SYSTEMATICS OF THE BLACKFLY SUBGENUS *TRICHODAGMIA* ENDERLEIN (DIPTERA: SIMULIIDAE: *SIMULIUM*) IN THE NEW WORLD

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To my wife Nathalie David-Hernández,
to my children Mina, Lani, Kiran, Ariadna and Ian
to my mother Francisca Triana,
my late father Alberto Martin,
to my sister Arais Martin,
to all my family in Cuba

CONTENTS

1. GENERAL INTRODUCTION

1.1. Background

Members of the family Simuliidae form a group of insects belonging to the Order Diptera. In the most recent World Inventory of Blackflies (ADLER & CROSSKEY, 2010) 26 genera and 2101 valid species of Simuliidae were recorded worldwide, of which approximately 12 genera and 359 recognized species are found in the Neotropics (COSCARÓN & COSCARÓN-ARIAS, 2007). Within Diptera, the Simuliidae are easily recognized by their small stout adult appearance with an unusually pronounced curved thorax, the presence of labral fans on the larval head capsule and pupae with respiratory gills (CROSSKEY, 1999). In spite of their antiquity (fossil forms have been found in geological beds dated to the Mesozoic period and lower Cretaceous, ~ 113-119 Ma), they are morphologically an extremely homogenous family (MOULTON, 2003). Because of this homogeneity, they have been generally neglected in spite of their great medical and veterinary significance (ADLER *et al.*, 2004; CURRIE & ADLER, 2008).

The Simuliidae, or blackflies as they are commonly known, belong to one of the insect orders with complete metamorphosis, the life stages being egg, larva, pupa and adult. Their life cycle comprises two stages, one aquatic (egg-larva-pupa) and one aerial (adult: female and male) (CROSSKEY, 1999). The adults often form "swarms" over the tree canopy or near water, where mating occurs. The female lays the eggs on the surface of running water where they gradually sink. The eggs are covered by an adhesive viscous substance (the gelatinous matrix), which help them to stick and keep clustered to a substrate (CROSSKEY, 1990). In most species oviposition occurs on rocks and vegetation, but these are always in very close association with running water or are found in the splash zone, so they are wetted immediately on oviposition (HUTCHINSON, 2007). In some species, eggs are laid in 1-6 gonatrophic cycles from which a larva emerges several days later. The simuliid larva does not have a fixed number of instars, six to nine instars being common, though seven is the average for most species. The larva has no true legs and the general form is worm-like. In most species, the larva posses a characteristic pair of labral fans, which they use to filter the water for bacteria and other organic matter on which they feed. The larva [= pharate pupa] of most species construct a cocoon made of silk within which they complete moult into a pupa. The pupa is a non-feeding stage and it has conspicuous gill filaments with which they breathe under water. From the mature pupae (often seen in field samples dark brown to black) the adults emerge in a conspicuous way. They emerge wrapped up in an air bubble, which then bursts on contact with the surface (CROSSKEY, 1990).

In the majority of Simuliidae species the female requires a blood meal for egg maturation, and it is this requirement that makes species in this family important as biting pests and in the transmission of parasites in both man and other warm-blooded animals. The most important parasites in man transmitted by simuliid blackflies are the nematodes *Onchocerca volvulus* (LEUCKART) and *Mansonella ozzardii* MANSON. The former species is responsible for the human disease "onchocerciasis" or river blindness, at present affecting 40 million people in the Afrotropical and Neotropical Regions (ADLER *et al.*, 2010; DAVIES, 1974; BASÁNEZ *et al.*, 2006; PAHO, 1974; WHO, 1995, 2002; YARZÁBAL *et al.*, 1985). Some species of Simuliidae can also transmit protozooans such as *Leucocytozoon* and trypanosomes, which infect both domestic and wild birds. Massive blackfly attacks have been known to cause mortality in cattle, pigs, and sheep which is attributed to toxic shock from the salivary injections during their bite (CURRIE & ADLER, 2008). Other economic impacts caused by blackflies are the loss of weight gain, reduced milk production, malnutrition and impotence (ADLER *et al.*, 2004; CURRIE & ADLER, 2008). Simuliidae have also been incriminated, though less frequently, in the transmission of the arbovirus that causes Venezuelan equine encephalitis (HUTCHINSON, 2007). In Latin America, some species of Simuliidae are thought to be responsible for outbreaks of the rare disease *Endemic Pemphigous Foliaceus* in Brazil, with *Simulium nigrimanum* MACQUART being the main culprit (EATON *et al.*, 1990; DIAZ *et al.*, 1989a,b). In addition, they are also the aetiological agent of the *Altamira Haemorrhagic Syndrome*, only known from the town of Altamira, Brazil (PINHEIRO, 1983; PINHEIRO *et al.*, 1974, 1986). The female of some species can show high anthropophily, bringing about severe effects on the tourist trade in certain areas. An example of this is *Simulium pertinax* (KOLLAR) which has caused a loss of millions of dollars to the tourist industry in the south-eastern coastal region of Brazil (ARAUJO-COUTINHO & LACEY, 1990; ARAUJO-COUTINHO *et al.*, 2003).

As well as medical importance of some species, simuliids are also "keystone" organisms in the ecology of running water, because of their unique ability to filter dissolved organic matter making it available to the food chain (CURRIE & ADLER, 2008; MALMQUIVIST *et al.*, 2001; 2004). They are also an important food source for salmonid fish and invertebrates such as Plecoptera or stoneflies (CURRIE & ADLER, 2008). In addition, blackflies are also important for environmental monitoring of freshwater contamination and stream degradation. This is mainly because immature stages (larvae and pupae) can be susceptible to both organic and inorganic pollution, for example effluent from sugar mills, slurry from farms, insecticides and fertiliser run off from farms and plantations) (FELD *et al.*, 2002; LAUTENSCHALGER & KIEL, 2005; WANTZEN, 2006; PRAMUAL & KUVANGKADILOK, 2010). Blackflies also have a particular evolutionary interest as a morphologically conservative group with very extensive cryptic speciation and reticulate evolution (ADLER *et al.*, 2004; CROSSKEY, 1999), the latter hampering a straight forward phylogenetic reconstruction (VRIESENDORP & BAKKER, 2005).

The Simuliidae as a whole still remains poorly known in spite of the efforts of R.W. CROSSKEY and other workers in cataloguing the natural history of blackflies and the taxonomy of world or regional Simuliidae fauna, for example ADLER & CROSSKEY (2008, 2009), ADLER *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), COSCARÓN *et al.* (2008), CROSSKEY (1988, 1990, 1993, 1999, 2002a), CROSSKEY & HOWARD (1997, 2004), and SHELLEY *et al.* (2010). There are various problems in the systematics of Simuliidae worldwide. Firstly, several regional simuliid faunas are still poorly studied and they are much in need of biodiversity surveys and revisionary studies, where many new morphospecies are still to be found (CURRIE & ADLER, 2008). Second, the supraspecific classification is currently unstable and problematic; many species or species-groups are placed in the wrong genus, and whether subgenera should be ranked as species groups or genera is still much debated. And thirdly, for many species their taxonomic limits remain poorly defined because of the presence of species complexes ("sibling species"). In this respect it is fair to point out that the Holarctic Region is relatively well known with the appearance of recent catalogues and other publications for the Diptera of the Nearctic and Palaearctic Regions (*e.g.* ADLER *et al.*, 2004; PETERSON, 1981; RUBTSOV & YANKOVSKY, 1988). On the contrary, the Simuliidae fauna of the biodiversity-rich Afrotropical, Neotropical, Oriental and Australasian Regions remain poorly understood, though the fauna of several pacific islands, Japan, Thailand, Argentina and Brazil have been fairly well covered. Most simuliid systematists follow the classification system of CROSSKEY & HOWARD (2004). However, other classification systems have been recently proposed (ADLER *et al.*, 2004), and the Simuliidae scientific community are not in agreement concerning the taxonomic position of many genera, especially those genera placed in the Tribe Simuliini. The same applies to species delineation, especially in vectors of *O. volvulus* or other pest species. Species boundaries for many simuliid species are poorly defined because of variation in the main diagnostic morphological characters. This together with differences in biology and biting behaviour might indicate the presence of sibling species. Therefore, these taxa will have to be studied employing DNA and/or cytogenetic techniques linked to morphological variation and examination of type material.

The objectives of this chapter are to provide an overview of the history of the current classification of the family Simuliidae and to explain how the classification of the Neotropical species relates to the phylogeny of this family.

1.2. History of the higher classification of Simuliidae

The monophyly of the family Simuliidae within Diptera and its relationships with other families within the suborder Nematocera is recognized by all previous workers (*e.g.* WOOD & BORKENT, 1989), but the relationships within the family are still problematic (ADLER *et al.*, 2004; CURRIE, 1988). The history of the classification of the Simuliidae has been outlined by SMART (1945), CROSSKEY (1999) and ADLER *et al.* (2004). This section deals with the most important studies that have contributed towards our current knowledge of the classification in Simuliidae (see TABLES 1-2). Even though this chapter will emphasize the history of the phylogeny and classification of simuliids in the Neotropical Region, their evolution in this area is viewed within the context of the world blackflies, thus references will be made to key papers from other regions.

The problem with the placement of simuliid species in genera, subgenera, tribes and subfamilies that we encounter today, dates back to the very early days when the genus *Simulium* was erected. The rank in classical taxonomy for recognizing a supraspecific taxon is, to a certain extent, subjective, as there is no universal or fixed criterion for defining subgenera, genera, tribes or subfamilies (CROSSKEY, 1998; 1990). Two trends can be identified in the development of classification of Simuliidae. On one hand, there is a system that does not employ subgeneric divisions, thus all the species are placed into numerous, but relatively small genera (*e.g.* ENDERLEIN, 1921; RUBTSOV, 1974). On the other hand, there is another system in which few genera are recognized, but some larger ones are divided into subgenera (*e.g.* EDWARDS, 1931; CROSSKEY & HOWARD, 1997, 2004; SMART, 1945). This is because of the many overlapping character found amongst the members of each subgenera. There is also a controversy on the usage of suprageneric categories (subfamilies), which vary in number (*e.g.* ENDERLEIN, 1921a - seven subfamilies; EDWARDS, 1931, SMART, 1945, CROSSKEY & HOWARD, 2004 - two subfamilies) depending on the author's opinion of the weight of certain morphological character given to the taxonomic ranking. For example, ENDERLEIN (1921a) used the hair on the wing veins as a good character at the subfamily level, while CROSSKEY & HOWARD (1997) relied more on the structure of the adults' genitalia.

The first known simuliid was described as a member of the mosquito genus *Culex* by LINNAEUS (1758). At the same time, other authors placed several species of Simuliidae in genera that now belong to other families of Diptera, for example *Tipula*, *Musca*, *Riagio*, and *Chironomus*. It was LATREILLE who first established the genus *Simulium* in 1802 to accommodate the "true" Simuliidae, and 32 years later NEWMAN (1834) created the "*Simuliites*", thus providing the modern basis of the classification of the family.

All known species of Simuliidae remained in *Simuliites* until ROUBAUD (1906a,b) proposed two subgenera *Pro-Simulium* and *Eu-Simulium*, which were then given generic rank by SURCOUF & GONZÁLEZ-RINCONES (1911). This arrangement remained more or less the same until MALLOCH (1914) recognized the taxonomic importance of the adult's wing venation in Simuliidae classification, which was in accord with the morphological studies being carried in other insect groups at that time. MALLOCH proposed that taxa with a "forked radial sector vein" comprised *Prosimulium* and those with "an unforked radial sector" belonged to *Simulium*. He also described a new genus *Parasimulium*, mainly on the basis of the absence of basal median cell. His taxonomic division prevailed for several years until a proliferation of scientific names in Simuliidae appeared between the 1920s to 1940s.

The splitting of the family Simuliidae into subfamilies and the array of generic and specific names was mainly due to the work of the German entomologist G. ENDERLEIN, who erected approximately five generic names with many of them only including a single species (monotypic) [see key publications of ENDERLEIN (1921a-c; 1922; 1925; 1929; 1930; 1934a,b; 1935; 1936)]. Even though ENDERLEIN'S classification system was compromised by employing characters that are now known to vary intra- and interspecifically, he was the first worker to propose a suprageneric classification of the family (TABLE 1) (ENDERLEIN, 1921a). In other publications, he divided further his subfamilies Nevermanniinae and Simuliinae into three and two tribes, respectively (ENDERLEIN, 1921b; 1936).

Contemporary to ENDERLEIN was the British worker F.W. EDWARDS who collected numerous species of Diptera during his trips to South America (Patagonia, Argentina and Chile) and to Java and Sumatra. In Simuliidae, he described many new species and re-described other poorly known taxa (EDWARDS, 1931; 1934). He also proposed a classification system, which recognized only two genera, *Parasimulium* and *Simulium*. The latter genus was divided into seven subgenera (*Austrosimulium*, *Eusimulium*, *Cnephia*, *Gigantodax*, *Morops*, *Prosimulium*, and *Simulium*). In his paper of 1934, he did not elaborate on his classification, but pointed out that the subgenera *Morops*, *Eusimulium* and *Simulium s.str.* could not be easily separated from each other. EDWARD'S 1934 paper is particularly relevant to Simuliidae phylogeny, because he stated that the forked radial sector of *Prosimulium* and *Parasimulium*, and the presence of a basal cell in the wing of *Prosimulium*, *Cnephia* and *Gigantodax* were "primitive features" and also that the submedian fold vein was not a true vein in this family. EDWARDS (1934) criticized the classification system of ENDERLEIN and outlined the main weakness of ENDERLEIN'S system, especially the presence and/or absence of hairs to separate species and even genera. It is now known that this character varies between adults even within population of the same species (SHELLEY *et al.*, 2002a). For example, females of *S. guianense s.l.* can have numerous hairs on the Sc wing vein, but these can be present or absent in the male, and in other instances females specimens from the same locality might or might not have hairs on the Sc wing vein.

The controversy and discrepancies in Simuliidae supraspecific classification were outlined by SMART in 1945, who provided a critical review of the system employed by ENDERLEIN and EDWARDS. The 1940s to 1960s represented a period in which most workers tried to synthesize the state of knowledge on blackfly taxonomy. SMART (1945) pointed out the deficiencies of the ENDERLEIN system, especially the use of variable morphological characters to define genera (*e.g.* setation of wing veins) and in not taking into account the morphology of the male and female genitalia. For EDWARD'S system, he commented on his failure to propose a more robust classification for the family on a worldwide basis and for not drawing attention to the relevance of his discoveries in the understanding of the phylogeny of Simuliidae. In this account, SMART (1945) proposed his own supraspecific classification recognizing only two subfamilies with no subgenera or tribes: Parasimuliinae, with only one genus *Parasimulium*, and Simuliinae that included *Prosimulium*, *Cnephia*, *Gigantodax*, *Austrosimulium* and *Simulium*. He also agreed that *Parasimulium* was the most primitive genus within the family and provided improvded diagnoses for these two subfamilies and genera. However, the revision of RUBTSOV in 1940 is worthy of mentioning here, because he only recognized five genera, with *Prosimulium* having two subgenera and *Simulium* with 16 subgenera. VARGAS' (1945a) catalogue of the Simuliidae of the Neotropical Region reflected his views of the state of the classification of the group at this time, which was more or less in accord with the then view of workers from other parts of the world.

Another contribution to the simuliid phylogeny was made by STONE (1949), who described the new genus *Gymnopais* in which the larva lacked labral fans, and a similar taxon, *Twinnia*, was later described by STONE & JAMBACK (1955). The labral fan is an important structure that is used by the larva to feed, so simuliid researchers had tried to infer its phylogenetic significance for generations. The absence of larval labral fans was so relevant to RUBTSOV that in 1955 he created the subfamily Gymnopaidinae to accommodate *Gymnopais* and *Twinnia*. In trying to reflect the latest discoveries in simuliid classification GRENIER & RAGEAU (1960) proposed a system with only three subfamilies: Parasimuliinae, Prosimuliinae and Simuliinae. These authors followed previous classifications and placed *Parasimulium* in its own subfamily (Parasimulinae), but did not recognize other variable characters such as wing venation to create subfamilies; thus they only recognized Prosimulinae ascontaining two tribes: Gymopaidini and Prosimulini. The subfamily Simuliinae included the tribes Cnephiini, Austrosimuliini, and Simuliini.

It was STONE in 1963, who thoroughly reviewed all genus-group names in the family Simuliidae, and proposed a generic synonymic list recognizing only 11 genera and 23 subgenera, and commented on the unsatisfactory world classification of Simuliidae. He outlined his views in his *Catalogue of the Diptera of America North of Mexico*. STONE departed from all previous classification systems and only recognized the subfamilies Prosimuliinae, with three tribes Gymnopaidini, Parasimuliini and Prosimuliini, and Simuliinae with no tribes.

The 1970s to 1980s brought the outstanding works of I.A. RUBTSOV and R.W. CROSSKEY on whom the present knowledge of blackfly classification is based. The work of these two authorities emphasizes the ongoing difference of opinions between simuliidologists even at the subfamily level. The work of RUBTSOV represented a major step forward in the classification of the Simuliidae on a worldwide basis reflecting the phylogenetic relationships in his treatise "*Evolution*, *phylogeny and classification of the Simuliidae*" (RUBTSOV, 1974). In this work he recognized three subfamilies, Parasimuliinae, Prosimuliinae and Simuliinae, nine subfamilies and 59 subgenera, and also provided zoogeographical considerations for this group. On the contrary, CROSSKEY (1988) considered only two subfamilies (Prosimuliinae and Simuliinae) and collated the latest taxonomic information about Simuliidae at this time.

A rather conservative approach was adopted more recently by CROSSKEY & HOWARD (1997, 2004) in their Inventory of World Black Flies [see also inventory updates in CROSSKEY (1999, 2002a) and ADLER & CROSSKEY (2008, 2009, 2010)]. This major effort shed light on the systematics of the group as a whole and it is this classification system that most western European taxonomists follow. In this system the subfamily Parasimuliinae is recognized together with Simuliinae, which have two tribes Prosimuliini and Simuliini. Studies on the genus *Crozetia* have also shaped our understanding of the classification of Simuliidae. DAVIES (1965, 1974) studied this genus and concluded that rudimentary, rake-like labral fans were primitive in Simuliidae. However, WOOD (1978) opposed this because he considered that this morphological character state was due to secondary loss in Simuliidae. The fully developed larval labral fans in *Parasimulium* (considered the most primitive taxon in Simuliidae) led CURRIE (1988) to propose that having complete labral fans for filter feeding was part of the ground plan of the Simuliidae. An extreme division of Simuliidae has been adopted by two key papers in the early 1990s. YANKOVSKY (1992) proposed the recognition of four subfamilies and nine tribes, while PY-DANIEL & MOREIRA SAMPAIO (1994a,b) recognized only two subfamilies, Gymnopaidainae and Simuliinae.

In the last four years several key contributions have been published that deal with the higher classification of the Simuliidae. The first one is the book on North American Simuliidae authored by ADLER *et al.* (2004), the second is the overview of the Simuliidae of the Neotropical Region published by COSCARÓN & COSCARÓN-ARIAS (2007), the third a Catalogue of the Simuliidae of the Neotropical Region by COSCARÓN *et al.* (2008), fourthly the yearly updates of the World Inventory of Simuliidae by ADLER & CROSSKEY (2008, 2009, 2010), and the fifth and more recently publication on *The Simuliidae of Brazil* by SHELLEY *et al.* (2010). The first publication recognized the use of the two subfamily system in Simuliidae: Parasimuliinae with no tribes and Simuliinae with the tribes Prosimuliini and Simuliini. COSCARÓN & COSCARÓN-ARIAS (2007) agreed with ADLER *et al.* (2004) and included all Neotropical simuliids in the subfamily Simuliinae. SHELLEY *et al.* (2010) also agreed with this classification system. In the three latest versions of the World Inventory of Blackflies, the two subfamily classification system has also been employed (ADLER & CROSSKEY, 2008, 2009, 2010), and this was also followed by COSCARÓN *et al.* (2008).

1.3. A phylogenetic approach to blackfly systematics

Phylogenetic reconstruction is an important tool in systematics and it is usually based upon a cladistic analysis of shared novel homologous characters between species (LEMEY *et al.*, 2009; MIRANDA-ESQUIVEL & MUÑOZ DE HOYOS, 1995; SCHUH & BROWER, 2009). This system, advocated by HENNIG (1965), revolutionized systematics and provided a robust analytical methodology in the form of most parsimonious trees being the best hypothesis for the phylogeny of a given group.

ADLER *et al.* (2010) have postulated that the estimation of a group's phylogeny can identify historical events leading to current biodiversity patterns, can provide a more objective classification that reflects the evolution of the group, and can help to understand the evolution of particular traits such as anthropophily. The classification of Diptera and Simuliidae has been affected by the use of cladistic methods as outlined by ADLER *et al.* (2004). The use of morphological characters from all life stages in Simuliidae is paramount in the systematics of this group (ADLER *et al.*, 2004) because it gives a more complete understanding of the various evolutionary novelties and hence of the phylogeny of the family as whole. Unfortunately, this principle has not always been applied (*e.g.* PY-DANIEL & MOREIRA SAMPAIO, 1994a,b). In addition, researchers have not always been in accord with regards to the "weight" applied to different morphological characters to the four life stages of simuliid taxa, which has resulted in different phylogenies and hence different classifications (*e.g.* COSCARÓN, 1987).

1.3.1 Morphological characters

Even though earlier workers had tried to put the Simuliidae classification in a phylogenetic context, it was only in the 1980s that cladistic analysis was applied to the simuliids to infer phylogenetic relationships based on genitalia, pupal abdominal chaetotaxy, number of gill filaments and cocoon shape, and larval head morphology and abdominal chaetotaxy.

It can be said that WYGODZINSKY & COSCARÓN (1962, 1973) were the first authors who tried to view the Simuliidae in a phylogenetic context. They only reviewed the "primitive" Prosimuliinae, but discussed their relationships in a sister-group context based on the morphology of all life cycle stages of the species and genera known at that time. The only author that has reviewed the evolution of Simuliidae on a world basis is RUBTSOV (1974), and his views concerning the evolutionary developments of certain characters were shown on the phylogenetic trees that he produced for the subfamilies Parasimuliinae and Simuliinae.

In 1982, WOOD & BORKENT discussed the phylogenetic position of the genus *Parasimulium*. Using the cladistic methods of ELDRIDGE & CRACRAFT (1980) and morphological characters of the antennae, legs and adult genitalia, they suggested the monophyly of *Parasimulium* and advocated that it was the sister group to all other simuliids. Their work supported the views of others based on non-cladistic approaches (*e.g.* STONE, 1969). However, WOOD & BORKENT (1982) advocated the inclusion of the immature stages of *Parasimulium* into the analyses as well as further data from another species, *P. melanderi*, in order to re-assess their conclusions because of the poor resolution of their phylogenetic tree. This was later achieved when BORKENT & WOOD (1986) described the first and second larval instars of *P. stonei*. Their study was significant because the larval morphology corroborated a close relationship between *Parasimulium* and other members of the tribe Prosimuliini.

In 1987, COSCARÓN published a phylogenetic analysis together with a supraspecific classification of the genus *Simulium* in the Neotropical Region. He considered that *Simulium* was monophyletic by the following apomorphies: pedisulcus well developed; basal cell of wing absent; basal sector of Radius short; presence of bifid to trifid hooks on pupal abdominal tergites VI-VII; abdominal tergites VIII-IX without hooks; thorax of pupa with fine and multibranched trichomes; third antennal segment of larva shorter than the first and second segments; and cervical sclerites separated from postocciput.

Even though COSCARÓN (1987) did not produce a data matrix for his analysis, he commented on the closeness of *Simulium* to the Holarctic genus *Eusimulium*. In the same paper, COSCARÓN divided many of the subgenera into "groups" and "subgroups", and even though he used morphological characters of the adults, such as genitalia characters, he emphasized that most of the "cladistic information" in Simuliidae were found in the immature stages (larva and pupae), especially the larval head morphology. He did not give reasons for this statement, and all his conclusions were biased towards the larval life stage.

The most complete cladistic analysis based on morphology to the late 1980s is that CURRIE (1988) [see also ADLER *et al.*, 2004]. CURRIE re-described material of species of *Parasimulium* and supported the hypothesis of sister-group relationships between *Parasimulium* (Parasimuliinae) and all other simuliids (Simuliinae). He also provided evidence for two monophyletic tribes within Simuliinae: Prosimuliini and Simuliini. One of the major changes in CURRIEs' phylogenetic analysis is that he restricted the tribe to include only the genera *Gymnopais*, *Helodon*, *Levitnia*, *Prosimulium*, *Urosimulium* and *Twinnia*. All other subgenera previously placed in Prosimuliini were transferred to Simuliini (*e.g. Gigantodax*, *Lutzsimulium* and *Mayacnephia*).

A subsequent morphological phylogenetic analysis by PY-DANIEL & MOREIRA SAMPAIO (1994a,b) only used characters from the immature stages, did not take into consideration *Parasimulium,* and did not provide a data matrix with scored characters. In this paper, they re-validated the subfamily Gymnopaidainae and only recognized one other subfamily, the Simuliinae. They also proposed the elimination of tribes within Simuliidae and elevated all subgenera of *Simulium s.l.* to genera, thereby restricting the distribution of *Simulium s.str.* to the Holarctic Region (CROSSKEY & HOWARD, 1997). The behaviour related to the construction of the cocoon of the different species were employed by STUART & HUNTER (1998a,b) to estimate phylogenetic relationships between species of the genus *Simulium*.

In 2000, CURRIE & GRIMALDI discussed the character states in support of the tribe Simuliini, especially the wing venation after the discovery of the fossil Cretaceous-age genus *Archicnephia*. In the same year, EVANS & ADLER (2000) also produce a phylogenetic tree of the Simuliini based on the internal morphology of the spermatheca, which proved to be a good morphological structure to infer cladistic relationships. They found that the different distribution of internal spicules and external sculpturing of the spermatheca were diagnostic for several of the genera they analyzed. Three years later, CRAIG *et al.* (2003) reviewed the findings of CURRIE & GRIMALDI (2000) in the context of their revision of the genus *Crozetia*. They agreed with the Parasimuliinae-Simuliinae subfamily taxonomic arrangement, with two tribes within Simuliinae, Prosimuliini and Simuliini. They also agreed that

Crozetia and all other Simuliini were monophyletic by having differentiated costal setae present, a subapical paramere and the presence of the calcipala.

ADLER *et al.* (2004) have also inferred a phylogeny for the family Simuliidae in which all CURRIE'S findings (1988) were taken into account. The authors discussed the monophyly of Simuliidae and expanded on the ground plan apomorphies based on 23 characters of adults, pupal, larvae and egg, and female feeding behaviour. More recently, the relationships of southern genera of Simuliidae have been discussed by GIL-AZEVEDO & MAIA-HERZOG (2007), who concluded that their study was in accord with the most parsimonious classification system in Simuliidae employed by ADLER *et al.* (2004). GIL-AZEVEDO (2010) also reviewed the taxonomy and proposed a phylogeny for the genus *Lutzsimulium* and related taxa in Brazil (*Kempfsimulium*). In his paper, he revalidated the genera *Araucnephia* and *Araucniphiodes*, and subsumed *Kempfsimulium* under *Lutzsimulium*.

The most recent paper exploring the phylogeny in Simuliidae is that of SAM-KYU & ADLER (2009). The authors used 13 larval gut characters in 45 species representing 17 subgenera and 15 genera in order to assess their utility in taxon diagnosis and phylogenetic inference. Larval gut morphology, in particular the esophageal armature, varied sufficiently among taxa permitting generic diagnoses. Their results supported a sister-group relationship between *Parasimulium* and the remaining simuliids. However, the gut morphology failed to support the monophyly of the tribes Simulini and Prosimulini (ADLER *et al.*, 2004); the sister-group relationships among the subgenera of the genus *Simulium* were also poorly supported, perhaps because of the limited use of characters in their data set.

1.3.2 Molecular characters

In recent years, technological advances have enabled the use of DNA sequences to estimate the phylogeny of many organisms using the polymerase chain reaction (PCR), automatic sequencing hardware and easy-to-use computer software. These biochemical techniques have been applied in systematics not only for the identification of taxa, but also to explore evolutionary process, biological clocks and phylogenetic trees (HILLIS & MORITZ, 1990; PAGE & HOLMES, 1998; MALLET & WILLMOTT, 2003; TOWNSON *et al.*, 1988).

With regards to Simuliidae evolution, molecular phylogenetic analyses have not, as yet, provided much insight into the supraspecific classification of Simuliidae (MOULTON, 2000; 2003). However, they have proved very useful for the identification of the vectors of *O. volvulus*, the separation of closely related taxa and for revealing the relationships between them (*e.g.* AGATSUMA *et al.*, 1993; BROCKHOUSE *et al.*, 1993; POST & FLOOK, 1992; PRUESS *et al.*, 1992; RODRÍGUEZ-PÉREZ *et al.*, 2004, 2006; SAWYER, 1991; SCARPASSA & HAMADA, 2003; TOÉ *et al.* 1997) [see also the review of these methods by ADLER *et al.*, 2004].

The first phylogenetic studies using molecular characters in Simuliidae stem from the works of SOHN *et al.* (1975), PRUESS *et al.*, (1992), XIONG & KOCHER (1991) and TANG *et al.* (1995; 1996). However, these early works suffered from a limitation in the quantity of data (only 350 bases) and taxon sampling (< five simuliid species) precluding the inference of meaningful conclusions (MOULTON, 2000). The only study that has addressed the molecular phylogeny of Simuliidae on a large scale is that of MOULTON (1997, 2000, 2003). MOULTON'S approach was to employ a larger number of genes [four nuclear (28S rDNA, EF-1 alpha, DDC, PEPCK) and two mitochondrial (12S, rDNA and ND2)], and representatives of 25 genera belonging to the subfamilies Parasimuliinae and Simuliinae. He also tested his conclusions by using species of six other families of Diptera (Drosophilidae, Ptychopterida, Dixidae, Culicidae and Thaumaleidae) as outgroups. MOULTON (2000, 2003) considered his own results to be troublesome, mainly because his choice of genes failed to adequately resolve most of the simuliid relationships, in comparison with the classification based on morphological characters currently employed at that time (CURRIE, 1988). Nevertheless, his study supported the recognition of Parasimuliinae (*Parasimulium s.l.*) and Simuliinae, with the latter being divided into two monophyletic tribes, Prosimuliini and Simuliini. In addition, MOULTON concluded that genera previously placed in Prosimuliini *sensu* CROSSKEY & HOWARD (2004) (*e.g. Araucnephia*, *Araucniphiodes*, *Cnesiamima*, *Lutzsimulium*, *Sulcinephia* and *Tlalocomyia*) belonged in the Tribe Simuliini. MOULTON (2000, 2003) also complimented the phylogenetic interpretation of CURRIE (1988) based on morphological characters, as

CURRIE'S interpretation "was impeccable" in inferring his phylogenetic and classificatory system. In the same papers, MOULTON advocated the rejection of any other classification system that did not reflect the sister-group relationship between *Parasimulium* and the remainder of Simuliidae, such as the classification of PY-DANIEL & MOREIRA SAMPAIO (1994a,b, 1995), because they contained unnatural groupings. The viewpoints of MOULTON (2000, 2003) and CURRIE (1988) have been taken into account by ADLER *et al.* (2004) in their studies of the Simuliidae of North America and northern Mexico, and this was also followed in some cases in the two most recent revisions of the family in the New World (COSCARÓN & COSCARÓN-ARIAS, 2007; SHELLEY *et al.*, 2010).

1.3.2.1. DNA barcoding

Since the proposal of HEBERT *et al.* (2003a,b) to use a small portion (ca 658 bp) of the mitochondrial gene cytochrome *c* oxidase subunit 1 (*COI*) as a standardised sequence (DNA barcode) for identification of animal species, this approach has been widely adopted. The technology behind this methodology has the potential for gathering molecular data relatively quickly, and in many groups of organisms the development of a *COI* library is becoming of paramount taxonomic importance with regards to the delineation of species boundaries and for species identification (JANZEN *et al.* 2005; CYWINSKA *et al.*, 2006).

However, the advent of DNA barcoding in taxonomy has been controversial (LANE, 2009) [for more details see **Chapter** 4 in this thesis], and its theoretical limitations have been exhaustively explored and outlined in the scientific literature. DNA barcoding detractors have argued that the approach is flawed because *a priori* taxonomic resolution is essential (MORITZ & CICERO, 2005); *COI* is unable to recognize hybrids because of maternal inheritance (MORITZ & CICERO, 2005; KRESS & ERICKSON, 2008); and the presence of introgression, heteroplasmy and pseudogenes (HLAING *et al.*, 2009) is very common in natural populations of species (which can mislead the results in phylogenetic analysis, especially non-monophyly). A further argument is that *COI*, as a mtDNA gene, is particularly prone to selective sweeps and its populations dynamics may be driven by intracellular symbionts (CYWINSKA *et al.*, 2006).

Nonetheless, in spite of these potential problems and limitations, empirical evidence is accumulating to show that in practice DNA barcoding is often very useful in species identification for many biodiversely rich groups of organisms such as butterflies (HEBERT *et al.*, 2003a; JANZEN *et al.* 2005), mosquitoes (CYWINSKA *et al.*, 2006; KUMAR *et al.*, 2007; RUIZ, 2010), tachinids (SMITH *et al.*, 2006; 2007; 2008), amphibians (SMITH *et al.*, 2007) and mammals (BORISENKO *et al.*, 2007; CLARE *et al.*, 2007). Barcoding has also proved to be a versatile tool for revealing cryptic species in butterflies (JANZEN *et al.* 2005), mosquitoes (CYWINSKA *et al.*, 2006) and other insects such as blackflies which may be taxonomically difficult, because identification is hampered due to cryptic species or phenotypic plasticity (RIVERA & CURRIE, 2009). It has also got particular value in facilitating the association between different developmental life stages (AHRENS *et al.*, 2007; RIVERA & CURRIE, 2009).

In Simuliidae, the first DNA Barcoding study was carried out for the Nearctic Region by RIVERA & CURRIE (2009). These authors examined 10 genera and 65 species of Simuliidae in North America. In the Neotropical Region only a small fraction (118 species) of the total fauna (340 nominal species) have been barcoded [see **Chapter 4**]. However, preliminary information have been obtained by PEPINELLI *et al.* (2009) for 63 nominal species of the genera *Gigantodax* (11 species), *Lutzsimulium* (three species), *Pedrowygomyia* (one species) and *Simulium* (48 species). From the genus *Simulium* PEPINELLI *et al.* (2009) have barcoded 11 anthropophilic species of which three taxa are known vectors of *O. volvulus* (*S. guianense s.l.*, *S. metallicum s.l.* and *S. oyapockense*). Similarly, L.M. HERNÁNDEZ [unpublished data; see http://www.boldsystems.org]. has barcoded 70 nominal species of the genera *Cnesia* (three species), *Gigantodax* (11 species), *Paraustrosimulium* (one species) and *Simulium* (53 species). Of the genus *Simulium* 14 species are anthropophilic of which five are known or suspected to be vectors of *O. volvulus* (*S. ganalesense*, *S. gonzalezi*, *S. guianense s.l.*, *S. metallicum s.l.*, *S. oyapockense* and *S. quadrivittatum*). More recently, HAMADA *et al.* (2010) described the new species *S. lithobranchium* from Brazil, based upon morphological differences of the male genitalia, the presence of dorsal tubercles in the larvae, and a high intraspecific genetic divergence (>4%) in the barcoding sequences they analyzed.

Because of the presence of aquatic (egg, larva and pupa) and aerial (adults) life stages in Simuliidae in combination with their structural homogeneity, the identification of this group is a difficult task. A further complication is the presence of known sibling species complexes in the family, which would require the examination of the larval salivary gland polytene chromosomes for identification. Therefore, blackflies provide good candidates for species identification facilitated by DNA barcoding.

1.3.3. Impact of other biochemical methods (enzyme electrophoresis and cuticular hydrocarbons) and cytogenetics on Simuliidae systematics

In the same way that general DNA technology has been applied to Simuliidae systematics, so have other genetical and molecular methods (studies on chromosomes, enzymes and cuticular hydrocarbons). Although none of these methods have shed light on the evolution of the family, they have been potent, especially the chromosomes, in the discovery of sibling species and the identification of vectors of river blindness, including the Neotropical Region (ADLER *et al.*, 2004, 2010; AGATSUMA *et al.*, 1986; HIRAI & UEMOTO, 1983; MILLEST, 1989, 1992; PHILLIPS *et al.*, 1985, 1986; PROCUNIER, 1988, 1989; PROCUNIER *et al.*, 1985, 1987; RIOS-VELÁSQUEZ *et al.*, 2002; ROTHFELS, 1979) [see also review papers in KIM & MERRIT, 1988].

The giant polytene chromosomes of the larval salivary gland have played an important role in the study of the epidemiology of onchocerciasis and its vectors in Africa, (the *S. damnosum* complex (*e.g.* POST, 1982a; 1986)) and also in Latin America (for example *S. exiguum* and *S. guianense* (CHARALAMBOUS *et al.*, 1993a,b; 1996; 1998; 2005; CONN, 1988; CONN *et al.*, 1989)). The principal researcher of cytotaxonomy in Simuliidae was KLAUS H. ROTHFELS, who dedicated his entire career to researching the chromosomal morphology in this family. In his numerous papers, he gave close insight into the complexity of the field of cytotaxonomy and proposed several speciation models in Simuliidae. In addition to species diagnosis, cytologists tried to draw phylogenetic conclusions, though with not much success, as "cytophylogenies" are unrooted. In addition, the chromosomes also become too scrambled by numerous inversions in distantly related species, and it is sometimes impossible to sort out the individual inversions and hence character definition becomes almost impossible (ROTHFELS, 1979). Few studies had addressed this issue except the papers of CHUBAREVA (1977) and ROTHFELS (1979), in which the authors had commented on the origin of the family Simuliidae. The latter studies reported that the chromosomes of the genus *Gymnopais* had five homologues segments similar to one of the most primitive genera in Chironomidae (*Orthocladius*). Thus, they inferred that *Gymnopais* might be the most primitive of all cytologically studied simuliids.

Cytotaxonomy has also played an important role in the continuing debate on the supraspecific classification of Simuliidae. This has been mainly applied to the delineation of certain genera and subgenera, which has resulted in the synonymisation of some of them. A classical example of the latter is the synonymy of the subgenera *Hearlea*, *Obuchovia*, *Hagenomayia*, *Shewellomyia* with *Hemicnetha* proposed by ADLER *et al.* (2004) on the basis of their general morphology and the presence of only three fixed inversions.

1.4. Development of a classification system for the Simuliidae in the Neotropical Region

1.4.1. Classical approaches to taxonomy, including supraspecific divisions in Neotropical Simuliidae

The previous sections covered the development of classification systems of the world Simuliidae and the early work on generic and subgeneric groupings whenever they relate to the Neotropical species. Before the publication of the World Simuliidae Catalogue by SMART (1945) and the New World Simuliidae by VARGAS (1945a), work on the Neotropical fauna progressed in line with research and control efforts on human onchocerciasis in Central America, as well as foci of the disease that became known subsequently in South America. This was a period when many new species were discovered and attempts made by several key workers to organise the specific names into supraspecific groups.

Initially, the main efforts on Neotropical simuliid taxonomy were those of VARGAS (1936; 1941a,b; 1942; 1943a,b; 1945a-c) and collaborators (VARGAS & DÍAZ NÁJERA, 1946; 1948a,b; 1949; 1951a,b; 1953a,b; 1954; 1956; 1957a,b 1958; 1958; VARGAS, MARTÍNEZ PALACIOS & DÍAZ NÁJERA, 1946) working in Mexico at a time when the public health importance of human onchocerciasis was being assessed. The work of VARGAS was valuable for its morphological interpretation of existing species and descriptions of new species, as well as its use and further definition of subgenera. VARGAS followed EDWARDS (1931, 1934) and RUBTSOV'S (1940) earlier work in dividing the genus *Simulium* into subgenera. He started his work (VARGAS, 1941a,b) with a revision of the taxonomic arrangements of the world Simuliidae made by several authors and provided a list of species and their distributions in Mexico. Twenty-two species names were recognized at this time. He then provided a review (VARGAS, 1942) of the development of the use of adult genitalia in supraspecific groupings by various authors together with his own figures and descriptions for some Mexican species. There followed a period of species descriptions and the grouping of species into subgenera, which suffered considerable rearrangement over a twenty-year period culminating in a subgeneric classification of the entire genus *Simulium* (VARGAS & DÍAZ NÁJERA, 1957b) with pictorial keys to the genera and subgenera of Simuliidae in Mexico added two years later (VARGAS & DÍAZ NÁJERA, 1959). It is on this foundation that the contemporary systematic organisation of the Neotropical Simuliidae has been developed. In the works of VARGAS & DÍAZ NÁJERA the authors discussed extensively the divisions and grouping of Mexican Simuliidae, and also provided a valuable discussion on ENDERLEIN'S criteria for supraspecific groupings. Key papers are those of VARGAS & DÍAZ NÁJERA (1953a,b) who, having examined the ENDERLEIN types from the Berlin Museum, extended their interest in subgeneric groupings to include species outside of Mexico that had been treated by ENDERLEIN.

In 1957b VARGAS & DÍAZ NÁJERA produced their final overview of the Mexican Simuliidae fauna with keys to the genera, subgenera of the genus *Simulium* and 68 species based on adult and pupal characters, together with a species distribution list for the country. The subgenera of *Simulium* that they recognized for the Mexican fauna were: *Byssodon*, *Eusimulium*, *Hemicnetha*, *Hearlea*, *Neosimulium*, *Notolepria*, *Psilopelmia* and *Simulium* s.s. Their final work in 1959 provided pictorial keys for medical entomologists and the subgenera of *Simulium* were reduced to seven because the two species of the subgenus *Byssodon* (*S. quadrivittatum* and *S. ganalesense*) were moved into the subgenus *Simulium*. Adults, pupae and larvae were figured in keys to the subgenera of *Simulium* using external and genital characters of adults, and morphology of the integument and gills for pupae. After VARGAS passed away, DÍAZ NÁJERA produced several more taxonomic papers mainly with descriptions of new species (DÍAZ NÁJERA *et al.*, 1965, 1969, 1981; DÍAZ NÁJERA & VULCANO, 1962A). DALMAT'S (1955) work in Guatemala provided details on the taxonomy of Simuliidae of this country and followed the most modern classification system for the Simuliidae available at that time, especially the work of VARGAS & DIAZ NÁJERA. DALMAT'S work also related species distributions to physical factors in relation to river blindness distribution.

Following the examination of some of the ENDERLEIN types STONE (1962) synonymized *Dasypelmoza*, *Ectemnaspis* and *Trichodagmia* described by ENDERLEIN in 1934a (see also ENDERLEIN 1934b) and *Grenieriella* VARGAS & DÍAZ NÁJERA (1951a) with *Chirostilbia* (ENDERLEIN, 1921). In 1963, STONE produced an annotated list of genus-group names for the world Simuliidae and divided the genus *Simulium* into several subgenera and genus group names. Furthermore, he recorded the great divergence of opinion as to the relative phylogenetic significance of the diagnostic characters and the extent of supraspecific classification within the family. This work was a milestone in terms of establishing diagnostic characters for each genus-group name, but the author predicted some mightbe found untenable with future experience. The characters in questioned were the presence or absence of Sc wing setation, legs, general morphology and general coloration.

In the late 1940s, PEDRO WYGODZINSKY and SIXTO COSCARÓN had started working on the taxonomy of the South American Simuliidae and later expanded this to cover the whole Neotropical Region. The work initially provided descriptions of new and poorly described species, but later involved the systematics of the whole family. The second author continues today. Their monumental contribution eventually covered the entire Neotropical Region and provided a comprehensive regional overview with species descriptions, subgeneric diagnoses and phylogenies of the subgenera based on morphological characters. Also in the 1940s, M.A.V. D'ANDRETTA (later referred to as M. A.

VULCANO) and C. D'ANDRETTA JR. worked on the Brazilian fauna and redescribed some of the Brazilian species described by ADOLFO LUTZ as well as describing some new species (see also PINTO, 1932) for this country. ORFILA'S (1939) work on the Simuliidae of Argentina was also important in terms of cataloguing the local fauna. In 1967, VULCANO provided a catalogue of the Simuliidae of the Neotropical Region containing information on type localities and distributions. The author commented on the lack of a universally agreed subgeneric classification for the family and consequently did not allot *Simulium* species to subgenera. Description of many new species was also the main role of JAIME RAMÍREZ PÉREZ in Venezuela, which he presented in his monograph "*Los Jejénes de Venezuela*" in 1983. Another catalogue for tropical South America, in which species lists by country were provided, was also published by VULCANO (1981).

In 1987, COSCARÓN organized the 243 Neotropical species then recognized into supraspecific groups based on a cladistic analysis of the genus *Simulium*. He also included in his analysis some Holarctic species of the subgenera *Byssodon*, *Eusimulium* and *Psilozia*, whose Nearctic distribution overlaps with the northern Neotropical Region. The author provided keys and diagnoses to subgenera, species lists and their geographical distribution.

The description of many new species in the Neotropical Region probably originated from the belief that such isolated and vast areas of South America will harbour different species. This rationale proved to be far from the truth when country-wide surveys started to take place in Brazil, Venezuela and Ecuador in the late 1970s mainly due to the efforts of A.J. SHELLEY and collaborators. SHELLEY began to study the Simuliidae using not only morphological methods, but also cytogenetics. He pioneered the application of a digital imaging analysis system to study the thoracic coloration patterns of adult simuliids. The colour of the thorax is still one of the most important external diagnostic characters on which species identification of Latin American Simuliidae is based (SHELLEY *et al.*, 2010). However, variation in this pattern was observed depending on the incidence of the light on the specimen. The discovery that the different disposition of the setae on the thorax produced a black or silver pattern showed that the "new species" had already been described from other areas of the Neotropical Region (SHELLEY *et al.*, 1997). This technique is being used to the present day and has been an invaluable tool in the taxonomic revision and delineation of several subgenera and species in the Neotropical Region (*e.g.* HERNÁNDEZ & SHELLEY, 2005; HERNÁNDEZ *et al.*, 2007, 2008; SHELLEY *et al.*, 2006, 2010).

The appearance of the book of COSCARÓN & COSCARÓN-ARIAS (2007) brought together all the current knowledge of the Simuliidae in the Neotropical Region. Their taxonomic interpretation of some subgenera was not in general agreement with the accepted classification system of ADLER *et al.* (2004) and ADLER & CROSSKEY (2008, 2009, 2010). For example, ADLER *et al.* (2004) regarded the subgenus *Hearlea* as a synonym of *Hemicnetha*. In addition, the subgenera *Cerqueirellum* and *Coscaroniellum* were treated as congeneric with *Psaroniocompsa* following the rationale of SHELLEY (1988a,b). All these subgenera are considered as valid in COSCARÓN & COSCARÓN-ARIAS (2007). The same applies to the subgenera *Thyrsopelma* and *Trichodagmia*. ADLER & CROSSKEY (2008, 2009) recognized the division of Simuliidae in fewer genera and subgenera with species placed into species-groups within each subgenus. The latter was the taxonomic rationale employed by SHELLEY *et al.* (2010) for their proposal of a new classification system mainly based on the simuliid fauna of Brazil. Nonetheless, SHELLEY *et al.* (2010) placed this fauna in a wider context of the current trends in the classification of Simuliidae in the New World. COSCARÓN *et al.* (2008) has also produced a new catalogue for the Neotropical Simuliidae, in which the classification of COSCARÓN & COSCARÓN-ARIAS (2007) was used. In this work, COSCARÓN *et al.* (2008) provided information about the type for each species and key taxonomic references for each taxa.

Even though the classification proposed by SHELLEY *et al.* (2010) draws upon COSCARÓN (1987) and COSCARÓN & COSCARÓN-ARIAS (2007) they disagree with the supraspecific classification with regards to *Cerqueirellum*, *Coscaroniellum*, *Ectemnaspis*, *Hearlea*, *Inaequalium* and *Psilopelmia*, and these were synonymized as follows: *Hearlea* and *Hemicnetha* under *Trichodagmia*; *Cerqueirellum*, *Coscaroniellum*, *Inaequalium* under *Psaroniocompsa*; and *Ectemnaspis* under *Psilopelmia*. In addition, SHELLEY *et al.* (2010) regarded the genera *Araucnephia*, *Araucniphiodes* and *Kempfsimulium*. as junior synonyms of the genus *Lutzsimulium*.This is also reflected at the species level, where numerous new specific synonymies were proposed as well as species revalidations and new placement of species in different subgenera and/or species groups [see Checklist, page 52-66 in SHELLEY *et al.*, 2010].

1.4.2. Phylogenetic approaches to Neotropical Simuliidae taxonomy

The first cladistic approach to Neotropical Simuliidae was that of PY-DANIEL & MOREIRA SAMPAIO (1994a) (as discussed in section **3.1**). They proposed the elimination of tribes and subgenera in Neotropical Simuliidae, raised all subgenera to genus and also revalidated the subfamily Gymnopaidinae without further explanation. The failure to take into account the genus *Parasimulium* has been criticized by MOULTON (2000; 2003). In essence, the work of PY-DANIEL & MOREIRA SAMPAIO (1994a) constitutes the only paper that included all known genera of Neotropical Simuliidae in a single analysis. Apart from PY-DANIEL & MOREIRA SAMPAIO (1994a), the other important phylogenetic study in Simuliidae in the Neotropics is that of COSCARÓN (1987) on the genus *Simulium*. He included one Nearctic taxon in his analysis, but did not provide the reasons for doing this, nor did he explain clearly his taxonomic decisions, especially his division of the genus *Simulium* into subgenera and species groups.

From then on several papers have appeared on South and Central American Simuliidae, but generally they have dealt with the phylogeny and validity of names at the subgeneric level within the genus *Simulium*, for example MIRANDA-ESQUIVEL & MUÑOZ DE HOYOS (1995) on the subgenera *Ectemnaspis-Psilopelmia*; MIRANDA-ESQUIVEL & COSCARÓN (2001) on *Trichodagmia-Thyrsopelma*; COSCARÓN & COSCARÓN-ARIAS (1997) on *Psaroniocompsa*, *Inaequalium*, and *Chirostilbia*; and STRIEDER & PY-DANIEL (2002) on *Inaequalium*. More recently, PINTO-SÁNCHEZ *et al.* (2005) produced a phylogeny of the genus *Gigantodax* and related taxa (*Gymnopais*, *Hearlea*, *Prosimulium*) combining the morphology of the adult, pupa and larva with cytological characters. They carried out this research in order to infer the relationship of *Gigantodax* and the newly described genus *Pedrowygomyia*. However, they restricted this study only to these genera and did not correlate their conclusions with other taxa on a world basis.

Although phylogenetic studies had already been carried out in the Neotropical Region (*e.g.* COSCARÓN, 1987; PY-DANIEL & MOREIRA SAMPAIO, 1994a,b), P.H. ADLER, D.J. CURRIE and J.K. MOULTON were the first authors to view the phylogeny of Neotropical Simuliidae in perspective with an to date world perpectives using cladistic analyses (ADLER *et al.*, 2004; CURRIE, 1988) and molecular methods (MOULTON, 2000; 2003). Although these papers have more or less resolved the basal lineage in Simuliidae and indicated a Gondwana relationship for the Australian and South American clades (*e.g.* *Paraustrosimulium*, *Gigantodax*, *Lutzsimulium*), little is known about the phylogeny of other Neotropical subgenera, especially those included in the tribe Simuliini.

In 2007, GIL-AZEVEDO & MAIA-HERZOG published some preliminary ideas on the phylogeny of several Neotropical genera. They included all the genera of Simuliidae found in the southern hemisphere and used *Prosimulium* and *Helodon* as outgroups. They carried out this research because the hypothesis concerning the phylogenetic relationships among the southern subgenera is poorly understood and has never been tested employing cladistics. Although they did not include *Parasimulium* (the most primitive genus) in their analysis, they used some representatives of the tribe Prosimuliini. Their main conclusion was that all the southern hemisphere Simuliidae genera belong in the tribe Simuliini rather than in Prosimuliini. This hypothesis has already been put forward by ADLER *et al.* (2004) and MOULTON (2000, 2003) integrating morphological and molecular characters, and was followed by the World Inventory of Simuliidae (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 2004). GIL-AZEVEDO (2010) has recently published a phylogeny of the genus *Lutzsimulium* in Brazil and employed six putative outgroups belonging to the genera *Araucnephia*, *Araucniphiodes, Gigantodax*, *Helodon*, and *Paraustrosimulium*, and the subgenus *Chirostilbia* in the genus *Simulium*. The authors proposed that *Lutzsimulium* was monophyletic being defined by 15 synapomorphies, and also proposed the revalidation of the genera *Araucnephia* and *Araucniphiodes*.

1.5. Current classification of the family Simuliidae in the Neotropical Region

The most recent classification on Neotropical Simuliidae is the book *The Blackflies (Diptera, Simuliidae) of Brazil* by SHELLEY *et al.* (2010). This work placed the Brazilian simuliid fauna within the context of the current taxonomic classification of Simuliidae, especially the work of ADLER *et al.* (2004) and the World Inventory of Blackflies by ADLER & CROSSKEY (2009, 2010). The classification system as put forward in these publications is followed here. More recently, GIL-AZEVEDO (2010) proposed the revalidation of the genera *Araucnephia* and *Araucniphiodes* based on a cladistic analysis. This revalidation is not followed in the current work because the overlapping morphological characters amongst *Araucnephia*, *Araucniphiodes* and *Lutzsimulium*. Work combining molecular markers with morphological traits is still much needed in order to address these issues.

At present, all Neotropical simuliids are placed in the subfamily Simuliinae. The family comprises eight genera and approximately 340 valid species and two *nomina nudae* in this region. The genus *Simulium* is the only one that has been divided into subgenera (see TABLE 2).

COSCARÓN & COSCARÓN-ARIAS (2004) and COSCARÓN *et al.* (2008) recognized 12 genera and 349 species in the Neotropical Region. Their interpretation with regards to the validity of certain genera, subgenera, species groups and species in the Neotropical Region disagrees with the work of ADLER *et al.* (2004), ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010). The reader should consult these publications for further details on generic, subgeneric and specific synonymies.

1.6. Perspectives and future developments

In the previous sections, the history of the development of the classification of World Simuliidae has been discussed and the taxonomy of the Neotropical simuliids has been put into perspective in the global context. Additionally, the ongoing differences in opinions between researchers with regard to the supraspecific categories in this family have also been highlighted.

Although steps have been taken to address the systematic problems of Simuliidae, there is much more work to be carried out to shed light on the taxonomy and phylogeny of the world simuliids (ADLER *et al.*, 2010), especially in the tribe Simuliini. Concerning the Neotropical Simuliidae, there is some "activity" at the much needed “alpha taxonomic level” for most of the genera, and more detailed work in a few species groups and vectors of river blindness, in which chromosome or enzyme studies has been carried out. Unfortunately, no overall agreement exists yet concerning the generic or subgeneric position for many species, or the validity of many subgenera.

Two schools of thought concerning the systematics of Simuliidae can be identified. One school advocates grouping of the family into numerous but rather small ["small" refers to the number species allotted to them] genera with no subdivisions (*e.g.* PY-DANIEL & MOREIRA SAMPAIO, 1994a,b; RUBTSOV & YANKOVSKY, 1984, 1988). Their argument is that the use of numerous named genera is more convenient for identification purposes (RUBTSOV, 1974). The second school advocates fewer genera with more numerous subgenera. The latter was proposed by R.W. CROSSKEY (see CROSSKEY & HOWARD, 1997, 2004) and is followed by several workers of World Simuliidae (*e.g.* ADLER *et al.*, 2004; SHELLEY *et al.*, 1997, 2010). CROSSKEY´S reasoning for this is that too many genera, which have been diagnosed on variable morphological characters, offer little biological information. It also unbalances the classification system of Simuliidae in comparison to other Diptera families (CROSSKEY, 1988).

CROSSKEY (1988) argued that a classification must be linked to a species phylogeny and changed in response to new phylogenetic findings. He stated that classifications are needed for practical reasons (taxon definition, identification), but phylogenies are not essential on a day-to-day basis. Simuliidae phylogeny potentially compromises the current classification of the family, and it is this compromise that is the "driving force” behind Simuliidae systematics and taxonomy nowadays. Fortunately, practising Simuliidae taxonomists now have an array of tools such as DNA markers, chromosomes, enzymes and cuticular hydrocarbons that can be used to unravel the many taxonomic problems in the family, not only at specific (sibling species) levels, but also at generic and suprageneric levels. Nonetheless, I envisage that the use of morphological characters will still play a major underlying role in our understanding of Simuliidae systematics worldwide.

1.7. Systematics of the blackfly subgenus *Trichodagmia* ENDERLEIN (Diptera: Simuliidae: *Simulium*) in the new world

As outlined in the previous sections, the family Simuliidae are significant to humans because many species are important biting pests in various parts of the world, and some species transmit the filarial nematode *O. volvulus* that causes human onchocerciasis. Members of the family Simuliidae also play an important role in freshwater ecosystems by recycling organic matter (including dissolved organic matter) from the water column, and they are good indicators of water quality. For these reasons, blackflies have been the subject of active research for many years. Nonetheless, they are morphologically conservative and the classification of the family Simuliidae remains unstable at the subgeneric and species group level, especially in the tribe Simuliini. Thus, many authors have attempted to apply a variety of different methods (morphotaxonomy, cladistics, DNA, cytogenetics, cuticular hydrocarbons) to unravel the taxonomic and evolutionary relationships among taxa.

An example of this classificatory instability is the subgenus *Trichodagmia*. The many taxonomic changes that have been proposed for this taxon (more details in **Chapter 2**) merely demonstrate the difficulty of the group, especially with respect to the position of the subgenus *Trichodagmia* in the tribe Simuliini and its phylogenetic relationships. The subgenus *Trichodagmia* also includes some of the main vectors of river blindness in South America (within the *S. guianense* species complex) as well as other highly anthropophilic species (*S. nigrimanum*). Several species within the subgenus *Trichodagmia* are species complexes (*S. guianense s.l.*, *S. virgatum s.l.*) which have been defined on the basis of the polytene larval chromosomes, making adult identification difficult or impossible, which is an impediment to the understanding of the transmission of onchocerciasis and to the current control campaigns of the disease in Latin America.

For these reasons, I undertook the revision of the subgenus *Trichodagmia* by employing an integrated taxonomic approach combining classical taxonomy, cladistic analysis (phylogenetics) and DNA barcoding. The objectives of this thesis are as follows: 1- To provide a morphotaxonomic revision of the subgenus *Trichodagmia*, with identification keys to separate all species groups and species, and to summarise the distribution, biology and medical importance of each taxa; 2- To determine whether the subgenus *Trichodagmia* is monophyletic and what are the relationships among its constituent species based on morphological characters of four life stages (larva, pupa, female, male); and 3- To test the robustness of DNA barcoding for the identification of the known species, and to test its potential for revealing cryptic diversity in this subgenus and related taxa.

1.8. APPENDIX 1. TABLES.

TABLE 1. First suprageneric classification system in Simuliidae by G. ENDERLEIN (ENDERLEIN, 1921a).

SUBFAMILIES	TRIBES	GENERA
Prosimuliinae		*Prosimulium*, *Taeniopterna*, *Cephia*, *Helodon*, *Parasimulium*
Cnesiinae		*Archinesia*, *Cnesia*
Ectemniinae		*Aspathia*, *Cryptotecmnia*, *Ectemnia*, *Pternaspatha*, *Psilozia*
Hellichiinae		*Hellichia*, *Astega*
Nevermanniinae		*Acropogon*, *Anasolen*, *Chylonectha*, *Cnetha*, *Dasyzopelmoza*, *Ectemnaspis*, *Friesia*, *Hemicnetha*, *Gomphostilbia*, *Miodasia*, *Morops*, *Nevermannia*, *Notolepria*, *Pselophochir*, *Psilopelmia*, *Psilonectha*, *Schonbaueria*, *Stilboplax*, *Titanopteryx*, *Wihelmia*
Stegopterninae		*Gigantodax*, *Mallochela*, *Stegopterna*
Simuliinae		*Boophthora*, *Byssodon*, *Chirostilbia*, *Dyscosphyria*, *Edwardsellum*, *Gynonychodon*, *Metomphalus*, *Odagmia*, *Pliodasina*, *Psaroniocompsa*, *Simulium*, *Thyrsospelma*, *Trichodagmia*

TABLE 2. Current number genera and species of Simuliidae in the Neotropical Region following ADLER & CROSSKEY (2009) and SHELLEY *et al.* (2010). For certain taxa I have followed the number of species as interpreted by COSCARÓN & COSCARÓN-ARIAS (2007) and this is highlighted with four asterisks (****).

SUBFAMILY	TRIBE	GENERA*	SUBGENERA	SPECIES
Simuliinae	Simuliini	*Cnesia*		3
		Cnesiamima		1
		Gigantodax		60
		Lutzsimulium		7
		Paraustrosimulium		1
		Pedrowygomyia		4
		Simulium	*Aspathia*	26
			Byssodon ****	1
			Chirostilbia	13
			Eusimulium ****	1
			Nevermannia ****	1
			Notolepria	9
			Psaroniocompsa **	47
			Psilopelmia **	60
			Psilozia ****	3
			Pternaspatha	29

TABLE 2. Continued.

SUBFAMILY	TRIBE	GENERA*	SUBGENERA	SPECIES
Simuliinae	Simuliini		*Trichodagmia***	62***
		Tlalocomyia	–	12
TOTAL: 1	1	8	11	340

* In the total number of genera, the genus *Mayacnephia* is recognized as a junior synonymy of *Tlalocomyia* following ADLER *et al.* (2004). The genera *Araucnephia*, *Araucnephioides*, and *Kempfsimulium* are recognized as junior synonyms of *Lutzsimulium* following SHELLEY *et al.* (2010). The revalidation of the the genera *Araucnephia* and *Araucnephioides* by GIL-AZEVEDO (2010) is not recognized in the current work.

** Within the genus *Simulium* SHELLEY *et al.* (2010) proposed the following subgeneric synonymies which are followed in this work: *Cerqueirellum* C*oscaroniellum* and *Inaequalium* are synonyms of *Psaroniocompsa*; *Ectemnaspis* is a synonymy of *Psilopelmia*; *Hearlea*, *Hemicnetha* and *Thyrsopelma* are synonyms of *Trichodagmia*.

***The recently described species *Simulium lithobranchium* by HAMADA *et al.* (2010) is included.

2. MORPHOTAXONOMY OF THE SUBGENUS *TRICHODAGMIA* ENDERLEIN

2.1. Summary

In this chapter, the morphotaxonomy of the 58 valid species of the New World subgenus *Trichodagmia* are reviewed. In addition, the taxonomy of two other species (*S. oviedoi* and *S. rivasi*) previously allotted to *Trichodagmia* is also reviewed. Full morphological descriptions of these 60 species based upon the adults, pupal and larval life stages is provided, in combination with a comprehensive taxonomic discussion, along with notes on distribution, biology and medical importance. The location and condition of the type material is given for all species with the known synonyms. The subgenus *Obuchovia* is here considered a **new junior synonymy** of *Trichodagmia*, and all its constituent species are now placed in the ALBELLUM species group to represent a Palaearctic element within this subgenus. Three new junior synonymies are here proposed: *Simulium chiriquiense* FIELD is a synonym of *S. ethelae* DALMAT **n. syn**.; *S. biuxinisa* COSCARÓN & IBÁÑEZ-BERNAL is a synonym of *S. paynei* VARGAS **n. syn**; and *S. keenani* FIELD is a synonym of *S. earlei* VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA **n. syn**. A neotype is designated for *S. lahillei* (PATERSON & SHANNON, 1927) and a lectotype for *S. pulverulentum* KNAB. *Simulium falculatum* ENDERLEIN is transferred from the TARSATUM species group of SHELLEY *et al.* (2010) to the CANADENSE species group based on the morphology of the female genitalia. Two species, *S. rivasi* RAMÍREZ PÉREZ and *S. oviedoi* RAMÍREZ PÉREZ, are transferred from the TARSATUM species group of SHELLEY *et al.* (2010) to the subgenus *Psilopelmia* based on the morphology of the male gonostyle and the ventral plate. Keys to separate all species groups and species based on the adults, pupae and larvae are also provided.

2.2. Introduction

The discovery of several onchocerciasis foci and the high anthropophily of many simuliid species in Central, South and North America, has greatly stimulated the systematics of Simuliidae in the Neotropical Region (LUNA DIAS *et al.*, 2004; SHELLEY, 1988a,b; SHELLEY *et al.*, 1987a,b, 2000), especially in those taxa which are vectors of river-blindness (SHELLEY *et al.*, 1997, 2010). Several species of *Trichodagmia* are of great economic importance with respect to river blindness transmission and their voracious attacks on both humans and livestock, and are a source for food consumption in some communities [reviewed by SHELLEY *et al.*, 2010].

The species included in *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010) are widely distributed in the New World. The majority of the taxa are found in swift fast flowing rivers with clear waters and/or waterfalls usually at altitudes between 600 to 1000 m (ADLER *et al.*, 2004; SHELLEY *et al.*, 2010). Species of *Trichodagmia* have a wide distribution range in the New World extending from northern Argentina, and southeast Brazil to Amazônia, the Guyana Shield, and southern Venezuela. The current synonymy of *Hemicnetha* under *Trichodagmia* (SHELLEY *et al.*, 2010) also extends the distribution of this taxon to North America (ADLER & CROSSKEY, 2008, 2009, 2010; ADLER *et al.*, 2004; MIRANDA-ESQUIVEL & COSCARÓN, 2001; SHELLEY *et al.*, 2010).

The classification system of Neotropical blackflies is unstable [as discussed in **CHAPTER 1**], mainly at the generic and subgeneric level in the Tribe Simuliini. Controversy still exists as to whether *Simulium s.l.* should include less subgenera (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; SHELLEY *et al.*, 2010) or wether all previous subgenera should be given generic rank (PY-DANIEL & MOREIRA SAMPAIO, 1994a,b, 1995). An example of the latter problem is the subgenus *Trichodagmia* ENDERLEIN 1934a.

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The most recent review of species of *Trichodagmia* is that of SHELLEY *et al.* (2010), who recognized four species groups (CANADENSE, ORBITALE, PICTIPES and TARSATUM) and 62 valid species in this subgenus. One of these species, *S. guianense s.l.*, is known to be a species complex and the primary vector of onchocerciasis (river blindness) in the highlands of the Amazônia focus in Brazil (CHARALAMBOUS *et al.*, 1996; SHELLEY, 1991; 1994, 2002; SHELLEY *et al.*, 1997, 2010). *Simulium guianense s.l.* is also involved in the transmission of onchocerciasis in the southern (Amazonian) focus of the disease in Venezuela (GRILLET *et al.*, 2005). Considerable anthropophily is found in several species of *Trichodagmia* that are responsible for sporadic outbreaks of disease. A well-known example *S. nigrimanum* MACQUART, which is thought to be the responsible for outbreaks of *Endemic Pemphigus Foliaceus* in Brazil, an apparently autoimmune reaction to the females' bites (EATON *et al.*, 1990). The rare condition known as the *Altamira Haemorrhagic Syndrome* is also attributed to bites of species in this subgenus (DÍAZ *et al.*, 1989a,b).

Other species of *Trichodagmia* are also well-known biting nuisances both to humans and cattle, *e.g.* *S. lahillei* (PATERSON & SHANNON) in Argentina, and *S. orbitale* LUTZ and *S. scutistriatum* (LUTZ) in the state of Rio Grande do Sul, Brazil (MIRANDA-ESQUIVEL & COSCARÓN, 2001). On the other hand, several species are regarded as strictly mammalophilic feeding on a large number of hosts such as cats, cattle, donkeys, horses, mules, goats, and sheep in the United States and other countries in South America, for example Guatemala (ADLER *et al.*, 2004; DALMAT, 1955). Larvae of *S. rubrithorax* form huge mats in fast flowing rivers and they have been recorded as a food source for Yanomami Indians in Brazil, where they collect larvae from waterfalls (SHELLEY & LUNA DIAS, 1989).

Trichodagmia was described by ENDERLEIN in 1934a to accommodate *Trichodagmia latitarse* [now a synonom of *S. townsendi* MALLOCH]. However, several authorities have employed a much broader concept to define this subgenus resulting in several subgeneric and specific synonymies in *Trichodagmia* (SHELLEY *et al.*, 2010) [see the following section in this chapter "**2.4.1. Previous Work**" for more details]. The objective of this chapter is to provide a morphotaxonomic review of the subgenus *Trichodagmia* in the New World, with descriptions of males, females, pupae and larvae, and notes on the species distribution and their biology and medical importance. In addition, keys to the species groups and species based on adults and immature stages (larva and pupa) are also given.

2.3. Material and methods

Most of the specimens used in this work are housed in the BMNH [=NHM] Simuliidae collection, although material from other natural history museums and institutions was also examined as noted in the sections "**Acronyms for Depositaries of Specimens Examined**" and "**Material Examined**". Identifications of all specimens based on the female, male, pupal or larval stage is often impossible because several species are morphologically identical in one or other stage. Consequently, adults reared from pupae in combination with the examination of the dissected gill histoblast in mature larvae collected at the same locality were used wherever possible, so that character suites of at least two life stages can be used for identification.

2.3.1. Collecting, rearing and preparation

The methodologies used in this paper largely follow those described by SHELLEY *et al.* (2010, Figs. 31-37, 39-44). For the collection of specimens also see the collecting protocol detailed by HERNÁNDEZ (2007) in www.blackflies.info.

Larvae and pupae were collected from all sorts of running water courses, removed from their substrate (*e.g.* rocks, leaves, tree logs) and placed in plastic bags to be screened later in the laboratory. All samples were properly labelled and placed in an insulated box containing a small quantity of ice to keep the temperature stable. Care was taken to remove most of the water from the bags so that the larvae and pupae did not drown.

At the collection site, larvae were immediately placed in a fresh mixture of Carnoy's solution for fuure cytogenetic studies. The Carnoy's was changed after an hour and again 24 hrs later. P.H. ADLER (pers. comm.) recommends that only up to a maximum of 18-20 larvae should be placed in a single vial containing Carnoy's and kept in a 4C° fridge, if good chromosomal preparations are to be obtained. Carnoy's solution is also an advantage because it fixes the colour pigments of the larva.

In the laboratory, mature pupae were placed individually in a rearing tube until the adult emerged. The adult was then preserved dry on a micro-pin on a strip of polyporous, which was itself pinned with the associated pupal exuviae in a polypropylene tube containing glycerine. Alternatively, were preserved in 70% ethanol with their pupal exuviae in a small genitalia glass tube plugged with cotton wool and contained in a larger (12 mm) tube stoppered with plastic or cotton wool in a jar of ethanol. All specimens were labelled with the information as shown in Figs. 31-35 of SHELLEY *et al.* (2010). Link reared specimens of each sex that were preserved in ethanol were dissected and mounted on cavity slides (SHELLEY *et al.*, 2010, Figs. 21-22). Dried, pinned material was dissected and mounted when necessary. Anthropophilic females which appeared while searching for the immature stages, were collected individually in small glass vials, and later killed in the lab using Acetyl Acetate and micropinned for identification and photography. When anthropophilic females were present an extra 15-20 minutes was spent at each collecting site in order to maximise the collection of biting females.

Dissection techniques followed HERNÁNDEZ & SHELLEY (2005) and HERNÁNDEZ *et al.* (2005). All life stages were individually dissected in 80% ethanol. The various body parts of the adults (head, thorax, and abdomen) and larvae (head and body, except gill histoblasts and anal gill) were placed in hot 10% KOH for 10-15 min. These body parts were then rinsed in water for 5-10 min and after two changes of 80% alcohol, all unwanted body tissues and membranes were removed. The remainder of the adult's body and pupa were dissected in 80% ethanol, and then transferred into Cellosolve (2-Ethoxyethanol). All body parts from the KOH were brought together with the remaining individual, and transferred to Cellosolve for 10-15 min and mounted on a cavity slide using Euparal® as the mounting medium. The adult's genitalia and female cibarium were dissected in a small drop of Phenolic Gum Copal (D.J. & D. Henshaw supplier).

For the larval stage, the gill histoblasts were first dissected in 80% ethanol and placed in 10-20% glacial acetic acid until the filaments were largely opened. These were then rinsed in water, one pass of alcohol, and then transferred to Cellosolve before being mounted in Euparal®. All slides were left to dry overnight and a coverslip with a drop of Euparal® was placed on top the following morning.

2.3.2. Digital imaging and measurements

All digital images used in this study were prepared using a composite image analysis system by Syncroscopy company [previously known as Synoptics], Cambridge, UK. This system overcomes the focussing problems caused by depth of field that previously precluded photography of three dimensional structures such as the scutum (for its pattern), and genitalia and mouthparts (LOWRY & SHELLEY, 1990). The functioning of the prototype system, as detailed by SHELLEY *et al.* (2000) [also see Fig. 23 of SHELLEY *et al.*, 2010], was upgraded with an DELL computer and Olympus compound microscope and Wild stereo microscope attached to a JVC-KY70 colour digital camera. This camera produces high quality images of 1289 X 1019 pixels of 4mb (HERNÁNDEZ & SHELLEY, 2005; HERNÁNDEZ *et al.*, 2005; SHELLEY *et al.*, 2010).

Variation of the scutal thorax pattern can occur in Simuliidae depending on the direction of the light source incident on the specimen (*e.g.* SHELLEY *et al.*, 1997, 2010; LOWRY & SHELLEY, 1992). Therefore, a standard positioning and standard type of light source were employed to capture this pattern (SHELLEY *et al.*, 2010). A fibre-optic light source was directed onto the anterior and posterior regions of the thorax, and the scutal pattern was captured for each position (Figs. 38-41 of SHELLEY *et al.*, 2010). Pinned dry specimen were mainly used for this procedure, as material recovered from alcohol using the method of SABROSKY (1966) was less satisfactory due to shrivelling and colour changes. All photographs are kept in the Simuliidae Digital Imaging Archive at the BMNH.

Names and definitions of the body structure and dimensions used in this work follows SHELLEY *et al.* (1997, 2000, 2010). Measurements were taken using the "Measurement module" in the Automontage software and are given in millimetres (mm). Body lengths for adults and pupae in alcohol were measured from material held in a lateral position by a bed of glass beads within a watch glass containing 80% ethanol. Body lengths of dry specimens were used when material was only available in this condition (as indicated in the text), and this measurement was taken with the specimen in lateral view. Gill length is given for the longest unbroken pupal gill filament from pupae in ethanol (SHELLEY *et al.*, 1997), although slide mounted specimens were used in few cases. Wing length and width were measured mainly from pinned specimens, but slide-mounted or specimens in alcohol were also used. Larval body length was also taken with the specimens positioned in lateral view in glass beads in 80% alcohol; the larval head length and width were measured with the head in dorsal view.

2.3.3. Preservation

All new material in this study was preserved using standard BMNH protocols (HERNÁNDEZ, 2007) in the dry [= pinned], slide, and spirit (ethanol) collections. Larvae were preserved in Carnoy's fluid in a refrigerator at 4ºC. A slide collection of chromosomal preparations of species complexes and their associated photographs are also stored in BMNH.

The Simuliidae collections were first databased using the software PARADOX, but are being transferred based onto a system (KE Emu) developed by "*KE Software*" for collections management for museums, galleries and herbaria. The curation of all material in this collection is based on the present classification of the family in the World Blackflies Inventory of ADLER & CROSSKEY (2008; 2009) adapted to incorporate the new arrangements that follow SHELLEY *et al.* (2010) and the current work. The spirit collection is still based on the world blackflies inventory of CROSSKEY & HOWARD (1997, 2004).

2.3.4. Structures used by other authors in taxonomic studies on Neotropical Simuliidae

Since the 1940s workers on Simuliidae have largely used the same sets of structures for genus, subgenus and species definition. The only near-comprehensive revisions of species in the Neotropical Region are those of COSCARÓN (1987) for *Simulium*, COSCARÓN & COSCARÓN-ARIAS (2007) for all species, and SHELLEY *et al.* (2010) mainly for the Brazilian simuliid fauna. In 1987 COSCARÓN used the following principal characters in his classification and phylogenetic reviews: In the female the general coloration, basal (=median) part of the cibarium and genitalia and to a lesser extent the tooth on the hind leg claw, the setae of the basal section of R, the absence or presence of hairs on the pleural membrane and katepisternum, spines in the spermatheca. In the male the general coloration, setation of the basal section of R and the genitalia. In the pupa the cocoon shape, gills, cephalothoracic tubercles and trichomes and abdominal chaetotaxy. In the larva the general abdominal morphology, head sclerites, hypostomium, mandible and number of rows on the posterior circlet. The same structures, with additional characters, were used by COSCARÓN & COSCARÓN ARIAS (2007) in their keys to the Neotropical fauna with the addition of the antennae and legs in order to embrace the different genera involved. A more comprehensive assessment of the pupal characters for the separation of several genera and subgenera in Neotropical species was made by SHELLEY *et al.* (2010), and the same broad approach is followed in this work.

Comprehensive accounts of taxonomic structures used in species descriptions are given by CROSSKEY (1990), ADLER *et al.* (2004), COSCARÓN & COSCARÓN ARIAS (2007) and SHELLEY *et al.* (2010). Several structures used in simuliid identification are given different names depending on the author. To facilitate the use of keys and descriptions, and for comparison with those of other authors, the names used in this work together with those commonly used by other authors for the same structure are listed below. Portuguese and Spanish words have been translated to English unless there is no English equivalent.

This work [after SHELLEY *et al.*, 2010]	Other authors
Basal cell	basal medial cell
Genital fork stem	genital fork median branch
Genital fork lateral arms	genital fork anterior branches

Gonapophysis	oviscapt, ovipositor lobe
Gonocoxite	basimere, basistyle, pieza basal, pieza lateral
Gonostyle	distimere, dististyle, pinceta
Nudiocular area	fronto-ocular triangle
Paramere	endoparameral organ, endoparameres
Paraproct	anal lobe, ovipositor lobe
Posterior circlet	anal disc, anal ring
Postgenal cleft	gular aperture
Rectal gill [with lobes and lobules]	anal gill [rectal papillae, diverticula]
Ventral papilla	ventral tubercle
Ventral plate	adminículo, basal plate
Tubercles (on pupa)	platelets

2.3.5. Methods Used in Taxonomic Research on Simuliidae in the Current Work

A diagnosis for the four species groups of *Trichodagmia* is provided in the current work. This has been based upon long series of specimens examined in the Simuliidae collection housed at the NHM [= BMNH] and the Simuliidae Digital Imaging Archive held at this institution. In addition, specimens from other museums and institutions, and original descriptions and figures in the literature were taken into account. In the case of published figures, subtle differences in certain characters such as scutal pattern and genitalia morphology have been treated with caution because of the variation that can be caused by age and condition of specimens, as well as different orientation of specimens on slides and incidence of the light source on colour pattern [see sections **2.3.1-2.3.4**, **"Collecting, Rearing and Preparation"**; **"Digital Imaging and Measurements"**; **and "Preservation"**].

I have consulted type specimens of valid species and their synonymies where possible, and used computer generated digital images to more objectively represent morphology than line drawings. I have obtained link-reared specimens from collection sites as often as possible in order to assess intraspecific variation (that has frequently been neglected in the Neotropical fauna of Simuliidae).

A general weakness in many of the previous works on the Neotropical Simuliidae has been the failure to analyse the variation in key morphological structures of some new species, which have sometimes been based on single or very few specimens, or only one or two life stages. Examples of these characters are wing vein setation that varies within populations and between sexes, leg coloration, number of pupal gill filaments and trichome branching, and presence or absence of tubercles or setae on the larval abdomen. Consequently, many "valid species" have become junior synonyms as character variation is taken into account from differen populations throughout the species distribution. These have been dealt with in synonymic reviews (*e.g.* SHELLEY *et al.*, 1984; HERNÁNDEZ *et al.* 2007a), subgeneric reviews (*e.g.* HERNÁNDEZ *et al.*, 2007b, 2008), countrywide revisions (*e.g.* SHELLEY *et al.*, 2002; 2010), species group reviews (*e.g.* SHELLEY *et al.* 2006) and routinely in published species descriptions and redescriptions [see **REFERENCES**].

I have attempted to base species descriptions on long series of link-reared specimens in comparison with type specimens, to obtain accurate definition of intraspecific variation using a standard technique. Where this has not been possible, I have relied on un-reared specimens in the BMNH and other institutions, and sometimes recourse had to be made to specimens that had been slide mounted by other specialists using their own techniques. In a few cases only published descriptions and illustrations by other authors have been available, for exampled the adult and larval morphology of species in the CANADENSE species group. The use of body, wing and gill lengths for distinguishing species was avoided where possible, because this can show seasonal and habitat variation (P.H. ADLER, A.J. SHELLEY, pers. comm.).

SHELLEY *et al.* (2010) did not include the larval morphology while describing species of Simuliidae from Brazil because this stage in many species is unknown and larvae preserved in ethanol rapidly deteriorate in colour with age and even, but to a lesser extent, in Carnoy's fixative. However, in order to provide descriptions for all *Trichodagmia* species in the New World, it was usually possible to obtain larval specimens from fresh collections or loaned from recent surveys made by other colleagues.

The use of some characters described by other authors was also avoided. For example, PY-DANIEL (1983) refers to the fronto-ocular area (AFO) [originating in WYGODZINSKY & COSCARÓN (1973) as the frontal angle] that consists of a lateral extension of the frons into the ommatidia of the female at the point of the nudiocular triangle. He used the dimensions of this area for distinguishing certain subgenera, for example *Cerqueirellum* and *Coscaroniellum*. I have not used this character because of the difficulty in accurately defining the area.

In general, I used a suite of diagnostic morphological characters for species descriptions and taxonomic placements following SHELLEY *et al.* (2010). These are as follows: in the female - general coloration, nudiocular triangle, cibarium, scutal pattern and leg coloration, eighth sternite and gonapophyses, paraproct and genital fork; in the male: general coloration, scutal and leg coloration, gonocoxite and gonostyle, ventral plate, median sclerite and paramere; in the pupa - cocoon coloration and form, gill filament number, branching and configuration; in the larva - general body coloration, presence or absence of setae on the abdomen, presence or absence of the ventral papillae, head coloration, morphology of the postgenal cleft and hypostomial teeth, morphology of the mandible, and presence or absence of sclerotised plates around the anal sclerite. Descriptions also include other characters that appear to vary at the individual level such as venation of the Sc and basal section of R, teeth on claw on hind leg as well as characters used by other authors that show little interspecific variation. The male gonostyle and the female paraproct were used as the major diagnostic character in the classification of species groups within the subgenus *Trichodagmia*. All these characters are used at varying levels of importance by revising authors.

The pupal chaetotaxy has been used by VARGAS and collaborators and the main characterto distinguish *Trichodagmia* from other subgenera within the genus *Simulium*. I have placed far less importance on this character because in all subgenera of the genus *Simulium*, the pupal abdomen has nine clearly defined segments that are usually membranous with small protective plates over the genital region, although in some more primitive species the cuticle is hardened and forms segmental tergites and sternites (SHELLEY *et al.*, 2010; Figs. 77-80). In the genus *Simulium s.l.,* the abdomen has forwardly directed hooks and spine combs, hooklets, hair-like setae and trichomes. The basic onchotaxy comprises 4+4 hooks on tergites III-IV and 2+2 hooks on sternites V-VII. The ninth abdominal segment can bear or not 1+1 terminal spines. In the pupa the main character that I used in species identification is the form of the gill and the number of filaments, and in some cases the form of the cocoon. CROSSKEY (1990) distinguished seven main types of cocoon for Simuliidae, but I have simplified this to either slipper-shaped, boot-shaped, or shoe-shaped, with or without fenestrations. Gill form is of more importance at the species and sometimes at species group level (*e.g.* the CANADENSE species group), where it can sometimes be a key character. However, this is not the case for all taxa.

2.3.6. General figures and terminology used in this work

The reader is referred to ADLER *et al.* (2004), CROSSKEY (1990), COSCARÓN & COSCARÓN ARIAS (2007) and, more recently, SHELLEY *et al.* (2010) for detailed accounts of the morphology of life stages of Simuliidae. The terminology used in this work is based on that used by SHELLEY *et al.* (2010).

Two terms are used that refer to morphospecies showing significantly different infra-specific taxonomic forms. If these are distinguished using cytological, zymological or molecular techniques, the morphospecies is referred to as a "complex of sibling species". If these are distinguished purely on morphology they are referred to as "morphoforms" and will only get species status when other disciplines confirm their seperate specific status. The term *sensu stricto* (*s.str.*) is used when reference is being made to the form or sibling species on which the first description of the morphospecies was based. The term *sensu lato (s.l.*) is used when reference is being made to a species complex or a species that consists of different morphoforms.

Descriptions of *Trichodagmia* species used in the current work are improved and expanded from the descriptions written by L. M. HERNÁNDEZ recent publication of *The Simuliidae of Brazil* (SHELLEY *et al.*, 2010), to take into account non-Brazilian populations of Brazilian species, to include non-Brazilian species, and to include larvae for all species. Full descriptions of the adults and pupa have been included here, together with the most relevant taxonomic changes for those taxa that occur in Brazil. The larval description for simuliid species found in Brazil were not treated by Shelley *et al.* (2010), but has been added in the current work. For all species groups and species, diagnosis for species groups, morphological descriptions for adults and immature stages and full taxonomic discussion is given. In this work, four life stages have been reviewed: the female, male, pupa and larva. The egg stage remains undescribed for most species of Simuliidae. In most cases, it is necessary to base the identification on a combination of characters for each life stage and an association of an adult with its pupal exuviae. External features were mainly viewed with a dissecting microscope using dry, spirit or slide material. Other characters were viewed on slides under a compound microscope.

A series of annotated figures outlining the general morphology of the life stages has been provided to facilitate understanding the species descriptions: female (Figs. 1-39), male (Figs. 40-64), pupa (Figs. 65-85) and larva (Figs. 86-99). The figures follow the scheme used for describing adults, pupa and larva for each species. Dimensions of these stages include range, arithmetic mean with standard deviation and number of specimens examined, when sufficient material was available.

FEMALE:

Head: A general image of the female mouthparts is given in Fig. 103 and some of the variation in the cibarium in Figs. 5-7. The nudiocular area (Fig. 2) of the eye varies from being developed to well developed. In larger species it can be seen with the naked eye. It is a useful character at the species level. The cibarium is unarmed or armed with teeth or tubercles in the region of the median margin; the cornuae can be developed and sclerotised (Figs. 5-7), but sometimes they are reduced. The cibarium is used in conjunction with other characters, but can be important for separating species into groups or subgenera.

Thorax: The coloration of the scutum and patterns of setae are important at the species, species group and subgenus level. A pattern, when present, usually consists of vittae (longitudinal bands) (Fig. 1) or cunae (triangles) (Fig. 2) on a differently coloured background. These are best viewed in pristine, dried pinned specimens; those dried from ethanol preservation often lose clear pruinose patterns because they can be devoid of hairs. Wing venation (Fig. 4) in *Trichodagmia* species correspond to the norm for the genus *Simulium* with a curved posterior branch of the cubital vein (Cu2) and basal cell absent. The presence or absence of setae on the basal section of the Radius and Subcosta veins appears to be stable in some species, but variable between populations in others. The leg coloration (Fig. 3) is included, but it has been of limited value in species identification. The presence or absence of basal teeth on the claws of the tarsal segments, especially the hind tarsi, has been found to vary intraspecifically and should be used with caution.

Abdomen: Coloration and pattern is important at species and subgenus levels. The form and the presence or absence of microtrichiae of the gonapophyses (Figs. 9-10, 30-39) of the eighth sternite are useful at the species group and to some extent the subgenus level. I refer to the paraproct form and dimension [following Shelley *et al.* (2010)] as the part of the paraproct at the level of the cercus and the length of its ventral extension (if present) in relation to the depth of the cercus (Figs. 8, 14-29). This is a change from previous publications where the paraproct was described in its entirety. The paraproct form is useful at the species, species group and subgenus levels (Figs. 9, 11, 14-29). The genital fork is variable in the degree of its development and form (Figs. 12) and can be used in some cases to distinguish species and species groups and/or subgenera, for example *S. tarsatum* and *S. tarsale* (Figs. 697, 698). The external sculpturing and internal setation of the spermatheca (Fig. 13) are of limited importance in species of *Trichodagmia.*

MALE:

Head: There are no characters on the head that are useful for species identification.

Thorax: The only important character on the thorax (Figs. 40, 41) is scutal coloration and setation. Scutal patterns when present consist of an orange, brown, dark brown to black scutum sometimes with silvery pruinose areas usually in the form of cunae, vittae or subrectangular vittae (Figs. 704-828).

Abdomen: Silver ornamentation of the abdomen is reported, but thought to be of limited value (Fig. 40), especially because the abdomen is often contracted in dry specimens. The genitalia are of great importance taxonomically from subgenus and species groups to species lebl, particularly the form of the gonocoxite and gonostyle. The genitalia are shown in ventral view in Fig. 42 and under each species description. SHELLEY *et al.* (2010) discussed in detail how the orientation of the gonostyle in slide preparations for imaging is particularly important. The gonocoxite and gonostyle are relatively flattened structures that lie under the posterior end of the abdomen of the male (Figs. 43-46). The ventral side of these structures is completely sclerotised and is not used in images or descriptions (Figs. 47-60). The dorsal side shows a membranous, unsclerotised area at the base of both the gonostyle and gonocoxite. Images are taken of this dorsal aspect with the two structures lying flat on a slide under a small coverslip. Other orientations will show different forms of the gonocoxite and especially the gonostyle (SHELLEY *et al.*, 2010, Fig. 64). Some authors describe the gonocoxite and gonostyle from an undissected slide mounted hypopygium (*e.g.* ADLER *et al.*, 2010), which rarely gives the same form as when the structure is dissected and placed flat under a coverslip. The ventral plate is important only at the species group and species level. The form is highly variable, ranging from a simple, flat to complex three-dimensional structure (Figs. 47-60). The median sclerite within the subgenus *Trichodagmia* is usually long and wide, with or without an apical incisure (Fig. 637) and is of limited use even at the species level. The paramere varies from usually undeveloped (ORBITALE species group) (Fig. 62) to developed (Figs. 61, 63-64) with apical teeth of varying size. The dissected paramere is such a small structure that it is difficult to arrange in a slide preparation, and consequently images in this work are not of a standard orientation.

PUPA:

Cocoon: Usually useful at the species group, subgeneric and generic level. It may be slipper-shaped (Fig. 65), shoe-shaped (Fig. 66), boot-shaped (Fig. 67), shoe-shaped without anterior fenestrations (Fig. 68), or shoe-shaped with anterolateral fenestrations (Fig. 69).

Gill: The most important diagnostic character on the thorax is the gill. This is highly variable morphologically and its number of branches, branching patterns, length, width and to a lesser extent integument are all of use at the species, species group and in some cases subgeneric level. The number of branches is less variable when they are few of them, but when there are more than 10 branches the number can vary intraspecifically and from one side of the pupa to the other. Species with filamentous gills most commonly have six, eight or 12 branches, although this number varies. I use the term configuration to indicate primary gill branch divisions from dorsal to ventral. Hence, a 3:3:2 configuration in a gill with eight filaments signifies that there are three primary branches, the dorsal and median with three secondary branches, and the ventral with two secondary branches. Samples of gills of various species to illustrate the broad range of variation are given in Figs. 75-84. The gill surface is covered with spicules that may be randomly distributed along the filament, in the form of rings or regularly distributed and well developed (SHELLEY *et al.*, 2010).

Head (*frontoclypeus*) and *Thorax*: The cuticular form of the frontoclypeus also varies and may be useful in some cases at all taxonomic levels (Figs. 70-72). For example, spines only occur in *S. hirtipupa* (Fig. 71), whereas rounded and/or spiny tubercles (or their absence) may occur in other species (Fig. 70). The form of the trichomes varies from simple, bifid to multibranched, or spiniform. Some species have irregular rugosities or markings that are good diagnostic characters (Fig. 72). When low numbers of branches occur on trichomes this is of little use at the species level because of intraspecific variation in the genus *Simulium*. However, in other subgenera, such as *Psilopelmia* in the Andean Region, multi-branched trichomes are useful for species identification (see review of COSCARÓN & COSCARÓN-ARIAS, 2007). Thickening of the frontoclypeus (carina) (Fig. 724) and irregular markings (Figs. 46) are seen in some species of the TARSATUM species group and can also be used as a diagnostic character.

The thoracic integument has similar variations as the frontoclypeus (*e.g.* Figs. 73, 74). Variation in tubercle and trichome form are sometimes useful at the species level.

Abdomen: The onchotaxy and form of the cuticle of the abdomen is important at the generic level (Figs. 85) (also Figs. 77-80 in SHELLEY *et al.*, 2010), but not at the subgeneric or species level. In *Trichodagmia* the common ground plan patterns is as follows: tergite I with 1+1 sublateral setae; tergite II normally with 4+4 spiniform setae; tergites III-IV with 4+4 submedian hooks; tergites V-VIII sometimes with small setae; tergite IX with 1+1 small terminal spines and weakly sclerotised. Sternite III without setae; sternites IV with simple lateral hooks; sternite V with 2+2 hooks; sternites VI-VII with well separated hooks. The anterior margin of tergites and/or sternites can have areas of spine combs, and in some species these are well developed resembling teeth. Within-species variation in the presence or absence of setae, trichomes, tubercles and hooks is very common, and hence is of little taxonomic importance. However, in several species the presence of bands of densely distributed rounded tubercles is diagnostic.

LARVA:

The general body shape and coloration is not diagnostic of species groups or species in the subgenus *Trichodagmia* (Figs. 86-88, 90).

Head: The positive or negative head pattern (Fig. 91) is commonly used to distinguish species, but this character has now been shown to vary even within the same cytotype (CHARALAMBOUS *et al.*, 1997). The hypostomium, especially the shape of the postgenal cleft and hypostomial teeth (Figs. 92-95), and the mandibles (Figs. 96, 97) is the most important taxonomic structure to separate species. The most common pattern is for the hyspotomium to have nine teeth that are evenly arranged along its anterior margin (Fig. 93). Tooth terminology has been described by ADLER *et al.* (2004): one median tooth, usually more prominent than the remainder teeth; 3+3 sublateral teeth, 1+1 lateral teeth; and small lateral serrations [paralateral teeth can be seen in some species]. On each lateral margin, the hypostomium has a single line of hypostomial teeth varying in number and length. In addition, 1+1 long simple trichomes can be seen near the posterior margin centrally. Nonetheless, variation from this common pattern can be seen with some species having the hypostomial teeth only distributed in the central region and prominently protruded forward (Fig. 95) or hypostomial teeth being reduced and positioned below the anterior margin (Fig. 94). Seven or eight hypostomial teeth has also been recorded in some species, but a higher number is quite common (Fig. 95). In addition, the 3+3 sublateral teeth sometimes have the pair adjacent to the median tooth most prominent than the median and lateral teeth, and 2+2 long or short and simple or bifid trichomes in the posterior region are also present. The shape of the postgenal cleft varies from deep, bell-shaped and triangular apically (Figs. 92) to short, broadly centrally, and rounded or with a tube-like incisure on apex (Figs. 94).

The morphology of the mandibular teeth can be of great value for species identification. In *Trichodagmia* the most common pattern is: mandible with three apical teeth the internal more prominent; mandibular comb with more than seven and/or eight to 17 teeth, and 1+1 mandibular serrations, the anterior often longer than posterior (Fig. 97). Variation in this pattern occurs in the numerous species examined [see under species descriptions]. I will refer to 'mandibular serrations', although CRAIG & CRAIG (1986) have proved that this is actually a sensillum (also ADLER *et al.*, 2010). Other larval head characters here described (such as antennal segments surpassing or not the apex of labral head fans, number of labral fan rays, and shape of cervical sclerite) are not good characters for species or species groups delineation.

Thorax: The most important taxonomic character on the thorax is the morphology of the dissected gill histoblast from mature larvae. These are seen as dark brown or black patches on either side of the thorax (Fig. 86). The number and configuration of the gill filaments is the only character for reliable species identification. However, this is sometimes difficult in closely related species with the same number of gill filaments and similar configuration of the gill filaments. The presence of sclerotised plates on the proleg, number of rows and teeth, and the presence or absence of setae are of limited use in identification.

Abdomen: In general, abdominal characters are of limited use at the species level, but the shape and length of the posterior arms of the anal sclerite can separate certain species. For example, in species of the CANADENSE species group such as *S. gorirossiae*, *S. johnsoni*, *S. larvispinosum* the posterior arms of the anal sclerite encircles the posterior circlet, which has prominent sclerotised ventrolateral or dorsolateral accessory plates (Figs. 87, 99). The shape and number of these plates are good characters for species separation. In addition, the presence or absence of ventral papilla, and sometimes the number of finger-like lobules in the rectal gills might be a good specific characters (Figs. 88-89). The presence of 1+1 dorsolateral tubercles (Fig. 90)can be diagnostic at the species level.

Other characters used in species descriptions, such as the presence or absence of setae on the integument, number of sclerotised proceses and hooks per row in the posterior circlet, number of branches on the anal gill are variable and easy to damage during dissection, and hence they are of limited use for species identification.

2.3.7. Acronyms used for depositaries of Simuliidae

The following acronyms are used for depositories of specimens referred to in the text and under **MATERIAL EXAMINED:**

AMNH	American Museum of Natural History, New York, USA.
BMNH	Department of Entomology, Natural History Museum, London, United Kingdom [Currently known as NHM].
CNC	Canadian National Collections, Ottawa, Canada.
CUAC	Clemson University Arthropods Collection, Clemson, South Carolina, USA.
CU	Cornell University, Ithaca, New York, USA.
DBAT	Dipartimento di Biologia Animale, Universita di Torino, Torino, Italy.
DERM*	Laboratorio de Entomologia de la Division de Endemias Rurales, Maracay, Aragua State, Venezuela. [Previously recorded as DDSV- Sección de Oncocercosis, Division de Dermatologia, Villa de Cura, Aragua State, Venezuela in SHELLEY *et al.*, 1997].
FSP	Faculdade de Saúde Pública, Universidade de São Paulo, Brazil.
ICBUSP	Coleção Entomológica do Departamento de Parasitologia do Instituto de Ciências Biomédicas da Universidade de São Paulo, Brazil.
ICNUC	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia
IDVC*	Instituto de Dermatología, Villa de Cura, Aragua, Venezuela [Previously recorded as IND, Instituto Nacional de Dermatología, Villa de Cura, Aragua in SHELLEY *et al.*, 1997].
IML	Instituto Miguel Lillo, Instituto Superior de Entomologia, Facultad de Ciencias Naturales, San Miguel de Tucumán, Argentina.
INBIO	Instituto de Biodiversidad, San José, Costa Rica.
INDRE	Instituto Nacional de Diagnósticos y Referencia Epidemiológicos, Mexico City, Mexico; formerly Instituto de Salubridad y Enfermedades Tropicales, ISET].
INPA**	Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
IOC	Laboratório de Simulídeos e Oncocercose (LSO), Instituto Oswaldo Cruz, Rio de Janeiro, Brazil.
MLP	Museo de Ciencias Naturales, La Plata, Argentina.
MCZ	Museum of Comparative Zoology, Harvard, USA.
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
MZUCR	Museo de Zoologia, Universidad de Costa Rica, San José, Costa Rica.
NM	Naturhistoriches Museum, Vienna (Wien), Austria.
NMHU	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany [as ZMHU – Zooligisches Museum der Humboldt-Universität, Berlin, Germany in SHELLEY *et al.*, 1997 and ZM by SHELLEY *et. al.*, 1989].
NMNH	Smithsonian Intitution, National Museum of Natural History, Washington, USA [Previously recorded as U S National Museum of Natural History in SHELLEY *et al.*, 1997].
SMT	Staatliches Museum für Tierkunde, Dresden, Germany.

* For notes on RAMIREZ PEREZ' Simuliidae collection see SHELLEY *et al.* (2010).
** For notes on the situation in INPA see SHELLEY *et al.* (2010).

2.4. Review of the subgenus *Trichodagmia* ENDERLEIN, 1934a

All subgenera considered to be synonymous with the subgenus *Trichodagmia* [*Dyarella*, *Grenieriella*, *Hearlea*, *Hemicnetha*, *Shewellomyia* and *Thyrsopelma*] were reviewed by SHELLEY *et al.* (2010). They did not include the subgenus *Obuchovia*, treated by ADLER *et al.* (2004) as a synonym of *Hemicnetha*, because it was only found in the Palaearctic Region [the latter subgenus was later revalidated by ADLER & CROSSKEY (2008)]. I have here reviewed the taxonomic status of the subgenus *Obuchovia* with regards to that of *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010).

I have largely drawn upon COSCARÓN'S treatment of the Neotropical fauna (1987), later updated by COSCARÓN & COSCARÓN ARIAS (2007) and more recently by SHELLEY *et al.* (2010). For those Nearctic elements incurring into the Neotropical Region, I have followed ADLER *et al.* (2004) in combination with the latest versions of the World Inventory of Blackflies by ADLER & CROSSKEY (2008, 2009, 2010).

2.4.1. Previous work

The previous works dealing with the taxonomy of subgeneric and species names related to *Trichodagmia* have been detailed by SHELLEY *et al.* (2010) and these are updated here. The taxonomic changes proposed by SHELLEY *et al.* (2010) are also discussed together with the changes that have occurred in the subgenera *Hagenomyia*, *Hearlea*, *Obuchovia*, and *Shewellomyia*.

ENDERLEIN (1934a) described several new species from the Neotropical Region from material deposited in the Dresden Museum, and from the Neotropical and other world regions in the Berlin Museum (NMHU) [see WERNER 1996a,b for current ENDERLEIN holdings in these two museums]. In his subfamily Simuliinae he described the new genera *Thyrsopelma* and *Trichodagmia* with two new species (*T. brasiliense* [=*S. orbitale* LUTZ, 1910] and *T. latitarse* [=*S. townsendi* MALLOCH, 1912]) as their respective type species. Generic diagnoses were based purely on wing setation, both having the basal section of R with several rows of hairs and the Sc and Radius haired. This character was used to separate them from the genera *Simulium* and *Odagmia* (=*Simulium s.str.*), which he described as having bare basal sections of R. In this and later papers (ENDERLEIN, 1934b, 1936) various new species were added to *Thyrsopelma* and *Trichodagmia* and these are dealt with under the introductions to species descriptions where they relate to Neotropical species. Additionally, ENDERLEIN (1936) referred to generic characters of *Trichodagmia* in his species description of *Trichodagmia distincta* LUTZ, 1910. He redescribed female *Trichodagmia* species as possessing in most cases enlarged first tarsal segments (except females from Sierra Córdoba in Argentina that EDWARDS examined) and dark, narrow, longitudinal stripes on the scutum. They differed in these two characters from females of his genera *Dasypelmoza* (=*Pternaspatha*) and *Friesia* (=*Simulium s.s.*)., which have narrow fore tarsal segments and different scutal patterns. ENDERLEIN (1934b) examined simuliids deposited in the Vienna Museum (NM) and described the new genus *Hemicnetha* in his subfamily Nevermanniinae with *H. mexicana* [=*S. paynei*] collected by BILIMEK from Mexico as the type species. In the definition of the genus, wing setation was again used as well as the morphology of the first tarsal segment of the male hind leg. In *Hemicnetha* the Sc of the male and female was unhaired and the Radius and basal section of R were lightly haired. It differed from *Cnetha* (=*Nevermannia*, see CROSSKEY, 1988) because of the bare Sc of the former. In *Hemicnetha* the first tarsal segment of the male hind leg was broad, flat and spindle-shaped. In 1936 ENDERLEIN placed *Thyrsopelma* with *Psaroniocompsa* and his new genus *Pliodasina* (=*Psaroniocompsa*) in the tribe Simuliini and *Trichodagmia* with *Odagmia* in the tribe Odagmiini.

The next period in Neotropical simuliid taxonomy involved VARGAS, whose underlying interest was identification of onchocerciasis vectors in Mexico. In 1942 VARGAS considered characters for the genera *Cnetha* ENDERLEIN, 1921a and *Hemicnetha* ENDERLEIN, 1934b to be very similar. In accordance with other authors he believed *Cnetha* to be a synonym of the genus *Simulium* together with the genus *Hemicnetha*, with its type species *H. mexicana.* To avoid homonymy with *S. mexicanum* BELLARDI, 1862 he proposed the new name *S. paynei* for ENDERLEIN's species and denominated it as *Simulium* (*Simulium*) *paynei nomen novum n.n.* In his world catalogue VARGAS (1945a) maintained the name *Hemicnetha* as a synonym of the genus *Simulium.* MAIA-HERZOG *et al.* (1984) pointed out an error in the Spanish summary of VARGAS & DÍAZ NÁJERA (1953a) where *H. mexicana* is referred to as a synonym of *S. barbatipes* - "*H. mexicana* ENDERLEIN, 1934 y *gueroa* SMART, 1944 es sinónimo de *Simulium barbatipes* (ENDERLEIN, [actually 1934a]". This is obviously a typographical error because the main text and English summary correctly reported VARGAS' earlier action.

In his paper on new names and data for New World Simuliidae VARGAS (1943a) reviewed the status of several of the genera previously published by ENDERLEIN. He followed EDWARDS' (1931, 1934) and RUBTSOV's (1940) treatment of some of ENDERLEIN'S generic names as synonymous with the genus *Simulium*. He referred to the characters used by ENDERLEIN (1934a) for erecting *Trichodagmia* as a new genus and incorrectly added information from ENDERLEIN's key on the frons, leg coloration and dimensions. These characters were actually used by ENDERLEIN for species identification within *Trichodagmia* and were not intergeneric. As VARGAS correctly detailed, additional information on leg characters and scutal pattern were given in ENDERLEIN (1936). VARGAS concluded that insufficient characters had been provided by ENDERLEIN to justify the new genus *Trichodagmia* and consequently synonymized it with the genus *Simulium*. Later, in the same paper for similar reasons of insufficient intergeneric characters he synonymized *Dasypelmoza* ENDERLEIN 1934a with EDWARD' subgenus *Eusimulium* of *Simulium*. To avoid creating homonyms he carried out the following name changes. *Dasypelmoza miniata* ENDERLEIN 1934a became *Simulium* (*Eusimulium*) *miniatum* and *Trichodagmia miniata* ENDERLEIN 1934b was given the new name *S. martinezi* [=*S. dinellii*]. *Trichodagmia angustitarsis* ENDERLEIN 1934a [=*S. jujuyense* PATTERSON & SHANNON 1927) was given the new name *S. hoffmanni* to avoid homonymy with *S. angustitarse* (LUNDSTRÖM, 1911). *Dasypelmoza macca* ENDERLEIN 1934a became *Simulium* (*Eusimulium*) *maccum*. In 1945a VARGAS, following EDWARDS' subgeneric system (1931, 1934), regarded ENDERLEIN's genera *Hemicnetha*, *Thyrsopelma* and *Trichodagmia* as being within the genus *Simulium*, but gave no indication as to which subgenus of EDWARDS' scheme they belonged.

VARGAS then began to regard many of the generic names of ENDERLEIN as subgenera. In 1946 VARGAS *et al.* erected the new subgenus *Dyarella* based on adult genitalia and larval characters with *S. mexicanum* BELLARDI as type species, and included *S. mathesoni* previously described from Mexico (VARGAS, 1943b) based on external characters and genitalia of the male. Their diagnosis for this subgenus is given in section **2.8 APPENDIX 2**. Later papers (VARGAS & DÍAZ NÁJERA, 1948a, 1948b, 1949) added extra characters from the female, male and pupa. VARGAS & DÍAZ NÁJERA (1953a) examined the two ENDERLEIN specimens of *S. paynei* (earlier described by VARGAS as *Hemicnetha mexicana*) and made preparations of the genitalia. They considered these specimens as conspecific with *S. mathesoni* VARGAS, 1943b and hence synonymized this name with the earlier described *S. paynei*. They then recognized the subgenus *Hemicnetha* for *S. paynei* and synonymized with it the (later described) subgenus *Dyarella*.

In the same paper VARGAS *et al.* (1946) mentioned the subgenus *Hearlea* to include five species of Simuliidae for the Mexican fauna and attributed the subgenus to RUBTZOV (1940). Rubtzov first mentioned the name *Hearlea* (with the species *S. canadense* described by HEARLE in 1932 while discussing the zoogeographical relationships between the Nearctic and Palearctic Regions. As the subgenus *Hearlea* had not been formally described at that time nor had a type species been designated, the name *Hearlea* became a *nomen nudum* under the ICZN (1999) rules. VARGAS *et al.* (1946) provided a key to separate the subgenus *Hearlea* from all other subgenera of Simuliidae in Mexico based on the male genitalia and also selected a type species, *S. canadense*. Therefore, VARGAS *et al.* (1946) become the authors of the subgeneric name *Hearlea* under the ICZN (1999) (articles 21 and 50), and this has been accepted by most authors (*e.g.* ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN, 1987; COSCARÓN & COSCARÓN-ARIAS, 2007; CROSSKEY, 1988; CROSSKEY & HOWARD, 1997, 2004).

In their notes on simuliid systematics VARGAS & DÍAZ NÁJERA (1951b) described *Grenieriella* as a new subgenus in *Simulium*. Subgenus diagnostic characters are given in section **2.8. APPENDIX 2**. *Simulium lahillei* PATERSON & SHANNON was selected as the type species and *S. chalcocoma* KNABA, *S. nigrimanum* MACQUART, 1846 [as *S. pruinosum* LUTZ], *S. orbitale* LUTZ and *S. guianense* WISE [as *S. pintoi* D'ANDRETTA & D'ANDRETTA] were placed in the subgenus. In the same paper these authors discussed some of the generic names proposed by ENDERLEIN including *Trichodagmia*, *Thyrsopelma* and *Hemicnetha.* They doubted the validity of *Thyrsopelma* because it was based on wing setation and female anterior tarsal morphology (characteristic of ENDERLEIN's subfamily Simuliinae) and included species from two zoogeographical regions, the Neotropical (Brazil and Bolivia) and Oriental. They argued that only adult genitalia morphology was adequate for a subgeneric diagnosis. Similar arguments were given concerning the doubtful validity of *Trichodagmia*, which they hinted at being a synonym of *Thyrsopelma* because it appeared later in the same paper and was not distinct based on ENDERLEIN's descriptions. They also questioned the inclusion of *Trichodagmia* in the tribe Odagmiini by ENDERLEIN, but with no explanation. They noted that species of their subgenus *Grenieriella* were different from *Odagmia* in that species of *Grenieriella* showed no notable widening or cone-shaped first tarsal segment of the hind leg as occurs in *Odagmia* [although in their diagnosis of *Grenieriella* they state that the posterior metatarsus of the male is cone-shaped or narrow]. They also questioned ENDERLEIN's diagnosis of *Hemicnetha* based on wing setation and male leg morphology and pointed out the variation in wing venation between species and even sexes in species of their subgenus *Grenieriella*. Apart from the juxtaposition of these names no obvious link was made between their subgenus *Grenieriella* and ENDERLEIN's genera *Trichodagmia*, *Thyrsopelma* and *Hemicnetha*, being apparently a coincidence that they included two species (*S. chalcocoma* and *S. orbitale*) that are the type species for ENDERLEIN's *Trichodagmia* and *Thyrsopelma* respectively. It was not until two years later that VARGAS & DÍAZ NÁJERA (1953a), having examined types of ENDERLEIN, tackled this situation. They referred to the inadequate descriptions, type designations, citations of localities and collectors and poorly defined classification system of ENDERLEIN and suggested that the situation could be partly rectified by an examination of the genitalia of females. They synonymised, based on the female genitalia, *Trichodagmia latitarsis* [spelled *latitaris*] ENDERLEIN, 1934a with *S. chalcocoma* KNAB, 1914a, which in 1951b they had placed in their new subgenus *Grenieriella*. As a consequence of this specific synonymy *Grenieriella* became a synonym of *Trichodagmia*.

VARGAS & DÍAZ NÁJERA (1953a) also dealt with *Thyrsopelma*. This originated as a genus of ENDERLEIN (1934a) with *T. brasiliense* as its type. They examined one female labelled as a type [actually a syntype according to WERNER, 1996a] from three females sent to ENDERLEIN by VON SELLO from Brazil and concluded that it was probably conspecific with *S. orbitale* LUTZ, 1910. However, they observed that the paraprocts of the type were more elongate than those of *S. orbitale* figured by D'ANDRETTA & D'ANDRETTA (1945), which they explained as possibly artefactual and were reticent to provide a synonymy. They listed *Thyrsopelma brasiliense* [regarded by VARGAS (1945a) as *Simulium* (*Eusimulium*) *brasiliense* following RUBTSOV, 1940] as a possible synonym of *Simulium orbitale* and did not accept *Thyrsopelma* as the subgenus for *S. orbitale* at this stage. Previously, VARGAS (1945a) had followed RUBTSOV (1940) in including *S. orbitale* as a synonym of *Simulium nigrimanum* Macquart in the subgenus *Simulium*. However, the figure and description of the latter authors indicated relatively elongate paraprocts. They did not come to a firm conclusion, but subsequent authors (COSCARÓN, 1987; CROSSKEY & HOWARD, 2004) cite *S. brasiliense* as a synonym of *S. orbitale* LUTZ and it was confirmed by Shelley *et al.* (2010) [see **Taxonomic Discussion** under *S. orbitale*]. In the same paper (VARGAS & DÍAZ NÁJERA, 1953a) they examined a poorly preserved specimen of *Trichodagmia laticalx* ENDERLEIN 1934a [=*Simulium* (*Trichodagmia*) *tarsatum*] and noted its similarity to *Simulium mexicanum* BELLARDI, 1862 [=*Simulium* (*Trichodagmia*) *tarsatum*], also in the subgenus *Hemicnetha* until SHELLEY *et al.* (2010). In their final revision of Mexican simuliids (VARGAS & DÍAZ NÁJERA, 1957a, 1959] the only subgenus of this group was *Hemicnetha*, whose diagnosis is the same as that given under *Dyarella* in section **2.8. APPENDIX 2** with the following extra details: female gonapophyses long reaching to or beyond ventral margin of cercus and without depressions, paraproct [as anal lobe] not in form of half moon directed ventrally [or anteriorly and parallel to ventral face of abdomen in 1959 pictorial key], flattened, rounded; branches of genital fork with prominent or small conical or flattened internal process. By the end of their work VARGAS' group thus recognised for the Neotropical Region the subgenus *Hemicnetha* with its synonym *Dyarella*, and *Trichodagmia* with its synonym *Grenieriella* and that, possibly, *Thyrsopelma* was also a synonym.

In 1962 STONE selected a lectotype for *Chirostilbia flavifemur* described by ENDERLEIN (1921a) from two females collected in Brazil. Both STONE (1962) and WERNER (1996a) referred to the wrong publication of ENDERLEIN (see ENDERLEIN 1921c) as the original description. CROSSKEY & HOWARD corrected this in 1997 and explained that the description of *Chirostilbia flavifemur* (ENDERLEIN 1921c) was preceded by a generic key to *Chirostilbia* (ENDERLEIN, 1921a), which contained sufficient information for the name *flavifemur* to be available because *Chirostilbia* was monospecific. ENDERLEIN (1921c) further referred to *Chirostilbia flavifemur* in a paper containing keys and lists to subfamilies, tribes and genera, which had already been previously discussed (ENDERLEIN, 1921a). STONE (1962) also examined a specimen from Paraguay labelled as *Chirostilbia flavifemur*, which he thought to be *S. pertinax* KOLLAR. He believed that the lectotype and paralectotype of *C. flavifemur* might have been conspecific with *S. pertinax* even though their "thoraxes were slightly redder and less shiny" and the "hind femur entirely yellow with no trace of a dark spot at the apex". He observed that the position of *pertinax* and *flavifemur* in the genus *Simulium* was uncertain, but that they appeared close to *chalcocoma* KNAB (=*latitarsis* ENDERLEIN), the type species of *Trichodagmia*, treated by VARGAS & DÍAZ NÁJERA (1953a) as a subgenus. He reasoned that if this group of species is considered sufficiently distinct to warrant a subgenus, *Chirostilbia* has priority and *Dasypelmoza* ENDERLEIN, *Ectemnaspis* ENDERLEIN, *Trichodagmia* ENDERLEIN and *Grenieriella* VARGAS & DÍAZ NÁJERA would become its synonyms. Even though this is not presented as a certainty in the text his paper begins with a list of synonyms in which these four subgenera appear as new synonyms of *Chirostilbia.* In 1963 STONE presented a list of genus-group names for the Simuliidae on a worldwide basis and maintained the subgeneric synonyms of *Chirostilbia* given in his previous paper based on their type species being similar to *Simulium pertinax* of the subgenus *Chirostilbia*. He gave a diagnosis for this subgenus as well as for *Hemicnetha*, which he accepted as a valid subgenus. He accepted the synonymy of *Dyarella* with *Hemicnetha* by VARGAS & DÍAZ NÁJERA (1953a). CROSSKEY (1981) followed the synonymy of *Trichodagmia* with *Chirostilbia*, accepted *Grenieriella* as a valid subgenus, but made no mention of the status of *Thyrsopelma.*

COSCARÓN (1987) then published the most comprehensive taxonomic revision of the genus *Simulium* for the Neotropical Region. He provided diagnoses to the genus and constituent subgenera and within these placed species into species groups [He used the word species "subgroup" instead of species "group" because in the same paper he had referred to the *blancasi*, *oviedoi* and *quadrivittatum* species "groups" as having an equivalent status to subgenus]. In his cladistical analysis of the then 243 species of Neotropical *Simulium*, he gave different weight to the morphological characters used in contemporary simuliid taxonomy. In adults he stated that he had placed more weight on the genitalia and female cibarium, and less on the presence or absence of a tooth on claws and setae on the basal section of R, because of intraspecific variation in these characters. Hairs on the pleural membrane and katepisternum and internal setae in the spermatheca were regarded as less important in species in this zoogeographical region. In the pupa increased emphasis was placed on abdominal chaetotaxy and cephalothoracic trichome morphology because other pupal characters were considered to vary intraspecifically. Larvae were considered very important for defining species groups in terms of their general morphology and morphology of the anal sclerite, hypostomium, mandible and number of rows of hooks in the posterior sucker. This paper has been the starting point and main information source for the subgeneric and species definitions. COSCARÓN's diagnoses for *Hemicnetha*, *Thyrsopelma* and *Trichodagmia* [as *Grenieriella*] are given in section **2.8 APPENDIX 2.**

There is some confusion over subgeneric groups throughout COSCARÓN's paper (1987) that is relevant to the current interpretation of the subgenus *Trichodagmia.* The latter concern to the priority given to the subgenera *Hemicnetha*, *Grenieriella* and *Thyrsopelma.* The latter problem has been detailed and corrected by SHELLEY *et al.* (2010), and the reader is referred to this publication for further details.

VARGAS & DÍAZ NÁJERA (1953a) had already sunk *Grenieriella* as a synonym of *Trichodagmia.* The diagnoses in COSCARÓN (1987) (section **2.8 APPENDIX 2**) are the most detailed for these Neotropical subgeneric names, but they present problems because some of the characters are not included for every subgenus, many of the characters (such as wing setation) are intraspecifically variable, and there is an overlap in character variation between each subgenus. COSCARÓN (1987) disagreed with STONE's (1963) inclusion of *Thyrsopelma* in *Chirostilbia*, but did not comment on the inclusion of *Trichodagmia.* To support his viewpoint COSCARÓN detailed the diagnostic characters of *Chirostilbia* that differ from *Thyrsopelma* as follows: female *Chirostilbia* species have claws with teeth, paraprocts more than twice as long as wide and pointed apically, gonapophyses with a slight sclerotised internal border, genital fork with strongly curved shaft, gonostyle shorter than gonocoxite and robust without apical spine, pupal gills filiform or widened and asymmetrical, multi-branched thoracic trichomes, larval integument without scales, second antennal segment of larva only slightly longer than first segment and smaller than third segment, lateral teeth of hypostomium sharp, anal ring with less than 90 rows of hooks with around 15 hooks in each row. COSCARÓN (1987) covered to a varying extent the subgenera *Hemicnetha*, *Thyrsopelma* and *Trichodagmia* [as *Grenieriella*] in a section on phylogeny, in keys and under a section on diagnoses of supraspecific taxa and these have been distilled in section **2.8. APPENDIX 2**. His diagnosis for each species group does not equally cover every character and hence comparisons for some of the characters are not possible. He regarded *Thyrsopelma* as related to *Grenieriella* and *Hemicnetha*, especially to the former because of the similarity in form of gonocoxite, gonostyle, parameres, pupal gills, composition of cocoon, and second antennal segment of the larva very developed and large numbers of rows of hooks in the posterior sucker. Differences between *Thyrsopelma* and the other two subgenera were stated to be in colour and thoracic ornamentation of both sexes and the morphology of the cibarium, gonapophyses, paraproct, ventral plate, tip of pupal gills and larval mandible.

In 1991 Coscarón produced a paper on the Simuliidae of southern South America (the southern cone consisting of Argentina, Chile, southern Bolivia, Paraguay, Uruguay and south-east Brazil) providing keys to all stages and descriptions and figures of selected species. In this work he maintained the same classification used in his 1987 paper, except that the term subgroup [within a subgenus] was replaced by group. This produces a problem in the case of the “BLANCASI group” which he regarded as equivalent to a subgenus. The three subgenera *Hemicnetha*, *Grenieriella* and *Thyrsopelma* were maintained.

Peterson *et al.* (1988) gave a description of the new blackfly species *S. hieroglyphicum*, which they placed in the subgenus *Hemicnetha*. The authors recognized about 22 species in this subgenus, which is largely Neotropical with two species also occurring in the Nearctic Region, and produced a key to species [only 21 species included]. Their view of *Hemicnetha* was broader than that of Coscarón (1987) and Crosskey (1988). They included all the *Hemicnetha* species previously cited by Coscarón (1987), but omitted *S. placidum* [synonymized by Hernández & Shelley (2005) with *S. mexicanum*, now *S. tarsatum*, that was regarded as a valid species by Coscarón (1987)] and *S. seriatum* [later synonymised with *S. tarsatum* by Hernández & Shelley (2005)] and *S. dehnei* [later synonymised by Shelley *et al.* (2002b) with *S. earlei*]. They included *S. conviti* as a valid species [previously synonymised with *S. paynei* by Maia-Herzog *et al.*, 1984], and *S. lahillei* and *S. muiscorum* [synonymised with *S. townsendi* by Hernández & Shelley, 2005], which Coscarón 1987 placed in *Grenieriella* [now *Trichodagmia*] and Crosskey (1988) placed in *Trichodagmia* and *Hemicnetha*, respectively. Crosskey & Howard (1997, 2004) included both species in *Trichodagmia* and in the latest World Inventory of Blackflies (Adler & Crosskey, 2010) accepted the species synonymy. Additionally, Peterson *et al.* (1988) included *S. oviedoi* and *S. rivasi*, which Crosskey (1988) had not assigned to a subgenus. However, these two species were placed together in the OVIEDOI species group [regarded as a subgenus] by Coscarón (1987), but were unplaced to subgenus in the OVIEDOI species group by Crosskey & Howard (1997, 2004). Coscarón & Coscarón Arias (2007) considered these two species as belonging to *Hemicnetha* as did Hernández *et al.* (2007), who placed them in their TARSATUM species group created by Hernández & Shelley (2005) to replace the MEXICANUM species group when they synonymised *S. mexicanum* with *S. tarsatum*, which was accepted by Adler & Crosskey (2008, 2009, 2010). I have now examined specimens of these two species, which appear to be more closely related to species of the subgenus *Psilopelmia* in which they have now been assigned [see **Taxonomic Discussion** under *S. oviedoi* and *S. rivasi*].

Py-Daniel & Moreira Sampaio (1994b) considered the changes in names of Neotropical species following their decision to upgrade subgenera of *Simulium* to genera (Py-Daniel and Moreira Sampaio, 1994a). They provided the name *bellardii* as a replacement name for *mexicanum* of Bellardi, 1862 [now a synonym of *S. tarsatum* Macquart – see Hernández & Shelley (2005)]. However, Crosskey & Howard (1997) pointed out that “they wrongly thought that their recognition of *Hemicnetha* as a genus (not as a subgenus of *Simulium*) required nomenclatural revision of the congeneric names *mexicanum* (*-a*) Bellardi, 1862 [as 1869], and *paynei* Vargas, 1942 (syn. *mexicanum* (*-a*) Enderlein, 1934b, preoccupied). Their restitution of the name *Hemicnetha mexicana* Enderlein is invalid under the International Code for Zoological Nomenclature (ICZN, 1999, Article 59b) since a name replaced before 1961, because of secondary homonymy, remains permanently invalid. There is no justification for their rejection of *mexicana* Bellardi, the senior homonym, and its replacement by their new name *bellardii*. The latter is an unnecessary replacement name, unusable and permanently invalid.” In 1995 Py-Daniel & Moreira Sampaio gave a list of the then 77 recognised Brazilian species placing them in their newly recognised genera.

Crosskey (1988), Crosskey & Howard (1997, 2004) and Adler & Crosskey (2008, 2009, 2010) only recognised the subgenera *Hemicnetha* and *Trichodagmia*, with *Thyrsopelma* and *Grenieriella* as synonyms of *Trichodagmia*, originally mooted by VARGAS & DÍAZ NÁJERA (1953a). CROSSKEY (1988) proposed this rationale for "inventory purposes only" until the subgeneric classification of *Simulium* in the Neotropical Region is regularised. In 2001, MIRANDA-ESQUIVEL & COSCARÓN justified their use of the two subgeneric names *Thyrsopelma* and *Trichodagmia* [previously treated by COSCARÓN (1987) as *Grenieriella*] with reference to a cladistical analysis. They used used 34 morphological characters of larvae, pupae, and (principally) adults, and some characters were different to those used by COSCARÓN (1987). They concluded that their cladogram justified the recognition of two subgenera, *Thyrsopelma* (inncluding *S. guianense*, *S. hirtipupa*, *S. itaunense*, *S. perplexum*, *S. orbitale* and *S. scutistriatum*) and *Trichodagmia* (as *Grenieriella*, including *S. chalcocoma*, *S. huairayacu*, *S. lahillei*, *S. muiscorum*, *S. nigrimanum*, *S. sumapazense* and *S. wygodzinskyorum*) as COSCARÓN had suggested. However, conflicting views are given in different parts of their paper for the diagnoses of these two subgenera. According to the abstract the subgenus *Thyrsopelma* was characterized by the shape of the hypostomial teeth, and *Trichodagmia* by the presence of cibarial teeth, an untoothed female tarsal claw and the size of the gonapophyses, its pupal gill tip sclerotisation, and by the larval integument being covered by lanceolate setae. In the text the monophyly of *Thyrsopelma* was said to rest on the shape of the hypostomial teeth, larval integument covered by lanceolate hairs, females' tarsal claws without teeth and the size of the gonapophyses, while that of *Trichodagmia* rests on the presence of cibarial teeth and pupal gill tip sclerotisation. They also merged the LAHILLEI and NIGRIMANUM species groups [as subgroups] of COSCARÓN (1987) because in their new analysis *S. wygodzinskyorum* [which had been later placed in *Trichodagmia* by COSCARÓN & PY-DANIEL (1989)] was basal to the clade in which all the other species were included. They also regarded *S. sumapazense*, described after COSCARÓN's cladistical analysis, as more closely related to *S. muiscorum* than *S. wygodzinskyorum.* Also the previous division (COSCARÓN, 1987) of *Thyrsopelma* into three species groups [as subgroups] was slightly rearranged with the members of the ORBITALE species groups divided into two closely related clades – *orbitale* with *itaunense* and *guianense* with *perplexum.* The interpretation of this new cladistical analysis of MIRANDA-ESQUIVEL & COSCARÓN (2001) therefore largely corresponded with the previous one of COSCARÓN, except that species groups were dropped "nomenclaturally in order to promote homogeneity". However, *S. pruinosum* was not included, presumably being accepted as a synonym of *S. nigrimanum* [see **Taxonomic Discussion** of *S. nigrimanum*], but this was not stated. In any case, whatever the taxonomic interpretation, it is not clear that this cladistical analysis was robust, because it relied on a particular interpretation of intraspecific morphological variation and of the relative importance of different morphological characters in supraspecific classification. However, it is possible that this cladistic analysis might have been premature until a clearer definition of morphological definition of species became available. This required a more thorough analysis of the species through observations on intraspecific variation in long series of specimens in conjunction with a more critical examination of primary types with special reference to their genitalia. This approach has recently been validated by the examination of mainly Neotropical ENDERLEIN types by HERNÁNDEZ & SHELLEY (2005) when 15 new synonyms were created, several of which fall within the subgenera *Hemicnetha* and *Trichodagmia sensu* CROSSKEY & HOWARD (1997, 2004).

IBÁÑEZ-BERNAL (1992) reviewed the Mexican species of *Hemicnetha* and provided descriptions of all stages of the twelve species as well as a diagnosis of the subgenus *Hemicnetha* [in keys and text]. The latest work on North American Simuliidae (ADLER *et al.*, 2004) also dealt with some species of *Hemicnetha* that occur in both the Neotropical and Nearctic regions. They subsumed the Neotropical subgenus *Hearlea*, the Palaearctic subgenus *Obuchovia* and the Nearctic *Shewellomyia* in *Hemicnetha* based on similarities in the adult genitalia. In the latest review of the Neotropical fauna COSCARÓN & COSCARÓN ARIAS (2007) accepted *Hemicnetha*, *Thyrsopelma* and *Trichodagmia* as subgenera with *Grenieriella* as a synonym of *Trichodagmia* and also accepted *Hearlea* as a valid subgenus.

The recent world inventory of the Simuliidae (ADLER & CROSSKEY, 2008, 2009, 2010) followed the arrangement for the subgenus *Hemicnetha* presented by ADLER *et al.* (2004) in which *Hearlea* and *Shewellomyia* (also as *Hagenomyia*) were recorded as synonyms of *Hemicnetha*, except that *Obuchovia* was removed from its synonymy with *Hemicnetha* and treated as a valid subgenus of *Simulium.* Within the subgenus *Hemicnetha* four species groups were recognised by ADLER *et al.* (2004) CANADENSE, PAYNEI, PICTIPES and TARSATUM. In the case of the subgenus *Trichodagmia* the inventory (ADLER & CROSSKEY, 2010) accepts *Grenieriella* and *Thyrsopelma* as synonyms. HERNÁNDEZ & SHELLEY (2005) dealt with species status in the subgenus *Hemicnetha*. *Simulium tarsatum* and *S. tarsale* were transferred from 'unplaced' to the subgenus *Hemicnetha*. One name was synonymised with *S. nigrimanum*, eight names with *S. tarsatum*, five with *S. townsendi* and *S. falculatum* was considered as valid within *Hemicnetha*. HERNÁNDEZ *et al.* (2007) then synonymised *S. mutucuna* with *S. rubrithorax* and regarded *S. oviedoi* and *S. rivasi* as part of the TARSATUM species group of *Hemicnetha*. More recently, SHELLEY *et al.* (2010) reviewed all simuliids found in Brazil and proposed a new classification system for all genera, subgenera and species groups that were largely represented in that country and put them into context with regards to the Neotropical fauna. They discussed in detail their synonymy of *Hemicnetha* under *Trichodagmia*, and recognised three species groups, the CANADENSE, ORBITALE and TARSATUM species groups, thus subsuming the previous species groups of ADLER *et al.* (2004).

With regards to the subgenus *Obuchovia*, SHELLEY *et al.* (2010) followed the concept of ADLER & CROSSKEY (2008). because all *Obuchovia* species are found only in the Palaearctic Region and the authors were not familiar with this taxon. As the subgenera *Obuchovia* and *Shewellomyia* have been regarded as being closely related to *Hemicnetha*, I here review both subgenera separately in order to provide an account of the history of their taxonomy.

The subgenus *Obuchovia* was first described by RUBTZOV (1947) to accommodate *S. albellum*. The taxonomic confusion that has occurred in *Obuchovia* has been detailed by CROSSKEY (1967), who stated the following: STONE (1963) considered the first and second publication of the name *Obuchovia* by RUBTZOV (1947, 1951) as invalid, therefore treated *Obuchovia* as dating from a later publication (RUBTZOV, 1956), in which there is a description and a citation of a type species (*Simulium auricoma* MEIGEN, 1818). But RUBTZOV'S paper (RUBTZOV, 1947) does in fact provide a group description for *Obuchovia* and fixes a type species, and *Obuchovia* is nomenclaturally valid from 1947 because in page 90 there is the wording "subgenus nov." followed by "Group XV *albellum*, sp.n.", and on page 105 of the same work a description is given of the main characters in this group". In the same paper, CROSSKEY also pointed out that he brought this problem to the attention of Dr. STONE, who also agreed in that *Obuchovia* should be regarded as a valid subgenus.

CROSSKEY (1967) separated *Obuchovia* into two species groups, the ALBELLUM and AURICOMA groups, based on the width and length of the fore tarsal segment. The main diagnostic characters of *Obuchovia* given by CROSSKEY (1967) and other key works can be found in section **2.8. APPENDIX 2**. A short overview of *Obuchovia* has been given by CROSSKEY & SANTOS GRÁCIO (1985) while describing a new species from Spain and Portugal. CROSSKEY & HOWARD (2004) considered *Obuchovia* as a valid subgenus, but this was not accepted by ADLER *et al.* (2004) who subsumed *Obuchovia* under *Hemicnetha*. Then, in 2008 *Obuchovia* was re-established by ADLER & CROSSKEY without further explanation. The authors did not recognise the previous species groups of CROSSKEY (1967) and CROSSKEY & HOWARD (2004) because of "the small size of the subgenus and the structural similarity of the included species". I have discussed the reasons for this taxonomic action with Drs R.W. CROSSKEY and P.H. ADLER during the course of this work and they seem to disagree in their interpretation of *Obuchovia*. CROSSKEY considered *Obuchovia* as a valid subgenus following the Palaearctic distribution of all species and the morphology of the male ventral plate (pers. comm. to L.M. HERNÁNDEZ, July 2008), but ADLER argued that "the morphological similarity and similar biology of species in *Obuchovia* with those of *Hemicnetha* did not render *Obuchovia* the status of a distinct taxon. I did not see any problem in having a broader concept of *Hemicnetha* for it to include a Palaearctic element after all the new discoveries I have encountered, while reviewing the North American and Arboreal simuliid fauna" (pers. comm. to L.M. HERNÁNDEZ, September, 2008).

SHEWELL (1959) erected the new subgenus *Hagenomyia* to accommodate the species *S. pictipes* described by HAGEN (1880) from the USA, and the new species *S. longistylatum*. He separated *Hagenomyia* from all other Nearctic *Simulium* subgenera by the male having a deeply cleft ventral plate, a conspicuous fringe of long hairs on the seventh abdominal sternite of the female, and a wholly reticulate structure of the cocoon [see section **2.8. APPENDIX 2** for full diagnostic characters]. By erecting this name, SHEWELL (1959) created a junior homonym for *Hagenomyia*, as this generic name was already assigned to an African neuropteran species described by BANKS (1911). In order to avoid this homonym PETERSON (1975) substituted *Hagenomyia* with the name *Shewellomyia*. This name was later synonimized with *Hemicnetha* by ADLER *et al.* (2004) for which the authors erected the PICTIPES species group. ADLER & CROSSKEY (2008, 2009, 2010) accepted this taxonomy in the latest versions of the World Inventory of Blackflies. SHELLEY *et al.* (2010) also recognized the PICTIPES species group to include the Nearctic species *S. claricentrum*, *S. innoxium* and *S. pictipes*.

2.4.2. Remarks

I have examined ENDERLEIN's descriptions of *Trichodagmia*, *Thyrsopelma* and *Hemicnetha* and made dissections to reveal the morphology of the genitalia and the female head of several species, mostly reported in HERNÁNDEZ & SHELLEY (2005) and SHELLEY *et al.* (2010). I also examined and dissected specimens belonging to type material of the subgenus *Hearlea* (as recognized by COSCARÓN *et al.*, 2004), and *Shewellomyia*. In addition, original descriptions by RUBTSOV (see **REFERENCES**) and material housed at the BMNH identified as *Obuchovia* (described and/or identified by R.W. CROSSKEY) were also examined.

ENDERLEIN's initial diagnoses of *Trichodagmia* and *Thyrsopelma* (ENDERLEIN, 1934a) were based on wing vein setae and were exactly the same as each other. His distinction between the presence of fine hairs on the basal section of vein R in *Hemicnetha* (ENDERLEIN, 1934b) compared to several rows of hairs in the other two genera is not reliable because it varies between species in these three supraspecific groups. Later, ENDERLEIN (1936) gave further diagnostic female characters for *Trichodagmia*, as usually having an enlarged first tarsal segment and usually dark, narrow, longitudinal stripes on the scutum. The diagnostic character for male *Hemicnetha* (ENDERLEIN, 1934b) was a broad, flat, spindle-shaped first tarsal segment of the hind leg, but with no reference to the other genera. The tarsal segment is also now known to be unacceptable as a generic diagnostic character because it varies in many species of *Hemicnetha* [= TARSATUM species group of SHELLEY *et al.*, 2010). Similarly, scutal pattern is variable at species level as the diagnoses show (and even ENDERLEIN observed), and leg morphology is also a character of limited value because it varies between male and female of the species, except in some subgenera. In order to appreciate the degree of confusion caused by ENDERLEIN's somewhat random and ineffective use of characters in his generic diagnoses of Neotropical species, SHELLEY *et al.* (2010) provided a table (Table 2, Pp: 629) in which they compared ENDERLEIN's (ENDERLEIN, 1934a,b, 1936) and CROSSKEY's (CROSSKEY & HOWARD, 1997) supraspecific placements using the names *Hemicnetha*, *Thyrsopelma* and *Trichodagmia* as examples. A large proportion of the specific name changes are a result of avoidance of homonymies caused by regarding ENDERLEIN'S genera as subgenera of *Simulium*, and other changes are the result of synonymies. The table clearly illustrates the wide range of subgenera that now contain these names.

I have analysed the use of the names *Grenieriella*, *Hearlea*, *Hemicnetha*, *Obuchovia Thyrsopelma*, *Shewellomyia*, and *Trichodagmia* by various authors, and species groups within these subgenera. I conclude that the subgeneric names *Grenieriella*, *Hearlea*, *Hemicnetha*, *Thyrsopelma*, and *Shewellomyia*, should be regarded as junior synonyms of *Trichodagmia* in accord with SHELLEY *et al.* (2010), with the subgenus *Obuchovia* to be added as a new synonym. The cladistic analysis carried out in **CHAPTER 3** "**Phylogenetic analysis of the subgenus *Trichodagmia* ENDERLEIN based on morphology**" support this rationale [see also **Chapter 6** section **5.3.** "**Implication on the classification of the subgenus *Trichodagmia***"]. In this work, I have followed the broader taxonomic concept of *Trichodagmia* as advocated by SHELLEY *et al.* (2010), who largely agree with CROSSKEY & HOWARD (1997, 2004) and ADLER & CROSSKEY (2008, 2009, 2010). These authorities advocate a minimal use of subgeneric and species group names in contrast to COSCARÓN (1987), who proposed far more divisions at these two supraspecific levels.

In the new classification of the subgenus *Trichodagmia* not all species clearly fit into groups because of the overlap in characters. My analysis has been based on type material wherever possible and, for many species, I have examined long series of link-reared specimens collected by myself and colleages in order to assess intraspecific variation. In all other cases when no specimens were available for examination, I had to rely on descriptions and figures produced by other authors. Many of these were made when the taxonomy of the Neotropical Simuliidae was less advanced and hence some of the key characters were not described and a certain amount of informed extrapolation has been used. I have placed less emphasis on larval morphology because of the morphological homogeneity of *Trichodagmia* species in this life stage and the relative dearth of modern descriptions. I have based the species groups only on structures that seem to show minimal intraspecific variation in the Neotropical fauna following SHELLEY *et al.* (2010). These are: scutal pattern, female nudiocular area and cibarium, and genitalia of adults; cocoon and gill morphology of pupae; and morphology of the larval hypostomium and postgenal cleft, and number and shape of hypostomial teeth and mandible. I have used a suite of these characters, and species have been placed in species groups where characters are similar. I have dealt with all the species in the ORBITALE and TARSATUM species groups (*sensu* SHELLEY *et al.*, 2010) and all species in the CANADENSE species group (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010). For species in the the subgenus *Obuchovia*, the classification of CROSSKEY (1967), CROSSKEY & GRACIO (1985), and ADLER & CROSSKEY (2008, 2009) was followed.

The most obvious characters separating the current CANADENSE, ORBITALE and TARSATUM species groups, and the species of *Obuchovia* [now the ALBELLUM species group] are the form of the female paraproct, and male gonostyle and paramere. The form of the male ventral plate varies within *Trichodagmia* and it is more difficult to use in separating these species groups, because of the variable development of the lateral shoulders, keel and median process in each species. This is not the case in the *Obuchovia* species, where the suboval shape of the male ventral plate is common in the majority of taxa I have examined (Figs. 150, 153, 156, 159, 164). In the remaining species groups, the possession of a well developed median process with no keel (*e.g.* Figs. 51, 57) lies at one extreme, and at the other end a well developed keel with no well defined median process (Fig. 56); between these one can find species with varying development of the median process and keel (*e.g.* Figs. 48-50, 54).

The internal classification of *Trichodagmia* has been derived from COSCARÓN's earlier work (1987), later revised by CROSSKEY & HOWARD (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), and updated by ADLER & CROSSKEY (2008, 2009, 2010), SHELLEY *et al.* (2010) and this work. A clear summary of the taxonomic changes here discussed is shown in **Appendix 2.9**, TABLE 1. In my classification of *Trichodagmia* the ORBITALE species group conforms with the subgenus *Trichodagmia* in the latest World Inventory of Simuliidae (ADLER & CROSSKEY, 2010) with account taken of new synonyms and transfer of species from other supraspecific taxa by SHELLEY *et al.* (2010). In the latter treatise, *Simulium albopictum* was synonymised with *S. orbitale* and *S. oviedoi* and *S. rivasi* transferred from the subgenus *Hemicnetha*. In this work, *S. ovideoi* and *S. rivasi* are now placed in the BICOLORATUM species group of the subgenus *Psilopelmia* [see section **2.4.3. Checklist of *Trichodagmia* species and groups** for valid species and synonymies]. *Simulium argentatum* recorded as a *Trichodagmia* species by CROSSKEY & HOWARD (1997) appeared under *Inaequalium* in their 2004 publication following its synonymy with *S. inaequale* by COSCARÓN & MIRANDA-ESQUIVEL (1998), and maintained by ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010), which followed the review of the subgenus *Inaequalium* by HERNÁNDEZ *et al.* (2007b).

In the latest revision of the Neotropical fauna by COSCARÓN & COSCARÓN ARIAS (2007) the species of the ORBITALE group of *Trichodagmia* were divided between the two subgenera that they recognise, *Thyrsopelma* and *Trichodagmia*. The subgenus *Hemicnetha* in COSCARÓN'S (1987) work (also in COSCARÓN & COSCARÓN-ARIAS, 2007) and in the World Inventory of Simuliidae (ADLER & CROSSKEY, 2008, 2009, 2010) now forms the TARSATUM species group of the subgenus *Trichodagmia* by SHELLEY *et al.* (2010). COSCARÓN & COSCARÓN-ARIAS (2007) grouped the Neotropical species of the subgenus *Hemicnetha* into the BRACHYCLADUM, MEXICANUM, OVIEDOI and PAYNEI species groups, while ADLER & CROSSKEY (2008) merged the BRACHYCLADUM and PAYNEI species groups under the PAYNEI species group, and the MEXICANUM and OVIEDOI species groups under the TARSATUM species group. This was largely based on the re-arrangements and synonymies of HERNÁNDEZ *et al.* (2007). Additionally, ADLER & CROSSKEY (2008) have placed the North American species of *Hemicnetha* in the PICTIPES species group (previously as *Shewellomyia*) and species of the subgenus *Hearlea* in the CANADENSE species group.

The most salient diagnostic characters of the species placed in the subgenus *Obuchovia* (*sensu* ADLER & CROSSKEY, 2009, 2010), overlaps with those taxa allotted in the ORBITALE, PICTIPES and TARSATUM species group. The main morphological traits in *Obuchovia* that stand up from the typical ground plan of other *Trichodagmia* species are the extremely elongate and cigarette-like shaped male gonostyle (Figs. 148, 151, 154, 157, 160, 162), the male median sclerite being approximately five times longer than wide (Figs. 149, 152, 155, 158, 163), the male ventral plate with lateral arms concave at mid point and diverging laterally (Figs. 150, 153, 156, 159, 164), and the presence of hooks and tubercles on tergites I-II in the pupa. These represent good characters at the species group level.

Based on the above morphological characters, the subgenus *Obuchovia* is subsumed in this work within *Trichodagmia* to form the ALBELLUM species group [see **Appendix 2.9**, TABLE 1]. This grouping also seems to be supported by the cladistic analysis carried out in **Chapter 3**. In spited of this re-arragenment, the ALBELLUM species group (ex subgenus *Obuchovia*) is in need of taxonomic revision, but it is beyond the scope of this work to review this taxon that only occurs in the Palaeartic Region. However a brief diagnosis is here provided, and it is also included in the keys to species groups within the subgenus *Trichodagmia* in order to help the identification of the ALBELLUM species group. The main diagnostic characters ALBELLUM species group are as follows:

FEMALE: Thorax (Figs. 100-111) commonly black sometimes with 1+1 silver spots at mid point on lateral margins or largely greyish [with light illumination anterior]; with posterior illumination thorax greyish or with 1+1 silver pruinose cunae and/or pruinose areas centrally; abdominal segments black with yellow markings (Figs. 112-115); nudiocular triangle often present, developed (Figs. 116, 117); cibarium without teeth, concave centrally (Figs. 121-125, 129, 132); wing setation as in *Trichodagmia*, with basal sector of Radius with or without setae in few specimens examined; legs largely pale yellow to brown with dark brown to black areas (Figs. 118-120), hind leg with or without basal tooth; gonapophyses well developed, longer than width of eighth sternite at mid point, largely membranous and setose (Figs. 122,. 126, 133); paraproct subrectangular, its ventral extension extending beyond junction with cercus, sometimes suboval apically and with internal margin membranous; cercus and paraproct covered with setae (Figs. 123, 127, 130, 134); genital fork with sclerotised stem and with well developed apical processes; internal posterior processes absent (Figs. 124, 128, 131, 135).

MALE: Thorax (Figs. 136, 137) black with silver pruinosities on anterior third or distinctly greyish [with light illumination anterior]; the pattern can reverse with light illumination posterior or be the same as with light illumination anterior; abdomen with silver pruinosities on tergites I and II (Fig. 146) or without visible pruinosities (Fig. 147); gonostyle extremely elongate, cigarette-shaped, lateral margins nearly straight with a ridge sometimes located at the base of gonostyles, or reaching mid length or apical third of gonostyle, covered by stout teeth (Figs. 148, 151, 154, 157, 160, 162) [see also COUVERT, 1968, Fig. 5a-c, Pp: 90], and without terminal spine; paramere sclerotised, with developed spines centrally, basal plate prominently developed (Figs. 149, 152, 155, 158, 161, 163); median sclerite very long, nearly five times longer than wide at mid point, with distinct apical incision (Figs. 149, 152, 155, 158, 161, 163); ventral plate well sclerotised, main body suboval with or without central keel, and developed or not centrally; basal arms well developed, sclerotised, strongly emarginated at mid point from where they divert laterally (Figs. 150, 153, 156, 159, 164).

PUPA: Cocoon shoe-shaped with compact fibres; gill with six filaments arranged in a 2:2:2 configuration in the vertical plane; pupal thorax with or without markings (Figs. 165, 168, 174) and trichomes; onchotaxy as in the TARSATUM and PICTIPES species groups, sometimes with tergites I, II with prominent spiniform trichomes, or simple hooks evenly distributed on band of rounded tubercles.

LARVA: The larvae of species in the ALBELLUM species group do not have clear cut morphological characters that separate them from other species in the subgenus *Trichodagmia* or the genus *Simulium s.l.* In the specimens I have examined (see **Material Examined**), the larval postgenal cleft is deep and triangular (Figs. 166, 167, 171, 172, 175); the hypostomium has nine teeth evenly distributed in the anterior margin (Figs. 167, 169, 171, 172); in most species the median tooth, sublateral and lateral teeth are well developed (Figs. 166-169), but they can sometimes be reduced (Figs. 172-175); and the mandibles have three apical teeth and two mandibular serrations (Figs. 170, 173, 176). In addition, the rectal gills have three branches with numerous finger-like tubercles and the posterior arms of the anal sclerite do not encircle the posterior circlet as in many species within the subgenus *Trichodagmia*.

2.4.3. Checklist of *Trichodagmia* species groups and species

Following the synonymy of the subgenera *Hemicnetha* by SHELLEY *et al.* (2010) and *Obuchovia* [this work] with the subgenus*Trichodagmia*, several species have been re-allocated. Thus, the subgenus *Trichodagmia* now contains three North American species – *S. claricentrum*, *S. innoxium* and *S. pictipes* previously placed in the PICTIPES species-group of *Hemicnetha* in ADLER *et al.* (2004) and ADLER & CROSSKEY (2008, 2009, 2010). The ALBELLUM species group contains all species recorded in Palaearctic Region previously assigned to the subgenus *Obuchovia.* The CANADENSE species-group contains all species of the subgenus *Hearlea* that were subsumed within *Hemicnetha* by ADLER *et al.* (2004). The recognition of *Hearlea* as a valid subgenus of the genus *Simulium* by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007) was not accepted by ADLER *et al.* (2004) nor by SHELLEY *et al.* (2010). However, ADLER *et al.* (2004)provided good reasons for recognizing *Hearlea* as a species group in the then valid subgenus *Hemicnetha*, and this has been followed in the current work.

All species groups and species are arranged in alphabetical order. Valid species are highlighted in italics and bold, while synonyms are given only in italics. The reader should refer to the section "**Species Descriptions, Distribution, Biology and Medical Importance, and Distribution**" for details on synonymies, type material and depositaries, and taxonomic discussion for each species.

ALBELLUM species group

All taxa in this species group are found in the Palaearctic Region. ADLER & CROSSKEY (2008, 2009, 2010) recognized 15 valid species in this species group.

Simulium adornatum **(RUBTSOV, 1956)**
Simulium albellum **RUBTSOV, 1947**
Simulium auricoma **MEIGEN, 1818**
    S. syriacum ROUBAUD, 1909 [In BEZZI, 1909]
    S. djerdapense BARANOV, 1937
Simulium biseriatum **RUBTSOV, 1940**
Simulium brevifile **(RUBTSOV, 1956)**
Simulium continii **(RIVOSECCHI & CARDINALI, 1975)**
Simulium emiliae **(RUBTSOV, 1976)**
Simulium galloprovinciale **GIUDICELLI, 1963**
Simulium ibericum **CROSSKEY & SANTOS GRÁCIO, 1985**
Simulium karasuae **(PANCHENKO, 1998)**
Simulium margaritae **(RUBTSOV, 1956)**
Simulium marocanum **BOUZIDI & GIUDICELLI, 1988**
Simulium popowae **RUBTSOV, 1940**
    Simulium terminasjanae TERTERYAN, 1952
    Simulium atrofuscum (RUBTSOV, 1956)
    Simulium popovae: incorrect subsequent spelling
    Simulium terminasjane: incorrect original spelling (alternative)
Simulium segusina **(COUVERT, 1968)**
    Simulium seguisina: incorrect subsequent spelling
Simulium transcaspicum **ENDERLEIN, 1921a**
    Simulium transcaspicum ENDERLEIN, 1921 [April] (unav., *nomen nudum*)
    Simulium trenscaspica: incorrect subsequent spelling
    Simulium ochrescentipes: RUBTSOV & YANKOVSKY, 1988 [not ENDERLEIN]

CANADENSE species group

This species group is highly speciose in Central America. It now contains 19 valid species with the transfer of *S. falculatum* from the TARSATUM species group of SHELLEY *et al.* (2010), and the new synonymy of *S. chiriquiense* under *S. ethelae.*

Simulium ayrozai **VARGAS, 1945**
Simulium burchi **DALMAT, 1951**

Simulium canadense HEARLE, 1932

Simulium fraternum TWINN, 1938

Simulium capricorne DE LEÓN, 1945

Simulium deleoni VARGAS, 1945

Simulium carolinae DE LEÓN, 1945

Simulium contrerense DÍAZ NÁJERA & VULCANO, 1962

Simulium dalmati VARGAS & DÍAZ NÁJERA, 1948b

Simulium delatorrei DALMAT, 1950

Simulium estevezi VARGAS, 1945

Simulium ethelae DALMAT, 1950

Simulium chiriquiense FIELD, 1967. **New Synonymy**

Simulium falculatum (ENDERLEIN, 1929)

Simulium coffeae VARGAS, 1945 (unnecessary substitute name for *Friesia falculata* ENDERLEIN, 1929)

Simulium gorirossiae VARGAS & DÍAZ NÁJERA, 1957

Simulium johnsoni VARGAS & DÍAZ NÁJERA, 1957

Simulium juarezi VARGAS & DÍAZ NÁJERA, 1957

Simulium larvispinosum DE LEÓN, 1948

Simulium menchacai VARGAS & DÍAZ NÁJERA, 1957

Simulium microbranchium DALMAT, 1949

Simulium nigricorne DALMAT, 1950

Simulium paracarolinae COSCARÓN, 2004 [In COSCARÓN, MIRANDA-ESQUIVEL, MOULTON, COSCARÓN-ARIAS & IBÁÑEZ-BERNAL, 2004]

Simulium temascalense DÍAZ NÁJERA & VULCANO, 1962

ORBITALE species group

This species group now contain 16 valid species following the recent synonymies in SHELLEY *et al.* (2010) and the description of *S. lithobranchium* by HAMADA *et al.* (2010). *Simulium oviedoi* and *S. rivasi* have now been transferred from the ORBITALE species group of SHELLEY *et al.* (2010) to the subgenus *Psilopelmia* following examination of further material.

Simulium duodenicornium PEPINELLI, HAMADA & TRIVINHO STRIXINO, 2005

Simulium guianense WISE, 1911 (complex)

Simulium pintoi D'ANDRETTA & D'ANDRETTA, 1945

Simulium ortizi RAMÍREZ PÉREZ, 1971

'A' CHARALAMBOUS, SHELLEY, MAIA-HERZOG & LUNA DIAS, 1996 (Cytoform)

'B' CHARALAMBOUS, SHELLEY, MAIA-HERZOG & LUNA DIAS, 1996 (Cytoform)

'C' CHARALAMBOUS, SHELLEY, MAIA-HERZOG & LUNA DIAS, 1996 (Cytoform)

'D' CHARALAMBOUS, SHELLEY, MAIA-HERZOG & LUNA DIAS, 1996 (Cytoform)

Simulium hirtipupa LUTZ, 1910

Simulium huairayacu WYGODZINSKY, 1953

Simulium itaunense D'ANDRETTA & GONZÁLEZ B., 1964

Simulium jeteri (PY-DANIEL, DARWICH, MARDINI, STRIEDER & COSCARÓN, 2005)

Simulium lahillei (PATERSON & SHANNON, 1927). New type designation.

Simulium lithobranchium HAMADA, PEPINELLI, MATTOS-GLÓRIA & LUZ, 2010

Simulium nigrimanum MACQUART, 1838

Simulium pruinosum LUTZ, 1910

Simulium spadicidorsum ENDERLEIN, 1934

Simulium nunesdemelloi HAMADA, PEPINELLI & HERNÁNDEZ, 2006

Simulium orbitale LUTZ, 1910

Simulium brasiliense (ENDERLEIN, 1934)

Simulium albimanum (incorrect subsequent spelling in LUTZ, 1909 of *nigrimanum*)

Simulium albopictum LANE & PORTO, 1940

***Simulium perplexum* SHELLEY, MAIA-HERZOG, LUNA DIAS & COUCH, 1989**
***Simulium scutistriatum* LUTZ, 1909**
***Simulium sumapazense* COSCARÓN & PY-DANIEL, 1989**
***Simulium townsendi* MALLOCH, 1912**
    Simulium chalcocoma KNAB, 1914
    Simulium ecuadoriensis ENDERLEIN, 1934
    Simulium latitarsis ENDERLEIN, 1934
    Simulium strigatum (ENDERLEIN, 1934)[1933]
    Simulium muiscorum BUENO, MONCADA & MUÑOZ DE HOYOS, 1979
***Simulium wygodzinskyorum* COSCARÓN & PY-DANIEL, 1989**

PICTIPES species group

The three species belonging to this group (*sensu* ADLER *et al.*, 2004) have only been found in the United States and Canada.

***Simulium claricentrum* ADLER, 1990**
***Simulium innoxium* COMSTOCK & COMSTOCK, 1895**
    Simulium aldrichianum (ENDERLEIN, 1936)
***Simulium pictipes* HAGEN, 1880**
    Simulium longistylatum SHEWELL, 1959

TARSATUM species group

Species in the TARSATUM species group have a wide distribution in the New World extending from northern Argentina to the United States and Canada. The group now contains 19 valid species after the synonymies proposed in this work.

***Simulium brachycladum* LUTZ, 1932 [In PINTO, 1932]**
    Simulium brevibranchium LUTZ & MACHADO, 1915 (*nomen nudum*)
***Simulium bricenoi* VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA, 1946**
    Simulium wirthi PETERSON & CRAIG, 1997
***Simulium cristalinum* COSCARÓN & PY-DANIEL, 1989**
***Simulium earlei* VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA, 1946**
    Simulium dehnei FIELD, 1969
    Simulium keenani FIELD, 1969. **New Synonymy**
***Simulium freemani* VARGAS & DÍAZ NÁJERA, 1949**
***Simulium guerrerense* VARGAS & DÍAZ NÁJERA, 1956**
***Simulium hieroglyphicum* PETERSON, VARGAS & RAMÍREZ PÉREZ, 1988**
***Simulium hinmani* VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA, 1946**
***Simulium hippovorum* MALLOCH, 1914**
***Simulium lobatoi* LUNA DIAS, HERNÁNDEZ, MAIA-HERZOG & SHELLEY, 2004**
***Simulium paynei* VARGAS, 1942** [new name for *Hemicnetha mexicana* ENDERLEIN, 1934]
    Simulium mathesoni VARGAS, 1943
    Simulium bilimekae SMART, 1944 [Unnecessary substitute name for *Simulium mexicanum* ENDERLEIN]
    Simulium acatenangoense DALMAT, 1951
    Simulium conviti RAMÍREZ PÉREZ & VULCANO, 1973
    Simulium biuxinisa COSCARÓN & IBÁÑEZ-BERNAL, 1995**. New Synonymy.**
***Simulium pulverulentum* KNAB, 1915. New type designation.**
***Simulium rubrithorax* LUTZ, 1909**
    Simulium magnum LANE & PORTO [In PORTO, 1940]
    Simulium major: LANE & PORTO, 1940
    Simulium mutucuna NUNES DE MELLO & VIEIRA DA SILVA, 1974
***Simulium smarti* VARGAS, 1936**

Simulium solarii **STONE, 1948**
Simulium tarsale **WILLISTON, 1896**
    Simulium clavipes MALLOCH, 1914
Simulium tarsatum **MACQUART, 1846**
    Simulium mexicanum BELLARDI, 1862
    Simulium seriatum KNAB, 1914
    Simulium aureopunctatum MALLOCH, 1914
    Simulium placidum KNAB, 1915
    Simulium lugubre LUTZ & NUÑEZ TOVÁR, 1928 [In LUTZ, 1928]
    Simulium turgidum (HOFFMANN, 1930)
    Simulium laticalx (ENDERLEIN, 1934)
    Simulium latidigitus (ENDERLEIN, 1936)
    Simulium bellardii (PY-DANIEL & MOREIRA SAMPAIO, 1994) [Unjustified replacement name for *Simulium mexicanum* BELLARDI – see CROSSKEY & HOWARD, 1997.]
Simulium virgatum **COQUILLETT, 1902 (complex)**
    Simulium cinereum BELLARDI, 1859 (Preoccupied)
    Simulium tephrodes SPEISER, 1904 [Replacement name for *Simulium cinereum* BELLARDI]
    Simulium rubicundulum KNAB, 1915
    Simulium chiapanense HOFFMANN, 1930
Simulium yepocapense **DALMAT, 1949**
    Simulium ardeni DALMAT, 1953

Species previously placed in the subgenus *Trichodagmia* but now transferred to the subgenus *Psilopelmia*

simulium oviedoi **RAMÍREZ PÉREZ, 1971**
Simulium rivasi **RAMÍREZ PÉREZ, 1971**

2.4.4. Taxonomy of the subgenus *Trichodagmia*

Subgenus *Trichodagmia* ENDERLEIN

Trichodagmia ENDERLEIN, 1934a [1933]: 288 (as genus). Type species: *townsendi*, MALLOCH [as *latitarsis*] (original designation). [Synonymy with genus *Simulium* by VARGAS, 1943a: 106; synonymy with *Chirostilbia* by STONE, 1962: 206; synonymy with *Grenieriella* by COSCARÓN, 1987: 37); revalidated by CROSSKEY, 1988: 481; synonymy with *Grenieriella* by COSCARÓN, 1991: 275; revalidated by CROSSKEY & HOWARD, 1997: 78]

Thyrsopelma ENDERLEIN, 1934a [1933]: 284 (as genus). Type species: *orbitale* [as *brasiliense*] (original designation). [Synonymy with genus *Simulium* by SMART, 1945: 489 and VARGAS, 1945a: 105; revalidated by COSCARÓN, 1987: 1; synonymy with *Trichodagmia* by CROSSKEY, 1988: 481; treated as a valid subgenus by MIRANDA-ESQUIVEL & COSCARÓN, 2001: 429 and COSCARÓN & COSCARÓN ARIAS, 2007: 597; treated as a synonym of *Trichodagmia* by CROSSKEY & HOWARD, 1997: 78, ADLER & CROSSKEY, 2008: 95, 2009: 99, 2010: 100, and more recently by SHELLEY *et al.*, 2010: 417.]

Hemicnetha ENDERLEIN 1934b: 190. Type species *virgatum s.l.* [as *H. mexicana*] (original designation as genus). [Synonymy with genus *Simulium* by VARGAS, 1942: 246; revalidated by COSCARÓN, 1987: 1; synonymy with *Trichodagmia* by SHELLEY *et al.*, 2010: 417.]

Hearlea RUBTSOV, 1940: 154 [Unavailable, *nomen nudum*.]

Hearlea VARGAS, MARTÍNEZ PALACIOS & DÍAZ NÁJERA, 1946: 104, 106 (as subgenus of *Simulium*). Type species: *canadense* (original designation). [Synonymised under *Hemicnetha* by ADLER *et al.*, 2004: 369; revalidation as a subgenus by COSCARÓN *et al.*, 2004: 4 and COSCARÓN & COSCARÓN-ARIAS, 2007: 561; considered as the CANADENSE species group in the subgenus *Hemicnetha* by ADLER & CROSSKEY, 2008: 44, 2009: 46, 2010: 100; considered as the CANADENSE species group of the subgenus *Trichodagmia* by SHELLEY *et al.*, 2010: 417.]

Dyarella VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA, 1946: 105. Type species *S. mexicanum* BELLARDI (original designation). [Synonymy with *Hemicnetha* by VARGAS & DÍAZ NÁJERA, 1953a: 148.]

Obuchovia RUBTZOV, 1947: 90, 105 (as subgenus of *Simulium*). Type species: *Simulium (Obuchovia) albellum* (original designation). [Synonymy with *Hemicnetha* by ADLER *et al.*, 2004: 369; revalidated by CROSSKEY & HOWARD, 2004: 47; considered a valid subgenus in ADLER & CROSSKEY, 2008: 67 and SHELLEY *et al.*, 2010: 415]. **New synonymy.**

Grenieriella VARGAS & DÍAZ NÁJERA, 1951b: 141 (as subgenus of *Simulium*). Type species: *S. lahillei* (original designation). [Synonymy with *Trichodagmia* by VARGAS & DÍAZ NÁJERA, 1953a: 147; synonymy with *Chirostilbia* by STONE, 1962: 206; revalidated by CROSSKEY, 1981: 17; synonymy with *Trichodagmia* by CROSSKEY, 1988: 481; treated as a valid subgenus by COSCARÓN, 1991: 275, but recognized as a synonym of *Trichodagmia* by CROSSKEY & HOWARD, 1997: 78, ADLER & CROSSKEY, 2010: 100.]

Hagenomyia SHEWELL, 1959: 83 (as subgenus of *Simulium*) (preoccupied). Type species *pictipes* (original designation). [Synonymy with subgenus *Hemicnetha* in ADLER *et al.* 2004: 166; synonymy with *Trichodagmia* by SHELLEY *et al.*, 2010: 417.]

Shewellomyia PETERSON, 1975: 111 (substitute name for *Hagenomyia* SHEWELL, therefore same type species). [Synonymy with subgenus *Hemicnetha* in ADLER *et al.* 2004: 166; synonymy with *Trichodagmia* by SHELLEY *et al.*, 2010: 417.]

In this work 73 valid species are recognized in the subgenus *Trichodagmia*. Within the subgenus five species groups are recognized: the ALBELLUM, CANADENSE, ORBITALE, PICTIPES and TARSATUM groups. The ALBELLUM species group is mainly Palaearctic, while the remaining species group are confined to the New World.

Diagnosis.

Adults: Medium to large brown to black flies (up to 5.0 mm) with or without scutal patterns [female, Figs. 285-417; male Figs. 704-826].

Female: Nudiocular area partially to well developed (Figs. 177-227). Cibarium variable, ranging from generally unarmed [including membrane with denticles attached to unarmed central trough – this character is probably more commonly found in species than has been described because the membrane may be lost during dissection], to armed with large pointed teeth (Figs. 229-282). Wing venation variable with Sc either bare or with setae, basal section of Radius usually with setae and often with more than one row (see Fig. 4). Claws generally with basal tooth. Gonapophyses membranous, setose and either triangular pointing posteriorly or ovoid and pointing to median line of abdomen, exceptionally with coarse hairs (Figs. 526-481). Paraproct varying from subtriangular to subrectangular with ventral extension from less than half to more than length of cercus often with membranous processes, with fine setae and coarse hairs (Figs. 584-641) [except in *S. falculatum* and *S. lobatoi* (Figs. 594, 630), respectively]. Genital fork variable with ends of lateral arms either arranged obliquely or parallel to transverse axis of abdomen, and anterior and posterior processes to lateral arms developed to greater or lesser extent (Figs. 644-703).

Male: Gonostyle either subrectangular and rounded distally with sinuous lateral margins and distal spine or spindle-shaped with one or more distal spines; gonostyle same length or longer than gonocoxite (Figs. 829-888). Ventral plate varying from rectangular with no lateral shoulders on main body and an underdeveloped median process to well developed lateral shoulders, and a keel and or fissure on the median process and main body and median process (Figs. 891-949). Paramere with well developed spines or no spines (Figs. 952-1009).

Pupa: Cocoon slipper, shoe or boot-shaped as in Figs. 65-69; gill with thick or thin filaments, sometimes swollen and prominent (CANADENSE species group) (Figs. 1011-1029), of variable length and with rounded, pointed or sclerotised tips (Figs. 1011-1073). The onchotaxy (Fig. 85) of *Trichodagmia* falls within the variation found in the genus *Simulium* (SHELLEY *et al.* 2010) and it is very similar across the species. Nonetheless, in certain species of the TARSATUM species group rounded tubercles are present on tergites I and II.

Larva: Medium to very large raging between 7.0 to 13.0 mm (Figs. 1078-1119). Abdominal cuticle normally without setae, except in some species of the ORBITALE species group. Hypostomium ranging from small and rounded apically to commonly deep and triangular (Figs. 1122-1171), with or without a tubular incision apically. Hypostomium commonly with nine teeth evenly distributed along anterior margin (Figs. 1174-1226), except in species such as *S. hieroglyphicum* and *S. lobatoi* where the teeth are centrally arranged and protrude forwards (Figs. 1218, 1223); median tooth most prominent, 3+3 sublateral teeth, 1+1 lateral teeth, and 1+1 lines of more than seven hypostomial teeth parallel to lateral margins (Figs. 1174-1216). Variation in this pattern of hypostomial teeth might occur. Mandible normally with three apical teeth; mandibular comb with seven or more teeth; and two mandibular serrations, anterior more prominent than posterior (Figs. 1229-1283). Posterior circlet not encircling anal sclerite, except in certain species of the CANADENSE species group (Fig. 1283-1289).

2.4.5. Identification keys to species groups of the subgenus *Trichodagmia*

Key to species groups

The most recent keys to separate species of *Trichodagmia* in the New World are those of ADLER *et al.* (2004) [North America], COSCARÓN & COSCARÓN-ARIAS (2004) [Neotropical Region] and SHELLEY *et al.* (2010) [Brazil]. The key of SHELLEY *et al.* (2010) has been here modified to include the ALBELLUM, CANADENSE and the PICTIPES species groups, and other taxa belonging to their ORBITALE and TARSALE groups which are found outside Brazil. In the current work, a key to separate the larval stage is also given.

The adults of species allotted in the subgenus *Trichodagmia* are difficult to identify on the basis of external morphology, especially the coloration pattern of the thorax. Therefore, dissection of the female and male genitalia, preferably in link-reared adults, have to be carried out in order to place specimens in the correct species group with certainty.

FEMALE

1. Ventral extension of paraproct weakly extending beyond the cercus, often with prominence at junction with cercus and 1 or 2 lobes apically, which are distinctly setose (Figs. 584-602); species mainly found in Central America with a single species found in North America (*S. canadense*) .... CANADENSE species group

\- Ventral extension of paraproct distinctly extending beyond the cercus without 1 or 2 lobes apically prominently setose (Figs. 603-641) [except in *S. lobatoi* of TARSATUM species group see Fig. 630]; species mainly distributed in the Neotropical Region with some elements in the Nearctic and Palaearctic Regions 2

2. Gonapophyses prominently developed, nearly two to three times longer than length of eighth sternite at mid point, sometimes distinctly acuminate apically and covered in microtrichiae (except in *S. lobatoi* in which gonapophyses are of same length as eighth sternite and covered by prominent black setae) (Figs. 562-571); ventral extension of paraproct suboval, subrectangular or subquadrangular (Figs. 621-641) 3

\- Gonapophyses not prominently developed, nearly same length as eighth sternite, varying from subrectangular, subtriangular to nearly subquadrangular, rounded apically (Figs. 544-558, 559-561); ventral extension of paraproct either same length as cercus (Figs. 603-617) or 1.5 to 2 times longer than cercus (Figs. 618-620); species found only in South America (ORBITALE species group) or in the Nearctic Region (PICTIPES species group) 4

3. With light source anterior, thorax black with distinct 1+1 silver spots on lateral margins or largely greyish without silver patterns (Figs. 100-111); species found in the Palaearctic Region .... ALBELLUM species group

\- With light source anterior black or brown to reddish brown, with or without a pattern, without 1+1 silver spots on lateral margins, largely greyish (see Figs. 362-417); species mainly found in the Neotropical Region with five taxa also found in the Nearctic Region (*S. freemani*, *S. hippovorum*, *S. paynei*, *S. solarii*, and *S. virgatum s.l.*) .... TARSATUM species group

4. Ventral extension of paraproct nearly same length as cercus (Figs. 618-620); paraproct sclerotised, subtriangular (Figs. 618-620); species only found in North America ....PICTIPES species group

- Ventral extension of paraproct nearly two times longer than cercus (Figs. 603-617); paraproct membranous and often pointed apically, having membranous setose tails at junction with cercus (Figs. 603-617); species only extending from northern Argentina to northern South America ....ORBITALE species group

MALE

1. Gonostyle spindle-like shape (Figs. 847-862); basal plate of parameres poorly developed (Figs. 970-983); species only extending from northern Argentina to northern South America ....ORBITALE species group
- Gonostyle prominently elongate (Figs. 148, 151, 154, 157, 160, 162, 829-846, 863-865) or flattened with sinuous margins (Figs. 866-888), but not spindle-shaped; basal plates of parameres well developed (Figs. 149, 152, 155, 158, 163, 952, 969, 984-1009); species found in South and North America, and the Palaearctic Region 2
2. Gonostyle elongate, often wider basally and narrowing towards apex, sometimes depressed at mid point, with internal ridge (Figs. 863-865) or distinct flap-like ridge basally (Figs. 829-846) 3
- Gonostyle elongated, but often very wide and of same width along its length, never with prominent flap-like ridge basally (Figs. 148, 151, 154, 157, 160, 162, 866-888).. 4
3. Ventral plate with anterior margin with prominent median cleft extending beyond mid-point almost to near posterior margin (Figs. 924-926); species only found in North America .... PICTIPES species group
- Ventral plate with anterior margin produced into a small process centrally (*e.g.* Figs. 891, 892, 896-900) or without a central process (*e.g.* Figs. 907), never with prominent cleft – if present always small and never reaching mid point of ventral plate (Fig. 893); species mainly found in Central America with a single species in North America (*S. canadense*) .... CANADENSE species group
4. Gonostyle cigarette-like shaped, without terminal spine (Figs. 148, 151, 154, 157, 160, 162); ventral plate suboval or subquadrangular, with long basal arms prominently concave at mid point and then diverging laterally (Figs. 150, 153, 156, 159, 164); species only found in the Palaearctic region. .... ALBELLUM species group
- Gonostyle often flattened, with lateral margins sinuous, and sometimes wide at mid-point or subapically, and with an apical or subapical spine (Figs. 866-888); ventral plate subrectangular or subquadrangular, never suboval, with developed subparallel basal arms, never prominently concave at midpoint or diverging laterally (Figs. 927-949); species commonly found in the Neotropical Region, five species also found in the Nearctic Region (*S. freemani*, *S. hippovorum*, *S. paynei*, *S. solarii*, and *S. virgatum s.l.*) .... TARSATUM species group

PUPA

In the following key specimens are sometimes difficult or impossible to identify to species group, if only pupae are available for identification. If well developed pharate pupae are available, dissection of the adults' genitalia can be made and this should indicate the species group. The most reliable way to identify the pupa is the examination of the gill configuration and number of filaments in conjunction with examination of link-reared adults.

1. Gill with nine filaments (Figs. 1046-1048); species only distributed in North America .... PICTIPES species group
- Gill with different number of filaments; species distributed in the Neotropical, Nearctic and Palaearctic Regions 2
2. Gill with at least one filament prominently more swollen than remaining filaments (*e.g.* Figs. 1013-1024, 1027) or distinctly longer (*e.g.* Fig. 1016) with ventral primary branch curved and encircling frontoclypeus (*e.g.* Figs. 1015, 1019) [see also variation in Figs. 1011-1029]; species mainly found in Central America with a single species also found in North America (*S. canadense*)............................... ....CANADENSE species group

- Gill with filaments not prominently swollen (Figs. 165, 168, 174, 1030-1073) and generally of about same length, but in case of different girth at least one filament longer than remaining filaments, and ventral primary branch not encircling the frontoclypeus (*e.g.* Figs. 84, 1058)............ 3
3. Gill with six filaments (Figs. 165, 168, 174, 1049, 1052, 1053).. 4
- Gill with more than six filaments (*e.g.* Figs. 1030-1045, 1050, 1055-1073)... 5
4. Gill filaments forwardly directed in 2:2:2 configuration in the vertical plane (Figs. 165, 168, 174), some species with markings in the pupal thorax; species only found in the Palaearctic Region ....ALBELLUM species group
- Gill filaments upwardly directed, all branching basally in a bunch in the vertical plate (Figs. 1052, 1054), thorax of pupa without markings (except in *S. bricenoi* and *S. hieroglyphicum*); species found in the New World ....TARSATUM species group
5. Gill with eight filaments (*e.g.* Figs. 1050, 1056, 1060-1066, 1072); cocoon with or without fenestrations ....TARSATUM species group [in part]
- Gill with more than eight filaments.. 6
6. Gill with 10 filaments (Figs. 1033, 1057, 1067, 1073)................TARSATUM species group [in part]
- Gill with more ten filaments.. 7
7. Gill with 12 filaments (*e.g.* Figs. 1030, 1036, 1037, 1041, 1043, 1071) [TARSATUM and ORBITALE species group, in part].. 8
- Gill with more than 12 filaments 9
8. Gill filaments pointed and sclerotised apically (*e.g.* Figs. 1030-1032, 1034, 1037, 1039, 1041)........... ....ORBITALE species group [in part]
- Gill filaments rounded and not sclerotised apically (Fig. 1071)... ....TARSATUM species group [in part]
9. Gill with 15 filaments (*e.g.* Figs. 1035, 1070) [TARSATUM and ORBITALE species group, in part] 10
- Gill with more than 15 filaments 11
10. Gill filaments pointed and sclerotised apically (Fig. 1035).........ORBITALE species group [in part]
- Gill filaments rounded apically (Fig. 1070).................................TARSATUM species group [in part]
11. Gill with 18 filaments (Figs. 1038, 1069)[TARSATUM and ORBITALE species group, in part].. 12
- Gill with more 18 filaments 13
12. Gill filaments splayed out and dividing at some distance from gill base (Fig. 1070)........................... ....TARSTUM species group [in part]
- Gill filaments clumped together in a bunch and dividing basally (Fig. 1038) ....ORBITALE species group [in part]
13. Gill with 19-23 filaments (Figs. 1039-1040) ....ORBITALE species group [in part]
- Gill with more than 23 filaments 14
14. Gill with 45-56 filaments, primary branches and secondary filaments of same girth (*e.g.* Fig. 1034). ....ORBITALE species group [in part]
- Gill with 60-90 filaments, primary branches with at least three filaments prominently of different girth than remainder filaments (Fig. 1058) ....TARSATUM species group [in part]

LARVA

There are few morphological characters to separate the larvae of currently described species in the subgenus *Trichodagmia* to species groups and/or species. The best character for larval identification is the configuration and number of the gill filaments in the dissected gill histoblast of the mature larva. When mature larvae are not found, identification to species is almost impossible.

1. Abdominal segment VIII with 1+1 ventral papillae (Fig. 87); posterior arm of the anal sclerite encircling the posterior circlet having accessory sclerotised plates composed of spiny processes (Figs. 87, 1283-1289); species found in Central America with a single element in North America (*S. canadense*)... CANADENSE species group [in part]

- Abdominal segment VIII without 1+1 ventral papillae; posterior arm of the anal sclerite not encircling the posterior circlet and without accessory sclerotised plates (Fig. 98); species found in the New World and the Palaearctic Region..2
2. Mature larva with dissected gill histoblast with gill filaments prominently swollen or very long, sometimes longer filament having small apically pointed and sclerotised smaller filaments .... CANADENSE species group [in part]
- Mature larva with dissected gill histoblast having all filaments of same length, if relatively swollen, smaller secondary branches rounded apically, never sclerotised...3
3. Mature larva with dissected gill histoblast with nine filaments......................PICTIPES species group
- Mature larva with dissected gill histoblast with different number of filaments 4
4. Larval thoracic and abdominal integument with distinct ovoid spiniform setae or covered by black spiniform setae...ORBITALE species group [in part]
- Larval thoracic and abdominal integument without ovoid or spiniform setae...................................... ....ALBELLUM, ORBITALE [in part], and TARSATUM species groups

2.4.6. Identification key to species of the New World CANADENSE species group.

FEMALE

The female of species in the CANADENSE species group are externally homogeneous and they cannot be reliably identified without examination of the genitalia, especially the paraproct. The use of the wing length range in the key in COSCARÓN & COSCARÓN-ARIAS (2007) to females of the CANADENSE species group was found inadequate for reliable species identification.

Simulium nigricorne, *S. temascalense* and *S. paracarolinae* are not included in the key because the female thoracic pattern is poorly described in the first two species, and the female of *S. paracarolinae* remains unknown. The reader should consult the description and figures of these species in the taxonomic section for each taxon.

1. Scutum with silvery submedian vittae joining 1+1 anterior silvery areas or spots (*e.g.* Figs. 289, 297, 303, 305) [with light source anterior] 2
- Scutum with silvery submedian vittae not joining 1+1 anterior silvery areas or spots [with light source anterior] (*e.g.* Figs. 287, 295)..10
2. Ventral extension of paraproct half-moon shaped, barely extending beyond cercus from where it curves backwards having small membranous internal tail (Figs. 15, 586) ....*S. canadense*
- Ventral extension of paraproct distinctly surpassing cercus, broadly subquadrangular or subrectangular in shape.. 3
3. Ventral extension of paraproct subquadrangular as in Figs. 16, 584, 590, 591.................................. 4
- Ventral extension of paraproct subrectangular as in Figs. 592, 594.. 5
4. Ventral extension of paraproct without lobes near junction with cercus and small rounded lobe apically (Figs. 15, 590) ....*S. dalmati*
- Ventral extension of paraproct with distinct lobe near junction with cercus and with fine, membranous lobe apically covered by long hairs (Fig. 584)..*S. ayrozai*
5. Ventral extension of paraproct rounded apically and without lobe near junction with cercus (*e.g* Figs. 591, 592, 594)... 6
- Ventral extension of paraproct with different shape as in Figs. 593, 597-598 8
6. Paraproct with internal surface nearer cercus sclerotised, external surface membranous (Fig. 592) . ...*S. estevezi*
- Paraproct with internal and external surfaces widely sclerotised (Figs. 591, 594)............................. 7
7. Cercus subrectangular, two and half times length of ventral extension of paraproct (Fig. 594)......... .... *S. falculatum*
- Cercus subquadrangular, one and half times length of cercus (Fig. 591) .... *S. delatorrei*
8. Ventral extension truncate apically (*e.g* Figs. 593, 598)... 9
- Ventral extension of paraproct with rounded extension apically and lobed at junction with cercus (Fig. 597) ....*S. juarezi*

9. Ventral extension of paraproct without lobe near junction with cercus (Fig. 598) .... *S. larvispinosum*
- Ventral extension of paraproct with lobe near junction with cercus (Fig. 593) .... *S. ethelae*
10. Ventral extension of paraproct with small lobe near junction with cercus and divided into three small membranous lobes apically (Fig. 595) .... *S. gorirossiae*
- Ventral extension of paraproct without three small membranous lobes apically (*e.g.* Figs. 585, 589, 596, 599) 11
11. Ventral extension of paraproct broad apically and aligned with posterior margin of cercus (Figs. 589, 599) .... *S. contrerense*, *S. menchacai*
- Ventral extension of paraproct finer apically and curving along posterior margin of cercus (*e.g.* Figs. 585, 587, 588, 596) 12
12. Ventral extension of paraproct prominently lobed on external margin (Fig. 585) .... *S. burchi*
- Ventral extension of paraproct without lobe on external margin (Figs. 587, 588, 596) 13
13. Ventral extension of paraproct with lobe at junction with cercus (Fig. 587) .... *S. capricorne*
- Ventral extension of paraproct without lobe at junction with cercus (Figs. 588, 596) .... *S. carolinae*, *S. johnsoni*

MALE

This key should be used with caution because the males of species in the CANADENSE species group are extremely homogeneous, and they cannot be reliably identified without examination of pupae from link-reared specimens (Coscarón & Coscarón-Arias, 2007). Most species are very similar in terms of thoracic pattern (Figs. 704-731) and gonostyle morphology (Figs. 829-846). However, the morphology of the ventral plate is a good character to separate some species in this group. Nonetheless, the apparent shape of the ventral plate, as well as the gonostyle, can be variable depending on the orientation of this structure on the slide, hence care must be taken when mounting the male genitalia as detailed in Shelley *et al.* (2010) and this work.

For some species, I have had to rely on other authors' drawings in order to derive the following key and for the descriptions of the male genitalia. Discrepancies were detected in the general morphology illustrated by the original drawings and my digital images. Therefore, a certain amount of interpretaion has had to be used, but relying more on my own observations.

Simulium falculatum, *S. paracarolinae* and *S. temascalense* are not included in the key because the males of these species are unknown.

1. Ventral plate with highly developed shoulders producing a deep median incision (Fig. 893) .... *S. canadense*
- Ventral plate with undeveloped shoulders and without deep median incision (*e.g.* Figs. 891, 892, 894-908) 2
2. Ventral plate prominently subquadrangular, with lateral margins concave in posterior third and central keel extending to posterior margin as in Figs. 899, 905 3
- Ventral plate not prominently subquadrangular, often subrectangular with central keel extending to mid point or less as in Figs. 891, 892, 904 4
3. Ventral plate with median keel extending from anterior to posterior margins (Fig. 905) .... *S. larvispinosum*
- Ventral plate with median keel extending to mid point of ventral plate (Fig. 899) .... *S. delatorrei*
4. Median plate broadly subrectangular as in Figs. 891, 892, 897, 902, 904 5
- Median plate broadly subquadrangular as in Figs. 895, 896, 901, 907 9
5. Median plate with central process originating from posterior margin, central process prominent .... (Fig. 897) .... *S. contrerense*
- Median plate with central process arising from mid point or anterior margin, central process small, sometimes folded over main body of ventral plate (Figs. 891, 892, 902, 904) 6
6. Anterior margin of ventral with both sides at base of central process distinctly concave (Fig. 891) . ... *S. ayrozai*
- Anterior margin of ventral not concave at base of central process (Figs. 892, 902, 904) 7

7. Posterior margin of ventral plate convex (Fig. 904) .... *S. juarezi*
- Posterior margin of ventral plate straight or weakly concave (Figs. 892, 902) 8
8. Ventral plate with central process arising from midpoint and reaching anterior margin (Fig. 892) .... *S. burchi*
- Ventral plate with central process arising from anterior margin (Fig. 902) .... *S. gorirossiae*
9. Ventral plate without central process on anterior margin (Figs. 895, 901) .... *S. capricorne*, *S. ethelae*
- Ventral plate with anterior margin with central process (*e.g.* Figs. 896, 898, 900, 903, 906-907) 10
10. Ventral plate with central process slightly produced beyond anterior margin centrally (Fig. 907) .... *S. microbranchium*
- Ventral plate with central process produced well beyond anterior margin centrally (Figs. 896, 898, 900, 903, 906) .... *S. carolinae*, *S. dalmati*, *S. estevezi*, *S. johnsoni*, *S. menchacai*

PUPA

Simulium falculatum and *S. paracarolinae* are not included in the key because their pupae are unknown.

1. Gill filaments prominently swollen, sometimes flattened or subcylindrical with pseudoannulations or wrinkles, but never with apically pointed and sclerotised secondary filaments (*e.g.* Figs. 1011-1015, 1017-1021, 1027, 1028) 6
- Gill filaments not prominently swollen, some filaments cylindrical, smooth, with secondary filaments pointed and sclerotised apically (*e.g.* Figs. 1016, 1022-1025, 1029) 2
2. Gill with longest filament relatively wider basally and narrowing towards end of filament (Figs. 1026, 1029) 3
- Gill with longest filament of approximately same girth along its length (*e.g.* Figs. 1022, 1023) 4
3. Gill with longest filament not sclerotised apically, with five small, pointed and apically sclerotised secondary filaments on basal third (Fig. 1029) .... *S. temascalense*
- Gill with longest filament sclerotised apically, with long single secondary filaments on basal third and up to four prominent, long branches, three of them having smaller pointed filaments and one single, rounded apically (Fig. 1026) .... *S. menchacai*
4. Gill with longest dorsal filament pointed, sclerotised apically, with a small pointed filament on basal third, two prominent branches bifurcating apically, and single filament, rounded apically (Fig. 1022) .... *S. gorirossiae*
- Gill with longest filaments rounded, unsclerotised apically, with secondary filaments with different configuration (Figs. 1023, 1025) 5
5. Gill with longest filament having small secondary filament on basal third, two branches dividing apically with two filaments each, and single long filament (Fig. 1023) .... *S. johnsoni*
- Gill with longest dorsal filament having on basal third, a small branch that bifurcate apically, two branches each bifurcating basally terminating into one, two or three tertiary, small filaments, and single small filament (Fig. 1025) .... *S. larvispinosum*
6. Gill with median primary branch prominently swollen and subtriangular, dorsal branch prominently swollen and rounded, ventral branch finger-like (Fig. 1017) .... *S. contrerense*
- Gill with primary branches swollen but with configuration as in Figs. 1011-1015, 1018-1020, 1021, 1024, 1018 7
7. Gill with filaments flattened or subcylindrical arranged in a C-like configuration (Figs. 1014, 1027) 8
- Gill with filaments cylindrical or flattened, but not arranged in a C-like configuration (Figs. 1011-1013, 1015, 1018-1020) 10
8 Gill filaments arranged in an opened C-like configuration, with dorsal filament curving at mid length from which it is forwardly directed (Fig. 1027) .... *S. microbranchium*
- Gill filaments arranged in a closed C-like configuration and not curving at mid length (Figs. 1021, 1028) 9
9. Dorsal primary branch pointed apically; ventral primary branch relatively more swollen than dorsal branch, especially beyond mid length (Fig. 1021); cocoon slipper-shaped as in Fig. 65 ....

....*S. ethelae*

\- Dorsal and ventral primary branch of same girth, cylindrical (Fig. 1028); cocoon shoe-shaped as in Fig. 66 .... *S. nigricorne*

10\. Gill with two prominently flat filaments (Fig. 1011) ....*S. ayrozai*

\- Gill with more than two, either cylindrical or subcylindrical, filaments (*e.g.* Figs. 1012, 1018-1020) 11

11\. Gill with median primary branch distinctly bulbous apically (*e.g.* Figs. 1012, 1013, 1018, 1024).....12

\- Gill with median primary branch not prominently bulbous apically (*e.g.* Figs. 1019, 1020) 14

12\. Gill with median primary branch prominently bulbous; dorsal and ventral primary branches comparetively much thinner (Fig. 1024).. *S. juarezi*

\- Gill with median primary branch not prominently bulbous; dorsal and ventral primary branches nearly of same length (Figs. 1012, 1013, 1018)..13

13\. Gill with median primary branch thinner basally and expanding beyond mid length toward apex (Fig. 1012) .... *S. burchi*

\- Gill with median primary branch swollen and cylindrical over entire surface (Fig. 1013)................... ....*S. canadense*

\- Gill with median primary branch apically capitate with 3-4 small, apical protuberances (Fig. 1018).. ....*S. dalmati*

14\. In lateral view, gill with median primary branch directed forward and prominently curving upwards at mid length from which it narrows towards apical region (Fig. 1020)...................*S. estevezi*

\- In lateral view, gill with median primary branch directed forward, only weakly curving at mid length from which it continues being of same width towards apical region (Fig. 1019)..................... ....*S. delatorrei*

LARVA

The larvae of species in the CANADENSE species group are externally homogeneous, except those taxa that have sclerotised accessory plates on the posterior region of the abdomen. The best character for larval identification are the configuration and number of the gill filaments in the dissected gill histoblast of the mature larva. As consequence great care should be taken when using keys for identification of larvae, and identification should be confirmed by the examination of link-reared adults, which have been collected preferably in the same locality as the mature larvae. When mature larvae are not found, identification to species is almost impossible. Once the species group has been established, the morphology of the postgenal cleft, hypostomium and mandible are species specific characters.

The following key has been modified from that of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and DÍAZ NÁJERA & VULCANO (1962a) to separate the larval stage of species in the CANADENSE group. COSCARÓN & COSCARÓN-ARIAS (2007) and DÍAZ NÁJERA & VULCANO (1962a) have used the body length, number of labral fans, number of rows of the posterior circlet and number of lobules in the rectal gill to separate the taxa in this species group, but it is now known that these characters vary depending upon availability of food in rivers as well as the strength of the current and season (P.H. ADLER, pers. comm.).

The larvae of *S. falculatum* and *S. nigricorne* are unknown, hence they have not been included in the larval key.

1\. Posterior region of abdomen of larva with accessory sclerotised plates bearing spiny process (*e.g.* Figs. 1283-1289) 2

\- Posterior region of abdomen of larva without accessory sclerotised plates..8

2\. Abdominal segment VIII with ventrolateral papillae (*e.g.* Figs. 87, 1287) 6

\- Abdominal segment VIII without ventrolateral papillae 3

3\. Posterior region of abdomen with only 1+1 conical sclerotised accessory dorsolateral plates (Fig. 1288) ....*S. paracarolinae*

\- Posterior region of abdomen with 2+2 sclerotised accessory dorsolateral plates (*e.g.* Figs. 1284-1286) 4

4\. Posterior region of abdomen without ventrolateral sclerotised accessory plates (Fig. 1283)..............

.... *S. carolinae*
- Posterior region of abdomen with sclerotised ventrolateral accessory plates...................................... 5
5. Posterior region of abdomen with sclerotised accessory plates having four weakly pointed conical processess (Fig. 1285); anal sclerite without dorsal subrectangular flattened sclerotised accessory plates (Fig. 1285).. *S. johnsoni*
- Posterior region of abdomen with sclerotised accessory plates with eight pointed conical processes, the most ventral more prominent (Fig. 1286) [best seen at high magnification – see species description]; anal sclerite with dorsal subrectangular flattened sclerotised accessory plates (Fig. 1286) .... *S. larvispinosum*
6. Posterior region of abdomen with sclerotised accessory plates having four acuminate processes and a line of another four processes covered in small spines (Fig. 1289) .... *S. temascalense*
- Posterior region of abdomen with sclerotised accessory plates of a different shape (*e.g.* Fig. 1287) 7
7. Posterior region of abdomen with sclerotised accessory plates with six pointed acuminate process (Fig. 1287); hypostomium with 11 hypostomial setae (Fig. 1187) .... *S. menchacai*
- Posterior region of abdomen with sclerotised accessory plates with seven pointed acuminate processes and other three covered by spines (Fig. 1284); hypostomium with 19 hypostomial setae (Fig. 1184) .... *S. gorirossiae*
8. Anterior margin of hypostomium concave (*e.g.* Figs. 1176, 1179, 1180)... 9
- Anterior margin of hypostomium relatively straight (*e.g.* Figs. 1174, 1177, 1182) 11
9. Hypostomium with 1+1 lines of five to seven hypostomial setae parallel to lateral margin (Fig. 1176) .... *S. canadense*
- Hypostomium with 1+1 lines of 16-18 hypostomial setae parallel to lateral margin (Fig. 1179-1180) 10
10. Mandible with mandibular comb with 12 teeth (Fig. 1234) ....*S. contrerense*
- Mandible with mandibular comb with eight teeth (Fig. 1235) .... *S. dalmati*
11. Hypostomium with less than nine teeth evenly distributed on anterior margin as in Figs. 1174, 1182) 12
- Hypostomium with nine teeth evenly distributed on anterior margin as in Figs. 1175, 1177.......... 13
12. Hypostomium with 1+1 line of eight hypostomial setae parallel to lateral margins (Fig. 1182).......... ....*S. estevezi*
- Hypostomium with 1+1 line of 12 hypostomial setae parallel to lateral margins (Fig. 1174)............. ....*S. ayrozai*
13. Hypostomium with more than 10 hypostomial setae parallel to lateral margins (*e.g.* Figs. 1175, 1177)... 14
- Hypostomium with 1+1 line of eight to 10 hypostomial setae parallel to lateral margins (*e.g.* Figs. 1181, 1183, 1186)... 16
14. Hypostomium with 12 hypostomial setae (Fig. 1177)... *S. capricorne*
- Hypostomium with more than 12 hypostomial setae.. 15
15. Hypostomium with 15 hypostomial setae (Fig. 1175); postgenal cleft dome-like shape without tube-like incision apically (Fig. 1123) .... *S. burchi*
- Hypostomium with 19 hypostomial setae;; postgenal cleft dome-like with tube-like incision apically (Fig. 1134). ....*S. microbranchium*
16. Rectal gill with 60-78 finger-like lobules...*S. delatorrei*
- Rectal gill with 45 or fewer finger-like lobules .... *S. ethelae*, *S. juarezi*

2.4.7. Identification key to species of the New World ORBITALE species group.

FEMALE

Simulium sumapazense and *S. jeteri* are not included in the key because of the lack of information concerning females.

1. Scutum largely black, sometimes marked with brown [light source anterior] (*e.g.* Figs. 315, 319, 321 340, 346) 2

- Scutum largely brown or reddish brown [light source anterior] (*e.g.* Figs. 325, 330, 336, 338, 350)... 7

2. With light source anterior, scutum with 1+1 median pear-shaped and 1+1 sublateral wide vittae extending from anterior to posterior margin (Fig. 346)..*S. townsendi*

- With light source anterior, scutum without a pattern (*e.g.* Figs. 315, 317, 319, 334, 340) 3

3. Paraproct broadly rectangular with ventral extension folded and directed internally (Fig. 613)......... .... *S. perplexum*

-. Paraproct of different shape as in Figs. 603-605, 609, 612.. 4

4. Ventral extension of paraproct narrow apically extending as a single finger-like membranous process (Fig. 605) ....*S. hirtipupa* [typical black form, and brown colour form]

- Ventral extension of paraproct not prominently narrow apically, extending as one or two membranous processes (*e.g.* Figs. 603-604, 607, 609, 612) 5

5. Ventral extension of paraproct at least length of cercus (Fig. 612)..*S. orbitale*

- Ventral extension of paraproct less than half length of cercus (*e.g.* Figs. 603, 604, 607,) 6

6. Paraproct with single, small, posterior membranous processes (*e.g.* Figs. 604, 607, 609) ....*S. guianense s.l.*, *S. itaunense*, *S. lithobranchium*

- Paraproct with two, small, posterior membranous processes (Fig. 603) ....*S. duodenicornium*

7. Scutum with indistinct pattern consisting of fine, median black line and in some species 1+1 submedian black lines [with light source anterior] (*e.g.* Figs. 336, 338, 344-350)............................... 8

- Scutum with distinct pattern consisting of 1+1 median, pear-shaped and 1+1 submedian, wide silver pruinose vittae extending from anterior to posterior margins [with light source anterior] (*e.g.* Figs. 332, 335, 350) 10

8. Cibarium with teeth (*e.g.* Figs. 254, 255) 9

- Cibarium without teeth (Fig. 258) ....*S. scutistriatum*

9. Ventral extension of paraproct with external margin distinctly curved at mid point (Fig. 610)......... ....*S. nigrimanum*

- Ventral extension of paraproct with external margin straight along its entire length (Fig. 611)......... ....*S. nunesdemelloi*

10 Ventral extension of paraproct subrectangular, with prominent process at junction with cercus (Fig. 617) .... *S. wygodzinskyorum*

- Ventral extension of paraproct bulbous, with weak process at junction with cercus (Figs. 606, 608) ....*S. huairayacu*, *S. lahillei*

MALE

Simulium sumapazense and *S. jeteri* are not included in the key because there is a lack of information concerning males.

1. Scutum largely black, sometimes marked with brown (*e.g.* Figs.732-743, 759-762) [except brown variation in *S. hirtipupa*, see species description] 2

- Scutum largely brown, dark brown or reddish brown (*e.g.* Figs. 746, 751, 755, 757, 763, 767)........10

2. With light source anterior thorax with pattern (*e.g.* Figs. 734, 736-741, 748, 753, 759,) 3

- With light source anterior thorax without pattern (Fig. 742) 6

3. With light source anterior silver pruinosity covering most of scutum (*e.g.* Figs. 734, 736, 737, 738, 739, 740); ventral plate subrectangular, median process well developed arising from anterior part of ventral plate with sparse, long hairs and not reaching level of lateral shoulders (Fig. 910) ....*S. guianense s.l.*

- With light source anterior silver pruinosity in front of submedian cunae (*e.g.* Figs. 748, 759, 753); ventral plate subrectangular, median process well developed and in variable position in relation to ventral surface of ventral plate, reaching or not level of lateral shoulders (*e.g.* Figs. 913, 915, 918)... 4

4. Median process of ventral pate originating from anterior margin or central depression (*e.g.* Figs. 913, 915) 5
- Median process of ventral plate originating from whole ventral surface (Fig. 918) .... *S. orbitale*
5. Median process of ventral plate prominently extending beyond lateral shoulders (Fig. 913) .... *S. itaunense*
- Median process of ventral plate not prominently extending beyond lateral shoulders (Fig. 915) .... *S. lithobranchium*
6. With light source anterior, scutum black with brown markings and fine central black line (*e.g.* Figs. 744, 765) 7
- With light source anterior, scutum black without brown markings, sometimes with fine central black line (*e.g.* Figs. 732, 742, 761) 8
7. Ventral plate with reduced main body and well developed lateral shoulders and median pear-shaped median process (Fig. 911) .... *S. hirtipupa* [brown form]
- Ventral plate with main body well developed, without lateral shoulders and median process triangular (Fig. 922) .... *S. townsendi*
8. Main body of ventral plate reduced, with median pear-shaped process; lateral shoulders well developed (Fig. 911) .... *S. hirtipupa* [typical black form]
- Main body of ventral plate well developed, with or without median, pear-shaped process; lateral shoulders relatively weakly developed (Figs. 909, 919) 9
9. Gonostyle subrectangular and as long as gonocoxite (Fig. 858); ventral plate wider than long, concave centrally without median process (Fig. 919) .... *S. perplexum*
- Gonostyle spindle-shaped, nearly two times longer than gonocoxite (Figs. 847); ventral plate with pear-shaped median process originating from anterior margin and extending beyond lateral shoulders (Fig. 909) .... *S. duodenicornium*
10. With light source anterior scutum with indistinct pattern (*e.g.* Figs. 751, 755, 757, 763) 11
- With light source anterior scutum with distinct pattern (*e.g.* Figs. 746, 767) 13
11. Ventral plate without median process or process weakly produced centrally (*e.g.* Figs. 916, 917); gonostyle often with two, three, five or more terminal or subterminal spines (Figs. 855, 856) .... *S. nigrimanum*, *S. nunesdemelloi*
- Ventral plate with prominent median process (*e.g.* Figs. 912, 914, 920, 923); gonostyle with single, stout terminal spine (Figs. 853, 859) 12
12. Ventral plate with median process subtriangular, main body of ventral plate distinctly covered with hairs and posterior margin prominently produced centrally (Fig. 914) .... *S. lahillei*
- Ventral plate with median process dome-shaped, main body of ventral plate not covered with hairs and posterior margin straight (Fig. 920) .... *S. scutistriatum*
13. With light source anterior, scutum with 1+1 submedian dark brown triangular vittae (Fig. 746); ventral plate with small median process (Fig. 912) .... *S. huairayacu*
- With light source anterior scutum with 1+1 sublateral silver pruinose vittae arising on anterolateral margins and extending to mid region of thorax (Fig. 767); ventral plate with prominent median process (Fig. 923) .... *S. wygodzinskyorum*

PUPA

1. Gill with 12 filaments 6
- Gill with 15 or more filaments 2
2. Gill with 15 filaments, prominently sclerotised apically (Fig. 1035) [best seen at high magnification – see species description] .... *S. jeteri*
- Gill with more than 15 filaments, not prominently sclerotised apically (*e.g.* Figs. 1034, 1038, 1039) [best seen at high magnification – see species descriptions] 3
3. Gill with 18 filaments, all rounded apically and arranged in a bunch (Fig. 1038) .... *S. nigrimanum*
- Gill with 19 or more filaments, all pointed apically (*e.g.* Figs. 1034, 1039, 1040) 4
4. Gill with 19 to 24 filaments (Figs. 1039, 1040) 5
- Gill with 45-56 filaments (Fig. 1034) .... *S. itaunense*

5. Gill with 22-23 long and fine filaments (Fig. 1040) .... *S. orbitale*
- Gill with 19 or 20 short and stout filaments (Fig. 1039) .... *S. nunesdemelloi*
6. Gill filaments pointed apically, but without sclerotised ends 7
- Gill filaments pointed apically, but with sclerotised ends 11
7. Gill configuration with a dorsal primary branch with 10 filaments upwardly directed and closed together; ventral primary branch with two secondary filaments directed towards ventral region of pupa curving upwards at mid point (Fig. 1033) .... *S. huairayacu*
- Gill with a different configuration pattern (*e.g.* Figs. 1036, 1043, 1044) 8
8. Gill with filaments of dorsal primary branch relatively shorter, stouter and wider basally than filaments of median and ventral primary branches (Fig. 1043) .... *S. sumapazense*
- Gill with filaments of primary branches relatively of same length and girth (Figs. 1036, 1044) 9
9. Gill with filaments grouped together as in Figs. 1036, 1044 10
- Gill with filaments splayed out as in Fig. 1045 .... *S. wygodzinskyorum*
10. Gill with filaments of dorsal primary branch dividing more apically as in Fig. 1036 .... *S. lahillei*
- Gill with filaments of dorsal primary branch dividing basally as in Fig. 1044 .... *S. townsendi*
11. Frontoclypeus and thorax of pupa densely covered with black spiniform setae as in Fig. 7 .... *S. hirtipupa*
- Frontoclypeus and thorax of pupa not covered with black spiniform setae 12
12. Gill with black tips of filaments short and thick (*e.g.* Figs. 1031, 1037, 1041) 13
- Gill with black tips of filaments long and fine (*e.g.* Figs. 1030, 1042) 15
13. Gill not covered by spicules; gill filaments configuration as in Fig. 1037 .... *S. lithobranchium*
- Gill covered by spicules; gill filaments configuration as in Figs. 1031, 1041 14
14. Gill filaments with annulations on distal part less accentuated with spicules; gill filaments configuration as in Fig. 1031 .... *S. guianense s.l.*
- Gill filaments with annulations on distal part accentuated by forwardly directed processes without spicules; gill filaments configuration as in Fig. 1041 .... *S. perplexum*
15. Gill filaments with dorsal and ventral branches in a straight line parallel to surface of cephalothorax (Fig. 1030); tergite II with band of rounded tubercles .... *S. duodenicornium*
- Gill filaments directed forwards, not arranged in vertical line with cephalothorax (Fig. 1042); tergite II without band of rounded tubercles .... *S. scutistriatum*

LARVA

The larvae of species in the ORBITALE species group are externally homogenous, except for those taxa that have the thorax and abdomen covered with ovoid setae (*e.g. S. duodenicornium*, *S. guianense s.l.*, *S. lithobranchium*, *S. orbitale*) or covered with black spiniform setae (*S. hirtipupa*). The best character for larval identification are the configuration and number of the gill filaments in the dissected gill histoblast of the mature larva. As consequence, great care should be taken when using keys for identification of larvae, and identification should be confirmed by the examination of link-reared adults, which have been collected preferably in the same locality as the mature larvae. When mature larvae are not found, identification to species is almost impossible. Once the species group has been established, the morphology of the postgenal cleft, hypostomium and mandible are species specific characters.

Simulium perplexum is not included in the key because its larva is unknown. The larva of *S. lahillei* and *S. itaunense* is poorly described, therefore I have to rely on other authors' diagnostic characters to include them in the key to larva.

1. Mature larva with dissected gill histoblast with more than 12 filaments 2
- Mature larva with 12 filaments 6
2. Mature larva with dissected gill histoblast with 15 filaments .... *S. jeteri*
- Mature larva with dissected gill histoblast with more than 15 filaments 3
3. Mature larva with dissected gill histoblast with 45 or more filaments .... *S. itaunense*
- Mature larva with dissected gill histoblast with less than 45 filaments 4

4. Mature larva with dissected gill histoblast with 18 filaments; hypostomium with teeth reduced, located below level of anterior margin (Fig. 1199)..*S. nigrimanum*
- Mature larva with dissected gill histoblast with 19-23 filaments; hypostomium with teeth developed and protruding forward on anteriorior margin (Figs. 1200, 1201) 5
5. Larval integument with simple setae; dissected gill histoblast with 19-20 stout and short filaments. ....*S. nunesdemelloi*
- Larval integument with ovoid setae (Fig. 89); dissected gill histoblast with 22-23 fine and long filaments ....*S. orbitale*
6. Dissected gill histoblast with filaments unsclerotised apically.. 7
- Dissected gill histoblast with filaments sclerotised apically 9
7. Postgenal cleft short and broad mesally (Fig. 1150); anterior margin of hypostomium concave and lateral teeth longer and higher than remaining teeth (Fig. 1205) .... *S. wygodzinskyorum*
- Postgenal cleft deep and pointed apically (*e.g.* Figs. 1139, 1142, 1148, 1149); anterior margin of hypostomium with margin straight and teeth different from above (*e.g.* Figs. 1194, 1197, 1203, 1204) 8
8. Hypostomium with median tooth and 1 + 1 lateral teeth reduced (Fig. 1204) ....*S. townsendi*
- Hypostomium with median tooth and sometimes 1 + 1 lateral teeth well developed (Figs. 1194, 1197, 1203).. *S. huairayacu*, *S. lahillei*, *S. sumapezense*
9. Thoracic and abdominal integument prominently covered with black spiniform setae .... *S. hirtipupa*
- Thoracic and abdominal integument without black spiniform setae 10
10. Hypostomium with 1+1 lines of 11 hypostomial setae (Fig. 1202); postgenal cleft deep, prominently triangular (Fig. 1147); thoracic and abdominal integument without setae...................... ....*S. scutistriatum*
- Hypostomium with 1+1 lines of 5-8 hypostomial setae (*e.g.* Figs. 1191, 1192, 1198); postgenal cleft broad mesally, not prominently triangular (*e.g.* Figs. 1136, 1137, 1143); thoracic and abdominal integument covered with oval setae 11
11. Abdominal segments I-VI with 1+1 dorso-lateral tubercles varying from poorly to well developed .... *S. lithobranchium*
- Abdominal segments I-VI without 1+1 dorso-lateral tubercles 12
12. Anterior margin of hypostomium concave centrally, median and sublateral teeth lower than lateral teeth (Fig. 1192); postgenal cleft as in Fig. 1137 ....*S. guianense*
- Anterior margin of hypostomium convex centrally, median and sublateral teeth at same level as lateral teeth (Fig. 1191); postgenal cleft as in Fig. 1136...*S. duodenicornium*

2.4.8. Identification key to species of the New World PICTIPES species group.

FEMALE

The females of the three species placed in the PICTIPES species group share a similar thoracic pattern and morphology of the genitalia. Hence, they cannot be reliably identified in the absence of link-reared specimens.

1. Genital fork with internal posterior process poorly developed and stem prominently expanded apically (Fig. 67).. *S. innoxium*
- Genital fork with internal posterior process prominently developed and stem relatively less expanded apically (Figs. 678, 680) .... *S. claricentrum*, *S. pictipes*

MALE

The males of the three species placed in the PICTIPES species group share a similar thoracic pattern. They can be reliably identified by the morphology of the ventral plate in link-reared specimens.

1. Ventral plate with lateral shoulders relatively less prominent and ventral margin distinctly acuminate (Fig. 924); thoracic pattern as in Figs. 769, 770 ....*S. claricentrum*

- Ventral plate with lateral shoulders relatively more prominent and ventral margin weakly concave or nearly straight (Figs. 925, 926); thoracic pattern as in Figs 771-776. 2
2. Ventral plate with lateral shoulders well developed and ovoid; basal arms short and expanded apically (Fig. 925) .... *S. innoxium*
- Ventral plate with lateral shoulders well developed and pear-shaped; basal arms long and relatively narrower apically (Fig. 926) .... *S. pictipes*

PUPA

1. Gill filaments expanded basally and tapering towards apex (Fig. 1048) .... *S. pictipes*
- Gill filaments approximately of same girth along its length (Figs. 1046, 1047) 2
2. Gill filaments lacking tuberculate sculpture in basal third to fourth of each filament (Fig. 1046) .... *S. claricentrum*
- Gill filaments with tuberculate sculptures in basal third to fourth of each filaments (Fig. 1047)........ .... *S. innoxium*

LARVA

The larvae of species in the PICTIPES species group are externally homogeneous The morphology of the hypostomial teeth is useful to species identification, but this character should be used in combination with the dissected gill histoblast in mature larvae. As consequence great care should be taken when using keys for identification of larvae, and identification should be confirmed by the examination of link-reared adults, which have been collected preferably in the same locality as the mature larvae. When mature larvae are not found, identification to species is almost impossible.

1. Hypostomium with anterior margin concave, median and 1 + 1 lateral teeth nearly at same height (Fig. 1206) .... *S. claricentrum*
- Hypostomium with anterior margin straight, median tooth more prominent than 1+ 1 lateral teeth (Figs. 1207-1208) 2
2. Hypostomium with 1+1 lines of eight hypostomial setae (Fig. 1208) .... *S. pictipes*
- Hypostomium with 1+1 lines of more 16-17 hypostomial setae (Fig. 1207) .... *S. innoxium*

2.4.9. Identification key to species of the New World TARSATUM species group

FEMALE

Simulium hieroglyphicum is included in the key based on the characters described in PETERSON *et al.* (1988).

1. Thorax black as in Figs. 366 367, 374, 375, 396-397, 404, 405 2
- Thorax orange tinged with brown or dark brown as in Figs. 384, 385, 388, 389, 398, 399, 414, 415) 8
2. Thorax without a pattern [with light source anterior] (*e.g.* Figs. 402, 406, 408, 410) 3
- Thorax with a pattern [with light source anterior] (*e.g.* Figs. 372, 394, 382, 412, 414) 6
3. Thorax prominently covered by clumps of golden hairs (*e.g.* Figs. 402, 410) 4
- Thorax covered by finer hairs irregularly distributed (*e.g.* Figs. 406, 408) 5
4. Genital fork with small anterior posterior processes (Fig. 698) .... *S. tarsatum*
- Genital fork prominent anterior posterior processes (Fig. 695) .... *S. smarti*
5. Paraproct ssubquadrangular (Fig. 638); gonapophyses with internal margins narrowing apically (Fig. 578); genital fork without internal posterior processes (Fig. 697) .... *S. tarsale*
- Paraproct subrectangular (Fig. 627); gonapophyses with internal margins diverging apically (Fig. 568); genital fork with internal posterior processes well developed (Fig. 687) .... *S. hieroglyphicum*
6. Gonapophyses distinctly wider at base and prominently pointed apically (Fig. 574) .... *S. pulverulentum*
- Gonapophyses not so wide at base and rounded apically (Figs. 566, 570, 580) 7
7. Cercus elongated, rounded apically (Fig. 629); gonapophyses only sclerotised on internal margins (Fig. 570) .... *S. hippovorum*

- Cercus subrectangular, relatively truncate apically (*e.g.* Figs. 625, 640); gonapophyses largely sclerotised over entire surface (Figs. 566, 580,) .... *S. freemani*, *S. virgatum s.l.*

8. Thorax with one median, straight line and 1+1 submedian vittae that diverge posteriorly and extend from anterior margin to mid length of scutum [with light source anterior] (Fig. 384); paraproct not extending much beyond junction with cercus, covered by prominent long black hairs (Fig. 630) .... *S. lobatoi*

- Thorax with different pattern with light source anterior as in Figs. 364, 366, 368, 370, 378, 388, 390, 392, 398, 404; paraproct extending well beyond cercus and often covered by short setae or microtrichiae (Figs. 622-624, 626, 628, 631-633, 635, 637) 9

9. Thorax orange brown (Fig. 398); paraproct subrectangular, devoid of hairs or microtrichiae apically (Fig. 635) .... *S. rubrithorax*

- Thorax brown to dark brown as in Figs. 364, 366, 368, 370, 378, 388, 390, 392, 404; paraproct subquadrangular, suboval, sometimes subrectangular, covered by hairs or microtrichiae apically (*e.g.* Figs. 622-624, 626, 628, 631-633, 637) 10

10. Gonapophyses small, nearly as long as width of eighth sternite at mid length (Figs. 564, 577) 11

- Gonapophyses very long, nearly 1.5 to 2.5 times longer that width of eighth sternite at mid length (*e.g.* Figs. 563, 565, 569, 572, 573, 577) 12

11. Thorax dark brown with median and submedian silver pruinosities on anterior third of scutum [with light source anterior] (Fig. 368); with light source posterior thorax with 1+1 submedian comma-shaped vittae with tails extending to mid point of scutum [best seen by slightly tilting the specimen] (Fig. 369) .... *S. cristalinum*

- Thorax brown without median and submedian silver pruinosities on anterior third of scutum [with light source anterior] (Fig. 404); with light source posterior 1+1 round, submedian silver pruinose vittae without tails on anterior third of scutum (Fig. 405) .... *S. solarii*

12. Thorax without pattern, only faint single black line in middle of thorax [with light source anterior] (Fig. 370) .... *S. earlei*

- Thorax with pattern [with light source anterior] (*e.g.* Figs. 362, 364, 376, 378, 386, 416) 13

13. Paraproct distinctly suboval (*e.g.* Figs. 631-633) .... *S. paynei*

- Paraproct rectangular or subquadrangular (*e.g.* Figs. 621, 622, 626, 628, 641) 14

14. Paraproct subquadrangular and expanded apically as in Fig. 622 .... *S. bricenoi*

- Paraproct subrectangular (*e.g.* Figs. 621, 626, 628, 641) 15

15. Paraproct well developed and distinctly sclerotised (*e.g.* Figs. 628, 641) 16

- Paraproct poorly developed, membranous and poorly sclerotised (*e.g.* Figs. 621, 626) 17

16. Gonapophyses with internal margins well separated, wide basally and prominently narrow and thinner apically (Fig. 569) .... *S. hinmani*

- Gonapophyses with internal margins closer together and not prominently narrow and thinner apically (Fig. 581) .... *S. yepocapense*

17. Cercus prominently suboval (Fig. 621); junction of cercus and paraproct with visible internal membranous tail (Fig. 621) .... *S. brachycladum*

- Cercus subrectangular (Fig. 626); junction of cercus and paraproct without internal membranous tail (Fig. 626) .... *S. guerrerense*

MALE

1. Thorax orange (*e.g.* Figs. 799, 800, 811, 812) 2

- Thorax brown, dark brown or black (*e.g.* Figs. 781-784, 797, 798, 817, 818, 823-834) 3

2. Thorax orange with faint median and 1+1 submedian silver pruinose vittae [with light source anterior] (Fig. 799); with light source posterior thorax dark brown without silver pruinosities (Fig. 780); ventral plate with anterior margin deeply concave at base of median process (Fig. 937) .... *S. lobatoi*

- Thorax orange with distinct 1+1 median and 1+1 submedian, wide silver pruinose vittae [with light source anterior] (Fig. 811); with light source posterior thorax orange with 1+1 fine silver pruinose vittae on central region of thorax (Fig. 812); ventral plate with anterior margin straight at base of median process (Fig. 943) .... *S. rubrithorax*

3. Thorax black, covered by clumps of golden setae (Figs. 813, 814, 819, 820) 4

\- Thorax dark brown to black, covered by irregularly distributed, semirecumbent golden, yellowish or whitish hairs (*e.g.* Figs. 785, 786, 794-796, 817, 818) 5

4. Ventral plate prominently produced centrally and basal arms distinctly expanded apically (Fig. 944); gonostyle elongate, with external margin distinctly concave on apical third and internal margin not produced (Fig. 883) .... *S. smarti*

\- Ventral plate relatively less produced centrally and basal arms pointed apically (Fig. 947); gonostyle flattened, with external margin weakly concave on apical third and internal margin prominently expanded (Fig. 886) .... *S. tarsatum*

5. Thorax dark brown to black with indistinct pattern [with light source anterior] (*e.g.* Figs. 785, 794, 795) 6

\- Thorax dark brown to black with distinct pattern [with light source anterior] (*e.g.* Figs. 787, 791, 809, 825) 8

6. Gonostyle elongate and cigarette-like shaped, with lateral margins weakly sinuous (Fig. 873) .... *S. hieroglyphicum*

\- Gonostyle flattened, with lateral margins strongly sinuous (*e.g.* Figs. 870, 874, 885) 7

7. Gonocoxite with antero-lateral angle strongly produced (Fig. 885) .... *S. tarsale*

\- Gonocoxite with antero-lateral angle not produced (Figs. 870, 874) .... *S. earlei*, *S. hinmani*

8. Ventral plate with an antero-median process forwardly produced (*e.g.* Figs. 927-930, 938-941, 945-946, 948) 11

\- Ventral plate without an antero-median process (Figs. 932, 933, 949) 9

9. Ventral plate with central region prominently convex, especially when examined in lateral view (Fig. 932); thorax varying from dark brown (Figs. 787, 788) [specimens from Mexico] to black (Figs. 789, 790) [specimens from USA] .... *S. freemani*

\- Ventral plate with central region not prominently convex (Figs. 933, 949); thorax with single colour forms 10

10. Ventral plate with anterior margin produced centrally; lateral shoulders of ventral plate distinct (Fig. 933) .... *S. guerrerense*

\- Ventral plate with anterior margin not produced centrally; lateral shoulders of ventral plate absent (Fig. 949) .... *S. yepocapense*

11. Ventral plate with antero-median process 1 to 2 times as long as width at base and tip of antero-median process not concave (Figs. 927, 930, 942) 12

\- Ventral plate with antero-median process varying from 2, 2.5 or 3 times as long as width at base and tip of antero-median process concave (*e.g.* Figs. 929, 936, 938-941, 945, 948) 14

12. Ventral plate with antero-median process as long as width at base and truncate apically; basal arms pointed apically (Fig. 942) .... *S. pulverulentum*

\- Ventral plate with antero-median process twice as long as width at base and rounded apically; basal arms rounded apically (Figs. 927, 930) 13

13. Anterior half of scutum with median, whitish, rectangular band and 1+1 white, submedian cunae containing small brown cunae with light source anterior (Fig. 777); scutal pattern indistinct with posterior light source (Fig. 778); ventral plate with anterior margin concave at base of antero-median process (Fig. 927) .... *S. brachycladum*

\- Anterior half of scutum with median, whitish, pear-shaped band with distal concavity and 1+1 white, submedian cunae with light source anterior (Fig. 783); scutal pattern changes from whitish to black and rest of scutum from brownish black to grey pruinose with posterior light source (Fig. 784); ventral plate with anterior margin straight at base of antero-median process (Fig. 930) .... *S. cristalinum*

14. Ventral plate with anterior margin at base of antero-median process prominently concave; lateral shoulders of ventral plate distinctly developed (Fig. 945) .... *S. solarii*

\- Ventral plate with anterior margin at base of antero-median process not prominently concave; lateral shoulders of ventral plate relatively weakly developed (*e.g.* Figs. 928, 936, 938-941, 948) 15

15. Ventral plate with antero-median process long, nearly three times longer than width at base; anterior margin of ventral plate at base of antero-median process gently concave (Fig. 948) ....

.... *S. virgatum s.l.*

\- Ventral plate with antero-median process relatively shorter, up to twice as long as width at base; anterior margin of ventral plate at base of antero-median process nearly straight (Figs. 928, 936, 938-941) 16

16\. Ventral plate with antero-median process wider basally; area between basal arms of ventral plate prominently subtriangular [as in *Hemicnetha mexicana* lectotype] (Figs. 938-941) .... *S. paynei*

\- Ventral plate with antero-median process relatively thinner basally; area between basal arms of ventral plate suboval (Figs. 928, 936) .... *S. bricenoi*, *S. hippovorum*

PUPA

The pupal gill configuration of *S. tarsale* has not been accurately illustrated nor described. Nonetheless, I have tentatively included it in the key to pupae following the characters given in STONE (1969).

1\. Gill with 6-8 filaments 2

\- Gill with more than eight filaments 8

2\. Gill with six filaments 3

\- Gill with eight filaments 4

3\. Gill filaments of approximately same length and pointed apically (Fig. 1049) [best seen at high magnification] .... *S. brachycladum*

\- Gill with some filaments of dorsal primary branch much shorter and less developed than remaining filaments, all filaments rounded apically (Figs. 1052, 1053) .... *S. cristalinum*

4\. Thorax of pupa rugose as like Fig. 72, but with raised rhomboid-like markings .... *S. bricenoi*

\- Thorax of pupa not rugose and without rhomboid markings 5

5\. Cocoon without fenestrations on anterior margin as in Fig. 66 6

\- Cocoon with fenestrations on anterior margin as in Fig. 69 7

6\. Thorax of pupa with prominent rounded tubercles, densely distributed over entire surface .... *S. freemani*

\- Thorax of pupa with small rounded, scarcely distributed tubercles only visible near base of gill or central region) .... *S. lobatoi*, (and probably *S. tarsale*)

7\. Gill filaments arranged in palmate configuration, with six filaments arising from common trunk and two filaments slightly separated from remainder filaments (Fig. 1060) .... *S. hippovorum*

\- Gill filaments not arranged in palmate configuration, with two primary branches having four filaments each (Figs. 1064, 1068, 1072) .... *S. paynei*, *S. rubrithorax*, *S. virgatum s.l.*

8\. Gill with 60-90 filaments, with basal primary filaments prominently swollen and longer than secondary filaments (Figs. 84, 1058); frontoclypeus and thorax of pupa with prominent loose rugosities (Figs. 72, 74) .... *S. hieroglyphicum*

Gill with 10-18 filaments, all of relative same girth (*e.g.* Figs. 1057, 1059, 1067, 1071, 1073); frontoclypeus and thorax of pupa without loose rugosities 9

9\. Gill with 10 filaments 10

\- Gill with more than 10 filaments 11

10\. Gill with dorsal primary branch with eight filaments and ventral primary branch with two filaments (Figs. 1057, 1059, 1067) .... *S. guerrerense, S. hinmani*, *S. pulverulentum*

-\. Gill with dorsal primary branch with four filaments and ventral primary branch with six filaments (Fig. 1073) .... *S. yepocapense*

11\. Gill with 12 filaments (Fig. 1071) .... *S. tarsatum*

\- Gill with more than 12 filaments 12

12\. Gill with 18 splayed out filaments, all dividing at different heights from gill base (Fig. 1069) .... *S. smarti*

\- Gill commonly with 15-17 filaments all relatively closed together (Figs. 1054, 1070) 13

13\. Cocoon with opening on anterior margin distinctly oblique and not covering gill filaments; gill with 15 filaments, all rounded apically (Fig. 1070) .... *S. solarii*

- Cocoon with opening on anterior margin not prominently oblique and not covering gill filaments; gill commonly with 16 filaments [specimens with 15 or 17 filaments have been examined], all pointed apically (Fig. 1054).......... *S. earlei*

LARVA

The larva of species within the TARSATUM species group species group are externally homogeneous. The best character for larval identification are the configuration and number of the gill filaments in the dissected gill histoblast of the mature larva. As consequence, great care should be taken when using keys for identification of larvae, and identification should be confirmed by the examination of link-reared adults, which have been collected preferably in the same locality as the mature larvae. When mature larvae are not found, identification to species is almost impossible. Once the species group has been established, the morphology of the postgenal cleft, hypostomium and mandible are species specific characters.

Simulium tarsale is not included in the key to larvae because of its poor morphological description.

1. Mature larva with dissected gill histoblast with 60-90 filaments, at least three of them prominently swollen and much longer than remaining filaments.......... *S. hieroglyphicum*
- Mature larva with dissected gill histoblast with 6-18 filaments, all of relatively same girth and length.......... 2
2. Mature larva with dissected gill histoblast with six filaments.......... 3
- Mature larva with dissected gill histoblast with more than six filaments.......... 4
3. Postgenal cleft triangular and pointed apically (Fig. 1156); mandible with two mandibular serration (Fig. 1265).......... *S. cristalinum*
- Postgenal cleft bell-shaped, broadly rounded apically (Fig. 1154); mandible with single mandibular serrations (Fig. 1263).......... *S. brachycladum*
4. Mature larva with dissected gill histoblast with eight filaments.......... 5
- Mature larva with dissected gill histoblast with more than eight filaments.......... 11
5. Anterior margin of hypostomium with teeth concentrated on central region and prominently protruded forwards (Fig. 1218).......... *S. lobatoi*
- Anterior margin of hypostomium with teeth evenly distributed along anterior margin (Figs. 1210, 1217, 1219, 1215).......... 6
6. Hypostomium with 1+1 lines of 8-9 hypostomial setae parallel to lateral margin (*e.g* Figs. 1215, 1217, 1219).......... 7
- Hypostomium with 1+1 lines of 13 hypostomial setae parallel to lateral margin (*e.g* Figs. 1213. 1221).......... 10
7. Hypostomium with median tooth, pair of sublateral teeth adjacent to median tooth and 1 + 1 lateral teeth rounded (Fig. 1225) [best seen at high magnification]; mandibular comb teeth as in Fig. 1279.......... *S. virgatum s.l.*
- Hypostomium with median pair of sublateral teeth adjacent to median tooth and 1 + 1 lateral teeth triangular and pointed apically (*e.g.* Figs. 1210, 1217, 1219) [best seen at high magnification]; mandibular comb teeth as in Figs. 1264, 1271, 1273.......... 8
8. Mandibular comb with 7-8 teeth; first, second and third mandibular teeth nearly of same length (Fig. 1273).......... *S. paynei*
- Mandibular comb with 10-12 teeth; mandibular comb teeth of different length as in Figs. 1264, 1271).......... 9
9. Mandibular comb with third tooth nearly as long as fourth tooth (Fig. 1271).......... *S. hippovorum*
- Mandibular comb with third tooth prominently longer than fourth tooth (Fig. 1264).......... *S. bricenoi*
10. Postgenal cleft triangular with tube-like incision apically (Fig. 1166).......... *S. rubrithorax*
- Postgenal cleft triangular without tube-like incision apically (Fig. 1158).......... *S. freemani*
11. Mature larva with dissected gill histoblast with 10-12 filaments.......... 12
- Mature larva with dissected gill histoblast with more than 12 filaments.......... 16
12. Mature larva with dissected gill histoblast with 10 filaments.......... 13

- Mature larva with dissected gill histoblast with 12 filaments .... *S. tarsatum*

13. Postgenal cleft small and rounded apically (Fig. 1161); postgenal bridge 1.5 times longer than hypostomium (Fig. 1161) .... *S. hinmani*

- Postgenal cleft deep and triangular apically (*e.g.* Figs. 1159, 1165, 1167, 1171); postgenal bridge as long as hypostomium 14

14. Hypostomium with median tooth much longer than 1 +1 lateral teeth (Fig. 1226)............................ .... *S. yepocapense*

- Hypostomium with median and 1 + 1 tooth different from above as in Figs. 1214, 1220, 1222-1223 15

15. Hypostomium with median tooth, sublateral and 1 + 1 lateral teeth well developed, all relatively of same length and at the same level (Fig. 1220) .... *S. pulverulentum*

- Hypostomium with median tooth reduced and much lower than 1+ 1 lateral teeth, sublateral teeth reduced (Fig. 1214) .... *S. guerrerense*

16. Mature larva with dissected gill histoblast with 18 filaments; hypostomial teeth arranged centrally on anterior margin (Fig. 1222) .... *S. smarti*

- Mature larva with dissected gill histoblast with 15-17 filaments; hypostomial teeth often evenly distributed on anterior margin (Figs. 1212, 1223) 17

17. Mature larva with dissected gill histoblast with 15 filaments; hypostomial teeth as in Fig. 1223; head coloration dark brown (Fig. 1115) or pale yellow (Fig. 1116) over entire surface.......... *S. solarii*

- Mature larva with dissected gill histoblast commonly with 16 filaments; hypostomial teeth as in Fig. 1212; head coloration prominently dark brown on basal half and pale on apical half ...... *S. earlei*

2.5. Morphological description, taxonomic discussion, distribution, biology and medical importance of species of the subgenus *Trichodagmia* in the New World.

The following diagnosis to species groups and description to species are presented in alphabetical order. The systematic arrangement follows that of ADLER & CROSSKEY (2008, 2009, 2010) with more recent taxonomic adjustments given by SHELLEY *et al.* (2010) or proposed in this work.

2.5.1. The CANADENSE species group.

All taxa in the CANADENSE species group are mainly found in Central America, with only one species extending into the USA and Canada. The CANADENSE species group now contain 20 valid species with the synonymy of *S. chiriquiense* under *S. ethelae* and the transfer of *S. falculatum* from the ORBITALE species group of SHELLEY *et al.* (2010).

The morphological descriptions here provided have been derived after examination of type material and numerous identified specimens mainly housed in the BMNH, INDRE, MLP and NMNH simuliid collections. However, some life stages were not available, especially larvae. In this case, I have based the descriptions here provided upon the species original descriptions, and the key papers of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and DALMAT (1955).

Diagnosis.

Female: Scutum black usually with pattern (Figs. 285-314). Nudiocular triangle developed but to medium depth (Figs. 177-193). Cibarium unarmed, sometimes with 1+1 small prominences in central trough (Figs. 229-246). Sc and basal section of Radius with or without setae. Claws with basal tooth. Gonapophyses subtriangular with internal margins well separated and sclerotised, remainder of gonapophyses membranous; gonapophyses covered with microtrichiae (Figs. 30-32, 526-543). Paraprocts generally extending weakly beyond cercus, subquadrangular to subrectangular; in most species paraproct narrow or with two membranous projections apically giving the appearance of a two-lobed paraproct, sometimes membranous tails present at junction with cercus; paraproct highly setose (Figs. 14-17, 584-602). Genital fork sclerotised, often with stem expanded apically, anterior processes well developed, internal process varying from undeveloped to developed, termination of lateral arms weakly straight (Figs. 644-662).

Male: Scutum black, with or without pattern (Figs. 704-731). Gonocoxite subquadrangular. Gonostyle elongate, four times longer than gonocoxite, sometimes weakly curved beyond mid point (*S. burchi*), and terminating in a single stout spine (Figs. 42, 43, 829-846). Ventral plate variable either subquadrangular with anterior margin weakly concave to subtriangular with developed lateral shoulders, and in some species a median process can be seen; ventral plate often without lateral shoulders and basal arms developed and subparallel; in most species the ventral plate has a central keel extending from anterior margin to nearly posterior region, prominently covered with long hairs (Figs. 47-50, 891-908). Paramere well developed with central long spines; basal plates prominently sclerotised and developed (Figs. 61, 952-969).

Pupa: Cocoon varying from slipper-shaped (Figs. 65, 1015) to shoe-shaped (Figs. 66), but never with fenestrations. Pupal gill filaments prominently swollen, either with pseudoannulations or small secondary branches; gill varying from two to 12 filaments; in certain species of the CANADENSE species group (*e.g S. carolinae*, *S. gorirossiae*, *S. johnsoni*, *S. larvispinosum*, *S. menchacai*, *S. temascalense*) the secondary filaments are distinctly sclerotised apically (Figs. 75-78, 1011-1029). Trichomes of the frontoclypeus and pupal thorax long, spiniform.

Larva: There are no clear cut diagnostic characters for the larvae of species in the CANADENSE species group, thus a suite of characters has to be taken into account in combination with diagnostic characters in link-reared adults from pupae collected in the same locality. Postgenal cleft often bell-shaped or deep and triangular with or without a tube-like incision apically (Figs. 1122-1135). Hypostomium often with nine evenly distributed teeth along anterior margin, although in certain taxa the teeth occur in central region of hypostomium; anterior margin of the hypostomium varying from straight to weakly concave centrally; median tooth well developed in most species (Figs. 1174-1190). Mandible with two or three apical teeth; mandibular comb with number of mandibular teeth as in other species of the subgenus *Trichodagmia* (Figs. 1229-1245). Abdominal larval integument without setae. In species certain species of the CANADENSE species group such as *S. gorirossiae* and *S. menchacai* (see Figs. 89, 99, 1267) the abdominal segment VIII has 1+1 ventral papillae, and the posterior arm of the anal sclerite encircles the posterior circlet having prominent sclerotised accessory plates (Figs. 98-99, 1283-1289). In the majority of species of the CANADENSE species group, the posterior arms of the anal sclerite never encircles the posterior circlet and it does not have sclerotised accessory plates (*e.g.* Fig. 98, 1078, 1079, 1080, 1083).

2.5.1. ***Simulium (Trichodagmia) ayrozai*** **VARGAS** (Figs. 14, 30, 48, 177, 229, 285, 286, 420, 526, 584,, 644, 704, 705, 829, 891, 952, 1011, 1122, 1174, 1229)

A zoophilic species only known from Guatemala and Mexico. The description here provided has been based upon examination of type material, identified material housed at BMNH, INDRE, MLP, MZUCR and NMNH, the original description of VARGAS (1945), and the reviews of COSCARÓN & COSCARÓN-ARIAS (2007), DÍAZ NÁJERA & VULCANO (1962A), and VARGAS & DÍAZ NÁJERA (1957b).

Simulium ayrozai VARGAS, 1945: 75. HOLOTYPE male (reared), MEXICO: Desierto de los Leones; 5.iii.1944, (*Martínez & Díaz N.*) (INDRE, 3676) [Examined.]

FEMALE. General body colour black. Body length (specimens pinned) 2.8-3.2 mm (mean = 3.0 mm, s.d. = 0.2, n = 3); wing length 3.2-3.4 mm (mean = 3.3 mm, s.d. = 0.1, n = 3), wing width 1.5-1.7 mm (mean = 1.5 mm, s.d. = 0.11, n = 3).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 177). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 229).

Thorax: scutum dark brown with evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent brown setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax largely silver pruinose with 1+1 submedian, X-shaped black vittae (Fig. 285); humeri and lateral margins silver pruinose; posterior margin black. With posterior illumination, thorax black with 1+1 median comma-shaped vittae on anterior third of thorax (Fig. 286). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length except on apical third, which is bare. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 420. Fore leg with coxa, trochanter, apical third of femur, basal and apical third of tibiae, and tarsal segments I-III dark brown; remainder of leg pale brown. Mid and hind legs with coxae, trochanters, apical third of femora and tibiae, basal half of tarsal segment I, and tarsal segments II-IV dark brown; remainder of leg pale yellowish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-II with anterior margin weakly silver pruinose; III-IX dark brown to black. Tergal plates well developed in pinned specimens examined. Sternites and genitalia black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses 1.5 times smaller than length of eighth sternite at mid point, nearly subsquare with weakly curved internal margins and densely covered by microtrichiae (Figs. 30, 526). Cerci subrectangular, covered with brown setae; paraproct small, subtriangular, nearly same length as cercus, with two membranous tails apically covered by long hairs; paraproct sclerotised on basal half and membranous apically densely covered with few prominent basal setae (Figs. 14, 584). Genital fork stout and sclerotised with stem expanded apically; termination of lateral arms with anterior margin straight and well developed; anterior processes well developed and blunt apically, posterior processes absent (Fig. 644). Spermatheca globular, without external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour black. Body length (specimens pinned) 3.0-3.8 mm (mean = 3.4 mm, s.d. = 0.4, n = 3); wing length 2.5-3.3 mm (mean = 3.0 mm, s.d. = 0.33, n = 4), wing width 1.-1.8 mm (mean = 1.4 mm, s.d. = 0.32, n = 4).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered with evenly distributed recumbent white hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with 1+1 subrectangular silver pruinose vittae extending from humeri to mid thorax, and weak silver pruinosity on middle of thorax; humeri silver pruinose; lateral and posterior margins black (Fig. 704). With posterior illumination, thorax black (Fig. 705). Humeri, lateral and posterior margins black. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation similar to that of female except Sc bare (as in the holotype). Leg coloration similar to female.

Abdomen: tergites dark brown to black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergites I, IV-VII (best seen in some specimens when tilted and viewed laterally). Genitalia dark brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle prominently elongate, three times longer than gonocoxite, weakly curved apically with small process basally and terminating in single stout spine; gonocoxite and gonostyle covered with long setae (Fig. 829). Ventral plate sclerotised, subrectangular, covered with long hair; anterior median process well developed with 1+1 distinct depression on anterior margin; lateral shoulders developed and basal arms well developed and subparallel (Fig. 891). Median sclerite long, about three times longer than wide at widest point, apparently without small apical incision (Fig. 891). Paramere with well developed and sclerotised basal process and numerous long spines along whole length (Fig. 952).

PUPA. Cocoon length dorsally 4.2-4.5 mm (n = 2), ventrally 4.2-5.0 mm (n = 2); pupa length 4.7-5.2 mm (n = 2); gill length 1.1 mm (n = 1).

Cocoon: shoe-shaped as in Fig. 66, black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture elevated.

Gill: light brown with two forwardly directed filaments arranged in vertical plane (Fig. 1011). Gill with two primary branches, one anterior and one posterior arising from short trunk. Filaments prominently swollen, rounded distally, with distinct pseudo-annulations, edges weakly smooth; all filaments approximately same length.

Head (*frontoclypeus*): 1+1 spiniform frontal and 1+1 spiniform facial trichomes in the few specimens examined. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and approximately five platelets in groups of two in frontal region, respectively; tubercles absent from entire surface.

Thorax: with 1-3 spiniform trichomes near margin of dorsal cleft; thorax with scarcely distributed tubercles, pointed tubercles only visible in the posterior regior of thorax.

Abdomen: similar to *S. contrerense* following COSCARÓN *et al.* (2004); abdominal tergite I without setae in the single specimen examined; tergite II with 4+4 long spiniform setae in row, 1+1 small simple setae anterior to outermost spiniform setae, and 2+2 small setae on lateral margin; tergites III-IV with 4+4 submedian simple hooks in longitudinal row, 1+1 small simple setae anterior to outermost hooks, and 2+2 or 1+1 small simple setae laterally; tergites V-IX without visible setae; tergite IX weakly sclerotised, without terminal spines. Spine combs only visible on anterior margin of tergites VI-IX, some well developed resembling teeth. Sternite IV without visible setae centrally but 1+1 small simple setae laterally; sternite V with 2+2 close bifid hooks; sternites VI-VII with 2+2 well separated simple or bifid hooks; sternites VIII-IX without setae visible setae; sternite IX weakly sclerotised. Spine combs not visible in the single specimen examined.

LARVA (Last instar). Body length 8.0-10.0 mm [Other measurements and the number not given in the description of VARGAS *et al.* (1946)]. Body colour dark grey (specimens preserved in alcohol).

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Head pattern positive. Cervical sclerites small joining postgenae posteriorly. Postgenal cleft dome-shaped, with narrow antero-median incision (Fig. 1122). Hypostomium strongly pigmented on anterior margin, with seven teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 2+2 sublateral teeth smaller than lateral teeth; 1+1 lateral tooth; 15-16 lateral serrations; 1+1 lines of approximately 12 hypostomial setae parallel to lateral margin; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1174). Antennal segments light pigmented; length of antennal segments I-III excluding the sensillum 1:1.5:1.0 mm. Mandible with two apical teeth, first one longer than second; mandibular comb with approximately eleven teeth, first fourth more prominent than remainder, two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1229). Lateral mandibular process single, large. Labral fans with more 52-54 rays.

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 46-52 rows of sclerotised process.

Abdomen: usually grey. Ventral papillae absent. Cuticle lacking setae, except area on anal sclerite. Anal sclerite well sclerotised with anterior arms extending to one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 150 rows of 24-27 simple hooks. Rectal gills with three branches with 12-15 finger-like per branch, dorsal lobes larger than the ventral ones.

Taxonomic Discussion. *Simulium ayrozai* was described by VARGAS in 1945 based on a reared male holotype, and three males, four females, 25 pupal exuviae and six larvae (all as paratypes, one female as allotype), collected in the Federal District, Mexico. Even though VARGAS (1945) collected six larvae, the larval stage was only formally described for the first time in VARGAS *et al.* (1946). The citation of mis-spellings of *S. ayrozai* (as *ayrosai*) can be found in ADLER & CROSSKEY (2008, 2009, 2010).

VARGAS (1945) stated in the original description of *S. ayrozai* that the male holotype was partially mounted and deposited at the INDRE Simuliidae collection with the number “3622”. I have examined the male holotype, which is in relatively good condition. The male holotype and its pupal exuviae and cocoon are preserved in alcohol, while three legs, one wing and its genitalia are mounted on a slide, but bearing the number “3676” (**Material Examined**). I have also examined three females and five males (all as paratypes), and a single female without type status deposited at INDRE and NMNH collections, respectively (**Material Examined**).

The female of *S. ayrozai* is similar to other species within the CANADENSE species group in which the silver pruinose pattern of the thorax reach the anterior margin (Figs. 285, 286). They cannot be readily separated without the examination of the pupal gill configuration. The males have distinct

1+1 silver pruinose subrectangular vittae (Figs. 704, 705), which are also present in the majority of the species in this group.

The best character to identify *S. ayrozai* is the configuration of the pupal gill filaments, which is unique within the CANADENSE species group in having two, prominently flat and large filaments covered with distinct annulations (Fig. 1011).

The larva of *S. ayrozai* can only be separated from other species of the CANADENSE species group by the examination of the dissected gill histoblast. Following the key of DÍAZ NÁJERA & VULCANO (1962a), the larva of *S. ayrozai* falls within the species in which the sclerotised secondary plates at the end of the abdomen are absent and the anterior margin of the hypostomium is more or less straight. In this respect, *S. ayrozai* is similar to *S. estevezi* in which the hypostomium has less than nine teeth on the anterior margin (see Figs. 1122, 1174). However, both species may be separated by the number of hypostomial setae. *Simulium ayrozai* has 12 setae (Fig. 1122), while *S. estevezi* has eight setae (Fig. 1182).

Simulium ayrozai was first described in the subgenus *Simulium* by VARGAS (1945), but was later placed in the subgenus *Hearlea* by VARGAS *et al.* (1946) and DÍAZ NÁJERA & VULCANO (1962a). This was accepted by CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed it in the JUAREZI species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. ayrozai* is now placed.

Distribution. *Simulium ayrozai* has only been recorded from Mexico and Guatemala (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. Nothing is known on the biology of *S. ayrozai*.

2.5.1.2. ***Simulium* (*Trichodagmia*) *burchi*** **DALMAT** (Figs. 178, 230, 287, 288, 421, 527, 585, 645, 706, 707, 830, 892, 953, 1012, 1078, 1123, 1175, 1230)

A relatively well-known species first described from Guatemala. The description here provided has been derived from examination of the type specimens, the original description of DALMAT (1951), examination of identified material housed at the MLP and NMNH Simuliidae collections, and the revisions of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and DALMAT (1955).

Simulium (*Hearlea*) *burchi* DALMAT, 1951: 42. HOLOTYPE female (reared; pupal exuviae in alcohol), GUATEMALA: El Quiché Department; Nebáj, Finca Micovez, Rio Micovez; 15.xi.1949, (*H.T.Dalmat*) (NMNH, accession no. 8X-3) [Examined.] [The collectors' names on the pinned specimens do not agree with those given in the original description by DALMAT (1951) as *J. Onofre Ochoa*, *Miguel A. Rodriguez* & *Herbert T. Dalmat.*]

FEMALE. General body colour black. Body length (specimens pinned, n = 2) 2.5 mm, wing length 1.4-2.9 mm; wing width 1.5 mm.

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 178). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 230).

Thorax: scutum black with evenly arranged, recumbent, golden hairs interspersed with recumbent black hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with two isolated 1+1 subquadrangular pruinose patches contiguous with anterior margin; three white pruinose bands on mid region joining white pruinose patches covering anterior fourth of scutum; humeri, lateral and posterior margins silver pruinose (Fig. 287). With posterior illumination, thorax black with 1+1 round, submedian silver pruinose vittae on anterior third of scutum, and one median and 1+1 submedian faint silver pruinose bands arising from mid length of scutum and extending to near posterior margins (Fig. 288). Scutellum black with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length, except apical third. Radius with numerous setae intermixed with distinct spines only at apex, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 421. Fore leg with coxa and trochanter brownish yellow; femur slight darkenened on outer surface and towards apex; tibia withish with apical third dark brown; tarsal segments black. Mid leg with coxa black; trochanter, femur, tibia, and basal half of tarsal segment I brown; apical third of femur, tibia, apical half of tarsal segment I, and tarsal segments II-IV dark brown. Hid leg with coxa, trochanter, apical third of femur, tibia, tarsal segment I, and tarsal segments II-IV dark brown; remainder of femur and tibia pale yellow; basal half of tarsal segment I whitish. Hind leg claw with basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IV velvet black, tergites VI-IX shiny black; tergites I-II with silver pruinosity on anterolateral margins. Tergal plates well developed. Sternites and genitalia dark black. Eighth sternite sclerotised with nine to 10 irregularly distributed setae on posterior margin; gonapophyses subtriangular, weakly sclerotised and densely covered with microtrichiae (Fig. 527). Cerci subquadrangular, covered with brown setae; paraproct subrectangular, weakly extending beyond cercus, ventral extension of the paraproct with small prominence at junction with cercus and apical region bent inwards in a heel-like shape, paraproct largely sclerotised with apical region membranous; paraproct covered with long setae centrally and small setae towards apex (Fig. 585). Genital fork stout and sclerotised with stem enlarged apically; termination of lateral arms with anterior margin straight; anterior and internal posterior processes well developed and blunt apically (Fig. 645). Spermatheca suboval, without external sculpturing and small internal spicules; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens pinned) 2.6-3.00 mm (mean = 2.8 mm, s.d. = 0.18, n = 4); wing length 1.6-2.7 mm (mean = 2.2 mm, s.d. = 0.46, n = 4), wing width 1.2-1.9 mm (mean = 1.5 mm, s.d. = 0.35, n = 3).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum velvet black covered with recumbent golden scales interspersed with recumbent black hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with silver pruinose area on anterior third of scutum and small silver pruinose band mesally; humeri, lateral and posterior margins black (Fig. 706). With posterior illumination, thorax, humeri, and lateral and posterior margins black (Fig. 707). Humeri Scutellum black with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female except Sc bare in the specimens I examined. Leg coloration as in female, but with apices of femora, tibiae and tarsal segments darker brown.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergites II-VII [best seen in some specimens when tilted and viewed laterally]. Genitalia black; sternal plates developed. Gonocoxite subquadrangular, with antero-lateral margins produced; gonostyle prominently elongate, three times longer than gonocoxite, with lateral margins weakly sinuous, narrower at mid point, and terminating in single stout spine; gonocoxite and gonostyle covered with long setae (Fig. 830). Ventral plate sclerotised, subrectangular, with anterior margin weakly concave centrally; main body of ventral plate with small median process that arises from posterior two thirds of ventral plate; lateral shoulders weakly developed; basal arms short, sclerotized and curved inwards; main body of ventral plate and median process covered by hairs (Fig. 892). Median sclerite nearly three times longer than wide, with small apical incision (Fig. 892). Paramere with well developed and sclerotised basal process and numerous long spines centrally (Fig. 953).

PUPA. Cocoon length dorsally 3.3-3.7 mm (mean = 3.5 mm, s.d = 0.14, n = 5), ventrally 4.0-4.5 mm (mean = 4.2 mm, s.d. = 0.22, n = 5); pupa length 3.1-3.6 mm (mean = 3.3 mm, s.d. = 0.25, n = 3); gill length 1.9-3.5 mm (mean = 2.8 mm, s.d. = 0.52, n = 13).

Cocoon: shoe-shaped as in Fig. 66, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with three swollen forwardly directed filaments in vertical plane. Gill with main trunk short giving rise to one set of primary branches, one dorsal, one median and one ventral; dorsal branch prominently swollen apically and directed forwards, median branch small, ventral branch curved at mid point and directed towards ventral region of pupa (Fig. 1012). Filaments stout, rounded distally, without spicules on surface and prominently annulated edges crenate; dorsal branch relatively more stout than ventral branch.

Head (*frontoclypeus*): with only 1+1 long, simple frontal and 1+1 long facial trichomes in the single specimen examined. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 4 platelets in single group laterally in frontal region; tubercles absent.

Thorax: with 1-2 spiniform trichomes on margin of dorsal cleft, one long, simple trichome at gill base, and 2+2 long simple setae on ventral margin; thorax with rounded tubercles more densely distributed on surface near dorsal cleft.

Abdomen: abdominal tergite I with 1+1 submedian small simple setae; tergite II with 4+4 spiniform setae in row, 1+1 small simple setae anterior to outermost spiniform setae, and 3+3 small simple setae on lateral margins; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 1+1 small simple setae anterior to outermost hooks; tergite V with no visible setae; tergite VI with 1+1 small submedian simple setae; tergites VII-IX with no visible setae, sternite IX weakly sclerotised without terminal spines. Spine combs on anterior margins of tergites V-IX, some developed to resemble teeth especially on tergites VII, VIII. Sternite III without visible setae; sternite IV with 3+3 small simple setae laterally; sternite V with 2+2 close simple hooks; sternites VI, VII with 2+2 well separated simple hooks; sternites VIII, IX without setae visible setae; sternite IX weakly sclerotised. Spine combs on anterior margin of sternites V-VIII.

LARVA (Last instar). Body length 6.9-7.4 mm (mean = 7.1 mm, s.d. = 0.20, n = 5), length of head capsule 0.6-0.7 mm (mean = 0.6 mm, s.d. = 0.05, n = 5); width of head capsule 0.6-0.7 mm (mean = 0.6 mm, s.d. = 0.05, n = 5). Body colour grey to tan with irregular dark patches on ventro-lateral areas of segments VI, VII (following DALMAT, 1955) (Fig. 1078).

Head: mainly dark brown. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Postgenal cleft deep, dome-shaped, subtriangular apically; postgenal bridge as long as hypostomium (Fig. 1123). Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 reduced sublateral teeth; 1+1 lateral teeth at same height as sublateral teeth; 6+6 small, lateral serrations; 1+1 lines of approximately 15 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1175). Antennal segments longer than labral fan stalk, antennal segments dark yellowish, length of antennal segments I-III excluding the sensillum 1.0:1.5:1.0 mm. Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with nine teeth, first fifth teeth more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1230). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 46-54 rays with fine, single line of spines in row interspersed with finer spinules.

Thorax: grey dorsally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 47-50 sclerotised processes of simple hooks.

Abdomen: usually grey dorsally, progressively paler ventrally. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised. Posterior circlet with 172-178 rows of sclerotised processes with simple hooks. Rectal gills with three branches, dorsal branch with 22 finger-like lobules and lateral branches with 28 finger-like lobules.

Taxonomic Discussion. *Simulium burchi* was described by DALMAT (1951) from a female holotype (accession number 8X-3), and four males, four females and six pupal exuviae (one male as allotype, accession numbers 8X-1, 8X-2, 8X-7, 8X-8, 8X-10, 8X-12, 8X-14; 9I-1, 9I-2) collected in Guatemala. A full description of the larva was later given by DALMAT (1955). The latter author stated that he deposited the holotype and allotype at the NMNH, while some paratypes were housed in his private collection, which is now housed at the NMNH. I have examined the pinned female holotype, which is in good condition. DALMAT (1951) stated that its pupal exuviae and cocoon were preserved in alcohol, but I was unable to locate them in the NMNH simuliid holdings. In addition, I have examined two pinned, reared females and one reared male together with several pupal exuviae all labelled as paratypes and housed at the NMNH Simuliidae collection. The male labelled as allotype (NMNH acc. no. 8x-10) is on three slides containing the legs, wings and genitalia, while its pupal exuviae is in alcohol; the remainder of the adult was not found at the NMNH holdings (**Material Examined**).

The adults of *S. burchi* cannot be separated from other species of the CANADENSE species group in the absence of the pupal gill configuration. *Simulium burchi* is best recognized by the pupal gill with three primary branches, the dorsal branch being prominently swollen towards the apex, the median branch small, finger-like, and the ventral branch bent at mid point and directed towards ventral region of pupa (Fig. 1012). In this respect, *S. burchi* is similar to *S. dalmati*, but in the latter species the ventral branch is directed forwards (Fig. 1018). Other species with distinctly swollen dorsal primary branches are *S. delatorrei* and *S. juarezi*, but the general configuration of the pupal gill filaments is different in these species (see Figs. 1019, 1024).

COSCARÓN & COSCARÓN-ARIAS (2007) stated that the larva of *S. burchi* differs from that of *S. dalmati* by its larger size, longer hypostomial bridge and smaller number of finger-like lobes on the rectal papillae [= anal gill]. In the authors' key to larva, *S. burchi* keyed out to the group of species without sclerotised accessory plates and the posterior circle having 172-178 rows of hooks and labral fans with 46-57 rays. However, the larva of *S. burchi* may only be readily identified from other closely related species by the morphology of the dissected gill histoblast in mature larva in combination with the pupal gill configuration in link-reared adults collected in the same locality.

Simulium burchi was placed in the subgenus *Hearlea* by DALMAT (1951). This has been accepted by CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010), but not recognized in COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007). The latter authors placed *S. burchi* in the JUAREZI species group in the valid subgenus *Hearlea*. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. burchi* is now placed.

Distribution. *Simulium burchi* has only been recorded from Guatemala and Mexico (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; DALMAT, 1955).

Biology and Medical Importance. DALMAT (1955) stated that he collected the immature stages of *S. burchi* in only two places in Guatemala (Aldea Yulvá, Cuilco and Nebaj, Quiché) between 7250 to 8800 feet. The pupae were taken from streams of approximately 1.5 m wide, varying from 3 to 8 inches in depth and with a pH of 6.4, always in cascades attached to stones, twigs and leaves. In Cuilco, pupal exuviae of *S. burchi* were found in rivers of sandy or hard clay riverbeds. COSCARÓN & COSCARÓN-ARIAS (2007) stated that *S. burchi* occurs in medium-sized torrential creeks on leaves, stones and twigs. Nothing is known on the female feeding behaviour.

2.5.1.3. ***Simulium (Trichodagmia) canadense*** **HEARLE** (Figs. 15, 31, 42, 43, 47, 61, 70, 75, 85, 98, 179, 231, 289-292, 422, 528, 586, 646, 708-711, 831, 832, 893, 894, 954, 955, 1013, 1079, 1124, 1176, 1231)

This is a common species distributed from British Columbia to southern Mexico, east into the Rocky Mountains and Black Hills of South Dakota, with an unusual record from central Florida. The description here provided has been based upon examination of type material, identified material housed at BMNH, CNC, CUAC, INDRE, MLP, MZUCR, and NMNH, the original description of HEARLE (1932) and TWINN (1938), and the revisions of ADLER *et al.* (2004), COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium virgatum canadensis HEARLE, 1932: 14. HOLOTYPE male, CANADA: British Columbia, Kamloops, Lanes Creek; 6.viii.1931, (*T.R.Molliet & R.T.Turner*) (CNC, type 3454) [Examined.]

Simulium (Simulium) fraternum TWINN, 1938: 53. HOLOTYPE male, USA: Utah, Davis Co., Farmington; 4.ix.1934, (*G.F.Knowlton & C.F.Smith*) (CNC, type 4452) [Examined.] [Synonymy by STAINS & KNOWLTON, 1943: 276.]

FEMALE. General body colour black. Body length (specimens pinned) 2.2-2.9 mm (mean = 2.5 mm, s.d. = 0.24, n = 9), wing length 2.3-3.1 mm (mean = 2.7 mm, s.d. = 0.26, n = 9), wing width 1.1-1.4 mm (mean = 1.4 mm, s.d. = 0.18, n = 9).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 179). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 231).

Thorax: scutum black evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent dark setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with 1+1 median, pear-shaped and 1+1 sublateral, wide, silver pruinose cunae extending from anterior to posterior margins; 1+1 black, subtriangular cunae on anterior third of scutum joining and 1+1 submedian black bands that extend length of scutum; humeri silver pruinose; lateral and posterior margins black (Figs. 289, 291). With posterior illumination, thorax black with 1+1 subtriangular, silver pruinose cunae on anterior third of scutum; humeri, weakly pruinose; lateral and posterior margins black (Figs. 290-292). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along basally, and bare apically. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius bare; basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 422. Fore leg with coxa, trochanter, apical third of femur, apical two thirds of tibia, and tarsal segments I-IV dark brown; remainder of leg pale brown. Mid and hind legs with coxae, trochanters, and apical third of femora, tibiae, tarsal segments I, and tarsal segments III, IV pale brown; basal three thirds of femora and basal two thirds of tibiae pale brown; basal half of tarsal segment sI, whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-V velvet black, VI-IX shiny black with silver pruinosity in posterior margin of segments I-II. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses half length of eighth sternite at mid point, almost square, membranous basally and sclerotised towards apex, densely covered with microtrichiae (Figs. 31, 528). Cerci hemispherical, covered with brown setae; paraproct small, subrectangular, nearly same length as cercus and sclerotised with small tail apically; paraproct densely covered with brown hairs (Figs. 15, 586). Genital fork stout and sclerotised; termination of lateral arms with anterior margin straights and well developed; anterior processes well developed and blunt apically; posterior processes developed (Fig. 646). Spermatheca globular, without external sculpturing and apparently without internal spicules; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens pinned) 2.6-3.2 mm (mean = 2.9 mm, s.d. = 0.21, n = 9), wing length 1.5-2.8 mm (mean = 2.3 mm, s.d. = 0.44, n = 9), wing width 0.9-1.5 mm (mean = 1.2 mm; s.d.= 0.23, n = 9).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered with irregular white recumbent hairs; posterior margin covered with recumbent setae interspersed with black hairs. Scutal pattern varies slightly with light incidence: with light source anterior, thorax black with 1+1 subrectangular silver pruinose cunae extending from antero-lateral margins to central region of thorax; 1+1submedian black cunae on anterior thirds of scutum; humeri silver pruinose; lateral and posterior margins black (Figs. 708, 710). With posterior illumination, thorax black with 1+1 silver small comma shaped cunae on anterior thirds of scutum;

humeri, lateral and posterior margins black (Figs. 709, 711). Scutellum black with golden, recumbent hairs and long, erect, dark brown setae on posterior margin. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Subcosta bare in the two specimens examined. Leg coloration as in female though slightly darker brown.

Abdomen: tergites black with silver pruinosities on antero-lateral margin of tergites II, VI, VII [best seen if specimen is tilted dorso-laterally], basal fringe with long, brown hairs. Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle elongated, 2.5 times longer than gonocoxite, with prominent basal process, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Figs. 42-43, 831-832). Ventral plate sclerotised, subrectangular, with carina on central region and without shoulders; anterior region concave with prominent incision centrally; basal arms developed and subparallel (Figs. 47, 893, 894). Median sclerite long, about three times longer than wide at widest point, with small incision apically (Figs. 893, 894). Paramere with well developed and sclerotised basal process and numerous long spines along whole length; internal membrane covered with numerous fine spinules (Figs. 61, 954, 955).

PUPA. Cocoon length dorsally 3.4-3.7 mm (mean = 3.5 mm, s.d = 0.09, n = 15), ventrally 3.4-4.1 mm (mean= 3.7 mm, s.d. = 0.18, n = 15); pupa length 3.1-4 mm (mean = 3.6 mm, s.d. = 0.28, n = 15); gill length 2.2-3.0 mm (mean = 2.6 mm, s.d. = 0.18, n = 15).

Cocoon: shoe-shaped as in Fig. 66, brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown with three swollen filaments downwardly directed filaments in vertical plane (Fig. 75, 1013). Gill with main trunk short giving rise to three distinctly swollen primary branches. In lateral view, anterior branch short and directed upward, towards central region of thorax; median and ventral primary branches relatively long and directed towards ventral region of pupa; median branch more prominently swollen than remaining branches (Figs. 75, 1013). Filaments stout, rounded distally, without spicules on surface with numerous ridges and crevice, edges weakly crenate; median primary filament longer than remaining filaments.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 3-4 platelets in two groups laterally in frontal region; tubercles rounded and well distributed over entire surface.

Thorax: with four spiniform trichomes near margin of dorsal cleft, one spiniform trichome on central region and one spiniform trichome on posterior region, 3+3 long, simple, trichomes near spiniform trichomes on dorsal cleft, and 2+2 simple trichomes on ventral margin of thorax; tubercles mostly rounded and densely distributed over entire surface.

Abdomen: abdominal tergite I with 1+1 simple, short setae laterally and 1+1 submedian groups of rounded tubercles on central region; tergite II with 3+3 or 4+4 submedian spiniform setae in longitudinal row mesally; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to outermost hooks, and 1+1 small, simple setae on lateral margins; tergites V-VII without visible setae; tergite IX weakly sclerotised without terminal spines. Spine combs on antero-lateral regions of tergites I-IX. Sternite III without setae; sternite IV with 1+1 sublateral simple hooks; sternite V with 2+2 close bifid hooks, 1+1 simple setae between and anterior to hooks; sternites VI, VII with well separated simple or bifid hooks; sternites VIII, IX without setae; sternite IX weakly sclerotised. Spine combs on anterior margins of sternites IV-IX (Fig. 85).

LARVA (Final instar). Body length 6.3-7.4 mm (mean = 6.7 mm, s.d. = 0.39, n = 4), length of head capsule 0.6-0.8 mm (mean = 0.7 mm, s.d. = 0.09, n = 4); width of head capsule 0.5-0.7 mm (mean = 0.6 mm, s.d. = 0.03, n = 4). Body colour dark grey dorso-laterally, whitish ventrally (specimens preserved in ethanol). General body form as in Fig. 1079

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule weakly wrinkled. Head pattern positive. Cervical sclerites elongated joined to postgena. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Fig. 1124). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 small, sublateral, teeth; 1+1 lateral teeth longer than sublateral teeth; approximately 5+5 lateral serrations; 1+1 lines of six hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1176). Sub-esophageal ganglion unpigmented. Antenna longer than labral fan stalk, segment I, basal and apical third of segment II, and segment III dark brown, central region of segment II whitish; length of antennal segments I-III excluding the sensillum 0.2:0.08-0.1:0.09-0.1 mm (n = 6). Mandible with two apical teeth, first one longer than second; mandibular comb with approximately 10 teeth, first three teeth more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1231). Lateral mandibular process absent. Maxillary palps heavily pigmented, one and a half times as long as wide at base. Labral fan with 30-43 rays (n = 6) each with fine, single line of spines in a row.

Thorax: pale grey dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 18-34 processes (n = 6). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with three filaments, with median filament more prominent than other filaments.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 106-128 rows of 19-23 simple hooks (n= 6). Rectal gills with three branches with approximately 10 finger-like lobes, anterior more prominent than remainder (in dorso-lateral view) (n = 6).

Taxonomic Discussion. *Simulium canadense* was described by HEARLE (1932) as *Simulium virgatum var. canadensis* based on a male holotype, one female (allotype), and 70 reared females and 40 males collected in British Columbia, USA. I have examined the male holotype (no. 3454), which is deposited at the CNC. The specimen is pinned and it is in good condition (see **Material Examined**). Digital images of its thorax and abdomen coloration pattern have been taken and they are now stored at the Simuliidae Digital Images Archives, BMNH. In addition, I have also examined the female allotype and numerous paratypes housed at CNC, plus identified specimens deposited in CNC, NMNH and BMNH Simuliidae collections (**Material Examined)**.

The taxonomy of *S. canadense* has been fully reviewed in the recent book of the *The Blackflies (Simuliidae) of North America* by ADLER *et al.* (2004). In this work, the authors discussed the distribution and bionomics of this species and detailed the most relevant literature dealing with its taxonomy. The same authors accepted the synonymy of *S. fraternum* with *S. canadense* of other authorities without explanation and I have the following comments to make. *Simulium fraternum* was described by TWINN (1938) based on males collected from Utah, Davies Co., USA. The pinned male holotype and its terminalia are deposited at the CNC, and they are in good condition (**Material Examined**). *Simulium fraternum* was first synonymised with *S. canadense* by STAINS & KNOWLTON (1943) without further explanation. VARGAS accepted this synonymy in 1943a, and recorded *S. canadense* in Mexico for the first time. VARGAS (1945) also discussed this synonymy and some differences in the male genitalia between *S. canadense*, *S. fraternum*, and the newly described species, *S. ayrozai*. However, this synonymy was not listed in the catalogues of SMART (1945), COSCARÓN (1987), COSCARÓN & COSCARÓN-ARIAS (2007), COSCARÓN *et al.* (2008) nor in the revision of the subgenus *Hearlea* by COSCARÓN *et al.* (2004). I have studied the original description of *S. fraternum*. Its general morphology, especially that of the thoracic pattern (Figs. 710-711) and genitalia (Figs. 832, 894, 955), fall within the morphological variation found in *S. canadense*. The general morphology of the ventral plate in the holotype of *S. fraternum* (Fig. 955) is different from that of *S. canadense* (Fig. 954), but this is due to the position of the ventral plate on the slide. Examination of the slide in different angles showed the presence of the concavity in the central region of the ventral plate, which is typical of *S. canadense*. In the absence of the pupal exuviae of *S. fraternum*, I therefore agree with STAINS & KNOWLTON'S (1943) synonymy for taxonomic stability.

The female of *S. canadense* is externally similar to other species in the CANADENSE species group of *Hemicnetha* (*sensu* ADLER *et al.*, 2004) in the silver pruinose thorax with 1+1 black bands extending from the anterior to posterior margins [light source anterior] (Figs. 289, 291). The males are also similar to other species of the CANADENSE group in the thorax with 1+1 subtriangular silver pruinose cunae on the anterior third of scutum [light source anterior] (Figs. 708, 710). The best character to recognise *S. canadense* is the configuration of the pupal gill filaments, which have three distinctly swollen filaments, the median being the most prominent and largely more swollen than the remaining filaments (Figs. 75, 1013). No other species of the CANADENSE species group has a similar gill configuration.

The mature larva of *S. canadense* may only be readily distinguished from other species by the examination of the dissected gill histoblast of larvae collected in the same locality from which link-reared adults were obtained. The gill histoblast of *S. canadense* is distinctively large with three swollen filaments.

Descriptions of adults, pupae and larvae of *S. canadense* may be found in COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007) [see also ADLER *et al.*, 2004 for key papers on descriptions of life stages].

The cytology of the *S. canadense* was briefly reviewed by GIBSON (in ROFTHELS, 1979) and ADLER *et al.* (2004). The latter papers also records the work of BROCKHOUSE & TANGUAY (1996) on the molecular systematics of the latter species based on the salivary gland proteins. ADLER *et al.* (2004) [citing GIBSON in ROFTHELS, 1979] stated that three fixed inversions separate the chromosomes of *S. canadense* from the standard banding sequence of *S. pictipes*. The analysis of ADLER *et al.* (2004) revealed that the inversion differences are in the chromosome arms IL and IIL, and that the nuclear organizer is located near the base of the IS arm. The latter authors also suggested that *S. canadense* might be a species complex given its broad distribution range.

Simulium canadense was placed in the subgenus *Hearlea* by VARGAS *et al.* (1959) and this has been followed in the World Inventory of Blackflies (CROSSKEY & HOWARD, 1997, 2004). However, ADLER *et al.* (2004) considered *Hearlea* as a synonym of *Hemicnetha*, and this has been followed in ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic action was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the JUAREZI species group of the valid subgenus *Hearlea*. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. canadense* is now placed.

Distribution. *Simulium canadense* is distributed from British Columbia, Canada, east to the Rocky Mountains and Black Hills of South Dakota (USA), and southern Mexico, with an unusual record from central Florida (Lake Tohopekaliga, Rt. 525A, Kissimmee) (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007).

Biology and medical importance. The biology, economic importance, hosts and cytology of *S. canadense* has been reviewed in ADLER *et al.* (2004). *Simulium canadense* is generally multivoltine, but in some streams it passes through one generation annually. The immature stages inhabit rocky streams several meters wide. Larvae can be found in water with temperature ranging from 0°C to more than 20°C. Larvae are affected by the turbulence of the water. In certain rivers larvae can be found attached to the trailing vegetation, but in other flows they are found on rocks. The females attacked unspecified "larger domestic animals"; few blood-fed females have been collected near blue grouse (*Dendragapus obscurus* SIBLEY AND MONROE). ADLER *et al.* (2004) stated that the larvae of *S. canadense* have been collected infected with mermithids nematodes of the genus *Gastronomies*, the microsporidian *Amblyospora fibrata* STRICKLAND, and the chytrid fungus *Coelomycidium simulii* DEBAIS. Hydropsychid and Ryachoohilid caddis flies have been reported as natural predators of *S. canadense* larvae.

2.5.1.4. *Simulium (Trichodagmia) capricorne* DE LEÓN (Figs. 17, 180, 232, 293, 294, 423, 529, 587, 647, 712, 713, 833, 895, 956, 1014, 1015 1080, 1125, 1177, 1232)

A relatively well-known species first described from Guatemala by DE LEÓN (1945). The description here provided has been derived from the original description, examination of identified material at the BMNH, INDRE, NMNH and MLP, and the reviews of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium capricornis DE LEÓN, 1945: 71. SYNTYPES pupal exuviae, GUATEMALA: Totonicapán Department, a la entrada de Totonicapán; [Without date or collector's name.]; Acatenango Department, Rio Samalá, km 169; [Without date or collector's name.] [SYNTYPES said to be in the collection of J. ROMEO DE LEÓN, but location of this collection unknown.]

Simulium (*Simulium*) *deleoni* VARGAS, 1945: 72. HOLOTYPE male (reared), MEXICO: Federal District, Desierto de los Leones; 5.iii.1944, (*A.Díaz Nájera & A.Martínez Palacios*) (INDRE, no. 3619) [Examined.] [Synonymy by COSCARÓN *et al.* 2004: 14.]

FEMALE. General body colour black. Body length (specimens pinned) 2.3-3.0 mm (mean = 2.5 mm, s.d. = 0.24, n = 6), wing length 1.5-3.0 mm (mean = 2.3 mm, s.d. = 0.44, n = 8), wing width 1.0-1.6 mm (mean = 1.3 mm, s.d. = 0.20, n = 8).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 180). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae, with small teeth visible on lateral margins of cornuae [only at higher magnification] (Fig. 232).

Thorax: scutum black with evenly arranged, recumbent, golden hairs interspersed with recumbent black hairs; posterior margin with evenly arranged, recumbent, golden hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax largely pruinose with 1+1 straight, median and 1+1 wide, sublateral vittae extending from anterior third of scutum to near posterior margin, anterior margins of median and sublateral vittae joining at anterior third of scutum; humeri and lateral margins with weak silver reflection; posterior margin black (Fig. 293). With posterior illumination, thorax black with 1+1 submedian silver round spots on anterior third [sometimes small tails reaching mid point of scutum can be seen in specimens devoid of setae]; humeri and lateral margins weakly pruinose; posterior margin black (Fig. 294). Scutellum black with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae on basal fourth-fifths. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius with few hairs. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 423. Fore leg with area on femur and tibia pale, remainder of legs dark brown. Mid and hind legs with coxae, trochanters, apex of femora, base and apex of tibiae, apical half of tarsal segment I, and tarsal segments II-IV dark brown; remainder of femora and tibiae pale yellow, and remainder of tarsal segment I white. Hind leg with curved claw bearting a basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites black, with pruinose reflections on posterior margin of tergite II. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with 12-13, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular, well separated, with internal margin weakly curved and sclerotised; gonapophyses densely covered with microtrichiae (Fig. 529). Cerci subhemispherical, covered with brown setae; paraproct subrectangular, extending beyond cercus; basal lobe of paraproct with small prominence, and ventral extension highly setose apically (Figs. 17, 587). Genital fork stout and sclerotised with stem weakly expanded; termination of lateral arms with anterior margin straight; anterior and internal posterior processes well developed and blunt apically (Fig. 647). Spermatheca globular, without external sculpturing and small groups of setae on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens pinned) 2.5-3.0 mm (mean = 2.7 mm, s.d. = 0.18, n = 5), wing length 1.9-2.5 mm (mean = 2.2 mm, s.d. = 0.16, n = 8), wing width 1.0-1.7 mm (mean = 1.2 mm; s.d. = 0.23, n = 8).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum velvet black covered with recumbent golden setae interspersed with recumbent black hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with 1+1 submedian pollinose areas on anterior third of scutum (Fig. 712). With posterior illumination, thorax black (Fig. 713). Humeri, lateral and posterior margins black. Scutellum black with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on anterolateral margins of tergite II-V [best seen in some specimens when tilted and viewed laterally]. Genitalia black; sternal plates developed. Gonocoxite subquadrangular, with produced anterolateral margins; gonostyle elongate, three times longer than gonocoxite, with margins weakly sinuous, gonostyle with basal flap-like process and terminating in single stout spine; gonocoxite and gonostyle covered with long setae (Fig. 833). Ventral plate sclerotised, subrectangular, with anterior margin weakly concave and fairly produced centrally; lateral shoulders undeveloped; basal arms sclerotised and curved inwards; main body of ventral plate covered with small hairs [in certain angles a central carina can be seen extending near posterior region] (Fig. 895). Median sclerite about four times longer than wide at widest point, with small apical incision [it appears curl up in the specimen I have examined] (Fig. 895). Paramere with well developed and sclerotised basal process and numerous long spines centrally, central membrane covered with small spinules (Fig. 956).

PUPA. Cocoon length dorsally 3.2-4.0 mm (mean = 3.5 mm, s.d. = 0.27, n = 8), ventrally 3.4-3.8 mm (mean = 3.6 mm, s.d. = 0.33, n = 8); pupa length 2.8-4.6 mm (mean = 3.5 mm, s.d. = 0.81, n = 8); gill length 2.8-3.4 mm (mean = 3.0 mm, s.d. = 0.23, n = 9).

Cocoon: often slipper-shaped as in Fig. 65 [though I have examined few specimens with nearly shoe-shaped cocoon], dark brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with two swollen filaments forwardly directed filaments in vertical plane (Figs. 1014, 1015). Gill configuration with main trunk short giving rise to two primary branches, one dorsal and one ventral arranged in close C-shaped form; dorsal branch prominently swollen, with pseudoannulations and basal prominence pointing towards anterior region of cocoon; ventral branch encircling lateral margin of frontoclypeus and prominently curved inward on apical third. Filaments stout, pointed distally, without spicules on surface and with ridges and crevices, edges crenate; dorsal branch longer and stouter than ventral branch.

Head (*frontoclypeus*): with 2+2 long, simple frontal and 1+1 spiniform, long facial trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-4 platelets in two groups laterally in frontal region; tubercles rounded only visible in facial region and lateral margins of frontal region.

Thorax: with 5+5 spiniform trichomes on margin dorsal cleft; thorax with rounded tubercles most densely distributed on surface of posterior region.

Abdomen: abdominal tergite I with 1+1 long, sublateral long simple setae; tergite II with 4+4 long spiniform setae in row, 1+1 small simple setae anterior to outermost spiniform setae; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 1+1 small simple setae anterior to outermost hooks, tergites V-VIII without visible setae on the two specimens examined; sternite IX weakly sclerotised, without terminal spines. Spine combs distribution on anterior margins of tergites VI, VII some developed resembling teeth. Sternites III, IV without visible setae; sternite V with 2+2 close bifid hooks; sternites VI, VII with 2+2 well separated simple or bifid hooks; sternites VIII, IX without visible setae; sternite IX weakly sclerotised. Spine combs on anterior margins of sternites III-VII.

LARVA (Final instar). Body length 7.0-7.3 mm (mean = 7.1 mm, s.d. = 0.17, n = 3), length of head capsule 0.6 mm (n = 5), width of head capsule 0.6 mm (n = 5). Body colour dark grey to tan without dark patches on ventro-lateral regions of segments VI, VII (preservation of specimens not stated in the original description, but probably in ethanol). General body form as in Fig. 1080.

Head: mainly dark brown, anterior region of cephalic apotome paler. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Postgenal cleft deep, bell-shaped, triangular apically; postgenal bridge 1.5 times longer than hypostomium (Fig. 1125). Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with pair adjacent to lateral teeth longer than remaining pairs; 1+1 lateral teeth; 6+6 small, lateral serrations;

1+1 lines of approximately six to eight hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1177). Antenna longer than labral fan stalk, antennal segments weakly pigmented; length of antennal segments I-III excluding the sensillum 0.01:0.07:0.1 mm (n = 1). Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately eight teeth, first three more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1232). Lateral mandibular process present. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 44-45 rays with fine, single line of spines in row interspersed with finer spinules.

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of 39-44 sclerotised processes.

Abdomen: usually grey dorsally. Ventral papillae absent. Cuticle lacking setae except few scale-like setae around anal sclerite. Anal sclerite well sclerotised with anterior arms enlarged, and posterior arms extending one third of diameter of posterior circlet anteriorly; area between arms sclerotised. Posterior circlet with 115-125 rows of sclerotised processes. Rectal gills with three branches, each branch with one larger finger-like lobule and three shorter, giving a total of 12 finger-like lobules.

Taxonomic Discussion. *Simulium capricorne* was described DE LEÓN in 1945 from an undisclosed number of pupae exuviae [= crisálida] collected in Guatemala. Because DE LEÓN did not select a holotype, these pupal exuviae are syntypes (ICZN, 1999). The syntypes are thought to be housed at the collection of J. ROMEO DE LEÓN, but the location of this collection is unknown. The taxonomy of *S. capricone* was later reviewed by DALMAT (1945), who also described the larva for the first time. Other taxonomic revisions dealing with this species are DÍAZ NÁJERA & VULCANO (1962a), COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), and VARGAS & DÍAZ NÁJERA (1957b).

In the recent revision of the subgenus *Hearlea*, COSCARÓN *et al.* (2004) synonymised *S. deleoni* with *S. capricorne* based on the similar configuration of their pupal gill filaments and I have the following comments to make. *Simulium deleoni* was described by VARGAS (1945) based on a reared male holotype, a female allotype, and 30 pupal exuviae collected in Mexico. I have examined the male holotype, which is housed in INDRE. Part of the adult and its pupal exuviae are preserved in alcohol, while three legs, one wing and its genitalia are mounted on a slide (see **Material Examined**). In addition, I have examined the female allotype, which is mounted on a slide, and a male paratype in alcohol. One leg, one wing and the genitalia of a female paratype are mounted on a slide (**Material Examined**). The general morphology of the male gonostyle and ventral plate of *S. deleoni*, and the cocoon shape and configuration of the gill filaments (Fig. 1015) fall within the variation found in *S. capricorne*. Therefore, I agree with the synonymy of COSCARÓN *et al.* (2004).The female and male of *S. capricorne* are externally similar to that of *S. ethelae* based on the scutal coloration pattern (Figs. 293, 294, 303-305, 712, 713, 722-725). Both species cannot be distinguished from other species in the CANADENSE species group without examination of the pupal gill filaments.

Simulium capricorne is best recognized by the pupal gill with two filaments, which are prominently swollen and arranged in a close, C-shape (Fig. 1014). In this respect, *S. capricorne* is similar to *S. ethelae*. However in the latter species, the dorsal and ventral branches are arranged in an open C-shape, while the dorsal branch is distinctly more slender (Fig. 1021). Another similar species is *S. microbranchium*, but the dorsal filament is relatively much shorter bending at a 45 degree angle at mid length (Fig. 1027).

Based on the key of DÍAZ NÁJERA & VULCANO (1962a), the larva of *S. capricorne* falls within the species group in which the abdomen does not have accessory sclerotised plates and the anterior margin of the hypostomium is straight. Within this group *S. capricorne* (Fig. 1177) is similar to *S. delatorrei, S. ethelae* and *S. juarezi* (Figs. 1128, 1130, 1186) because the hypostomium has nine teeth evenly distributed on the anterior margin. *Simulium capricorne* can be further distinguished from *S. delatorrei* by the labral fans with 44-45 rays (following COSCARÓN *et al.*, 2004). *Simulium ethelae* is keyed out by the shorter and less triangular postgenal cleft (Figs. 1183). Nonetheless, the best character to identify *S. capricorne* is the configuration of the dissected gill histoblast in mature larvae.

Distribution. *Simulium capricorne* is only known from Guatemala and Mexico (ADLER & CROSSKY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. Little is known on the biology of *S. capricorne*. DÍAZ NÁJERA & VULCANO (1962a) stated that it inhabits areas located at high altitude in streams with low water temperature.

2.5.1.5. *Simulium* (*Trichodagmia*) *carolinae* DE LEÓN (Figs. 181, 233, 295, 296, 424, 530, 588, 648, 714, 715, 834, 896, 957, 1016, 1081, 1126, 1178, 1233, 1283)

This is a well known species recorded from Guatemala and Mexico. The description here provided has been derived from the original description of DE LEÓN (1945), examination of identified material at the BMNH, NMNH and MLP, and the reviews of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium carolinae DE LEÓN, 1945: 73. SYNTYPES pupae and larvae, GUATEMALA: Quezaltenango Department, Salto de Zunil, waterfall near to Zunil, 1900m; [Without date or collector's name.] [Syntypes said to be deposited at the J. ROMEO DE LEÓNS' collection, but location of this collection unknown.]

FEMALE. General body colour black. Body length (specimens pinned) 2.1-2.4 mm (mean = 2.2 mm, s.d. = 0.13, n = 6), wing length 2.1-2.7 mm (mean = 2.3 mm, s.d. = 0.23, n = 6), wing width 0.9-1.4 mm (mean = 1.1 mm, s.d. = 0.17, n = 6).

Head: dichoptic covered with dark red eyes and nudiocular area developed (Fig. 181). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 233).

Thorax: scutum black evenly arranged, recumbent, yellowish hairs interspersed with black fine, semi-recumbent black setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax with black background, with 1+1 silver pruinose median straight vittae extending from anterior to posterior margins, and 1+1 large, submedian subtriangular vittae, largely pollinose that join the median vittae at mid point of scutum; humeri weakly pruinose; lateral and posterior margins black (Fig. 295). With posterior illumination, thorax black with 1+1 subtriangular, silver pruinose cunae on anterior third of scutum [faint brownish vittae can be seen on posterior margin with certain lights]; humeri, weakly pruinose; lateral and posterior margins black. Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity (Fig. 296). Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta withsingle setae in central area or with line of setae from base to one third before apex in the few specimens examined. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 424. Fore leg with coxa, trochanter, femur, apical third of tibia, and tarsal segments I-IV dark brown; remainder of tibia yellowish. Mid and hind legs with coxae, trochanters, femora, apical third of tibiae, apical half of tarsal segment I, and tarsal segments II-IV dark brown; remaider of tibiae yellowish; basal half of tarsal segment I pale yellow. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-V velvet black, VI-IX shiny black with silver pruinosity in posterior margin of segments I, II. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin, and same length as eighth sternite at mid point; gonapophyses nearly half length of eighth sternite at mid point, subtriangular, weakly sclerotised but membranous apically, densely covered with microtrichiae (Fig. 530). Cerci subrectangular, covered with brown setae; paraproct subrectangular, extending beyond cercus, weakly sclerotised without a tail apically; paraproct densely covered with brown hairs (Fig. 588). Genital fork stout and sclerotised with stem expanded apically; termination of lateral arms with anterior margin straight and well developed;

anterior and internal posterior processes (Fig. 648). Spermatheca subglobular, apparently without external sculpturing and internal spicules not visible; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens pinned) 2.3-2.9 mm (mean = 2.6 mm, s.d. = 0.23, n = 5), wing length 2.2-2.8 mm (mean = 2.4 mm, s.d. = 0.23, n = 5), wing width 1.0-1.3 (mean = 1.2 mm, s.d. = 0.14, n = 5).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black, covered with irregular yellow recumbent hairs interspersed with black hairs; posterior margin covered with recumbent setae interspersed with black erect hairs. Scutal pattern varies slightly with light incidence: with light source anterior, thorax black with 1+1 subrectangular silver pruinose cunae on anterior third of scutum; humeri weakly silver pruinose; lateral and posterior margins black (Fig. 714). With posterior illumination, thorax black; humeri, lateral and posterior margins black (Fig. 715). Scutellum black with golden, recumbent hairs and long, erect, dark brown setae on posterior margin. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Sc bare in the specimens I have examined. Leg coloration pattern similar to that of female though darker brown.

Abdomen: tergites black with silver pruinosities on antero-lateral margin of tergites II, III, V-VII [best seen if specimen is tilted dorso-laterally], basal fringe with long, brown hairs. Genitalia black; sternal plates developed. Gonocoxite subquadrangular with antero-lateral margin produced; gonostyle elongated, three times longer than gonocoxite, with ridge basally and terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 834). Ventral plate sclerotised, subrectangular, with anterior and posterior margins slightly straight; body of ventral plate with central process triangular and pointed apically, all covered by long hairs; lateral shoulders weakly developed, basal arms well developed and curved inwards (Fig. 896). Median sclerite about three times as long as width at mid point, without apical incisure (Fig. 896) . Paramere with well developed and sclerotised basal process and numerous long spines along whole length (Fig. 957).

PUPA. [DALMAT (1955) gave measurements as follows: Cocoon length (basally) 3.00 mm. Other measurements and numbers of specimens examined were not given in this latter publication nor in the original description of *S. carolinae*].

Cocoon: slipper-shaped as in Fig. 65, brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown with nine, fairly enlarged filaments forwardly directed filaments in vertical plane (Fig. 1016). Gill configuration similar to that of *S. larvispinosum*; main trunk short giving rise to three distinctly primary branches: one dorsal, one median and one ventral. Dorsal primary branch prominently enlarged with two smaller filaments basally, which are sclerotised apically; median branch with five smaller secondary filaments all sclerotised apically; ventral branch single, distinctly curved (Fig. 1016). Filaments stout, pointed distally, without spicules or ridges on surface, edges fairly straight; median primary filament longer than remainder filaments.

Head (frontoclypeus): [not described in DALMAT, 1955].

Thorax: with six spiniform trichomes near margin of dorsal cleft; tubercles densely distributed over entire surface [tubercles shaped not described in DALMAT, 1955].

Abdomen: [chaetotaxy not described because of lack of material; see DALMAT (1955) for details].

LARVA (Final instar). [Body length 7.8 mm following DALMAT, 1955. Other measurements and numbers of specimens examined not given in the original description nor the latter publication]. Body colour grey to brown dorso-laterally, with irregular dark patches on ventro-lateral regions of segments VI, VII [preservation of specimens not stated, probably in spirit].

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule weakly wrinkled. Head pattern positive. Postgenal bridge deep, bell-shaped, subtriangular apically (Fig. 1081). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth evenly distributed along anterior margin; all teeth nearly same length and reduced; 1+1 lines of eight hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1126). Antennal segments pigmented; length of antennal segments I-III excluding the sensillum 0.1:0.04:0.1 mm (n = 1). Mandible with two apical teeth nearly same length; mandibular comb with approximately 12 teeth, first three teeth more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1178). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with more 44-45 rays with fine, single line of spines in row.

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of 45-46 sclerotised processes.

Abdomen: usually grey dorsally, without bands. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised, with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms; posterior arm completely encircling posterior circlet; at junction of anterior and posterior arms 2+2 dorso-lateral triangular sclerotised accessory plates (Fig. 1283). Posterior circlet with 196-204 rows of sclerotised processes. Rectal gills with three branches, each of outer branches with one broad lobe and eight slender lobes, while the median has 11 lobes giving a total of 29 finger-like lobes.

Taxonomic Discussion. *Simulium carolinae* was described by DE LEÓN (1945) based on an unknown number of larvae and pupae collected in Quezaltenango Department, Guatemala. As DE LEÓN did not clearly state which of the two life stages he designated as a holotype, these specimens are syntypes (ICZN, 1999). The syntype series of *S. carolinae* are said to be deposited in the J. ROMEO LEÓN collection, but the location of this collection is unknown.

The adults' thoracic pattern of *S. carolinae* falls without the variation found in species of the CANADENSE species group (Figs. 295, 296, 714, 715) from which they cannot be easily identified in the absence of link-reared adults.

The best character to identify *S. carolinae* is the configuration of the pupal gill filaments (see Fig. 1016) and the morphology of the larva, especially the shape of the sclerotised accessory plates near the anal sclerite (Fig. 1283). The gill of *S. carolinae* is similar to that of *S. gorirossiae*, *S. johnsoni* and *S. larvispinosum* in the dorsal primary branch prominently elongated and more swollen than the remaider of filaments (Figs. 77, 1022, 1023, 1025). However, the number and distribution of the basal secondary filaments may be used to separate these species (Figs. 1016).

The larva of *S. carolinae* is best recognized by the presence of 2+2 dorso-lateral short, prominent sclerotised processess on the posterior arms of the anal sclerite (Fig. 1283).

Descriptions of all life stages of *S. carolinae* may be found in COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955), DE LEÓN (1945) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium carolinae was placed in the subgenus *Hearlea* by DALMAT (1955). This has been accepted by COSCARÓN (1987) and CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic arrangement has not been recognized in COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the CAROLINAE species group of their valid subgenus *Hearlea*. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. carolinae* is now placed.

Distribution. *Simulium carolinae* has only been recorded from Guatemala and Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. Little is known on the biology of female and immature stages of *S. carolinae*. DE LEÓN (1945) recorded pupae at an altitude 1,600m.

2.5.1.6. *Simulium (Trichodagmia) contrerense* DÍAZ NÁJERA & VULCANO (Figs. 76, 182, 234, 425, 531, 589, 649, 835, 836, 897, 958, 1017, 1179, 1234)

A zoophilic species only known from Mexico. The description here provided has been based upon examination of type material and identified specimens housed at INDRE, the original description of DÍAZ NÁJERA & VULCANO (1962a) and the revisions of COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium (Hearlea) contrerense DÍAZ NÁJERA & VULCANO, 1962a: 94. HOLOTYPE male (reared), MEXICO: Federal District, Los Dínamos, Contreras; 20.v.1962, (*I.Córdova Ruiz*) (INDRE, no. 6519) [Examined.]

FEMALE. General body colour black. [Measurements and number of specimens examined not given in the original description.]

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 182). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts and maxillary palps dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed and sclerotised cornuae, without teeth and prominently concave on central trough (Fig. 234).

Thorax: scutum dark brown covered with evenly arranged, recumbent, golden setae. [Scutal pattern poorly known and it has not been figured because of lack of material.] Based on the description of DÍAZ NÁJERA & VULCANO (1962a) and apparently with the light source anterior to specimen, scutum with 1+1 silver pruinose spots occupying anterior third of scutum and separated by black space, 1+1 silver bands emerging from mid scutum not touching anterior silver spots; lateral margins silver pruinose. The pattern has not been described with the light source posterior. Scutellum black with black bristles. Postnotum black with silver pruinosity. Pleura dark brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length or bare. Radius with numerous setae intermixed with distinct spines, basal section of radius apparently bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 425. Fore leg with coxa, trochanter, basal two thirds of femur dark brown; apical third of femur, basal and apical third of tibia, and tarsal segments dark brown to black; remainder of tibia whitish. Mid and hind leg with same coloration pattern as fore leg, except that basal one to two thirds of tarsal segment I whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown, with central region of each segment prominently black. Tergal plates developed. Sternites yellowish [and probably the genitalia]. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses one and a half times length of eighth sternite at mid point, almost square with curved internal margin, weakly sclerotised on internal margins, densely covered with microtrichiae (Fig. 531). Cercus subrectangular, covered with brown setae; paraproct 1.5 times longer than cercus, subrectangular, basal lobe of paraproct prominently pointed, ventral extension with small prominence apically; apical two thirds of paraproct sclerotised; paraproct covered with small brown setae and microtrichiae towards apex. (Fig. 589). Genital fork stout and sclerotised; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed, posterior processes weakly developed (Fig. 649). Spermatheca not examined.

MALE. General body colour black. [DÍAZ NÁJERA & VULCANO (1962a) gave measurements for the body length 6.0 mm for a specimen in ethanol. Other measurements and numbers of specimens examined not given in the original description.] [COSCARÓN & COSCARÓN-ARIAS, 2004 recorded the wing length as 5.0 mm. The authors did not give other measurements or the number of specimens examined].

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum velvet black covered with golden setae. Scutal pattern poorly known and it has not been figured because of lack of material. Based on the description of DÍAZ NÁJERA & VULCANO (1962a) and apparently with light source anterior, scutum strongly velvet black with silver pruinosity in the anterior and posterior third, and lateral margins. The pattern has not been described with the light source posterior. Humeri and lateral margins silver pruinose. Scutellum brown with golden, recumbent hairs and long, erect, black setae. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Sc haired. Leg coloration as in female.

Abdomen: Tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II. Genitalia black. Gonocoxite subquadrangular; gonostyle elongate with margin nearly straight, four times longer than gonocoxite and having distinct projection basally; gonocoxite with stout single apical spine; gonocoxite and gonostyle covered with long setae (Fig. 835-836). Ventral plate weakly sclerotised, subrectangular; ventral plate with prominent shoulders, either longer or smaller than dome-like median process [this depends on the correct positioning of the ventral plate on the slide]; posterior margin of ventral plate straight, basal arms subparallel, sclerotised apically (Fig. 897). Median sclerite as in Fig. 897. Paramere with well developed and sclerotised basal process and numerous long spines along whole length, central membrane covered with fine spinules (Fig. 958).

PUPA. [COSCARÓN & COSCARÓN-ARIAS, 2004 recorded the dorsal cocoon length as 6.0 mm. Other measurements and number of specimens examined were not given in the original description]; gill length 3.5 mm (n = 1).

Cocoon: shoe-shaped as Figs. 66 [not slipper-shaped as originally described] brown to black, composed of thick, coalesced fibres with no reinforced rim to anterior aperture, margin of aperture gradually elevated.

Gill: dark brown with three forwardly and ventrally directed filaments in vertical plane (Figs. 76, 1017). Gill with dorsal and median branches prominently swollen, dorsal rounded apically and median distinctly triangular and pointed apically; ventral branch finger-like, much smaller than other branches and directed to ventral region of pupa extending up to frontoclypeus. Filaments without spicules on surface, edges weakly sinuous.

Head (*frontoclypeus*): with 1+1 frontal and 1+1 facial spiniform, prominent trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and two laterally in frontal region, respectively; tubercles rounded only visible on lateral margin in frontal region.

Thorax: with 4+4 long, spiniform, and 2-3 small simple trichomes at base of gill; tubercles absent.

Abdomen: abdominal tergite I with 1+1 submedian simple setae on posterior margin and 1+1 submedian long simple setae on anterior margin, group of rounded tubercles on anterior margin centrally; tergite II with 3+3 submedian spiniform setae in longitudinal row, 2+2 simple, small setae anterior to outermost spiniform setae, and 3+3 small simple setae on lateral margins; tergites III and IV with 4+4 submedian simple hooks in longitudinal row, 2+2 simple small setae anterior and 1+1 small simple setae lateral to most lateral of hooks, respectively, and 3+3 small simple setae on lateral margins; tergite V with 2+2 submedian small setae and 3+3 small setae on lateral margins; tergite VI with 1+1 small median setae on posterior margin; tergite VII without setae; tergite VIII with 1+1 small simple setae on lateral margins; tergite IX weakly sclerotised, without terminal spines. Spine combs distribution on anterior margins of tergites V-IX. Sternite III with 2+2 small simple setae on lateral margins; sternite IV with 4+4 median small simple setae and 2+2 small simple setae on lateral margins; sternite V with 2+2 close submedian simple hooks, and 1+1 small simple setae anterior to innermost of simple hook, and 1+1 small simple setae at both sides of hooks; sternites VI, VII with 2+2 well separated simple or bifid hooks in row on posterior margins, 1+1 or 2+2 small simple setae anterior or between outermost hooks; sternites VIII, IX with no visible setae. Spine combs on anterior margin of sternites IV-IX.

LARVA (Last instar). [DÍAZ NÁJERA & VULCANO (1962a) recorded the body length as 12.6 mm. Other measurements and numbers of specimens examined were not given in the original description.] General coloration greyish yellow.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Head pattern positive. Postgenal cleft subtriangular. Hypostomium strongly pigmented on anterior margin, with approximately eight apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 or 2+2 reduced sublateral teeth; 1+1 lateral teeth sometimes same length as median tooth; 12+12 lateral serrations; 1+1 lines of 17-18 hypostomial setae parallel to lateral margins; 1+1 long and 1+1 small simple setae in posterior half of hypostomium (Fig. 1179). Length of antennal segments I-III excluding the sensillum 1.0:2.2:1.9 mm. Mandible with two apical teeth, first one longer than second; mandibular comb with approximately 12 teeth, first four more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1234). Lateral mandibular process absent. Cephalic fan with than 42 rays or more with fine, single line of spines in row.

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of sclerotised processes.

Abdomen: usually yellowish spotted with dark green. Ventral papillae absent. Cuticle lacking setae. Posterior circlet with 185 rows of simple hooks. Rectal gills with three branches, each with one larger bulb-like lobe and 22 small lobules; in total 60-66 lobes can be found.

Taxonomic Discussion. *Simulium contrerense* was described by DÍAZ NÁJERA & VULCANO (1962a) based on a reared male holotype, a reared female (as allotype), and 15 pupal exuviae and eight larvae (all as paratypes) collected from the Federal District, Mexico. The authors also examined two penultimate instar larvae collected from Nevado de Toluca, Mexico State in Mexico. I have examined the male holotype which is housed at INDRE. The holotype and its pupal exuviae are mounted on four slides, all with labels "INDRE 6519". The specimen is in relatively good condition, though three legs are missing (see **Material Examined**). I have also examined the female allotype (INDRE no. 6520), which is mounted on four slides. The allotype is in relatively good condition, though the spermatheca is missing from the slide. In addition, I have examined a slide only containing the genitalia of a male and a further slide containing a pharate female (all labelled as paratypes) also housed at INDRE Simuliidae collection (**Material Examined**).

The thoracic pattern of adult *S. contrerense* is poorly known and they might not be reliably separated from other taxa in the CANADENSE species group without examination of the pupal gill configuration. The prominent swollen gill filaments places *S. contrerense* in the JUAREZI species group of the subgenus *Hearlea* (*sensu* COSCARÓN & COSCARÓN-ARIAS, 2007). Within this group, *S. contrerense* can be easily recognized by the distinctly swollen dorsal branch, the median primary branch pointed apically and the relatively finger-like ventral primary branch, which is directed towards the ventral region of the pupa (Fig. 1017). Other species with swollen primary branches are *S. burchi*, *S. canadense*, *S. delatorrei* and *S. juarezi*, but the general morphology of the pupal gill filaments is different in these taxa (see Figs. 1012, 1013, 1019, 1024).

Following the key of DÍAZ NÁJERA & VULCANO (1962a), the larva of *S. contrerense* falls within the species without sclerotised secondary plates in the posterior region of the abdomen, and the anterior margin of the hypostomium more or less concave. Within this group, the larva of *S. contrerense* may be separated from other species by the hypostomium with 1+1 lateral teeth as long as the median tooth and 3+3 extremely reduced sublateral teeth (Fig. 1179). However, the best character to recognise this species in the larval stage is the configuration of the dissected pupal gill histoblast in mature larvae collected in the same locality from where link-reared adults have been obtained.

Simulium contrerense was placed in the subgenus *Hearlea* by DÍAZ NÁJERA & VULCANO (1962a), and this has been accepted by CROSSKEY & HOWARD (1997, 2004). ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action subsequently followed by ADLER & CROSSKEY (2008, 2009, 2010). However, the latter was recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who still maintain *Hearlea* as a valid subgenus. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. contrerense* is now placed.

Distribution. *Simulium contrerense* has only been recorded from Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. Nothing is known on the biology of *S. contrerense.* VARGAS & VULCANO (1962a) stated that larvae were collected at Nevado de Toluca, Mexico State at an altitude of 3000 m. Toluca peak is one of the four highest volcanos in Mexico, and it is densely covered by coniferous trees and broadleafed plants (WIKIPEDIA, 2010).

2.5.1.7. *Simulium* (*Trichodagmia*) *dalmati* VARGAS & DÍAZ NÁJERA (Figs. 16, 32, 183, 235, 297, 298, 426, 532, 590, 650, 716, 717, 837, 898, 959, 1018, 1127, 1180, 1235)

This is a zoophilic species only known from Mexico. The description here provided has been derived from the examination of type specimens and identified material deposited at BMNH, INDRE, MLP, and NMNH, the original description of VARGAS & DÍAZ NÁJERA (1948), and the reviews of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), VARGAS & DÍAZ NÁJERA (1957a) and VARGAS, MARTÍNEZ & DÍAZ NÁJERA (1946).

Simulium (Hearlea) dalmati VARGAS & DÍAZ NÁJERA, 1948c: 337. HOLOTYPE male. MEXICO, Veracruz State, Cumbres de Acultizingo; 31.viii.1948, (*Israel Córdova*) (INDRE, no. 3934] [Examined.]

FEMALE. General body colour black. Body length (specimens pinned) 3.0 mm (n = 1), wing length 2.4-3.0 mm (n = 2), wing width 1.1-1.2 mm (n = 2).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 183). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth, anterior margin concave centrally (Fig. 235).

Thorax: scutum black with evenly arranged, semi-recumbent, yellowish setae, interspersed with fine, semi-recumbent brown setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with 1+1 median pear-shaped and 1+1 submedian wide triangular silver pruinose vittae extending from anterior to posterior margins; 1+1 submedian silver pruinose cunae on anterior third of scutum; median fine black line extending from anterior to posterior margins; humeri light brown, lateral and posterior margins black (Fig. 297). With posterior illumination, thorax dark brown to black, with 1+1 submedian cunae with fine tails reaching mid region of scutum; humeri and lateral margins faintly silver pruinose; posterior margin black (Fig. 298). Scutellum dark brown with recumbent white hairs intermixed with long brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 426. Fore leg with coxa, trochanter and femur light brown; external surface of tibiae whitish; apical third of tibiae and tarsal segment I-IV dark brown. Mid leg with trochanter and two thirds of femur and tibia pale brown; coxa, apical third of femur and tibiae, apical half of tarsal segment II and tarsal segments III-IV dark brown; basal half of tarsal segment I whitish. Hind leg with trochanter, basal two thirds of femur, basal half of tibia yellowish; apical third of femur, apical half of tibia, apical third of tarsal segment I and apical third of tarsal segment II and tarsal segments II-IV dark brown; basal two thirds of tarsal segment I and base of tarsal segment II whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-V velvet black IX black, segment VI-VII shiny brown; segment II with silver pruinose ornamentation. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular with curved internal margin, weakly sclerotised, densely covered with microtrichiae (Figs. 32, 590). Cercus subrectangular, covered with brown setae; paraproct small, extending beyond and as wide as cercus with small produced process; paraproct covered with prominent brown hairs and smaller setae apically (Figs. 16, 590). Genital fork stout and sclerotised, except stem not sclerotised; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed, posterior processes weakly developed (Fig. 650). Spermatheca not examined but probably similar to that of *S. capricorne*.

MALE. General body colour dark brown to black. Body length (specimens pinned, n = 2) 3.1-3.5mm, wing length 2.4-2.5mm, wing width 1.1-1.3 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black with evenly distributed recumbent yellow hairs interspersed with black hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with 1+1 subrectangular vittae extending from antero-lateral margin to central region of scutum (Fig. 716). With posterior illumination scutum black (Fig. 717). Humeri lightly pruinose; lateral and posterior margins black. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc mostly bare. Leg coloration as in female but darker.

Abdomen: Tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergites II, V, VI [best seen in some specimens when tilted and viewed laterally]. Genitalia brown; sternal plates developed. Gonocoxite subquadrangular, with one antero-lateral margin produced; gonostyle prominently elongate, nearly two times longer than gonocoxite, with lateral margins weakly straight and curved on apical third, with flap-like process basally and terminating in single stout spine; gonocoxite and gonostyle covered with long setae (Fig. 837). Ventral plate sclerotised, subrectangular; main body of ventral plate with anterior margin produced centrally into triangular process; lateral shoulders developed, basal arms well developed, subparallel (Fig. 898). Median sclerite about three times longer than wide at mid point, without apical incision [it appears curled up in some specimens I examined] (Fig. 898). Paramere with well developed and sclerotised basal process and numerous long spines along whole length (Fig. 959).

PUPA. [COSCARÓN *et al.* (2004) recorded cocoon length (dorsally) as 5.0 mm. Other measurements and number of specimens examined not given in this paper]; gill length 1.6 mm (n = 1).

Cocoon: shoe-shaped as in Fig. 66, brown, composed of coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown with three upwardly, forwardly and ventrally directed filaments arranged in vertical plane (Fig. 1018). Gill with main trunk short with to three primary branches, one dorsal, one median and one ventral. Dorsal branch swollen, with prominent annulations, capitate apically and forwardly directed. Median branch short, upwardly directed reaching region of dorsal cleft. Ventral branch ventrally directed, swollen and encircling frontoclypeus. Filaments stout, with dorsal and ventral primary branches rounded apically and ventral primary branch pointed apically; filaments without spicules on surface, edges weakly crenate; dorsal and ventral branches longer than median branch.

Head (*frontoclypeus*): with few irregularly distributed tubercles.

Thorax: with few irregularly distributed tubercles.

Abdomen: [chaetotaxy not examined because of lack of material, but probably with similar pattern to that of *S. capricorne* and other species found in the CANADENSE species group].

LARVA (Last instar). Body length 9.0 mm [Other measurements and number of specimens examined not given in the original description]. Body colour greyish green dorso-laterally, whitish ventrally (specimens probably preserved in spirit).

Head: mainly dark brown. Head pattern negative. Postgenal cleft bell-shaped, with narrow antero-median incision; postgenal bridge 1.5 times longer than hypostomium (Fig. 1127). Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed in anterior margin; median tooth sharp, well developed and most prominent; 3+3 reduced sublateral teeth; 1+1 lateral teeth longer than sublateral teeth; 4+4 small, lateral serrations; 1+1 lines of approximately 16 hypostomial setae parallel to lateral margins; 2+2 long, simple setae in posterior half of hypostomium (Fig. 1180). Antenna as long as labral fan stalk, all segments pale; length of antennal segments I-III excluding the sensillum 0.1:0.07:0.1 mm (n = 1). Mandible with two apical teeth, first one longer than second; mandibular comb with approximately nine teeth, first four more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1235). Lateral mandibular process absent. Cephalic fan with more 44-46 rays with fine, single line of spines in a row.

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised.

Abdomen: usually grey. Ventral papillae absent. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 164 rows of sclerotised simple hooks. Anal gill with three branches each with 5-7 small, finger-like lobes.

Taxonomic Discussion. *Simulium dalmati* was described by VARGAS & DÍAZ NÁJERA (1948c) based on a male holotype (no. 3934), a female allotype (no. 3935), and eight males and four females, and numerous larvae and pupal exuviae (all as paratypes) collected in Veracruz State, Mexico. I have examined the holotype and the allotype, and one female and one male paratype housed at INDRE. The holotype is good condition. It has been glued to a card point by the ventral side of the thorax; three legs, left wing and its genitalia are mounted on a slide (**Material Examined**). The female allotype is also glued to a card point, while its right wing, right legs and genitalia are mounted on a slide (**Material Examined**).

The adults' thoracic pattern of *S. dalmati* are similar to several other species in the CANADENSE species group (Figs. 297, 298, 716, 717). The female may only be readily separated by the morphology of the paraproct (Figs. 16, 590) in combination with the configuration of the gill filaments in link-reared adults (Fig. 1018). The male may only be identified by the examination of the pupal gill configuration.

The best character to identify *S. dalmati* is the morphology of the pupal gill filaments. Within the CANADENSE species group, the pupal gill configuration of *S. dalmati* is similar to species such as *S. ayrozai*, *S. burchi*, *S. delatorrei*, *S. estevezi* in which the dorsal primary branch is swollen, the median is shorter than the remaining branches, and the ventral is also stout and partly encircling the frontoclypeus (Figs. 1011, 1012, 1019, 1020). However, *S. dalmati* may be separated by having a capitate dorsal primary branch, more pointed median primary branch and the ventral primary branch prominently swollen (Fig. 1018). In the latter species the pupal gill configuration is different (Figs. 1011, 1012, 1019, 1020).

Following the key of DÍAZ NÁJERA & VULCANO (1962a) the larva of *S. dalmati* belongs to the species in which the sclerotised accessory plates are absent in the terminal region of the abdomen and the anterior margin of the hypostomium is concave. The larva may be readily separated by the lateral hypostomial teeth directed forwards and shorter than the median tooth, the presence of nine hypostomial teeth and 1+1 lines of 16 hypostomial setae (Fig. 1180). The most similar species is *S. canadense*, but in this species the larva has eight hypostomial teeth and 1+1 lines of 6-7 hypostomial setae (Fig. 1176).

Simulium dalmati was placed in the subgenus *Hearlea* by VARGAS & DÍAZ NÁJERA (1957b), and this has been accepted by key Simuliidae catalogues, *e.g.* COSCARÓN (1987) and CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic action was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the JUAREZI species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. dalmati* is now placed.

Distribution. *Simulium dalmati* has only been recorded from Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. Little is known on the biology and female feeding habits of *S. dalmati*. DÍAZ NÁJERA & VULCANO (1962a) stated that this species inhabits areas located at high altitude in streams with low water temperatures.

2.5.1.8. ***Simulium* (*Trichodagmia*) *delatorrei*** DALMAT (Figs. 184, 236, 299, 300, 427, 533, 591, 651, 718, 719, 838, 899, 960, 1019, 1082, 1128, 1181, 1236)

This is a zoophilic species only known from Mexico and Guatemala. The description here provided has been based upon examination of type material and identified specimens housed at BMNH, MLP and NMNH, the original description of DALMAT (1950), and the revisions of COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium (Dryarella) delatorrei Dalmat, 1950: 137. HOLOTYPE female (reared), GUATEMALA: Totonicapán Department, Catarata Panajochel, Sololá; 24.ii.1949, (*H.T.Dalmat & Jaime Rosales*) (NMNH, accession number 6P-8) [Examined.]

FEMALE. General body colour black. Body length 2.0-3.0 mm (mean = 2.6 mm, s.d. = 0.36, n = 7); wing length 2.0-3.0 mm (mean = 2.5 mm, s.d. = 0.34, n = 7), wing width 1.0-1.5 mm (mean = 1.3 mm, s.d. = 0.16, n = 7).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 184). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts and maxillary palps dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed and sclerotised cornuae; anterior margin concave on central trough and without teeth, tough small serrations can be seen on the internal margin of cornuae [only visible at higher magnification] (Fig. 236).

Thorax: scutum black with evenly arranged recumbent golden setae interspersed with dark hairs. Scutal pattern varying with light direction. With anterior illumination, thorax with 1+1 pear-shaped vittae and 1+1 wide triangular vittae extending from anterior to posterior margins; humeri and posterior margin silver pruinose; lateral margins black (Fig. 299). With posterior illumination, thorax black with 1+1 submedian rounded spots with small tails on anterior third of scutum; greyish areas on posterior region can be seen in specimens devoid of hairs; humeri silver pruinose; lateral and posterior margins black (Fig. 300). Scutellum black with black bristles. Postnotum black with silver pruinosity. Pleura dark brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae except apex. Radius with numerous setae intermixed with distinct spines, basal section of radius bare in the holotype. Basal tuft of long, dark setae. Leg coloration and proportions as Fig. 427. Fore leg with coxa and trochanter yellow; femur and tibia yellow except for small apical dark band on tibia; tarsal segments black. Mid leg with coxa dark brown, trochanter yellow, femur yellow with small patches on dorsal surface, tibia largely yellow but dark brown apically; basal half of tarsal segment I, its distal half and remainding tarsal segments black. Hind leg as mid leg except tarsal segment I yellow on basal two thirds. Hind leg claw curved with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown to black. Tergal plates developed. Sternites black. Eighth sternite sclerotised with short, irregularly distributed setae on posterior margin; gonapophyses as long as eighth sternite at mid point, subtriangular, well separated and internal margins curved; gonapophyses weakly sclerotised, densely covered with microtrichiae (Fig. 533). Cercus subquadrangular, covered with brown setae; paraproct subrectangular, extending beyond junction with cercus; ventral extension narrow apically; paraproct covered with small brown setae and microtrichiae towards apex. (Fig. 591). Genital fork stout and sclerotised stem relatively expanded apically; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed, internal posterior processes weakly developed (Fig. 651). Spermatheca suboval, without external sculpturing and small groups of setae on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour black. Body length 2.9 mm (mean = 2.9 mm, n = 3); wing length 1.9-2.6 mm (mean = 2.3 mm, s.d. = 0.340 n = 4), wing width 0.8-1.3 mm (mean = 0.9 mm, s.d. = 0.23, n = 4).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum velvet black covered with silvery grey pruinosity sometimes interspersed with narrow adpressed pale yellow scales. Scutal pattern varies slightly with light incidence: with light anterior scutum black with 1+1 silver pruinose areas on anterior third of scutum (Fig. 718). With posterior illumination, thorax black (Fig. 719). Humeri, lateral and posterior margins black. Scutellum velvet black with black pilosity Postnotum black with silvery grey pruinosity. Wing setation as in female, except Subcosta with few hairs along short section at its base (Dalmat, 1995) [I have examined specimens with bare Sc wing vein]. Leg coloration as in female.

Abdomen: Tergites velvet black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II. Genitalia black. Gonocoxite subquadrangular; gonostyle elongate, nearly three times longer than gonocoxite, slightly curved inwards in some specimens, with flap-like process basally and terminating in stout, single, apical spine; gonocoxite and gonostyle covered with long setae (Fig. 838). Ventral plate weakly sclerotised, subquadrangular; ventral plate with shoulders weakly developed and anterior margin produced centrally into short process covered in long hairs [a central carina extending to posterior third of ventral plates can be seen]; basal arms subparallel, sclerotised apically (Fig. 899). Median sclerite approximately three times longer than wide with no visible apical incision [the median sclerite was curled up in all specimens I examined] (Fig. 899). Paramere with well developed and sclerotised basal process and numerous long spines along whole length, central membrane covered with fine spinules (Fig. 960).

PUPA. Cocoon length dorsally 3.3-3.7 mm (mean = 3.5 mm, s.d = 0.14, n = 5), ventrally 4.0 -4.5 mm (mean = 4.2 mm, s.d. = 0.22, n = 5); pupa length 3.1-3.6 mm (mean = 3.3 mm, s.d. = 0.25, n = 3); gill length 1.9-3.5 mm (mean = 2.8 mm, s.d. = 0.52, n = 13).

Cocoon: slipper-shaped as in Fig. 65, brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture gradually elevated.

Gill: dark brown with three backwardly, forwardly and ventrally directed filaments in vertical plane (Fig. 1019). Gill configuration with main trunk short giving rise to set of three primary branches, one dorsal, one median and one ventral. Dorsal branch finger-like, shorter than remainder of branches and directed slightly backwards and inwards to median region of pupal thorax. Median primary branch prominently swollen, with prominence on ventral margin at mid point from which it bends upward. Ventral branch directed ventrally encircling the frontoclypeus. Filaments stout, with pseudoannulations, edges weakly sinuous; dorsal branch most prominent and longer than remainder branches.

Head (*frontoclypeus*): with 1+1 frontal and 1+1 facial spiniform, prominent trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 3-4 four laterally in two groups in frontal region; rounded tubercles densely distributed over surface.

Thorax: with 2-3 long, spiniform trichomes on dorsal cleft, one spiniform trichome on posterior region and one long simple trichome on ventral margin of pupa.

Abdomen: abdominal tergite I without visible setae in single specimen examined; tergite II with 3+3 submedian spiniform setae in longitudinal row, 2+2 simple, small setae lateral to outermost spiniform setae; tergites III, IV with 4+4 submedian simple hooks in longitudinal row; tergites V-IX without visible setae; tergite IX weakly sclerotised without terminal spines. Spine combs distribution on anterior margin of tergites VI-IX. Sternite V with 2+2 close submedian simple hook; sternites VI, VII with 2+2 well separated simple or bifid hooks in row on posterior margins; sternite VIII without setae; sternites III, IV, and IX damaged in the single specimen examined.

LARVA (Last instar). Body length 6.3-7.6 mm (mean = 7.2 mm, s.d. = 0.53, n = 5), length of head capsule 0.6-0.8 mm (mean = 0.7 mm, s.d. = 0.08, n = 5); width of head capsule 0.6-0.7 (mean = 0.6 mm, s.d. = 0.05, n = 5). General coloration grey (specimens in spirit) (Fig. 1082)

Head: mainly brown, anterior region of cephalic apotome weakly yellowish. Head pattern negative. Postgenal cleft bell-shaped, wider at mid point with narrow antero-median incision; postgenal bridge as long as hypostomium (Fig. 1128). Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, the mid pair more reduced than outermost pairs; 1+1 lateral teeth at same length as longest sublateral teeth; 5+5 lateral serrations; 1+1 lines of eight hypostomial setae parallel to lateral margins; 1+1 long and 1+1 small simple setae in posterior half of hypostomium (Fig. 1181). Antennal segments surpassing apex of labral fan stalk, lightly pigmented; length of antennal segments I-III excluding the sensillum 0.1:0.07:0.1 mm (n = 1). Mandible with two apical teeth, first one longer than second; mandibular comb with approximately eight teeth, first four more prominent than remainder teeth; two mandibular serrations, anterior more prominent than posterior (Fig. 1236). Lateral mandibular process absent. Labral fans with 39-40 rays with fine, single line of spines in each row (n = 1).

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of 40-42 sclerotised processes (n = 1).

Abdomen: greyish. Ventral papillae absent. Cuticle lacking setae. Posterior circlet with 114 rows of 12-22 simple hooks (n = 1). Rectal gills with three branches, each with 24-25 small finger-like lobules giving a total of 74 lobules (n = 1).

Taxonomic Discussion. *Simulium delatorrei* was described by DALMAT in 1950 based on a female holotype, and eight females, four males and 24 pupae (as paratypes) collected in Guatemala. The larva was later described and figured for the first time by DALMAT (1955) and also by DÍAZ NÁJERA & VULCANO (1962a). I have examined the holotype, which is housed at the NMNH Simuliidae collection. The specimen is mounted on five slides containing the head, wings, legs and the genitalia (see **Material Examined**); the remainder of the adult, and its pupal exuviae and cocoon were not found in the NMNH holdings. I have also examined three reared males and five reared females all labelled as paratypes (one male as allotype) and deposited at the NMNH (**Material Examined**). In addition, I have examined two reared females and one pupal exuviae (all paratypes) and one larva housed at the MLP (**Material Examined**). I have taken digital images of the key diagnostic characters of the holotype and allotype of *S. delatorrei*, which are now stored in the Simuliidae Digital Images Archives at the BMNH. I have also examined within the type series of *S. delatorrei* at the NMNH a single female labelled as paratype, with accession number 5W-3 that does not agree with the diagnostic characters of *S. delatorrei.* This specimen bears a white identification label in COSCARÓN's hand "*Simulium (Psilopelmia) haematopotum* 2000". I agree with COSCARÓN's identification and I have labelled this specimen accordingly.

The general morphology of the adult's scutal pattern (Figs. 299, 300, 718, 719), pupal gill configuration (Fig. 1019) and larval morphology (Figs. 1128-1236) of *S. delatorrei* falls within the variation found in other species in the CANADENSE species group, especially *S. estevezi*. Adults of *S. delatorrei* can only be readily identified by the configuration of the pupal gill filaments (Fig. 1019) in link-reared specimens. The larva may only be readily separated from that of *S. estevezi* and *S. juarezi* by the configuration of the dissected gill histoblast in mature larvae collected at the same locality, where link-reared adults have been obtained.

The pupa of *S. delatorrei* has distinctly swollen filaments resembling a horn-like structure (Fig. 1019) with prominent striations on its surface, and the median primary branch weakly bends at mid length from which it continues being of the same width towards the apical region. In *S. estevezi* the median primary branch does curve prominently at mid length and it narrows down towards the apical region of the median branch; all branches lack striations (Figs. 1020) [see also **Taxonomic Discussion** under *S. estevezi* for further details].

Simulium delatorrei was first placed in the subgenus *Dryarella* [now a synonym of *Trichodagmia*, see SHELLEY *et al.*, 2010] by DALMAT (1950), who later transferred it to the subgenus *Hearlea.* The latter taxonomic action has been accepted by most authors, *e.g.* COSCARÓN (1987), CROSSKEY & HOWARD (1997, 2004), DALMAT (1955), VARGAS & DÍAZ NÁJERA (1957b) and DÍAZ NÁJERA & VULCANO (1962a). ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed in the latest versions of the World Inventory of Blackflies (ADLER & CROSSKEY, 2008, 2009, 2010). However, the latter was not accepted by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed *S. delatorrei* in their JUAREZI species group of the valid subgenus *Hearlea.* More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. delatorrei* is now placed.

Distribution. *Simulium delatorrei* has only been recorded from Guatemala and Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and medical importance. The immature stages of *S. delatorrei* were found by DALMAT (1950) attached to leaves in emergent vegetation, stones, twigs and pine needles in streams. The same author stated that *S. delatorrei* is found in the highlands of Guatemala at altitudes between 5250 to 9470 feet, in narrow run-off ditches, one to ten feet wide. The streams varied from four inches deep to one foot, pH 6.4-7.4, and water temperatures of 8°C to 19°C. The streambeds were always composed of sand, with small and large stones, and at times with mud. Nothing is known on the female feeding habits.

2.5.1.9. ***Simulium* (*Trichodagmia*) *estevezi*** **VARGAS** (Figs. 185, 237, 301, 302, 428, 534, 592, 652, 720, 721, 839, 900, 961, 1020, 1129,1182, 1237)

A relatively well-known species only found in Mexico. The description here provided has been based upon examination of type material and other identified species housed at MLP, MZUCR and NMNH, and the original description of VARGAS (1945) and the revisions of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium (Simulium) estevezi VARGAS, 1945b: 71. HOLOTYPE male (not associated with pupal exuviae), MEXICO: Oaxaca State, San Felipe del Agua, 1600 mts; 11.xii.1943, (*A.Martínez Palacios*) (INDRE, no. 3554) [Examined.]

FEMALE. General body colour black. [COSCARÓN *et al.* (2004) recorded the wing width as 3.6 mm. Other measurements and numbers of specimens examined not given in the latter paper or the original description].

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 185). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts and maxillary palps dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and fine and small teeth on margin of cornuae and central trough [only visible at higher magnification]; anterior margin concave on central trough (Fig. 237).

Thorax: scutum black with evenly arranged recumbent golden setae interspersed with dark hairs. Scutal pattern varying with light direction. With anterior illumination, thorax with 1+1 median pear-shaped vittae and 1+1 wide triangular vittae extending posteriorly for two thirds from anterior margin; humeri and lateral margins silver pruinose; posterior margin black (Fig. 301). With posterior illumination, thorax black with 1+1 submedian rounded spots with small tails on anterior third of scutum [greyish areas on posterior region can be seen with certain lights]; humeri silver pruinose; lateral and posterior margins black (Fig. 302). Scutellum black with black bristles. Postnotum black with silver pruinosity. Pleura dark brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae except on apical third. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as Fig. 428. Fore leg with trochanter, apex of femur, base and apex of tibia, and tarsal segments I-IV dark brown; remainder of femur and tibia pale yellowish; coxa not examined. Mid leg not examined. Hind leg with coxa, part of trochanter, apex of femur and tibia, apical half of tarsal segment I, and tarsal segments II-IV dark brown; remainder of femur and tibia pale yellow; basal half of tarsal segment I whitish. Hind leg claw curved with small basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX black. Tergal plates developed. Sternites black. Eighth sternite sclerotised with short, irregularly distributed setae on posterior margin; gonapophyses as long as eighth sternite at mid point, subtriangular, well separated and internal margin curved; gonapophyses membranous, but weakly sclerotised on internal margins and densely covered with microtrichiae (Fig. 534). Cercus subrectangular, covered with brown setae; paraproct subrectangular, extending beyond junction with cercus; ventral extension rounded apically; paraproct covered with small brown setae and microtrichiae towards apically. (Fig. 592). Genital fork stout and sclerotised with stem expanded apically; termination of lateral arms with anterior margin straight and well developed; anterior processes well developed, internal posterior processes weakly developed (Fig. 652). Spermatheca not examined.

MALE. General body colour black. [COSCARÓN *et al.* (2004) recorded the body length as 2.6 mm; wing length 2.9 mm. Other measurements and numbers of specimens were not given in the latter paper or the original description.]

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum velvet black covered with silvery grey pruinosity. Scutal pattern varies slightly with light incidence: with light anterior, scutum black with 1+1 silver pruinose areas on anterior third of scutum (Fig. 720). With posterior illumination, thorax black (Fig. 721). Humeri weakly pruinose; lateral and posterior margins black. Scutellum velvet black with black pilosity. Postnotum black with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: Tergites velvet black, basal fringe with long, brown hairs [silver ornamentation not recorded as single specimen available had been dissected]. Gonocoxite subquadrangular, with one antero-lateral margin weakly produced; gonostyle elongate, nearly two times longer than gonocoxite, wide at base somewhat narrower at mid point, with flap-like ridge and terminating in single stout spine; gonocoxite and gonostyle covered with long setae (Fig. 839). Ventral plate sclerotised, subquadrangular; main body of ventral plate developed and lateral shoulders weakly developed, anterior margin produced centrally into short process prominently covered by hairs; a short carina extending centrally up to mid point of ventral plate can be seen; basal arms subparallel, sclerotised apically (Fig. 900). Median sclerite very long, nearly three times longer than wide at mid point, without visible apical incision (Fig. 900). Paramere with well developed and sclerotised basal process and numerous long spines along whole length, central membrane covered with fine spinules (Fig. 961).

PUPA. [COSCARÓN *et al.* (2004) recorded the cocoon length dorsally as 2.8 mm, basally as 3.6 mm. Other measurements and number of specimens examined not given in the latter paper or in the original description]; gill length 2.3-2.5 mm (n = 2).

Cocoon: slipper-shaped as in Fig. 65, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture gradually elevated.

Gill: dark brown with three backwardly, forwardly and ventrally directed filaments in vertical plane (Fig. 1020). Gill configuration similar that of *S. delatorrei.* Main trunk short giving rise to set of three primary branches, one dorsal, one median and one ventral. Dorsal primary branch prominently swollen, sometimes narrow apically. Median branch finger-like and shorter than remaining branches. Ventral branch directed ventrally encircling the frontoclypeus, sometimes curved at mid point. Filaments stout, with pseudoannulations, edges weakly sinuous; dorsal branch most prominent and longer than remaining branches.

Head (*frontoclypeus*): with 1+1 frontal and 1+1 facial spiniform, prominent trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 3-4 four laterally in two groups in frontal region, respectively; rounded tubercles densely distributed over surface.

Thorax: with 2-3 long, spiniform trichomes on dorsal cleft, one spiniform trichome on posterior region and one long simple trichome on ventral margin of pupa; tubercles weakly pointed and distributed over entire surface except posteriorly.

Abdomen: abdominal tergite I without visible setae, but row of rounded tubercles on central region; tergite II with 3+3 submedian spiniform setae in longitudinal row, 4+4 simple, small setae lateral to outermost spiniform setae; tergites III and IV with 4+4 submedian simple hooks in longitudinal row, 1+1 small setae anterior to outermost hooks, and 2+2 small simple setae laterally; tergites V-IX without visible setae; tergite IX weakly sclerotised without terminal spines. Spine combs on anterior margins of tergites VI-IX. Sternites III and IV with 3-4 small setae centrally; sternite V with 2+2 closed submedian bifid hooks; sternites VI, VII with 2+2 well separated simple or bifid hooks in row on posterior margins; sternites VIII, IX without visible setae. Spine combs on anterior margins of sternites IV-VII.

LARVA (Last instar). [COSCARÓN *et al.* (2004) recorded the body length as 7.0 mm. Other measurements and numbers of specimens examined not given in the latter paper nor in the original description]. General coloration grey (specimens probably preserved in ethanol).

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Head pattern positive. Postgenal cleft bell-shaped, wider at mid point short and narrow antero-median incision; postgenal bridge 1.5 times longer than hypostomium (Fig. 1129). Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, pair most basal to median tooth reduced; 1+1 lateral teeth; 5+5 lateral serrations; 1+1 lines of eight hypostomial setae parallel to lateral margins; 1+1 long and 1+1 small simple setae in posterior half of hypostomium (Fig. 1182). Antennal segments extending beyond apex of labral fans stalk, lightly pigmented; length of antennal segments I-III excluding the sensillum 0.1:0.07:0.1 mm (n = 1). Mandible with two apical teeth, first one longer than second; mandibular comb with 11 teeth, first five more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1237). Lateral mandibular process absent. Labral fans with 44-50 rays each with fine, single line of spines in row.

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of sclerotised processes.

Abdomen: grey. Ventral papillae absent. Cuticle lacking setae. Posterior circlet with 98-100 rows of simple hooks. Rectal gills with three branches, each with 8-10 small finger-like lobules giving a total of 24-30 lobules [numbers of specimens examined not given in the original description].

Taxonomic Discussion. *Simulium estevezi* was described by VARGAS (1945) based on a male holotype, a female allotype and three pupal exuviae collected in Oaxaca State, Mexico. The larva was first illustrated by DÍAZ NÁJERA & VULCANO (1962a), and later by VARGAS & DÍAZ NÁJERA (1945) and COSCARÓN & COSCARÓN-ARIAS (2007). VARGAS (1945) stated in the original description that the male holotype was mounted on a slide in Canada Balsam and deposited at INDRE with the accession number “3554”. However, I have examined at INDRE a specimen labelled in VARGAS’ hand “male holotype”, which is partially pinned. The specimen is in relatively good condition and it has been glued to a card point by the ventral side of thorax. Only one antennal segment, the left wing, the three legs of the left hand side and the genitalia are mounted on a slide; the remainder of the specimen is pinned (**Material Examined**). I have also examined the pinned female allotype (INDRE no. 3555), which has been partially dissected. The specimen is in relatively good condition being glued to a card point by the ventral side of the thorax; three legs, one wing and its genitalia are on a slide (see **Material Examined**).

The adults’ thoracic pattern of *S. estevezi* is very similar to that of other species allotted to the CANADENSE species group (Figs. 301, 302, 720, 721). The pupal gill configuration (Fig. 1020) and larval morphology (Figs. 1129, 1182, 1237) fall within the morphological variation found in *S. delatorrei* indicating that both species might be conspecific. However, in link-reared specimens of *S. estevezi* the female paraproct does not have the ventral extension narrow apically (Fig. 592) as in *S. delatorrei* (Fig. 591). In addition, the genital fork in *S. estevezi* has the stem prominently expanded apically (Fig. 652), which is different from that of *S. delatorrei* (Fig. 651). In the male *S. estevezi* the gonostyle is visibly more elongated with its margins straight (Fig. 839). In *S. delatorrei* the gonostyle is distinctly more curved (Fig. 838). Based on the latter morphological differences, I prefer to maintain *S. estevezi* and *S. delatorrei* as valid species until more material is available to assess their taxonomic status.

Simulium estevezi was placed in the subgenus *Simulium* by VARGAS (1945), but later in the subgenus *Hearlea* by VARGAS & DÍAZ NÁJERA (1945), and this has been accepted by all key catalogues, *e.g.* COSCARÓN (1987) and CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* within *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic action was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the JUAREZI species group in their valid subgenus *Hearlea*. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. estevezi* is now placed.

Distribution. *Simulium estevezi* is only known from Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004).

Biology and medical importance. Nothing is known on the biology of *S. estevezi*. The allotype label stated that is was collected at 1600m.

2.5.1.10. *Simulium* (*Trichodagmia*) *ethelae* DALMAT (Figs. 49, 65, 186, 238, 303-306, 429, 535, 593, 653, 722-725, 840, 901, 962, 1021, 1083, 1130, 1183, 1238)

A relatively well-known species originally described from Guatemala by DALMAT (1950), and also recorded from Mexico, Costa Rica and Panama. The description here provided has been based upon an examination of the type specimens, identified material housed at BMNH, INDRE, MLP, MZUCR and NMNH, the original description of DALMAT (1955) and the revisions of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium (Hearlea) ethelae DALMAT, 1950: 143. HOLOTYPE female, GUATEMALA: Sololá Department, Rio Los Arcos, near Los Encuentros; 4.xi.1948, [Without collector's name but probably H.T.Dalmat] (NMNH, accession no. 3"0"-1) [Examined.]

Simulium (*Hearlea*) *chiriquiense* FIELD, 1967: 194. HOLOTYPE female (reared), PANAMA: Chiriquí Province, Cerro Punta; 11.v.1954, (*Fleming*, *McGrath & Shalla*) [Depositary unknown-see **Taxonomic Discussion**.] **New synonymy**.

FEMALE. General body colour black. Body length (specimens pinned) 2.1-2.8 mm (mean = 2.4 mm, s.d. = 0.25, n = 9), wing length 2.2-2.9 mm (mean = 2.5 mm, s.d. = 0.26, n = 9), wing width 1.2-1.5 mm (mean = 1.3 mm, s.d. = 0.10, n = 9).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 186). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 238).

Thorax: scutum black covered with evenly arranged, recumbent, golden hairs interspersed with recumbent black hairs; posterior margin with evenly arranged, recumbent, golden hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax largely pruinose with a straight, median and 1+1 wide, sublateral vittae extending from anterior third of scutum to almost posterior margin, anterior margins of vittae joining at anterior third of scutum; humeri and posterior margin with weak silver reflections; lateral margin black (Figs. 303, 305). With posterior illumination, thorax black with 1+1 submedian round silver spots on anterior third, and small, median and 1+1 sublateral large faint pruinosities; humeri weakly pruinose; lateral and posterior margins black (Figs. 304, 306). Scutellum black with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length, except apical third which is bare. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 429. Fore leg with coxa, trochanter and femur pale yellow; basal two thirds of tibiae whitish, apical third tibia and tarsal segments I-IV dark brown to black. Mid and hind leg with coxae, trochanters, femora, basal and apical thirds of tibiae, and tarsal segments I-IV brown; mid part of tibiae whitish. Hind leg claw with basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IV velvet black, tergites VI-IX shiny black; tergites I, II with silver pruinosities on antero-lateral margins. Tergal plates well developed. Sternites and genitalia dark black. Eighth sternite sclerotised with five long, irregularly distributed setae on posterior margin and approximately 14-15 smaller setae at level of gonapophyses; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular, with internal margin weakly curved, apical two thirds of gonapophyses sclerotised, remainder membranous; gonapophyses densely covered with microtrichiae (Fig. 535). Cercus subhemispherical, covered with brown setae; paraproct subrectangular, extending beyond cercus; basal lobe of paraproct with small prominence, and ventral extension highly setose apically (Fig. 593). Genital fork stout and sclerotised; termination of lateral arms with anterior margins straight; anterior and internal posterior processes well developed and blunt apically (Fig. 653). Spermatheca globular, without external sculpturing and small groups of 3-4 spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens pinned) 2.1-3.2 mm (mean = 2.6 mm, s.d. = 0.36, n = 9), wing length 2.4-2.7 mm (mean = 2.5 mm, s.d. = 0.13, n = 9), wing width 0.9-1.7 mm (mean = 1.3 mm; s.d. = 0.21, n = 9).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum velvet black covered with recumbent golden setae interspersed with recumbent black hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with 1+1 submedian pollinose areas on anterior third of scutum (Figs. 722, 724). With posterior illumination, thorax velvet black (Figs. 723, 725). Humeri, lateral and posterior margins black. Scutellum black with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare. Leg coloration as in female, hind tarsal segment swollen.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites III-VII (best seen in some specimens when tilted and viewed laterally). Genitalia black; sternal plates developed. Gonocoxite subquadrangular, with produced antero-lateral margin; gonostyle elongate, with margins nearly straight terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 840). Ventral plate sclerotised, subrectangular, without shoulders and/or median process but with central keel prominently covered by hair; posterior margin of ventral plate curved centrally, basal arms subparallel and sclerotised apically; main body of ventral plate covered with small hairs (Figs. 49, 901). Median sclerite about three times longer than wide at widest point, with small incision (appears curled up in the few specimens examined) (Fig. 901). Paramere with well developed and sclerotised basal process and numerous long spines centrally, central membrane covered with small spinules (Fig. 962).

PUPA. Cocoon length dorsally 3.1-3.7 mm (mean = 3.4 mm, s.d = 0.17, n = 11), ventrally 3.1-4.2 mm (mean = 3.6 mm, s.d. = 0.30, n = 11); pupa length 2.9-4.3 mm (mean= 3.5 mm, s.d. = 0.48, n = 11); gill length 2.0-3.1 mm (mean = 2.6 mm, s.d. = 0.32, n = 14).

Cocoon: slipper-shaped as in Fig. 65, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with two swollen filaments forwardly directed filaments in vertical plane (Fig. 1021). Gill with main trunk short giving rise to two sets of primary branches one dorsal and one ventral, both branches curved inwards nearly at midpoint in an open C-shape; dorsal branch with small prominence basally, ventral branch extending along anterior margin of cocoon. Filaments stout, rounded distally, with spicules on surface and with ridges and crevices, edges crenate; dorsal branch relatively stouter than ventral branch.

Head (*frontoclypeus*): with 2+2 long, simple frontal and 1+1 spiniform, long facial trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-4 platelets in two groups laterally in frontal region; rounded tubercles only visible in facial region and lateral margins of frontal region.

Thorax: with 3-4 spiniform trichomes on margin dorsal cleft, one spiniform trichome at gill base, one spiniform trichome on posterior region, one spiniform trichome on alar region, and 2+2 small simple setae oin ventral margins; thorax with rounded and pointed tubercles most densely distributed on surface of posterior region.

Abdomen: abdominal tergite I with 1+1 submedian, 1+1 sublateral long simple setae, and 2-3 small simple setae on lateral margins; tergite II with 4+4 long spiniform setae in row, 1+1 small simple setae anterior to outermost spiniform setae, and 2+2 small setae on lateral margins; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 1+1 small simple setae anterior to outermost hooks, and 2+2 small simple setae laterally; tergites V-VII with 1+1 submedian small simple setae; tergites VIII and IX without visible setae; tergite IX sclerotised without terminal spines. Spine combs on antero-lateral regions of tergites V-IX, some developed to resemble teeth on tergites VIII, IX. Sternite III without visible setae; sternite IV with 2+2 small simple setae laterally; sternite V with 2+2 close bifid hooks; sternites VI, VII with 2+2 well separated simple or bifid hooks; sternites VIII, IX without setae ; sternite IX weakly sclerotised. Spine combs on anterior margin of sternites IV-IX.

LARVA (Final instar). Body length 6.4-7.1 mm (mean = 6.7 mm, s.d. = 0.27, n = 5), length of head capsule 0.7-0.8 mm (mean = 0.7 mm, s.d. = 0.05, n = 5); width of head capsule 0.6-0.7 (mean = 0.6 mm, s.d. = 0.05, n = 5). Body colour dark grey dorso-laterally, whitish ventrally (specimens preserved in alcohol and/or Carnoy's). General body form as in Fig. 1083.

Head: mainly dark brown, anterior region of cephalic apotome paler. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites elongate and joined to posterior margin of postgena. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge 1.5 times longer than hypostomium (Fig. 1130). Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with the pair adjacent to base of median tooth longer than the remainder; 1+1 lateral tooth, sometime longer than sublateral teeth; 5+5 small, lateral serrations; 1+1 lines of approximately eight hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1183). Sub-esophageal ganglion unpigmented. Antenna nearly as long as labral fan stalk, antennal segments dark brown, except white area near base of segment II; length of antennal segments I-III excluding the sensillum 0.08-0.1:0.06-0.1-0.09:0.1 mm (n = 4). Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately 12 teeth, first four more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1238). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 45-53 rays each with fine, single line of spines in a row interspersed with finer spinules (n = 5).

Thorax: grey dorsally, darker grey ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 35-45 sclerotised processes of 12-17 simple hooks (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with two swollen filaments.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except few setae around anal sclerite. Anal sclerite well sclerotised with anterior arms enlarged, and posterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 100-120 rows of sclerotised process with 18-19 simple hooks (n = 4). Rectal gills with three branches, each branches with 13-14 finger-like lobules (n = 3).

Taxonomic Discussion. *Simulium ethelae* was described by DALMAT (1950) based on a reared female holotype (acc. number 3"0"-1), a pharate male allotype (acc. number 5V-7), and four females, one male and 27 pupal exuviae (as paratypes, acc. numbers 3"0"-2, 6, 5; 6A, 6C, 6B, 6D, 6W-11, 6W10, 5y-9, 5V-11) collected in Guatemala. The male was later fully redescribed by DALMAT (1955) based on link-reared specimens. In the original description DALMAT (1955) indicated that the holotype and allotype were housed at the NMNH, while paratypes were deposited in his collection. I have examined the female holotype, which is housed at the NMNH. The holotype has been micropinned and it is in poor condition. It has lost one antennal segment, the abdomen and three legs (**Material Examined**). In addition, I have examined one pinned female (as paratype) and two pinned males with a green label in H.T. DALMAT'S hand "IDEOTYPES", all housed at the NMNH (**Material Examined**). No other type material were found in the Simuliidae holdings at this institution.

The taxonomy of *S. ethelae* has been recently reviewed by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who also provided a brief description of the life stages. COSCARÓN *et al.* (2004) suggested that a closely related species, *S. chiriquiense*, might be a junior synonym of *S. ethelae.* I have studied the original description of *S. chiriquiense* and examined numerous link-reared adults, pupal exuviae and larvae collected in Costa Rica identified as this species and have the following comments to make. *Simulium chiriquiense* was described by FIELD in 1967 based on females, males and pupal exuviae collected in the Chiriquí Province, Panama. It was later recorded from Costa Rica by VARGAS *et al.* (1977). Although FIELD (1967) designated a female as holotype no depositary was given in the original description. The holotype is thought to be housed at the NMNH, but Dr. F.C. THOMPSON has informed L.M. HERNÁNDEZ (pers. comm.) that no type material of species described by FIELD is deposited in this museum, hence it is considered lost. In addition, I have also examined several pupal exuviae and adults identified by M. VARGAS as *S. chiriquiense* deposited at the MZUCR (see **Material Examined**). All morphological characters of *S. chiriquiense*, especially the adults' thoracic pattern (Figs. 305, 306, 724, 725) and number of pupal gill filaments and configuration (Fig. 1021) fall within the morphological variation found in *S. ethelae.* Therefore, I consider the two species to be conspecific.

The adult's of *S. ethelae* cannot be separated from other species of the CANADENSE species group without the examination of the pupal gill configuration (Fig. 1021). *Simulium ethelae* is best recognized by the pupal gill with two largely swollen primary branches, the dorsal being strongly corrugated and the ventral extending around the opening of the cocoon. Both branches are bent in an open C-shaped configuration (Fig. 1021). In this respect, *S. ethelae* is more closely related to *S. capricorne*, although in the latter species the filaments are much wider basally, and the dorsal branch has a longer basal prominence (Fig. 1014; see also DALMAT, 1955, Fig. 309). The pupa of *S. microbranchium* is also very similar to that of *S. ethelae*, but both primary branches are more widely open and the dorsal branch does not have a basal prominence (Fig. 1027).

In the key of DÍAZ NÁJERA & VULCANO (1962a), the larvae of *S. ethelae* may be separated from the closely related species by the posterior region of the abdomen without sclerotised accessory expansions, the anterior margin of hypostomium straight with nine teeth, and the labral fans with 34-37 rays. However, the best character to identify larvae of *S. ethelae* is the morphology of the dissected gill histoblast, in combination with the configuration of the pupal gill filaments in link-reared adults collected at the same locality as mature larvae.

Descriptions of life stages of *S. ethelae* may be found in COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN -ARIAS (2007), DALMAT (1955) and FIELD (1967) [as *S. chiriquiense*].

Simulium ethelae was placed in the subgenus *Hearlea* by DALMAT (1951), which has been recorded in key catalogues, *e.g.* COSCARÓN (1987), CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter has not been recognized in COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who still maintained *Hearlea* as a valid subgenus and placed *S. ethelae* in the JUAREZI species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. ethelae* is now placed and this is followed in the current work.

Distribution. *Simulium ethelae* has been recorded from Costa Rica, Guatemala and Mexico (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; **Material Examined**).

Biology and Medical Importance. VARGAS *et al.* (1977) recorded larvae and pupae of *S. ethelae* (as *S. chiriquiense*) in streams at 500 m to 2790 m of altitude, with water temperatures varying from 11-16 C° and flowing very fast in Costa Rica. I have found immature stages of *S. ethelae* (as *S. chiriquiense*) in Costa Rica attached to rocks and trailing vegetation in medium to large fast flowing rivers with clear water, rocky streambeds, and water temperatures of 13-15ºC and pH 7 (L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data). They were collected mainly in areas of gallery and primary forest in the Central Mountain Range between 1200 to 2000 m altitude. No females were collected biting man during field work.

2.5.1.11. *Simulium* (*Trichodagmia*) *falculatum* ENDERLEIN (Figs. 187, 239, 307, 308, 430, 536, 594, 654)

This is a poorly known species from Mexico. The description here provided is based upon examination of the female holotype.

Friesia falculata ENDERLEIN, 1929: 327. HOLOTYPE female, MEXICO: Bora del Monte; [Without date.], (*Purpus S.V.*) (ZMHU) [Examined]. [COSCARÓN, 1987: 36 regarded this species as possibly synonymous with *Simulium* (*Hemicnetha*) *paynei* VARGAS, but ADLER *et al.* 2004: 373 and HERNÁNDEZ & SHELLEY *et al.* 2005: 853 accepted it as a valid species; treated as *species inquirendae* by COSCARÓN & COSCARÓN-ARIAS, 2007: 560; considered a valid species in ADLER & CROSSKEY, 2009: 47, 2010: 48, and SHELLEY *et al.* 2010: 65.]

Simulium coffeae VARGAS, 1945c: 4. [Unnecessary replacement name for *F. falculata*; see also ADLER *et al.*, 2004 and HERNÁNDEZ & SHELLEY *et al.*, 2005 for further details.]

FEMALE. General body colour black. Body length (specimen pinned, n = 1) 3.4 mm, wing length 3.6 mm, wing width 1.7 mm.

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 187). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus covered with pale, semi-recumbent setae and frons with long, erect, black hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellar segments black. Cibarium with developed, sclerotised cornuae and without teeth in central trough (Fig. 239).

Thorax: scutum black with grey pruinosity and irregularly arranged recumbent golden setae, interspersed with fine black setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with inverted Y-shaped median grey pruinose vitta, and 1+1 submedian wide greyish pruinose vittae, extending from anterior third of scutum nearly to posterior margin; humeri, lateral and posterior margins black (Fig. 307). With posterior illumination, thorax black with 1+1 grey pruinose, comma shaped cunae with tails extending to mid region of scutum; humeri, anterior and posterior margins black (Fig. 308). Scutellum black, devoid of hairs on single specimen examined. Postnotum black with faint grey pruinosity. Pleura dark brown to black with grey pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta without hairs. Radius with single line of setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 430. Foreleg with coxa pale brown; trochanter, femur, and tibia dark brown; tarsi black. Mid leg with coxa missing; trochanter, femur, tibia, and apical half of basitarsus and remaining of tarsal segments dark brown; basal half of basitarsus whitish Hind leg with coxa pale brown; trochanter, femur, tibia and apical third of basitarsus and remaining tarsal segments dark brown; basal two thirds of basitarsus whitish. Claws strongly curved with distinct basal tooth. Halteres pale cream with brown base.

Abdomen: tergites I-IX black, segment I with faint pruinosity dorsally). Tergal plates developed. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with approximately 17 long, irregularly distributed setae on posterior margin; gonapophyses shorter, membranous, narrow apically and internal margins weakly sclerotised; gonapophyses covered with small setae distributed over entire surface (Fig. 536). Cercus subrectangular, covered with distinct, long, brown setae; paraproct crescent-shaped, sclerotised except apical third which is weakly membranous, and slightly extending beyond junction with cercus (Fig. 594). Genital fork stout and sclerotised; termination of lateral arms with anterior margins straight and well developed, apically blunt; anterior processes well developed; posterior processes absent (Fig. 654). Spermatheca globular, without external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. Unknown.

PUPA. Unknown.

LARVA. Unknown.

Taxonomic Discussion. *Simulium falculatum* was described by ENDERLEIN (1929) as *Friesia falculata* from a single female collected in Bora del Monte, Mexico by S.V.Purpus. Later, VARGAS (1945c) published the replacement name *S. coffeae* for *S. falculatum* referring to a previous paper (VARGAS, 1943a,b) in which he dealt with several names pertaining to this species. He supposed that *S. falculatum* (as *F. falculata*) was preoccupied by *S. falcula* (ENDERLEIN, 1921a) [as *Wilhelmia falcula*, mis-spelled as *jalcula* (see CROSSKEY & HOWARD, 1997)], a European species. Under the INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE (ICZN, 1999: 9, article 10.6), the name *S. coffeae* represents an unjustified replacement name because *F. falculata* and *W. falcula* are not homonyms.

The taxonomy of *S. falculatum* has been recently reviewed by HERNÁNDEZ & SHELLEY (2005), who also provided information about the condition of the female holotype. The authors dissected the holotype, and based on the structure of the cercus and paraproct, placed this species as a valid species within the subgenus *Hemicnetha*, because of its external morphological similarities with *S. paynei* (see also SHELLEY *et* *al.*, 2010). The same authors also discussed the similarity of *S. falculatum* with some species of the subgenus *Hearlea*; especially *S. ayrozai* and *S. carolinae*. ADLER *et al.* (2004) also dealt with the taxonomy of this species, and kept it within their valid subgenus *Hemicnetha*. This taxonomic change has been followed by ADLER & CROSSKEY (2008, 2009), but it was not recognised by COSCARÓN & COSCARÓN-ARIAS (2007) who considered it as *species inquirendae*. SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia* and placed *S. falculatum* in the TARSATUM species group.

I have re-examined all digital images held at the Simuliidae Digital Imaging Archive at the BMNH of *S. falculatum* ,and compared with it the original description given in ENDERLEIN (1929) and identified specimens of the CANADENSE species group by DALMAT and VARGAS & DIAZ NÁJERA housed at the BMNH, CNC, MLP, NMNH and INDRE collections, and have the following comments to make. The overall external morphology of *S. falculatum* is very similar to species in the TARSATUM species group, *e.g. S. paynei*, *S. virgatum s.l.* However, the morphology of the paraproct does not fall within the variation found in the species of the TARSATUM species group, because the paraproct only extends slightly beyond the cercus, and it is rounded apically and not setose (Fig. 594). HERNÁNDEZ & SHELLEY (2005) showed slight differences between the right and left paraprocts in this species, but discussed that this can be explained by the position of this structure in the slide as shown by SHELLEY *et al.* (2010). The general morphology of the paraproct of *S. falculatum* is most similar to that of species now assigned to the CANADENSE species group [the subgenus *Hearlea* as reviewed in COSCARÓN *et al.* (2004)], especially *S. ayrozai* and *S. carolinae* (Figs. 584, 588). Nonetheless, differences in the thoracic pattern (Figs. 307, 308), cibarium (Fig. 239) and genital fork (Fig. 654) can be seen in *S. falculatum*. Based on the latter morphological differences, and in the absence of other life stages, I here consider *S. falculatum* as a valid species in the CANADENSE species group for taxonomic stability until topotype material can be collected in order to assess its taxonomic status.

Distribution. *Simulium falculatum* has only been recorded from its type locality in Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined** in HERNÁNDEZ & SHELLEY, 2005).

Biology and Medical Importance. Nothing is known on the biology of *S. falculatum*.

2.5.1.12. *Simulium* (*Trichodagmia*) *gorirossiae* VARGAS & DÍAZ NÁJERA (Figs. 87, 99, 188, 240, 431, 537, 595, 655, 841, 902, 963, 1022, 1084, 1131, 1184, 1239, 1284)

This is a zoophilic species only known from Mexico and Guatemala. The description here provided has been based upon examination of type specimens and other identified material housed at BMNH, MLP, MZUCR, the original description of VARGAS & DÍAZ NÁJERA (1957b) and the revisions of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium (Hearlea) gorirosii VARGAS & DÍAZ NÁJERA, 1957b: 199. HOLOTYPE female, MEXICO: Chiapas State, Mariscal, Finca Guadalupe Zajú; iii.1946, (*Díaz Nájera*) (INDRE, no. 6427) [Examined.]

FEMALE. General body colour black. [COSCARÓN *et al.* (2004) recorded the wing width as 3.2 mm. Other measurements and numbers of specimens examined were not given in their paper nor in the original description].

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 188). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 240).

Thorax: scutum velvet black covered by silver vestiture. The scutal pattern is poorly known and it is not illustrated because of lack of material. Based on the description of VARGAS & DÍAZ NÁJERA, (1957b) [and probably with light source anterior], the scutal pattern varies. Thorax black with 1+1 silver vittae joined to submedian subtriangular silvery spots; lateral margins silver pruinose. Pattern unknown with posterior illumination. Postnotum black with silver pruinosity. Pleura black with silver pruinosity.

Costa of wing with dense distribution of spines and setae. Subcosta with line of setae except on apical third. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 431. Coxa, trochanter, apical third of femur and tibia, and tarsal segments I-IV dark brown; remainder of femur and tibiae pale brown. Mid and hind legs with coxae, trochanters, apical thirds of femora and tibiae and patches on internal surface of femora, apical half of tarsal segment I, apex of tarsal segment II, and tarsal segments II-IV dark brown; remainder of femora and tibiae paler brown; basal third of tarsal segment I and base of tarsal segment II whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites black. Tergal plates developed. Sternites and genitalia dark black. Eighth sternite sclerotised with short irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular with curved internal margins, weakly sclerotised toward internal margins, remainder membranous; gonapophyses with covered with microtrichiae (Fig. 537. Cercus subrectangular, covered with brown setae; paraproct subtriangular, extending beyond junction with cercus; ventral extension of the paraproct with two lobes apically, one lobe subdivided in three smaller finger-like lobules; paraproct densely covered with prominent hairs (Fig. 595). Genital fork stout and sclerotised with stem expanded apically; termination of lateral arms with anterior margins straight and well developed; anterior processes well developed; internal posterior processes weakly developed (Fig. 655). Spermatheca globular, with weak external sculpturing and groups of 2-3 internal spicules; area of insertion of spermathecal duct membranous.

MALE. General body colour black. [COSCARÓN *et al.* (2004) recorded the wing width as 3.0 mm. Other measurements and numbers of specimens examined not given in the latter paper nor in the original description.]

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black. Scutal pattern poorly known and it is not illustrated because of lack of material. Based on the description of VARGAS & DÍAZ NÁJERA, (1957b) [and apparently with light source anterior] the thorax is black with anterior third silver pruinose. The scutal pattern is unknown with light posterior to specimen. Humeri and lateral margins dark brown with pruinose areas. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare and R with only spines in the two specimens examined. Leg coloration as in female.

Abdomen: tergites dark brownish black, basal fringe with long, brown hairs. Gonocoxite subquadrangular with one antero-lateral margin weakly produced; gonostyle elongate, about two and half times longer than gonocoxite, wide basally and narrow at mid point, with flap-like ridge basally and terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 841). Ventral plate weakly sclerotised, subrectangular, covered with long hair; anterior median process developed and central keel covered with long hairs; lateral shoulders slightly developed and basal arms well developed and subparallel (Fig. 902). Median sclerite not examined. Paramere with well developed and sclerotised basal processes and numerous long spines along whole length (Fig. 963).

PUPA. [COSCARÓN *et al.* (2004) gave measurements as follows: Cocoon dorsal length 1.5-1.7 mm; basal length 2.4-2.7 mm. Other measurements and numbers of specimens examined were not given in the latter paper nor in the original description]; gill length 1.9-2.0 mm (n = 2).

Cocoon: slipper-shaped as in Fig. 65, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: dark brown with filaments pointing upwards, forwards and ventrally in vertical plane. Gill configuration similar to that of *S. johnsoni* and *S. larvispinosum*: gill with main trunk short giving rise to two sets of primary branches, one dorsal and one ventral. Dorsal primary branches with seven secondary filaments arranged as follows: one longer filament wider at base, narrowing towards apex, and directly upward, one small filament on basal third of longest filaments, four filaments in 2+2 arrangement, and one basal single finger-like filament, curved and directed towards surface of pupa. Ventral primary branch single, very long and curved upwards at midpoint and nearly encircling frontoclypeus (Fig. 1022). Filaments stout pointed and sclerotised apically, with small spicules on surface, edges crenate; dorsal secondary filament of the dorsal primary branch longer than remaining filaments.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial long spiniform simple trichomes. Frontoclypeus platelets not visible in single specimen examined; tubercles rounded and well distributed over entire surface.

Thorax: with 4+4 spiniform trichomes near margin of dorsal cleft, one spiniform trichome on central region and 1-2 spiniform trichomes on ventral margin of thorax; tubercles rounded with some pointed most densely distributed on gill base and postero-dorsal region of thorax.

Abdomen: [chaetatotaxy not described because of lack of material].

LARVA (Final instar). [COSCARÓN *et al.* (2004) recoded the body length as 6.5-7.0 mm. Other measurements and numbers of specimens examined not given in their paper nor in the original description.] Body colour light yellowish grey (preservation of specimens not stated, but probably in ethanol) (Figs. 87, 1084).

Head: mainly yellow brown. Postgenal cleft triangular, pointed apically; postgenal bridge wide, 1.5 times longer than hypostomium (Fig. 1131). Hypostomium strongly pigmented on anterior margin, with nine apical teeth distinctly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth the pair most basal to median tooth longer than remainder; 1+1 lateral teeth; lateral serrations absent; 1+1 lines of approximately eighteen hypostomial setae parallel to lateral margins (Figs. 1184). Antennal segments extending beyond apex of labral fan stalk, segments pale brown; length of antennal segments I-III excluding the sensillum 0.9-0.1:0.1:0.1 mm (n = 2). Mandible with two apical teeth, first one longer than second; mandibular comb with eight teeth, first four more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1239). Lateral mandibular process present following COSCARÓN *et al.* (2004). Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with more 50-52 rays with fine, single line of spines in a row.

Thorax: grey dorsally. Cuticle without setae. Proleg with plate heavily sclerotised process of 47-55 teeth.

Abdomen: usually grey. Abdominal segment VIII with 1+1 ventro-lateral papillae weakly sclerotised. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms; posterior arm encircling posterior circlet; posterior circlet with heavily sclerotised accessory plates consisting of 2+2 dorso-lateral conical process and 1+1 ventro-lateral processes of 8+8 conical spiny processes (Fig. 1284). Posterior circlet with 272-283 rows of 30-35 simple hooks. Rectal gills with three branches with 6-10 finger-like lobes giving a total of 18-30 lobules.

Taxonomic Discussion. *Simulium gorirossiae* was described by VARGAS & DÍAZ NÁJERA (1957b) based on a male holotype (no. 6427), one female (allotype, no. 6428), one female and one male (paratypes, no. 6429, 6430), and approximately 25 immature pupal exuviae [all as paratypes] collected in Mexico. The larva was also described in this paper, but no larvae were designated as paratypes. The larva was fully illustrated later by DÍAZ NÁJERA & VULCANO in 1962a. I have examined a slide labelled as "*Simulium gorirossiae* Holotype" housed at INDRE that only contains the male genitalia. The slide also bears in VARGAS'S handwriting the locality information and the number system (INDRE no. 6427) given in the original description of this species (**Material Examined**). The remaining structures of the holotype were not found in the INDRE Simuliidae holdings (H. HUERTAS - pers comm. to L.M. HERNÁNDEZ). I have also examined the female allotype, which has been dissected and it is now on a slide that contains its head, genitalia and gill filaments; the remaining structures of the allotype were not found in the INDRE collection. I have examined two further slides containing three legs and one wing of a female and male also at INDRE. The remaining structures of the latter specimens could not be found in this collection (H. HUERTAS pers. comm. to L.M. HERNÁNDEZ). I have taken digital images of salient taxonomic characters of the type material of *S. gorirossiae*, which are now deposited in the BMNH Simuliidae Digital Archive.

The general morphology of adult *S. gorirossiae*, especially the female paraproct (Figs. 595) and male gonostyle (Fig. 841) falls within the variation found in species of the CANADENSE species group from which they cannot be separated without examination of the pupal gill filaments in link-reared specimens.

The gill configuration of *S. gorirossiae* (Fig. 1022) is most similar to that of *S. larvispinosum* (Figs. 77, 1025). However, in *S. gorirossiae* the dorsal primary branch has seven secondary filaments, the longest secondary filament being wider basally, narrowing to the apex with sclerotised tips. Furthermore, in *S. gorirossiae* the small filament in the basal third of the longest filament is single (Fig. 1022). In *S. larvispinosum* the dorsal primary branch has 13 secondary filaments, the longest secondary dorsal filament is swollen and of the same width over its entire length, and it is rounded and unsclerotised apically. The small filaments at the basal third of the longest filament are prominently swollen and bifid (Figs. 77, 1025).

The larva of *S. gorirossiae* can be readily separated from that of *S. larvispinosum* by the presence of secondary accessory sclerotised plates having 2+2 long dorso-lateral conical process and 1+1 ventro-lateral accessory plates consisting of seven long conical processes covered by short spicules (Figs. 1284) [see also pictorial key to larva of DÍAZ NÁJERA & VULCANO, 1962a)]. A similar species is *S. menchacai*, but its secondary plates only have 1+1 conical processes that are relatively much shorter, and the 1+1 ventro-lateral accessory plates have 4-5 conical processes, with the most ventral being the longest (Fig. 1287).

Another closely related species to *S. gorirossiae* is *S. johnsoni*, but in this species the pupal gill configuration (Fig. 1023) and the larval morphology, especially the structure of the sclerotised accessory plates is rather different (Figs. 1284, 1285).

Simulium gorirossiae was placed in the subgenus *Hearlea* by VARGAS & DÍAZ NÁJERA (1957b), and this has been accepted by most workers, *e.g.* COSCARÓN (1987) and CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic action was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed *S. gorirossiae* in the CAROLINAE species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. gorirossiae* is now placed.

Distribution. *Simulium gorirossiae* has only been recorded in Mexico and Guatemala (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. Little is known on the biology of *S. gorirossiae*. VARGAS & DÍAZ NÁJERA (1957b) stated that it was collected in Teocelo Waterfalls, a mountainous region in the Teocelo city, Veracruz State.

2.5.1.13. ***Simulium* (*Trichodagmia*) *johnsoni* VARGAS & DÍAZ NÁJERA** (Figs. 189, 241, 309, 310, 432, 538, 596, 656, 726, 727, 841a, 903, 964, 1023, 1132, 1185, 1240, 1285)

This is a zoophilic species only known from Mexico. The description here provided has been derived from the examination of type and other material deposited at INDRE, MLP, MZUCR and NMNH, the original description of VARGAS & DÍAZ NÁJERA (1957b), and the reviews of COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium (*Hearlea*) *johnsoni* VARGAS & DÍAZ NÁJERA, 1957b:203. HOLOTYPE male (reared), MEXICO: Veracruz State; Cascada de Teocelo; v.1946, (*J.Parra*) [Examined.] (INDRE, no. 6431).

FEMALE. General body colour black. [COSCARÓN *et al.* (2004) recorded the wing length as 3.1 mm. Other measurements and numbers of specimens examined were not given in the latter paper nor in the original description.]

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 189). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs.

Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth and concave trough (Fig. 241).

Thorax: scutum black with evenly arranged, recumbent, white hairs interspersed with long, erect black hairs on posterior margin. Scutal pattern varying slightly with illumination. With anterior illumination, thorax largely pollinose on black background with 1+1 indistinct submedian black vittae [pollinose areas with bluish reflections can be seen with certain lights]; humeri and posterior margins weakly silver pruinose; lateral margins black (Fig. 309). With posterior illumination, thorax black with 1+1 silver round spots on anterior third of scutum; humeri weakly pruinose; lateral and posterior margins black (Fig. 310). Scutellum black with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 432. Fore leg with coxa, trochanter, femur, basal and apical thirds of tibia, and tarsal segments I-IV dark brown; mid region of tibiae white. Mid leg with coxa, trochanter, base and apex of femur, apical third of tibia, apical half of tarsal segment I, and tarsal segments II-IV dark brown; remainder of femur and tibia pale yellowish, and basal half of tarsal segment I whitish. Hind leg with coxa, trochanter, apical third of femur, apical third of tibia, apical half of tarsal segment I, and apical third of tarsal segment II, and tarsal segments II-IV dark brown; remainder of femur and tibia pale brown to yellowish, basal half of tarsal segments I and II whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites black with silver pruinosity on lateral margins of segment II. Tergal plates well developed. Sternites and genitalia dark black. Eighth sternite sclerotised with 10 long irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular and well separated with internal margin lightly curved; gonapophyses with basal half membranous, apical half sclerotised, covered by microtrichiae (Fig. 538). Cercus rectangular; paraproct sclerotised, without membranous process apically or at junction with cercus; cercus and paraproct covered with brown setae (Fig. 596). Genital fork stout and sclerotised with termination of stem swollen; termination of lateral arms with anterior margins curved and well developed; anterior processes and internal posterior process well developed and blunt apically (Fig. 656). Spermatheca not examined because of lack of material.

MALE. General body colour black. Body length (specimens pinned, n = 1) 2.9 mm, wing length 2.5 mm, wing width 1.2 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered with evenly distributed recumbent yellowish hairs interspersed with semi-erect brown hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with silver pruinose band on anterior third of scutum [some bluish reflections on the silver band can be seen with certain lights] (Fig. 726). With posterior illumination, thorax dark brown to black (Fig. 727). Humeri pale brown; lateral and posterior margins dark brown to black. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare in the single specimen examined. Leg coloration as in female.

Abdomen: tergites dark brown to black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites V-VII [best seen in some specimens when tilted and viewed laterally]. Genitalia brown; sternal plates developed. Gonocoxite subquadrangular, with one antero-lateral margin produced; gonostyle prominently elongate, three times longer than gonocoxite, with lateral margins weakly sinuous, narrower at mid point, with a ridge basally, and terminating in single stout spine; gonocoxite and gonostyle covered with long setae (Fig. 841a). Ventral plate sclerotised, subquadrangular, main body with anterior margin produced centrally into small triangular process; lateral shoulders weakly developed, basal arms well developed, subparallel (Fig. 903). Median sclerite not examined. Paramere with well developed and sclerotised basal process and numerous long spines along entire length (Fig. 964).

PUPA. [Coscarón *et al.* (2004) gave measurements as follows: Basal length 3.1 mm; dorsal length 2.9.mm. Other measurements and numbers of specimens examined were not given in their paper or the original description]. Gill length 2.3-4.0 mm (mean = 3.3 mm, s.d. = 1.1, n = 4).

Cocoon: slipper-shaped as in Fig. 65, dark brown to black, composed of thick, compact fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with filaments upwardly, forwardly and ventrally directed in vertical plane. Gill with main trunk short giving rise to two sets of primary branches, one dorsal and one ventral. Dorsal primary branches with seven secondary filaments arranged as follows: one long filament swollen along its length and directly upwards, one small filament on basal third of longest filament, four filaments at base of longest filament directed forwards, and small, curved filament at base of longest filament backwardly directed. Ventral primary branch single, very long and nearly encircling frontoclypeus (Fig. 1023). Filaments stout, with longest filament of dorsal branch rounded apically, remainder of secondary filaments and ventral primary branch prominently sclerotised apically; filaments without spicules on surface, edges weakly crenate.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial long spiniform simple trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 3-4 platelets in two groups laterally in frontal region; tubercles absent.

Thorax: with 4+4 spiniform trichomes near margin of dorsal cleft, one spiniform trichome on central region and 1-2 spiniform trichomes on ventral margin of thorax; rounded tubercles most densely distributed on gill base and postero-dorsal region of thorax.

Abdomen: abdominal tergite I without visible setae and distinct band of tubercles along posterior margin; tergite II with 4+4 submedian spiniform setae in longitudinal row with circumjacent rounded tubercles; tergites III, IV with 4+4 submedian simple hooks; tergites V-VII without setae; tergite IX weakly sclerotised without terminal spines. Spine combs were not described because of the poor condition of the few specimens available. Sternite V with 2+2 close bifid hooks; sternites VI, VII with well separated simple hooks; sternites VIII, IX without setae. Sternite IX and spine combs were not described because of the poor condition of the few specimens available.

LARVA (Final instar). [Coscarón *et al.* (2004) recorded the body length as 8.5 mm. Other measurements and numbers of specimens examined were not given in their paper nor in the original description]. Body colour grey (preservation of specimens not stated, but probably in ethanol).

Head: mainly yellowish. Postgenal cleft bell-shaped, with narrow antero-median incision; postgenal bridge wide, 1.5 times longer than hypostomium (Fig. 1132). Hypostomium strongly pigmented in anterior margin, with eight to nine apical teeth distinctly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth; 1+1 lateral teeth; 5+5 small, lateral serrations; 1+1 lines of approximately eleven hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1185). Antenna pale brown; length of antennal segments I-III excluding the sensillum 0.1:0.1:0.1 mm (n = 1). Mandible with two apical teeth, first one longer than second; mandibular comb with seven teeth, first three more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1240). Lateral mandibular process present. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 54-56 rays each with fine, single line of spines in row.

Thorax: grey dorsally. Cuticle without setae. Proleg with plate heavily sclerotised process.

Abdomen: usually grey. Ventral papillae absent from segment VIII. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms; posterior arms with 2+2 dorso-laterally sclerotised accessory plates and 1+1 ventro-lateral accessory plates consisting of five processes (Fig. 1285). Posterior circlet with 242 rows of 26-36 simple hooks. Rectal gills with three branches with seven finger-like lobes per branch.

Taxonomic Discussion. Vargas & Díaz Nájera (1957b) described *S. johnsoni* based on a male holotype, four females (one as allotype), two males, and an extra specimen of unknown sex collected from Veracruz and Oaxaca States, Mexico. The larva was later described for the first time by Díaz

NÁJERA & VULCANO (1962a) based on specimens collected at San Felipe del Agua in Oaxaca State, Mexico (**Material Examined)**. I have examined the male holotype, which is housed at INDRE (no 6431) and mounted on one slide. I have also examined the female allotype (no. 6432) and two other female paratypes (nos. 6433, 6434) mounted on three slides (**Material Examined**). The holotype is in relatively good condition, though the slide only contains part of a maxillary palp, the male genitalia, one side of the pupal thorax and a gill of one side. The paramere and one gonostyle are partially damaged; the remainder of the holotype was not found in the INDRE Simuliidae collection (H. HUERTAS - pers. comm. to L.M. HERNÁNDEZ). The slide containing the allotype is also in good condition, though it only includes one pupal gill filament and the female paraprocts. The remainder of the allotype is missing and could not be found at INDRE (H. HUERTAS - pers. comm. to L.M. HERNÁNDEZ) (**Material Examined**).

The thoracic pattern of female *S. johnsoni* is unique within the CANADENSE species group by being highly pruinose with some bluish reflections leaving 1+1 black submedian vittae, which extends from the anterior to posterior margins (Fig. 309, 310). The male has the most common thoracic pattern with a silver pruinose band on the anterior third of scutum (Figs. 726, 727). However, the best character to identify *S. johnsoni* is the pupal gill configuration in link-reared specimens.

The pupal gill configuration pattern of *S. johnsoni* (Fig. 1023) falls within the morphological variation found in *S. gorirossiae* (Fig. 1022), indicating that these two species might be conspecific. Nonetheless, larvae identified as *S. johnsoni* can be separated from those of *S. gorirossiae* by the presence of four prominent dorsal accessory sclerotised plates and 1+1 ventro-lateral accessory plates with only five short processes (Fig. 1285). In *S. gorirossiae* the ventro-lateral accessory plates have eight prominent conical processes (Fig. 1284) [see also DÍAZ NÁJERA & VULCANO, 1957b; Figs. 67-75]. The larva of *S. larvispinosum* is also morphologically similar to that of *S. johnsoni*, but it can be readily separated from *S. johnsoni* by the presence of 1+1 dorsal rectangular flattened accessory plates (Fig. 1286) [see also COSCARÓN & COSCARÓN-ARIAS, 2007]. Because of the lack of material and based on the morphological differences discussed, I prefer to maintain *S. johnsoni* and *S. gorirossiae* as valid species until more material is available in order to assess their taxonomic status.

Simulium johnsoni was placed in the subgenus *Hearlea* by VARGAS & DÍAZ NÁJERA (1957b), and this has been accepted by most workers, *e.g.* COSCARÓN (1987), CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic action was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the CAROLINAE species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. johnsoni* is now placed.

Distribution. *Simulium johnsoni* has only been recorded from Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. Nothing is known on the biology of *S. johnsoni.*

2.5.1.14. *Simulium* (*Trichodagmia*) *juarezi* VARGAS & DÍAZ NÁJERA (Figs. 242, 539, 597, 657, 842, 904, 965, 1024, 1186, 1241)

This is a zoophilic species only known from Mexico. The description here provided has been based upon examination of identified material housed at INDRE, MLP and MZUCR, the original description of VARGAS & DÍAZ NÁJERA (1957b), and the revisions of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium (Hearlea) juarezi VARGAS & DÍAZ NÁJERA, 1957b: 205. HOLOTYPE male, MEXICO: Oaxaca State, Ixtlán, El Estudiante; 12.x.1948, *(I.Córdova)* (INDRE, 6435) [Holotype said to be housed at INDRE, but not found at present in the institution, H. HUERTAS - pers. comm. to L.M. HERNÁNDEZ 2008 - see **Taxonomic Discussion**].

FEMALE. General body colour black. [COSCARÓN *et al.* (2004) recorded wing width as 3.3-3.8 mm. Other measurements and numbers of specimens examined were not given in the original description.]

Head: dichoptic with dark red eyes and nudiocular area developed. Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth, anterior margin weakly concave on central trough (Fig. 242).

Thorax: scutum dark brown with evenly arranged recumbent white hairs. Scutal pattern is poorly known and it has not been illustrated because of lack of material. Based on the description of COSCARÓN *et al.* (2004) [and probably with anterior illumination] thorax dark brown with 1+1 median pear-shaped vitta and 1+1 sublateral wide rounded silver pruinose vittae extending from anterior to posterior margins; humeri greyish; lateral and posterior margins brown. The thoracic pattern is unknown with light source posterior. Scutellum brown with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with 2-3 hairs. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration following COSCARÓN *et al.* (2004): Fore leg with coxa, trochanter, femur, tibia and tarsal segments black except anterior region of tibiae which is white. Mid leg with coxa and trochanter black; femur and tibia brown with apical third black, basal half of tarsal segment I brown, remainder of segment I and tarsal segments II-IV black. Hind leg with coxa, trochanter, femur, tibia and tarsal segments black. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergite I brown with black spots centrally. Tergal plates well developed. Sternites and genitalia dark brown. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, almost square with curved internal margins, weakly sclerotised, densely covered with long hairs (Fig. 539). Cercus subrectangular, covered with brown setae; paraproct subrectangular extending beyond cercus; ventral extension of paraproct with prominence at junction with cercus and narrower apically; paraproct sclerotised densely covered with prominent brown hairs (Fig. 597). Genital fork stout and sclerotised; termination of lateral arms with anterior margins curved and well developed; anterior processes well developed and blunt apically, posterior processes undeveloped (Fig. 657). Spermatheca not examined.

MALE. General body colour black. [COSCARÓN *et al.* (2004) recorded the wing length as 3.2-3.6 mm. Other measurements and numbers of specimens examined were not given in their paper nor in the original description.]

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered by semirecumbent white hairs. Scutal pattern is poorly known and it has not been illustrated because of lack of material. Based on the description of COSCARÓN *et al.* (2004) [and probably with light source anterior] thorax black with 1+1 silver pruinose vittae on anterior third arising from antero-lateral margins and extending to centre of scutum; greyish area between silver pruinose vittae, single black lines extending from anterior to posterior margins. The thoracic pattern is unknown with posterior illumination. Humeri greyish; lateral and posterior margins black. Scutellum brown. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare. Leg coloration as in female though slightly darker brown.

Abdomen: tergites black, without pruinose ornamentation, basal fringe with long, brown hairs Genitalia brown; sternal plates developed as in *S. capricorne.* Gonocoxite subquadrangular with one antero-lateral margin produced; gonostyle elongate, twice as long as gonocoxite, with margins weakly sinuous and terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 842). Ventral plate weakly sclerotised, subrectangular; main body of ventral plate developed and anterior margin emarginated centrally, without central process; lateral shoulders weakly developed, basal arms well developed and subparallel (Fig. 904). Median sclerite not described because of lack of material. Paramere with well developed and sclerotised basal processes and numerous long spines along whole length (Fig. 965).

PUPA. [COSCARÓN *et al.* (2004) recoded the cocoon length dorsally as 3.2-3.5 mm; basally as 2.3-4.0 mm. Other measurements and numbers of specimens examined were not given in the original description]; gill length 2.8-3.1 mm (n = 2).

Cocoon: slipper-shaped as in Fig. 65, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: dark brown with three swollen filaments upwardly, forwardly and ventrally directed and in vertical plane (Fig. 1024). Gill with main trunk short giving rise to three primary branches, one dorsal, one median and one ventral. Dorsal branch apex directed upwards, relatively shorter, wide basally and narrower towards apex; median branch directed forwards, extremely enlarged and bulbous, sometimes with tubercles; ventral branch directed ventrally, 1.5 times longer than dorsal primary branch, somewhat bent on apical third. Filaments stout, rounded distally, without spicules on surface with numerous pseudoannulations and crevices, edges crenate; median primary filament more prominent than remaining filaments.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial spiniform trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 5 platelets in two groups laterally in frontal region; tubercles rounded, densely distributed over entire surface.

Thorax: with 3+3 spiniform trichomes near margin of dorsal cleft, one spiniform trichome on central region and one spiniform trichome on posterior region, and 2+3 long simple trichomes on ventral margin of thorax; tubercles rounded and well distributed over entire surface.

Abdomen: [chaetotaxy not described because of lack of material, but probably with same pattern as in other species of the CANADENSE species group].

LARVA (Final instar). [COSCARÓN *et al.* (2004) recorded the body length as 7.5 mm. Other measurements and numbers of specimens examined were not given in the original description.] Body colour dark green with yellow spots dorso-laterally, yellowish ventrally [specimen preservation not stated, but probably in ethanol].

Head: black, anterior region of cephalic apotome yellowish. Postgenal cleft deep and bell-shaped. Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth; 1+1 lateral teeth, longer than 3+3 sublateral teeth; 10+10 lateral serrations; 1+1 lines of approximately 8-10 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1186). Antennal segments lightly pigmented [measurement not given because of lack of material]. Mandible with two apical teeth, first one longer than second; mandibular comb with approximately eleven teeth, first fifth more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1241). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 50 rays each with fine, single line of spines in a row.

Thorax: greenish dorso-laterally. Cuticle without setae. Proleg with plate heavily sclerotised.

Abdomen: usually greenish dorsally, progressively paler ventrally. Ventral papillae absent. Cuticle lacking setae except spiny area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with approximately 145 rows of 17 simple hooks. Rectal gills with three branches each with 5-7 finger-like lobules per branch giving a total of 15-21 lobules; median lobules larger than remainder.

Taxonomic Discussion. *Simulium juarezi* was described by VARGAS & DÍAZ NÁJERA (1957b) based on a male holotype, one female allotype and one male, two females (partially pinned and mounted on slides) and 10 pupal exuviae (in alcohol) (all as paratypes) collected in the state of Oaxaca, Mexico. The larva was later described for the first time by DÍAZ NÁJERA & VULCANO (1962a). The illustration of the genitalia of the holotype was apparently based upon a pharate pupa (VARGAS & DÍAZ NÁJERA, 1957b) mounted on a slide. The holotype (no. 6435), the allotype (no. 6436), the two paratypes (nos. 6437-38) and all pupal exuviae were said to be deposited at INDRE, but no type material was found at this institution (H. HUERTAS - pers. comm. to L.M. HERNÁNDEZ, 2008). However, records of loans made showed that four type specimens were lent to VICTOR PY-DANIEL (INPA) in 1986. Numerous attempts to contact VICTOR PY-DANIEL by H. HUERTAS and myself during the course of this work in order to retrieve or borrow this material were unsuccessful.

The adult thoracic pattern of *S. juarezi* and its general morphology, especially the female and male genitalia (Figs. 539, 597, 657, 842, 904, 965) fall within the variation found in species of the CANADENSE species group. Adult *S. juarezi* may only be separated by the examination of the pupal gill configuration in link-reared specimens.

The best character to identify *S. juarezi* is the gill configuration of its pupa, which is unique within the CANADENSE species group in having the dorsal primary branch directed upwards, and the median primary branch extremely swollen and bulbous, and directed forwards (Fig. 1024). No other species in this species group has a similar gill configuration.

In the key to larvae of DÍAZ NÁJERA & VULCANO (1962a) *S. juarezi* may be separated from other closely related species by the posterior region of the abdomen without sclerotised accessory plates, anterior margin of hypostomium straight with nine teeth and labral fans with more than 37 rays. In this respect, *S. juarezi* is similar to *S. delatorrei* and *S. capricorne* from which it can only be distinguished by the morphology of the dissected gill histoblast in mature larvae.

Simulium juarezi was placed in the subgenus *Hearlea* by VARGAS & DÍAS NÁJERA (1957b), which was accepted in key catalogues, *e.g.* COSCARÓN (1987), CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter was not recognized in COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who still maintained *Hearlea* as valid subgenus and placed *S. juarezi* in their JUAREZI species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. juarezi* is now placed.

Distribution. *Simulium juarezi* has only been recorded from Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN *et al.*, 2004; COSCARÓN & COSCARÓN-ARIAS, 2007; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. Nothing is known on the biology of *S. juarezi*.

2.5.1.15. *Simulium* (*Trichodagmia*) *larvispinosum* DE LEÓN (Figs. 77, 190, 243, 311, 312, 433, 540, 598, 658, 728, 729, 844, 905, 966, 1025, 1133, 1187, 1242, 1286)

A zoophilic species only known from Guatemala and Mexico. The description here provided has been derived from the original description of DE LEÓN (1948), examination of identified material housed at NMNH, MLP and MZUCR collections, and the revisions of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium (Hearlea) larvispinosum DE LEÓN, 1948: 5. SYNTYPES females, males, pupal exuviae and larvae (males and females apparently reared), GUATEMALA: Suchitepéquez Department, Chicacao Municipy, Finca Olas de Mocá, in small waterfall; [Without date or collector's name.] [Syntypes said to be deposited in the private collection of J. ROMEO DE LEÓN, but location of this collection unknown.] [Synonymised with *S. carolinae* by VARGAS & DÍAZ NÁJERA, 1948: 337; revalidation by DALMAT, 1955: 267 and accepted by most authors, *e.g.* ADLER & CROSSKEY (2008, 2009, 2010), COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007) and SHELLEY *et al.* (2010).]

FEMALE. General body colour black. Body length (specimens pinned) 2.7-2.9 mm (mean = 2.8 mm, s.d. = 0.11, n = 4); wing length 2.1-2.7 mm (mean = 2.3 mm, 0.30, n = 3), wing width 1.3-1.4 mm (n = 2).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 190). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown.

Cibarium with well developed, sclerotised cornuae and without teeth, with 1+1 thick prominences at base of cornuae; anterior margin concave on central trough (Fig. 243).

Thorax: scutum dark brown covered with evenly arranged recumbent white hairs interspersed with long erect black hairs especially on posterior margin. Scutal pattern varying slightly with illumination. With anterior illumination, thorax largely silver pollinose on black background with 1+1 black rounded vittae on anterior third of scutum, separated from 1+1 submedian black vittae that arise on mid length of thorax and diverge laterally on posterior margin; faint brownish line centrally with certain lights; humeri silver pruinose, lateral and posterior margins black (Fig. 311). With posterior illumination, thorax black with 1+1 rounded silver pruinose vittae on anterior third; faint greyish areas on central region of thorax; humeri silver pruinose; lateral and posterior margins black (Fig. 312). Scutellum dark brown with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae except bare apically. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 433. Fore leg with coxa, trochanter, apex of femur, base and apex of tibiae, and tarsal segments I-IV dark brown; remainder of femur and tibia pale brown. Mid and hind legs with coxae, trochanters, apex of femora and tibiae, and apical half of tarsal segments I, and tarsal segments II-IV dark brown; remainder of femora and tibiae pale brown; remainder of tarsal segment I whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites black with silver pruinosities on tergites I, II. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly 1.5 times longer than eighth sternite at mid point, subtriangular, with curved internal margins, weakly sclerotised and densely setose (Fig. 540). Cercus subrectangular, covered with brown setae; paraproct subrectangular extending beyond junction with cercus; ventral extension of paraproct subquadrangular apically; paraproct sclerotised basally and membranous and highly setose on apex (Fig. 598). Genital fork stout and sclerotised with stem expanded apically; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed and blunt apically, posterior processes developed (Fig. 658). Spermatheca globular, with weak external sculpturing and single small internal spicules; area of insertion of spermathecal duct membranous.

MALE. General body black. [DALMAT (1955) and COSCARÓN *et al.* (2004) recorded the body length as 3.2 mm, wing length as 3.4 mm, wing width as 1.4 mm. The numbers of specimens examined was not given in the latter paper.]

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered by recumbent whitish hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with 1+1 silver pruinose areas on anterior third of scutum, and 1+1 faint grey bands on central region with certain lights; humeri silver pruinose; lateral and posterior margins black (Fig. 728). With posterior illumination, thorax black [with certain lights faint pruinosities can be seen on lateral margins] (Fig. 729); humeri silver pruinose; lateral and posterior margin black. Scutellum black with golden, recumbent hairs and long, erect black setae. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Sc pilose in specimens I examined. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II. Genitalia black; sternal plates developed. Gonocoxite subquadrangular with one antero-lateral margin produced; gonocoxite elongate, 2.5 times longer than gonocoxite, slightly narrower and curved towards apex, and terminating in single spine; gonocoxite and gonostyle covered with long setae (Fig. 843). Ventral plate prominently subquadrangular, sclerotised, with anterior margin produced centrally into very small triangular process; main body of ventral plate with central keel extending from dorsal to ventral margins and distinctly covered with hairs; lateral shoulders absent, basal arms well developed and subparallel (Fig. 905). Median sclerite about three times longer than wide at widest point, without visible apical incision (Fig. 905). Paramere with well developed and sclerotised basal process and numerous long spines along entire length (Fig. 966).

PUPA. [COSCARÓN *et al.* (2004) recorded the cocoon basal length as 3.4 mm. DALMAT (1955) gave measurements for the length of the cocoon base as 3.4 mm; greatest width as 1.9 mm; greatest height as 1.4 mm. Other measurements and numbers of specimens examined were not given in the latest paper]; gill length 2.2-3.0 mm (mean = 2.6 mm, s.d. = 0.18, n = 5).

Cocoon: slipper-shaped as in Fig. 65, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: dark brown with 12-14 filaments upwardly and ventrally directed in vertical plane (Fig. 77, 1025). Gill with main trunk short giving rise to two primary branches one dorsal and one ventral. Dorsal primary branch with 11-12 secondary branches arranged as follows: one very long anterior branch expanded throughout its entire length, upwardly directed towards anterior region of pupal thorax, two small filaments arising from short trunk on basal third, and 6-7 secondary filaments arising from short trunk that divide into two branches having 5 and 3 filaments, respectively; single small pointed filament on the longest filaments and opposite to basal branches directed towards pupal thorax. Ventral filament extremely long, curved directed towards frontal region of frontoclypeus. Filaments stout, with longest filament rounded distally, remaining filaments pointed and sclerotised; surface of filaments covered by small spicules, edges weakly crenate; dorsal secondary filament of anterior primary branch longer than remainder of filaments.

Head (*frontoclypeus*): with 2+2 frontal long simple and 1+1 facial spiniform trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in two groups laterally in frontal region; tubercles rounded and only distributed in central region.

Thorax: with 3+3 spiniform trichomes near margin of dorsal cleft, one spiniform trichome in posterior region, and 1-2 long simple trichomes on ventral margin of thorax; rounded tubercles around base of gill and pointed on posterior region, all tubercles scarcely distributed over entire surface.

Abdomen: abdominal tergite I without visible setae or tubercles; tergite II with 3+3 submedian spiniform setae in longitudinal row mesally, and 1+1 simple setae laterally to outermost spiniform setae; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 2+2 simple short setae anterior to outermost hooks; tergites V-IX without visible setae; tergite IX sclerotised without terminal spines. Spine combs on antero-lateral regions of tergites V-VII. Sternite III, IV without setae; sternite V with 2+2 close simple or bifid hooks; sternites VI, VII with well separated simple or bifid hooks; sternites VIII, IX without visible setae; sternite IX weakly sclerotised. Spine combs on anterior margin of sternite IV-VIII.

LARVA (Final instar). [COSCARÓN *et al.* (2004) recorded the body length as 8.5 mm. Other measurements and numbers of specimens examined were not given in their paper nor in the original description]. Body colour grey (specimens preservation not stated, but probably in alcohol).

Head: mainly brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites elongated adjoining basal margin of apotome. Postgenal cleft deep, bell-shaped, with finger-like incision apically; postgenal bridge 1.5 times smaller than hypostomium (Fig. 1133). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth distinctly concentrated in central region; median tooth sharp, well developed and most prominent; 3+3 reduced sublateral teeth; 1+1 reduced lateral teeth; lateral serrations not visible; 1+1 lines of approximately 16 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1187). Antenna longer than labral fan stalks; length of antennal segments I-III excluding the sensillum 0.1:0.07:0.1 mm. Mandible with two apical teeth, first one longer than second; mandibular comb with approximately seven teeth, first five longer than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1242). Lateral mandibular process absent. Maxillary palps heavily pigmented, one and a half times as long as wide at base. Labral fans with 48-50 rays each with fine, single line of spines in a row.

Thorax: grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 45-50 processes.

Abdomen: usually grey. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms; posterior arms of anal sclerite encircling posterior circlet, having prominent sclerotised accessory plates as follows: 2+2 dorso-lateral conical processes, 1+1 ventro-lateral accessory plates composed of five conical process, the most ventral prominently produced, and 1+1 dorso-lateral flattened accessory plates (Fig. 1286). Posterior circlet with 152 rows of sclerotised processes of 23-26 simple hooks. Rectal gills with three branches each with 6-8 finger-like lobules giving a total of 18-24 lobules.

Taxonomic Discussion. *Simulium larvispinosum* was described by DE LEÓN in 1948 based on one male, one female and an unspecified number of pupal exuviae and larvae collected in Guatemala. As no types were designated, these specimens are therefore considered as syntypes (ICZN, 1999). DALMAT (1955) stated that the syntype material of *S. larvispinosum* was deposited in the private collection of J. ROMEO DE LEón, but the location and state of this collection is unknown.

VARGAS & DÍAZ NÁJERA (1948b) reviewed the taxonomy of *S. larvispinosum* and synonymised this species with *S. carolinae*. However, DALMAT (1955) stated that both taxa could be easily recognised by the different morphology of the larval and pupal life stages and also by the adult genitalia, hence he revalidated *S. larvispinosum*. The latter taxonomic change have been accepted by most workers (COSCARÓN *et al.*, 2004; COSCARÓN & COSCARÓN-ARIAS, 2007; CROSSKEY & HOWARD, 1997, 2004; ADLER & CROSSKEY, 2008, 2009; SHELLEY *et al.*, 2010) and it is followed in this work.

The general morphology of adult *S. larvispinosum*, especially the thoracic pattern (Figs. 311, 312, 728, 729) and the morphology of the female paraproct (Fig. 540) and male gonostyle (Fig. 843) falls within the variation found in species of the CANADENSE species group, hence they cannot be easily identified in the absence of link-reared specimens.

The best character to separate *S. larvispinosum* is the configuration of the pupal gill filaments (Figs. 77, 1025). In this respect, the pupal gill configuration of *S. larvispinosum* is most similar to that of *S. johnsoni* because the dorsal filament of the anterior primary branch is more swollen thoughtout its entire length (Fig. 1023). Nonetheless, *S. larvispinosum* can be separated by the number and configuration of the secondary branches located at the base of the dorsal longest filament of the anterior primary branch (Figs. 77, 1025). Another similar species is *S. temascalense*, but in this taxon the longest filament of the anterior primary branch is prominently more acuminate distally than in *S. larvispinosum* (see Fig. 1029). More material is needed to assess this morphological variation with regard to the taxonomic status of *S. larvispinosum* and *S. temascalense.*

In the key to larvae in DÍAZ NÁJERA & VULCANO (1962a) *S. larvispinosum* may be separated from other closely related species by the posterior region of the abdomen with accessory sclerotised plates and abdominal segment VIII without anal papillae. *Simulium carolinae*, *S. johnsoni*, and *S. temascalense* also shared these characters with *S. larvispinosum*, but the latter species may be separated by the different configuration and number of the accessory sclerotised plates (Fig. 1286) and the presence of 1+1 dorsally flattened accessory plates (following COSCARÓN *et al.*, 2004).

Simulium larvispinosum was placed in the subgenus *Hearlea* by DE LEÓN (1948) and this has been accepted by VARGAS & DÍAS NÁJERA (1957b), COSCARÓN (1987) and CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic change was not recognized by COSCARÓN *et al.* (2004; 2008) and COSCARÓN & COSCARÓN-ARIAS (2007), who still maintained *Hearlea* as valid subgenus and placed *S. larvispinosum* in their CAROLINAE species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. larvispinosum* is now placed.

Distribution. *Simulium larvispinosum* is only known from Guatemala and Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. Nothing is known on the biology and medical importance of *S. larvispinosum*.

2.5.1.16. *Simulium* (*Trichodagmia*) *menchacai* VARGAS & DÍAZ NÁJERA (Figs. 78, 191, 244, 434, 541, 599, 659, 844, 906, 967, 1026, 1188, 1243, 1287)

This is a poorly known species which has only been found in Oaxaca State, Mexico. The description here provided has been derived from the original description of VARGAS & DÍAZ NÁJERA (1957b), examination of type material housed at INDRE, examination of identified material housed at MLP, and the revisions of COSCARÓN *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955) and DÍAZ NÁJERA & VULCANO (1962a).

Simulium (Hearlea) menchacai VARGAS & DÍAZ NÁJERA, 1957b: 208. HOLOTYPE male (not associated with pupal exuviae), MEXICO: Oaxaca State, San Felipe del Agua; 14.x.1948, (*I.Córdova*) (INDRE, no. 6423) [Examined.]

FEMALE. General body colour black. [COSCARÓN *et al.* (2004) recorded the wing length as 3.5 mm. Other measurements and numbers of specimens examined were not given in their paper nor the original description.]

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 191). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth, with 1+1 thick prominences at base of cornuae; anterior margin concave on central trough (Fig. 244).

Thorax: scutum black with evenly arranged recumbent yellow hairs. Scutal pattern poorly known and it has not been illustrated because of lack of material. Based on the descriptions of VARGAS & DÍAZ NÁJERA (1957b) and COSCARÓN *et al.* (2004) [and probably with anterior illumination], the thorax is dark brown to black with 1+1 median greyish median bands, 1+1 silver pruinose vittae not adjoining 1+1 vittae joining silver spots on apical third. The pattern is unknown with posterior illumination. Scutellum dark brown with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 434. Fore leg with coxa, trochanter, external surface of femur, basal external surface and apical third of tibia, and tarsal segments I-IV dark brown; internal surface of femur and mid part of tibia pale brown. Mid and hind legs with coxae, trochanters, apex of femora and tibiae, and apical half of tarsal segments I, and tarsal segments II-IV dark brown; remainder of femora and tibiae pale brown; remainder of tarsal segment I whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.to

Abdomen: tergites black with yellow bands on central region. Tergal plates well developed. Sternites and genitalia brownish. Genitalia similar to that of *S. larvispinosum*. Eighth sternite sclerotised with few long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as eighth sternite at mid point, subtriangular, with curved internal margins, weakly sclerotised on internal margins and densely setose (Fig. 541). Cercus subrectangular, covered with brown setae; paraproct subrectangular extending beyond junction with cercus; ventral extension of paraproct subquadrangular apically; paraproct sclerotised and highly setose on apex (Fig. 599). Genital fork stout and sclerotised with stem expanded apically; termination of lateral arms with anterior margin curved and well developed; anterior processes and blunt apically, internal posterior processes developed (Fig. 659). Spermatheca globular, without external sculpturing and internal spicules in groups of 1-2 spicules; area of insertion of spermathecal duct membranous.

MALE. General body black. [COSCARÓN *et al.* (2004) recorded the wing length as 3.5 mm. Other measurements and number of specimens examined were not given in their paper nor in the original description.]

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black. Thoracic pattern poorly known, and apparently varying with light incidence. Based on the description of VARGAS & DÍAZ NÁJERA (1957b) and COSCARÓN *et al.* (2004) [with light illumination anterior], the thorax is black with 1+1 silver pruinose areas on anterior third of scutum arising on antero-lateral margins. The pattern is unknown with posterior illumination. Scutellum brown with golden, recumbent hairs and long, erect black setae. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Subcosta with 2-3 setae. Leg coloration as in female.

Abdomen: tergites black with pruinose ornamentation on antero-lateral margins, basal fringe with long, brown hairs. Genitalia black; sternal plates developed similar to that of *S. larvispinosum*. Gonocoxite subquadrangular with one anterolateral margin produced; gonocoxite elongate, 2.5 times longer than gonocoxite, slightly narrower basally and terminating in single spine; gonocoxite and gonostyle covered with long setae (Fig. 844). Ventral plate subquadrangular, sclerotised, with anterior margin produced centrally into small triangular process; main body of ventral plate with central keel extending from dorsal to ventral margins and prominently covered with hairs; lateral shoulders undeveloped, basal arms well developed and subparallel (Fig. 906). Median sclerite twice as long as wide at widest point, with visible apical incision (Fig. 906). Paramere with well developed and sclerotised basal processes and numerous long spines along whole length (Fig. 967).

PUPA. [COSCARÓN *et al.* (2004) recorded the cocoon dorsal length as 3.0 mm; basal length as 3.5 mm. Other measurements and number of specimens examined were not given in their paper or in the original description]; gill length 1.5-2.0 mm (n = 3).

Cocoon: slipper-shaped as in Fig. 65, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: dark brown with 11-12 upwardly, forwardly and ventrally directed filaments in vertical plane (Fig. 78, 1026). Gill with main trunk short giving rise to two primary branches, one dorsal and one ventral. Dorsal primary branch with 10 secondary branches arranged in four groups as follows: first group with two filaments upwardly directed, the anterior acuminate apically and longer than posterior; second group arising from long trunk and divided into 2+1 filaments; third group arising from long trunk divided at mid length into two horn-like filaments, with one subapical small filament and one smaller filament at base of trunk; fourth group with single, finger-like filaments curved towards thorax of pupa. Ventral primary branch single, very long, directed ventrally but bending upwards at mid length (Figs. 78, 1026). Filaments stout, all filaments pointed and sclerotised apically; surface of filaments covered by small spicules, edges weakly crenate; dorsal secondary filament of anterior primary branch longer than remaining filaments.

Head (*frontoclypeus*): with 2+2 long frontal and 1+1 long facial spiniform trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups of dorso-lateral and 2-3 platelets in one group laterally in frontal region; tubercles absent.

Thorax: with 2+2 spiniform trichomes near margin of dorsal cleft, one long simple trichome in posterior region, and 1-2 long simple trichomes on ventral margin of thorax; tubercles rounded and densely distributed over entire surface.

Abdomen: abdominal tergite I with 1+1 small setae laterally and line of tubercles along posterior margin; tergite II with 3+3 submedian spiniform setae in longitudinal row, and 2-3 simple setae lateral to outermost spiniform seta; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 2+2 simple short setae anterior to outermost hooks; tergites V-IX without setae; tergite IX sclerotised without terminal spines. Spine combs not visible on anterior margins of tergites. Sternites III, IV without visible setae; sternite V with 2+2 close simple hooks; sternites VI, VII with well separated simple hooks; sternites VIII, IX without visible setae; sternite IX weakly sclerotised. Spine combs on anterior margin of sternites IV-VIII.

LARVA (Final instar). [DALMAT (1955) and COSCARÓN *et al.* (2004) recorded the body length as 7.5-8.0 mm. Other measurements and number of specimens examined were not given in their paper nor in the original description.] Body colour dark green with yellowish abdomen distally (specimen preservation not stated, but probably in ethanol).

Head: mainly brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Postgenal bridge deep, bell-shaped. Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth distinctly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, the pair adjacent to median tooth most prominent; 1+1 lateral teeth; 5+5 lateral serrations; 1+1 lines of approximately fifteen hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1188). Antennal segment yellowish, except apical region of segment III which is black. Mandible with three apical teeth, first one longer than second; mandibular comb with approximately nine teeth, first four longer than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1243). Lateral mandibular process absent. Labral fan with 50-55 rays each with fine, single line of spines in a row.

Thorax: greenish. Cuticle without setae. Proleg with plate heavily sclerotised band of sclerotised processes.

Abdomen: usually greenish. Ventral papillae present on abdominal segment VIII, surrounded by small setae. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms; posterior arms of anal sclerite encircling posterior circlet, having prominent sclerotised accessory plates as follows: 2+2 dorso-lateral conical processes, 1+1 ventro-lateral accessory plates composed of nine acuminate processes, the first 5-6 most prominent; all accessory plates covered with smaller pointed processes (Fig. 1287). Posterior circlet with 310 rows of sclerotised processes of simple hooks. Rectal gills with three branches each with 6-12 finger-like lobules giving a total of 18-36 lobules.

Taxonomic Discussion. *Simulium menchacai* was described by VARGAS & DÍAZ NÁJERA (1957b) based on a male holotype, one female allotype, and one female, one male and 10 pupae exuviae (all as paratypes) collected in Mexico. The larva was first fully described by DÍAZ NÁJERA & VULCANO (1962a). The male holotype (no. 6423) and female allotype (no. 6424) and all paratypes are said to be housed at INDRE. However, I have been in recent correspondence with H. HUERTAS at INDRE, who has confirmed that neither the holotype, nor the allotype nor many of the paratypes are found in this collection (pers. comm. to L.M. HERNÁNDEZ). Nonetheless, paperwork of loans made to this collection showed that the holotype and allotype were borrowed by VICTOR PY-DANIEL (INPA) in 1986. Numerous attempts to contact PY-DANIEL by H. HUERTAS and myself to retrieve this material were unsuccessful. I have only been able to examine a single slide containing the male genitalia (and labelled as paratype) housed at INDRE (see **Material Examined**).

The female (Figs. 191, 244, 541, 599, 659) and male (Figs. 844, 906, 967) general morphology of *S. menchacai* fall within the variation found in species of the CANADENSE species group, hence they cannot be readily separated without examination of the pupal gill filament in link-reared specimens.

The best character to identify *S. menchacai* is the pupal gill configuration. The gill of *S. menchacai* is unique in that the filaments of the anterior primary branch are arranged in four groups, with the most anterior group with two filaments directed forwards, the longest prominently acuminate apically (Figs. 78, 1026). No other described species in the CANADENSE species group has a similar pupal gill configuration.

In the pictorial key to larvae of DÍAZ NÁJERA & VULCANO (1962a), *S. menchacai* keyed out to *S. gorirossiae* and *S. temascalense* based on abdominal segment VIII with 1+1 ventro-lateral papillae. However, *S. menchacai* can be separated from the latter two species by the different shape of the ventro-lateral sclerotised accessory plates (Fig. 1287).

Simulium menchacai was placed in the subgenus *Hearlea* by VARGAS & DÍAZ NÁJERA (1957b), and this has been accepted by Simuliidae workers, *e.g.* COSCARÓN *et al.* (1987), CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic action was not recognized by COSCARÓN *et al.* (2004; 2008) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the CAROLINAE species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. menchacai* is now placed.

Distribution. *Simulium menchacai* has only been found in Mexico (Adler & Crosskey, 2008, 2009, 2010; Crosskey & Howard, 1997, 2004; **Material Examined**).

Biology and medical importance. Nothing is known on the biology of *S. menchacai.*

2.5.1.17. ***Simulium (Trichodagmia) microbranchium*** **Dalmat** (Figs. 50, 192, 245, 313, 314, 435, 542, 600, 660, 730, 731, 845, 907, 968, 1027, 1134)

A zoophilic species only known from Guatemala. The description here provided has been derived from examination of the type material housed at the NMNH, other material housed at BMNH and NMNH simuliids collections, and the revisions of Dalmat (1955), Coscarón *et al.* (2004) and Coscarón & Coscarón -Arias (2007).

Simulium (Simulium) microbranchium Dalmat, 1949: 538. HOLOTYPE female (reared), GUATEMALA: Sololá Department, Rio Los Arcos near Los Encuentros; 4.xi.1948, (*Luis de la Torre & H.T.Dalmat*) (NMNH, ac. No. 0004) [Examined.]

FEMALE. General body colour black. Body length (specimen pinned) 2.4-2.5 mm (mean = 2.4 mm, s.d. = 0.05, n = 4), wing length 2.9-3.0 mm (mean = 3.0 mm, s.d. = 0.17, n = 4), wing width 1.0-1.5 mm (mean = 1.2 mm, s.d. = 0.22, n = 4).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 192). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed sclerotised cornuae, with 1+1 prominences on central trough and without teeth (Fig. 245).

Thorax: scutum black covered with evenly arranged, recumbent, golden hairs interspersed with long, erect black hairs on posterior margin. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with silver pruinose submedian vittae not adjoining anterior 1+1 silver subtrapezoidal spots, but adjoining silvery pollinose area on posterior margin (Fig. 313). With posterior illumination, thorax black with 1+1 silver spots on anterior third of scutum (Fig. 314). Scutellum black with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura dark brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 435. Fore leg with coxa, trochanter, femur and two thirds of tibia light brown; apical third of tibia and tarsal segments I-IV dark brown. Mid leg with coxa brown, apex of trochanter, apex of femur, apical half of tarsal segment I and tarsal segments II-IV dark brown; remainder parts of legs pale yellow. Hind leg with trochanter, two thirds of femur and tibia pale brown; coxa, apical third of femur and tibia, apical half of tarsal segment I and tarsal segments II-IV dark brown; basal half of tarsal segment I whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites black. Tergal plates well developed. Sternites and genitalia dark black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular with curved internal margins, weakly sclerotised, densely covered with long hairs (Fig. 542). Cercus subquadrangular, covered with brown setae; paraproct small, subtriangular extending beyond and around cercus; cercus and paraproct covered by long hairs, ventral extension of the paraproct setose apically (Fig. 600). Genital fork stout and sclerotised; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed and blunt apically, posterior processes weakly developed (Fig. 660). Spermatheca globular, with weak external sculpturing and no visible internal spicules; area of insertion of spermathecal duct weakly membranous.

MALE. General body black. Body length (specimens pinned) 2.6-3.4 mm (mean = 3.0 mm, s.d. = 0.32, n = 6), wing length 2.6-3.3 mm (mean = 2.8 mm, s.d. = 0.27, n = 5), wing width 0.9-1.5 mm (mean = 0.23, s.d. = 5).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black dark covered with recumbent yellowish hairs intersperse with black setae. Scutal pattern varies slightly with light incidence: with light source anterior thorax black with 1+1 silver pruinose areas on anterior third of scutum (Fig. 730). With posterior illumination, thorax black (Fig. 731). Humeri weakly pruinose, lateral and posterior margins black. Scutellum dark brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum dark brown to black with silvery grey pruinosity. Wing setation as in female, except Sc bare. Leg coloration as in female.

Abdomen: tergites velvet black dark, basal fringe with long black hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergite VIII (best seen in some specimens when tilted and viewed laterally). Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle elongate, wider basally and tapering toward apex, terminating in stout apical spine; gonocoxite and gonostyle covered with long setae (Fig. 845). Ventral plate sclerotised, subquadrangular, covered with short hairs; main body of ventral with anterior margin concave centrally, ventral margin convex and distinct keel centrally prominently covered by hairs; lateral shoulders developed and basal arms well developed and subparallel (Figs. 50, 907). Median sclerite nearly three times longer than wide at mid point, without visible apical incision [it appears curled up in the two specimens examined] (Fig. 907). Paramere with well developed and sclerotised basal processes and numerous long spines along whole length (Fig. 968).

PUPA. [DALMAT (1955) and COSCARÓN *et al.* (2004) recorded the cocoon length dorsally as 3.5 mm. Other measurements and number of specimens examined not given in their paper nor in the original description]; gill length 1.7 mm (n = 1).

Cocoon: slipper-shaped as in Fig. 65, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with two swollen filaments projecting forwards in vertical plane (Fig. 1027). Gill with main trunk short giving rise to two distinctly swollen primary branches one dorsal and one ventral. Both branches arranged in an open C-shape, with dorsal branch bent at a 45 degree angle (Fig. 1027). Filaments stout, rounded distally, without spicules on surface with numerous ridges and crevices, edges weakly crenate; dorsal primary filament longer than ventral.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in one group laterally in frontal region; tubercles rounded and only visible on facial region and lateral margins of frontal region.

Thorax: with 3-4 spiniform trichomes near margin of dorsal cleft, one spiniform trichome on central region and one spiniform trichome on posterior region, 1-2 spiniform trichomes on ventral region; tubercles rounded and lightly distributed over entire surface.

Abdomen: abdominal tergite I without setae in the single specimen examined; tergite II with 4+4 long spiniform setae in row, 1+1 small simple setae anterior to outermost spiniform setae; tergites III, IV with 4+4 submedian simple hooks in longitudinal row; tergites V-IX without setae; tergite IX without terminal spines. Spine combs only visible on anterior margins of tergites VI-VIII. Sternites II-IV without setae; sternite V with 2+2 close bifid hooks; sternites VI, VII with 2+2 well separated simple hooks; sternites VIII, IX without setae. Spine combs absent in anterior margins of sternites.

LARVA (Final instar). [DALMAT (1955) and COSCARÓN *et al.* (2004) gave recorded the body length as 7.7 mm. Other measurements and number of specimens examined not given in the latter paper]. Body colour dark grey.

Head: mainly dark brown. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Postgenal bridge small, bell-shaped, subtriangular with tube-like extension apically. Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth evenly distributed in central region; median tooth sharp; 3+3 sublateral teeth; 1+1 lateral teeth, longer than sublateral tooth and at level of median tooth; 1+1 lines of approximately nineteen hypostomial setae parallel to lateral margins (Fig. 1134). Antennal segments not examined. Mandible with two apical teeth well separated from each other [description of remainder of mandibular teeth not given in DALMAT, 1955]. Lateral mandibular process not examined. Maxillary palps not examined. Cephalic fan with 56-57 rays.

Thorax: grey Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 37-59 processes.

Abdomen: usually grey. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 194-206 rows of 45-46 simple hooks. Rectal gills with three lobes each with approximately 25 small, finger-like lobes.

Taxonomic Discussion. *Simulium microbranchium* was described by DALMAT (1949) based on a reared female holotype, and two males and 13 pupal exuviae (paratypes, one male labelled as allotype) collected in Guatemala. I have examined the female holotype, which is housed at the NMNH. The holotype is mounted on five slides containing the head, cibarium, wings and genitalia; the remainder of the adult and its pupal exuviae were not found in the NMNH collections (L.M. HERNÁNDEZ, May.2010). I have also examined the male allotype at the NMNH. The specimen is on three slides containing the legs, genitalia and the pupal gill filaments; the remainder of the adult was not found at the NMNH Simuliidae collection (**Material Examined**). I have taken digital images of key diagnostic characters of the holotype and allotype, which are now held at the BMNH Simuliidae Digital Images Archive. In addition, I have examined at the NMNH one pinned female and two males labelled as paratypes, and a further female paratype housed at MLP (see **Material Examined**).

Adults of *S. microbranchium* cannot be separated from other species in the CANADENSE species group based on their thoracic pattern (Figs. 313, 314, 730, 731). They have to be identified by reference to the gill configuration in link-reared adults in combination with the morphology of the genitalia.

The pupal gill configuration of *S. microbranchium* (Fig. 1027) is very similar to that of *S. ethelae* (Fig. 1021), but it can be recognized by the much shorter and straighter dorsal branch, which does not have a short prominence basally and it bends at a 45 degree angle at mid length from where it is directed forwards (Fig. 1027). In *S. ethelae* the gill configuration is different (Fig. 1021), never bending at a 45 degree angle dorsally.

I have been unable to find reliable morphological characters to separate the larva of *S. microbranchium* from other species in the CANADENSE species group. However, COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN (2007) stated that the larva of *S. microbranchium* may be identified by the body length being less than 7.0-7.7 mm, posterior portion of the abdomen without sclerotised accessory plates, hypostomium with anterior margin straight, anal papillae with 72-78 finger-like lobules and posterior circle with 194-206 rows of sclerotised processes.

Simulium microbranchium was first placed in the subgenus *Simulium* by DALMAT (1950). However, the same author placed it in the subgenus *Hearlea* in 1951 and provided a full re-description of the adults and the pupal gill. The taxonomy of the species was later reviewed in DALMAT (1955), who also described the larva of *S. microbranchium* for the first time. Further descriptions of *Simulium microbranchium* might be found in COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN (2007).

The taxonomic placement of *S. microbranchium* of DALMAT (1955) was accepted in the first two versions of the World Inventory of Blackflies by CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* under *Hemicnetha* and recognized the CANADENSE species group, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic action was not accepted by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who still considered *Hearlea* as a valid subgenus. More recently, SHELLEY *et al.* (2010) followed the classification of ADLER *et al.* (2004) classification of *Hemicnetha*, synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group where *S. microbranchium* is now placed.

Distribution. *Simulium microbranchium* is only known from Guatemala (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. Little is known on the biology and medical importance of *S. microbranchium*. DALMAT (1955) stated that the latter species preferred altitudes of 6000 feet often with larvae and pupae found in waterfalls.

2.5.1.18. *Simulium (Trichodagmia) nigricorne* DALMAT (Figs. 601, 661, 846, 908, 969, 1028)

This species still remains poorly known only being recorded from Guatemala. I was unable to examine material of *S. nigricorne*, therefore the description here provided has been based on the original description of DALMAT (1950), and the reviews of COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium (Hearlea) nigricornis DALMAT, 1950: 148. HOLOTYPE pharate male pupa, GUATEMALA: Chimaltenango Department, Acatenango, Rio Laguneta, Finca Tehuyá Luch; 26.ii.1949, (*Carlos R. Santizo P. & Juan Marroquín G.*) [Holotype with accession number Acat. 589-8 is said to have been deposited in DALMAT'S private collection, but this collection is now housed at the NMNH, F.C. THOMPSON – pers. comm. to L.M. HERNÁNDEZ, May.2010. The holotype was not found during a visit by L.M. HERNÁNDEZ to this institution and it is presumably lost.]

FEMALE. [DALMAT (1950) stated that only the head and the genitalia were available to him for description.]

Head: dichoptic with dark red eyes. Cibarium with well developed, sclerotised cornuae and without teeth, anterior margin indented centrally (after COSCARÓN *et al.*, 2004).

Abdomen: Genitalia: Eighth sternite not described in original description. Cercus subquadrangular, covered by long dark hairs; paraproct subrectangular, extending beyond junction with cercus, weakly sclerotised mesally and setose and subquadrangular apically; paraproct densely covered with long hairs (Fig. 601). Genital fork stout and sclerotised with stem expanded apically; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed and blunt apically, posterior processes developed (Fig. 661). Spermatheca not described.

MALE. [DALMAT (1950) stated that only the genitalia of a pharate male of *S. nigricorne* exists, therefore key taxonomic characters remain unknown].

Abdomen: Genitalia: Gonocoxite subquadrangular with one antero-lateral angle produced; gonostyle elongate, twice as long as gonocoxite at mid point, with margins fairly straight, and terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 846). Ventral plate weakly sclerotised, subquadrangular, with anterior margin produced centrally into small pointed process; main body of ventral plate developed with central keel covered by long hairs and extending to near posterior margin; lateral shoulders undeveloped, basal arms well developed and subparallel (Fig. 908). Median sclerite not described. Paramere with well developed and sclerotised basal processes and numerous long spines along whole length (Fig. 969).

PUPA. [DALMAT (1950) provided measurements for the cocoon length: basally, 2.9 mm, maximum 3.6 mm; gill length 0.9 mm. Other measurements and number of specimens examined were not given in the original description.]

Cocoon: shoe-shaped [not slipper-shaped as published in DALMAT (1950, 1955)], brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: dark brown with two swollen filaments forwardly directed in vertical plane (Fig. 1028). Gill with main trunk short giving rise to two sets of primary branches, one dorsal and one ventral arranged in a closed C configuration. Dorsal primary branch arising from short trunk bending at an angle, region above curvature swollen and then immediately narrowing at mid length and larger apically. Ventral primary branch also swollen encircling frontoclypeus (Fig. 1028). Filaments stout, rounded distally, without spicules on surface but with distinct pseudoannulations, edges crenate; dorsal primary branch longer than ventral primary branch.

Head (*frontoclypeus*): [with few tubercles, DALMAT (1955)].

Thorax: [with numerous tubercles, DALMAT (1955)].

Abdomen: [chaetotaxy not here described because of lack of material, but further details in DALMAT (1955)].

LARVA (Last instar). Unknown.

Taxonomic Discussion. *Simulium nigricorne* was described by DALMAT (1950) based only on a pharate male pupa holotype (accession no. Acat. 589-8), one reared female allotype (accession Acat 589-8A), and three paratypes pupal exuviae (accession nos. Acat 590-11, 604-16, 667-3) collected in Guatemala. The paratype 604-15 was said to be deposited at the NMNH and the remainder of the specimens in DALMAT'S collection, which is now at the NMNH. However, no type material of *S. nigricorne* was found at the NMNH collections (L.M. HERNÁNDEZ, May.2010). The three paratype pupal exuviae cited by COSCARÓN *et al.* (2004) as deposited at the NMNH were not located at this institution.

The external general morphology of female and male *S. nigricorne* is poorly known. The morphology of the female (Figs. 601, 661) and male (Figs. 846, 908, 969) genitalia fall within the variation of other species in the CANADENSE species group, from which it cannot be easily separated without examination of the configuration of the pupal gill filaments.

Based on the current published descriptions, *S. nigricorne* can only be reliably identified by the pupa with two swollen primary branches arranged in a close, C-like configuration (Fig. 1028). In this respect, the gill configuration of *S. nigricorne* is similar to that of *S. ethelae* and *S. microbranchium* (Figs. 1021, 1027). However, the gill of *S. ethelae* has the dorsal primary branch more pointed apically and of the same width along its entire length (Fig. 1021). In *S. microbranchium* both primary branches are arranged in a distinct open, C-like configuration and the dorsal branch is relatively much thinner (Fig. 1027). The morphological variation of the pupal gill filaments of *S. nigricorne*, *S. microbranchium* and *S. ethelae* is poorly known, thus further material is needed in order to assess their taxonomic status.

Simulium nigricorne was placed in the subgenus *Hearlea* by COSCARÓN *et al.* (2004) and this has been accepted by ADLER & CROSSKEY (2008, 2009, 2010) and CROSSKEY & HOWARD (2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009). The latter taxonomic action was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed *S. nigricorne* in the CAROLINAE species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. nigricorne* is now placed.

Distribution. *Simulium nigricorne* has only been reported from Guatemala (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN *et al.*, 2004; COSCARÓN & COSCARÓN-ARIAS, 2007; DALMAT, 1955).

Biology and medical importance. DALMAT (1950) recorded larvae and pupae of *S. nigricorne* in two streams flowing from the Pacific slope of the Volcán Acatenango at 4000 to 5000 feet. The streams are two feet wide, one inch deep, with water temperature varying between 15°C to 19°C, pH 7.2. The stream beds were composed of sand, small and large stones, and much emergent vegetation. The pupae were always collected on large stones and rocks. Nothing is known on the female feeding habits of this species.

2.5.1.19. *Simulium (Trichodagmia) paracarolinae* COSCARÓN, ESQUIVEL, MOULTON, COSCARÓN-ARIAS, IBÁÑEZ-BERNAL (Fig. 1135, 1189, 1244, 1288)

This is a recently described species from Guatemala of which the adult and the pupal life stages remain unknown. The description here provided has been derived from the original description of COSCARÓN *et al.* (2004) and three larvae housed at MLP.

Simulium (Hearlea) paracarolinae COSCARÓN *et al.*, 2004: 32. HOLOTYPE larva, GUATEMALA: Solalá, Atitlan, Santa Alicia, Finca Monte de Orio, Río Catarata, (accession no. 12K, 36B); 24.iii.19451, (*Dalmat, H.*) (AMNH) [Examined.]

FEMALE. Unknown.

MALE. Unknown.

PUPA. Unknown.

LARVA (Mature larva). [COSCARÓN *et al.* (2004) recorded the body length as 7.0-8.5 mm. Other measurements and number of specimens examined were not given in the original description]. General body coloration light brown (specimens in ethanol).

Head: cephalic apotome mainly light brown, darkened basally, with darkened median longitudinal stripe on basal third and 1+1 small submedian spots near midline. Cervical sclerites not described. Postgenal cleft subtriangular, without antero-median incision (Fig. 1135). Hypostomium strongly pigmented on anterior margin, with approximately 10 teeth protruding in median region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with pair adjacent to base of median tooth longer than remainder; 1+1 lateral teeth, with smaller tooth at base, laterally; 1+1 lateral serrations; 1+1 lines of approximately 11-12 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1189). Antennal segments I-III pale brown; segment II whitish; length of antennal segments I-III excluding the sensillum 1:1.6:1.0 mm. Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately 14 teeth, first three comb teeth longer and more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1244). Lateral mandibular process absent. Maxillary palps heavily pigmented, two and a half times as long as wide at base. Labral fans with 44-48 rays following COSCARÓN *et al.* (2004) [the number of specimens examined was not given in the latter publication].

Thorax: [thoracic characters were not provided in the original description].

Abdomen: [coloration not given in the original description.] Anal sclerite with ventral struts heavily sclerotised, relatively short, not encircling posterior circle although enclosing approximately one third of it; accessory plates comprised of 1+1 well sclerotised, dorso-lateral conical plates covered with small setae (Fig. 1288). Posterior circlet with 398-400 rows of 42-48 hooks. Rectal gills with three branches each with 6-7 lobules giving a total of 18-21 lobules, median lobe largest.

Taxonomic Discussion. *Simulium paracarolinae* was described by COSCARÓN *et al.* (2004) based only upon a holotype larva and 23 larvae (all as paratypes) collected from Solalá Department, Guatemala. The adult and pupal life stages are unknown. The holotype is said to be housed at the AMNH, but I have not been able to examine it. However, I have studied the original description of this species and three larvae identified and examined by the original authors, which are deposited at MLP (see **Material Examined**).

COSCARÓN *et al.* (2004) stated that the presence of accessory plates on the anal sclerite and a curved anterior hypostomial margin placed *S. paracarolinae* in the CAROLINAE species group, for which the larva is known for all species. The authors also argued that *S. paracarolinae* could represent the unknown larva of *S. nigricorne*, but stated that the pupal morphology of *S. nigricorne* (Fig. 1028) suggested that it corresponds to a species group having different larval characters such as absence of accessory plates on the distal region of the abdomen and the anterior margin of the hypostomium straight. In addition, they also argued that the "mandible morphology and postgenal cleft is different" from this species.

The general larval morphology of *S. paracarolinae* is similar to that of *S. carolinae*. However, in the latter species the posterior arms of the anal sclerite have 2+2 dorso-lateral accessory plates (Fig. 1283), while in *S. paracarolinae* they only have 1+1 dorso-lateral accessory plates (Figs. 1288).

Simulium paracarolinae was placed in the subgenus *Hearlea* by COSCARÓN *et al.* (2004) and this has been accepted by several authorities, *e.g.* ADLER & CROSSKEY (2008, 2009), CROSSKEY & HOWARD (2004). However, Adler *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010). The latter taxonomic change was not recognized by

COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the CAROLINAE species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. paracarolinae* is now placed.

Distribution. *Simulium paracarolinae* is only known from Guatemala (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN *et al.*, 2004; **Material Examined**).

Biology and Medical Importance. Nothing is known on the biology of this species (COSCARÓN *et al.*, 2004).

2.5.1.20. *Simulium* (*Trichodagmia*) *temascalense* DÍAZ NÁJERA & VULCANO (Figs. 193, 246, 436, 543, 602, 662, 1029, 1190, 1245, 1289)

This is a poorly known species which has only been found in Mexico. The description here provided has been based upon examination of the female holotype housed at INDRE and the original description of DÍAZ NÁJERA & VULCANO (1962a).

Simulium (Hearlea) temascalense DÍAZ NÁJERA & VULCANO, 1962a: 102. HOLOTYPE female (reared), MEXICO: Michoacán Department, Temascal, 2800 m; 3.xii.1961, (*I.Córdova Ruiz*) [INDRE, no. 6518] [Examined.] [DÍAZ NÁJERA & VULCANO (1962a) gave a different number for the holotype in the original description - see **Taxonomic Discussion**.]

FEMALE. General body colour black. [Measurements and number of specimens examined were not given in the original description.]

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 193). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown to black. Cibarium with well developed, sclerotised cornuae and without teeth or prominences at base of cornuae (Fig. 246).

Thorax: scutum dark brown with whitish hairs interspersed with black setae. The scutal pattern is poorly known and it has not been illustrated because of lack of material. Following the descriptions of DÍAZ NÁJERA & VULCANO (1962a), COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007) the scutum has a 1+1 thin silvery vittae not adjoining anterior 1+1 subtriangular silvery spots. The pattern is unknown with posterior illumination. Scutellum yellowish with recumbent golden hairs intermixed with long, black bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae. Radius with numerous setae intermixed with distinct spines only apically, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 436 (teneral specimen). Coxa, trochanter, femur, tibia and tarsal segments I-IV pale brown. Mid leg with coxa missing; trochanter, apical thirds of femur and tibia, apical half of tarsal segments I, II dark brown; remainder of femur and tibia pale brown; basal half of tarsal segment I whitish; remainder of tarsal segments pale brown. Hind leg with coxa, trochanter, apical thirds of femur and tibia, apical half of tarsal segment I dark brown; remainder of femur and tibia pale brown; basal half of tarsal segment I whitish; remainder of tarsal segments missing. Halteres cream yellow with brown base.

Abdomen: tergites black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly 1.5 times longer than eighth sternite at mid point, almost square with curved internal margin, weakly sclerotised, covered with only few setae basally (Fig. 543). Cercus subrectangular, covered with brown setae; paraproct subtriangular extending beyond junction with cercus; ventral extension of paraproct with small membranous tail and rounded apically; paraproct covered with long dark hairs, and densely setose apically (Fig. 602). Genital fork stout and sclerotised, with stem strongly expanded apically; termination of lateral arms with anterior margin straight and well developed; anterior processes well developed and blunt apically; internal posterior processes developed (Fig. 662). Spermatheca missing from single specimen I examined.

MALE. Unknown.

PUPA. [DÍAZ NÁJERA & VULCANO (1962a) and COSCARÓN *et al.* (2004) gave a measurement for the cocoon: basal length 3.0 mm. Other measurements and number of specimens examined were not given in the latter paper]; gill length 2.9 mm (n = 1).

Cocoon: [cocoon shape not described in the original description], cocoon composed of compact fibres.

Gill: light brown with eight stout filaments upwardly, ventrally and forwardly directed in vertical plane (Fig. 1029). Gill with main trunk short giving rise to two sets of primary branches, one dorsal and one ventral. Dorsal primary branches with seven secondary filaments arranged as follows: one filament directed upwards, prominently long and wide basally, but narrower towards apex; four or five secondary filaments at basal third of longer filament, one filament slightly more separated from remaining four filaments; and single filaments at base of longer filaments directed upwards and on to pupal thorax. Ventral primary branch with single, long filament directed ventrally but curved upwards on apical third. Filaments stout, pointed and sclerotised distally, without spicules on surface, edges weakly crenate; dorsal filament of anterior primary branch longer than remaining filaments.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial long spiniform trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and four platelets in two groups laterally in frontal region; tubercles absent.

Thorax: with 3+3 spiniform trichomes near margin of dorsal cleft, one spiniform trichome on central region and one spiniform trichome on ventral margin of thorax; tubercles mostly rounded and only densely distributed on posterior region near dorsal cleft.

Abdomen: abdominal tergite I with 1+1 simple short sublateral setae and band of prominently pointed tubercles along posterior margin, and few pointed tubercles on anterior margin centrally; tergite II with 3+3 submedian spiniform setae in longitudinal row mesally, 3+3 long simple setae laterally to outermost spiniform setae, line of pointed tubercles posterior to spiniform setae centrally and few pointed tubercles on anterior margin; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to outermost hooks, and 2+2 small, simple setae on lateral; margin; tergite V with 1+1 median and 1+1 submedian small simple setae; tergites VI-IX without setae; tergite IX weakly sclerotised without terminal spines. Spine combs on submedian region of anterior margins of V-VIII. Sternites III, IV without visible setae; sternite V with 2+2 close simple hooks; sternite VI with 2+2 well separated simple hooks, sternite VII with 1+1 (probably other pair lost) well separated simple setae; sternites VIII, IX without setae, sternite IX weakly sclerotised. Spine combs on anterior margins of sternites III-VI.

LARVA (Final instar). [DÍAZ NÁJERA & VULCANO (1962a) and COSCARÓN *et al.* (2004) recorded the body length as 8.0 mm. Other measurements and number of specimens examined were not given in the latter paper]. Body colour dark green (specimens preservation not stated, but probably in ethanol).

Head: mainly yellowish. Head pattern negative. Postgenal bridge small, wide centrally without apical incision. Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth evenly distributed on anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with the pair adjacent to base of median tooth longer than remainder; 1+1 lateral teeth; 2+2 small paralateral teeth; and 5+5 lateral serrations; 1+1 lines of approximately fifteen hypostomial setae parallel to lateral margins; 2+2 small simple setae in posterior half of hypostomium (Figs. 1190). Antennal segments not examined. Mandible with two apical teeth, first one longer than second; mandibular comb with approximately ten teeth, first four more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1245). Lateral mandibular process absent. Labral fan with about 50 rays each with fine, single line of spines in a row.

Thorax: dark green. Cuticle without setae. Proleg with plate heavily sclerotised band of sclerotised process.

Abdomen: usually dark green. Abdominal segment VIII with 1+1 ventro-lateral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms; posterior arm encircling posterior circlet with 2+2 dorso-lateral conical accessory plates, 1+1 ventro-lateral accessory plates consisting of spiny lateral projections, and 1+1 dorso-lateral flattened plates (Fig. 1289). Posterior circlet with 242 rows of 45-46 sclerotised process of 25-26 simple hooks. Rectal gills with three branches each with 7-9 finger-like lobules given a total of 21-27 lobules.

Taxonomic Discussion. *Simulium temascalense* was described by DÍAZ NÁJERA & VULCANO in 1962a based upon a reared female holotype, four female pupal exuviae, and an undisclosed number of larvae collected in Michoacán Department, Mexico. The larva was also described in the same paper based on specimens collected in San Felipe del Agua found sympatrically with *S. johnsoni*. The male still remains unknown. DÍAZ NÁJERA & VULCANO (1962a) also stated that the holotype was partially mounted in Canada Balsam and registered it with the number "5118". I have examined two slides labelled as "*Simulium temascalense* Holotype female" housed in the INDRE Simuliidae collection. The female holotype has been fully dissected and it is mounted on two slides. Both slides are in good condition, though the pupal thorax is damaged on both sides. The slides contain the adult's body parts and pupal exuviae, except the spermatheca and the cocoon. The female thorax, one fore leg and one wing are not on the slides, and no other type material of this species was found at INDRE (H. HUERTAS - pers. comm. to L.M. HERNÁNDEZ, 2010) (**Material Examined**). In addition, both slides bear a handwritten accession number "6518", which does not agree with the number employed by DÍAZ NÁJERA & VULCANO (1962a) in their original description *S. temascalense*. Nonetheless, the slides have the locality information and identification labels in DÍAZ NÁJERA'S hand and the general morphology of this specimen agrees with the description and figures given in the original description of DÍAZ NÁJERA & VULCANO (1962a) of *S. temascalense*. Therefore, I am confident that these two slides represent the holotype of *S. temascalense* and I have labelled them accordingly (**Material Examined**).

The female general morphology, especially the genitalia (Figs. 543, 602, 662) and the pupal gill configuration (Fig. 1029) of *S. temascalense* is very similar to that of *S. johnsoni* (Fig. 1023). However, *S. temascalense* can be separated by the dorsal branch of the pupal gill being prominently narrow apically, and the smaller pointed branches near the base closer together (Fig. 1029). In *S. johnsoni* the dorsal branch is markedly more swollen apically and the pointed, smaller branches near the base twice as long and well separated (Fig. 1023).

The larva of *S. temascalense* is also very similar to that of *S. johnsoni*. However, the larva of *S. temascalense* has the dorso-lateral sclerotised processes much longer and the ventro-lateral sclerotised accessory plates with nine conical processes (Fig. 1289) (DÍAZ NÁJERA & VULCANO, 1962a). In *S. johnsoni* the dorso-lateral sclerotised processes are smaller and the ventro-lateral accessory plates only have five conical processes (Fig. 1285).

Simulium temascalense was placed in the subgenus *Hearlea* by DÍAZ NÁJERA & VULCANO (1962a) and this has been accepted by most authorities, *e.g.* COSCARÓN (1987), CROSSKEY & HOWARD (1997, 2004). However, ADLER *et al.* (2004) subsumed the subgenus *Hearlea* with *Hemicnetha*, an action followed by ADLER & CROSSKEY (2008, 2009). The latter taxonomic arrangement was not recognized by COSCARÓN *et al.* (2004) and COSCARÓN & COSCARÓN-ARIAS (2007), who placed this species in the CAROLINAE species group. More recently, SHELLEY *et al.* (2010) synonymised *Hemicnetha* under *Trichodagmia*, and recognized the CANADENSE species group, where *S. temascalense* is now placed.

Distribution. *Simulium temascalense* has only been recorded from Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN *et al.*, 2004; COSCARÓN & COSCARÓN-ARIAS, 2007; **Material Examined**).

Biology and Medical Importance. The immature stages of *Simulium temascalense* were collected attached to rocks in a waterfall of very cold water (DÍAZ NÁJERA & VULCANO, 1962a). Nothing is known on the female feeding behaviour.

2.5.2. The ORBITALE species group.

The ORBITALE species group now contains 16 species. It largely results from merging of the LAHILLEI, NIGRIMANUM and MUISCORUM species groups [as subgroups] of the subgenus

Grenieriella and the HIRTIPUPA, SCUTISTRIATUM and ORBITALE species groups [as subgroups] of the subgenus *Thyrsopelma* in COSCARÓN (1987) and includes the subsequently published *S. duodenicornium*, *S. lithobranchium*, *S. perplexum*, *S. sumapazense* and *S. wygodzinskyorum* (as detailed in SHELLEY *et al.*, 2010; this work). The *species inquirendae Thyrsopelma striginotum* ENDERLEIN in COSCARÓN (1987) was recognized by CROSSKEY & HOWARD (1997, 2004) as a valid species in the PERTINAX species group of the subgenus *Chirostilbia*. However, HERNÁNDEZ *et al.* (2007) placed this species as a junior synonym of *S. spinibranchium* where no species groups are recognized [see also revision of the subgenus *Chirostilbia* in HERNÁNDEZ *et al.*, 2008]. Species in the ORBITALE group of SHELLEY *et al.* (2010) coincide completely with those listed under *Trichodagmia* in CROSSKEY & HOWARD (1997, 2004) except that the latter authors list *S. albopictum* as a synonym of *S. orbitale* [see under species descriptions], and *S. chalcocoma* (and its synonyms) and *S. muiscorum* as synonyms of *S. townsendi* following the work of HERNÁNDEZ & SHELLEY (2005) and the recently described *S. duodenicornium* and *S. jeteri*.

Female: Scutum brown or grey usually without pattern (except *S. huairayacu*, *S. lahillei*, *S. townsendi* and *S. wygodzinskyorum* with pattern as in typical TARSATUM species group) (Figs. 315-351). Nudiocular triangle only partially developed to medium depth (Figs. 194-207). Cibarium unarmed, but in some cases with fine denticles and tubercles as in *S. orbitale* and *S. townsendi* and exceptionally with well developed teeth as in *S. huairayacu* and *S. nigrimanum* (Figs. 247-260). Sc and basal section of Radius with or without setae. Claws exceptionally with basal tooth. Gonapophyses ovoid to crescent shaped, directed towards median line of abdomen or posteriorly, membranous, unsclerotised and covered with microtrichiae (Figs. 33-35, 544-558). Paraprocts generally small, subtriangular or subrectangular, setose and with coarse hairs, membranous with some sclerotised areas and with ventral extension slightly produced or longer than cercus, rounded apically and in several species with one or more small membranous processes, which may be developed to different extents, with well developed, lobular membranous apex folded over towards centre of venter of abdomen or, exceptionally, with well developed, subrectangular paraproct, rounded distally [as in *S. huairayacu*, *S. lahillei*, *S. nigrimanum*, *S. nunesdemelloi*, *S. scutistriatum*, *S. townsendi* and *S. wygodzinskyorum*], and with blunt teeth on apical third of posterior margin as in *S. scutistriatum* (Figs. 18-21, 603-617). Genital fork with well developed ends to lateral arms parallel to transverse axis of abdomen, twice as wide as deep (Figs. 663-677), mainly unsclerotised and with anterior processes usually developed and sclerotised, inner posterior processes well developed.

Male: Scutum brownish to black, with or without pattern; pattern composed of varying degrees of silver pruinose areas on brown to black scutum, giving appearance of silver scutum with black areas ranging from median black vitta through median black vitta plus 1+1 lateral oval areas to all three areas combined in form of anchor (Figs. 732-768). Gonocoxite wider than long, except in *S. orbitale* and *S. perplexum* in which it is almost square; gonostyle 1.25 to three times longer than gonocoxite, except same length in *S. perplexum* (Figs. 44, 847-862). Gonostyle spindle-shaped, except in *S. perplexum*, in which it is more subrectangular (Figs. 44, 847-862), with terminal spine (sometimes 3-8 as in *S. nigrimanum*); Ventral plate variable with posteriorly directed median process ovoid, largely separated from body of ventral plate and covered with long hairs, keel absent or rudimentary and lateral shoulders well developed, or with median process of varying development, less hirsute and incorporated in ventral plate with no developed lateral shoulders as in *S. huairayacu*, *S. lahillei*, *S. nigrimanum* and *S. scutistriatum*, or with well developed median process, small keel and no lateral shoulders as in *S. wygodzinskyorum* (see also COSCARÓN & PY-DANIEL, 1989) or with well developed lateral shoulders as in *S. hirtipupa*, or without median process but with lateral shoulders as in *S. perplexum* or with no median process, reduced lateral shoulders and enlarged keel as in *S. townsendi* (Figs. 51-54, 909-923). Paramere poorly developed without spines (Figs. 62, 970-983).

Pupa: Cocoon shoe-shaped, without fenestrations (Fig. 66). Pupal gill filaments (up to 56) generally short ranging from one fifth to one third length of pupa, pointed and in some species with prominent sclerotised black tips, except in *S. nigrimanum*, which has rounded tips to gill as seen in species of the TARSATUM species group (Figs. 79-81, 1030-1045). Trichomes simple, usually fine but sometimes spiny; tubercles rounded or pointed with limited distribution in facial region of frontoclypeus and on gill base, alar and dorsal regions of thorax. In *S. hirtipupa* frontoclypeus and thorax covered with densely distributed stout spiniform black setae (Fig. 71).

Larva: There are not clear cut diagnostic characters for the larva of species in the ORBITALE species group. The larva has to be examined in combination with link-reared adults and pupae collected in the same locality. Morphological characters for larvae in this species group are: postgenal cleft either bell-shaped, deep and triangular apically or short and broadly rounded apically (Figs. 94, 1136-1150). Hypostomium often with nine evenly distributed teeth along anterior margin (Figs. 94, 1191-1205), but in several species (*e.g. S. guianense s.l.*, *S. hirtipupa*) the teeth can be reduced (Figs. 1192, 1193), sometimes positioned below level of anterior margin (*S. nigrimanum*); anterior margin of hypostomium straight (Figs. 94, 1199) or concave centrally, in which case 1+1 lateral teeth appearing more prominent (*e.g.* Fig. 1150). Number of mandibular teeth similar to species pertaining to other species groups (*e.g.* Figs. 1246-1262); in certain species (see Fig. 1253, 1255) the most salient character in the mandibles is that the anterior margin is prominently truncate at the level of the mandibular comb. Abdominal larval integument often without setae, but ovoid setae are found in species such as *S. duodenicornium*, *S. lithobranchium*, *S. guianense* and *S. orbitale*. In *S. hirtipupa* abdomen with prominent spines, while in *S. lithobranchium* 1+1 dorso-lateral tubercles on tergites I-VI present (Fig. 1092). Posterior arm of anal sclerite never encircling posterior circlet.

2.5.2.1. *Simulium* (*Trichodagmia*) *duodenicornium* PEPINELLI, HAMADA & TRIVINHO-STRIXINO (Figs. 18, 33, 80, 194, 247, 315, 316, 437, 544, 603, 663, 732, 733, 847, 909, 970, 1030, 1085, 1136, 1191, 1246)

This is a south-eastern Brazil species, morphologically closely related to *S. guianense s.l.* The description here provided is based upon the original description, and adults and immature stages collected at and near the type locality in Brazil by A.J. SHELLEY & A.P.A. LUNA DIAS.

Simulium duodenicornium PEPINELLI *et al.*, 2005: 17. HOLOTYPE male (reared), BRAZIL: São Paulo State, Joanópolis County, Mantequeira Mountains, Cachoeira dos Pretos, Cachoeira stream, [headwaters of Rio Piracicaba], 22°57'S 46°10'W; 22.v.2004, (*W.Pepinelli & N.Hamada*)(MZUSP).

FEMALE. General body colour black. Body length 2.8 mm (n = 1); wing length 2.5 mm (n = 1), wing width 1.1 mm (n = 1).

Head: frons, clypeus and occiput dark brown with silver pruinosity; nudiocular triangle slightly developed (Fig. 194). Mouthparts brownish yellow. Antenna with silver pubescence, scape, pedicel and proximal area of first flagellomere brownish yellow, subsequent flagellomeres dark brown. Cibarium unarmed but with small tubercles in central trough, lateral arms well developed and sclerotised (Fig. 247).

Thorax: scutum black, with numerous, short, broad brass-coloured setae distributed regularly in groups; central line without setae (Figs. 315, 316). Scutellum and pleural region brown with golden hairs; postnotum black. Costa of wing with setae intermixed with spines. Subcostal wing vein bare. Radius with single line of setae interspersed with spine, basal sector of Radius with lines of long dark setae. Coloration and proportion of legs as in Fig. 437. Foreleg with coxa, trochanter, femur and basal three fourths of tibia light brown, distal fourth and tarsus dark brown; mid leg coxa, trochanter, femur and basal three fourths of tibia light brown, distal fourth of tibia dark brown, basal three fourths of basitarsus and basal third of second tarsomere light brown, rest of tarsus dark brown; hind leg coxa, trochanter and femur mid brown, basal half of tibia mid brown distal half dark brown, basal two thirds of basitarsus and second tarsomere light-brown rest of tarsus dark brown. Claw without basal tooth.

Abdomen: abdominal tergites dark brown. Basal fringe with thin, long, golden hairs. Eighth sternite sclerotised with long irregularly placed setae on posterior margin, gonapophyses rounded and touching centrally (Fig. 33, 544). Cercus hemispherical, paraproct subtriangular with two membranous projections, both covered with long brown setae (Fig. 18, 603). Genital fork stout and sclerotised; terminations of lateral arms well developed with anterior margins straight; anterior processes well developed and pointed apically; posterior processes well developed and subtriangular (Fig. 663). Spermatheca subspherical, with internal microspines; spermathecal duct and area of attachment unpigmented.

MALE. General body colour black. Body length 2.8 mm (n = 1); wing length 2.4 mm (n = 1) and width 1.2 mm (n = 1).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black with densely distributed golden setae (Figs. 732, 733). Scutellum dark-brown, postnotum black, pleural region dark-brown. Wing setation as in female. Leg coloration as in female. Abdominal tergites black; basal fringe with long, fine, golden hairs. Tergites, in lateral view, with silver pruinosity. Genitalia brown. Gonocoxite subrectangular; gonostyle conical with one or two acute apical spines (Fig. 847). Ventral plate subrecatnagular, concave dorsally with well developed lateral shoulders and prominent highly setose median process arising from middle of body of ventral plate (Fig. 909). Median sclerite rectangular with apical incision (Fig. 909). Paramere weakly sclerotised and poorly developed with no spines (Fig. 970).

PUPA. Cocoon length dorsally 4.0-4.4 mm (mean = 4.1 mm, n = 5), ventrally 2.9-3.4 mm (mean = 3.2 mm, n = 5); pupa length 3.9-4.1 mm (mean = 4.0mm, n = 5).

Cocoon: shoe-shaped as in Fig. 66, thick and hard, without central projection on anterior margin.

Gill: with 12 short, thick and rigid filaments, pointed and sclerotised distally; most dorsal and ventral filaments in a straight line parallel to surface of cephalothorax (Figs. 80, 1030).

Head (*frontoclypeus*): with 2+2 short, stout and simple frontal trichomes and 1+1 facial trichomes, thicker and longer than the frontal. Frontoclypeus with small rounded tubercles, especially visible in facial region.

Thorax: with 5 +5 spiniform trichomes dorsally.

Abdomen: tergite I with 1+1 sublateral setae; tergite II with 4 +4 stout setae, 2 +2 fine sublateral setae and many small, tubercles, especially in the antero to the median region of the tergite; tergites III and IV each with 4 +4 anteriorly directed pairs of hooks on posterior margin; tergites VI-IX with groups of spine combs on anterior margin. Sternites III-IX with antero-median group of spine combs; sternites V-VII with 2+2 stout, bifid hooks.

LARVA (Final instar). [The description here provided has been derived from the original description and larvae collected at Cachoeira de Pilão, near the type locality of *S. duodenicornium* in Brazil]. Body length 6.2-7.5 mm (mean = 6.9mm, n = 5); length of head capsule 0.5-0.6 mm (mean = 0.53 mm, n = 5); width of head capsule 0.7-0.8 mm (mean = 0.82, n = 5). Body colour greyish black (specimens fixed in Carnoy's solution and/or alcohol). General body form as in Fig. 1085.

Head: head capsule with negative pattern. Cervical sclerite small, elliptical, free in membrane ach with thin, elongated sclerite anteriorly. Postgenal cleft subtriangular, widest medially, with thin, dark membrane covering its entire surface; postgenal bridge 0.5 times as long as hypostomium (Fig. 1136). Subesophageal ganglion not pigmented. Antennal segments as long as labral fan; distal and proximal articles smaller than median article; length of antennal segments excluding the sensillum 1:2.5-2.6:0.9 mm (n = 5). Hypostomium with pigmented anterior margin and six or seven reduced teeth; median tooth small and same height as adjancent sublateral teeth; sublateral teeth very reduced, sometime only visible the pair adjacent to median tooth; 1+1 developed lateral teeth more prominent that remainder teeth; 1 or 2 lateral serration; 1+1 lines of eight hypostomial teeth parallel to lateral margins (Fig. 1191) [PEPINELLI *et al.* (2005) described the hypostomial teeth as follows: apical teeth and lateral teeth larger and more blunt than remaining teeth; three small median teeth, and four larger, blunt intermediate teeth; lateral serrations absent and 7 or 8 setae per side]. Mandibular teeth as in Fig. 1246. Labral fan with 53-59 primary rays (n = 5).

Thorax: body covered with ovoid setae. Proleg with plate heavily sclerotised with band of approximately 178–184 rows with 26–31 hooks (*n* = 3). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 12 filaments arranged in three primary branches and pointed and sclerotised apically.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle with ovoid setae. Anal sclerite well sclerotised with anterior arms shorter in length than posteroventral arms. Posterior circlet with 178-184 rows (n = 4) of 26-32 hooks (n = 4). Anal papillae with three branches, each with 25-27 finger-like lobes (n = 4).

Taxonomic Discussion. *Simulium duodenicornium* was described by PEPINELLI *et al.* (2005) based on numerous males and females, larvae and pupal exuviae collected in the State of São Paulo, Brazil. The pinned male holotype is said to be deposited at MZUSP, but I have been unable to examine this specimen neither any specimen belonging to the type series. Nonetheless, I have examined 1 link-reared female and male, and numerous topotype pupal exuviae and larvae housed at the BMNH (**Material Examined)**. More recently, I have been in correspondence with MATEUS PEPINELLI, who has informed me that the holotype is still in his private collection and it will be deposited at MZUSP at a later date. He has also confirmed that the holotype is in good condition, with its pupal pelt mounted on a slide. PEPINELLI *et al.* (2005) also stated that five larvae and five pupal exuviae (as paratypes) are housed in the BMNH (as NHM), but this material has not yet been deposited at the BMNH Simuliidae collection.

The taxonomy of this species has been recently reviewed by SHELLEY *et al.* (2010). *Simulium duodenicornium* is closely related to several species in the ORBITALE species group. For a comparison see "**Taxonomic Discussion**" under *S. orbitale* in this work.

Distribution. *Simulium duodenicornium* has only been recorded from its type locality in the Mantequeira Mountains of São Paulo State (ADLER & CROSSKEY, 2008, 2009, 2010; SHELLEY *et al.*, 2010; **Material Examined**).

Biology and Medical Importance. The authors stated that larvae and pupae of *S. duodenicornium* were collected in one stream, which had a bed composed of sand, small stones and boulders. They were found on stems, leaves and roots of emergent vegetation, in the areas were the flow was faster and highly turbulent at 902 m. The authors recorded in May 2004 water temperature of 15.6ºC, pH 7.3, and electrical conductivity 14µs/cm. No females were collected biting man during the fieldwork.

SHELLEY *et al.* (2010) stated that larvae and pupae of *S. duodenicornium* were collected at the type locality, attached to roots on trailing vegetation. However, in another stream near Itajubá, Brazil, large numbers of larvae and pupae were found attached to rocks in fast flowing water. No biting occurred during collection.

2.5.2.2. ***Simulium (Trichodagmia) guianense*** **WISE (complex)** (Figs. 19, 79, 195, 248, 317-320, 438, 545, 604, 664, 734-741, 848, 910, 971, 1031, 1086, 1137, 1192, 1247)

This is a common and widespread species in Brazil. It is the primary vector of human onchocerciasis in highland areas of the Amazônia focus and, consequently, has been the most investigated species of the subgenus.

Simulium guianense WISE, 1911: 252. LECTOTYPE female, GUYANA: Essequibo River, 1908 (*Melville*) (BMNH) [Lectotype designation by SMART, 1940: 5]. [Examined.]

Simulium pintoi D'ANDRETTA & D'ANDRETTA, 1945: 101. HOLOTYPE male, BRAZIL: São Paulo State, Salto de Piraçicaba, Piraçicaba, 28.vii.944 (*Vulcano Andretta & Andretta Jr.*) [Depository unknown]. [Synonymy with *S. guianense* by SHELLEY *et al.*, 1997: 40.]

Simulium ortizi RAMÍREZ PÉREZ, 1971: 336. HOLOTYPE [sex unspecified, but female], VENEZUELA: Bolivar State, San Felix, Rio Caroni, [Without collection date] (*J.Ramírez Pérez*) (DERM). [Synonymy with *S. pintoi* by RAMÍREZ PÉREZ *et al.*, 1982: 55; synonymy with *S. guianense* by SHELLEY *et al.*, 1997: 40.]

'A' Cytoform CHARALAMBOUS *et al.*, 1996: 113.
'B' Cytoform CHARALAMBOUS *et al.*, 1996: 113.
'C' Cytoform CHARALAMBOUS *et al.*, 1996: 113.

FEMALE. General body colour black. Body length 1.9-3.3 mm (mean = 2.7 mm, s.d. = 0.3, n = 59); wing length 1.7-2.7 mm (mean = 2.2 mm, s.d. = 0.2, n = 56), wing width 0.7-1.5 mm (mean = 1.0mm, s.d. = 0.1, n=51).

Head: dichoptic with dark red eyes; nudiocular area slightly developed (Fig. 195). Frons, clypeus and occiput black with grey pruinosity; frons and clypeus with dense vestiture of recumbent brass-coloured setae. Mouthparts brown. Antennae dark brown with scape, pedicel and first flagellomere light brown. Cibarium not armed with teeth (Fig. 248), but small denticles and coloured bumps resembling tubercles present in central trough in a population from Mucajai only seen at high magnification as shown by SHELLEY *et al.* (1989b, Fig. 4); cornuae undeveloped and sclerotised.

Thorax: scutum, including paranotal folds, scutellum and humeri dark grey with feint silvery grey pruinosity. Scutum and scutellum with numerous, short, broad, brass-coloured, fine or scale-like setae arranged irregularly in small groups. Scutal pattern varying only slightly with illumination. With anterior illumination, thorax dark grey to black (Fig. 317, 319). With posterior illumination, thorax dark grey to black with feint silver grey pruinosity on anterior third (Fig. 318, 320); in freshly emerged specimens fine median line runs two thirds length of the scutum from the anterior border occurs where no scales present. Pleural region dark grey and brown with silvery grey pruinosity. Postnotum dark grey with light silvery grey pruinosity. Costa of wing with sparse distribution of hairs and spines. Subcosta either bare or with up to six fine setae in distal half. Basal sector of radius with single row of hair-like setae on basal two thirds, a single row of spine-like setae interspersed with hair-like setae on distal third; basal tuft of dark hairs. Leg proportions and coloration as in Fig. 438. Legs brown and white banded as follows: fore leg with coxa, trochanter and femur light brown, tibia light brown with anterior surface white and upper border dark brown, and tarsus black; mid leg coxa dark grey pruinose, trochanter and femur light brown, tibia grey, basitarsus white with black distal articulation and rest of tarsi black; hind leg coxa dark grey pruinose, trochanter light brown, femur black except proximal articulation, tibia black with distal articulation and outer distal half of margin white, basitarsus with basal three quarters white and distal quarter black, rest of tarsi black . Scale-like hairs on femora and tibiae of mid and hind legs as in *S. exiguum* [see SHELLEY *et al.*, 2010]. Claw curved and slender without basal tooth. Haltere light yellow with dark brown stem.

Abdomen: abdominal tergites I-IV velvet black with silver pruinosity covering tergite II, tergites V-IX shiny black. Tergal plates well developed. Sternites and genitalia black. Eighth sternite highly sclerotised in posterior two-thirds with 1+1 groups of 13-24 well developed setae; gonapophyses large, membranous, not meeting centrally and densely covered in fine setae (Fig. 545). Cerci hemispherical; paraprocts broadly quadrangular with dorsally exposed part sclerotised and more ventral part membranous with small tail-like projection pointing internally close to gonapophyses; whole paraproct densely covered in setae (Fig. 18, 604). Genital fork short, with highly developed terminations to lateral arms and sclerotised anterior processes (Fig. 664). Spermatheca oval, highly sclerotised, with internal sculpturing and few small spicules; width of membranous area of insertion of spermathecal duct large, about half maximum width of spermatheca.

MALE. General body colour black. Body length 1.9-3.1 mm (mean = 2.5 mm, s.d. = 0.3, n = 31); wing length 1.5-2.3 mm (mean = 1.9mm, s.d. = 0.2, n = 29); wing width 0.6-1.1 mm (mean = 0.8 mm, s.d. = 0.1, n = 21).

Head: holoptic with dark red eyes. Clypeus black with silvery grey pruinosity and many, long, dark, upright setae. Mouthparts black, antennae black with scape, pedicel and first flagellomere orange-brown.

Thorax: scutum velvet black with varying degrees of silvery grey pruinosity and covered by evenly distributed recumbent golden hairs. Scutal pattern varies slightly with light incidence, the clearer pattern being seen with posterior lighting (Fig. 734). The same pattern is seen with anterior lighting, but less distinctly (Fig. 735). Variation in this pattern occurs across the distribution of the species. In all cases the silver ornamentation covers most of the scutum except for a broad, median vitta that runs from anterior border posteriorly for about three quarters of scutal length and 1+1 lateral oval areas in the central part of the scutum. The median vitta varies from subrectangular to subtriangular and in the form of a capital T (Figs. 736-741). The lateral areas vary from large and oval to a small, indistinct area.

Humeri and paranotal folds black with silvery grey pruinosity. Scutellum velvet black on anterior half and black with silvery grey pruinosity on posterior half, postnotum black with silvery grey pruinosity. Pleural region black with silvery grey pruinosity. Scutum and postnotum covered in short, recumbent golden hairs and posterior margin of scutellum with strong, brown bristles curved anteriorly. Wing venation as in female except basal sector of Radius and Subcosta bare. Leg coloration as in female except light brown and grey areas black in fully coloured specimens. Haltere lemon yellow with orange-brown base.

Abdomen: abdominal tergites velvet black, basal fringe light brown. Silver ornamentation as follows: tergite II all silver except for posterior edge and median area of posterior half of segment, most of lateral area of tergites V-VII and lower margin of tergite VIII. Sternites yellowish brown with well developed black sternal plates on segments III-VIII. Genitalia dark brown. Gonocoxite subrectangular, gonostyle elongate, pyriform with large blunt distal spine (Fig. 848) and sometimes smaller accessory spine. Ventral plate sclerotised, subrectangular with shallow, apical (posterior) depression, well developed, parallel basal (anterior) arms and setose, ventral, pyriform, median prolongation not reaching apical level of well developed lateral shoulders (Fig. 910). Median sclerite rectangular with deep incision at narrower apex (Fig. 910). Paramere poorly developed with no spines and little sclerotisation (Fig. 971).

PUPA. Cocoon length dorsally 2.0-3.1 mm (mean = 2.5 mm, s.d. = 0.3, n = 35); ventrally 2.2-3.6 mm (mean = 2.8 mm, s.d. = 0.3, n = 37); pupa length 1.9-3.1 mm (mean = 2.4 mm, s.d. = 0.3, n = 37); gill length 0.5-0.9 mm (mean = 0.7 mm, s.d. = 0.1, n = 36).

Cocoon: shoe-shaped as in Fig. 66, light to dark brown; rim of aperture not reinforced and without central protuberance. Cocoon of smooth and gelatinous appearance with no obvious fibres.

Gill: light brown with twelve filaments arranged in form of antlers (Fig. 79, 1031), main trunk giving rise to three primary branches, dorsal with six filaments, median with four filaments and ventral with two filaments. Branching of filaments in basal two thirds of gill. Filaments short with distal dark pointed ends, their more distal surfaces with spicules in annular arrangement.

Head: with 2+2 small, unbranched frontal trichomes, and 1+1 small, unbranched, facial trichomes; surface of head with scattered platelets on periphery and base of frontal region, rounded tubercles on facial and based of frontal region.

Thorax: with up to 4+4 simple or sometimes bifid, poorly developed, antero-dorsal trichomes. Surface of thorax with sparsely developed platelets mainly on dorsal and ventral margins and rounded and pointed tubercles around base of gill, dorsal cleft and alar region.

Abdomen: tergite II with 4+4 fine hooks in line on posterior border of segment; tergites III-V with 4+4 well developed simple hooks; tergites VI-IX with patches of poorly developed spine combs on antero-lateral margins; tergite IX with no obvious terminal spines. Abdominal sternite IV with 1+1 simple, short, unsclerotised spines; sternite V with 2+2 bifid or sometimes trifid hooks; sternites VI and VII with 2+2 bifid or trifid hooks; 1+1 patches of spine combs on postero-lateral borders of sternites IV-VIII.

LARVA (Final instar). Body length 3.9-6.0 mm (mean = 5.1 mm, s.d. = 0.6, n =2 9); width of head capsule 0.5 -0.7 mm (mean = 0.6mm, s.d. = 0.05, n = 28); length of head capsule 0.5-0.8 mm (mean = 0.7 mm, s.d. = 0.08, n = 29). Body colour usually white with greyish brown markings, but occasionally completely creamy white. General body form as in Fig. 1086.

Head: light yellow and translucent with faint positive head spot pattern or head spots concolorous; chromatophores visible through cephalic apotome in many individuals. Head capsule with few, randomly distributed setae on all surfaces. Postgenal cleft large, as wide as long, rounded anteriorly, postgenal bridge about two thirds as long as hypostomium (Fig. 1137). Hypostomium with strongly pigmented anterior margin and eleven apical teeth; median tooth weakly developed; sublateral teeth varying from 3+3 to 5+5 teeth, which are more prominent than median tooth; 1+1 laterl teeth longer than median and sublateral teeth; lateral serrations absent; 1+1 lines of five hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1192). Antennal segments long, unpigmented; length of antennal segments excluding the sensillum 0.07-0.09:0.09-0.1:0.05-0.07

mm (n = 4). Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately eight teeth, first to fifth teeth longer than remainder teeth; two mandibular serrations, the anterior more prominent than posterior (Fig. 1247). Lateral mandibular process absent. Maxillary palps about three times as long as breadth at base. Labral fan with 35-49 rays, all with single line of fine microspinules (n = 5).

Thorax: cream with grey anterior collar and occasionally amorphous, grey central area on dorsum and grey central patch on venter of proleg and a single grey central patch on ventral surface of thorax posterior to proleg. Dorsal surface of cuticle, except for intersegmental margins, covered in numerous, small, platelet-shaped setae that appear simple under the light microscope; ventral surface glabrous. Proleg plates lightly sclerotised with about twelve processes. Pupal respiratory histoblast light brown and showing black pointed ends to filaments, claviform.

Abdomen: cream with single complete grey ring on first four anterior narrow segments, more obvious dorsally; posterior segments grey dorsally with white intersegmental areas, whitish cream ventrally. Ventral nerve cord grey. Ventral papillae absent. Dorsal surface of cuticle, except for intersegmental margins, covered in short platelet-shaped setae; ventral surface glabrous except for some setae scattered around posterior venter of abdomen. Anal sclerite highly sclerotised with posterior arms extending to about 34th to 38th row of posterior circlet hooks. Posterior circlet with 117-124 rows of 25-30 hooks (n = 4). Anal gill trilobed, each lobe with 12-14 finger-like lobules (n = 3).

Taxonomic Discussion. WISE (1911) first described *S. guianense s.l.* from eleven females collected by Melville while biting man on the Essequibo River and tributaries of its upper reaches in Guyana. Details of the taxonomy of this species are fully reviewed in SHELLEY *et al.* (1997). Since then, more paralectotypes were discovered in the NHM and this is discussed in SHELLEY *et al.* (2004). More recently, SHELLEY *et al.* (2010) gave further details on the taxonomy of this species and discussed its distribution and biology in Brazil.

Simulium guianense s.l. is a relatively well studied species because of its rôle as a primary vector of human onchocerciasis in the highland areas of the Amazonia focus of the disease in Brazil and Venezuela (BASÁÑEZ *et al.*, 1988; SHELLEY, 1988a; SHELLEY *et al.*, 1987, 1997, 2001). It was suspected of being a complex of sibling species largely because of variations in biting behaviour. CHARALAMBOUS *et al.* (1996) then showed the presence of four distinct cytotypes in Brazil collected in different localities: cytotype A from Goiás State (Rio Tocantins and Rio Mucambão), B from Amapá State (Rio Oyapoque), C from Maranhão State (Rio Tocantins) and D from Pará State (Rio Xingu). Further evidence that more cytotypes of *S. guianense* might be found has been given by SHELLEY *et al.* (2002a), who observed morphological differences in the larvae and wing venation of adults in two populations of this species from Goiás State (Rio Verdão and Rio Doce). This population has been recently named as the new species *S. lithobranchium* by HAMADA *et al.* (2010). The variation in the scutal pattern in the males of *S. guianense s.l.* (Figs. 734-741) and any link that it may have to cytotype needs further study. In the *S. damnosum* complex in Africa male scutal pattern variation is useful in some cases as a character for cytotype identification, but considerable variation has been noted in the *soubrense/sanctipauli* subgroup suggesting that variation within cytotype probably also occurs (CHEKE *et al.*, 1987; DANG & PETERSON, 1980; MEREDITH *et al.*, 1983).

Simulium guianense s.l. is externally similar to *S. duodenicornium*, *S. lithobranchium*, *S. itaunense*, *S. orbitale* and *S. perplexum* (see "**Taxonomic Discussion**" under *S. orbitale* for full details). Further taxonomic descriptions of *S. guianense* can be found in COSCARÓN (1991) [as *S. pintoi*], D'ANDRETTA & D'ANDRETTA (1945) [as *S. pintoi*], RAMÍREZ PÉREZ (1971) [as *S. ortizi*] and SHELLEY *et al.* (2000; 2010).

COSCARÓN (1987) placed *S. guianense* in the ORBITALE subgroup of the subgenus *Thyrsopelma* and this position was later maintained by MIRANDA-ESQUIVEL & COSCARÓN (2001) in their cladistical analysis of the subgenera *Thyrsopelma* and *Trichodagmia.* However, ADLER & CROSSKEY (2008, 2009, 2010) and CROSSKEY & HOWARD (1997) placed *S. guianense* in the subgenus *Trichodagmia*, an action followed by SHELLEY *et al.* (2010) and this work. COSCARÓN & COSCARÓN-ARIAS (2007) allotted *S. guianense* in the subgenus *Thyrsopelma* and accepted all the synonyms listed in SHELLEY *et al.* (1997).

Distribution. *Simulium guianense s.l.* has a widespread distribution in Brazil being found in the states of Amapá, Amazonas, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Pernambuco, Rio de Janeiro, Roraima, São Paulo and Tocantins (ADLER & CROSSKEY, 2008, 2009, 2010; SHELLEY *et al.*, 2010; **Material Examined**). Elsewhere, it has been recorded in French Guiana (HAMADA & FOUQUE, 2001; **Hamada & Grillet, 2001**), Guyana, Suriname and Venezuela (ADLER & CROSSKEY, 2008, 2009, 2010).

Biology and Medical Importance. *Simulium guianense s.l.* is found in large (300 m), fast flowing, sunlit rivers, in Brazil, but the less common anthropophilic populations appear to have a more discrete distribution and in some cases are collected breeding in smaller rivers (SHELLEY, 2002). Immature stages can be collected on submerged plants, especially species of the family Podostemaceae. In Guyana, SHELLEY *et al.* (2004) collected *S. guianense s.l.* on submerged vegetation in a 50m wide river with rocky beds. COSCARÓN (1991) recorded this species from Argentina in small, deep, fast flowing and clear water rivers with rocky beds. GOMES & PY-DANIEL (2002) analysed the chemical composition of the breeding grounds in Brazil. Forty species of microalgae were found in the guts of last stage larvae by GOMES *et al.* (2002). Zoophilic populations were recorded at Catrimani and Mucajai (SHELLEY *et al.*, 1997) and in French Guiana (HAMADA & FOUQUE, 2001). In the Venezuelan part of the focus *S. guianense s.l.* is anthropophilic in highland areas and zoophilic at lowland sites and recent work in this area has covered factors affecting biting rhythms (GRILLET *et al.*, 2005).

This species is the primary vector of human onchocerciasis in highland areas of the Amazônia focus, where it bites man more predominantly in Auaris and Serra dos Surucucus, being present in only small numbers at Toototobi. The absence of cibarial teeth is one of the factors that contribute to the efficiency of this species as a vector. PESSOA *et al.* (2008) referred to the publications of MIRANDA-ESQUIVEL & COSCARÓN (2001) and PY-DANIEL *et al.* (2005) in which they referred to the presence of teeth in *S. guianense s.l.* Some populations show tubercles, not teeth, that will have no effect on microfilarial integrity. PESSOA *et al.* (2008) concluded that other mechanisms probably govern vectorial efficiency apart from cibarial morphology. Several factors, apart from cibarial armature, affect *O. volvulus* transmission and these have been detailed by several authors, *e.g.* REID (1994); SHELLEY (1988a, 1988b), SHELLEY & COSCARÓN (2001), SHELLEY *et al.* (1990).

2.5.2.3. *Simulium* (*Trichodagmia*) *hirtipupa* LUTZ (Figs. 71, 196, 249, 321-324, 439, 546, 605, 665, 742-745, 849, 911, 972, 1032, 1087, 1138, 1193, 1248)

A species that only occurs in Brazil and which has a distinctive pupa covered by black spiniform setae.

Simulium hirtipupa LUTZ, 1910: 260. NEOTYPE female (reared), BRAZIL: Minas Gerais State, Fazenda Barra do Turvo, BR 139, (site 453-6); 16.v.1979, (*A.J.Shelley & A.P.A.Luna Dias*) (BMNH) [Examined.] [Holotype lost, hence Neotype designation by MAIA-HERZOG *et al.*, 1985: 483; neotype also lost; new specimen labelled as neotype in this work - see "**Taxonomic Discussion**".]

FEMALE. General body colour black. Body length (specimens preserved in alcohol) 2.3-3.6 mm (mean = 3.2 mm, s.d. = 0.62, n = 4), (specimens dried) 2.3-2.7 mm (mean = 2.7 mm, s.d. = 0.22, n = 10); wing length 1.8-2.8 mm (mean = 2.4 mm, s.d. = 0.32, n = 10), wing width 0.7-1.5 mm (mean = 1.1 mm, s.d. = 0.25, n = 10).

Head: dichoptic with dark red eyes and nudiocular area slightly developed (Fig. 196). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with pale, semi-recumbent setae interspersed with long, erect, black hairs. Mouthparts dark brown. Antennae with scape and pedicel dark brown, rest of flagellar segments black. Cibarium with sclerotised cornuae and unarmed central trough (Fig. 249).

Thorax: scutum black with evenly arranged groups of recumbent, white, broad setae, interspersed with fine black setae mainly on anterior margin; posterior margin with evenly arranged broad, recumbent, white setae. Scutal pruinosity varying slightly with illumination. With anterior illumination, thorax black; humeri brown with silver pruinosity on antero-lateral margins; lateral and posterior margin black (Fig. 321). With posterior illumination, thorax black with greyish pruinosity on anterior margin to two thirds length of scutum; humeri and lateral margins silver pruinose; posterior margin black (Fig. 322). Scutal pattern variation was observed in specimens from Rio Caramajibe in Alagoas State, with females having 1+1 median and 1+1 submedian to lateral broad brown vittae running full length of thorax, being more obvious with anterior light source (Figs. 323, 324). Scutellum dark brown with recumbent, white hairs intermixed with long, black bristles, especially on posterior margin. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta bare. Radius with line of setae intermixed with distinct spines, basal section of radius with single line of setae. Variation in setation has been observed. MAIA-HERZOG *et al.* (1985) recorded females with radius bare and COSCARÓN (1991) described females with basal section of Radius with 2-3 lines of hairs, Sc with around 11 marks, which appear to be hair insertions, but hairs were never seen, and males with basal section of Radius and Subcosta veins bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 439. Foreleg with coxa, base of trochanter and two thirds of femur brown, middle of tibia whitish; apex of trochanter and tibia, base and apex of femur, and tarsal segments dark brown. Mid and hind legs dark brown, except basal two thirds of tarsal segment I and base of tarsal segment II white. Claws curved with small tooth. Halteres cream with brown base.

Abdomen: tergites I-IV velvet black and tergites V-VIII shiny black, with silver pruinosity on anterior margin of tergites I and II. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses subtriangular, membranous, half as wide as eighth sternite at mid point, with small setae distributed over entire surface (Fig. 546). Cercus hemispherical; paraproct subtriangular with distinct tail-like projection pointing internally, close to gonapophyses; cerci and paraprocts covered by long, brown setae (Fig. 605). Genital fork stout and sclerotised; termination of lateral arms with anterior margin straight and well developed; anterior processes well developed and blunt apically; posterior processes well developed and subtriangular (Fig. 665). Spermatheca globular, with reticulate external sculpturing and with small spicules; area of insertion of spermathecal duct one about two thirds maximum width of spermatheca.

MALE. General body colour black. Body length (specimens preserved in alcohol) 3.8-4.0 mm (mean = 3.8 mm, s.d. = 0.62, n = 3); (specimens pinned) 2.2-3.6 mm (mean = 3.0 mm, s.d. = 0.38, n = 9); wing length 1.0-2.4 mm (mean = 2.1 mm, s.d. = 0.43, n = 9), wing width 0.8-1.9 mm (mean = 1.2 mm, s.d. = 0.31, n = 9).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark with golden, recumbent hairs. Scutal pattern slightly varies with light incidence: with anterior light source thorax grey (Fig. 742); with light source posterior to specimen anterior fourth greyish pruinose and median, thin dark line extending from anterior margin for one third length of scutum (Fig. 743). In specimens from Rio Caramajibe in Alagoas State scutum dark brown with anterior light source and brown with darker median line and pruinose reflections with posterior light source (Figs. 744, 745). Humeri silver pruinose, lateral and posterior margins of scutum black. Scutellum dark brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum black with silvery grey pruinosity. Wing setation as in female, except bare basal section of radius. Leg coloration as in female.

Abdomen: tergites velvet black, basal fringe with long, black hairs. Silver pruinose ornamentation as follows: anterior and lateral margin of tergite II, and lateral margins of tergites V-VIII [best seen when viewed laterally]. In some specimens pruinose reflections can be seen on posterior margin of segment II and segments III, IV and V mesally. Genitalia black; sternal and tergal plates developed. Gonocoxite quadrangular; gonostyle elongate, narrow apically, about three times longer than maximum width of gonocoxite at mid point, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 849). Ventral plate subrectangular with reduced main body, highly developed lateral arms, median process with a distinct keel and subparallel basal arms (Fig. 911). Median sclerite long, about four times longer than width of ventral plate at mid point, with small apical incision (Fig. 911). Paramere weakly sclerotised and poorly developed with no spines (Fig. 972).

PUPA. Cocoon length dorsally 3.3 – 4.0 mm (mean = 3.5 mm, s.d. = 0.24, n = 18), ventrally 3.3 – 4.7 mm (mean = 4.0 mm, s.d. = 0.42, n = 18); pupa length 2.9 –4.7 mm (mean =4.8 mm; s.d. = 0.42, n = 18); gill length 0.9-1.6 mm (mean = 1.2, s.d. = 0.17, n = 18).

Cocoon: shoe-shaped as in Fig. 66, light to dark brown composed of compact and coalesced fibres, with reinforced rim to anterior aperture, margin of aperture not elevated.

Gill: light brown with 12 upwardly directed filaments arranged in bunch in vertical plane. Gill configuration with filaments branching basally at different heights (Fig. 1032); main trunk short, giving rise to three sets of primary branches, two internal and one external; the external and the most dorsal of the internal set with 4 secondary basal branches; the ventral of the internal set with four branches bifurcating on basal third of gill. Filaments stout, pointed distally, with distinctive small, dark brown in rings around diameter spicules, edges crenate; all filaments approximately same length.

Head (*frontoclypeus*): frontal and facial trichomes were not examined as all specimens have the frontoclypeus prominently covered with long black spiniform setae (Fig. 71) [Coscarón (1991) said that the frontal trichomes were bifid in the specimens he studied. Py-Daniel *et al.* (2005) stated that long fine and hyaline trichomes are found on the head and thorax of *S. hirtipupa*, which are only visible by careful examination, where these trichomes are located in the family Simuliidae].

Thorax: covered with prominent black spiniform setae, and up to three long, simple setae; groups of smaller spines and rounded tubercles on posterior third of thorax.

Abdomen: tergite I with 1+1 simple, long, submedian setae on anterior margin and 1+1 groups of rounded tubercles; tergite II covered by spines mainly on anterior margin, 1+1 groups of spines near posterior margins and sometimes with 2+2 long, simple setae sublaterally; tergite III with 4+4 submedian spines in row, 1+1 small setae in middle of spines, 1+1 simple setae anterior to most lateral spines and groups of spine combs on posterior margin [in one specimen the sublateral seta is bifid on the left side]; tergites IV-V with 4+4 simple hooks in row, 2+2 small simple setae anterior to most lateral hooks and 1+1 small setae sublaterally; tergites VI, VII and VIII with spine combs on anterior margin; tergite IX without terminal spines, weakly sclerotised. Abdominal sternite IV with 3+3 submedian setae and spine combs on anterior margin; sternite V with 1+1 submedian and 1+1 sublateral, simple setae and spine combs on anterior margin; sternite VI with 2+2 close, simple, median hooks, 1+1 small setae anterior to most lateral hooks and spine combs on anterior margin; sternites VII-VIII with 2+2 well separated simple spines and spine combs on anterior margins [sometimes 1+1 small setae can be seen posteriorly to most lateral hooks]; sternite IX weakly sclerotised, with spine combs on anterior margins.

LARVA (Final instar). Body length 6.8-7.0 mm (n = 2); length of head capsule 0.9 mm (n = 2); width of head capsule 0.7 mm (n = 2). General body form as in Fig. 1087

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Fig. 1138). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth distinctly reduced and evenly distributed along anterior region and all nearly at same level; median tooth weakly developed [sometime more developed than remaining teeth]; 3+3 sublateral teeth, weakly developed and same level as medium tooth; 1+1 lateral teeth, longer than median and sublateral teeth; lateral serrations absent; 1+1 lines of five hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1193). Sub-esophageal ganglion unpigmented. Antennal segments nearly longer than labral fan stalk, segments I-III dark brown, length of antennal segments I-III excluding the sensillum 0.08:0.09-0.1:0:07-0.1 mm (n = 3). Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately six teeth, five teeth smaller than other tooth; one prominent mandibular serration (Fig. 1248). Lateral mandibular process not seen. Maxillary palps heavily pigmented, one and a half times as long as wide at base. Labral fan with 34-52 rays all with fine, single line of spines in a row (n = 4).

Thorax: grey purplish dorsally and brown tinges ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 32-42 processes of 14-15 hooks (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 12 filaments, pointed and sclerotised apically.

Abdomen: usually with purple bands and brown tinges dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae on segments I, II, but remaining segments with prominent spiny setae, especially segments V, VIII. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 135-130 rows of 23-25 simple hooks (n = 3). Rectal gills with three branches each with approximately 12 finger-like lobes (n = 2).

Taxonomic Discussion. *Simulium hirtipupa* was described by Lutz (1910) from a pupal exuviae collected in Lassance, Minas Gerais State, Brazil being given this name for the very dense and spiny setae on the pupal head and thorax. The holotype is lost, hence MAIA-HERZOG *et al.* (1985) designated a neotype and provided a full description of all life stages. The neotype (a reared female) was collected at Buritizeiro near the type locality in Minas Gerais State by A.P.A.Luna Dias and P.R.Garritano on 10.i.1985. SHELLEY *et al.* (2010) reviewed the taxonomy of *S. hirtipupa*, and stated that they have previously examined the neotype, which was deposited in IOC but this specimen has also been lost (L. GIL-ACEVEDO, pers. comm. to A.J. SHELLEY). I have examined numerous specimens of *S. hirtipupa* from several Brazilian states including Minas Gerais deposited at the BMNH. Following the ICZN (1999), I therefore here select a pinned, reared female specimen collected at Fazenda Barra do Turvo and labelled it as a neotype (see **Material Examined**). I have taken digital images of its thoracic pattern (Figs. 321, 322), which are now stored at the Simuliidae Digital Images Archive at the BMNH.

The morphological differences between *S. hirtipupa* and all other closely related species within the ORBITALE species group are given in the "**Taxonomic Discussion**" under *S. orbitale*.

COSCARÓN (1987, 1991), COSCARÓN & COSCARÓN-ARIAS (2007) and SHELLEY *et al.* (2010) has given full descriptions and illustrations of the life stages of *S. hirtipupa*.

COSCARÓN (1987) placed *S. hirtipupa* in its own subgroup in the subgenus *Thyrsopelma*. Later, MIRANDA-ESQUIVEL & COSCARÓN (2001) maintained it in the same subgenus, and this has been followed in the recent revision of the Neotropical Simuliidae (COSCARÓN & COSCARÓN-ARIAS, 2007). More recently, ADLER & CROSSKEY (2008, 2009, 2010), CROSSKEY & HOWARD (1997, 2004) and SHELLEY *et al.* (2010) placed this species in the ORBITALE species group of the subgenus *Trichodagmia*, which is followed in the current work.

Distribution. *Simulium hirtipupa* is only found in Brazil in the states of Amapá, Bahía, Mato Grosso do Sul, Minas Gerais and São Paulo (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; HAMADA *et al.*, 2003; SHELLEY *et al.*, 2010; **Material Examined**). The finding of specimens by HAMADA *et al.* (2003) in Amapá Stated represents the first record of *S. hirtipupa* for the north of Brazil. It has been also been collected in Mato Grosso do Sul State sympatric with *S. nigrimanum* and *S. subpallidum*.

Biology and Medical Importance. The immature stages of *S. hirtipupa* can be collected in small to medium (2-10 m wide), fast flowing rivers, with pupae attached to rocks and dead leaves, branches and tree roots in parts of the river where the current is faster (SHELLEY *et al.*, 2010). The alimentary habits of females of *S. hirtipupa* are unknown in Brazil, although they are probably zoophilic.

2.5.2.4. *Simulium (Trichodagmia) huairayacu* WYGODZINSKY (Figs. 197, 250, 325, 326, 440, 547, 606, 666, 746, 747, 850, 912, 973, 1033, 1088, 1139, 1194, 1249)

A species closely related to *S. lahillei*, originally described from Tucumán Province, Argentina. The description here provided has been derived from examination of paratype specimens housed at IML, the original description of WYGODZINSKY (1953), and identified material deposited at the AMNH, BMNH and MLP Simuliidae collections.

Simulium huairayacu WYGODZINSKY, 1953: 310. HOLOTYPE male (reared), ARGENTINA: Tucumán Province, Arroyo Matadero, entre Raco y Siambón; 26.vi.1949, (*Wygodzinsky, P.*) (IML).

FEMALE. General body colour dark brown to brownish orange. Body length (specimens pinned) 3.1-3.2 mm (mean = 3.2 mm, n = 3), wing length 2.9-3.4 mm (mean = 3.3 mm, n = 3), wing width 1.4-1.7 mm (mean = 1.8, n = 3)

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 197). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with erect brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and small teeth on central trough (Fig. 250).

Thorax: scutum dark, reddish brown with evenly arranged, recumbent, whitish setae, interspersed with fine, semi-erect brown setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown with 1+1 median, pear-shaped and 1+1 sublateral, wide, silver pruinose vittae, extending from anterior to near posterior margin of scutum; humeri faintly silver pruinose; lateral and posterior margins dark brown to black (Fig. 325). With posterior illumination, thorax dark brown to dark reddish brown, with 1+1 submedian, silver pruinose vittae on anterior third of scutum; humeri weakly silver pruinose; lateral and posterior margins black (Fig. 326). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length except apical third. Radius with numerous setae intermixed with distinct spines, basal section of radius with setae. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 440. Fore leg with coxa, trochanter femur, and internal surface of tibia brown; external surface of tibia silver pruinose; tarsal segments black. Mid and hind legs with coxae, apical half of tibiae, third of tarsal segments I and II, and tarsal segments III, IV dark brown; trochanters and femora brown; basal half of tibiae and basal two thirds of tarsal segments I, and II pale yellowish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown with silver pruinosity on antero-lateral margins of segments II and VI. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite weakly sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular with curved internal margin, membranous and densely covered with hairs (Fig. 547). Cercus subrectangular, covered with brown setae; paraproct long, subtriangular, two and half times longer than cercus, weakly sclerotised on basal half and membranous apically; paraproct densely covered with prominent brown hairs basally and small, stout microtrichiae on apex (Fig. 606). Genital fork stout and sclerotised; termination of lateral arms with anterior margin concave and well developed; anterior processes well developed and blunt apically, posterior processes well developed (Fig. 666). Spermatheca globular, without external sculpturing and groups of four to five, irregularly distributed spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour dark brown to black. Body length (specimens pinned) 2.7-3.4 mm (mean = 2.9 mm, s.d. = 0.30, n = 4), wing length 2.3-3.2 mm (mean = 2.7 mm, s.d. = 0.40, n = 4), wing width 1.5-1.8 mm (mean = 1.6 mm, s.d. = 0.20, n = 4).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark black covered by evenly distributed recumbent golden hairs with greenish reflection with certain lights. Scutal pattern varying with light incidence: with light source anterior, thorax black with silver pruinosity on anterior third [in pristine specimens 1+1 black comma-shaped vittae are visible on anterior third of scutum] (Figs. 746); humeri, lateral and posterior margins dark brown to black. With posterior illumination, thorax black (Fig. 747). Variation on this pattern was recorded in link-reared specimens recently collected in Cordoba Province, Argentina. With light incidence anterior 1+1 black comma-shaped vittae on anterior third of scutum. With light posterior, thorax dark brown to black with 1+1 triangular-shaped vittae on anterior third of scutum; humeri, lateral and posterior margins dark brown to black. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation similar to female, except Sc bare. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergites II and VI-VIII (best seen in some specimens when tilted and viewed laterally). Genitalia brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle spindle-shaped with dorsal and ventral margins sinuous, often terminating in single, stout spine [in some specimens two spines can be seen; see also WYGODZINSKY, 1953a: 312, Fig. 112.]; gonocoxite and gonostyle covered with long setae (Fig. 850). Ventral plate sclerotised, subrectangular; main body of ventral plate covered with long hair with ventral margin distinctly triangular centrally; anterior median process often well developed centrally; lateral shoulders slightly to well developed and basal arms well developed and subparallel (Fig. 912). Median sclerite long, about three times longer than wide at widest point, with deep incision extending to its base (Fig. 912). Paramere well developed with sclerotised basal processes, without long spines centrally (Fig. 973).

PUPA. Cocoon length dorsally 2.6-4.4 mm (mean = 3.7 mm, s.d = 0.53, n = 13), ventrally 5.5-6.5 mm (mean = 5.9 mm, s.d. = 0.30, n = 10); pupa length 4.2-5.1 mm (mean = 4.6 mm, s.d. = 0.28, n = 10); gill length 0.9-1.9 mm (mean = 1.5, s.d. = 0.25, n = 13).

Cocoon: shoe-shaped as in Fig. 66, dark brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown 12 upwardly directed filaments arranged in bunch in vertical plane (Fig. 1033). Gill configuration with filaments branching basally at different heights; main trunk short, giving rise to two sets of primary branches, one dorsal and one ventral; dorsal branch with filaments upwardly directed arranged in bunch and consisting of 10 filaments; ventral branch directed ventrally and weakly directed towards head of pupa with only two secondary filaments dividing at gill base (Fig. 1033). Filaments stout, pointed distally, with tubercles and irregular rugosities on surface, edges weakly smooth; all filaments approximately same length.

Head (*frontoclypeus*): without frontal or facial trichomes in the few specimens examined. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in groups of two or three laterally in frontal region; tubercles rounded and well distributed over entire surface in facial region.

Thorax: with up to five multibranched long trichomes near margin of dorsal cleft, and one multibranched trichome on central and alar region; tubercles rounded and distributed over entire surface.

Abdomen: abdominal tergite I with 1+1 simple, short setae laterally and triangular tubercles well distributed over entire surface; tergite II with 4+4 submedian spiniform setae, and 1+1 small simple setae anterior to outermost spiniform; tergites III and IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to most lateral of the hooks, and 1+1 lateral small simple setae; tergites V-VII with 1+1 small sublateral simple setae; tergite VIII without setae; tergite IX weakly sclerotised and terminating in 1+1 small spines. Spine combs distribution as follows: 1+1 groups on antero-lateral margins of tergites II-VII, and well developed trichomes resembling teeth on tergite VIII. Sternite III with 1+1 submedian small simple setae; sternite IV with 1+1 submedian and 1+1 lateral small simple setae; sternite V with 1+1 close, simple hooks and two sublateral, simple setae; sternites VI-VII with 2+2 well separated, simple, median hooks; sternites VIII, IX without setae. Spine combs distribution on antero-lateral margins of sternites III-VIII.

LARVA (Final instar). Body length 8.7-10.71 mm (mean = 9.3 mm; s.d. = 0.90, n = 5); length of head capsule 0.8-1.7 mm (mean = 1.0 mm, s.d. =0.37, n = 5); width of head capsule 0.6-1.5 mm (mean = 0.8 mm, s.d. = 0.35, n = 5). Body colour dark grey dorso-laterally, whitish ventrally (specimens fixed in alcohol). General body form as in Fig. 1088.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, rounded apically; postgenal bridge nearly one and half times as long as hypostomium (Fig. 1139). Hypostomium strongly pigmented on anterior margin, often with nine apical teeth weakly developed and not protruding in central region; median tooth well developed and most prominent; 3+3 sublateral teeth adjacent to median teeth; 1+1 lateral teeth at same height as sublateral teeth; 2-3 lateral serrations; 1+1 lines of approximately 6-8 hypostomial setae parallel to lateral margins; 1+1 long, simple or bifid setae in posterior half of hypostomium (Fig. 1194). Sub-esophageal ganglion lightly pigmented. Antennal segments smaller than labral fan stalk, segment I light to dark brown, base of segment II and segment III dark brown; length of antennal segments I-III excluding the sensillum 0.1:0.05-0.5:0.05-0.7 mm (n = 5). Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately seven teeth, first four longer than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1249). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 42-48 rays (n = 5), each with fine, single line of microspinules in a row.

Thorax: greyish dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 18-25 processes (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 12 filaments, all branching from common trunk and divided into three branches, filaments pointed.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 163-200 rows of 25-36 simple hooks (n = 4). Rectal gills with three lobes of approximately 8-15 small, finger-like lobules each (n = 5).

Taxonomic Discussion. *Simulium huairayacu* was described by WYGODZINSKY (1953) based on numerous females, males, pupae and larvae collected in several streams in Tucumán Province, Argentina. WYGODZINSKY (1953) selected a holotype which is now housed at the IML (see **Material Examined**). I have been unable to examine the male holotype of *S. huairayacu*, but in recent correspondence with GUILLERMO CLAPS, Curator of Diptera at IML he stated the following: “A male labelled as holotype and a female paratype (as allotype), and some paratypes of *S. huairayacu* are housed in the Simuliidae collections at IML. The male holotype and female paratype are in good condition, but the female allotype is not”. I have been able to examine one male and one female labelled as paratypes and mounted on the same pin housed at this institution (**Material Examined**).

The female and male of *S. huairayacu* (Figs. 325, 326, 746, 747) are externally similar to that of *S. lahillei* (Figs. 330-333, 751, 752) by the brownish orange coloration of the thorax. Dichoptic males occur in *S. huairayacu*, and these have been discussed by WYGODZINSKY (1953). The adults of the latter two species can only be separated by the configuration of the pupal gill filaments. *Simulium huairayacu* and *S. lahillei* both have 12 pupal gill filaments (Figs. 1033, 1036), but in *S. huairayacu*, the filaments are grouped in two primary branches, one dorsal and one ventral. The dorsal branch has 10 secondary filaments, all arranged in a bunch and directed upwards, while ventral branch has only two filaments directed towards ventral region of pupa (Fig. 1033). In *S. lahillei* the filaments are divided into two primary branches, one external with eight filaments and one internal with four filaments, all upwardly directed (Fig. 1036).

The larva *S. huairayacu* and that of *S. lahillei* may only be distinguished by the general configuration and number of filaments of the dissected gill histoblast in mature pupae [see also WYGODZINSKY, 1953]. The latter author also stated that the larva of *S. huairayacu* is morphologically identical to the larva of *S. lahillei*, except it is smaller and has relatively finer antennal segments.

A full description of all life stages of *S. huairayacu* may be found in COSCARÓN & COSCARÓN-ARIAS (2007) and WYGODZINSKY (1953).

Simulium huairayacu was placed in the subgenus *Grenieriella* by WYGODZINSKY (1953). ADLER & CROSSKEY (2008, 2009, 2010), COSCARÓN & COSCARÓN-ARIAS (2007) and SHELLEY *et al.* (2010) placed it in the ORBITALE species group of the subgenus *Trichodagmia*.

Distribution. *Simulium huairayacu* has only been recorded from Argentina, Bolivia and Perú (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; CROSSKEY & HOWARD, 1997, 2004).

Biology and Medical Importance. COSCARÓN & COSCARÓN-ARIAS (2007) stated that the immature stages of *S. huairayacu* can be collected in small to medium-sized torrential creeks in clear, cold water, frequently found together with *S. lahillei*. I have collected immature stages of this species in Tucumán Province, Argentina in a stream 10 m wide and 30 cm deep, with fast flowing and murky waters with lichens and huge boulders. The females did not bite humans during the field work (L.M. HERNÁNDEZ, unpublished data).

2.5.2.5. *Simulium (Trichodagmia) itaunense* D'ANDRETTA & GONZÁLEZ B. (Figs. 13, 34, 52, 198, 251, 327, 328, 441, 548, 607, 667, 748, 749, 851, 913, 974, 1034, 1089, 1140, 1195, 1250)

A well-known zoophilic species only recorded in Brazil.

Simulium itaunensis D'ANDRETTA & GONZÁLEZ B., 1964: 106-108. HOLOTYPE male (reared), BRAZIL: São Paulo State, Itatinga (Fazenda Itaúna); 17.vii.1957 (*C.D'Andretta Jr.*) (MZUSP, no. 856).

FEMALE. General body colour black. Body length (specimen in alcohol) 4.2 mm (n = 1), (specimens pinned) 2.9-3.4 mm (mean= 2.9 mm, s.d. = 0.17, n=3); wing length 2.8-3.1 mm (mean = 2.9 mm, s.d. = 0.17, n=3), wing width 1.4-1.5 mm (mean = 1.5 mm, s.d. = 0.09, n = 3).

Head: dichoptic with dark red eyes and nudiocular area slightly developed (Fig. 198). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with recumbent white setae interspersed with dark, semi-erect black setae. Mouthparts dark brown to black. Antennae with scape and pedicel dark brown, rest of flagellar segment black. Cibarium unarmed or with undeveloped tubercles in the central trough some of which have extremely fine denticles (only visible at high magnification); cornuae well developed and sclerotised (Fig. 251) [STRIEDER (2004) stated that cibarium in this species is armed with small tubercles (see Fig. 4, page 295), but these were not seen in any specimen that we studied].

Thorax: scutum black, covered by recumbent, white setae. Scutal pattern varying only slightly with illumination. With anterior illumination, thorax black; humeri brownish with faint grey pruinosity; lateral and posterior margins black (Fig. 327). With posterior illumination, thorax black with grey pruinosity on anterior two thirds of scutum; lateral and posterior margins black (Fig. 328). Humeri brownish and weakly pruinose. Scutellum black with recumbent white setae interspersed with long, black bristles. Postnotum black with silver pruinosity. Pleura dark brown to black with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta nearly bare with only few setae in basal third (only setae insertions were visible in the few dissected specimens we examined). Radius with line of setae intermixed with spines; basal section of Radius with hairs arranged in double line on basal third. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 441. Foreleg with coxa, trochanter and femur pale brown, tibia with basal and apical third and tarsal segments dark brown, pale yellow mesally. Mid and hind legs with coxa, apex of hind femur, apex of mid and hind tibia and basitarsal segment I and II dark brown; trochanter, mid femur, basal half of hind femur, basal half of mid and hind tibia yellowish brown; basal two thirds of basitarsal segment I and II pale yellow. Claws curved without distinct basal tooth. Halteres cream with brown base.

Abdomen: tergites I-IX shiny black, covered with recumbent white setae; tergite I silver pruinose on antero-lateral margin. Tergal plates developed; sternal plates undeveloped. Sternites greyish black; genitalia black. Eighth sternite sclerotised with irregularly distributed setae on posterior margin; gonapophyses crescent shaped, well developed and touching centrally with apices curved in anterior direction, membranous and rounded distally, highly setose over entire surface (Figs. 34, 548). Cerci subhemispherical, covered with brown setae; paraproct subtriangular, nearly same length as cercus, with small membranous process with hairs and setae and weakly sclerotised anteriorly; paraproct covered with prominent brown setae interspersed with small setae (Fig. 607). Genital fork stout and sclerotised; termination of lateral arms with anterior margin straight and developed; anterior and posterior processes well developed (Fig. 667). Spermatheca globular, without external sculpturing and with single spicules on internal surface; area of insertion of spermathecal duct weakly sclerotised, two fifths maximum width of spermatheca (Fig. 13).

MALE. General body colour black. Body length (specimens pinned) 3.4-3.9 mm (mean = 3.7 mm, s.d. = 0.19, n = 4), wing length 2.7-2.9 mm (mean = 2.8 mm, s.d. = 0.06, n = 4), wing width 1.3-1.6 mm (mean = 1.4 mm, s.d. = 0.14, n = 4).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black with grey pruinosity, covered with golden, recumbent hairs. Scutal pattern, irrespective of light direction, consisting of 1+1 submedian, rounded silver pruinose vittae on anterior one third (Figs. 748, 749). Humeri weakly silver pruinose; lateral and posterior margins of scutum black [light source anterior or posterior], weakly silver pruinose when specimens viewed at an angle. Scutellum black with recumbent golden hairs interspersed with long, erect black hairs on posterior margin. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Subcosta with fewer setae. Leg coloration as in female except legs darker brown.

Abdomen: tergites black distinctly covered by golden, recumbent hairs, basal fringe with long, brown hairs. Silver pruinose ornamentation on abdominal segments as follows: anterior margin of tergites IV and V [in dorsal view] and antero-lateral margin of segments II and V-VII [best seen when specimen viewed laterally]. Genitalia black; tergal plates poorly and sternal plates well developed. Gonocoxite subquadrangular; gonostyle spindle-shaped, 3.5 times longer than length of gonocoxite at mid point, with a single, stout spine [sometimes with another smaller one]; gonocoxite and gonostyle covered with long setae (Fig. 851). Ventral plate sclerotised, subrectangular with well developed lateral shoulders, prominent, median, pear-shaped process arising from posterior margin covered with long hairs; basal arms straight, sclerotised and weakly narrow apically (Figs. 52, 913). Median sclerite prominent, ovoid, nearly as long as width of ventral plate, with distinct incision to half of its length (Fig. 913). Paramere weakly sclerotised and poorly developed with no spines (Fig. 974).

PUPA. Cocoon length dorsally 3.7-4.3 mm (mean = 4.0 mm, s.d.= 0.21, n=9), ventrally 4.5-4.9 mm (mean = 4.7 mm, s.d.= 0.14, n=9); pupa length 4.1-5.5 mm (mean = 4.9 mm; s.d. = 0.39, n = 9); gill length 0.7-1.2 mm (mean = 0.9 mm, s.d. = 0.17, n = 11).

Cocoon: shoe-shaped as in Fig. 66, light to dark brown composed of thick coalesced fibres, with reinforced rim to anterior aperture; margin of aperture weakly elevated.

Gill: light brown with 45-56 upwardly directed filaments arranged in bunch in vertical plane [specimens with 50 filaments are commonly found]. Gill configuration with main trunk short, giving rise to four sets of primary branches, three external and one internal (Fig. 1034). Primary branches bifurcate further into secondary branches that are highly variable in number of filaments, all branching at different heights. In gills with the lowest number of filaments the configuration is as follows: most dorsal of external branch often with 17 filaments, median 8 and ventral 7; internal set of filaments often consisting of 14 filaments. Variation of this pattern occurs on all primary branches. Filaments stout, pointed and highly sclerotised distally, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 simple, spiniform, facial trichomes; frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and 2-3 platelets in groups of 2 laterally in frontal region, respectively; tubercles rounded, densely distributed in facial region and absent from frontal region.

Thorax: with 4+4 distinct spiniform trichomes near margin of dorsal cleft and 2+2 simple trichomes on central region of thorax; tubercles mostly rounded on ventral margin near base of gill and pointed on posterior part of dorsal margin.

Abdomen: tergite I with spine combs on posterior margin; tergite II with 3+3 submedian and 1+1 sublateral spiniform setae in longitudinal row and 1+1 long, simple setae anterior to most lateral spiniform setae; tergites III and IV with 4+4 submedian, simple hooks in longitudinal row, sometimes 1+1 small, simple setae anterior to most lateral hooks and 1+1 small, simple setae laterally; tergites V-

VII with 1+1 small simple setae laterally; tergite IX sclerotised without terminal spines. Groups of spine combs on anterior margin of tergites I-VIII. Abdominal sternite III with 1+1 submedian and 2+2 sublateral small, simple setae; sternite IV with 2+2 submedian, spiniform setae; V with 2+2 submedian, close bifid hooks; sternites VI-VII with 2+2 well separated bifid hooks. Abdominal sternites III-VIII with groups of spine combs on anterior margin.

LARVA (Final instar). [The description of the larva of *S. lahillei* has been derived from PY-DANIEL *et al.* (1985). Body measurements were not given in the latter publication.] Body colour varying from pale grey to pale green (specimens preserved in alcohol). General body form as in Fig. 1089.

Head: mainly dark brown, anterior region of cephalic apotome darker. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, wide at mid line and pointed apically; postgenal bridge nearly as long as hypostomium (Fig. 1140). Hypostomium strongly pigmented on anterior margin, with approximately 10 teeth weakly developed in central region; two median teeth [PY-DANIEL *et al.* (1985) stated that this condition might be teratological], poorly developed; 3+3 sublateral and 1+1 lateral teeth nearly same length; 1+1 very reduced lateral serrations; 1+1 lines of six hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1195). Sub-esophageal ganglion not examined. Antennal segments longer than labral fan stalk; coloration of antennal segments not given in PY-DANIEL *et al.* (1985); length of antennal segments I-III excluding the sensillum 1:2:2:1.2 mm. Mandible with three apical teeth, first one longer than second and third teeth; mandibular comb with approximately 11 teeth, first six more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1250). Lateral mandibular process absent. Maxillary palp morphology not described in PY-DANIEL *et al.* (1985). Labral fan with 47-48 rays each with fine, single line of spines in a row.

Thorax: pale grey to pale green. Cuticle with small setae. Proleg with plate heavily sclerotised. Pupal respiratory gill histoblast not described in PY-DANIEL *et al.* (1985).

Abdomen: pale grey to pale green. Ventral nerve cord not described in PY-DANIEL *et al.* (1985). Ventral papillae absent. Cuticle with petaloid setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 133 rows of 17-22 simple hooks (number of specimens examined not given). Rectal gills with three lobes.

Taxonomic Discussion. The taxonomy of *S. itaunense* has been fully discussed in HERNÁNDEZ *et al.* (2005). A comparison between *S. itaunense* and related species of the ORBITALE group is given under *S. orbitale*. PY-DANIEL *et al.* (1985) provided the first larval description of *S. itaunense*.

COSCARÓN & COSCARÓN-ARIAS (2007) placed *S. itaunense* in the subgenus *Thyrsopelma* [= *Trichodagmia*], but I here accept its placement in the ORBITALE species group following the work of SHELLEY *et al.* (2010). ADLER & CROSSKEY (2008, 2009, 2010) considered this species as a member of the valid subgenus *Trichodagmia*.

Distribution. *Simulium itaunense* has only been recorded in Brazil from the states of Rio Grande do Sul, Santa Catarina and São Paulo (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; SHELLEY *et al.*, 2010; STRIEDER, 2004a,b; **Material Examined**).

Biology and Medical Importance. In Brazil, the immature stages of *S. itaunense* are found in small rivers (3 m wide) with clear water and sandy, river beds (A.J. SHELLEY & A.P.A. LUNA DIAS, unpublished data). STRIEDER (2004a) recorded the larvae and pupae on Podostemaceae and on rocks in fast flowing, clear water streams. He also stated that the females of *S. itaunense* bite horned cattle in Rio Grande do Sul. STRIEDER & CORSEUIL (1992), and STRIEDER *et al.* (1992) recorded females of *S. itaunense* biting bovines the waterfall Verão, Rio Grande do Sul, Brazil.

2.5.2.6. *Simulium (Trichodagmia) jeteri* (PY-DANIEL, DARWICH, MARDINI, STRIEDER & COSCARÓN) (Figs. 329, 750, 852, 1035, 1090, 1141, 1196, 1251)

This is a poorly known species from southern Brazil. All stages were described by PY-DANIEL *et al.* (2005) based on pharate pupae, pupal exuviae and larvae. Their description of the adults is superficial, most of the photographs are indistinct and hence insufficient to enable species identification. The species may be distinguished from other species of the subgenus *Trichodagmia* by the pupal gill. The following description has been distilled from the description and photographs for this species by the original authors. For details on other characters not used in the standard species descriptions, the reader is referred to the original description. I cannot verify the description of *S. jeteri* because I was unable to examine type specimens or other material.

Thyrsopelma jeteri PY-DANIEL *et al.*, 2005: 465. HOLOTYPE female extracted from pupa and its pupal exuviae. BRAZIL: Rio Grande do Sul State, Município de Barracão, Espigão Alto, Arroio Marmeleiro; 2.ix.1988, (*Py-Daniel*, *V.*, *Darwich*, *S.*, *Mardini*, *L.* & *Barbosa*, *U.C*) (INPA).

FEMALE. General coloration as in Fig. 329. Nudiocular triangle well developed. Claw of hind leg without tooth.

MALE. General coloration brown (Fig. 750). Gonostyle longer than gonocoxite, spindle-shaped and terminating in a blunt spine (sometimes smaller subapical spine present) (Fig. 852).

PUPA. Cocoon length dorsally 2.1-2.5 mm (n = 5), ventrally 2.5-2.9 mm (n = 4); gill length 0.6-0.8 mm.

Cocoon: shoe-shaped as in Fig. 66, light brown and not covering gills. Texture smooth and with no median anterior projection dorsally.

Gill: light brown with 15 upwardly directed filaments arranged in bunch. Gill configuration with filaments branching at different heights; main trunk short giving rise to two set of primary branches, one external and one internal. The external branch have one dorsal one median and one ventral secondary branches with four, two and three filaments each, respectively. The internal branch have one dorsal and one ventral secondary branch each with four and two filaments, respectively (Fig. 1035). Filaments short, covered with fine spiniform tubercles, narrower distally, each terminating in sclerotised spine; all filaments relatively of same length.

Head (*frontoclypeus*): with 1+1 frontal and 1+1 simple, reduced facial trichomes; frontoclypeus with numerous rounded tubercles or without tubercles.

Thorax: with 4+4 with several groups of trichomes variously distributed; tubercles rounded when present and with varying distributions.

Abdomen: tergite I with 1+1 long simple trichomes with or without denticules arranged in 1+1 groups on anterior margin; tergite II with 1+1 long simple setae and 1+1 short median setae and 4+4 short hooks and no anterior denticules; tergites III-IV with 2+2 simple median setae and 1+1 simple hooks on posterior margin; tergite V with 5+5 or 6+6 simple setae with small denticules on anterior margin (1+1 setae are smaller on lateral margins); tergite VI with 2+2 short simple setae without anterior denticules; tergite VII with 2+2 setae and small denticules on anterior margin; tergite IX without setae with anterior denticules; tergite IX with small terminal spines. Sternal segments III-IV with 1+1 groups of denticules on anterior margin; sternite V with denticules resembling teeth on anterior margin and 3+3 simple setae; sternite VI with denticules resembling teeth on anterior margin, 2+2 simple setae and 2+2 bifid or trifid hooks; sternite VII with denticules on anterior margin, 3+3 simple small setae and 2+2 prominent bifid hooks; sternite VIII with denticules resembling teeth anteriorly to innermost hook, 2+2 bifid hooks.

LARVA (Final instar). Body length 5.2-5.6 mm [other head measurements not given in original description]. Body colour dark grey to yellowish white (specimens preserved in Carnoy's solution and/or alcohol). General body form as in Fig. 1090.

Head: mainly dark brown. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft varying from circular to subtriangular; postgenal bridge 1.25 times as long as hypostomium (Fig. 1141). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth weakly developed on anterior margin [PY-DANIEL *et al.*, 2005 recorded one extra lateral tooth that is sometimes visible in few specimens]; median, 3+3 sublateral and lateral teeth of approximately same length; paralateral teeth often absent, though one paralateral tooth can sometime s be seen.; lateral serrations absent; 1+1 lines of 5-7 hypostomial setae parallel to lateral margins (Fig. 1196). Sub-esophageal ganglion not examined. Antenna longer than labral fan stalk [coloration not given in the original description], length of antennal segments I-III excluding the sensillum 1:1.7-1.8:1.1-1.5 mm. Mandible with two apical teeth; mandibular comb with approximately 8-9 teeth, first three longer than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1251). Lateral mandibular process present. Maxillary palps heavily pigmented. Labral fan with 51-56 rays each with fine, single line of spines in row.

Thorax: coloration not given in the original description. Cuticle apparently without setae. Proleg with plate heavily sclerotised. Pupal respiratory gill histoblast short and rounded; dissected gill histoblast with 15 filaments.

Abdomen: coloration not given in the original description. Ventral nerve cord greyish. Ventral papillae absent. Cuticle with subpetaloid setae. Anal sclerite well sclerotised; no sclerotised areas between arms.s Posterior circlet with 130-164 rows of 14-19 simple hooks. Rectal gills not examined (number of specimens examined not given in the PY-DANIEL *et al.*, 2005).

Taxonomic Discussion. *Simulium jeteri* has been recently described by PY-DANIEL *et al.* (2005) based on females, males, pupae and larvae collected from Rio Grande do Sul, Brazil. The type material is said to be deposited at INPA under the care of VICTOR PY-DANIEL, but I have been unable to examine it. SHELLEY *et al.* (2010) have recently reviewed the taxonomy of this species.

PY-DANIEL *et al.* (2005) provided comparisons of *S. jeteri* with other species of *Trichodagmia* based on the number of filaments in the pupal gill and morphological characters of the larvae. The latter are highly variable and are size dependent and were not regarded by SHELLEY *et al.* (2010) as species diagnostic characters. COSCARÓN & COSCARÓN-ARIAS (2007) provided a short diagnosis for the pupa and larva based on the original description. From the descriptions and photographs provided by the authors, it is impossible to compare this species with any other species in *Trichodagmia.* The presence of a spindle-shaped gonostyle (Fig. 852) places it the ORBITALE species group (*sensu* SHELLEY *et al.*, 2010) and the 15 filaments in the gill make it unique in this species group (Fig. 1035). The general morphology of the pupal gill filaments of *S. jeteri* is similar to that of *S. duodenicornium* and *S. scutistriatum*, but in the latter species the gill have 12 filaments arranged in a rather different configuration (Figs. 1030, 1042). Based on the number of gill filaments and the lack of material at hand, I agree with SHELLEY *et al.* (2010) and maintain *S. jeteri* as a valid species.

PY-DANIEL *et al.* (2005) placed *Simulium jeteri* (as *Thyrsopelma jeteri*) in the genus *Thyrsopelma.* This taxonomic arrangement has not been followed in the recent World Inventory of Blackflies by ADLER & CROSSKEY (2008, 2009, 2010), who considered *Thyrsopelma* as a subgeneric synonym of *Trichodagmia.* The latter taxonomic problem has been discussed in detail SHELLEY *et al.* (2010).

Distribution. *Simulium jeteri* has only been collected in four localities in the state of Rio Grande do Sul (ADLER & CROSSKEY, 2008, 2009, 2010; PY-DANIEL *et al.*, 2005; SHELLEY *et al.*, 2010).

Biology and Medical Importance. Larvae and pupae of *S. jeteri* were found in rocky bottomed, fast flowing crystalline waters with sparse vegetation on the margins (PY-DANIEL *et al.*, 2005). The authors provide a list of the physico-chemical characteristics of the type locality with a water temperature of 11°C and a pH of 6.08. recorded.

2.5.2.7. *Simulium (Trichodagmia) lahillei* (PATERSON & SHANNON, 1927) (Figs. 53, 199, 252, 330-333, 442, 549, 608, 668, 751, 752, 853, 914, 975, 1036, 1091, 1142, 1197, 1252)

A relatively well-known species, which has only been recorded from southern South America (Argentina).

Eusimulium lahillei PATERSON & SHANNON, 1927: 740. NEOTYPE female, ARGENTINA: Tucumán Province, Famaillá; 18.ix.1949, (*Romaña & Wygodzinsky*) (NMHU) [Examined.] **New type designation**.

FEMALE. General body colour dark reddish brown. Body length (specimens pinned) 3.6-4.4 mm (n = 2), wing length 3.6 (n = 2), wing width 1.2-1.3 mm (n = 2).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 199). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with erect brown hairs. Mouthparts parts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and small teeth in central trough (Fig. 252).

Thorax: scutum dark reddish brown with evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent brown setae; posterior margin with long white recumbent hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark reddish brown with 1+1 pear-shaped median and 1+1 wide, submedian, grey pruinose vittae, beginning near anterior border of scutum and extending to near posterior margin; humeri pale brown, lateral and posterior margins dark reddish brown (Figs. 330, 332). With posterior illumination, thorax dark reddish brown, with 1+1 submedian, comma shaped, silver pruinose cunae on anterior third of scutum [in some specimens fine brown line on central region of scutum extending from the anterior to posterior margins]; humeri and lateral margins grey pruinose; posterior margin dark reddish brown (Figs. 331, 333). Scutellum dark reddish brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark reddish brown with silver pruinosity. Pleura dark reddish brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length, except apical third. Radius with numerous setae intermixed with distinct spines, basal section of radius with irregular lines of setae. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 442. Coxa, femur, trochanter and external surface of tibia whitish to pale brown; internal surface of tibia and tarsal segments dark brown. Mid and hind legs with trochanters, base of femora and base of basitarsi whitish; coxae, apical half of tibiae, apical half of basitarsi, and remaining tarsal segments dark brown; apical two thirds of femora and basal two thirds of tibiae pale brown. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown to black, silver reflection on dorsal and lateral margins of tergite II and on lateral margins of tergites IV-VII. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite weakly sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses 1.5 times longer than eighth sternite at mid point, membranous and highly setose (Fig. 549). Cercus suboval, covered with brown setae; paraproct nearly three times longer than cercus, subrectangular, weakly sclerotised on anterior margin, rounded apically; paraproct covered by long brown setae at junction with cercus and stout, short setae toward apex (Fig. 608). Genital fork with slender and sclerotised stem; termination of lateral arms with anterior margin weakly straight; anterior processes well developed and blunt apically, posterior processes strongly developed (Fig. 668). Spermatheca globular, with no external sculpturing and irregularly distributed spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour dark reddish brown. Body length (specimens pinned) 2.9-3.6 (n = 2), wing length 2.6 mm (n = 1), wing width 1.2 (n = 1).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark reddish brown covered with recumbent yellowish hairs on anterior margin and whitish towards posterior margin. Scutal pattern varies slightly with light incidence: with light source anterior thorax dark reddish brown, slightly darker on central region forming wide, pear-shaped mark that extends from anterior to posterior margins; humeri dark brown, sometimes weakly pruinose; lateral margin dark brown to black with faint pruinosity; posterior margin dark brown [in some specimens a central dark brown line is seen on anterior third of scutum] (Fig. 751). With posterior illumination, thoracic pattern as with anterior light incidence, except 1+1 round, submedian, silver pruinose spots on anterior third of scutum; humeri pruinose with certain lights. (Fig. 752). Scutellum dark brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum dark brown with faint silver grey pruinosity. Wing setation as in female. Legs as in female.

Abdomen: tergites dark brown to black with yellow marking on antero-lateral margins, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites VII, VIII (best seen when specimen tilted and viewed laterally). Genitalia brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle spindle-shaped, with dorsal and ventral margins sinuous, nearly same length as gonocoxite terminating in two stout spines; gonocoxite and gonostyle covered with long setae (Fig. 853). Ventral plate sclerotised, subrectangular, covered with long hair; main body with anterior median process well developed in central region; ventral margin prominently developed centrally; lateral shoulders and basal arms well developed, basal arms subparallel (Figs. 53, 914). Median sclerite long, about three times longer than wide at widest point, with prominent incision (Fig. 914). Paramere weakly developed, with basal arms sclerotised and numerous minute spines centrally (Fig. 975)

PUPA. Cocoon length dorsally 3.2-4.2 mm (mean = 3.7 mm, s.d = 0.47, n = 4), ventrally 4.9-5.6 mm (mean = 5.3 mm, s.d. = 0.29, n = 4); pupa length 3.9-4.9 mm (mean = 4.0 mm, s.d. = 0.61, n = 2); gill length 1.3-2.3 mm (mean = 1.6, s.d. = 0.34, n = 5).

Cocoon: shoe-shaped as in Fig. 66, dark brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown with 12 upwardly directed filaments arranged in bunch in vertical plane (Fig. 1036). Gill configuration with filaments branching basally at different heights; main trunk short, giving rise to three sets of primary branches, one internal and two external: the more external consists of one dorsal branch with six secondary branches that bifurcate at different heights and one ventral with two filaments; the internal branch consists of four secondary branches that bifurcate at some distance from base of gill at different heights. In some specimens secondary filaments of dorsal external primary branches bifurcated more basally and internal primary branch of all secondary filaments bifurcate at same level (see WYGODZINSKY, 1949, p. 313, Fig. 6 D, E). Filaments stout, pointed distally, without spicules on surface, but covered with granules, edges weakly smooth; all filaments approximately same length.

Head (*frontoclypeus*): trichomes absent in the single specimen examined [WYGODZINSKY, 1951 stated that the trichomes were apparently absent]; frontoclypeus covered by fine granules.

Thorax: trichomes absent in the single specimen examined [WYGODZINSKY, 1951 stated that the trichomes were apparently absent]; thorax covered by fine granules.

Abdomen: abdominal tergite I with 1+1 trifid, long setae laterally; tergite II with 4+4 spiniform simple short setae in longitudinal row; tergites III and IV with 4+4 submedian simple hooks in longitudinal row; tergites V-IX without setae; tergite IX with 1+1 terminal spines, weakly sclerotised. Spine combs distribution on antero-lateral margins of tergites VI-VIII, some resembling teeth on tergites VII and VIII. Sternites III, IV without setae; sternite V with 2+2 close simple hooks; sternites VI, VII with 2+2 well separated simple hooks. All sternites without visible spine combs.

LARVA (Penultimate instar). [I have not been able to obtain mature larvae of *S. lahillei*. Therefore, the description here provided has been derived from three penultimate instar larvae housed at the BMNH and MLP, and the description of WYGODZINSKY (1949) and COSCARÓN & COSCARÓN-ARIAS (2007)]. Body length 9.5-10.0 mm (n = 3); length of head capsule 0.8-1.0 mm (n = 3); width of head capsule 0.7-0.8 (n = 3). Body colour dark grey dorso-laterally, whitish ventrally (specimens preserved in alcohol). General body form as in Fig. 1091.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge 1.5 times as long as hypostomium (Fig. 1142). Hypostomium strongly pigmented on anterior margin, with nine apical teeth distinctly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, central slightly smaller than other two teeth; 1+1 lateral teeth nearly as long as sublateral teeth; approximately 6+6 lateral serrations; 1+1 lines of approximately eight hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1197). Sub-esophageal ganglion lightly pigmented. Antennal segments longer than labral fan stalk, segments I-III pale to dark brown; length of antennal segments I-III excluding the sensillum 0.06:0.1:0.06 mm (n = 1). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately 11 teeth, first, second and fourth more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1252). Lateral mandibular process absent. Maxillary palps heavily pigmented, one and a half times as long as wide at base. Labral fan with 50-60 rays each with fine, single line of spines in row.

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 34 processes (n = 1). Pupal respiratory gill histoblast not examined.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except hairs and scales on anal sclerite. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 179 rows of 31 simple hooks (n = 1) [WYGODZINSKY (1949) recorded 300-360 rows (mean = 320) with 30-40 simple hooks.] Rectal gills with three lobes of 14 small, finger-like lobules (n = 1) [COSCARÓN & COSCARÓN-ARIAS (2007) recorded 10 diverticula on each lobe].

Taxonomic Discussion. *Simulium lahillei* was described by PATERSON & SHANNON (1927) as *Eusimulium lahillei* based on six syntype females collected from Quebrada de Lules, Tucumán Province, Argentina by R.C.Shannon. Unfortunately, all syntypes have been lost (S. COSCARÓN, pers. comm. to L.M. HERNÁNDEZ, March.2005).

The life stages of *S. lahillei*, including the eggs, were later redescribed by WYGODZINSKY (1949) from numerous specimens collected in Tucumán Province, Argentina, who also discussed its systematic position within *Simulium s.l.* In addition, WYGODZINSKY (1949) provided illustrations for all main taxonomic characters and, at this time, stated that he collected females of *S. lahillei* biting horses in Monte Cabello, Argentina. In a subsequent paper, WYGODZINSKY (1953) gave additional distribution records for *S. lahillei* and found females biting humans in Córdoba Province, Argentina. Several attempts were made to locate the material studied by WYGODZINSKY in 1949, 1953a and at the MLP Simuliidae holdings. However, only one male with number "IMR no. 898" was located in this institution. I have also examined at the NMHU one male and one female (both reared and on the same pin) with number "I.M.R. 825" and bearing identification labels in WYGODZINSKY'S hand. The latter numbering system agrees with the one adopted by WYGODZINSKY (1953). Therefore, following the ICZN (1999, article 72.5), I have selected the female as a neotype and labelled it accordingly. I have taken digital images of its thoracic pattern, which is now deposited in the Simuliidae Digital Image Archive at the BMNH (see **Material Examined**). The specimen is in relatively good condition, though the central region of the thorax is slightly collapsed (Figs. 330, 331). It has been glued to a card point by its right side together with its pupal pelt.

In Argentina, the adults of *S. lahillei* are externally most similar to *S. huairayacu* in the brownish red coloration of the thorax (*e.g.* Figs. 330-333, 751, 752). However, *S. lahillei* can be readily distinguished by the pupal gill with 12 upwardly directed filaments arranged in three primary branches, which divide into secondary branches at different heights (Fig. 1036). In *S. huairayacu*, the pupal gill filaments are divided into two primary branches, one dorsal consisting of 10 filaments all arranged in a bunch and upwardly directed, and one ventral with only two forwardly directed secondary filaments (Fig. 1033). Other species with similar coloration of thorax are *S. itaunense* and *S. scutistriatum*, both occurring in Brazil. However, these species can be easily separated from *S. lahillei* by the different configuration of the gill filaments (Figs. 1034, 1042).

The larva of *S. lahillei* remains poorly known, hence it cannot be reliably separated from other species of *Trichodagmia*.

A full description of *S. lahillei* may be found in WYGODZINSKY (1943, 1953) and COSCARÓN & COSCARÓN-ARIAS (2007). VARGAS & DÍAZ NÁJERA (1951) gave additional information on the morphology of the female genitalia.

Simulium lahillei was placed in the subgroup LAHILLEI of the subgenus *Grenieriella* by COSCARÓN (1987). CROSSKEY & HOWARD (1997) placed this species in the subgenus *Trichodagmia*, an action followed by ADLER & CROSSKEY (2008, 2009, 2010), SHELLEY *et al.* (2010) and this work.

Distribution. *Simulium lahillei* has been recorded from Argentina, Bolivia, Colombia and Perú (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. The immature stages of *S. lahillei* have been found in creeks of median discharge, fast current and clear water, attached in groups to stones near the surface, frequently in winter and at the beginning of spring (COSCARÓN & COSCARÓN-ARIAS, 2007). WYGODZINSKY (1949, 1953) and COSCARÓN & COSCARÓN-ARIAS (2007) recorded females of *S. lahillei* biting horses and humans in northern Argentina. SHELLEY & COSCARÓN (2001) stated that this species is probably the most important vector of *Mansonella ozzardi* in northern Argentina.

2.5.2.8.*Simulium (Trichodagmia) lithobranchium* HAMADA, PEPINELLI, MATTOS-GLÓRIA & LUZ (Figs. 90, 200, 253, 334, 335, 443, 550, 609, 669, 753, 754, 854, 915, 976, 1037, 1092, 1143, 1198, 1253)

This is a newly described species from Brazil, externally similar to *S. duodenicornium* and *S. guianense s.l.* *Simulium litobranchium* is the first named simuliid species in the Neotropical Region using a combination of morphological characters and *COI* DNA Barcoding. The description and measurements here provided have been derived from the original description of HAMADA *et al.* (2010) and the examination of topotype material collected in Rio Verdão and Rio Doce, Goiás State, Brazil held at the BMNH Simuliidae collection. This material was previously identified by SHELLEY *et al.* (2002a) as an "atypical variation of *S. guianense s.l.* with abdominal tubercles in the larva".

Simulium lithobranchium HAMADA *et al.*, 2010: 24. HOLOTYPE (male), BRAZIL: Goiás State, Montividiu municipality, Ponte de Pedra River, 17°10'S 50°50'W, 761 masl; 21.v.2006, (*N.Hamada*, *M.Pepinelli* *& V.Landeiro*) (INPA).

FEMALE. General body colour black. Body length 2.3-2.4 mm (n = 2); wing length 2.3-2.4 mm (n = 2), wing width 1.1-1.2 mm [HAMADA *et al.* (2010) gave measurements as follows: Body length 1.8 mm (s.d. = 0.08, n = 5); wing length 2.1 mm (s.d. = 0.1, n = 11), wing width 1.0 mm (s.d. = 0.03, n = 11)].

Head: dichoptic with dark red eyes; nudiocular area slightly developed (Fig. 200). Frons, clypeus and occiput black with grey pruinosity; frons and clypeus with dense vestiture of recumbent brass-coloured setae. Mouthparts brown. Antennal scape, pedicel and first segment brownish yellow, remaining segments darker brown. Cibarium not armed with teeth (Fig. 253); cornuae developed and sclerotised.

Thorax: scutum, including paranotal folds, scutellum and humeri dark black covered by golden hairs distributed in small groups. Scutal pattern varying only slightly with illumination. With anterior illumination, thorax to black (Fig. 334). With posterior illumination, thorax dark grey to black with feint silver grey pruinosity on anterior margin (Fig. 335). Pleural region black with silvery grey pruinosity. Postnotum brown with silvery grey pruinosity. Costa of wing with sparse distribution of hairs and spines. Subcosta with hairs on mesal half. Radius with spines interspersed with hairs; basal section of radius with single row of hair-like setae; basal tuft of dark hairs. Variation in wing setation pattern was recorded by SHELLEY *et al.* (2002a): haired or bare Sc with fine setae in the distal half, and the basal section of Radius with three unven rows of hairs. Leg proportions and coloration as in Fig. 443. Front leg with coxa, apex of trochanter, femur, internal surface of tibia brown; base of trochanter and external surface of tibia whitish; apex of tibia and tarsal segments I-IV dark brown. Mid and hind legs with coxae, trochanters, apical half of femora and tibiae, apical third of tarsal segment I and tarsal segments II-IV dark brown; basal half of trochanters, tibiae, and basal two thirds of tarsal segment I whitish spotted with brown. Claw curved and slender without basal tooth. Haltere light yellow with dark brown stem.

Abdomen: abdominal tergite II with lateral silver pruinosity; tergites VI-VIII brown dorsally. Tergal plates well developed. Sternites and genitalia black. Eighth sternite unsclerotised with 1+1 groups of 19 well developed setae; gonapophyses small, membranous, not meeting centrally and covered in microtrichiae (Fig. 550). Cercus subtriangular; paraprocts broadly quadrangular with dorsally exposed part sclerotised and more ventral part membranous with tail-like projection pointing internally close to gonapophyses; whole paraproct densely covered in setae (Fig. 609). Genital fork short, with highly developed terminations to lateral arms and sclerotised anterior processes; posterior processes developed (Fig. 669). Spermatheca subspherical, with cuticular microspines in pentagonal pattern; area of insertion of spermathecal duct large unpigmented.

MALE. General body colour black. [HAMADA *et al.* (2010) gave measurements and range as follows: Body length 1.7 mm (s.d. = 0.14, n = 5); wing length 2.0 mm (s.d. = 0.09, n = 10); wing width 1.0 mm (s.d. = 0.025, n = 10]. Body length 2.1-2.9 mm (n = 2); wing width 1.4 mm (n = 2), wind width 0.9-1.1 mm (n = 2)

Head: holoptic with dark red eyes. Clypeus black with silvery grey pruinosity and many, long, dark, upright setae. Mouthparts black, antennae black with scape, pedicel and first flagellomere brownish yellow, remainder of antennal segments darker brown.

Thorax: scutum velvet black covered by evenly distributed recumbent golden hairs. Thorax, irrespective of light incidence, black with 1+1 sublateral silver areas on anterior third of scutum; humeri faintly pruinose; lateral and posterior margins black (Figs. 753, 754). Scutellum dark brown to black covered by golden setae. Postnotum brown with silver pruinosity. Pleural region black with silvery grey pruinosity. Wing venation as in female except Sc bare as recorded in HAMADA *et al.* (2010), but SHELLEY *et al.* (2002) recorded specimens with the basal section of Radius with an uneven double row of hair-like setae. Leg coloration as in female except darker coloured. Halteres lemon yellow with orange-brown base.

Abdomen: abdominal tergites velvet black, basal fringe light brown. Silver ornamentation on lateral margins of tergites II, and V-VII. Sternites brown with well developed black sternal plates. Genitalia dark brown. Gonocoxite subquadrangular rectangular; gonostyle spindle-shaped, expanded basally and elongate thinner apically terminating in single, prominent spine (Fig. 854). Ventral plate sclerotised, subquadrangular, covered with long hair only on median process; main body with well developed, pear-shaped anterior process on central region that arises from mid third of ventral plate extending or not extending beyond apex of lateral shoulders; anterior margin concave and ventral margin straight; lateral shoulders developed; basal arms developed, subparallel and strongly sclerotised (Fig. 915). Median sclerite rectangular with deep incision at narrower apex (Fig. 915). Paramere poorly developed with no spines and little sclerotisation (Fig. 976).

PUPA. Cocoon length dorsally 2.7-3.8 mm (mean = 3.0 mm, s.d. = 0.38, n = 7); ventrally 3.2-3.6 mm (mean = 3.3 mm, s.d. = 0.16, n = 6); pupa length 2.5-3.7 mm (mean = 3.0 mm, s.d. = 0.46, n = 6); gill length 0.5-0.7 mm (mean = 0.6 mm, s.d. = 0.06, n = 8).

Cocoon: shoe-shaped as in Fig. 66 [HAMADA *et al.* (2010) recorded the shape of the cocoon for *S. lithobranchium* as boot-shape], light to dark brown; rim of aperture not reinforced and without central protuberance; cocoon of thick fibres.

Gill: light brown with 12 filaments upwardly directed (Fig. 1037); main trunk giving rise to two primary branches; one external and one internal. External branch with three secondary branches: one dorsal, one median and one ventral, with four, two and two secondary filaments each. Internal primary branch with four filaments; all filaments divide at some distance from gill base. Filaments short with small distal dark pointed ends; all filaments of same girth.

Head (frontoclypeus): with 2+2 small, unbranched frontal trichomes, and 1+1 small, unbranched, facial trichomes; surface of head with scattered platelets on periphery and base of frontal region and rounded tubercles on facial and frontal region.

Thorax: with up to 5+5 short, thick simple trichomes or sometimes 1+1 bifid; 1+1 thick longer trichomes on lateral margin. Surface of thorax without tubercles dorsally; dorsal posterior region with majority of tubercles pointed, but some rounded in area below tracheal trunk of gill filaments.

Abdomen: tergite I with 1+1 simple small simple setae on lateral margins; tergite II with 4+4 stout spiniform setae in row, 2+2 small sublateral setae, and numerous small rounded tubercles in anteromedian region; tergites III, IV with 4+4 simple hooks in row along posterior margins; tergites V-VIII without setae. Spine combs on anterior margins of tergites V-IX. Sternites III, IV without visible setae; sternite V with 2+2 close bifid hooks; sternites VI, VII with 2+2 well separated bifid hooks. Spine combs on anterior margins of sternites III-IX.

LARVA (Final instar). Body length 4.5-5.3 mm (mean = 4.9 mm, s.d. = 0.4, n = 3); width of head capsule 0.6 -0.8 mm (mean = 0.7 mm, s.d. = 0.1, n = 3); length of head capsule 0.5-0.6 mm (mean = 0.5 mm, s.d. = 0.05, n = 3). Body colour usually light to dark greyish green (specimens in Carnoy's solution or ethanol). General body form as in Figs. 90, 1092.

Head: dark brown with positive and negative head patterns. Head capsule with few, randomly distributed setae on all surfaces. Postgenal cleft large, as wide as long, rounded anteriorly, postgenal bridge about half length of hypostomium (Fig. 1143). Hypostomium with strongly pigmented anterior margin and approximately nine poorly developed apical teeth evenly distributed along anterior margin; median tooth weakly developed; 3+3 sublateral teeth varying in length, poorly differentiated; 1+1 lateral teeth, more developed than median and lateral teeth; 1-2 lateral serrations; 1+1 lines of 6-7 hypostomial setae parallel to lateral margins (Fig. 1198). Antennal segments as long as labral fan stalk, all segments slightly pigmented; length of antennal segments I-III excluding the sensillum 0.06-0.09:0.05:0.06 mm (n = 3) [HAMADA *et al.* (2010) gave ratio as follows: 1.7:0.8:0.9 mm; number of specimens examined not given in this paper]. Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately nine to ten teeth; two mandibular serrations, anterior more develoed than posterior [HAMADA *et al.*, 2010 stated that they found specimens with single mandibular serration] (Fig. 1253). Lateral mandibular process absent. Maxillary palps about three times as long as breadth at base. Labral fan with 46-54 rays, all with single line of fine microspinules (n = 2) [HAMADA *et al.* (2010) gave ranges as follows: 42-56 rays, mean = 49, s.d. = 5, n = 7].

Thorax: cream with grey coloration anteriorly and posteriorly. Dorsal surface of cuticle, except for intersegmental margins, covered in numerous, small, oval-shaped setae that appear simple under the light microscope; ventral surface glabrous. Proleg plates sclerotised with about 12 processes. Pupal respiratory histoblast light brown; dissected gill histoblast with 12 smooth filaments all of same length and showing small black pointed ends.

Abdomen: dark gray and paler ventrally, specially towards end of abdomen. Ventral nerve cord grey. Ventral papillae absent. Dorsal surface of cuticle, except for intersegmental margins, covered in short oval-shaped setae; ventral surface glabrous except for some setae scattered around posterior venter of abdomen. Abdominal segments I-V or 1-VI with 1+1 dorso-lateral tubercles varying from poorly to well developed (Fig. 1092). Anal sclerite highly sclerotised with posterior arms 0.5 times length of ventral arms. Posterior circlet with 139-166 rows of 22-26 hooks (mean = 24, n = 4). Anal gill trilobed, each lobe with 24 finger-like lobules (n =2) [HAMADA *et al.* (2010) gave ranges as follows: 24, 28 and 28 per branch, *n* = 9].

Taxonomic Discussion. *Simulium lithobranchium* was described by HAMADA *et al.* (2010) based on numerous adults, pupae exuviae and larvae collected in Delfinópolis (Minas Gerais State) and Montividiu (Goiás State) municipalities, Brazil. The male holotype has been pinned and is deposited at INPA, but I have not been able to examine it. However, I have examined topotypes link-reared adults, pupae and larvae of this species from Rio Dulce and Rio Verdão held at the BMNH simuliid collection (**Material Examined**).

In Brazil, the female of *S. lithobranchium* is externally similar to other species described in the ORBITALE species group (*sensu* SHELLEY *et al.*, 2010), especially *S. duodenicornium* and *S. guianense s.l.*, by having the scutum black, covered by golden hairs distributed in small groups (Figs. 334, 335). However, the morphology of the cercus and paraproct distinguished this species (see Fig. 609) from the latter taxa (Figs. 603, 604). The male thoracic pattern of *S. lithobranchium* is most similar to that of *S. itaunense* and *S. orbitale* in having 1+1 sublateral silver cunae on anterior margin [with light source anterior] (Fig. 753-754). Nonetheless, *S. lithobranchium* can be easily separated from *S. itaunense* and *S. orbitale* by the morphology of the ventral plate, especially the median process arising nearly from the middle of the main body and reaching the level of the lateral shoulders (Fig. 915). In *S. orbitale* the median process arises from the ventral margin of the ventral plate (Fig. 918), while in *S. itaunense* it arises from the anterior margin (Fig. 913). The general morphology of the ventral plate in *S. lithobranchium* is also similar to that of *S. duodenicornium* and *S. guianense s.l.* (Figs. 909, 910), but in *S. duodenicornium* the thorax does not have a distinct pattern irrespective of light direction (Figs. 732, 733). The males of *S. guianense s.l.* are easily recognized by the broadly pruinose thorax with central and 1+1 submedian black vittae [with light source anterior to specimen] (Figs. 734-741). In the figure of the ventral plate given in HAMADA *et al.* (2010, Fig. 38), the median process in *S. lithobranchium* does not extend beyond the apex of the lateral margin, while in the specimens I have examined it does (Fig. 915). This difference could be due to how the structure was positioned while mounted on a slide as detailed by SHELLEY *et al.* (2010).

The number of gill filaments (12 filaments) of *S. lithobranchium* (Fig. 1037) is also shared by other species in the ORBITALE species group recorded in Brazil: *S. duodenicornium*, *S. guianense s.l.*, *S. hirtipupa* and *S. scutistriatum* (Fig. 1037). However, the pupa of *S. hirtipupa* is easily distinguished from that of *S. lithobranchium* by the prominent black spiniform setae on the frontoclypeus and pupal thorax (Fig. 71), while *S. scutistriatum* can be identified by having the end of the pupal gill filaments prominently sclerotised (Fig. 1042). *Simulium duodenicornium* also has the end of the gill filaments prominently sclerotised, but all filaments are arranged in a straight line parallel to the surface of the cephalothorax (Figs. 80, 1030). The pupal gill configuration of *S. lithobranchium* is most similar to that of *S. guianense s.l.* (Figs. 79, 1031), but in the latter species the filaments are covered by spicules in an annular arrangement (SHELLEY *et al.*, 2010, Fig. 1218). The surface of the gill filaments in *S. lithobranchium* is smooth.

The larva of *S. lithobranchium* cannot be easily from other species in the ORBITALE species group, which have the dorsal surface covered by ovoid setae. The best character that distinguishes the larvae of this species is the presence of 1+1 dorsal tubercles on the abdominal segments I-V or I-VI (Figs. 90, 1092; see also SHELLEY *et al.*, 2002a: 99, Fig. 2).

SHELLEY *et al.* (2002a) discussed the morphological variation in the larvae and wing venation of a population that they identified as "atypical variation of *S. guianense s.l.* with abdominal tubercles in the larva". They found that reared adults obtained from localities at Rio Verdão and Rio Doce in Goiás state showed differences in the setation of the Sc and basal section of the radial veins, while the larvae have prominent 1+1 tubercles on the dorsal surface of segments I-VI. However, the latter authors refrained to name a new species until cytological and molecular studies were carried out to determine their taxonomic status, because of the variation found in this character in other species such as various cytotypes of *S. damnosum s.l.* in Africa. This was the main purpose of the paper of HAMADA *et al.* (2010), in which they carried out morphological studies linked to DNA barcoding on specimens collected from similar localities as detailed by SHELLEY *et al.* (2002a). HAMADA *et al.* (2010) found a >4% divergence in the sequences of the barcoding region of the *COI* gene among the species they analyzed (*S. duodenicornium*, *S. guianense s.l.*, *S. lithobranchium* and *S. scutistriatum*), thus confirming their argument to erect a new species for the population with larvae having dorsal tubercles on the abdomen (Fig. 1092). Larval specimens collected from the type locality of *S. lithobranchium* were cytologically screened by S. LUTZ (INPA-Manaus), but unfortunately he did not obtain good chromosome preparations (pers. comm. to A.J. SHELLEY).

HAMADA *et al.* (2010) mentioned the difference of opinion on the validity of the subgenera *Thrysopelma* and *Trichodagmia* of other authors, but followed the classification of MIRANDA-ESQUIVEL & COSCARÓN (2001) and placed *S. lithobranchium* in the subgenus *Thyrsopelma*. SHELLEY *et al.* (2010) [and also this work] have detailed the reasons for the recognition of *Thyrsopelma* as a junior synonym of *Trichodagmia*. I have followed the classification scheme of SHELLEY *et al.* (2010) and placed *S. lithobranchium* in the ORBITALE species group of the subgenus *Trichodagmia*.

Distribution. *Simulium lithobranchium* has only been recorded from the states of Goiás and Minas Gerais in Brazil (HAMADA *et al.*, 2010; **Material Examined**). SHELLEY *et al.* (2002a) also recorded it from the same states [as an atypical form of *Simulium guianense s.l.*]

Biology and Medical Importance. HAMADA *et al.* (2010) collected immature stages of *S. lithobranchium* in three rivers varying in width from 30 to 40 meters together with *S. guianense*. The streams have a bed of sand , small stones and boulders, with water temperatures between 17 to 19ºC, pH from 6.5 to 7.3 and a low electrical conductivity (below 15µ/cm). Larvae and pupae were collected on leaves of Podostomaceae, submerged branches and leaves of riparian vegetation and submerged grass. SHELLEY *et al.* (2002a) recorded larvae and pupae of *S. lithobranchium* [as an atypical form of *Simulium guianense s.l.*] in small numbers attached to submerged vegetation in a fast flowing stretch of the 8m wide Rio Verdão and at the 10m wide Rio Doce. Both flow through farmland. HAMADA *et al.* (2010) and SHELLEY *et al.* (2002a) stated that females *S. lithobranchium* were not found biting man during fieldwork.

2.5.2.9. *Simulium (Trichodagmia) nigrimanum* MACQUART (Figs. 3, 4, 7, 66, 81, 94, 201, 254, 336, 337, 444, 551, 610, 670, 755, 756, 855, 916, 977, 1038, 1093, 1144, 1199, 1254)

This is a common man-biting species originally described from São Paulo State in Brazil and still regarded as a *species inquirendae* by some authors.

Simulium nigrimanum MACQUART, 1838: 88. LECTOTYPE female (not male as published by MACQUART), BRAZIL: São Paulo State, [Collection date and collector un-known] (MNHN). [Lectotype designation by SHELLEY *et al.*, 1984: 146]. [Publication date incorrectly cited as 1837 by VARGAS (1945a) and D'ANDRETTA & D'ANDRETTA (1945)] [Examined.]

Simulium pruinosum LUTZ, 1910: 250. LECTOTYPE female, BRAZIL: Minas Gerais State, Lassance, Rio das Velhas, [Without collection date and collector's name.] (IOC no. 141) [Examined.] [Lectotype designation by VULCANO, 1959: 41.; synonymy by SHELLEY *et al.* 1984: 46, revalidation by PY-DANIEL, 1989a: 256; synonymy by CROSSKEY & HOWARD, 2004: 75; latter synonymy followed in ADLER & CROSSKEY, 2008: 95, 2009: 99, 2010: 101; COSCARÓN & COSCARÓN-ARIAS, 2007: 609; COSCARÓN *et al.*, 2008: 49; and SHELLEY *et al.*, 2010: 433.]

Trichodagmia spadicidorsum ENDERLEIN, 1934b: 194. LECTOTYPE female, BRAZIL: São Paulo; [Without date or collector's name] (NMHU) [Examined.] [Lectotype designation and synonymy by HERNÁNDEZ & SHELLEY, 2005: 11; synonymy followed in ADLER & CROSSKEY, 2008: 95, 2009: 99, 2010: 101; COSCARÓN & COSCARÓN-ARIAS, 2007: 609; COSCARÓN *et al.*, 2008: 50; and SHELLEY *et al.*, 2010: 433.]

FEMALE. General body colour brown. Body length 3.3-4.1 mm (mean = 3.5mm, s.d. = 0.21, n = 13), wing length 2.6-3.2 mm (mean = 2.9 mm, s.d. = 0.16, n = 17), wing width 1.1-1.5 mm (mean = 1.3 mm, s.d. = 0.1, n = 17).

Head: dichoptic with dark red eyes and nudiocular area slightly developed (Fig. 201). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus covered with pale, semi-recumbent setae interspersed with erect black hairs and frons with long, erect, black hairs. Mouthparts parts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellar segments dark brown. Cibarium with well developed, sclerotised cornuae and single row of stout, blunt teeth in central trough (Figs. 7, 254).

Thorax: scutum dark brown to brownish black and no pattern, with numerous, recumbent, brass-coloured hairs interspersed with semi-erect black hairs. With light anterior, scutum dark brown, lateral margins dark brown to black (Fig. 336). With posterior light, scutum with faint pruinosity on anterior two thirds; humeri silver pruinose (Fig. 337). Scutum, irrespective of light direction, with feint darker median line extending from anterior to posterior margins. Scutellum dark brown with recumbent white hairs intermixed with long, black bristles. Postnotum dark brown with silver pruinosity. Pleura dark brown with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcostal wing vein with line of setae (but bare in specimens from Colombia). Radius with double row of hairs in basal section and spines interspersed with hairs in distal half. Basal tuft of long, dark setae (Fig. 4). Leg coloration and proportions as in Figs. 3, 444. Coxa, trochanter and femur of fore leg light brown, tibia and tarsus brown to black; coxa, trochanter and femur of mid leg light brown, tibia brown to black with white basal articulation, tarsus brown to black with basal two thirds of basitarsus white; coxa and trochanter of hind leg brown, femur dark brown, tibia brown to black with white basal articulation, tarsus brown to black with basal half of basitarsus and second tarsomeres white. Claws with well developed basal tooth. Halteres cream with brown base.

Abdomen: matt black with tergites VI-IX shiny black. Sternites black, genitalia brown. Eighth sternite with highly sclerotised posterior margins and 1+1 groups of up to six setae; gonapophyses well developed, membranous and covered in fine setae (Fig. 551). Cerci hemispherical, paraprocts well developed and subrectangular with part extending beyond cercus membranous, setose and with scale-like setae apically as in *S. scutistriatum* (Fig. 610). Genital fork (Fig. 670) slightly sclerotised with well developed lateral arms and anterior processes. Spermatheca oval, sclerotised with lines of fine, internal spicules; area of insertion of spermathecal duct about one fourth maximum width of spermatheca.

MALE. General body colour brown. Body length 2.9-3.8 mm (mean = 3.4 mm, s.d. = 0.37, n = 4), wing length 2.3-3.1 mm (mean = 2.6 mm, s.d. = 0.34, n = 4), wing width 1.1-1.4 mm (mean = 1.2 mm, s.d. = 0.14, n = 4).

Head: holoptic with red eyes. Rest of coloration as in female.

Thorax: dark brown with feint median dark stripe and with no pattern and numerous adpressed, brass-coloured hairs. With anterior light source 1+1 white median cunae and 1=1 white and yellowish submedian larger cunae on anterior margin (Fig. 755). With light posterior to specimen anterior margin with grey pruinosity (Fig. 756). Humeri, lateral and posterior margins of scutum dark brown to black. Scutellum dark brown with brass coloured, recumbent hairs and long, erect, dark brown setae. Postnotum dark brown to black with silvery grey pruinosity. Wing setation as in female except Subcosta with either no setae or one seta basally or in mid section of vein. Radius as in female except single line of fine setae in basal half. Leg coloration as in female.

Abdomen: abdominal tergites velvet black with silver pruinosity covering tergite II and lateral margins of tergites V-VIII [best seen when specimen viewed laterally]. Genitalia dark brown; tergal plates developed. Gonocoxite longer than wide; gonostyle slender, pyriform almost 50% longer than gonocoxite and with three to eight stout spines at distal tip (Fig. 855). Ventral plate subrectangular, sclerotised, with no keel and bluntly pointed on median part of posterior margin, median part of anterior margin bluntly pointed and basal arms well developed slightly bow-shaped and strongly sclerotised; lateral shoulders small and curved (Fig. 916). Median sclerite small, about three times longer than wide at widest point, with small apical incision (Fig. 916). Paramere membranous poorly developed without spines (Fig. 977).

PUPA. Cocoon length dorsally 2.5-3.3 mm (mean = 2.9 mm, s.d. = 0.23, n = 13), ventrally 3.1-4.3 mm (mean = 3.7 mm, s.d. = 0.32, n = 8), pupa length 2.8-5.1 mm (mean = 3.5 mm, s.d. = 0.68, n = 9), gill length 1.3-1.7 mm (mean = 1.5 mm, s.d. = 0.22, n = 3).

Cocoon: shoe-shaped as Fig. 66, light brown, gelatinous in appearance, composed of thick coalesced fibres. Margin of anterior aperture reinforced, weakly to strongly elevated and with central protuberance.

Gill: white consisting of a bunch of 18 short, upwardly directed filaments branching at various heights in basal half. Filaments all approximately same length, fine, edges crenate and ends rounded (Figs. 81, 1038).

Head (frontoclypeus): with 2+2 frontal, simple trichomes and 1+1 facial, bifid simple, trichomes; frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and about 5 platelets in groups of 1 or 2 laterally in frontal region, respectively; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region.

Thorax: with 5+5 small, simple trichomes and 1 bifid to four-branched trichome near alar region; few tubercles on anterior half of thorax, but pointed and densely distributed on postero-lateral margin and base of gill.

Abdomen: tergite I with 1+1 submedian, small, simple setae and 2+2 simple setae sublaterally and rounded tubercles on posterior margin; tergite II with 4+4 submedian spines in longitudinal row, 1+1 small simple setae anterior to outermost spine and 1+1 small, simple setae on lateral margin; tergites III and IV with 4+4 submedian, simple hooks in longitudinal row, sometimes 2+2 simple, short setae anterior to most lateral spines and 1+1 small setae laterally; tergites V-VIII with spine combs on antero margin; tergite IX without terminal spines, weakly sclerotised. Abdominal sternite III with 1+1 submedian and 2+2 sublateral small setae and spine combs on anterior margin; sternite IV with 1+1 long and 2+2 small, simple, median setae, 2+2 sublateral, simple setae and spine combs on anterior margin; sternite V with 2+2 close, simple median hooks, 2+2 small, simple, submedian setae, 1+1 small, simple setae laterally and groups of spine combs on anterior margin; sternites VI-VII with 2+2 well separated, simple hooks and groups of spine combs on anterior margin; sternite VIII with spine combs on anterior margin.

LARVA (Final instar). Body length 4.1-7.1 mm (mean = 5.6 mm; s.d. = 0.89, n = 15); length of head capsule 0.5-0.8 mm (mean = 0.6 mm, s.d. = 1.10, n = 15); width of head capsule 0.4-0.7 mm (mean = 0.5 mm, s.d. = 0.10, n = 15). Body colour dark grey dorso-laterally, whitish ventrally (specimens fixed in Carnoy's solution and/or alcohol). General body form as in Fig. 1093.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, rounded apically; postgenal bridge nearly one and half times as long as hypostomium (Fig. 1144). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth weakly developed and not protruding in central region; median tooth well developed and most prominent; 3+3 sublateral teeth adjacent to median tooth; 1+1 lateral teeth, longer than median and sublateral teeth; lateral serrations absent; 1+1 lines of approximately 6-9 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1199). Sub-esophageal ganglion lightly pigmented. Antenna smaller than labral fan stalk, all segments light brown whitish on apex of segment II and base of segment III; length of antennal segments I-III excluding the sensillum 0.1-0.2:0.02-0.06:0.07-1.1 mm (n = 6). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately 10 teeth, second, third and fourth teeth longer than first; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1254). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 32-46 fans (n = 6), rays with fine, single line of microspinules in a row.

Thorax: greyish dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 33-62 processes (n = 6). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 18 filaments, all branching from a common trunk and some filaments weakly pointed.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 118-144 rows of 14-19 simple hooks (n = 4). Rectal gills with three lobes of approximately 12 small, finger-like lobules each (n = 2).

Taxonomic Discussion. *Simulium nigrimanum* was described by MACQUART (1838) based on specimens collected from the north of São Paulo, Brazil at a locality referred to as "nord de la Capitaineire de Saint-Paul". In their paper on specific synonymies of Neotropical species SHELLEY *et al.* (1984) examined the two extant female types of *S. nigrimanum* in the MNHN and concluded that in MACQUART'S description the reference to male (as female) was a typographical error and synonymised *S. pruinosum* with *S. nigrimanum*. This has not been accepted by two authorities (PY-DANIEL, 1989; COSCARÓN, 1991), who preferred to maintain *S. pruinosum* as a valid species and *S. nigrimanum* as a *species inquirendae*. PY-DANIEL (1989) agreed that the two specimens in the MNHN and *S. pruinosum* are conspecific, but did not accept our explanation concerning a typographical error. ADLER & CROSSKEY (2008) and CROSSKEY & HOWARD (1997, 2004) maintained the synonymy. A similar situation occurred with *S. tarsatum* described by MACQUART in 1846 (see HERNÁNDEZ & SHELLEY, 2005).

The taxonomy of *S. nigrimanum* has been recently reviewed by SHELLEY *et al.* (2010), who also discussed the different opinions on the validity of *S. pruinosum*. COSCARÓN (1987) separated *S. nigrimanum* with its synonym *S. pruinosum* into a "subgroup" of its own within the subgenus *Grenieriella*. However, in 1991 the situation became rather confusing when the same author formed the *pruinosum* group for *S. pruinosum* within the subgenus *Grenieriella*. This was a consequence of PY-DANIEL'S revalidation (1989) of the name *S. pruinosum* from its synonymy with *S. nigrimanum* by SHELLEY *et al.* (1984). In his list of synonyms of *S. pruinosum* COSCARÓN included *S. nigrimanum* as its synonym, even though the latter predates the former species. He also regarded his reference to *S. nigrimanum* in 1987 and that of SHELLEY *et al.* (1984) as pertaining to *S. pruinosum*. In 2001 MIRANDA-ESQUIVEL & COSCARÓN then placed *S. nigrimanum* in the subgenus *Trichodagmia*, thereby reverting to its status in COSCARÓN (1987) and presumably again accepting *S. pruinosum* as its junior synonym. CROSSKEY & HOWARD (1997, 2004) placed *S. nigrimanum* and its synonym *S. pruinosum* in *Trichodagmia*. In the latest Neotropical revisions COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) accepted the synonymy of *S. pruinosum* with *S. nigrimanum* by SHELLEY *et al.* (1984).

ENDERLEIN (1934b) described *Trichodagmia spadicidorsum* based on three syntype females collected in Brazil. COSCARÓN (1987) included *T. spadicidorsum* as a possible synonym of *S. distinctum*, but did not include it in his 1991 paper. CROSSKEY & HOWARD (1997, 2004) followed COSCARÓN (1987) and also included *S. spadicidorsum* as a possible synonym of *S. distinctum*. HERNÁNDEZ & SHELLEY (2005) examined ENDERLEIN'S type material of *T. spadicidorsum*, removed it as a synonym of *S. distinctum* and synonimized it with *S. nigrimanum*. This has been followed by ADLER & CROSSKEY (2008, 2009, 2010), COSCARÓN & COSCARÓN-ARIAS (2007) and SHELLEY *et al.* (2010). SHELLEY *et al.* (2000) illustrated the ventral plate and median sclerite of *S. nigrimanum* based on a male collected in the Minaçu area, Rio Tocantins on 28.ix.1995 by M. Camargo during a study of the simuliid species occurring in the secondary onchocerciasis focus at Minaçu in central Brazil. LUNA DIAS *et al.* (2004) examined this specimen and found that it is of the closely related species *S. lobatoi*.

Simulium nigrimanum is similar to other *Trichodagmia* species with brown thorax that lack a pattern on both the female and male thoraxes (*e.g. S. nunesdemelloi*) (Figs. 336-339, 755-758), but it is distinguished by its pupa with eighteen filaments with rounded ends (Fig. 1038). It is further recognized by the distinctive female paraproct (Fig. 610) and the male genitalia, especially the gonostyle with 3-8 distinct, stout spines apically (Fig. 855). Variation in the number of spines of the male gonostyle in *S. nigrimanum* has been seen even in the same specimen. VULCANO (1959) illustrated a specimen with up to nine spines at the tip of the gonostyle.

Full descriptions of *S. nigrimanum* may be found in COSCARÓN (1991) [as *S. pruinosum*], COSCARÓN & COSCARÓN-ARIAS (2007), SHELLEY *et al.* (2000; 2010) and VULCANO (1959) [as *S. pruinosum*].

Distribution. *Simulium nigrimanum* is a fairly common species in Brazil occurring in the states of Espírito Santo, Federal District, Goiás, Mato Grosso, Minas Gerais, Mato Grosso, Mato Grosso do Sul, Paraná, São Paulo and Tocantins (CROSSKEY & HOWARD, 1997, 2004; ADLER & CROSSKEY, 2008, 2009, 2010). Elsewhere, it has been recorded from Colombia, Paraguay and Venezuela (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; SHELLEY *et al.*, 2010).

Biology and Medical Importance. *Simulium nigrimanum* breeds in small to medium fast flowing rivers on rocks and plant roots and twigs, but Minaçu, Goiás it was occasionally found breeding in larger rivers. RAPP PY-DANIEL & PY-DANIEL (1984) collected larvae of this species from streams with 1.19m/s water velocity, 1.7 m wide and 10-30 cm deep.

The female of *S. nigrimanum* might be zoophilic in some places in Brazil, but in many areas in this country (*e.g.* Mato Grosso do Sul) they will bite humans voraciously usually in early morning and late afternoon. The bite of females of this species can cause severe bruise-like allergic reactions and swelling of the limbs in some people (L.M. HERNÁNDEZ, unpublished data). *Simulium nigrimanum* is considered a potential vector of *Onchocerca volvulus* in the Minaçu onchocerciasis focus (SHELLEY *et al.*, 2000, 2001). It has also been suspected of causing *Endemic Pemphigus foliaceus* in part of Brazil, an autoimmune skin blistering reaction, which is possibly in response to its saliva (EATON *et al.*, 1998; DÍAZ *et al.*, 1989a,b).

2.5.2.10. *Simulium (Trichodagmia) nunesdemelloi* HAMADA, PEPINELLI & HERNÁNDEZ (Figs. 202, 255, 338, 339, 445, 552, 611, 671, 757, 758, 856, 917, 978, 1039, 1094, 1145, 1200)

This is a fairly newly described species that was collected in the Alto Rio Negro region, in the northwestern part of Amazonas State, Brazil. The following description has been based on the authors' original description and digital images held at the BMNH.

Simulium nunesdemelloi HAMADA *et al.*, 2006: 23. HOLOTYPE male (apparently not associated with pupal exuviae), BRAZIL: Amazonas State, São Gabriel da Cachoeira County 00º10'S 67º01'W, Rio Negro, 8.x.1998 (*N.Hamada*, *R.L.M.Ferreira* & *L.Aquino*) (INPA).

FEMALE. General body color brownish. Body length (specimen preserved in alcohol) 2.0 mm (n= 1); wing length 2.1–2.2 mm (n = 2), wing width 0.9 mm (n = 2).

Head: dichoptic with red eyes and nudiocular triangle not developed (Fig. 202). Frons, clypeus, and occiput with silvery blue pruinosity and semi-recumbent brown setae interspersed with long black hairs. Mouthparts dark brown. Antennae with silver pubescence; pedicel, scape, and first flagellomere brownish yellow, following flagellomeres increasingly dark brown. Cibarium with sclerotised cornuae, central area with well developed sharp teeth (Fig. 255).

Thorax: scutum dark, brownish orange with silver hairs, clumped in small group. Scutum with median and 1+1 submedian narrow, black vittae running from anterior to posterior margins irrespective of light incidence (Figs. 338-339). Scutellum brownish orange, with golden and dark brown hairs; postnotum brown. Costa of wing with spines and setae. Subcosta bare (except one female with a single seta distally. Basal section of Radius bare. Leg coloration and proportions as in Fig. 445. Foreleg with coxa, trochanter, and femur light brown; tibia, and tarsal segments I–IV brown. Mid leg with coxa, trochanter, and femur light brown, distal articulation of femur brown; tibia brown; tarsal segment I whitish basally with distal fourth brown, tarsal segments II–IV brown. Hind leg with coxa, femur, and tibia brown; trochanter and basal two thirds of tarsal segment I light brown, distal third brown, rest of tarsus dark brown. Femora and tibiae of mid and hind legs with narrow scale-like setae. Tarsal claw with subbasal tooth. Halteres whitish, brown basally.

Abdomen: tergites I-IV dark brown and tergites VI–VIII shiny brown, with silver pruinosity on median part of tergite II. Eighth sternite sclerotised with 1+1 submedian to lateral groups of long dark setae on posterior margin; gonapophyses well developed, lobular, unsclerotised and with numerous small setae over entire surface (Fig. 552). Cercus hemispherical; paraproct subrectangular with lobular, setose ventral projection almost length of cercus (Fig. 611). Genital fork with well developed ends to lateral arms parallel to transverse axis of abdomen, twice as wide as deep (Fig. 671), mainly unsclerotised and with anterior processes usually developed and sclerotised and posterior processes well developed. Spermatheca subspherical, with internal cuticular setae; spermathecal duct and area of attachment unsclerotised.

MALE. General body color brownish. Body length (specimens preserved in alcohol) 2.0–2.4 mm (n = 2). Wing length 2.3 mm (n = 1), wing width 0.9 mm (n = 1).

Head: holoptic with dark red eyes. Rest of coloration as in female.

Thorax: scutum brownish-orange with golden hairs, clumped in small groups. Median and 1+1 submedian narrow, black vittae running from anterior to posterior border, irrespective of light direction (Figs. 757, 758). Scutellum brownish-orange with golden hairs and thin, median, dark band. Postnotum black with silver pruinosity. Wing with Sc and base of R bare. Legs with same color pattern as in female.

Abdomen: tergites black; basal fringe with thin, long, black hairs and golden highlights; tergites II–VII with silver pruinosity. Genitalia dark brown. Gonocoxite rectangular; gonostyle elongate, almost double length of gonocoxite length and with one or two terminal spines (Fig. 856). Ventral plate (Fig. 917) subrectangular with median part of anterior margin dome-shaped and with setae; basal arms well developed and sclerotised. Median sclerite not examined. Paramere weakly sclerotised and poorly developed with no spines (Fig. 978).

PUPA. [Measurements following HAMADA *et al.* (2006), n = 5: Cocoon mean length dorsally 2.5 mm; pupal length 2.4 mm].

Cocoon: shoe-shaped as in Fig. 66, light brown consisting of compact and coalesced fibers with lightly reinforced rim to anterior aperture; most of gill concealed within cocoon.

Gill: light brown with 19 or 21 filaments projecting anteriorly in a bunch. Filaments short, stout, pointed and sclerotised distally with rows of brown spicules along length, margins crenate (Fig. 1039).

Head (*frontoclypeus*): frontal trichomes 3–5 branched and longer than dorsal simple or bifid trichomes; tubercles absent or scarce on dorsal region, mostly present on facial region.

Thorax: five pairs of two to four branched trichomes and one pair of bifid, thick, long lateral trichomes; tubercles scarce, but when present they are found on posterior region and on area below trunk of gill filaments.

Abdomen: tergite I with 1+1 sublateral setae, tergite II with 4+4 short, stout setae, tergites III and IV with 4+4 anteriorly directed hooks on posterior margin. Tergites without spine combs. No spine comb-like spines present on tergites. Sternites III–VIII with groups of spine combs on anterior margins; sternites V-VII with 2+2 long hooks.

LARVA (Final instar). [Measurements taken from original description; the authors did not provide the range, n = 5: Mean body length 6.2 mm (s.d. = 0.71, n = 5); head capsule, mean lateral length 0.50 mm (s.d = 0.02, n = 5]. General coloration variable, from light to dark grayish green (Fig. 1094) (specimens fixed in Carnoy's solution).

Head: head capsule (in dorsal view) with dark region on midline and along basal margin, with small, simple setae. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, dome-like shaped and roundly apically; postgenal bridge 0.57 times as long as hypostomium (Fig. 1145). Subesophageal ganglion slightly pigmented. Antennal segments as long as labral fan stalk; antennal segment II longer than segments III and I, antennal segment II longer than segment I; length of antennal segments I-III excluding sensillum 1:1.4–1.75:0.8–0.9 mm. Labral fan with 41–43 primary rays. Hypostomium (Fig. 1200) with nine evenly distributed teeth along anterior margin; median tooth and 3+3 sublateral teeth of similar length, not well differentiated; 1+l teeth nearly all at same level as median and sublateral teeth; 3–5 lateral serrations; hypostomium with 4–6 hypostomial setae parallel to lateral margins. Lateral mandibular process absent. Mandible [after HAMADA *et al.* 2006] with one apical, two small external; three subapical (first subequal to third and both smaller than second, or all subequal), six or seven internal teeth; one mandibular serration and one small mandibular sensillum (*sensu* CRAIG & CRAIG, 1986).

Thorax: gill histoblast large with sclerotised distal end of filaments pointing toward ventral region of body; gill histoblast dissected with 19 to 20 filaments.

Abdomen: body with simple setae on dorsal region of abdomen, and near anal sclerite; ventral tubercles absent. Anal sclerite highly sclerotised with posterior arms extending to about 34th to 38th row of posterior circlet hooks. Posterior circle bearing 143-150 rows (n = 2) with 21-24 hooks (n = 4). Rectal gills with three lobes, each with 29-30 finger-shaped lobules.

Taxonomic Discussion. *Simulium nunesdemelloi* was described by HAMADA *et al.* (2006) based on numerous adults, pupae and larvae collected at Rio Negro and Rio Tiquié, Amazonas state, Brazil. The pinned reared male holotype is housed at INPA Simuliidae collection and it is in good condition.

The taxonomy of *S. nunesdemelloi* has been recently reviewed by SHELLEY *et al.* (2010). The female and male of *S. nunesdemelloi* are very similar to adults of *S. nigrimanum* and *S. scutistriatum*. The males in the latter species have a ventral plate without a developed central region (Figs. 916, 917, 920), and the females have a subtriangular paraproct covered by microtrichiae (Fig. 610, 611, 614). However, they species can be readily distinguished by the configuration and number of the pupal gill filaments: 19-20 in *S. nunesdemelloi* (Fig. 1039), 18 in *S. nigrimanum* (Figs. 81, 1038) and 12 in *S. scutistriatum* (Fig. 1042). The pupal gill configuration and number of *S. nunesdemelloi* is most similar to that of *S. orbitale*, but the filaments are much thicker and crenulated (Fig. 1038) than in *S. orbitale* (Fig. 1040). In addition, the cephalic and thoracic trichomes of *S. nunesdemelloi* are not spiniform as those in *S. orbitale*.

The larva of *S. nunesdemelloi* can be recognized from other species of *Trichodagmia* by the following combination of characters: absence of racket-shaped scales on the dorsal region of abdomen, rounded postgenal cleft (Fig. 1145), and dissected gill histoblast with 19-20 gill filaments with heavily sclerotised tips. HAMADA *et al.* (2006) further pointed out that the larva of *S. nunesdemelloi* can be separated from other larvae of *Trichodagmia* by the end of the gill histoblast with ends pointing towards the ventral region of the body. I could not find a reliable character to separate larvae of *S. nunedemolloi* from those of *S. orbitale* (Figs. 1146).

HAMADA *et al.* (2006) did not assign *S. nunesdemelloi* to any subgenus within *Simulium s.l.* because it shared characters of species of the subgenera *Trichodagmia* and *Thyrsopelma*. In the recent World Inventory of Blackflies ADLER & CROSSKEY (2008, 2009, 2010) placed *S. nunesdemelloi* in the subgenus *Trichodagmia*, where no species groups were proposed. This has been reviewed by SHELLEY *et al.* (2010), who allotted this species to the subgenus *Trichodagmi*a in the ORBITALE species-group, and this has been followed in the current work.

Distribution. *Simulium nunesdemelloi* has only been recorded from the state of Amazonas, Brazil (ADLER & CROSSKEY, 2008, 2009, 2010; HAMADA *et al.*, 2006; SHELLEY *et al.*, 2010; **Material Examined**).

Biology and Medical Importance. The immature stages of *S. nunesdemelloi* have been collected in forested areas in large rivers (Rio Negro and Rio Tiquié) with widths of 1.65 km and 70 m, respectively, attached to Podostomaceae. All pupae and larvae were attached to Podostomaceae leaves growing on rocky substrate in highly turbulent water, usually at depths below 0.5 m. The temperature of the water was approximately 26°C and PH 4.5-5.2. Females of this species have never found biting humans (HAMADA *et al.*, 2006).

2.5.2.11. *Simulium* (*Trichodagmia*) *orbitale* LUTZ (Figs. 20, 35, 44, 51, 62, 88, 89, 203, 256, 340, 341, 446, 553, 612, 672, 759, 760, 857, 918, 979, 1040, 1095, 1146, 1201, 1255)

This is a common species in southern Brazil.

Simulium orbitale LUTZ, 1910: 231. NEOTYPE female, BRAZIL: Minas Gerais State, Benjamin Constant, ii. 1910 (*A.Lutz*) (IOC) [Examined.] [Neotype designation by D'ANDRETTA & D'ANDRETTA, 1945: 100.]

Simulium albimanum LUTZ, 1909: 127, 132. [Incorrect subsequent spelling of *S. nigrimanum* LUTZ, not MACQUART: see D'ANDRETTA & D'ANDRETTA, 1945: 86 & SHELLEY *et al.*, 1984: 147.]

Thyrsopelma brasiliense ENDERLEIN, 1934a: 284. LECTOTYPE female, BRAZIL: [Collection date and collector unknown.] (NMHU) [Examined.] [Synonymy by VARGAS & DIAZ NÁJERA, 1953a: 146; lectotype designation and confirmed synonymy by SHELLEY *et al.*, 2010: 440; synonymy mistakingly attributed to VARGAS (1951b) by SHELLEY *et al.*, 1910: 440.]

Simulium albopictum LANE & PORTO, 1940: 193. HOLOTYPE female, BRAZIL: Paraná State, Cambará, 29/30.vii.1936 (*G. H. de Paula Souza*) (FSP) [Examined.] [Synonymy with *S. guianense* by MIRANDA-ESQUIVEL & COSCARÓN, 2001: 430; treated as a *species inquerenda* by COSCARÓN & COSCARÓN-ARIAS, 2007: 626 and COSCARÓN *et al.*, 2008: 49; confirmation of synonymy with *S. orbitale* and lectotype designation by SHELLEY *et al.*, 2010: 440, still regarded as a valid species in ADLER & CROSSKEY, 2008: 94, 2009: 99, 2010: 101.]

FEMALE. General body colour black. Body length (specimens pinned) 2.1 mm (mean = 2.1 mm, s.d. = 0.02, n = 3), wing length 1.5-2 mm (mean = 1.2 mm, s.d. = 0.73, n = 3), wing width 0.9-2.1 mm (mean = 1.6 mm, s.d. = 0.62, n = 3).

Head: dichoptic with dark red eyes and nudiocular area slightly developed (Fig. 203). Frons, clypeus and occiput black; clypeus covered with broad, white recumbent setae and frons with broad, white setae interspersed with long, erect, black hairs. Mouthparts parts black. Antennae with scape and pedicel brown rest of flagellar segments black. Cibarium without teeth and with well developed, sclerotised cornuae (Fig. 256).

Thorax: scutum black with groups of evenly arranged, broad, recumbent whitish silver setae and longer, darker, recumbent hairs on posterior margin. Scutum without distinct pattern irrespective of light direction (Figs. 340, 341). Scutellum dark brown with broad, recumbent, white hairs and long, black bristles mainly on posterior margin. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta with line of setae occupying up to nearly two thirds of vein length. Radius with line of setae intermixed with distinct spines, basal section of radius with line of setae. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 446. Fore legs with coxa, trochanter, femur and two thirds of tibia yellowish; apex of tibia and tarsal segments dark brown. Mid and hind legs with coxa, apex of femur, two thirds of tibia and apex of tarsal segments I - IV mid brown; trochanters and base of tibiae yellowish; two thirds of tarsal segment I and base of segment II whitish. Claw weakly curved without tooth. Halteres cream with brown base.

Abdomen: tergites I-IX black, with faint silver pruinosity on tergite II laterally and brown mottled on segment I posteriorly and segments III, V and VII anteriorly. Tergal plates well developed. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses subtriangular, membranous, nearly as long as eighth sternite at mid point, with small setae distributed over entire surface (Fig. 35, 553). Cerci subrectangular, covered with distinct, long, brown setae; paraproct subtriangular, weakly sclerotised dorsally, with two tail-like, setose projections on membranous part; paraproct covered with prominent brown setae (Fig. 20, 612). Genital fork stout and sclerotised; termination of lateral arms with anterior margin straight and well developed; anterior processes reduced; posterior processes well developed and subquadrangular (Fig. 672). Spermatheca globular, with weak external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct two thirds maximum width of spermatheca.

MALE. General body colour black. Body length (specimens pinned) 2.1 mm (n = 1), wing length 1.5 mm (n = 1), wing width 0.9 mm (n = 1).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum brownish black with golden, recumbent hairs. Scutal pattern shows little variation with light incidence being brownish black with 1+1 broad, silver vittae beginning on antero-lateral margins and running diagonally towards mid line of scutum and ending in posterior third of thorax (Figs. 759, 760). Humeri, lateral and posterior margins of scutum silver pruinose [best seen when specimen viewed laterally]. Scutellum dark brown with golden, recumbent hairs and long, erect, dark setae. Postnotum brown with silvery grey pruinosity. Wing setation mostly as in female, except Sc with setae only on basal third. Leg coloration similar to female, except coxae, trochanters, femora and tibiae dark brown.

Abdomen: tergites black, except silver pruinosity on lateral margins of segment II and segments IV - VI ventro-laterally; basal fringe with long, brown hairs; tergal plates developed. Gonocoxite subquadrangular; gonostyle elongate, two time longer than gonocoxite length at mid point, widened on basal two thirds and terminating in single, stout, spine; gonocoxite and gonostyle covered with long setae (Fig. 857). Ventral plate subrectangular and weakly sclerotised; main boyd of ventral plate well developed, concave on anterior margin and with prominent, median, pear-shaped process arising from posterior margin covered by long hairs and not extending beyond apices of well developed lateral shoulders; basal arms straight, sclerotised and narrow apically (Fig. 918). Median sclerite prominent, nearly as long as width of ventral plate, with distinct incision for half of its length (Fig. 918). Paramere weakly sclerotised and poorly developed with no spines (Fig. 979).

PUPA. Cocoon length dorsally 2.5–2.8 mm (n = 2), ventrally 2.1–2.9 mm (n = 2); pupa length 3.1–3.5 mm (n = 2); gill length 1.1–1.4 mm (mean = 1.2 mm, s.d. = 0.13, n = 4).

Cocoon: shoe-shaped as in Fig. 66, light brown composed of thick coalesced fibres, with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with 20-23 upwardly directed filaments arranged in bunch in vertical plane. Gill configuration variable with filaments branching at different heights (Fig. 1040); basic pattern with main trunk short, giving rise to two sets of primary branches, two external and two internal: the most dorsal of the external set consisting of eight secondary branches and the ventral one of four, all bifurcating a different heights; the internal consisting of two secondary branches, with the most dorsal having seven filaments and the ventral with three, all branching at different heights. Gill filament number variation was found on dorsal branches of external and internal set having either seven or eight filaments each, and in one specimen some filaments of dorsal external set were shorter. Filaments stout, pointed and weakly sclerotised distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (frontoclypeus): with 2+2 frontal and 1+1 facial small, simple trichomes; frontoclypeus with group of platelets mesally, 1+1 dorso-laterally and 2-3 platelets in groups of 3 or 4 laterally in frontal region, respectively; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region.

Thorax: with 3+ 3 large, simple trichomes near margin of dorsal cleft and two to three simple trichomes on alar region; tubercles rounded and densely visible ventrally on alar region and gill base, and pointed to postero-lateral margin of dorsal cleft.

Abdomen: tergite I with 1+1 submedian, simple setae; tergite II with 2+2 sublateral, simple setae and 1+1 submedian, small setae; tergite III with 4+4 submedian spines in longitudinal row and 1+1 simple, long setae lateral to outermost spine; tergites IV and V with 4+4 submedian hooks in longitudinal row and sometimes 2+2 or 3+3 simple, short setae anterior to most lateral hooks; tergites VI with 4 submedian setae and spine combs on anterior margin; tergite VII with 1+1 submedian, simple, small setae and spine combs on anterior margins; tergite VIII with spine combs on antero-lateral margins; tergite IX weakly sclerotised, without terminal spines. Abdominal sternites III and IV with spine combs on anterior margins; sternite V with 2+2 close, bifid to trifid hooks in a row and spine combs on anterior margin; sternite VI-VII with 2+2 well separated, bifid to trifid hooks and groups of spine combs on anterior margin; sternite VIII with spine combs on anterior margin.

LARVA (Final instar). Body length 4.0-5.0 mm (mean = 4.7 mm, s.d. = 0.43, n = 5); length of head capsule 0.5-1.1 mm (mean = 0.66 mm, s.d. = 0.25, n = 5); width of head capsule 0.4-0.5 mm (mean = 0.4 mm, s.d. = 0.05, n = 5). Body colour with pale greenish bands dorso-laterally, and with yellowish and whitish tinges (specimens preserved in Carnoy's solution). General body form as in Fig. 88, 89, 1095.

Head: mainly pale yellow over entire surface. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern weakly negative. Cervical sclerites elongate, fused to occiput. Postgenal cleft not deep, dome-shape, rounded apically; postgenal bridge nearly twice length of hypostomium (Fig. 1146). Hypostomium strongly pigmented on anterior margin, with nine poorly developed apical teeth, evenly distributed on anterior margin, anterior margin concave in central region; median tooth small; 3+3 sublateral teeth, sometimes pair adjacent to median tooth smaller than outermost pair; 1+1 lateral teeth, nearly at the same level as median and lateral teeth; 1+1 paralateral teeth; lateral serrations absent; 1+1 lines of three to six hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1201). Sub-esophageal ganglion lightly pigmented. Antennal segments longer than labral fan stalk, all segments pale yellow; length of antennal segments I-III excluding the sensillum 0.05-0.08:0.06-0.1:0.04-0.07 mm (n = 5). Mandible with three apical teeth, first one more prominent than second and third; mandibular comb with nine teeth, fourth and nine teeth less developed than teeth first, second and third teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1255). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with more 29-40 rays with fine, single line of spines in a row (n = 4).

Thorax: pale yellow with green tinges. Cuticle densely covered with ovoid setae. Proleg with plate heavily sclerotised with band of approximately 26 rows of sclerotised processes of 12 simple hooks (n = 1). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 22 filaments, all branching from common trunk, and sclerotised and pointed apically.

Abdomen: usually with green bands on pale yellow background grey dorsally, progressively paler ventrally, especially towards posterior where segments white. Ventral nerve cord unpigmented. Ventral papillae absent. Cuticle prominently covered with ovoid setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 90-116 rows of sclerotised processes of 21-26 simple hooks (n = 3). Rectal gills with three branches of approximately 11-13 small, finger-like lobules (n = 2).

Taxonomic Discussion. In 1909 LUTZ collected and described numerous females from Avanhandava, northern São Paulo State and believed them to be conspecific with *S. nigrimanum*, a species previously described by MACQUART (1838) from the same region. LUTZ commented that although MACQUART had only described the male and that his own collections were females, they belonged to the same species. In 1910, LUTZ provided a slightly revised description of the female and new descriptions of the male, pupa and larva. He concluded that MACQUART'S description of the male *S. nigrimanum* was of a different species and consequently gave the name *S. orbitale* to his now new species. The male genitalia of *S. orbitale* were first illustrated by PINTO (1932) in his study of the Simuliidae of Central and South America based on specimens from Rio Saõ Francisco, Minas Gerais State. In 1909 LUTZ referred to *S. nigrimanum sensu* LUTZ not MACQUART as *S. albimanum* and hence the name *S. albimanum* became a synonym of *S. orbitale*, which was the actual species to which he was referring (see reviewed by SHELLEY *et al.*, 1984). In 1945 D'ANDRETTA & D'ANDRETTA provided full descriptions of all stages of *S. orbitale*, which they regarded as belonging to the subgenus *Eusimulium*, together with a list of previous references and misidentifications of this species. They stated that the holotype of *S. orbitale* had been lost and designated a neotype female from Benjamin Constant, Minas Gerais State, collected in 1910 by Lutz. Additionally, they examined LUTZ' original *S. orbitale* specimens and concluded that two species were present, *S. orbitale* and a new species that they described as *S. pintoi* [later synonymised with *S. guianense s.l.* by SHELLEY *et al.*, 1997].

In the recent book of *The Simuliidae of Brazil* SHELLEY *et al.* (2010) were unable to locate LUTZ' specimens, but examined the neotype of *S. orbitale* and reared specimens that were conspecific. Since many of the interspecific morphological characters used for separating species in *Trichodagmia* are similar for *S. orbitale* and *S. guianense*, and D'ANDRETTA AND D'ANDRETTA (1945) did not give clear figures of the female paraprocts of *S. guianense* [as *S. pintoi*] and *S. orbitale*, a good interspecific character, SHELLEY *et al.* (2010) were unable to assess whether all the figures in this latter paper refer only to *S. guianense* [as *S. pintoi*] or in some cases to *S. orbitale*. In the same book (SHELLEY *et al.*, 2010) also selected a lectotype for *Thyrsopelma brasiliense* ENDERLEIN and synonymised *S. albopictum* with *S. orbitale*. The latter authors mistakingly attributed the synonymy of *T brasiliense* with *S. orbitale* to (VARGAS, 1951b). This synonymy should be attributed to VARGAS & DÍAZ NÁJERA (1953a). Apparently, the reference of VARGAS (1951a) was an error in citing the paper of VARGAS & DÍAZ NÁJERA (1951b), in which the authors mention the subgenus *Trichodagmia*. I have studied all type material and specimens examined by SHELLEY *et al.* (2010) within the context of the current work (see **Material Examined** in the latter publication).

Several species of the ORBITALE species group of the subgenus *Trichodagmia* are externally similar in the female. The scutum of *S. orbitale* is similar to that of *S. duodenicornium*, *S. guianense s.l.*, *S. hirtipupa*, *S. itaunense* and *S. perplexum* in that it is black, without a pattern and has broadened setae arranged in groups (Figs. 315, 316, 317-324, 327, 328, 342, 343). Females may be distinguished to a certain extent by the cibarium morphology, but are most easily distinguished by the paraprocts. The presence of well developed cornuae in *S. hirtipupa* and *S. orbitale* (Figs. 20, 605, 612) separates these two species from *S. duodenicornium*, *S. guianense s.l.* and *S. itaunense* (Figs. 603, 604, 607), which have undeveloped cornuae. In the ventral extension of the paraproct *S. orbitale* and *S. duodenicornium* have a small, membranous, tail-like projection ventrally (Figs. 603, 612) while in *S. hirtipupa* it is well developed (Fig. 605), but in *S. orbitale* the paraproct is more membranous and developed next to the cercus (Fig. 612). In *S. guianense s.l.* the paraproct is similar to that of *S. orbitale*, except that there is no membranous tail projecting ventrally, but a small membranous tail emerging from beneath (inner surface) the paraproct and projecting ventrally (Fig. 604). In *S. perplexum* the paraproct is broadly rectangular and in place of the tail the paraproct is extended and doubled under ventrally (Fig. 613). These species are also not easy to distinguish in males using the scutal pattern: *S. duodenicornium* (Figs. 732, 733), *S. hirtipupa* (Figs. 742-745) and *S. perplexum* (Figs. 761, 762) have no pattern as in females, *S. itaunense* (Figs. 748, 749) and *S. orbitale* (Figs. 759, 760) show a similar pair of silver cunae, while *S. guianense s.l.* (Figs. 734-741) has a distinctive pattern. Species determination in the male is most satisfactory using the genitalia. *Simulium perplexum* is immediately distinguished by its subrectangular gonostyle (Fig. 858) compared to the typical spindle-shaped gonostyle of *Trichodagmia* of the other five species. However, differences are evident in the morphology of the ventral plate. *Simulium hirtipupa* is easily distinguished by the reduced main body of the ventral plate and the highly developed lateral arms and median process with a distinct keel (Fig. 911). Similarly, *S. perplexum* is distinctive because of the total absence of the median process and keel (Fig. 919). *Simulium duodenicornium*, *S. guianense s.l.*, *S. itaunense* and *S. orbitale* are more similar, though slight differences may be seen. *Simulium itaunense* has a well developed median process emerging from the plate margin and has a small keel (Fig. 913), while in the other three species (Figs. 909, 910, 918) the central process arises from the whole of the central portion of the body of the ventral plate and has no keel.

The number of pupal gill filaments is useful in separating the above related species. *Simulium orbitale* has 20 to 22 filaments (Fig. 1040) [COSCARÓN (1991) recorded specimens of *S. orbitale* with 21 to 23 filaments], *S. itaunense* has 45-56 (Fig. 1034) while *S. duodenicornium*, *S. guianense s.l.* and *S. hirtipupa* all possess 12 gill filaments (Figs. 1030, 1031, 1032). *Simulium hirtipupa* (Fig. 1032) is unique in the presence of distinctive small spinules on the filaments, *S. guianense s.l.* has spicules, while *S. duodenicornium* lacks spicules. *Simulium duodenicornium* and *S. guianense s.l.* have a very similar gill configuration with the former distinguished by shorter and wider filaments that are splayed out over an angle of 180°, compared to the bunched gill and longer gill filaments of the other three species. The other species in Brazil with 12 filaments is *S. scutistriatum* (Fig. 1042); the gill configuration is similar to that of *S. guianense s.l.* and so pupae need to be reared to adults for species identification. Other species not present in Brazil occurring in Andean countries in the subgenus *Trichodagmia* that have 12 gill filaments of similar morphology are *S. huairayacu*, *S. muiscorum*, *S. sumapazense* and *S. wygodzinskyorum*, and *S. perplexum* from Guyana. These all have different gill configurations and where both adults are known show distinct morphological differences to the Brazilian species discussed above. Another good character for separating some of the closely related species is the presence or absence of spiniform setae on the frontoclypeus. Only *S. hirtipupa* has many black spiniform setae, while the other species show rounded tubercles to varying extents (Fig. 71). PEPINELLI *et al.* (2005) noted the absence of the row of simple hooks on tergite V of *S. guianense s.l.* pupae from French Guiana as an additional character, but these are present in our *S. guianense* specimens excluding French Guiana. They also recorded the presence of tubercles on tergite II, not seen in any other species of *Trichodagmia.*

The larva of *S. orbitale* may be separated from other Brazilian species now placed in the ORBITALE species group by the greenish general coloration of the body (Figs. 88, 89, 1095), head capsule pale yellow, the dissected gill histoblast with 20-22 filaments, and the hypostomium with reduced apical teeth, which are evenly distributed along anterior margin (Figs. 1201). It may be separated from that of *S. nunesdemelloi* with difficulty by the dissected gill histoblast with longer and thinner filaments, which are relatively shorter and stouter in *S. nunesdemelloi.*

COSCARÓN (1987) placed *S. orbitale* in the subgroup ORBITALE of the subgenus *Thyrsopelma* and this subgenus was maintained for the species in MIRANDA-ESQUIVEL & COSCARÓN (2001). COSCARÓN & COSCARÓN-ARIAS (2007) maintained *Thyrsopelma* as a valid subgenus, where they included *S. orbitale* together with other six species and no division into species groups. ADLER & CROSSKEY (2008, 2009, 2010), CROSSKEY & HOWARD (2004) and, more recently, SHELLEY *et al.* (2010), included *S. orbitale* in the subgenus *Trichodagmia* which is followed in the current work.

Distribution. *Simulium orbitale* is commonly found in southern Brazil, in the states of Minas Gerais, Mato Grosso do Sul, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo. Elsewhere, it has been reported from Argentina, Colombia and Paraguay (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN, 1991; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. In Brazil the immature stages are found on Podostemaceae (D'ANDRETTA & D'ANDRETTA, 1945). COSCARÓN (1991) collected *S. orbitale* in fast flowing rivers at a depth of 50cm in Argentina. In Brazil, larvae and pupae are found on submerged vegetation in fast flowing, small rivers usually associated with rapids or near waterfalls. DELLOME FILHO (1992) found a preference for yellow over green polypropylene threads by larvae in a river in Paraná State in southern Brazil. DARWICH *et al.* (1989) recorded what they described as "occasional phoresis" in *S. orbitale* based on the presence of larvae and emerged pupae as well as simuliid eggs on the gastropod *Asolene (Pomella)* *megastoma* (SOWERBY) in southern Brazil. They also found larvae of two species of *Simulium* (*Psaroniocompsa*) on the same species of mollusc, but the identification to this subgenus needs verifying.

The females are zoophilic in Brazil (SHELLEY *et al.*, 2010). LUTZ (1910) collected females biting around the eyes of horses, the reason for his specific name *orbitale*. The alimentary habits of the adults of this species elsewhere in this region are poorly known. WYGODZINSKY (1953) reported *S. orbitale* biting man in Argentina, but admitted that because of the difficulty in separating this species from *S. guianense s.l.* [as *S. pintoi*] the latter species may have been involved. COSCARÓN (1991) knew of no reports on its alimentary habits. Females showed a preference for bovine baits over canine in southern Brazil (STRIEDER & CORSEUIL, 1992).

2.5.2.12. *Simulium (Trichodagmia) perplexum* SHELLEY, MAIA-HERZOG, LUNA DIAS & COUCH

(Figs. 54, 204, 257, 342, 343, 447, 554, 613, 673, 761, 762, 858, 919, 980, 1041)

This is a poorly known species originally described from Guiana (as British Guiana), which is closely related to *S. guianense s.l.* The description here provided has been based upon examination of the type material housed at the BMNH and the original description of SHELLEY *et al.* (1989).

Simulium (*Trichodagmia*) *perplexum* SHELLEY *et al.*, 1989: 343. HOLOYPE female, GUYANA: Kaieteur Falls, Potaro River; 1.ix.1937, (*O.W.Richards & J.Smart*) (BMNH) [Examined.]

FEMALE. General body colour black. Body length 1.6-2.2 mm (mean = 2.0 mm, s.d. = 0.2, n = 4); wing length 1.6-2.9 mm (mean = 2.0, s.d. = 0.48, n = 4), wing width 0.8-1.5 mm (mean = 1.0, s.d. = 0.26, n = 4).

Head: coloration and morphology (Figs. 204, 257) as in *S. guianense*, except antennae longer and thinner, and cibarium with small tubercles in central trough (Fig. 257).

Thorax: coloration and morphology as in *S. guianense* (Figs. 342, 343), except basal section of radius with no setae. Legs coloration as in Fig. 447; claw of hind leg with well developed basal tooth, and scales absent on legs.

Abdomen: abdominal tergites II-VII with lateral dark bands, velvet black with silver pruinosity covering tergite II, tergites V-IX shiny black. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised in posterior with 1+1 groups of 12-13 well developed setae; gonapophyses small membranous, not meeting centrally and densely covered in fine setae (Fig. 554). Cercus subquadrangular; paraproct with internal extension well developed and sclerotised, and not membranous as in *S. guianense* (Fig. 613). Genital fork with lateral arms less developed than in *S. guianense* (Fig. 673). Spermatheca oval and well sclerotised as in *S. guianense*, with internal sculpturing of spicules arranged in a line; area on insertion of spermathecal duct membranous.

MALE. General body colour black as in *S. guianense s.l.* Body length (n = 2) 2.1-2.4 mm; wing length 2.0-2.9 mm; wing width 1.0-1.2 mm.

Head: coloration and morphology as in *S. guianense s.l.*, except antennae longer and thinner, pedicel, scape and first two flagellomeres orange-brown.

Thorax: coloration and morphology as in *S. guianense s.l.* . Scutum, humeri and paranotal folds velvet black; darker median line extending from anterior scutal border for two thirds length of scutum with light source anterior to specimen (Fig. 761). With light source posterior to specimen scutum light grey with dark median line as in female (Fig. 762). Scutum covered in groups of golden scale-like setae with green reflections and long dark brown setae, especially on anterior and posterior borders. The male is easily separated from that of *S. guianense s.l.*, which has a silver and grey pattern to the scutum (see Figs. 734-741). Legs as in *S. guianense s.l.* except scales absent.

Abdomen: as in *S. guianense s.l.* Genitalia different to *S. guianense s.l.* in that gonostyle broader at base and hence subtriangular in form, with smaller distal pointed spine instead of larger terminally rounded spine of *S. guianense*. Gonocoxite almost square compared with subrectangular gonocoxite of *S. guianense s.l.*, which is wider than long (Fig. 858). Ventral plate similar in general morphology to that of *S. guianense s.l.*, except basal arm narrower and main body of ventral plate shallower and without protuberance (Figs. 54, 919). Median sclerite subrectangular, basal margin with fine spines and distal margin with an incision extending to mid length of sclerite (Fig. 919). Paramere as in Fig. 980.

PUPA. Gill length 0.7 mm (n = 1) [Other measurements not given because of lack of material].

Cocoon, *head* (*frontoclypeus*), and *thorax* as in *S. guianense s.l.* Pupal gill similar to *S. guianense s.l.* except annulations on more distal parts of gill filaments more accentuated with forwardly-directed processes rather than spicules (Fig. 1041). Abdominal chaetotaxy was not studied due to the poor quality of the material at hand.

LARVA (Final instar). Unknown.

Taxonomic Discussion. SHELLEY *et al.* (1989) described *S. perplexum* based on 17 females, 14 males, one pharate male pupa and two pupal skins collected from Kaieteur, Amatuk and Warratuk Falls, Guyana. I have examined the female holotype, which is housed at the BMNH. The specimen is in good condition and it has been micro-pinned through the posterior margin of the thorax, though this has not obscured the coloration pattern (Figs. 342, 343) (**Material Examined**).

SHELLEY *et al.* (1989; 2010) gave details on the external morphological similarity between the adults and pupal exuviae of *S. perplexum* and *S. guianense s.l.* The adults of *S. perplexum* are externally similar to those of *S. guianense s.l.* from which they can only be separated by the lack of pattern on the male thorax (Figs. 342, 343, 761, 762), the general morphology of the female paraproct (Fig. 613), and the male gonostyle (Fig. 858) and ventral plate (Figs. 54, 919). The pupal gill configuration is very similar in both species (Figs. 1031, 1041). However, they can be separated by the different shape of the annulations on the more distal part of the gill filaments, which are accentuated with forwardly directed processes in *S. perplexum*, while in *S. guianense s.l.* the flaments are covered by spicules (SHELLEY *et al.*, 2004, Figs. 109-112).

The larval stage of *S. perplexum* still remains unknown, therefore comparisons cannot be made with that of *S. guianense s.l.* or other closely related species.

MIRANDA-ESQUIVEL & COSCARÓN (2001) in their cladistical analysis of the subgenera *Thyrsopelma* and *Trichodagmia* placed *S. perplexum* in the ORBITALE subgroup of the subgenus *Thyrsopelma*. COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) placed *S. perplexum* in their valid subgenus *Thyrsopelma* and accepted all the synonyms listed in SHELLEY *et al.* (1997). However, ADLER & CROSSKEY (2008; 2009, 2010), CROSSKEY & HOWARD (1997, 2004) and SHELLEY *et al.* (2010) have placed *S. perplexum* in the subgenus *Trichodagmia*, an action followed in this work.

Distribution. *Simulium perplexum* has only been recorded from Guyana (ADLER & CROSSKEY, 2008, 2019, 2010; SHELLEY *et al.*, 1989, 2004).

Biology and Medical Importance. Pupae of *S. perplexum* were collected attached to submerged vegetation in the family Podostomaceae by SMART (1940), who identified them as *S. guianense s.l.* in the rainforest where Kaieteur Falls is located. The females of *Simulium perplexum* are anthropophilic and they can be easily confused with those of *S. guianense s.l.*

2.5.2.13. *Simulium* (*Trichodagmia*) *scutistriatum* LUTZ (Figs. 205, 258, 344, 345, 448, 555, 614, 674, 763, 764, 859, 920, 981, 1042, 1096, 1147, 1202, 1256)

This is an uncommon species only found in the south-eastern area of Brazil and more recently recorded from the state of Bahía. The description here provided have been upon examination of the female holotype and material collected and identified by N. HAMADA and housed at INPA.

Simulium scutistriatum LUTZ, 1909: 133. HOLOTYPE female, no. 12.639, BRAZIL: Rio de Janeiro, Itaguaí, [Collection date unknown.] (*D.Madeira*) (IOC). [Examined.]

FEMALE. General body colour dark reddish brown. Body length (in alcohol) 3.6-5.0 mm (mean = 4.1 mm, s.d. = 0.47, n = 8), (pinned) 3.3 mm (n = 2); wing length 2.4-3.0 mm (mean =2.8 mm, s.d. = 0.20, n=7), wing width 1.2-2.7 mm (mean = 1.5 mm, s.d. = 0.48, n = 8).

Head: dichoptic with dark red eyes and nudiocular area slightly developed (Fig. 205). Clypeus brown, frons and occiput dark brown to black, with silvery grey pruinosity; clypeus and frons covered with yellowish, semi-recumbent setae interspersed with long, erect, black hairs. Mouthparts parts dark brown. Antennae with scape and pedicel pale brown, rest of flagellar segments dark brown to black. Cibarium with well developed, sclerotised cornuae and small tubercles with very fine teeth on central trough (only visible with high magnification) (Fig. 258).

Thorax: scutum dark reddish brown with faint grey pruinosity and evenly arranged groups of recumbent, brass-coloured, broadened setae, interspersed with fine, semi-erect, black setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax with 1+1 pear-shaped, reddish brown vittae running from anterior margin to two thirds of scutum length; 1+1 wide, greyish, sublateral vittae, which show black markings on anterior margins with some lights; humeri dark brown (Fig. 344). With posterior illumination, thorax having 1+1 median, pear-shaped, reddish brown vittae and 1+1 large, sublateral pruinose vittae covering anterior margins to half length of thorax; humeri silver pruinose (Fig. 345). Thorax, irrespective of light direction, divided by a median dark brow line running from anterior margin to apex of median, pear-shaped; posterior and lateral margins dark brown to black. Scutellum dark brown with recumbent white hairs intermixed with long, erect, black bristles. Postnotum dark brown with silver pruinosity. Pleura dark brown to black with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta with line of setae along entire length. Radius with numerous setae intermixed with distinct spines, basal section of Radius with three irregular rows of setae along entire length. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 448. Fore legs with coxae, trochanters, femora, and two thirds of tibiae yellowish to light brown, apex of tibiae and tarsi dark brown to black. Mid legs with coxae, trochanters, femora, and two thirds of tibiae and first tarsal segment brown; apex of tibiae and first tarsal segment plus tarsal segments II, III and IV dark brown to black. Hind legs with coxae, femur, tibiae, first and second tarsal segments dark brown apically; trochanter and rest of femur light brown; half of tibiae, and half of first and second tarsal segments pale yellow. Claw weakly curved with small basal tooth. Halteres pale yellow with brown base.

Abdomen: tergites I-IX black, except yellow on anterior margin of segments I and II mesally, and brown mottled on anterior margin of segments V and VIII; all segments without silver pruinosity. Tergal plates well developed. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses short, rounded, and membranous, with small setae distributed over entire surface (Fig. 555). Cerci subrectangular, covered with distinct, long, black setae; paraproct subrectangular, with internal membranous process, weakly sclerotised, ventral extension nearly three times longer than cercus and covered with prominent brown setae basally and setose on anterior margin, apically (Fig. 614). Genital fork stout and sclerotised; termination of lateral arms with anterior margin nearly straight and well developed; anterior and posterior well developed (Fig. 674). Spermatheca globular, without apparent external sculpturing and small internal spicules; area of insertion of spermathecal duct membranous about one third maximum width of spermatheca.

MALE. General body colour dark, reddish brown to black [specimens recovered from alcohol by SABROSKY'S method (1966)]. Body length (specimens preserved in alcohol) 3.8-4.2 mm (n = 2), pinned 3.9 mm (n = 1); wing length 2.2-2.7 mm (mean = 2.8 mm, n = 3), wing width 1.1-1.4 mm (mean = 1.3 mm, n = 3).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark brown with golden, recumbent hairs interspersed with recumbent black hairs. Scutal pattern varies slightly with light incidence: with anterior light source thorax dark with 1+1 median, pear-shaped and 2-2 submedian, broad, reddish brown vittae that extend to lateral margins (Fig. 763); humeri yellowish to pale brown; lateral and posterior margins dark brown to black. With light source posterior to specimen thorax dark brown with weak silver pruinosity on central region (Fig.

764); humeri pale brown; lateral and posterior margins dark brown to black. Scutellum yellowish with golden, recumbent hairs interspersed with long, erect, dark brown setae. Postnotum dark brown with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: tergites dark brown, basal fringe with long, brown hairs. Silver pruinose ornamentation on antero-lateral margins of tergites II-VII. Genitalia dark brown; tergal plates developed; sternal plates poorly developed. Gonocoxite subquadrangular; gonostyle spindle-shaped terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 859). Ventral plate sclerotised, subrectangular, covered by short hairs; keel not developed covered by long hairs; basal arms well developed and subparallel (Fig. 920). Median sclerite as long as wide with apical incision (Fig. 920). Paramere with well developed and sclerotised basal process, with distinct central membranous area covered by small hairs (Fig. 981).

PUPA. Cocoon length dorsally 3.6-4.6 mm (mean = 3.9 mm, s.d. = 0.39, n = 10), ventrally 4.2-6.2 mm (mean = 5.4 mm, s.d. = 0.54, n = 11); pupa length 3.6-5.6 mm (mean = 4.6 mm; s.d. = 0.62, n = 10); gill length 1.1-2.0 mm (mean = 1.5 mm, s.d. = 0.28, n = 11).

Cocoon: shoe-shaped as in Fig. 66, dark brown composed of thick coalesced fibres, with reinforced rim to anterior aperture, margin of aperture strongly elevated.

Gill: light brown with 12 upwardly directed filaments arranged in a bunch in vertical plane. Gill Configuration with filaments branching basally at different heights (Fig. 1042); main trunk short, giving rise to four sets of primary branches, two external and two internal; the most external consists of one dorsal with four secondary branches that bifurcate at different height and a ventral with two filaments bifurcating at some distance from base; the internal consists of two primary branches, one dorsal with four filaments branching at different height and one ventral with two filaments bifurcating more apically than the ventral branch of the external set of filaments. Variation on the pupal configuration pattern was examined in specimens collected at Chapada Diamantina, Bahía State, in which filaments from external and internal branches bifurcate more apically. Filaments stout, prominently pointed and sclerotised distally, without spicules on surface, edges straight; dorsal filament of the internal set longer than rest of filaments.

Head (frontoclypeus): with 2+2 frontal and 1+1 facial small, simple trichomes; frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and 4-5 platelets in groups of 3 laterally in frontal region, respectively; tubercles rounded and densely distributed over entire surface.

Thorax: with three simple trichomes on alar region; tubercles mainly rounded but pointed posteriorly on dorsal cleft, tubercles densely distributed over entire surface.

Abdomen: tergite I with pointed tubercles densely distributed over posterior margin and 2+2 simple, sublateral setae; tergite II with 3+3 median setae in row, 3+3 sublateral and 2+2 lateral, small setae, and pointed tubercles on anterior margin; tergites III and IV with 4+4 submedian hooks in a longitudinal row, 1+1 simple, small setae anterior to most lateral hooks [on left side in one specimen 4 sublateral setae can be seen]; tergite V with few spine combs on anterior margin; tergites VI-VIII with groups of spine combs on antero-lateral margin; tergite IX without terminal spines, weakly sclerotised. Abdominal sternite III and IV with 1+1 median, 2+2 submedian, 2+2 sublateral, small, simple setae and spine combs mainly on anterior margin [in ventral view, most lateral setae are more prominent than most internal ones and resemble spines]; sternite V with 2+2 close, simple, median hooks; sternites VI-VII with 2+2 well separated, simple or bifid hooks in a row on posterior margins and groups of spine combs anteriorly; sternite IX with spine combs on lateral margins.

LARVA (Final instar). Body length 10.1-11.6 mm (mean = 10.8 mm, s.d. = 0.56, n = 6); length of head capsule 0.8-0.9 mm (mean = 0.9 mm, s.d. = 0.08, n = 6); width of head capsule 0.8 mm (mean = 0.8 mm, s.d. = 0.03, n = 6). Body colour dark grey with brown tinges dorso-laterally, whitish ventrally (specimens fixed in Carnoy's solution). General body form as in Fig. 1096.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, rounded apically; postgenal bridge nearly one and half times as long as hypostomium (Fig. 1147). Hypostomium strongly pigmented on anterior margin, with nine apical teeth, all teeth distinctly reduced and evenly distributed along anterior margin; median tooth weakly developed; 3+3 sublateral teeth adjacent to median teeth of same length sometimes with smaller teeth at the base; 1+1 lateral teeth, longer than median and sublateral teeth; 3+3 lateral serrations; 1+1 lines of 11 hypostomial setae parallel to lateral margins; 1+1 prominent and 1+1 small simple setae in posterior half of hypostomium (Fig. 1202). Sub-esophageal ganglion lightly pigmented. Antennal segments longer than labral fan stalk, all segments light brown; length of antennal segments I-III excluding the sensillum 0.1:0.1-0.2:0.08-0.1 mm (n = 6). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately 11 teeth, first four teeth longer than remainder; two mandibular serrations, sometimes joined at base to form a single structure, in which case the anterior is more developed than posterior (Fig. 1256). Lateral mandibular process absent. Maxillary palps heavily pigmented, one and a half times as long as wide at base. Labral fan with 57-72 rays each with fine, single line of microspinules in a row (n = 4)

Thorax: greyish dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 57-72 rows of sclerotised processes with 35-42 of simple hooks (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 12 filaments, arranged in four primary branches, and pointed and heavily sclerotised apically.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 188-250 rows of sclerotised processes of 42-50 simple hooks (n = 4). Rectal gills not everted in the few specimens examined.

Taxonomic Discussion. *Simulium scutistriatum* was described by LUTZ (1909) based on one female collected by Sr. David Madeira in Itaguahy (Itaguaí), Rio de Janeiro State. I have examined the pinned female holotype, which is housed at IOC. The holotype is in poor condition with head, one fore leg, mid legs and hind tarsal segments missing; its abdomen and one wing are mounted on a slide (**Material Examined**).

A full description (only female) and comparisons of *S. scutistriatum* with other simuliid species can be found in MAIA-HERZOG *et al.* (1984). More recently, SHELLEY *et al.* (2010) also reviewed the taxonomy of this species and compared with similar species.

The female scutal pattern of *S. scutistriatum* is similar to other simuliid species found in Brazil, *e.g.* *S. brachycladum*, *S. lobatoi* and *S. virgatum s.l.*, by the thorax orange to dark brown with large pruinose areas and a median dark brown line running from anterior to posterior margins (Figs. 344, 345). However, it is readily distinguished from the latter species by the absence on the thorax of a bow-shaped, dark brown vittae and evenly arranged groups of recumbent, brass-coloured, broadened setae, interspersed with fine semi-erect black setae (with light source anterior) (Fig. 344) (see also "**Taxonomic Discussion**" under *S. lobatoi* for further comparisons and Figs. 384, 385). *Simulium scutistriatum* is easily recognised by the structure of the female paraproct, which is very long with its ventral extension nearly three times longer than length of cercus and not expanded apically (Fig. 614). The males of *S. scutistriatum* are similar in scutal pattern to those of *S. lobatoi* and *S. virgatum s.l.* in being orange (*e.g.* Figs. 763, 764, 799, 800) compared to that of *S. brachycladum*, which is black (Figs. 777, 778). Males of *S. scutistriatum* are distinguishable from those of *S. lobatoi* and *S. virgatum s.l.* in having a spindle-shaped gonostyle (Fig. 859), an undeveloped keel on the ventral plate (Fig. 920) and parameres without teeth (Fig. 981).

The best character to recognize *S. scutistriatum* is the number and configuration of gill filaments. The highly sclerotised and prominently pointed ends of the gill are also found in *S. itaunense* and *S. jeteri* (Figs. 1034, 1035), but the number of filaments easily separates these two species (50 in *S. itaunense* and 15 in *S. jeteri*) from *S. scutistriatum* (12 filaments) (Fig. 1042). Other species with less pointed and 12 gill filaments occurring in Brazil are *S. guianense s.l.* and *S. hirtipupa*. In *S. guianense s.l.* the gill pattern is different with dorsal primary branch with six filaments, a median with four and a ventral with two filaments (Figs. 79, 1031). *Simulium hirtipupa* is easily identified by the presence of prominent black spiniform hairs on the thorax and frontoclypeus (Fig. 71). COSCARÓN'S (1991) key to pupae separated *S. guianense s.l.* (as *S. pintoi*) from *S. scutistriatum* by differences in the shape of the tubercles, which he stated were all pointed in *S. scutistriatum*. The specimens I examined from Brazil (see **Material Examined**) all have rounded tubercles on the frontoclypeus, and they are well distributed over the entire surface. They are mainly rounded on the thorax, except along the postero-lateral margin of the dorsal cleft where they are pointed.

The larva of *S. scutistriatum* may only be separated from species in the ORBITALE species group of the subgenus *Trichodagmia* by the dissected gill histoblast of mature larvae having 12 sclerotised and apically pointed filaments, which clearly separate it from other similar species such as *S. itaunense* (50 filaments) and *S. orbitale* (22 filaments) [see also section **2.4.7 Key to larva**].

COSCARÓN (1987) placed *S. scutistriatum* as the only member of the SCUTISTRIATUM species group in the subgenus *Thyrsopelma* and it is maintained in this subgenus by MIRANDA-ESQUIVEL & COSCARÓN (2001), COSCARÓN *et al.* (2008) and COSCARÓN & COSCARÓN-ARIAS (2007). ADLER & CROSSKEY (2008, 2009, 2010), CROSSKEY & HOWARD (1997, 2004) included *S. scutistriatum* in *Trichodagmia*. SHELLEY *et al.* (2010) allotted this species to the ORBITALE species group in this subgenus, which has been followed in the current work.

Distribution. *Simulium scutistriatum* has only been recorded from Brazil, where it is uncommon being found in the south-eastern area of this country in the States of Bahía, Rio de Janeiro, Goiás, Minas Gerais and São Paulo (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; see also **Material Examined** in SHELLEY *et al.*, 2010).

Biology and Medical Importance. Little is known of the biology of this species in Brazil. LUTZ (1910) recorded its presence between 0 to 900m at the localities of Xerém, Mendes, Juiz de Fora and Teresópolis in south east Brazil. The females are apparently zoophilic (SHELLEY *et al.*, 2010).

2.5.2.14. *Simulium* (*Trichodagmia*) *sumapazense* COSCARÓN & PY-DANIEL (Figs. 259, 449, 556, 615, 675, 860, 921, 982, 1043, 1097, 1148, 1203, 1257)

This is a poorly known species only found in Colombia. I was unable to obtain material of *S. sumapazense*. Therefore, the description here provided has been derived from the original description in COSCARÓN & PY-DANIEL (1989), examination of the holotype and the description and illustrations given in MUÑOZ DE HOYOS (1996). Characters not described here were not provided in the latter publications.

Simulium sumapazense COSCARÓN & PY-DANIEL, 1989: 321. HOLOTYPE pupal exuviae, COLOMBIA: Cundinamarca Province, Páramo de Sumapaz, 3700 m; 30.vi.1965, (*P. & B.Wygodzinsky*) [Examined.] [In the original description the holotype is said to be deposited at the AMNH, but it is still housed at MLP - see "**Taxonomic Discussion**".]

FEMALE (Pharate). General body colour black. Wing length 3.1 mm [remaining measurements not given].

Head: dichoptic and nudiocular area developed. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed and sclerotised cornuae, anterior margin slightly concave centrally with minute teeth on central region and on margin of cornuae (Fig. 259).

Thorax: scutellum and postnotum dark brown. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length. Radius with numerous setae intermixed with distinct spines apically, basal section of radius with setae. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 449 [coloration not described]. Hind leg claw with small basal tooth. Halteres cream yellow with brown base.

Abdomen: sternites dark brown. Eighth sternite sclerotised with 30 long, irregularly distributed setae on posterior margin; gonapophyses membranous, subtriangular and rounded at apex, nearly half length of eighth sternite at mid point and densely covered with microtrichiae (Fig. 556). Cercus hemispherical, covered with brown setae; paraproct subhemispherical, with small visible projection at junction with cercus, covered by long brown setae basally and microtrichiae distally (Fig. 615). Genital fork stout, sclerotised, termination of lateral arms with anterior margin curved and well developed; anterior processes well developed and blunt apically; posterior processes weakly developed (Fig. 675). Spermatheca globular, without external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE (Pharate). General body colour dark brown. [COSCARÓN & COSCARÓN-ARIAS (2007) recorded the wing length as 3.1 mm. Other measurements and the number of specimens examined were not given in the latter paper.]

Head: holoptic with dark red eyes. Clypeus with long black hairs.

Thorax: scutum dark brown with black hairs. Scutellum brown black hairs. and long erect dark brown setae. Postnotum dark brown. Wing setation as in female, but only 4-5 hairs. Leg coloration as in female.

Abdomen: gonocoxite subquadrangular; gonostyle spindle-shaped, with sinuous margins and terminating on stout spine; gonocoxite and gonostyle covered with long setae (Fig. 860). Ventral plate strongly sclerotised, subrectangular; main body covered by small setae, without developed shoulders; anterior median process small, and basal arms well developed and subparallel (Fig. 921). Median sclerite wide at mid length with apical incision. Paramere with well developed and sclerotised basal process and small teeth centrally and on membrane (Fig. 982).

PUPA. [COSCARÓN & COSCARÓN-ARIAS (2007) recorded the cocoon length dorsally as 3.3 mm, ventrally as 3.7 mm; gill length as 0.9-1.9 mm. The number of specimens examined was not given in the original description nor in the latter paper.]

Cocoon: shoe-shaped as in Fig. 66, [not slipper-shaped [= zueco] as described by COSCARÓN & PY-DANIEL, 1989], brown composed of thick, coalesced fibres (appearing gelatinous on slide) with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown with 12 upwardly directed filaments arranged in bunch in vertical plane (Fig. 1043). Gill configuration with filaments branching basally near or at different heights some distance from gill base; main trunk short and wide, giving rise to two sets of primary branches, one internal and one external: external primary branch divided into two secondary branches, one anterior and one posterior, both having four filaments each; internal primary branch with four filaments (Fig. 1043). Gill filament variation was examined in a paratype, in which the filaments of the posterior secondary branch divide more apically. Filaments stout, pointed and unsclerotised distally, without spicules on surface, edges weakly crenate; filaments of anterior secondary branch of external primary branch relatively shorter than remaining filaments.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial long, multiramous trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups of 13 platelets dorso-laterally and 2-3 platelets in one group in frontal region; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region; facial region with prominent carina extending across of frontoclypeus.

Thorax: with 5+5 long, multibranched trichomes near margin of dorsal cleft, one long, multibranched trichome on alar region and one long, multibranched trichome on central region; tubercles absent from central region of thorax, but rounded and well distributed tubercles only visible at base of gill, and pointed on postero-dorsal margin near the dorsal cleft.

Abdomen: tergite I with pointed tubercles and 1+1 simple trichomes centrally; tergite II with 3+3 spiniform setae in row along posterior margin; tergites III, IV with 4+4 simple hooks along posterior margins and 2+2 sublateral small simple trichomes; tergites V-IX without trichomes; tergite IX without terminal spine. Spine combs distribution on antero-lateral margins of tergites II and VIII. Sternite III without setae; sternite IV with 2+2 closed submedian simple hooks on posterior margin; sternites V, VI with 4+4 simple, close, submedian hooks along posterior margins; sternites VIII, IX with no visible trichomes or setae; sternite IX without terminal spines. Spine combs on anterior margins of sternites IV and VII, VIII.

LARVA (Last instar). [MUÑOZ DE HOYOS (1996) and COSCARÓN & COSCARÓN-ARIAS (2007) recorded the body length as 7.6 mm. Other measurements, general coloration and the number of specimens examined were not given in the latter papers]. General boyd form as in Fig. 1097.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Postgenal bridge deep, bell-shaped, subtriangular and widest at mid point; postgenal bridge two and half times smaller than hypostomium (Fig. 1148). Hypostomium strongly pigmented on anterior margin, with nine apical teeth in central region; median tooth more prominent that sublateral teeth; 3+3 sublateral teeth; 1+1 lateral teeth; no lateral serrations; 1+1 lines of approximately nine hypostomial setae parallel to lateral margins, the first five longer than remainder teeth; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1203). Antennal segments longer than labral fan stalk, all segments pigmented; lengthof segments I-III except sensillum 1:1.5-1.9:0.7:1.0 mm. Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately eight teeth, first four more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1257). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with more 40-44 rays with fine teeth.

Thorax: [coloration, cuticle chaetotaxy not given in the redescription of MUÑOZ DE HOYOS (1996)]. Dissected gill histoblast with 12 filaments.

Abdomen: [coloration of abdomen, and ventral nerve cord not given in the original description or redescription in MUÑOZ DE HOYOS (1996)]. Ventral papillae absent. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly, no sclerotised areas between arms. Posterior circlet with 150 rows of 24-26 simple hooks. Rectal gills with three lobes each having 26, 20, 26 secondary finger-like lobules.

Taxonomic Discussion. *Simulium sumapazense* was described from a single pupal exuviae and a pharate male collected from Páramo Sumapaz and Guasca in Colombia by COSCARÓN & PY-DANIEL (1989). Both holotype (pupal exuviae) and paratype (pharate male) were said to be deposited at the AMNH. However, both specimens are still housed in the MLP. Simuliidae collections with a label stating "to be sent to the AMNH" (L.M. HERNÁNDEZ, unpublished information). The holotype has one gill and all pupal abdominal segments damaged (**Material Examined**). The female, male and larva and a redescription of the pupa of *S. sumapazense* were later published by MUÑOZ DE HOYOS (1996).

The adults of *Simulium sumapazense* might only be recognized by the examination of the pupal gill filaments in link-reared specimens. The best character to recognize this species is the configuration of the pupal gill filaments. The pupa has 12 forwardly directed filaments, which are unsclerotised apically (Fig. 1043). This character readily separates *S. sumapazense* from other species of *Trichodagmia* with 12 filaments (*e.g. S. guianense s.l.*, *S. hirtipupa* and *S. perplexum*) (Figs. 1031, 1032, 1041). In Colombia, the general morphology of the pupal gill filaments of *S. sumapazense* is most similar to that of *S. wygodzinskyorum* (Fig. 1045). However, in *S. wygodzinskyorum* the tubercles in the frontoclypeus are widely distributed over its entire surface and the anterior secondary branch of the dorsal primary branch appear to have all filaments longer than the remaining filaments (Fig. 1045). In addition, the base of the dorsal branch is less stout and wider than in *S. sumapazense* (see Fig. 1045). It is likely that when numerous reared specimens of *S. sumapazense* are examined, the pupal gill configuration pattern and distribution of tubercles might fall within the variation found in *S. wygodzinskyorum*. Variation in tubercle distribution and configuration of the pupal gill filaments is common in Simuliidae, for example see HERNÁNDEZ *et al.* (2007b) for species of *Inaequalium* [now in the subgenus *Psaroniocompsa*], and SHELLEY *et al.* (2006) in the AMAZONICUM species-group of the subgenus *Psaroniocompsa*. This variation was the main reason for which the latter authors proposed numerous synonymies in Neotropical blackflies. Because of the paucity of available material of *S. sumapazense*, I maintain this species as a valid taxon until further material is available to assess its taxonomic status.

The larva of *S. sumapazense* is most similar to that of *S. wygodzinskyorum* in the dissected gill filaments with 12 stout filaments. However, both species may be separated by the morphology of the postgenal cleft, which is deeper and less wide centrally in *S. sumapazense* (Fig. 1148) than in *S.*

wygodzinskyorum (Fig. 1150). In addition, the median tooth in *S. sumapazense* is more prominent than in *S. wygodzinskyorum* (Fig. 1203).

COSCARÓN & PY-DANIEL (1989) placed *S. sumapazense* in the subgenus *Grenieriella*, but CROSSKEY & HOWARD (1997, 2004), ADLER & CROSSKEY (2008, 2009, 2010), COSCARÓN & COSCARÓN-ARIAS (2007), COSCARÓN *et al.* (2008) and SHELLEY *et al.* (2010) placed *S. sumapazense* in the subgenus *Trichodagmia*, which is followed in the current work.

Distribution. *Simulium sumapazense* has a limited distribution only being found in the high mountainous areas of Colombia (ADLER & CROSSKEY, 2008 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; MUÑOZ DE HOYOS & MIRANDA-ESQUIVEL, 1996; MUÑOZ DE HOYOS & COSCARÓN, 1999; **Material Examined**).

Biology and Medical Importance. COSCARÓN & PY-DANIEL (1989) and MUÑOZ DE HOYOS & MIRANDA-ESQUIVEL (1997) recorded *S. sumapazense* in the Páramo Sumapaz in Colombia at altitudes between 2650 to 3700 m. MUÑOZ DE HOYOS (1996) stated that *S. sumapazense* is a species of Andino/Páramo forests with preference for fast running, cold (7°C) clear water streams of pH 6.3. Larva and pupae are found attached to rocks sympatric with species of the genus *Gigantodax*.

2.5.2.15. *Simulium* (*Trichodagmia*) *townsendi* MALLOCH (Figs. 21, 206, 260, 346-349, 500, 557, 616, 676, 765, 766, 861, 922, 983, 1044, 1098, 1149, 1204, 1258)

Simulium townsendi MALLOCH, 1912: 651. HOLOTYPE female, PERU: Rio Charape; 13.vii.1911, (*C.H.T.Townsend*) (NMNH, no. 15306). [Examined.]

Simulium chalcocoma KNAB, 1914a: 85. HOLOTYPE female, PERU: Tincochchoca, 7000 ft; 10.viii.1911, (Yale Peruvian Expedition) (NMNH, type no. 18350). [Examined.] [Synonymy by HERNÁNDEZ & SHELLEY, 2005: 12.]

Simulium chalcocomense [Incorrect subsequent spelling by VARGAS, 1945b: 125, cited in VULCANO, 1967: 16.9, CROSSKEY & HOWARD, 1997: 79, 2004: 78, and ADLER & CROSSKEY 2008: 96, 2009: 99.]

Trichodagmia ecuadoriensis ENDERLEIN, 1934b: 193. LECTOTYPE female, ECUADOR: Tambillo; 1895, (*S.Otto*) (NMHU) [Examined.] [Synonymy with *S. chalcocoma* by COSCARÓN, 1987: 38; synonymy and lectotype designation by HERNÁNDEZ & SHELLEY, 2005: 13.]

Simulium equadoriensis [Incorrect subsequent spelling by LEÓN & WYGODZINSKY, 1953: 28, cited by CROSSKEY & HOWARD, 1997: 79, 2004: 78; ADLER & CROSSKEY, 2008: 96, 2009: 99, 2010: 101.]

Simulium aequatoriense [Incorrect subsequent spelling by VARGAS, 1945b: 109, cited by CROSSKEY & HOWARD, 1997: 79, 2004: 78; ADLER & CROSSKEY, 2008: 96, 2009: 99, 2010: 101.]

Trichodagmia latitarsis ENDERLEIN, 1934a: 289. LECTOTYPE female, BOLIVIA: Mapiri, Lorenzopato; 28.iv.1903, [Without collector's name.] (NMHU) [Examined.] [Synonymy with *S. chalcocoma* by VARGAS & DÍAZ NÁJERA, 1953: 140; synonymy with *S. townsendi* and lectotype designation by HERNÁNDEZ & SHELLEY, 2005: 13.]

Simulium latitarsus [Incorrect subsequent spelling by VARGAS, 1945a: 154, cited by CROSSKEY & HOWARD, 1997: 79, 2004: 78; ADLER & CROSSKEY 2008: 96, 2009: 99.]

Trichodagmia strigata ENDERLEIN, 1934a: 290. LECTOTYPE female, PERU: Mamara; 3.1911, (*O. Garlepp*) (NMHU) [Examined.] [Lectotype designation by WERNER, 1996a: 251; synonymy by HERNÁNDEZ & SHELLEY, 2005: 13.]

Simulium (*Hemicnetha*) *muiscorum* BUENO *et al.*, 1979: 581. HOLOTYPE male, COLOMBIA: Municipio de La Calera, Departamento de Cundinamarca, Cordillera Oriental, Río Teusacá; [Without date or collector's name.] (ICNUC) [Synonymy with *S. townsendi* by HERNÁNDEZ & SHELLEY, 2005: 13; regarded as a valid species by COSCARÓN & COSCARÓN-ARIAS, 2007: 608 and COSCARÓN *et al.*, 2008: 49; recognized junior synonymy of *S. townsendi* by ADLER & CROSSKEY, 2008: 95, 2009: 99, 2010: 101; SHELLEY *et al.*, 2010: 64; and the current work.]

FEMALE. General body colour black. Body length (specimens pinned, one in spirit) 2.9-4.8 mm (mean= 3.6 mm, s.d. = 0.74, n = 4), wing length 3.1-3.4 mm (mean = 3.2 mm, s.d. = 0.16, n = 4), wing width 1.4-1.6 mm (mean = 1.5 mm, s.d. = 0.10, n = 4).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 206). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthpart parts black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and with teeth on central trough (Fig. 260).

Thorax: scutum black with evenly arranged, recumbent, yellowish setae; posterior margin with recumbent yellowish setae. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with pear-shaped, median and 1+1 submedian, wide silver pruinose vittae, beginning near anterior border of scutum and extending to posterior margin; humeri pale brown; lateral and posterior margins black (Figs. 346, 348). With posterior illumination, thorax black, with 1+1 silver-pruinose comma shaped vittae extending from anterior third of scutum to nearly mid region of thorax; humeri pale brown; lateral margins weakly pruinose; posterior margin black. (Figs. 347, 349). Scutellum dark brown with recumbent yellow hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length except on apical third, which is bare. Radius with numerous setae intermixed with distinct spines, basal section of radius with several rows of hairs. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 500. Fore leg with coxa, trochanter, femur, tibia and tarsal segments dark brown. Mid leg with coxa, apical half of trochanter, tibia, femur, apical two thirds of tarsal segment I, and tarsal segments II-IV dark brown; basal are of trochanter, tibiae, and external surface of femur basally whitish. Hind leg with coxa, ventral region of trochanter, trochanter, tibia, femur, apical half tibia and tarsal segment I, dark brown; anterio region of trochanter, basal half of tibiae and tarsal segment I white. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX black. Tergal plates well developed in pinned specimens examined. Sternites and genitalia black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly 1.5 times as long as length of eighth sternite at mid point, almost square nearly converging towards middle, membranous and densely covered with microtrichiae (Fig. 557). Cerci subrectangular covered with brown setae; paraproct long, subtriangular, nearly two and half times longer than cercus, sclerotised over entire surface with distinct projection at junction with cercus; cercus and paraproct densely covered with prominent brown hairs and few basal setae (Figs. 21, 616). Genital fork stout and sclerotised; termination of lateral arms with anterior margins straight and well developed; anterior processes well developed and blunt apically; posterior processes well developed (Fig. 676). Spermatheca globular, without external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal membranous.

MALE. General body colour dark brown to black. Body length (specimens pinned) 3.6 mm, wing length 3.1 mm, wing width 1.7 mm (n = 1)

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: [single specimen recovered from alcohol by SABROSKY'S method (1969)] scutum dark brown covered with recumbent whitish hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax dark brown with faint 1+1 silver pruinosities on antero-lateral margins; humeri, lateral and posterior margins dark brown (Fig. 765). With posterior illumination, thorax dark brown; humeri, lateral and posterior margins dark brown (Fig. 766). Scutellum brown with white, recumbent hairs interspersed with long, erect, dark brown setae on posterior margin. Postnotum brown with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergites II, VI, VII (best seen in some specimens when tilted and viewed laterally). Genitalia dark brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle spindle-shaped with dorsal and ventral margins sinuous, often terminating in single, stout spine [in some specimens subapical stout spine present]; gonocoxite and gonostyle covered with long setae (Fig. 861). Ventral plate weakly sclerotised, subrectangular, covered with long hair; main body with anterior median process and keel well developed; lateral shoulders slightly developed and basal arms well developed and subparallel (Fig. 922). Median sclerite long, about 2.5 times longer than wide at widest point, with apical incision extending to mid point of sclerite (Fig. 922). Paramere poorly with well developed and sclerotised basal process, without stout spines and numerous microspines on membrane (Fig. 983).

PUPA. Cocoon length dorsally 3.1-3.7 mm, ventrally 4.4-5.2 mm; pupa length 4.5-5.4 mm; gill length 1.5-1.8 mm (n = 2)

Cocoon: shoe-shaped as in Fig. 66, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: dark brown with 12 upwardly directed filaments arranged in bunch in vertical plane (Fig. 1044). Gill configuration with filament branching at different heights; main trunk short, giving rise to four sets of primary branches each with three secondary filaments (Fig. 1044). Filaments stout, pointed distally, with spicules encircling surface, edges crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 1+1 frontal and 1+1 facial small, simple trichomes (sometimes difficult to see). Frontoclypeus without visible trichomes in the few specimens examined [COSCARÓN & COSCARÓN-ARIAS (2007) stated that frontal and facial trichomes have 7-12 and 2-5 branches, respectively]; group of platelets mesally, 1+1 groups dorso-laterally and 4 platelets in groups of two laterally in frontal region, respectively; tubercles rounded densely and well distributed over entire surface.

Thorax: with no trichomes in the few specimens examined [COSCARÓN & COSCARÓN-ARIAS (2007) stated that 2-5 trichomes are present each with 3-5 branches]; tubercles mostly rounded densely and well distributed over entire surface.

Abdomen: abdominal tergite I with 1+1 sublateral, bifid, long trichomes and rounded tubercles densely distributed along posterior margin; tergite II with 4+4 submedian, spiniform setae in longitudinal row, and 1+1 small simple setae on lateral margins; tergites III, IV with 4+4 simple hooks in row along posterior margins; tergites V-IX without setae; tergite IX weakly sclerotised, without terminal spines. Spine combs distribution as follows: entire length of anterior margin of tergite II and 1+1 groups on antero-lateral margins of tergites III-IX. Sternites III-IV with 1+1 submedian, small simple setae; sternite V with 2+2 closed simple hooks in row on posterior margin, 1+1 bifid long trichomes anterior to outer hooks; tergites VI, VII with 2+2 well separated, simple hooks on posterior margin; sternites VIII, IX without setae. Spine combs on anterior margins of sternites III-IX.

LARVA (Final instar). Body length 7.9-8.8 mm (mean = 8.4 mm, s.d. = 0.33, n = 5); length of head capsule 0.7-0.9 mm mean (mean = 0.8 mm, s.d. = 0.10, n = 5); width of head capsule 0.7-0.8 mm (mean = 0.7 mm, s.d. = 0.04, n = 5). Body colour dark grey dorso-laterally, whitish ventrally (specimens fixed in alcohol). General body form as in Fig. 1098.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Small setae absent on all surfaces and head capsule not wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, rounded apically; postgenal bridge nearly one and half times length of hypostomium (Fig. 1149). Hypostomium strongly pigmented on anterior margin, with nine weakly developed apical teeth, evenly distributed on anterior margin; median tooth poorly developed and as long as sublateral teeth; 3+3 sublateral teeth; 1+1 poorly developed lateral tooth; 5+5 lateral serrations; 1+1 lines of approximately 11 hypostomial setae parallel to lateral margins; 1+1 long, bifid setae in posterior half of hypostomium (Fig. 1204). Sub-esophageal ganglion lightly pigmented. Antenna slightly longer than labral fan stalk, all segments light brown; length of antennal segments I-III excluding the sensillum 0.07-0.1:0.07-0.1:0.07-0.1 mm (n = 5). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately eight teeth, first four teeth more prominent than remainder; two mandibular serrations, anterior more prominent than posterior [sometimes posterior serration extremely reduced] (Fig. 1258). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 34-46 rays each with fine, single line of microspinules in a row (n = 5).

Thorax: greyish dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 28-31 process of 14-15 simple hooks (n = 5). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 12 filaments, all branching from common trunk.

Abdomen: usually grey dorsally and ventrally. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except towards region of anal sclerite. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 132-162 rows of 20-31 simple hooks (n = 5). Rectal gills with three branches having 57-67 small finger-like lobules (n = 4) [BUENO *et al.* (1979) stated that that the posterior circlet has 189-197 rows of 26 simple hooks, and the anal gill has three branches of 35, 11 and 35 finger-like lobules each.]

Taxonomic Discussion. The taxonomy of *S. townsendi* has been recently reviewed by HERNÁNDEZ & SHELLEY (2005), who designated two lectotypes for *Trichodagmia ecuadoriensis* and *T. latitarsis*, and considered the following species conspecific with *S. townsendi*: *S. chalcocoma*, *T. ecuadoriensis*, *T. latitarsis* and *S. muiscorum*. In addition, the authors also commented on the variation found in the thoracic pattern and the female paraproct in the latter four species, which they regarded as intraspecific (see Figs. 71-76 in HERNÁNDEZ & SHELLEY, 2005). COSCARÓN & COSCARÓN-ARIAS (2007) in their review of Neotropical Simuliidae accepted all the above synonymies except *S. muiscorum*, and this was also followed in his catalogue COSCARÓN *et al.* (2008). They stated that they considered *S. muiscorum* as a valid species only because "this species shows differences such as the large size and short paraproct". All synonymies in HERNÁNDEZ & SHELLEY (2005) were discussed in detail, and all morphological differences were fully illustrated using digital images based on the dissected type material and other specimens (see **Material Examined** in this publication). HERNÁNDEZ & SHELLEY (2005) also argued that the differences in the paraproct morphology could be due to the positioning of this structure on the slide. Their views have been followed in the most recent World Inventory of Blackflies by ADLER & CROSSKEY (2008, 2009, 2010) and more recently by SHELLEY *et al.* (2010). The latter have also been followed in the current work.

The female of *S. townsendi* is easily distinguished from other species of *Trichodagmia* recorded in Colombia, Peru and Ecuador by the black thorax with 1+1 median, pear-shaped and 1+1 submedian silver pruinose vittae (Figs. 346-349) [also see the female description of tthorax]. The males can be distinguished by the dark brown coloration of the thorax (Figs. 765, 766) and the shape of the ventral plate, which has the anterior margin produced centrally (Fig. 922).

The best character to distinguish pupae of *S. townsendi* is the configuration of the pupal gill, which have 12 upwardly directed filaments arranged in four primary branches (Fig. 1044). Species such as *S. guianense s.l.*, *S. hirtipupa* and *S. perplexum* also have a 12-filamented pupa, but they all can be identified by the different configuration of the pupal gill filaments in combination with link-reared adults (Figs. 1031, 1032, 1041).

The larva of *S. townsendi* has a dissected gill histoblast with 12 pointed, apically unsclerotised filaments, which it also shares with other species of the ORBITALE species group. However, *S. townsendi* may be separated from the other species by the reduced median tooth and the lateral teeth of the hypostomium (Figs. 1149, 1204). Larvae of this species may only be distinguished by the morphology of the filaments in the dissected gill histoblast in combination with the configuration of the pupal gill in link-reared adults collected in the same locality as mature larvae.

COSCARÓN & COSCARÓN-ARIAS (2007) placed *S. townsendi* [as *S. muiscorum* and *S. townsendi*] in the subgenus *Trichodagmia*, in which no species groups were recognized. In the latest revision of the World Inventory of Blackflies ADLER & CROSSKEY (2008, 2009, 2010) followed these authors. More recently, *S. muiscorum* has been placed by SHELLEY *et al.* (2010) in their ORBITALE species group, which has been followed in the current work.

Distribution. *Simulium townsendi* has been recorded from Bolivia, Colombia, Ecuador and Perú (ADLER & CROSSKEY, 2008, 2009, 2010; also see **Material Examined** in HERNÁNDEZ & SHELLEY (2005), and SHELLEY *et al.* (2010).

Biology and Medical Importance. BUENO *et al.* (1979) collected *S. townsendi* [as *S. muiscorum*] in relatively polluted rivers with high concentrations of organic matter. These authors stated that the larvae and pupae of *S. townsendi* are found attached to rocks or aquatic vegetation in torrential creeks of clear, cold water with rocky bottoms. They also stated that females bite cattle in Colombia.

2.5.2.16. *Simulium (Trichodagmia) wygodzinskyorum* COSCARÓN & PY-DANIEL (Figs. 207, 350, 351, 501, 558, 617, 677, 767, 768, 862, 923, 1045, 1150, 1205, 1259)

This is a poorly known species only recorded from Peru and Ecuador. The description here provided is based upon the examination of the type material, the original description of COSCARÓN & PY-DANIEL (1989) and identified specimens housed at the MLP and AMNH.

Simulium wygodzinskyorum COSCARÓN & PY-DANIEL, 1989: 318. HOLOTYPE female (reared), PERU: Junin, San Ramón, Estancia El Naranjal, 1000m; 20/27-vi.1965 (*P. & B.Wygodzinsky*) (AMNH) [Examined.]

FEMALE. General body colour dark brown. Body length (specimens pinned) [single specimen available already dissected], wing length 2.5 mm; wing width 1.1 mm].

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 207). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts parts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed and sclerotised cornuae, with minute teeth along anterior margin to base of cornuae.

Thorax: scutum dark reddish brown covered by irregularly arranged white, recumbent setae intermixed with black semi erect setae mainly on posterior margin. Scutal pattern varying slightly with illumination. With anterior illumination, thorax reddish brown, with 1+1 median, pear-shaped and 1+1 sublateral, wide silver pruinose bands extending from anterior to posterior margins; median line and 1+1 submedian dark brown bands extending from anterior margin to near posterior margin; humeri lightly brown; lateral and posterior margins dark brown to black (Fig. 350). With posterior illumination thorax, dark reddish brown with faint median line and 1+1 submedian bands; in the single specimen examined, the holotype, feint 1+1 silver pruinose bands can be seen on anterior margin; humeri silver pruinose; lateral and posterior margins dark brown (Fig. 351). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length. Radius with numerous setae intermixed with distinct spines apically, basal section of radius with setae. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 501 Front leg with coxa, trochanter, femur and tibia dark brown; tarsal segments black. Mid leg with coxa, trochanter, femur, basal two thirds of tibiae and tarsal segments brown. Hind leg with coxa, trochanter, apical third of tibiae, femur, apical half of tarsal segment I, and tarsal segment II-IV dark brown; basal two thirds of tibiae and tarsal segment I pale yellow. Hind leg claw with small basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites dark brown. Tergal plates developed. Sternites dark brown. Eighth sternite sclerotised with 6-10 long, irregularly distributed setae on posterior margin; gonapophyses membranous, subtriangular and rounded at apex, nearly half length of eighth sternite at mid point and densely covered with microtrichiae (Fig. 558). Cercus hemispherical, covered with brown setae; paraproct subrectangular and rounded apically, with small projection at junction with cercus; paraproct covered by long brown setae basally and microtrichiae distally (Fig. 617). Genital fork stout, sclerotised, termination of lateral arms with anterior margins curved and well developed; anterior processes well developed and blunt apically; posterior processes prominently developed (Fig. 677). Spermatheca globular, without external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour brown orange. Body length (specimen pinned, n = 1) 3.0 mm, wing length 2.7 mm, wing width 1.4 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum orange brown covered with recumbent whitish hairs. Thoracic pattern varying slightly with light incidence: with light anterior thorax brownish orange with 1+1 silver pruinose vittae extending from antero-lateral margins towards central region of thorax, dark brown line on central region extending from anterior to posterior margins; humeri, lateral and posterior margins brownish orange (Fig. 767). With posterior illumination thorax, humeri, lateral and posterior margins brownish orange (Fig. 768). Scutellum brown with golden, recumbent yellow hairs and long erect dark brown setae. Postnotum dark brown with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female though darker (COSCARÓN & PY-DANIEL, 1989).

Abdomen: tergites I-IV dark brown, tergite II with pruinosity on anterior margin; remaining tergites not examined [they had already been dissected in the single specimen examined]. Sternal plates developed. Gonocoxite quite damaged but apparently subquadrangular; gonostyle spindle-shaped, with sinuous margins and terminating in stout spine; gonocoxite and gonostyle covered with long setae (Fig. 862). Ventral plate strongly sclerotised, subrectangular; main body of ventral plate covered by small setae, with well developed shoulders; anterior median process prominently developed and basal arms well developed and subparallel (Fig. 923). Median sclerite not examined. Paramere with well developed and sclerotised basal processes and small teeth centrally and on membrane.

PUPA. Cocoon length dorsally 2.5-3.3 mm, ventrally 2.5-3.0 mm; gill length 1.0-1.2 mm [Other measurements not given in the original description, n = 1].

Cocoon: slipper-shaped as in Fig. 65, brown, composed of thick, coalesced fibres (appearing gelatinous) with reinforced rim to anterior aperture, margin of aperture elevated.

Gill: light brown with 12 upwardly directed filaments arranged in bunch in vertical plane. Gill configuration with filaments branching at different heights; main trunk short, giving rise to three sets of primary branches, one internal and two external: the more external consists of one dorsal branch with four secondary branches that bifurcate at different heights, and ventral branch with six filaments, arranged in two branches, one anterior with four filaments and one posterior with two filaments; the internal primary branch with only two filaments (Fig. 1045). Filaments stout, pointed and unsclerotised distally, covered with spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (frontoclypeus): with 2+2 frontal and 1+1 facial stout, simple trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups of eight platelets dorso-laterally and 2-4 platelets in groups of one or two laterally in frontal region; tubercles rounded, well distributed over entire surface.

Thorax: dorsal trichomes missing on the few specimens examined; tubercles rounded and densely distributed dorsally, with pointed tubercles on alar region.

Abdomen: several pupal abdominal segments were damaged in the few specimens examined, but the chaetotaxy in some of them is as follows: tergite II with 3+3 spiniform submedian setae on central region; tergite III without setae; tergites IV and V with 4+4 simple hooks along posterior margins. Sternite III without setae; sternite IV with 2+2 submedian simple hooks on posterior margin, 1+1 simple trichomes lateral to outermost hooks, 1+1 simple trichomes on sublateral margins; sternite V with 2+2 submedian simple closely together and 1+1 well spaced simple hooks along posterior margin, and 2+2 small simple trichomes anterior to innermost hooks; sternites VI-VIII with no visible trichomes or setae; sternite IX weakly sclerotised with 1+1 small terminal spines. Spine combs on anterior margins of sternites III-VIII, some well developed resembling teeth on sternite VIII.

LARVA (Penultimate instar). [I have been unable to obtain mature larvae of *S. wygodzinskyorum*. COSCARÓN & PY-DANIEL (1989) stated in their larval description of *S. wygodzinskyorum* that the material they have examined belonged to an immature larva, and hinted that they were not sure of their identification. I have examined this material on which I based the description provided here.] [Body length and head measurements were not given in original description].

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal bridge deep, bell-shaped, subtriangular and widest at mid point; postgenal bridge two and half times shorter than hypostomium (Fig. 1150). Hypostomium strongly pigmented on anterior margin, with nine apical teeth in central region; median tooth small and at same level of sublateral teeth; 3+3 sublateral teeth, with the pair adjacent to base of median tooth longer than remainder; 1+1 lateral teeth, more prominent than median and sublateral teeth; 2+2 small, lateral serrations; 1+1 lines of approximately seven hypostomial setae parallel to lateral margin; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1205). Sub-esophageal ganglion not examined. Antenna longer than labral fan stalk, apex of segment I, base of segment II and segment III whitish, remainder of antennal segments pale brown; length of antennal segments 1.0:1.4:1.0 mm. Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately 11 teeth, first four more prominent than remainder, two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1259). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with more 30-32 rays with fine teeth (n = 1).

Thorax: [colouration not given in original description]. Cuticle chaetotaxy not described in original description. Proleg with plate heavily sclerotised with 6 groups of teeth of 3-5 each (n = 1). Form and configuration of gill histoblast not given in original description.

Abdomen: [coloration of abdomen, ventral nerve cord and ventral papillae not given in original description]. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly, no sclerotised areas between arms. Posterior circlet with 185 rows of 25-28 simple hooks (n = 1). Rectal gills with three lobes each having 16 secondary finger-like lobuless (n = 1).

Taxonomic Discussion. *Simulium wygodzinskyorum* was described by COSCARÓN & PY-DANIEL (1989) based on one female holotype, two males, and several pupal exuviae and larvae [all as paratypes] collected from San Ramón, Estancia El Naranjal, Peru by P. & B. Wygodzinsky. I have examined the female holotype, which is deposited at the AMNH. The holotype is in relatively good condition. It has been glued to a card point on the right side. Its head, abdomen, genitalia and one hind leg are on a small triangular plastic card attached to the same pin; the pupa has been glued to another card point and it is attached to the same pin together with the adult. I have also examined a male labelled as allotype and a pharate male deposited at AMNH and MLP, respectively (**Material Examined**).

In Argentina, the female of *S. wygodzinskyorum* cannot be externally separated from that of *S. lahillei* and *S. huairayacu* because the thorax is relatively reddish brown with 1+1 pear-shape median and 1+1 submedian silver pruinose bands extending from anterior to posterior margins [light source anterior] (Figs. 350, 351). The male of *S. wygodzinskyorum* can be readily distinguished from the latter two species by the darker brown thorax with 1+1 silver pruinose bands that extend from the antero-lateral margins reaching the central region of the thorax [light source posterior] (Fig. 767). In *S. huairayacu* the thorax is completely black (Fig. 746) and in *S. lahillei* the thorax is dark brown with 1+1 small rounded silver spots on the anterior third of thorax [with light posterior] (Fig. 751).

The best character to separate *S. wygodzinskyorum* from *S. lahillei* and *S. huairayacu* is the configuration of pupal gill filaments (Figs. 1033, 1036, 1045). The pupal gill configuration of *S. wygodzinskyorum* is most similar to that of *S. sumapazense* (Fig. 1043), but it may be readily identified by the gill filaments being stouter basally, and the presence of round and densely distributed tubercles on the entire surface of the frontoclypeus and thorax of the pupa (also see **Taxonomic Discussion** under *S. sumapazense*).

The larva of *S. wygodzinskyorum* still remains poorly described; hence it cannot be readily separated from other morphologically related species in the subgenus *Trichodagmia*, *e.g. S. sumapazense*.

Simulium wygodzinskyorum was originally placed in the subgenus *Grenieriella* by COSCARÓN & PY-DANIEL (1989), but it has been allotted to the subgenus *Trichodagmia* by CROSSKEY & HOWARD (1997, 2004) and COSCARÓN & COSCARÓN-ARIAS (2007). More recently, ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010) placed *S. wygodzinskyorum* in the ORBITALE species group within the subgenus *Trichodagmia*.

Distribution. *Simulium wygodzinskyorum* has only been recorded from Ecuador and Perú (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; COSCARÓN-ARIAS, 2003; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. The biology of *S. wygodzinskyorum* is poorly known. The immature stages were collected at an altitude of 1000 m by COSCARÓN & PY-DANIEL (1989). Nothing is known about the female's feeding behaviour.

2.5.3. The PICTIPES Species Group.

This species group only contains three species as recognized by ADLER *et al.* (2004), ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010).

Diagnosis.

Female: Scutum black usually with pattern (Figs. 352-361). Nudiocular triangle developed (Figs. 208-210). Cibarium unarmed (Figs. 261-263). Sc and basal section of Radius with or without setae. Claws without basal tooth. Gonapophyses subquadrangular, well separated centrally, membranous to weakly unsclerotised and covered with microtrichiae (Figs. 36, 559-561). Paraproct subtriangular or subrectangular, two times longer than cercus, setose and with hairs, sclerotised, rounded apically (Figs. 22-23, 617-620). Genital fork sclerotised, with well developed basal arms and developed anterior and inner posterior processes (Figs. 677-680).

Male: Scutum black, with or without pattern (Figs. 767-776). Gonocoxite subquadrangular, wider than long, with external antero-lateral margin prominently expanded (Figs. 45, 862-865). Gonostyle elongate, nearly four times longer than gonocoxite, with distinct basal ridge and without stout apical spine [in some specimens subterminal spiniform setae can be seen at higher magnification] (Figs. 45, 862-865). Ventral plate sclerotised, with deep central incision extending to beyond mid point giving appearance of bilobed structure; lateral shoulders absent; basal arms subparallel (Figs. 55, 923-926). Parameres with basal plates developed and with distinct spines centrally (Figs. 63, 984-986).

Pupa: Cocoon boot-shaped, without fenestrations (Fig. 67). Pupa with nine gill filaments, arranged in circular manner, often with two filaments of internal branch directed back towards the pupal thorax; filaments with rounded tips (Figs. 82, 1045-1048). Gill filaments with tuberculate sculptures, except in *S. claricentrum*. Trichomes simple; tubercles rounded, well distributed in facial region of frontoclypeus and pupal thorax.

Larva: There are no clear cut diagnostic characters for the larvae of species in the PICTIPES species group. The larvae have to be examined in combination with link-reared adults and pupal exuviae collected in the same locality. In general, larvae in this group have the postgenal cleft bell-shaped, deep and triangular apically (Figs. 1151-1153). Hypostomium with seven to nine teeth evenly distributed along anterior margin (Figs. 1206-1208), often with median tooth most developed, sometimes with intermediate teeth between sublateral teeth. Mandible with mandibular comb with nine to eleven teeth and two mandibular serrations (Figs. 1260-1262). Abdominal integument without setae. Posterior arms of anal sclerite never encircling the posterior circlet.

2.5.3.1. ***Simulium (Trichodagmia) claricentrum*** **ADLER** (Figs. 22, 36, 208, 261, 352, 353, 502, 559, 618, 678, 769, 770, 863, 924, 984, 1046, 1099, 1151, 1206, 1260)

This is a well-known species only recorded from the USA. The description here provided has been derived from the original description (ADLER, 1990), examination of type material and specimens identified by P.H.ADLER housed at the CUAC and BMNH.

Simulium claricentrum ADLER, 1990: 437. HOLOTYPE male (reared), USA: Pennsylvania, Sixteen Creek, Junction of Washington Street & Shadduck Road, Northeast (town), Erie Co., 42°11'N79°50'W; 10.x.1998, (*P.H.Adler & C.R.L.Adler*) (NMNH) [Examined.]

FEMALE. General body black. Body length (specimens pinned, n = 3) 3.0-3.7 mm, wing length 2.9-3.2 mm, wing width 1.5-1.6 mm.

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 208). Frons, clypeus and occiput brown, with silvery grey pruinosity; clypeus covered with pale, semi-recumbent setae and frons with erect, dark brown hairs. Mouthparts dark brown to black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae without teeth (Fig. 261).

Thorax: scutum black, largely pruinose covered by semirecumbent white hairs; dark brown with faint grey pruinosity and evenly arranged recumbent, whitish setae; posterior margin with semi erect white hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax largely silver pruinose, with 1+1 fine, X-shaped black vittae extending from anterior to posterior margins of thorax, and one fine, median, weakly brown line extending from anterior to posterior margins; sometimes 1+1 rounded vittae on postero-lateral margins can be seen in well preserved specimens; humeri, part of lateral margin, and posterior margin pruinose (Fig. 352). With posterior illumination, the pattern reverses with all pruinose areas becoming black and 1+1 rounded silver pruinose spots on anterior third of scutum can be seen (Fig. 353); humeri faintly paler brown; lateral and posterior margins black. Scutellum black with semi-erect white hairs intermixed with long, brown bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta with four to five setae at mid length in the specimen examined. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 502. Fore leg with coxa, trochanter, femur, tibia and tarsal segments black. Mid and hind legs with trochanters, basal half of femur and tarsal segment I brownish; remainder of legs black. Claws moderately curved without distinct basal tooth. Halteres cream with brown base.

Abdomen: tergites I-III dark brown to velvet black, VI-IX shiny black. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with long setae on posterior margin; gonapophyses small, half length of eight sternite at mid point, weakly sclerotised in central border and interspersed with microtrichiae (Fig. 559). Cercus subrectangular, about twice as broad as long, with posterior margin straight and corners rounded; paraproct subrectangular with ventral margin rounded and long dorsal finger-like extension (Fig. 618). Genital fork stout and heavily sclerotised, stem expanded anteriorly; anterior process weakly developed; posterior process well developed anterior processes on lateral arms (Fig. 678). Spermatheca subspherical, with cuticular microspines; area of insertion of spermathecal duct membranous.

MALE. General body colour similar to female. Body length (specimens pinned, n = 2) 2.7-3.0 mm, wing length 2.3-2.4 mm, wing width 1.2-1.4 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered with golden, recumbent hairs. Scutal pattern varies slightly with light incidence. With light anterior, thorax black with 1+1 triangular, silver pruinose vittae on anterior third of scutum (Fig. 769). With light posterior, thorax black (Fig. 770). Humeri, lateral and posterior margins of scutum black. Scutellum brown with golden, recumbent hairs and long, erect dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female except Sc without setae.

Abdomen: tergites black, basal fringe with long, brown hairs. Silver pruinose ornamentation on antero-lateral margins of tergite II [best seen when specimens tilted laterally]. Genitalia black; tergal plates developed; sternal plate undeveloped. Gonocoxite subquadrangular; gonostyle nearly four times longer than gonocoxite, elongate without terminal spine (Fig. 863). Ventral plate broadly subrectangular with prominent cleft centrally; main body without shoulders, but with two lobes relatively less developed than in *S. pictipes*, ventral margin of ventral plate weakly acuminate centrally; basal arms sclerotised, subparallel, weakly curving inwards (Fig. 924). Median sclerite very long, about 3.5 times longer than wide at widest point, Y-shaped without apical incision (Fig. 924). Paramere with well developed and sclerotised basal processes and numerous spines, central membrane with spines (Fig. 984).

PUPA. Cocoon length dorsally 3.6–5.1 mm (mean = 4.3, s.d. = 0.48, n = 10); ventrally 4.5-5.6 mm (mean = 5.2 mm, s.d. = 0.32, n = 10); pupa length 3.1-5.6 mm (mean = 4.4 mm, s.d. = 0.70, n = 10); gill length 1.4-3.8 mm (mean = 2.0 mm, s.d. = 0.69, n = 10).

Cocoon: boot-shaped as in Fig. 67, light to dark brown composed of thick open fibres resembling loops, with reinforced rim to anterior aperture, margin of aperture weakly elevated with fenestrations.

Gill: light brown with nine upwardly-directed filaments arranged in bunch in vertical plane. Gill configuration variable with filaments branching at different heights (Fig. 1046); main trunk short, giving rise to four pairs of primary branches plus single filament that curves ventrolaterally and often wraps around frontoclypeus; primary branches widened basally. Filaments thin, weakly tapered, not covered with small tubercles, edges weakly crenate; ventral filaments sometimes longer than dorsal filaments.

Head (frontoclypeus): with 1+1 frontal and 1+1 facial simple long trichomes; frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and six platelets in two groups laterally in frontal region, respectively; tubercles rounded and densely distributed over entire surface.

Thorax: with 2+2 long simple trichome on dorsal cleft, 2+2 simple small trichomes on central region, 1+1 long simple trichome on posterior region, and 2+2 long simple trichomes on ventral margin of alar region; thorax with rounded tubercles well distributed over entire surface, few pointed tubercles on dorsal cleft posteriorly.

Abdomen: chaetatoaxy similar to that of *S. innoxium*: tergite I with 1+1 setae; tergite II with 4+4 stout submedian spines in longitudinal row and 3+3 simple, short median setae, and three simple setae laterally to outermost median setae; tergites III, IV with 4+4 submedian spines in longitudinal row, two small simple setae anterior and between outermost hooks, and 3-4 small, simple setae laterally; tergites V-VII bare or with one small seta each; tergite VIII with 3-6 hook-like setae along posterior margin and 2+2 small setae laterally; tergite IX with 1+1 terminal spines. Spine combs on anterior margins of tergites VIII, IX. Sternite III with 1+1 median, 2+2 submedian and 1+1 lateral long simple setae; sternites IV, V with 2+2 close simple hooks, 2+2 long spiniform setae lateral to outermost simple hooks, and 1+1 long spiniform setae on lateral margins; sternites VI, VII with 2+2 well separated simple or bifid hooks in row on posterior margins, 1+1 or 2+2 long simple setae mesally, 1+1 long simple, setae between outermost hooks, and 1+1 long simple setae on lateral margins; sternite VIII sclerotised with 1+1 long simple setae laterally, sternite IX sclerotised, without visible setae or trichomes. Spine combs on antero-lateral region of sternites III-VIII.

LARVA (Last instar). Body length 7.0-8.8 mm (mean = 7.8 mm, s.d. = 0.78, n = 5); length of head capsule 1.0-1.2 mm (mean = 1.1. mm, s.d. = 0.07, n = 10); width of head capsule 0.7-0.8 (mean = 0.7 mm, s.d. = 0.04, n = 10). Body colour piebald dorso-laterally, whitish ventrally in some segments (specimens fixed in alcohol). General body form as in Fig. 1099.

Head: pale to dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, broader at mid point and rounded apically; postgenal bridge nearly as long as hypostomium (Fig. 1151). Hypostomium strongly pigmented on anterior margin, with seven apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 2+2 sublateral teeth; 1+1 lateral tooth, nearly same height as sublateral teeth; 3-4 lateral serrations; 1+1 lines of nine hypostomial setae parallel to lateral margins; 1+1 or 2+2 long simple setae on posterior half of hypostomium (Fig. 1206). Sub-esophageal ganglion darkly pigmented. Antennal segments longer than labral fan stalk; segments I-II pale brown dorsally, III brown; length of antennal segments I-III excluding the sensillum 0.09-0.1:0.1:0.06-0.1 mm (n = 5). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately eleven teeth, first two more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1260). Lateral mandibular process absent. Maxillary palps heavily pigmented, one and a half times as long as wide at base. Labral fans with 50-61 rays (n = 5) each with row of fine, single line of spines interspersed with small spinules.

Thorax: reddish brown and whitish ventrally. Cuticle with short, multibranched, dark brown setae. Proleg with plate heavily sclerotised with band of approximately 25-39 sclerotised processes of 14 simple hooks (n = 3) [ADLER (1990) stated the presence of 61-64 processes (n = 5)]. Pupal respiratory gill histoblast dark brown; dissected gill histoblast with nine filaments.

Abdomen: usually piebald, progressively paler ventrally, especially towards posterior segments. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 80-100 rows of 26-31 simple hooks (n = 5). Rectal gills not everted in all specimens examined [ADLER (1990) examined larvae with three-lobed rectal gills].

Taxonomic Discussion. *Simulium claricentrum* was described by ADLER (1990) based on females, males, pupae and larvae collected in the state of Pennsylvania, USA. The taxonomy of this species has been recently reviewed by ADLER *et al.* (2004), who also discussed its cytology, biology, distribution and medical importance in North America. I have examined the male holotype of *S. claricentrum*, which is housed at the NMNH Simuliidae collection. The specimen has been pinned by the right pleuron and it is in good condition; its pupal exuviae and a larval head are stored in a microvial containing glycerine attached to the pinned adult (**Material Examined**). In addition, I have also examined numerous pinned, link-reared adults (all labelled as paratypes) in combination with numerous identified specimens housed in BMNH, CNC and NMNH (see **Material Examined**).

The females of *S. claricentrum* are externally indistinguishable from those of *S. pictipes* and *S. innoxium*. The females of these species have distinct 2+2 median and 2+2 submedian silver pruinose vittae on the scutum (see Figs. 352-361). They can only separated by the number and configuration pattern of the pupal gill filaments. The male also externally resembles that of *S. pictipes*, but they can be distinguished by the morphology of the ventral plate. In *S. claricentrum* the main body of the ventral plate does not have shoulders, the two lateral lobes are relatively less prominently developed than in *S. pictipes*, and the ventral margin of the ventral plate is weakly acuminate centrally (Fig. 924). In *S. pictipes*, the ventral plate has the two lateral lobes prominently developed and the ventral margin is straight (Fig. 926).

The pupa of *S. claricentrum* can be separated from the other species in the PICTIPES species-group by the median and ventral branches being relatively wider basally (Fig. 1046) and the lack of tuberculate sculptures in the basal third to fourth of each gill filament (ADLER, 1990; ADLER *et al.*, 2004).

The dissected gill histoblast of the larva of *S. claricentrum* has nine gill filaments, which it also shares with *S. pictipes* and *S. innoxium*. ADLER (1990) stated that the larva of *S. claricentrum* can only be distinguished by the piebald pigmentation of the body and the paler head capsule. The larva of *S. pictipes* and *S. innoxium* have a dark grey general coloration, but the head capsule in *S. pictipes* is a darker brown in the region of the cephalic apotome. In *S. innoxium* the head is strongly darker brown over its entire surface [see Figs. 1099, 1100, 1101 for coloration pattern].

The cytology of *S. claricentrum* has been studied by ADLER (1990) and further reviewed in ADLER *et al.* (2004). The latter authors stated that this species can be chromosomally separated from *S. pictipes* by the presence of well-defined centromere bands. BEDO (1975) identified specimens as *S. pictipes* cytoform "A" and POST (1982b) found a sex-linked inversion (3L-3) in populations of this cytoform. ADLER *et al.* (2004) established that the latter cytoform corresponds to *S. claricentrum.*

Descriptions and illustrations of life stages of *S. claricentrum* may be found in ADLER (1990) and ADLER *et al.* (2004).

ADLER *et al.* (2004) placed *S. claricentrum* in the PICTIPES species group of the subgenus *Hemicnetha*, which has been followed in ADLER & CROSSKEY (2008, 2009, 2010). More recently, SHELLEY *et al.* (2010) subsumed the subgenus *Hemicnetha* under *Trichodagmia* and recognized the PICTIPES group within this subgenus, where *S. claricentrum* is now placed.

Distribution. *Simulium claricentrum* ranges from the southern shores of Lake Erie southwest into Oklahoma in the USA. It has only been recorded in this country from the states of Arkansas, Pennsylvania, Missouri, New York, Oklahoma, and Tennessee (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. Larvae and pupae of *S. claricentrum* form aggregate in moss-like clumps in swift, smooth bottomed streams of shale, siltstone, or travertine, with small cascades (ADLER *et al.*, 2004). The latter authors collected larvae in less than 10 cm beneath the water flows in streams 10-20 m wide with 10-19ºC water temperature, and stated that the larval drift peaks during the night. ADLER *et al.* (2004) also stated that larvae hatch in about four days. In the southern half of the range of its distribution larvae of *S. claricentrum* overwinter as eggs in Pennsylvania, and four generations are produced in Arkansas. In Oklahoma, larvae and pupae can be found all year round, but adults do not oviposit from about November to March.

The females and males of *S. claricentrum* form swarms downstream during mating, with coupled pairs falling to the ground where copulation occurs for only seconds. The females are thought to be mammophilic, although no records exist. It does not pester humans (ADLER *et al.*, 2004).

ADLER *et al.* (2004) recorded infection in larvae with the microsporidian *Polydispyrenia simulii* (LUTZ & SPLENDORE) and the fungi *Genistellospora homothallica* LICHTWARDT and *Harpellela melusinae* LÉGER & DUBOSCQ-C.

2.5.3.2. ***Simulium* (*Trichodagmia*) *innoxium*** **COMSTOCK & COMSTOCK** (Figs. 209, 262, 354-357, 503, 560, 619, 679, 771, 772, 864, 925, 985, 1047, 1100, 1152, 1207, 1261)

This is a North American species recently resurrected from synonymy with *S. pictipes* by ADLER *et al.* (2004). A pest species of horses and cattle that sometimes attack humans in the USA.

Simulium innoxium COMSTOCK & COMSTOCK, 1895: 452. NEOTYPE male, UNITED STATES OF AMERICA: New York State, Tompkins Co., Ithaca, Fall Creek; 1.vii.1886, [Collector's name unknown.] (CU) [Neotype designation by ADLER *et al.*, 2004: 375.]

Schoenbaueria aldrichiana ENDERLEIN, 1936: 120. HOLOTYPE female, UNITED STATES OF AMERICA: New York State, Tompkins Co., Ithaca, Fall Creek; 18.vii.1928, (*G.Enderlein*) (ZMHU) [Synonymised with *S. innoxium* by STONE, 1964: 42.] [Examined.]

FEMALE. General body colour black. Body length (specimens in spirit) 3.3-4.5 mm (mean = 4.0 mm, s.d. = 0.25, n = 10), wing length 2.9-3.5 mm (mean = 3.2 mm, s.d. = 0.19, n = 10), wing width 1.1-1.9 mm (mean= 1.5 mm, s.d. = 0.30, n = 10).

Head: dichoptic with dark red eyes and nudiocular area developed (Fig. 209). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-erect brown hairs. Mouthparts dark black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae, with minute teeth at base (only visible at higher magnification) (Fig. 262).

Thorax: scutum black evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent dark setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with 1+1 median, pear-shaped and 1+1 submedian, wide, silver pruinose bands, all band with a darker brown tinge centrally; humeri and posterior margin silver pruinose, lateral margins black (Figs. 354, 356) With posterior illumination, thorax black with 1+1 sub triangular, silver pruinose cunae on anterior third of scutum; humeri, weakly pruinose; lateral and posterior margins back (Figs. 355, 357). Scutellum black with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae. Radius with numerous setae intermixed with distinct spines, basal section of radius without hairs in all specimens examined. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 503. Fore leg with coxa, trochanter, femur, tibia and tarsal segments dark brown to black. Mid leg with coxa, trochanter, femur, tibia and tarsal segment dark brown. Hind leg with coxa, ventral surface of trochanter, femur, tibia, apical half of tarsal segment I, and tarsal segment II-IV dark brown; remainder of trochanter paly brown, basal half of tarsal segment I white. Hind leg claw without basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX black, with tergite II having prominent silver bands laterally. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses half length of eighth sternite at mid point, well separated centrally and broadly almost square, membranous basally and sclerotised towards apex, gonapophyses sparsely covered with microtrichiae (Fig. 560). Cercus subrectangular, sclerotised, covered with brown setae; paraproct extending beyond cercus by length of cercus, subtriangular, sclerotised with small membranous tail at junction with cercus; paraproct densely covered with brown hairs (Fig. 619). Genital fork stout and sclerotised; termination of lateral arms with anterior margins straight and well developed; anterior processes well developed and blunt apically; posterior processes developed (Fig. 679). Spermatheca globular, without external sculpturing and apparently without internal spicules; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens in spirit, n = 2) 3.8 mm, wing length 2.8-2.9 mm, wing width 1.4-1.5 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered with irregular golden recumbent hairs; posterior margin covered with recumbent golden setae interspersed with black hairs. Scutal pattern varies slightly with light incidence: with light anterior, thorax black with 1+1 subrectangular silver pruinose cunae extending from antero-lateral margins to central region of thorax; humeri silver pruinose; lateral and posterior margins black (Fig. 771). With posterior illumination, thorax black; humeri and lateral margins faintly pruinose; posterior margin black (Fig. 772). Scutellum black with golden, recumbent hairs and long, erect, dark brown setae on posterior margin. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Sc bare in the two specimens examined. Leg coloration as in female.

Abdomen: tergites black with silver pruinosities on antero-lateral margins of tergites II, V, VI [best seen if specimens are tilted dorso-laterally], basal fringe with long, brown hairs. Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle elongated, 2.5 times longer than gonocoxite, with prominent basal process; gonocoxite and gonostyle covered with long setae (Fig. 864). Ventral plate sclerotised, broadly subrectangular, prominently cleft in dorsal region, without shoulders; basal arms developed and subparallel (Fig. 925). Median sclerite long, about 2.5 times longer than wide at widest point, without apical incision (Fig. 925). Paramere with well developed and sclerotised basal processes and numerous long spines centrally; internal membrane covered with numerous fine spinules (Fig. 985).

PUPA. Cocoon length dorsally 5.6-6.4 mm (mean = 5.9 mm, s.d = 0.29, n = 5), ventrally 6.1-8.4 mm (mean = 7.1 mm, s.d. = 0.75, n = 5); pupa length 3.9-5.8 mm (mean = 5.0 mm, s.d. = 0.72, n = 5); gill length 1.8-2.6 mm (mean = 2.1 mm, s.d. = 0.31, n = 5).

Cocoon: shoe-shaped as in Fig. 67, brown, composed of thick fibres arranged in broad loops with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: pale with nine swollen filaments forwardly directed filaments in vertical plane (Fig. 1047). Gill configuration with main trunk short giving rise to two primary branches, one internal and one external. External branch with four secondary filaments, sometimes with most ventral directed towards and around frontal region of pupa. Internal branch with two branches, one dorsal and one ventral of three and two secondary filaments, respectively. In all specimens examined the third filament of the dorsal branch is directed backward towards the dorsal region of the thorax (Fig. 1047). Filaments stout, rounded distally, without spicules on surface with numerous ridges and crevices, edges weakly crenate; sometimes filaments of external primary branch longer than remaining filaments.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial long simple trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 4-5 platelets in two groups laterally in frontal region; tubercles rounded and well distributed over entire surface.

Thorax: with 1-2 simple trichomes near margin of dorsal cleft and one long simple trichome on central region, tubercles rounded and densely distributed over entire surface.

Abdomen: abdominal tergite I with 1+1 simple, long median setae, 1+1 long, simple, submedian setae, and 1+1 long setae on lateral margin, all tergites covered with well distributed pointed and rounded tubercles over entire surface, tergite covered with small pointed tubercles, especially on lateral region; tergite II with 4+4 submedian spiniform setae in longitudinal row mesally, sometimes one long simple seta between outermost spiniform setae or one long bifid setae antero-lateral to outermost setae, and 1+1 spiniform setae on lateral margins, tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, long setae anterior to outermost hooks; tergites V-VII with 1+1 long submedian simple setae and 1+1 long simple setae on lateral margins; tergite VIII with 1+1 long simple setae laterally; tergite IX sclerotised terminating in 1+1 apical spines. Spine combs on antero-lateral region of tergites VI-VIII. Sternite III with 1+1 median, 2+2 submedian and 1+1 lateral long simple setae; sternites IV, V with 2+2 close simple hooks, 2+2 long spiniform setae lateral to outermost simple hooks, and 1+1 long spiniform setae on lateral margins; sternites VI, VII with 2+2 well separated simple or bifid hooks in row on posterior margins, 1+1 or 2+2 long simple setae mesally, 1+1 long simple, setae between outermost hooks, and 1+1 long simple setae on lateral margins; sternite VIII sclerotised with 1+1 long simple setae laterally; sternite IX sclerotised, without visible setae or trichomes. Spine combs on antero-lateral regions of sternites III-VIII.

LARVA (Final instar). Body length 10.3-13.4 mm (mean = 11.5 mm, s.d. = 1.2, n = 5), length of head capsule 0.8-1.1 mm (mean = 0.9 mm, s.d. = 0.10, n = 5); width of head capsule 0.7-1.0 mm (mean = 0.8 mm, s.d. = 0.10, n = 5). Body colour dark grey (specimens preserved in alcohol). General body form as in Fig. 1100.

Head: mainly dark brown, anterior region of cephalic apotome yellow. Numerous small setae present on all surfaces and head capsule weakly wrinkled. Head pattern positive. Cervical sclerites elongated, weakly free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Fig. 1152). Hypostomium strongly pigmented on anterior margin, with 7-8 teeth apical teeth distributed along anterior margin; median tooth sharp, well developed and more prominent than remainder teeth; 2+2 or 3+3 small, sublateral teeth; 1+1 lateral teeth same height as sublateral teeth; approximately 11+11 small lateral serrations; 1+1 lines of approximately 13-14 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1207). Sub-esophageal ganglion lightly pigmented. Antenna smaller than labral fan stalk, all antennal segments dark brown segment I, length of antennal segments I-III excluding the sensillum 0.08-0.1:0.1:0.09-0.1 mm (n = 4). Mandible with three apical teeth, second tooth smaller than first and third; mandibular comb with fourteen teeth, first four teeth more prominent than remainder teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1261). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 44-54 rays (n = 5) each with fine, single line of spines in a row interspersed with smaller spinules.

Thorax: dark grey. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 26-40 sclerotised processes of 12-15 simple hooks (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with nine filaments.

Abdomen: usually dark grey dorsally. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 97-113 row of sclerotised processes of 21-31 simple hooks (n = 5). Rectal gills with three lobes of 6-7, 7-14 and 12 finger-like lobules in each branch, some lobules wider than remainder (n = 2).

Taxonomic Discussion. ADLER *et al.* (2004) discussed in detail the taxonomic problems surrounding *S. innoxium* and *S. pictipes*, and also all the misidentifications involving the former species. These authors applied the name *S. innoxium* [erected by COMSTOCK & COMSTOCK in 1895] to all the specimens previously identified by other authors as *S. pictipes* from New York. In addition, they also designated a neotype collected from New York, which is deposited at CU. However, I have not been able to examine this material.

ENDERLEIN (1936) described the species *Schoenbaueria aldrichiana* based on a pinned female holotype collected in New York. The latter name was first treated as a synonym of *S. innoxium* by STONE (1964) without further explanation, and this has been followed by most authorities (*e.g.* ADLER *et* *al*., 2004; ADLER & CROSSKEY, 2008, 2009, 2010). I have examined the pinned female holotype of *S. aldrichiana*, which is housed at the ZMHU (see **Material Examined**). The specimen is in relatively good condition. It has been micropinned through the katespisternum and the end of the micropin is visible in the posterior region of the thorax; one leg is missing while one wing is fairly damaged. Another wing is mounted on a micro slide. Both the pinned adult and the micro slide bear a label in ENDERLEIN'S handwriting "*Schoenbaueria aldrichiana* Type". I have taken digital images of its thoracic pattern, wing and abdomen, which are now stored in the Simuliidae Digital Image Archive at the BMNH. I have studied the original description of *S. aldrichiana* by ENDERLEIN (1936), and compared it with the general morphology of *S. innoxium*. The thoracic pattern (Figs. 356, 357) and the general morphology and leg coloration of *S. aldrichiana* fall within the variation found in *S. innoxium*, though it is also similar to that of *S. claricentrum* and *S. pictipes* (Figs. 352, 353, 358, 359). However, in the absence of the pupal exuviae of *S. aldrichiana*, I agree with STONES' (1964) synonymy for taxonomic stability.

The female and male thoracic pattern of *S. innoxium* is similar to that of *S. pictipes* from which it cannot be easily distinguished based on their external morphology (Figs. 352-355, 358, 359). The best character to distinguish *S. innoxium* from *S. pictipes* and *S. claricentrum* within the PICTIPES species group is the configuration of the pupal gill filaments. In *S. innoxium* the third dorsal branch of the internal primary branch curves at mid point and it is directed toward the dorsal region of the pupal thorax (Fig. 1047). In *S. pictipes* and *S. claricentrum* the pupal gill filaments have a different configuration (Figs. 82, 1046, 1048) [see **Taxonomic Discussion** under *S. pictipes*].

The larva of *S. innoxium* cannot be easily separated from those of *S. pictipes* without examination of link-reared adults and pupae collected in the same locality.

The cytology of *S. innoxium* was studied by BEDO (1975), who identified specimens as the cytoform *S. pictipes* "B". ADLER *et al.* (2004) agreed that the latter cytoform corresponds to *S. innoxium*.

Simulium innoxium was placed in the PICTIPES species group of the subgenus *Hemicnetha* by ADLER *et al.* (2004). The latter taxonomic arrangement has been accepted by ADLER & CROSSKEY (2008, 2009, 2010). More recently, SHELLEY *et al.* (2010) synonymised the subgenus *Hemicnetha* with *Trichodagmia* and recognized the PICTIPES species group, where *S. innoxium* is now placed.

Distribution. *Simulium innoxium* is widely distributed around the Great Lakes, and southwards to Alabama and Missouri being most common in the Appalachian highlands (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. The biology, economic importance, hosts and cytology of *S. innoxium* have been reviewed by ADLER *et al.* (2004). Larvae and pupae of *Simulium innoxium* form moss-like clusters and carpets on the crest and surfaces of waterfalls and dams, and on boulders or flat sedimentary rocks in swift rivers. Larvae have been found at water temperatures of 30°C. The females are anautogenous with an average fecundity of 188 to more than 200 eggs per ovarian cycles. The males form swarms at about 2 m above the water, but settle later close to the surface above the pupal beds.

The females of *S. innoxium* can be pests of horses and cattle as they feed on their ears, sometimes repelling other species. They have also been taken from the ears of mules. *Simulium innoxium* can be attracted to humans, although only two such records have been documented. They also serve as surrogate vectors of the bovine parasite *Onchocerca linealis* and the human parasite *O. volvulus*, and are poor experimental hosts of *Leucocytozoon smithi* (LAVERN &LUCET) (ADLER *et al*., 2004).

Larvae of *S. innoxium* occasionally contain infections of the fungus *Coelomycidium simulii* DEBAIS and the microsporidian *Polydispyrenia simulii* (LUTZ & SPELDORE). Trichomycete fungi in the larval gut often infect 100 % of the population. Other Trichomycete species such as *Genistellospora homothallica* LICHWARDT, *Pennela* nr. *hovassi* and *Simuliomyces microsporus* LICHWARDT have been found in the larval hindgut (ADLER *et al*., 2004), as well as protists such as *Paramoebidium chattoni* (LUGER & DUBOSCQ), *P. curvum* LICHWARDT and an unidentified species of *Paramoebidium*.

2.5.3.3. *Simulium (Trichodagmia) pictipes* HAGEN (Figs. 23, 45, 55, 63, 67, 82, 210, 263, 358-361, 504, 561, 620, 680, 773-776, 865, 926, 986, 1048, 1101, 1153, 1208, 1262)

This is a zoophilic North American species, which has been recently reviewed by ADLER *et al.* (2004).

Simulium pictipes HAGEN, 1880: 305. SYNTYPES [27 pupae with cocoons (one pharate female, four pharate males), 24 exuviae with cocoons, eight empty cocoons, six pupal exuviae fragments in ethanol], USA: New York State, Clinton Co., Adirondack Mountains, Ausable River; viii.1879, (*R.P.Edes & H.P.Bowditch*) (MCZ).

Simulium (*Hagenomyia*) *longistylatum* SHEWELL, 1959: 84. HOLOTYPE male, CANADA: Quebec, Baia Comeau, Outardes River; 21.vii.1955, (*L.S.Wolse*) (CNC, no. 6695) [Examined.] [Synonymy by ADLER *et al.*, 2004: 337.]

FEMALE. General body colour brown. Body length (specimens pinned) 3.4-4.5 mm (mean = 3.8 mm, s.d. = 0.34, n = 8), wing length 2.5-3.5 mm (mean = 3.1 mm, s.d. = 0.32, n = 8), wing width 1.5-1.9 mm (mean = 1.7 mm, s.d. = 0.12, n = 10).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 210). Frons, clypeus and occiput brown, with silvery grey pruinosity; clypeus covered with pale, semi-recumbent setae and frons with erect, dark brown hairs. Mouthparts dark brown to black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae without teeth (Fig. 263).

Thorax: scutum black, largely pruinose covered by semirecumbent white hairs; dark brown with faint grey pruinosity and evenly arranged recumbent, whitish setae; posterior margin with semi erect white hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax largely silver pruinose, with 1+1 fine, X-shaped black vittae extending from anterior to posterior margins of thorax, 1+1 rounded vittae on postero-lateral margin, and one fine, median, weakly brown line extending from anterior to posterior margins ; humeri, part of lateral margins, and posterior margin pruinose (Figs. 358, 360). With posterior illumination, the pattern reverses with all pruinose areas becoming black, 1+1 rounded silver pruinose spots on anterior third of scutum (Figs. 359, 361); humeri faintly paler brown; lateral and posterior margins black. Scutellum black with semi-erect white hairs intermixed with long, brown bristles. Postnotum black with silver pruinosity. Pleura black with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta bare. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 504. Fore leg with coxa, trochanter, femur, tibia and tarsal segments I-IV dark brown to black. Mid and hind leg coxae, apical third of femora, tibiae and tarsal segments I, and tarsal segments II-IV black; remainder of femora and tibiae, except basal third of tibiae dark brown; basal third of tibiae and basal half of tarsal segment I yellow brown. Claws strongly curved with a distinct basal tooth. Halteres cream with brown base.

Abdomen: tergites I-IV dark brown to velvet black, V-IX shiny black. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with long setae on posterior margin; gonapophyses small, half length of eighth sternite at mid point, weakly sclerotised on central border and interspersed with microtrichiae (Fig. 561). Cercus subrectangular, about twice as broad as long, with posterior margins straight and corners rounded; paraproct subrectangular, sclerotised, extending beyond junction with cercus and covered with small setae apically (Figs. 23, 620). Genital fork stout and heavily sclerotised, stem expanded anteriorly; anterior and posterior processes well developed (Fig. 680). Spermatheca subspherical, without visible cuticular microspines; area of insertion of spermathecal duct membranous.

MALE. General body colour black. Body length (specimens pinned) 3.1-3.9 mm (mean = 3.5 mm, s.d. = 0.26, n = 8), wing length 1.8-3.0 mm (mean = 2.5 mm, s.d. = 0.36, n = 8), wing width 1.3-1.9 mm (mean = 1.5 mm, s.d. = 0.18, n = 8).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered with golden, recumbent hairs. Scutal pattern varies slightly with light incidence. With light anterior, thorax black with 1+1 subrectangular, silver pruinose vittae extending from antero-lateral margins towards central region of thorax; humeri and posterior margin silver pruinose, lateral margins black (Figs. 773, 775). With posterior light, thorax black (Figs. 774, 776);

humeri dark brown; lateral and posterior margins black. Scutellum brown with golden, recumbent hairs and long, erect dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female.

Abdomen: tergites dark brown to black, basal fringe with long, brown hairs. Silver pruinose ornamentation on lateral margins of tergites II, III, V, VI [best seen when specimens tilted laterally]. Genitalia black; tergal plates developed; sternal plate undeveloped. Gonocoxite subquadrangular; gonostyle nearly four times longer than gonocoxite, prominently elongate, with lateral margin straight, distinct ridge basally and without terminal spine (Figs. 45, 865). Ventral plate broadly subrectangular, sclerotised, with cleft prominent centrally and extending beyond midpoint; main body of ventral plate without prominent shoulders and basal arms sclerotised, subparallel; ventral plate with small setae (Figs. 55, 926). Median sclerite long, about 3.5 times longer than wide at widest point, without apical incision (sometimes it appears curled up in some specimens) (Fig. 926). Paramere with well developed and sclerotised basal processes and numerous spines, central membrane with spines (Fig. 986).

PUPA. Cocoon length dorsally 5.2-6.5 mm (mean = 5.9 mm, s.d. = 0.41, n = 10); ventrally 5.7-7.4 mm (mean = 6.6, s.d. = 0.57, n = 10); pupa length 3.7-4.9 mm (mean = 4.3 mm, s.d. = 0.31, n = 10); gill length 1.8-2.3 mm (mean = 1.9 mm, s.d. = 1.15, n = 10).

Cocoon: boot-shaped as in Fig. 67, light to dark brown composed of thick coalesced fibres, with reinforced rim to anterior aperture, margin of aperture weakly elevated with fenestrations.

Gill: light brown with nine forwardly-directed filaments arranged in vertical plane. Gill configuration as in Figs. 88, 1048; main trunk short, giving rise to two sets of primary branches, one external and one internal. The external branch consists of one dorsal, one median and one ventral branches each with three, two and one secondary filaments, respectively. The internal branch consists of one dorsal and one ventral branches each having two two secondary filaments. Filaments stout, swollen basally and tapering apically; all filaments distinctly covered with minute tubercles on surface, edges weakly crenate; filaments varying in length, with the ventral filaments of the external primary branch longer than remainder of filaments.

Head (frontoclypeus): with 2+2 frontal and 1+1 facial long simple trichomes, frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and 4-5 platelets in two groups laterally in frontal region, respectively; tubercles rounded and well distributed over entire surface.

Thorax: with one to two simple long trichomes on dorsal cleft, one long simple trichome on central region and one long simple trichome on ventral margin of alar region; tubercles rounded, densely distributed over entire region surface.

Abdomen: chaetatotaxy similar to that of *S. claricentrum* and *S. innoxium*: tergite I with 1+1 simple, long median setae, 1+1 long, simple, submedian setae, and 1+1 long setae on setae on lateral margins, all tergite covered with well distributed pointed and rounded tubercles over entire surface, tergite covered with pointed tubercles, especially on lateral region; tergite II with 4+4 submedian spiniform setae in longitudinal row mesally, sometimes one long simple setae between outermost spiniform setae or one long bifid setae antero-lateral to outermost setae, and 1+1 spiniform setae on lateral margins, tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, long setae anterior to outermost hooks; tergites V-VII with 1+1 long submedian simple setae and 1+1 long simple setae on lateral margins; tergite VIII sclerotised with 1+1 long simple setae laterally; tergite IX sclerotised terminating in 1+1 apical spines. Spine combs on antero-lateral region of tergites VI-VIII. Sternite III with 1+1 median, 2+2 submedian and 1+1 lateral long simple setae; sternites IV, V with 2+2 close simple hooks, 2+2 long spiniform setae lateral to outermost simple hooks, and 1+1 long spiniform setae on lateral margin; sternites VI, VII with 2+2 well separate simple or bifid hooks in row on posterior margin, 1+1 or 2+2 long simple setae mesally, 1+1 long simple, setae between outermost hooks, and 1+1 long simple setae on lateral margins; sternite VIII sclerotised with 1+1 long simple setae laterally; sternite IX sclerotised, without visible setae or trichomes. Spine combs on antero-lateral regions of sternites III-VIII, some resembling teeth on lateral margin of tergite VIII.

LARVA (Last instar). Body length 9.9-11.9 mm (mean = 11.0 mm, s.d. = 0.80, n = 5); length of head capsule 0.9-1.1 mm (mean = 1.0 mm, s.d. = 0.0.7, n = 5); width of head capsule 0.7-0.8 mm (mean =

0.7 mm, s.d. = 0.04, n = 5). Body colour dark grey dorso-laterally, whitish ventrally (specimens fixed alcohol). General body form as in Fig. 1101.

Head: whitish to brown dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Fig. 1153). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth distinctly evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth; 1+1 lateral teeth all at same level as sublateral teeth; approximately 11+11 small, lateral serrations; 1+1 lines of eight hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1208). Sub-esophageal ganglion lightly pigmented. Antenna reaching apex of labral fan stalk, segment I, apex of segment II and segment III dark brown; length of antennal segments I-III excluding the sensillum 0.07-0.1:0.1-0.2:0.07-0.1 mm (n = 5). Mandible with three apical teeth, first one longer than second and third; mandibular comb with eight teeth, first and eighth tooth smaller than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1262). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with 41-57 rays (n = 5) each with single line of microspinules in row and interspersed with finer spinules.

Thorax: dark grey dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 29-33 rows of sclerotised processes of 15-20 simple hooks (n = 5). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with nine filaments.

Abdomen: usually dark grey dorsally and paler ventrally, especially towards posterior segments. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 93-108 rows of sclerotised process of 21-28 simple hooks (n = 5). Rectal gills not everted in all specimens I examined.

Taxonomic Discussion. *Simulium pictipes* was described by HAGEN (1880) from syntypes (one pharate female, four pharate males, and numerous pupal exuviae and larvae) collected in the state of New York. All syntypes are listed by ADLER *et al.* (2004) as housed at the MCZ, but I have been unable to examine this material. ADLER *et al.* (2004) reviewed the taxonomic confusion of *S. pictipes* and *S. innoxium*, also compared the former species with the closely related species, *S. longistylatum* (see ADLER & CROSSKEY, 2010). I have examined numerous specimens identified as *S. pictipes* and *S. longistylatum* housed at the CNC and CUAC collections. In addition, I have also examined the type specimens of *S. longistylatum* and have the following comments to make. *Simulium longistylatum* was described by SHEWELL (1959) from adults collected in Quebec, Canada. The male holotype, which is in good condition, and numerous paratypes (also in good condition), are deposited at the CNC Simuliidae collection. I have taken digital images of the holotype and a female paratype, which are now held at the Simuliidae Digital Imaging Archives at the BMNH. I have studied the adult's general morphology of *S. longistylatum*, and compared it with specimens identified as *S. pictipes* housed at CUAC. The general morphology of the female and male thoracic patterns (Figs. 360, 361, 775, 776), female wing venation, legs coloration, and genitalia falls within the variation found in *S. pictipes.* Based on these findings, I agree with the synonymy of ADLER *et al.* (2004).

The females of *S. pictipes* cannot be separated from those of *S. claricentrum* or *S. innoxium* without examination of the pupal gill configuration (Figs. 358-361). The males may be externally separated from *S. claricentrum* by the presence of 1+1 subrectangular silver cunae on the thorax that arise from the anteroateral margins and they are directed towards the central region of the scutum (Figs. 773-776). In *S. claricentrum* the silver cunae are subtriangular arising on the anterior margin and they are directed towards the posterior region of thorax (Figs. 769, 770). The morphology of the ventral plate can be used to separate both species, showing a more prominent cleft centrally in *S. pictipes* (Figs. 55, 926) than in *S. claricentrum* (Fig. 924).

The pupa of *Simulium pictipes* is not easily separated from *S. claricentrum* and *S. innoxium*, all of which possess nine gill filaments (Figs. 1046, 1047, 1048). However, in *S. pictipes* and *S. claricentrum* all filaments are directed forwards (Figs. 1046, 1048), while in *S. innoxium* the dorsal filaments of the internal branch are backwardly directed and towards the dorsal region of the thorax (Fig. 1047). *Simulium pictipes* may be separated from *S. claricentrum* by the width of the gill filaments, which are relatively more swollen basally and then taper beyond the mid point of the gill (Figs. 82, 1048). In *S. claricentrum* the pupal gill filaments are distinctly thinner along their entire length (Fig. 1046).

The larva of *S. pictipes* may only be separated from that of *S. innoxium* by the presence of 1+1 lines of eight hypostomial setae (Fig. 1208). It can be further recognized from *S. claricentrum* by the anterior margin of the hypostomium being straight [see **Key to larva** in section **2.4.8**]

POST (1982b) mentioned that a sex-link inversion (1S-1) is present in specimens of *S. pictipes* (as *S. longistylatum*).

Simulium pictipes was placed in the PICTIPES species group of the subgenus *Hemicnetha* by ADLER *et al.* (2004), and the latter taxonomic arrangement has been accepted by ADLER & CROSSKEY (2008, 2009, 2010). More recently, SHELLEY *et al.* (2010) synonymised the subgenus *Hemicnetha* with *Trichodagmia* and recognized the PICTIPES species group, where *S. pictipes* is now placed.

Distribution. *Simulium pictipes* has the most northerly distribution in the USA and Canada of all species in the PICTIPES species group. It tracks the Precambrian Shield west into Saskatchewan, northern Alberta, and the Northwest territories (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010).

Biology and Medical Importance. The biology, economic importance, hosts and cytology of *S. pictipes* have been discussed by ADLER *et al.* (2004). Larvae and pupae of *S. pictipes* occupy moss-like aggregations in the clear torrential currents of waterfalls and swift rocky rivers and lake outfalls. Early instars tolerate slower currents than later instars, but nearly all have a low water velocity threshold near 10 cm/sec. The females emerge with immature eggs but at least some females are autogeneous. The eggs are deposited in large masses in the water splashed zones; a single egg mass deposited by many females can contain up to 100,00 eggs. At least two generations are produced annually with larvae of the first generation emerging in May. The males of this species form swarms within 1-3 m over waterfalls. The females feed on nectar of *Vaccinium* sp. and a single female was collected in the ear of a moose [*Alces alces* (LINNANEUS)] (ADLER *et al.*, 2004). The latter authors stated that they have occasionally netted this species in swarms around humans, and that they were only aware of two records as biting man.

ADLER *et al.* (2004) recorded larvae of *S. pictipes* infected with mermithid nematodes and had taken many males trapped in webs of the spider *Lariniodes patagiatus* (CLERK).

2.5.4. The TARSATUM species group.

SHELLEY *et al.* (2010) merged the BRACHYCLADUM and PAYNEI species groups [as sub-groups] with MEXICANUM of the subgenus *Hemicnetha* in COSCARÓN (1997), CROSSKEY & HOWARD (2004) ADLER *et al.* (2008, 2009, 2010), and added more recently published species. The MEXICANUM species group was renamed TARSATUM following the synonymy of *S. mexicanum* with the previously described *S. tarsatum* (HERNÁNDEZ & SHELLEY, 2005). The name change has been accepted in the most recent World Inventory of Blackflies (ADLER & CROSSKEY, 2008, 2009, 2010).

The TARSATUM species group now contains 19 species following the synonymy of *S. biuxinisa* with *S. paynei* [this work] and other taxonomic changes detailed by HERNÁNDEZ *et al.* (2005) and SHELLEY *at al.* (2010): *Simulium seriatum* and its synonyms *S. laticalx* and *S. latidigitus* were synonymised with *S. tarsatum*; *S. strigatum* was made a synonym of *S. townsendi*, which was moved from "unplaced species" to the ORBITALE species group; and *S. tarsale* (and its synonym *S. clavipes*) was moved from "unplaced to subgenus" to the TARSATUM species group (HERNÁNDEZ *et al.*, 2005). The reasons given by COSCARÓN & COSCARÓN-ARIAS (2007) for not recognizing the synonymies discussed and illustrated in the works of HERNÁNDEZ *et al.* (2005) and SHELLEY *at al.* (2010) have not been accepted in the current work [see **Taxonomic Discussion** under relevant species].

Diagnosis.

Female: Scutum yellowish brown to black with pattern in various forms or sometimes without pattern (Figs. 362-417). Nudiocular area triangular often well developed (Figs. 211-227). Cibarium unarmed or with denticles on membrane attached to central trough (Figs. 264-282). Sc with setae, basal section of Radius bare or setose. Claws with well developed basal teeth. Gonapophyses very long and triangular (except in *S. lobatoi*, Fig. 571), posteriorly pointing, mostly membranous with slight sclerotisation on inner margin, with microtrichiae and in some species setae (Figs. 10, 562-581). Paraprocts large (except in *S. lobatoi*, Figs. 25, 630), broadly rectangular rounded distally, membranous with light sclerotisation and setose, usually with lanceolate setae distally and in some species (*S. brachycladum*, *S. cristalinum*, *S. pulverulentum* and *S. solarii*) margins of paraprocts not well defined (Figs. 26, 29, 621-629, 631-640). Genital fork with ends of lateral arms well developed and in a continuous line with the lateral arms and hence oblique to the transverse axis of the abdomen, three times as wide as deep, well sclerotised with anterior processes well developed inner, posterior processes sometimes well developed (Figs. 681-701).

Male: Scutum brown to black with or without pattern (Figs. 777-826). Gonostyle well developed, subrectangular with sinuous edges and terminal spine (Figs. 46, 866-888). Ventral plate up to four times as wide as long to almost square with a variously developed median process joined to small to well developed ventral keel and fissure in median process and main body, no or relatively undeveloped lateral shoulders (see under species descriptions) (Figs. 56-58, 927-949). Parameres with basal plates well developed and with many long spines (Figs. 64, 987-1009).

Pupa: Cocoon shoe-shaped with or without fenestrations as in Figs. 68, 69, exceptionally slipper-shaped (*e.g. S. yepocapense* similar to Fig. 65). Pupal gill filaments generally shorter than pupa, with up to 90 filaments that are rounded or pointed apically, but not sclerotised (Figs. 83, 84, 1049-1073). Head trichomes simple or bifid, tubercles rounded and only present in facial region; thickened margin between frons and clypeus in some species as in Fig. 70. Pupal cephalothorax without prominent spines, but with limited distribution (mid line and base of gill) of pointed or rounded tubercles, trichomes simple to bifid. In some species, irregular markings or rugosities are visible in the frontoclypeus and thorax (as in Figs. 72, 74).

Larva: There are no reliable diagnostic characters for the larva of the TARSATUM species group. These have to be examined in combination with link-reared adults collected in the same locality. In general, the larvae of species in this group have a deep postgenal cleft that is triangular apically (Figs. 1154-1171). Hypostomium often with seven, eight or nine teeth evenly distributed along anterior margin (Figs. 1209-1226), but in species such as *S. lobatoi* and *S. solarii* the teeth are prominently elevated centrally and protrude forward. Mandibles with three apical teeth; mandibular comb with more than seven teeth; mandible often with 1 + 1 mandibular serrations, but a single serration was also recorded (see Figs. 97, 1263-1280). Larval integument without ovoid setae. Posterior arm of anal sclerite never encircling posterior circlet.

2.5.4.1. ***Simulium* (*Trichodagmia*) *brachycladum*** **LUTZ AND PINTO** (Figs. 24, 37, 211, 264, 362, 363, 505, 562, 621, 681, 777, 778, 866, 927, 987, 1049, 1102, 1154, 1209, 1263)

This is a zoophilic species commonly found in the north and southeast of Brazil.

Simulium brachycladum LUTZ & PINTO in PINTO, 1932: 690. LECTOTYPE pupa no. 2756, BRAZIL: Pernambuco State, Tapera, [Collection date unknown] (*D.Bento Pickel*) (IOC). [Examined]. [Lectotype designation by MAIA-HERZOG *et al.* 1984: 341.]

Simulium brevibranchium LUTZ & MACHADO, 1915: 46. [*Nomen nudum*, formally described as *S. brachycladum* by LUTZ & PINTO in PINTO, 1932: 690.]

FEMALE. General body colour dark brown. Body length (specimens pinned) 2.6-3.6 mm (mean = 3.1 mm, s.d. = 0.29, n = 10), wing length 2.4-2.9 mm (mean = 2.7 mm, s.d. = 0.13, n = 10), wing width 1.2-1.5 mm (mean = 1.3 mm, s.d. = 0.11, n = 10).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 211). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with pale, erect setae interspersed with long, erect, black hairs. Mouthparts parts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellar segments black. Cibarium with well developed, sclerotised cornuae and small, irregular teeth lateral to central trough to which is attached a membrane covered by denticles (Fig. 264).

Thorax: scutum dark brown covered with grey pruinosity and evenly arranged recumbent, whitish setae, interspersed with fine black setae specially on anterior and posterior margin; posterior margin with long dark hairs. Scutal pattern varying with illumination. With anterior illumination, thorax dark brown with 1+1 median, pear-shaped and 1+1 sublateral, triangular, wide, grey pruinose vittae extending from one third to two thirds length of scutum; 1+1 submedian, brown vittae connecting anterior and posterior margin in a lyre-shaped pattern (Fig. 362); humeri dark brown with faint grey pruinosity; lateral margins dark brown. With posterior illumination, thorax dark brown with 1+1 comma-shaped, silver pruinose vittae extending from anterior margin to two thirds length of scutum [silver pruinosity visible in some specimens]; humeri silver pruinose; posterior margin dark brown to black (Fig. 363). Irrespective of light direction a fine, median, dark brown line extends from anterior to posterior margins. Scutellum dark brown with semi-erect white hairs intermixed with long, black bristles. Postnotum dark brown with silver pruinosity. Pleura dark brown to black with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta with line of setae in basal two thirds. Radius with numerous setae intermixed with distinct spines apically, basal section of radius generally bare but sometimes two or three setae are seen apically. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 505. Foreleg with coxa, trochanter and femur light to mid brown, tibia dark brown on basal and apical two thirds with central region white. Mid and hind legs with coxa dark brown, trochanter and femur mid brown with apical third of femur dark brown, tibia and tarsal segments dark brown except for white yellowish areas on central region of femur and basal two thirds of tarsal segment I and basal third of segment II. Claws strongly curved each with distinct basal tooth. Halteres cream with brown base.

Abdomen: tergites I-V velvet black, VI-IX shiny black, segment I and II with silver pruinosity on central region, except accentuated on tergite II. Tergal plates well developed. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with irregularly distributed setae on posterior margin; gonapophyses long, about 1.5 times longer than width of eighth sternite at mid point, weakly sclerotised and distinctly narrow apically, with small setae distributed over entire surface (Figs. 37, 562). Cerci hemispherical, covered with long, brown setae; paraproct broadly subrectangular, poorly defined, with sclerotised areas and some setae, most prominent basally and with small membranous protuberance basally (Figs. 621). Genital fork stout and heavily sclerotised; lateral arms with well developed anterior and posterior processes (Fig. 681). Spermatheca globular, apparently without external sculpturing or spicules on internal surface; area of insertion of spermathecal duct two fifths maximum width of spermatheca.

MALE. General body colour dark brown to black. Body length (specimens pinned) 2.4-3.6 mm (mean = 3.0 mm, s.d. = 0.38, n = 9), wing length 1.6-2.4 mm (mean = 2.2 mm, s.d. = 0.25, n = 10), wing width 0.9-1.3 mm (mean = 1.1 mm; s.d. = 0.12, n = 10).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum brownish black with golden, recumbent hairs. Scutal pattern varies slightly with light incidence: with anterior light source thorax brownish black with 1+1 small, median, rectangular and 1+1 submedian, comma-shaped silver pruinose vittae with dark brown cunae within anterior third (Fig. 777). With light source posterior to specimen thorax dark brown with silver pruinosity (Fig. 778). Irrespective of light direction thorax divided by fine dark brown line. Humeri silver pruinose; lateral and posterior margins of scutum dark brown to black. Scutellum dark brown with pale, semi-erect setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: tergites black, sometimes mottled brown on anterior margin; basal fringe with long, brown hairs. Silver pruinose ornamentation as follows: anterior margin of tergites I, whole of tergite II and antero-lateral margin of tergites III-VII. Genitalia black; sternal and tergal plates developed. Gonocoxite subquadrangular; gonostyle subrectangular, with dorsal and ventral margins sinuous and terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 866). Ventral plate weakly sclerotised with main body reduced and poorly developed lateral shoulders; anterior median process and keel highly developed and covered by small hairs, basal arms well developed, almost parallel and deeply sclerotised apically (Fig. 927). Median sclerite long, nearly four times longer than wide at widest point, with distinct apical incision (Fig. 927). Paramere with well developed and sclerotised basal process and numerous stout spines (Fig. 987).

PUPA. Cocoon length dorsally 3.2-4.3 mm (mean = 3.8 mm, s.d. = 0.29, n = 16), ventrally 4.4-5.8 mm (mean = 5.2 mm, s.d. = 0.33, n = 16); pupa length 3.2-4.3 mm (mean = 3.8 mm; s.d. = 0.35, n = 16); gill length 1.7-2.2 mm (mean = 1.9 mm, s.d. = 0.16, n = 15).

Cocoon: shoe-shaped as in Fig. 66, light to dark brown composed of thick coalesced fibres, with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown with 6 upwardly directed filaments arranged in bunch in vertical plane. Gill configuration with main trunk short, giving rise to two sets of primary branches, one external and one internal; external consists of 4 secondary branches and internal of two secondary branches, all filaments bifurcating basally. Filaments stout, pointed distally, with small spicules on surface, edges weakly crenate; usually all filaments approximately same length [in some specimens the most internal set of filaments is shorter than the other filaments (Fig. 1049).

Head (frontoclypeus): with 2+2 frontal and 1+1 facial simple trichomes [sometimes the most internal frontal trichome is bifid]; frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and 2-3 platelets in two or three groups laterally in frontal region, respectively; tubercles absent in frontal region, but mostly pointed (few rounded) and distributed in 1+1 groups laterally in facial region.

Thorax: with 2+2 simple trichomes near margin of dorsal cleft and two to four simple trichomes on central region; tubercles mostly pointed and only visible on postero-dorsal margin of dorsal cleft, and rounded on ventral margin near base of gill.

Abdomen: tergite I with 1+1 submedian, simple setae; tergite II with 3+3 submedian spines in longitudinal row, 1+1 small, simple setae lateral to outermost spines, 3+3 sublateral, simple setae; tergites III and IV with 4+4 submedian, simple hooks in longitudinal row, sometimes 1+1 or 2+2 small, simple, setae anterior to most lateral spines and 1+1 sublateral simple setae; tergites V with 1+1 or 2+2 submedian spiniform setae, 2+2 sublateral and 1+1 lateral, small simple setae; tergite VI with 1+1 submedian and 1+1 sublateral small setae; tergite IX without terminal spines, weakly sclerotised. Groups on spine combs as follows: posterior margin of tergite I, anterior and posterior margin of tergite II, and anterior margin of tergites III-VIII. Abdominal sternite IV with 1+1 sublateral, small simple hooks; sternite V with 2+2 close, simple median hooks; sternites VI-VII with 2+2 well separated hooks. Groups of spine combs on anterior margin of sternite III-VIII.

LARVA (Last instar). Body length 6.7-8.3 mm (mean = 7.6 mm, s.d. = 0.5, n = 5); length of head capsule 0.8-1.6 mm (mean = 1.3 mm, s.d. = 0.3, n = 5); width of head capsule 0.6-1.6 mm (mean = 1.2 mm, s.d. = 0.41, n = 5). Body colour whitish (in specimens fixed in alcohol). General body form as in Fig. 1102.

Head: mainly pale brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern lightly positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Fig. 1154). Hypostomium strongly pigmented on anterior margin, with nine apical teeth evenly distributed on anterior margin; median tooth sharp, more developed than remainder; 3+3 sublateral teeth; 1+1 lateral tooth, nearly same length or longer than basal sublateral tooth; 1+1 small, lateral serrations; 1+1 lines of approximately six hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1209). Sub-esophageal ganglion unpigmented. Antennal segments longer than labral fan stalk, all segment pale brown; length of antennal segments I-III excluding the sensillum 0.07-0.1:0.07-0.1:0.04-0.09 mm (n = 5). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately nine teeth, first three more prominent than remainder; only one mandibular serration (Fig. 1263). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with 49-53 rays each with fine, single line of spines in row (n = 5).

Thorax: white dorsally with greyish tinges ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 23-39 rows of sclerotised processes of 10-19 hooks (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with six filaments, all branching basally.

Abdomen: usually grey, progressively paler ventrally especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 107-124 rows of 22-26 simple hooks (n = 5). Rectal gills with three branches, each with 5 finger-like lobules giving a total of 15 lobules (n = 2).

Taxonomic Discussion. *Simulium brachycladum* was described by LUTZ & PINTO (in PINTO, 1932) from pupae and males collected at Tapera, Pernambuco State and São Felix, Bahía State. PINTO (1932) erroneously cited in the index the year of publication for *Simulium brachycladum* as 1931, but his paper was published in 1932 and no reprints were distributed prior to this volume. This error was subsequently recorded in the catalogue of VARGAS (1945) and VULCANO (1967). Subsequent mis-spelling of *S. brachycladum* [as *S. brachycladium*] and wrong species author citation can be found in SMART (1945) and VARGAS *et al.* (1946).

MAIA-HERZOG *et al.* (1984) discussed the taxonomic problems involving this species, its synonyms and type depositories, and also provided full descriptions of all life stages. They also documented the *nomen nudum* created by LUTZ & MACHADO (1945) while referring to "*Simulium brevibranchium*". COSCARÓN (1991) also discussed *S. brachycladum* and provided new distribution records in Brazil. More recently, SHELLEY *et al.* (2010) reviewed the taxonomy of this species and compared it with the closely related species, *S. cristalinum*. They (also referring to COSCARÓN & PY-DANIEL, 1989) separated *S. brachycladum* from *S. cristalinum* by the following combination of characters: females with basal region of the cibarium with teeth relatively shorter, Lutz's organ longer than half length of the palps and paraproct more "excavated" in median posterior region; males with gonostyle shorter and more sinuous laterally, ventral plate with longer keel (approximately twice as long as wide at base) and weekly concave laterally; pupa relatively longer, with cocoon more elevated and gill filaments approximately twice as long as in *S. cristalinum*.

The adults of *S. brachycladum* can be externally distinguished from that of *S. cristalinum* by the coloration of the thorax. The scutal pattern of females of *S. brachycladum* shows a distinct submedian lyre-shaped pattern (Figs. 362, 363), while *S. cristalinum* has a similar but more indistinct pattern originating from pronounced cunae on the anterior margin of the scutum (Figs. 368, 369). In Brazil, the female scutal pattern of *S. brachycladum* is most similar to that of *S. rubrithorax* [see SHELLEY *et al.* (2002b) for discussion on *S. rubrithorax*]. Apart from this character, the other closely related Brazilian species (*S. cristalinum* and *S. rubrithorax*) may only be distinguished from that of *S. brachycladum* in the female by the form of the paraproct (see Figs. 24, 621, 623, 635). In males the scutal pattern (Figs. 777, 778) and morphology of the ventral plate (Figs. 927) are sufficient to separate *S. brachycladum* from the other two species (see Figs. 783, 784, 811, 812, 930, 943).

The most reliable morphological character that easily separates *S. brachycladum* from *S. cristalinum* is the pupal gill configuration (Figs. 1049, 1052-1053) and sometimes the length of the pupal gill filaments. COSCARÓN & PY-DANIEL (1989) gave filaments length of 0.7–0.8 mm for *S. cristalinum* [0.6-0.7 mm by SHELLEY *et al.*, 2010], and COSCARÓN (1991) recorded 1.5 mm for *S. brachycladum* [1.7-2.2 mm by SHELLEY *et al.* 2010]. In this respect, the pupa of *S. brachycladum* is also similar to *S. oviedoi* and *S. rivasi*, but they can be separated by the different morphology of the tubercles on the pupal thorax.

The larva of *S. brachycladum* can only be distinguished from other Brazilian species in the TARSATUM species group by the dissected gill histoblast with six filaments, which are all branching basally and pointed apically. In this respect, *S. brachycladum* is most similar to *S. cristalinum* from which it can be separated by the morphology of the hypostomium and the number of mandibular serrations (Figs. 1154, 1263) [see **Taxonomic Discussion** under *S. cristalinum*].

CROSSKEY & HOWARD (1997, 2007), COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) placed *S. brachycladum* in the BRACHYCLADUM species group of the subgenus *Hemicnetha*. ADLER & CROSSKEY (2008, 2009, 2010) placed it in the PAYNEI species group in the latter subgenus.

More recently, SHELLEY *et al.* (2010) subsumed the PAYNEI species group and the subgenus *Hemicnetha* under the TARSATUM species group of the subgenus *Trichodagmia*, where *S. brachycladum* is now placed.

Distribution. *Simulium brachycladum* has only been recorded in Brazil, where it is a relatively common species found in the states of Bahía, Espírito Santo, Minas Gerais, Paraíba, Pernambuco, Rio de Janeiro & São Paulo (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN, 1991; CROSSKEY & HOWARD, 1997, 2004; PEPINELLI *et al.*, 2003; also see **Material Examined** by SHELLEY *et al.*, 2010 and the current work).

Biology and Medical Importance. The immature stages of *S. brachycladum* can be collected in medium to fast flowing, clear rivers with rocky beds (COSCARÓN, 1991). The larval stages of *S. brachycladum* [as *Hemicnetha brachyclada*] have been recently studied by ANDRADE *et al.* (2004), who recorded seven larval stages for this species in semi-natural conditions. The same authors also reviewed the control of *S. brachycladum* in Brazil and advocated for the mechanical control of the stream flow in rivers in the state of Rio Grande do Norte. The alimentary habits of females are unknown although they are presumed to be zoophilic (MAIA-HERZOG *et al.*, 1984). SHELLEY *et al.* (1995) recorded its oviposition behaviour in the state of Pernambuco. ANDRADE *et al.* (2000) recorded the presence of larvae and pupae of this species in the gut content of fish in the family Poecilidae.

2.5.4.2. *Simulium (Trichodagmia) bricenoi* VARGAS, MARTÍNEZ PALACIOS & DÍAZ NÁJERA (Figs. 93, 96, 97, 212, 265, 364-367, 506, 563, 622, 682, 779-782, 867, 868, 928, 929, 988, 989, 1050, 1051, 1103, 1155, 1210, 1264)

An uncommon species externally similar to *S. paynei* and *S. virgatum s.l.*

Simulium (*Dyarella*) *bricenoi* VARGAS *et al.*, 1946: 115. HOLOTYPE male (reared), MEXICO: Mexico State, 2645 m; 12.iii.1944, (*A.Díaz Nájera*) (INDRE) [Examined.]

Simulium wirthi PETERSON & CRAIG, 1997: 212: HOLOTYPE male (reared), USA: New Mexico: County Grant, Gallinas Creen, Railroad Canyon, Rt. 152, 1890 m; 15.v.1992, (*B.V.Peterson & M.E.Craig*) (NMNH) [Examined.] [Synonymy by ADLER *et al.*, 2004: 371; synonymy followed by ADLER & CROSSKEY, 2008: 45, 2009: 48, 2010: 2010, SHELLEY *et al.*, 2010: 64, and this work; synonymy ommited in COSCARÓN *&* COSCARÓN-ARIAS, 2007: 539 and COSCARÓN *et al.* 2008: 32.]

FEMALE. General body colour black. Body length (specimens pinned) 3.0-4.2 mm (mean = 3.8 mm, s.d. = 0.42, n = 7), wing length 3.4-4.0 mm (mean = 3.7 mm, s.d. = 0.18, n = 7), wing width 1.5-1.2 mm (mean = 1.7 mm, s.d. = 0.18, n = 7).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 212). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 265).

Thorax: scutum black with evenly arranged recumbent whitish setae, interspersed with fine, semi-recumbent golden setae; posterior margin with long golden hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with 1+1 median, pear-shaped and 1+1 wide, sublateral vittae extending from anterior margin nearly to posterior margin; humeri silver pruinose; lateral and posterior margins black (Figs. 364, 366). With posterior illumination, thorax black with 1+1 silver pruinose cunae on anterior third of scutum, and weak grey pruinose area on posterior region of thorax; humeri silver pruinose lateral and posterior margins black (Figs. 365, 367). Scutellum dark brown with recumbent golden hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 506. Fore leg with coxa, trochanter, and basal three quarters of femur pale brown; apical third of femur, basal and apical one third of tibia and tarsal segments dark brown, remainder of tibia whitish. Mid and hind legs with coxae, apical third of femora, basal ventral margin and apical third of tibiae, apical two thirds of tarsal segments I-IV dark brown; trochanters, basal external surface of femora and tibiae, and basal two thirds of tarsal segment I white. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown to black and brown. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with five long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular, densely covered with setae and microtrichiae (Fig. 563). Cercus hemispherical, covered with brown setae; paraproct subrectangular, nearly same width of cercus basally but more bulbous and expanded towards apex, weakly sclerotised; paraproct and cercus densely covered with prominent brown hairs, and paraproct densely covered with microtrichiae over entire surface (Fig. 622). Genital fork stout and sclerotised, expanded apically; termination of lateral arms with anterior margins curved and well developed; anterior processes well developed and blunt apically, posterior processes developed (Fig. 682). Spermatheca globular, without external sculpturing and one or two groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens pinned) 3.0-4.4 mm (mean = 4.0 mm, s.d. = 0.46, n = 10), wing length 2.1-3.5 mm (mean = 2.9 mm, s.d. = 0.41, n = 10), wing width 1.4-1.9 mm (mean = 1.6 mm; s.d. = 0.15, n = 10).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black covered by evenly distributed whitish hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax black, with 1+1 submedian pruinose vittae, extending from anterior to posterior margins of scutum; humeri and lateral lightly pruinose; posterior margin black (Figs. 779, 780). With posterior illumination, thorax black with median and 1+1 sublateral vittae extending from anterior to posterior margins of scutum; humeri weakly pruinose; lateral and posterior margins black (Figs. 781, 782). In some specimens, the median pruinose vitta is relatively indistinct. Scutellum brown with whitish hairs interspersed with brown setae on posterior margin. Postnotum dark brown with grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II (best seen in some specimens when tilted and viewed laterally). Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle subrectangular with dorsal straight and ventral margins sinuous, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Figs. 867, 868). Ventral plate sclerotised, subrectangular, covered with long hair; anterior median process prominently developed with distinct depression apically; lateral shoulders slightly developed and basal arms well developed and subparallel; main body of ventral plate and anterior process distinctly covered by long hairs (Figs. 928, 929). Median sclerite long, about three times longer than wide at widest point, with small apical incision (Figs. 928, 929). Paramere with well developed and sclerotised basal processes and numerous long spines along centrally, membrane distinctly covered with spinules (Figs. 988, 989).

PUPA. Cocoon length dorsally 3.2-5.5 mm (mean = 4.6 mm, s.d. = 0.57, n = 17), ventrally 4.5-6.8 mm (mean = 5.0 mm, s.d. = 0.61, n = 15); pupa length 3.4-5.5 mm (mean = 4.6 mm, s.d. = 0.55, n = 14); gill length 1.5-3.1 mm (mean = 2.3 mm, s.d. = 0.48, n = 17).

Cocoon: shoe-shaped as in Fig. 69, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture strongly elevated with distinct fenestrations.

Gill: light brown with eight upwardly directed filaments arranged in bunch in vertical plane (Figs. 1050, 1051). Gill with filaments branching basally at different heights; main trunk short, giving rise to two sets of primary branches, one internal and two external: the more external consists of one dorsal branch with four secondary branches that bifurcate at different heights and one single ventral; the internal branch consists of three secondary branches that bifurcate at different heights. Filaments stout, rounded distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes, and 1+1 small, sublateral, simple trichomes between frontal and facial trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 4 platelets in one group laterally in frontal region, respectively; tubercles absent in frontal region, but rounded and well distributed in facial region.

Thorax: with 1-2 simple trichomes near margin of dorsal cleft, 1-4 simple trichomes on alar region, and one simple trichome on central region posteriorly; tubercles rounded only visible at base of gill and antero-lateral margins near dorsal cleft. Thorax prominently rugose with raised, irregularly distributed reticulate markings.

Abdomen: tergite I with 1+1 submedian simple short trichomes and 2+2 simple sublateral trichomes; tergite II with 3+3 submedian spines in longitudinal row, 3+3 simple, short trichomes lateral to outermost spine and 2+2 lateral small simple trichomes; tergites III and IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to most lateral of hooks, and 3+3 or 4+4 lateral simple small trichomes; tergite V with 1+1 submedian simple trichomes and 3+3 sublateral and 3+3 lateral simple trichomes; tergite VI with 1+1 lateral small simple trichome; tergites VII-IX without trichomes; tergite IX without terminal spines. Spine combs distribution as follows: central region and posterior margin of tergite I, and anterior margin of tergites II-VII. Sternite III without trichomes or spine combs; sternite IV with 3+3 submedian simple trichomes; sternite V with 2+2 close simple hooks and 2+2 simple trichomes to outermost hooks; sternites VI-VII with 2+2 well separated simple hooks in row along posterior margin; sternites VIII-IX without trichomes. Spine combs on anterior margin of sternites IV-V.

LARVA (Final instar). [I was unable to obtain fresh larval specimens of *S. bricenoi*., thus the description here provided has been derived from PETERSON & CRAIG (1997), IBÁÑEZ-BERNAL (1992), and upon few specimens housed at CUAC]. Body length 8.2-8.6 mm (n = 2); length of head capsule 0.9-1.9 mm (mean = 1.1 mm, s.d. = 0.5, n = 4); width of head capsule 0.7-1.5 (mean = 0.9 mm, s.d. = 0.5, n = 4). Body colour variegated black and white, with black marks ventrally (specimens fixed in alcohol). General body form as in Fig. 1103.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Figs. 93, 1155). Hypostomium strongly pigmented on anterior margin, with nine apical teeth distinctly protruding from anterior margin in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, most adjacent to median teeth longer than remainder, and 1+1 lateral teeth; 5+5 small lateral serrations; 1+1 lines of approximately nine hypostomial setae parallel to lateral margins; 1+1 or 2+2 long, simple setae in posterior half of hypostomium (Fig. 1210). Sub-esophageal ganglion lightly pigmented. Antennal segments nearly as long as labral fan stalk, segment I, apex of segment II and segment III dark brown, one third of segment II pale whitish; length of antennal segments I-III excluding the sensillum 0.1:0.1:0.09-1.1 mm (n = 4). Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately 11 teeth, first three teeth more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Figs. 96, 97, 1264) . Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 53-55 fine, single line of different length of microtrichiae (n = 2).

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 54 rows of hooks (n = 2). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 8 filaments, all branching from a common trunk and rounded apically.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 195-196 rows of 40-41 simple hooks (n = 2).

Rectal gills not everted in the two specimens examined [IBÁÑEZ-BERNAL (2002) stated that larvae have three lobes with 6-12 small, finger-like lobules (n = 1)].

Taxonomic Discussion. *Simulium bricenoi* was described by VARGAS *et al.* (1946) from a male holotype, 50 females and males (one female as allotype), numerous pupae, and one VI instar larva collected from Mexico State, Mexico. Subsequent mis-spelling of the species name can be found in VARGAS & DÍAZ NÁJERA (1957) [as *S. briseñoi*]. VARGAS *et al.* (1946) stated that the male holotype was partially mounted and housed at INDRE. I have examined a slide labelled as "*S. bricenoi* HOLOTIPO" at INDRE Simuliidae holdings. The slide is in good condition and it contains both wings, all legs and the male terminalia; the remaider of the holotype is not found at INDRE collections and it is presumed lost (H. HUERTAS - pers. comm. to L.M. HERNÁNDEZ, 2009) (**Material Examined**).

ADLER *et al.* (2004) recently reviewed the taxonomy of *S. bricenoi* and also discussed its cytology and natural history in the United States. The authors tentatively associated the *S. virgatum s.l.* forms C & D of MUHAMMAD (1988) with *S. bricenoi*, but advocated further study to confirm this finding. In the same paper, ADLER *et al.* (2004) synonymised *S. wirthi* with *S. bricenoi* because the small differences in the cocoon and gill branching between the two species were regarded as intraspecific variation. I have examined the type material of *S. wirthi* and have the following comments to make. *Simulium wirthi* was described by PETERSON & CRAIG (1992) from numerous females and males, larvae and pupal exuviae collected in New Mexico (see **Material Examined**). The reared pinned male holotype, 16 females and eight males (all pinned and labelled as paratypes), are housed in the NMNH. I have examined the holotype, which is mounted on a micropin; its pupal pelt is stored in a microvial containing glycerine attached to the pinned adult. I have studied the adult's thoracic pattern (Figs. 366, 367, 781, 782), the female head (cibarium and nudiocular area), wing venation, leg coloration, the morphology of the female (Figs. 563, 622, 682) and male genitalia (Figs. 868, 929, 989), the pupal gill configuration (Fig. 1051) and morphology of the larva. The general morphology of *S. wirthi* falls within the morphological variation found in *S. bricenoi*, therefore I agree with the synonymy of ADLER *et al.* (2004).

The female of *S. bricenoi* is externally similar to the black form of *S. virgatum s.l.*, from which it may only be separated by the relatively rounded and less sclerotised paraproct (Fig. 622). *Simulium paynei* is also morphologically similar to *S. bricenoi*, and they cannot be easily separated on their general morphology or their genitalia. The external coloration in the male of *S. bricenoi* is very similar to that of *S. virgatum s.l.* and *S. paynei*, but they can be separated by the gonostyle being more prominently sinuous and expanded centrally in *S. bricenoi* (Figs. 867, 868). The morphology of the gonostyle in the other two species is different (see Figs. 877-880, 887). The shape of the ventral plate easily separate *S. virgatum s.l.* (Fig. 948) from that of *S. bricenoi* (Figs. 928, 929), although the general shape of the ventral plate of *S. virgatum s.l.* is similar to that of *S. paynei* (Figs. 938-941).

The prominent fenestrations near the cocoon opening and the general configuration of the pupal gill filaments of *S. bricenoi* resemble that of *S. paynei*, *S. rubrithorax* and *S. virgatum s.l.* (as in Fig. 69). However, *S. bricenoi* can be reliably separated by the pupal thorax with distinct irregular, rhomboid-like markings over the entire surface, which are never present in the numerous specimens I have examined of *S. paynei*, *S. rubrithorax* and *S. virgatum s.l.*

The larva of *S. bricenoi* cannot be separated from that of *S. paynei*, *S. rubrithorax* and *S. virgatum s.l.* in the absence of other life stages. The number and arrangement of teeth of the larval hypostomium is regarded as a good character to separate closely related species in Simuliidae. However, in the case of *S. bricenoi*, a different number of hypostomial teeth has been given by PETERSON & CRAIG (1992) (as *S. wirthi*) [seven teeth] and IBÁÑEZ-BERNAL (1992) [nine teeth]. In all the specimens I have examined nine teeth were visible on the hypostomium. In addition, variation in the number of sublateral teeth occurs in this species. I have examined one specimen in which two sublateral teeth are less developed than the remainder of the teeth. In the same specimen, a smaller mandibular serration can be seen at some distance from the main mandibular serration [the latter is only visible at higher magnifications].

The cytology of *S. bricenoi* was reviewed by ADLER *et al.* (2004), who stated that this species has chromocentric chromosomes. The authors further added that *S. bricenoi* has a Y-linked inversion in the IIL arm, although they admitted they did not study the chromosomes in great detail.

Description of life stages of *S. bricenoi* may be found in COSCARÓN & COSCARÓN-ARIAS (2007), IBÁÑEZ-BERNAL (1992), PETERSON & CRAIG (1997) [as *S. wirthi*], and VARGAS *et al.* (1946).

Simulium bricenoi was placed in the MEXICANUM species group within the subgenus *Hemicnetha* by ADLER *et al.* (2004), CROSSKEY & HOWARD (1997, 2004), COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008). However, this species was allotted to the TARSATUM species group by ADLER & CROSSKEY (2008, 2009, 2010) following the paper of HERNÁNDEZ *et al.* (2007a). More recently, SHELLEY *et al.* (2010) placed it in their TARSATUM species group of the subgenus *Trichodagmia* because of their synonymy of *Hemicnetha* under *Trichodagmia.*

Distribution. *Simulium bricenoi* has only been found in Mexico and the United States (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; COSCARÓN & COSCARÓN-ARIAS, 2007; **Material Examined**).

Biology and Medical Importance. Little is known of the biology of *S. bricenoi*. IBÁÑEZ-BERNAL (1992) predicted that the immature stages might be found in cold clear waters in mountain rivers above 1700 m of altitude. ADLER *et al.* (2004) recorded larvae from December through May in the United States, though one pupa has been recorded in October (ADLER *et al.*, 2004). The female feeding habits of this species is poorly known, although it is presumed that they are mammophilic. One female has been recorded feeding on humans in the laboratory (ADLER *et al.*, 2004; VARGAS *et al.*, 1946).

2.5.4.3. ***Simulium* (*Trichodagmia*) *cristalinum*** **COSCARÓN & PY-DANIEL** (Figs. 213, 266, 368, 369, 507, 564, 623, 683, 783, 784, 869, 930, 990, 1052-1053, 1156, 1211, 1265)

This is a poorly known species from Brazil only found in Roraima State. I have been unable to obtain larvae of *S. cristalinum*. Therefore, the description here provided for the larval stage has been based upon the original description of COSCARÓN & PY-DANIEL (1989).

Simulium (*Hemicnetha*) *cristalinum* COSCARÓN & PY-DANIEL, 1989: 312. HOLOTYPE pharate male, BRAZIL: Roraima State, Igarapé Cristalino, Br 174, 17.x.1987, (*Coscarón & V.Py-Daniel*) (INPA).

FEMALE. General body colour brown. Body length (specimen pinned, n = 1) 2.1 mm, wing length 1.7 mm, wing width 0.9 mm.

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 213). Frons, clypeus and occiput brown, with silvery grey pruinosity; clypeus covered with pale, semi-recumbent setae and frons with erect, dark brown hairs. Mouthparts dark brown to black. Antennae brown. Cibarium with well developed, sclerotised cornuae with lateral, small, irregular teeth and membrane with denticles attached to central trough (Fig. 266).

Thorax: scutum dark brown with faint grey pruinosity and evenly arranged recumbent, whitish setae; posterior margin with recumbent, whitish setae. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown to black with 1+1 submedian and 1+1 sublateral black vittae that diverge posteriorly (Fig. 368). With posterior illumination, pattern same except vittae silvery grey, pruinose (Fig. 369). Humeri weakly silver pruinose; lateral and posterior margins black. Irrespective of light direction a fine, median, black line extending from anterior to posterior margins. Scutellum dark brown with semi-erect white hairs intermixed with long, brown bristles. Postnotum with silver pruinosity. Pleura dark brown with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta with line of few setae in basal half. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 507. Fore leg with coxa, trochanter and femur brown; middle of tibia yellowish remainder of tibia and tarsi black. Mid leg with coxa, apex of femur, one third and apex of tibia, apex of basitarsal segment I and remainder of tarsal segments dark brown; trochanter and two thirds of femur pale brown; base of tibiae and one third of basitarsal segment I pale yellowish. Hind leg with coxa, femur, two thirds of tibia, half of basitarsal segment I, apex of basitarsal segment II and remaining of tarsal segment dark brown; trochanter, apex of femur, tibia, basal half of basitarsus and apex of basitarsal segment II pale yellow. Claws strongly curved with a distinct basal tooth. Halteres cream with brown base.

Abdomen: tergites I-V velvet black, VI-IX shiny black; tergites I-II yellowish on anterior margin and tergite II silver pruinose on posterior margin. Tergal plates well developed. Sternites and genitalia dark brown to black. Eighth sternite weakly sclerotised with long setae on posterior margin; gonapophyses long, about 1.5 times longer than width of eighth sternite at mid point, narrow distally and sclerotised in basal median border with setae interspersed with microtrichiae (Fig. 564). Cerci with straight margin; paraproct membranous, poorly defined, but subquadrangular and rounded apically, partly sclerotised and nearly twice as long as wide basally with small membranous protuberance and few setae basally (Fig. 623). Genital fork stout and heavily sclerotised, with well developed anterior processes on lateral arms (Fig. 683). Spermatheca globular, apparently with external sculpturing and spicules on internal surface; area of insertion of spermathecal duct approximately half width of spermatheca.

MALE. General body colour similar to female. Body length (specimen pinned, n = 1) 1.9 mm; wing length 1.5 mm, wing width 0.8 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark brownish black with golden, recumbent hairs. Scutal pattern varies slightly with light incidence: with anterior light source thorax dark brownish black with 1 median, pear-shaped (distinctly concave posteriorly) and 1+1 submedian, silver pruinose comma-shaped cunae on anterior third (Fig. 783). With light source posterior to specimen the silver pruinose pattern becomes brown and rest of scutum greyish pruinose (Fig. 784). Humeri, lateral and posterior margins of scutum dark brown to black. Scutellum brown with golden, recumbent hairs and long, erect dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female.

Abdomen: tergites dark brown to black, basal fringe with long, brown hairs. Silver pruinose ornamentation as follows: posterior margin of tergite II and ventro-lateral margins of segment V-VI [best seen when specimens tilted laterally]. Genitalia dark brown to black; tergal plates developed; sternal plate undeveloped. Gonocoxite subquadrangular; gonostyle nearly twice as long as gonocoxite, relatively wide with sinuous margins and stout spine apically (Fig. 869). Ventral plate similar to that of *S. brachycladum*, except main body slightly more developed, lateral arms and anterior median process less developed and basal arms curved internally and pointed apically (Fig. 930). Median sclerite very long, about four times longer than wide at widest point, with small apical incision [it appears curled up in the single specimen examined] (Fig. 930). Paramere with well developed and sclerotised basal process and numerous spines (Fig. 990).

PUPA. Cocoon length dorsally 2.2 – 2.4 mm (n = 2); ventrally 2.7 –3.0 mm (n = 2); pupa length 2.7-3.3 mm (n = 2); gill length 0.6-0.7 mm (mean = 0.6 mm, s.d. = 0.06, n = 4).

Cocoon: shoe-shaped as in Fig. 66, light to dark brown composed of thick coalesced fibres, with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with six upwardly directed filaments arranged in bunch in vertical plane [one specimen with five filaments on the right gill has been examined]. Gill configuration variable with filaments branching at different heights (Figs. 1052, 1053); main trunk short, giving rise to two sets of primary branches, one external and one internal, the external consists of 4 secondary branches and the internal of two secondary branches. Filaments stout, weakly pointed distally [some filaments appeared to be rounded distally], with small spicules on surface, edges weakly crenate; all filaments varying in length, with the ventral filament of the internal set being the longest. Variation in the length and development of the pupal gill filametns was seen between the left and right in specimens from Brazil (Fig. 1053).

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial simple trichomes, and 1+1 sublateral, simple trichomes between frontal and facial trichomes; frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and 4-5 platelets in two groups laterally in frontal region; tubercles absent in frontal region, but pointed and only visible on facial region.

Thorax: with 5+5 or 8+8 simple trichomes; thorax with pointed tubercles on dorsal and posterior region and base of gill, ventrally.

Abdomen: tergite I with pointed tubercles on central part of segment and postero-lateral margins; tergite II with 3+3 submedian spines in longitudinal row and 2+2 simple, short and 1+1 long setae lateral to outermost spine; tergites III and IV with 4+4 submedian spines in longitudinal row; tergites V-VIII damaged; tergite IX without terminal spines, weakly sclerotised. Spine combs distribution as follows: 1+1 groups on antero-lateral margins of tergites II- IV and anterior margins of remaining segments. Abdominal sternite III with 2+2 submedian, simple, small trichomes; sternite IV with 2+2 submedian, simple trichomes, the outermost lateral trichome more prominent that the innermost trichome; sternite V with 2+2 close, simple median hooks; sternites VI-VII with 2+2 simple, well separated hooks; sternite IX weakly sclerotised. Abdominal sternites III-VIII with spine combs on anterior margin.

LARVA (Final instar). [The following measurements were taken from the original description of COSCARÓN & PY-DANIEL (1989); the number of specimens examined was not given in this paper: Body length 5.8-6.3 mm; length of head capsule not given; width of head capsule 0.5-0.6 mm]. Body colour greyish green (specimens in ethanol).

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, rounded apically; postgenal bridge as long as hypostomium (Fig. 1156). Hypostomium strongly pigmented on anterior margin, with nine apical teeth weakly developed and evenly distributed on anterior margin; median tooth well developed and most prominent; 3+3 sublateral teeth adjacent to median teeth; 1+1 lateral teeth of same length as sublateral teeth; 2-3 very small lateral serrations [sometimes difficult to see]; 1+1 lines of approximately 9-10 hypostomial setae parallel to lateral margin; 2+2 long, simple setae in posterior half of hypostomium (Figs. 1211). Sub-esophageal ganglion not examined Antennal segments longer than labral fan stalk, all segments lightly pigmented; length of antennal segments I-III excluding the sensillum 1:1.6-1.7:1 mm. Mandible with three apical teeth, first one longer than remainder; mandibular comb with approximately eight teeth, first four teeth more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior, which is reduced (Fig. 1265). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with more 36-40 rays each with fine, single line of microspinules in row.

Thorax: greyish green dorsally and ventrally. Cuticle without setae. Proleg not described. Pupal respiratory gill histoblast dark brown; dissected gill histoblast with six filaments, all branching near base of gill.

Abdomen: usually greyish green dorsally. Ventral nerve cord not examined. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 189 rows of 28-29 simple hooks. Rectal gills with three lobes of approximately 5-6 finger-like lobules each.

Taxonomic Discussion. *Simulium cristalinum* was described by COSCARÓN & PY-DANIEL (1989) from pharate females and males, as well as pupae and larvae collected at Igarapé Cristalino, Roraima State, Brazil. The authors provided descriptions of all life stages and illustrations of most taxonomic characters commonly used to identify simuliid species. The holotype is said to be housed at INPA, but I have been unable to examine this specimen. However, I have examined one female and one male labelled as paratypes deposited at MLP (see **Material Examined** in SHELLEY *et al.*, 2010).

The taxonomy of *S. cristalinum* have been recently reviewed by SHELLEY *et al.* (2010), who also provided morphological comparisons for all life stages *S. cristalinum* with that of *S. brachycladum*. COSCARÓN & PY-DANIEL (1989) stated that *S. cristalinum* is the sister species of *S. brachycladum* from which it can be distinguished by the different morphology of the cibarial teeth (Fig. 266), female paraproct (Fig. 623), male ventral plate (Fig. 930), and the shorter gill filaments (Fig. 1052). SHELLEY *et al.* (2010) concluded that these two taxa can only be reliably separated by the length and configuration of the pupal gill filaments [see **Taxonomic Discussion** under *S. brachycladum*]. Variation in the length and number of pupal gill filaments occurs in *S. cristalinum.* I have examined one female pupa with five filaments on the right gill (two of them not fully developed) and six on the left side, which also showed differences in filament branch height and length (Fig. 1053; see also SHELLEY *et al.*, 2019, Plate 127, Fig. 1229). More material is required in order to assess this variation.

The larva of *S. cristalinum* is externally similar to that of *S. brachycladum* in that the dissected gill histoblast has six filaments, but they may be separated by the shape of the postgenal cleft, and the number of mandibular serrations. In *S. cristalinum* the postgenal cleft is relatively more triangular and pointed apically (Fig. 1156) and the mandible has two mandibular serrations (Fig. 1265). In *S. brachycladum* the postgenal cleft is wider basally (Fig. 1154) and the mandibles have only one mandibular serration (Fig. 1263).

COSCARÓN & PY-DANIEL (1989), COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) placed this species in the BRACHYCLADUM group of the subgenus *Hemicnetha*, an action followed by CROSSKEY & HOWARD (1997, 2004). However, ADLER & CROSSKEY (2008, 2009, 2010) considered *S. cristalinum* as a member of their PAYNEI species group, and more recently SHELLEY *et al.* (2010) placed *S. cristalinum* in the TARSATUM species group which is followed in this work.

Distribution. *Simulium cristalinum* has only been collected from Igarapé Cristalino (its type locality) and near Uiramutão, R. Cotingo in Roraima State (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & PY-DANIEL, 1989; CROSSKEY & HOWARD, 1997, 2004; see **Material Examined** in SHELLEY *et al.*, 2010).

Biology and Medical Importance. Little is known on the biology of *S. cristalinum*. The immature stages of have been collected in fast flowing, clear water streams with rocky riverbeds or in waterfalls. The female feeding habits are unknown (COSCARÓN & PY-DANIEL, 1989).

2.5.4.4. ***Simulium* (*Trichodagmia*) *earlei*** **VARGAS, MARTÍNEZ PALACIOS & DÍAZ-NÁJERA** (Figs. 214, 267, 370, 371, 508, 565, 624, 684, 785, 786, 870, 931, 991, 1054, 1104, 1157, 1212, 1266)

Simulium (*Dyarella*) *earlei* VARGAS *et al.*, 1946: 118. HOLOTYPE male, MEXICO: Temixco, Morelos, 3.vii.1945, (*A.Díaz-Nájera*) (INDRE) [Examined.]

Simulium keenani FIELD, 1969: 157. HOLOTYPE female (reared), PANAMA: Canal Zone, road junction K-6 and K-9; 20.iii.1956, [Collector's name not stated but presumably G. Field.] [Depositary of the holotype cited as in NMNH, but the material is now considered lost; there is no record of this type being deposited in the NMNH, F.C. THOMPSON: pers. comm. to L.M. HERNÁNDEZ]. **New synonymy**.

Simulium dehnei FIELD, 1969: 162. HOLOTYPE female, PANAMA: Canal Zone, Rodman Naval Base, 25.iii.1955, (*G.Field*) [Future depositary cited as NMNH, but material now considered lost; there is no record of this type having been deposited in the NMNH, F.C. THOMPSON, pers. comm. to L.M. HERNÁNDEZ.] [Synonymy by SHELLEY *et al.*, 2002b: 141 and followed by ADLER & CROSSKEY, 2008: 45, 2009: 48, 2010: 48, and this work; considered a probable synonym of *S. earlei* by COSCARÓN & COSCARÓN-ARIAS, 2007: 553, AND synonymy later accepted byCOSCARÓN *et al.*, 2008: 30.]

FEMALE. General body colour dark brown. Body length (specimens preserved in alcohol) 3.1-3.4 mm (mean = 3.3 mm, s.d. = 0.14, n = 4), wing length 2.5-2.9 mm (mean = 2.8 mm, s.d. = 0.23, n = 4), wing width 1.2-1.5 mm (mean = 1.4 mm, s.d. = 0.13, n = 4).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 214). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus covered with pale, semi-recumbent setae and frons with long, erect, black hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellar segments black. Cibarium with well developed, sclerotised cornuae and small, irregular teeth in the central trough and internal margins of cornuae (Fig. 267).

Thorax: scutum dark brown with faint white pruinosity and evenly arranged groups of recumbent, whitish, broadened setae, interspersed with fine black setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown with 1+1 large, greyish white, wedge-shaped vittae beginning on anterior border of scutum and running for two thirds length of scutum; 1+1 blackish, round vittae on anterior margin and area between grey vittae black; humeri and lateral margins silver (Fig. 370). With posterior illumination, thorax dark brown with faint pruinosity and a median longitudinal and 1+1 submedian posteriorly diverging lines in central region of scutum; posterior margin black (Fig. 371). Scutellum dark brown with recumbent white hairs intermixed with long, black bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with sparse distribution of spines and setae. Subcosta with line of setae in distal half. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 508. Forelegs with coxae, trochanters, femora, and middle of tibiae yellowish to light brown, remainder of tibiae and tarsi dark brown to black. Mid and hind legs mid to dark brown, except for lighter brown on trochanters, base of femora and tibiae, central portion of tibiae, basal half to two thirds of tarsal segment I, and base of tarsal segments II. Claws strongly curved with a distinct basal tooth. Halteres cream with brown base.

Abdomen: tergites I-IX black and brown mottled with very faint overall silver pruinosity, except accentuated on tergite II. Tergal plates undeveloped in the few specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses very long, membranous, narrow apically, with small setae distributed over entire surface (Fig. 565). Cerci subrectangular, covered with distinct, long, brown setae; paraproct subrectangular, membranous, except on external margin, which is weakly sclerotised, with small triangular process basally; paraproct with prominent brown setae basally and highly setose apically (Fig. 624). Genital fork stout and heavily sclerotised; termination of lateral arms with anterior margin straight and well developed, apically blunt; anterior processes well developed; posterior processes well developed and triangular (Fig. 684). Spermatheca globular, with weak external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct one fifth maximum width of spermatheca.

MALE. General body colour dark brown to black. Body length (specimens preserved in alcohol) 3.1-3.7 mm (mean = 3.3 mm, s.d. = 0.33, n = 3), wing length 2.7-3.7 mm (mean = 2.8 mm, s.d. = 0.05, n = 3), wing width 0.9-1.4 mm (mean = 1.2 mm, s.d. = 0.25, n = 3).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark brown with golden, recumbent hairs. Scutal pattern varies slightly with light incidence: with anterior light source thorax brown (Fig. 785). With light source posterior to specimen 1+1 broad, silver vittae beginning near anterior margin and diverging posteriorly, occupying three fourths length of scutum (Fig. 786). Humeri, lateral and posterior margins of scutum dark brown to black. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Silver pruinose ornamentation as follows: whole of tergite II, tergites III, IV on antero-lateral margins and 1+1 lateral areas on tergites VI and VII. Genitalia black; sternal and tergal plates undeveloped. Gonocoxite subquadrangular; gonostyle subrectangular with dorsal and ventral margins sinuous, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 870). Ventral plate subquadrangular, weakly sclerotised, well developed with long hairs and distinct apical depression in place of keel, spatula-shaped basal arms (Fig. 931). Median sclerite very long, about four times longer than wide at widest point, with small apical incision (appears curled up in all specimens examined) (Fig. 931). Paramere with well developed and sclerotised basal process and numerous long spines along whole length (Fig. 991).

PUPA. Cocoon length dorsally 3.0 – 3.7 mm (mean = 3.3 mm, s.d. = 0.24, n = 10), ventrally 5.5 – 5.6 mm (mean = 5.5 mm, s.d. = 0.37, n = 10); pupa length 4.0 – 4.1 mm (mean = 4.1 mm; s.d. = 0.40, n = 10); gill length 1.3 mm (mean = 1.3, n = 9).

Cocoon: shoe-shaped as in Fig. 66, light to dark brown composed of thick coalesced fibres, with reinforced rim to anterior aperture and central protuberance, margin of aperture weakly to strongly elevated.

Gill: light brown with 16 (sometimes 15 or 17) upwardly-directed filaments arranged in a bunch in vertical plane. Gill configuration variable with filaments branching at different heights, but mostly basally (Figs. 1054); common pattern as follows: main trunk short, giving rise to two sets of primary branches: the more external consists of 4 primary branches the two most anterior being unbranched and the two more posterior with three and four branches respectively; the internal consists of two primary branches the anterior with three filaments and the posterior with four filaments. Filaments stout, pointed distally, with small spicules on surface, edges crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial simple trichomes, and 1+1 sublateral, simple trichomes between frontal and facial trichomes; frontoclypeus with distinct group of platelets mesally, 1+1 dorso-laterally and 2-3 platelets in two to three groups laterally in frontal region, respectively; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region.

Thorax: with 5+5 large, bifid to five-branched trichomes near margin of dorsal cleft and three simple trichomes on alar region; tubercles mostly rounded (few pointed at base of gill), only visible on ventral region, at base of gill and postero-lateral margin of dorsal cleft.

Abdomen: tergite I with 2+2 simple, long trichomes laterally and rounded tubercles on posterior margin; tergite II with 3+3 submedian spines in longitudinal row and 1+1 simple, long setae lateral to outermost spine; tergites III and IV with 4+4 submedian spines in longitudinal row, sometimes 1+1 simple, short setae anterior to most lateral spines; tergites V-VI with 5+5 small, simple setae in longitudinal row; tergite VII with 1+1 small, simple trichomes sublaterally; tergite IX without terminal spines, weakly sclerotised. Spine combs distribution as follows: 1+1 groups on antero-lateral margins of tergites II-VII, and on posterior margins of I and II. Sternite III with 3+3 simple, small trichomes and simple hook laterally; sternite IV with 2 sublateral and 2 median, small, simple setae, 1+1 simple hooks laterally and spine combs on anterior margin; sternite V with 2+2 close, simple median hooks, 2 small, simple setae and 1+1 stout teeth laterally, and groups of spine combs on anterior margin; sternites VI-VII with 2+2 well separated hooks, distinct tooth on lateral margin and groups of spine combs on anterior margin, especially laterally; sternite IX weakly sclerotised apically with spine combs on anterior margin.

LARVA (Last instar). Body length 8.2-10.0 mm (mean = 9.0 mm, s.d. = 0.66, n = 5); length of head capsule 0.9-1.0 mm (mean = 0.9 mm, s.d. = 0.04, n =5); width of head capsule 0.7-0.8 (mean = 0.7 mm, s.d. = 0.05, n = 5). Body colour dark grey with greenish tint dorso-laterally, whitish ventrally (specimens preserved in Carnoy's solution and/or alcohol). General body form as in Fig. 1104

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft small, rounded apically; postgenal bridge 1 to 1.5 times longer than hypostomium (Fig. 1157). Hypostomium strongly pigmented on anterior margin, with eight or nine apical teeth evenly arranged on anterior margin sometimes with all teeth, except median, below or at same level; median tooth more prominent than remainder; 3+3 or 2+3 sublateral teeth, sometimes very reduced; 1+1 lateral teeth reduced and at same level as sublateral teeth; 6+6 small, lateral serrations; 1+1 lines of 7 hypostomial setae parallel to lateral margins [few specimens with 10 setae have been examined]; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1212). Sub-esophageal ganglion lightly pigmented. Antenna same length as labral fan stalk; antennal segments lightly pigmented; length of antennal segments I-III excluding the sensillum 0.1:0.1:0.09-0.1 mm (n = 3). Mandible with three apical teeth, first longer than second and third; mandibular comb with approximately 13 teeth, first three more prominent than remainder; one mandibular serration in specimens I have examined (Fig. 1266 [IBÁÑEZ-BERNAL (1992) illustrated specimens with two mandibular serration, the anterior smaller than the posterior]. Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with 44-50 rays each with fine, single line of spines in a row (n = 3).

Thorax: pale grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 30-35 processes (n = 3). Pupal respiratory gill histoblast dark brown; dissected gill histoblast often with 16 filaments.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 135-138 rows of sclerotised processes of 30-40 simple hooks (n = 3) [IBÁÑEZ-BERNAL (1992) gave ranges of 190-220 rows of 28-30 simple hooks. Rectal gills with three lobes of 7-9 finger-like lobules, dorsal lobules more prominent than ventral lobules (n = 1).

Taxonomic Discussion. *Simulium earlei* was described VARGAS *et al.* (1946) based on females, males, pupae and larvae collected at Temixco, in Morelos State, Mexico. I have examined the legs, wing and genitalia of the male holotype and a female paratype both mounted on a slides, and a pinned male paratype, all housed at INDRE Simuliidae collections (see SHELLEY et al., 2002b; **Material Examined**).

The taxonomy of *S. earlei* has been thoroughly reviewed by SHELLEY e*t al.* (2002b), who also discussed the morphological variation of the pupal gill filaments and proposed *S. dehnei* as junior synonym of *S. earlei* [note subsequent mis-spellings as *S. deheni* by COSCARÓN, 1987, and as *S. earli* byVARGAS & DÍAZ NÁJERA (1957b)]. In the same paper, the authors noted the close morphological similarity of *S. keenani* with *S. earlei* (see also IBÁÑEZ-BERNAL, 1992), but they did not synonymise the species "because of lack of material and some differences in the pupal gill configuration". Since then I have collected numerous adults and immature stages of *S. earlei* in Costa Rica, and I have the following comments to make. *Simulium keenani* was described by FIELD (1969) from a female holotype, and one male and one female (as paratypes) collected from Canal Zone, Panama in 20.March.1956 probably by FIELD. FIELD (1969) stated that a holotype and paratypes of *S. keenani* would be deposited in the NMNH. However, there is no record of this material at the NMNH and it is now presumably lost (F.C. THOMPSON, pers. comm. to L.M. HERNÁNDEZ). I have re-examined the original description and figures of *S. keenani* and compared it with numerous specimens of *S. earlei*, and found that *S. keenani* falls within the variation found in *S. earlei.* I regard the small differences in the pupal gill configuration as intraspecific, hence I consider both species conspecific.

In Central America, the female of *S. earlei* is externally similar to *S. solarii* and *S. guerrerense* by possessing a dark brown thorax with 1+1 silver pruinose lateral vittae [with light source anterior] (Figs. 370, 376, 404). The male is externally similar to that of *S. yepocapense* (Figs. 785, 825) from which it can only be distinguished by the configuration of the pupal gill filaments.

The best character that readily identifies *S. earlei* is the presence of 15 to 17 pupal gill filaments (commonest number is 16 filaments) all arranged in the vertical plane (Fig. 1054). In this respect, *S. earlei* is most similar to *S. solarii*, but in the latter species the filaments are all arranged in bunch (Fig. 1070), while in *S. earlei* are more widely spread out (Fig. 1054). Other species with a similar number of gill filaments in the pupa is *S. smarti*, but the number of gill filaments (18 filamens - as in the original description of VARGAS, 1942) and gill configuration (Fig. 1069) readly separate *S. smarti* from *S. earlei.*

The larva of *S. earlei* may be separated from other Central American species in the TARSATUM species group (*sensu* SHELLEY *et al.*, 2010) by the central region of the head prominently dark brown compared to light brown to yellowish in other species, and the dissected gill histoblast normally with 16 filaments. Apart from these characters, the larva of *S. earlei* resembles those of other species in the TARSATUM species group [see also Figs. 1157, 1212, 1266 for morphological features in the hypostomial teeth and mandible, respectively].

Descriptions of life stages of *S. earlei* may be found in COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955), IBÁÑEZ-BERNAL (1992) and SHELLEY *et al.* (2002b).

Simulium earlei was placed in the MEXICANUM species group by COSCARÓN (1987) and this was accepted by CROSSKEY & HOWARD (1997, 2004). HERNÁNDEZ & SHELLEY (2005) replaced the MEXICANUM species group name with the TARSATUM species group, which has was accepted by ADLER & CROSSKEY (2008) and SHELLEY *et al.* (2010), although COSCARÓN & COSCARÓN-ARIAS (2007) still recognized the MEXICANUM species group.

Distribution. *Simulium earlei* has a limited distribution in the Neotropical Region, only occurring in Central America (Belize, Costa Rica, Guatemala, Mexico and Panamá) (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN, 1987; CROSSKEY & HOWARD, 1997, 2004; IBÁÑEZ-BERNAL, 1992; see also

Material Examined in SHELLEY *et al*., 2002b; 2010). It is a relatively uncommon species in Costa Rica (L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data).

Biology and Medical Importance. SHELLEY *et al.* (2002b) collected the immature stages of *S. earlei* in Belize in large (10 to 30 m wide), fast flowing rivers, with pupae and larvae attached to rocks and dead leaves in parts of the river where the current is faster. It has been collected in Costa Rica in similar habitats in the Central mountain range at altitudes of 428 m in streams of 6m wide and 5m deep with moderate water flow (L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data). IBÁÑEZ-BERNAL (1992) reported it occurring between 200 m to 1.700 m in Mexico, while in Guatemala it has been found in the mountains of the Central and Coastal Departments (DALMAT, 1955).

The female feeding behaviour of *S. earlei* is unknown (IBÁÑEZ-BERNAL, 1992), though SHELLEY *et al.* (2002) stated that the females are zoophilic in Belize. They also appear to be zoophilic in Costa Rica (L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data).

2.5.4.5. *Simulium (Trichodagmia) freemani* VARGAS & DÍAZ NÁJERA (Figs. 57, 215, 268, 372-375, 509, 566, 625, 685, 787-790, 871, 932, 992, 1055, 1056, 1105, 1158, 1213, 1267)

This is a relatively poorly known, zoophilic species which is only found in Central America and the United States. The description here provided has been derived from the original description, examination of the type material, and identified specimens housed at the BMNH and CUAC collections.

Simulium (Dryarella) freemani VARGAS & DÍAZ NÁJERA, 1949: 289. HOLOTYPE male (reared), MEXICO: Oaxaca State, Etla, San Pablo; 21.i.1949, (*Francisco Reyes Salgado*) (INDRE, no. 3964) [Examined.]

FEMALE. General body colour dark brown. Body length (specimens pinned) 4.5 mm (n = 1); wing length 3.0-4.1 mm (n = 2), wing width 1.8 mm (n = 1). Body length (specimen in ethanol) 3.7 mm; wing length 2.1 mm (n = 1), [wing width not given because wing was in poor condition].

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 215). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae, with fine teeth on membrane on central trough and small and finer teeth on margin of cornuae [best seen at higher maginification] (Fig. 268).

Thorax: scutum dark brown to black with evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent brown setae mainly on posterior margin. Scutal pattern varying slightly with illumination. In type material [specimens from Mexico], the female appears to have been preserved in alcohol and later pinned. Thus, with light source anterior, thorax is dark brown to black with 1+1 median, pear-shaped and 1+1 sublateral wide dark brown vittae, 1+1 submedian comma-shaped black markings, and one fine median black line extending from anterior to posterior margins; humeri pale brown; lateral and posterior margins black (Fig. 372). With posterior illumination, thorax dark brown with faint 1+1 silver pruinose vittae on black background on anterior third of scutum, fine median black line extending from anterior to posterior margins; humeri, pale brown; posterior and lateral margins dark brown to black (Fig. 373). In well preserved pinned material [specimens from USA] with light anterior, thorax black with 1+1 silver pruinose, pear-shaped vittae and 1+1 wide silver-pruinose vittae extending from anterior to posterior margin; humeri pale yellow; lateral and posterior margins black (Fig. 374). With light source posterior, thorax black with distinct 1+1 median silver pruinose rounded vittae in anterior third of scutum; humeri and lateral margins silver pruinose; posterior margin black (Fig. 375). Scutellum dark brown to black with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown to black with silver pruinosity. Pleura dark brown to black with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae in material from the United States. Radius with numerous setae intermixed with distinct spines, basal section of radius without setae in specimens from the USA. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 509. Fore leg with coxa and trochanter pale brown; femur and tibia dark brown, tarsal segments black. Mid leg with coxa, apex of femur, apical two thirds of tibia, apical third of tarsal segments I, II, and tarsal segments III-IV dark brown to black; trochanter pale brown; basal third of tibia and basal third of tarsal segment I whitish. Hind leg with coxa, internal surface and apical third of femur, tibiae, apical half of tarsal segment I, and tarsal segment II-IV dark brown; trochanter and remainder of femur pale brown; basal half of tarsal segment I white. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I, II and antero-lateral margins of tergites III, IV pale brown; tergites V-VIII shiny black. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with approximately ten long, irregularly distributed setae on posterior margin; gonapophyses nearly 1.5 times longer than eighth sternite at mid point, subtriangular, with internal margins curved anteriorly and straighter toward apex, internal margins of gonapophyses sclerotised, remainder membranous; gonapophyses densely covered with microtrichiae basally and long hairs apically (Fig. 566). Cerci subrectangular, covered with brown setae; paraproct subquadrangular small, , same length as cercus, weakly sclerotised on basal half and membranous apically; paraproct densely covered with prominent brown hairs and few basal setae (Fig. 625). Genital fork stout and sclerotised; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed and blunt apically, posterior processes well developed (Fig. 685). Spermatheca globular, without external sculpturing and with groups of irregularly distributed, single spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour dark brown to black. Body length (specimens pinned) 4.8 mm (n = 1); wing length 2.5-3.6 mm (n = 2), wing width 1.3-1.6 mm (n = 2). Body length (specimen in spirit, n =1) 4.1 mm; wing length 3.9 mm, wing width 1.9 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark brown to black covered by semi-recumbent golden hairs in the type material. In pristine specimens, thorax black covered by white hairs. Scutal pattern varies slightly with light incidence: In type material [specimens from Mexico], irrespective of light incidence, thorax dark brown with 1+1 submedian small black comma-shaped vittae on anterior third of scutum; fine black line on central region extending from anterior to posterior margins; humeri pale brown weakly silver pruinose; lateral and posterior margins black with faint pruinosity (Figs. 787, 788). In specimens from the USA with light source anterior, thorax with 1+1 median and 1+1 submedian, wide silver pruinose areas on anterior third of scutum; humeri weakly yellowish, lateral margins black (Fig. 788, 789). With light source posterior thorax black with 1+1 faint silver pruinose vittae extending from anterior to posterior margins; humeri lightly pruinose; lateral and posterior margins black. Scutellum dark brown with golden or white recumbent hairs intermixed with long, erect, dark brown setae. Postnotum dark brown to black with silvery grey pruinosity. Wing setation as in female except Sc bare in the specimens examined (holotype and material from the USA). Leg coloration as in female.

Abdomen: tergites dark brown to black, basal fringe with long, brown hairs. Tergite I pale white laterally, pruinose ornamentation on antero-lateral margins of tergites V-VII [best seen in some specimens when tilted and viewed laterally]. Genitalia dark brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle subrectangular with dorsal and ventral margins sinuous, terminating in single, stout subapical spine; gonocoxite and gonostyle covered with long setae (Fig. 871). Ventral plate sclerotised, subtriangular, covered with long hair; body of ventral plate prominently developed centrally [best seen in lateral view]; shoulders undeveloped and basal arms well developed and subparallel (Figs. 57, 932). Median sclerite long, about two and half times longer than wide at widest point, apparently with apical incision (Fig. 932), but curled. Paramere with well developed and sclerotised basal process and numerous long spines along whole length (Fig. 992).

PUPA. Cocoon length dorsally 3.0-4.7 mm (mean = 3.7 mm, s.d = 0.70, n = 5), ventrally 4.2-5.7 mm (mean = 5.1 mm, s.d. = 0.68, n = 5); pupa length 4.5-6.5 mm (mean = 5.4 mm, s.d. = 0.79, n = 5); gill length 1.2-2.0 mm (mean = 1.6, s.d. = 0.29, n = 6).

Cocoon: shoe-shaped as in Fig. 66, brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated without fenestrations.

Gill: light brown with eight upwardly directed filaments arranged in bunch in vertical plane (Figs. 1055-1056). Gill with main trunk short, giving rise to two sets of primary branches one external and one internal, each with four secondary branches, all arising near gill base. Filaments stout, rounded distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus)*: with 2+2 frontal and 1+1 facial small, simple trichomes, and 1+1 small, sublateral, simple trichomes between frontal and facial trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in two groups laterally in frontal region; tubercles rounded and well distributed over entire surface.

Thorax: with 1-4 simple trichomes near margin of dorsal cleft, one trichome on posterior region, and 2-4 simple trichomes on alar region and near ventral margin of pupa; tubercles rounded and densely distributed over entire surface.

Abdomen: abdominal tergite I with 1+1 submedian, simple, short setae and rounded tubercles densely distributed along posterior margin; tergite II with 3+3 submedian spiniform setae in longitudinal row, 3+3 simple short setae lateral to outermost spiniform setae, and 2+2 small simple setae on lateral margin; tergites III and IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to most lateral of hooks, and 3+3 sublateral simple setae; tergites V-VII with 3+3 or 2+2 submedian small simple setae in row on posterior margin and 2+2 or 1+1 small simple setae laterally; tergite VIII with 1+1 submedian small simple setae; tergite IX without setae and weakly sclerotised. Spine combs distributed on antero-lateral margins of tergites II-IV, and also on posterior margins of tergites I-IV. Sternite III with 2+2 submedian small simple setae; sternite IV with 2+2 submedian small simple setae, and 3+3 small simple setae laterally; sternite V with 2+2 close submedian simple hooks, and 2+2 small simple setae lateral to outermost hooks; sternites VI, VII with 4+4 well separated hooks in row on posterior margin, 1+1 small simple setae between innermost hooks and 3+3 or 4+4 small, simple setae lateral to hooks and near lateral margins; sternite VIII with 3+3 submedian small simple setae, and 2+2 small simple setae on lateral margin; sternite IX without terminal spines. Spine combs distributed on anterior margin of sternites III-VIII.

LARVA (Only penultimate instar available). Body length 9.3-9.9 mm (mean = 9.6 mm, s.d. = 0.3, n = 3); length of head capsule 0.8-1.8 mm (mean = 1.1 mm, s.d. = 0.43, n = 4), width of head capsule 0.7-1.7 mm (mean = 1.0 mm, s.d. = 0.45, n = 4). Body colour dark grey dorso-laterally, whitish ventrally (specimens preserved in alcohol). General body form as in Fig. 1105.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly 1.5 times longer than hypostomium (Fig. 1158). Hypostomium strongly pigmented on anterior margin, with nine apical teeth distinctly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with the pair adjacent to base of median tooth longer than remainder, two outermost sublateral teeth nearly totally underneath anterior margin; 1+1 lateral teeth, longer than basal sublateral tooth; 8+8 small, lateral serrations only clearly visible at higher magnification; 1+1 lines of 13-14 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1213). Sub-esophageal ganglion unpigmented. Antenna same length as labral fan stalk, segments I-III pale to dark brown; length of antennal segments I-III excluding the sensillum 0.08-0.1:0.1:0.07-0.09 mm (n = 4). Mandible with three apical teeth, second smaller than first and third; mandibular comb with seven teeth, first four teeth more prominent than remainder teeth; two mandibular serrations, anterior slightly longer than posterior (Fig. 1267). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan swollen basally with 47-49 rays each with fine, single line of spines in a row (n = 2).

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 30-46 rows of 13-14 hooks (n = 2). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with eight filaments, all branching from common trunk and pointed apically.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms swollen, extending two thirds diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 229-290 rows of 40 simple hooks (n = 2). Rectal gills with three lobes each with approximately 11-13 finger-like lobules (n = 2).

Taxonomic Discussion. *Simulium freemani* was described by VARGAS & DÍAZ NÁJERA in 1949 based on a male holotype, four females and 16 pupal exuviae (all as paratypes) collected in Oaxaca State, Mexico. The coloration, dorsal profile and head morphology of the larva was illustrated for the first time by ADLER *et al.* (2004). I have examined the male holotype, which is housed at INDRE. The specimen is in relatively good condition, and is mounted on a card triangle on its left side. Its left wing, left three legs, abdomen and genitalia are on a slide. The cocoon and pupal exuviae are preserved in ethanol (**Material Examined**). I have also examined a pinned female allotype at INDRE; one wing, three legs and its genitalia are mounted on a slide. In addition, I have examined at INDRE another male paratype also on a slide (**Material Examined**).

The female of *S. freemani* (Figs. 372-375) is externally similar to the dark brown to black form of *S. virgatum s.l.* (Figs. 412-415) from which it can only be distinguished by the configuration of the cocoon in link-reared specimens. The male is also externally similar to that of *S. virgatum s.l.* (Figs. 787-790, 821-824), but they are easily separated by the general morphology of the ventral plate (Figs. 57, 932, 948). In *S. virgatum s.l.* the ventral plate has an antero-median process prominently developed (Fig. 948), which is absent in *S. freemani* (Figs. 57, 932). *Simulium paynei* is also morphologically very similar to *S. freemani*, but the shape of the ventral plate easily separates them (Figs. 59, 932, 938-941).

The best character to identify *S. freemani* is the number of the gill filaments (Figs. 1055, 1056) and the morphology of the cocoon. In *S. freemani* the pupa has eight gill filaments, a character that it shares with *S. bricenoi*, *S. paynei*, *S. rubrithorax*, and *S. virgatum s.l.* However, *S. freemani* can be separated from these species by the absence of prominent fenestrations on the anterior margin of the cocoon. *Simulium bricenoi* can be recognised by the presence of rhomboid-like markings in the pupal thorax. *Simulium rubrithorax* and *S. virgatum s.l.* can only be separated by the combination of the configuration of the pupal gill filaments in link-reared adults and the morphology of the male genitalia (see Figs. 882, 887, 943, 948, 1003, 1008).

The larva of *S. freemani* cannot be reliably separated from other species in the TARSATUM species group in which the dissected gill histoblast has eight filaments. In the **Key to larva** in **section 2.4.9** it can be separated from that of *S. rubrithorax* by the absence of a tube-like incision in the apex of the postgenal cleft (Figs. 1158, 1166). The different morphology of the hypostomial teeth may also be used to separate larvae of *S. freemani* and *S. virgatum s.l.* (Figs. 1213, 1225).

Two colour forms appear to occur in link-reared specimens of *S. freemani*, in which the gill configuration and number of gill filaments agree with the pattern described for this species. In specimens from Mexico, the female and male are brown (Figs. 372, 373, 787, 788), while in specimens from the USA the specimens are black (Figs. 374, 375, 789, 790). This color variation might indicate the presence of a species complex in *S. freemani*, but this requires further study. The cytotaxonomy of *S. freemani* has been reviewed by ADLER *et al.* (2004), who studied the chromosomes of larvae collected from Box Elder, Utah, USA. The authors stated that in this species the chromosomes are non-chromocentric and that they have a subterminal nucleolus organizer in IS, leaving a small terminal piece of the chromosome detached from the remainder of the arm.

Full descriptions of adults, pupae and larvae of *S. freemani* might be found in ADLER *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), IBÁÑEZ-BERNAL (1992), and VARGAS & DÍAZ NÁJERA (1949).

CROSSKEY & HOWARD (1997, 2004) placed *S. freemani* in the MEXICANUM species group of the subgenus *Hemicnetha*. ADLER *et al.* (2004) allotted this species to their PAYNEI species group, but COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) still maintained it in the MEXICANUM species group because they did not recognize the synonymy of *S. mexicanum* under *S. tarsatum* by HERNÁNDEZ & SHELLEY (2005). However, this synonymy has been accepted by the recent

World Inventory of Blackflies (ADLER & CROSSKEY *et al.*, 2008, 2009, 2010). More recently, SHELLEY *et al.* (2010) subsumed the PAYNEI species group under the TARSATUM species group in the subgenus *Trichodagmia*, where *S. freemani* is currently placed.

Distribution. *Simulium freemani* has been recorded from northern Utah through Arizona, New Mexico in the USA southwards into Central America (ADLER *et al.*, 2004; ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS (2007); **Material Examined**). The record of *S. freemani* for Costa Rica (ADLER & CROSSKEY, 2008, 2009) is doubtful as this taxon has not been found during a countrywide survey of Simuliidae in this country (L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data).

Biology and Medical importance. Little is known on the biology of *S. freemani*. ADLER *et al.* (2004) found larvae and pupae from March through August in the United States, and they are probably present throughout the year. The authors argued that females might be mammalophilic. COSCARÓN & COSCARÓN-ARIAS (2007) stated that the immature stages of *S. freemani* can be collected in rocky streams at 1600-2000 m, and that the female feeding habit is unknown.

2.5.4.6. *Simulium* (*Trichodagmia*) *guerrerense* VARGAS & DÍAZ NÁJERA (Figs. 216, 269, 376, 377, 510, 567, 626, 686, 791, 792, 872, 933, 993, 1057, 1106, 1159, 1214, 1268)

This is a zoophilic species only known from Mexico externally very similar to *S. pulverulentum*.

Simulium (Hemicnetha) guerrerense VARGAS & DÍAZ NÁJERA, 1956: 51. HOLOTYPE male (reared, but not associated with pupal exuviae), MEXICO: Guerrero State, Ayutla; xii.1945, (*A.Díaz, N.*) (INDRE, no. 6412) [Examined.]

FEMALE. General body colour dark brown. Body length (specimen pinned, n = 1) 2.4 mm, wing length 2.4 mm, wing width 1.1 mm.

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 216). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 269).

Thorax: scutum dark brown with evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent brown setae. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown with 1+1 median, pear-shaped vittae and 1+1 wide silver pruinose vittae visible on middle of thorax; humeri faint silver pruinose; lateral and posterior margins dark brown (Fig. 376). With light posterior, thorax dark brown with weak silver pruinosity on central region, and 1+1 brown lines diverging posteriorly towards lateral margins; humeri silver pruinose; lateral and posterior margins dark brown to black (Fig. 377). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length except apical third. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 510. Fore leg with coxa, trochanter, basal half of femur and mid tibia pale brown; apical half of femur, basal and apical regions of tibia, and tarsal segments I-IV dark brown to black. Mid leg with coxa, apex of femur, two thirds of tibia, apical quarter of tarsal segment I, and tarsal segments II-IV dark brown; coxa, trochanter, basal thirds of femur, and small basal spot on tibia pale brown, basal half of tarsal segment I whitish. Hind leg with with coxa, apical third of femur, two thirds of tibia, apical half of tarsal segment I and tarsal segments II-IV dark brown; coxa, trochanter, and small ring on base of tibia pale brown; basal half of tarsal segment I whitish. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I, II pale brown; tergites III-VIII dark brown. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown. Eighth sternite sclerotised with approximately 13 long, irregularly distributed setae on posterior margin; gonapophyses nearly two times longer than eighth sternite at mid point, subtriangular, with curved internal margins at junction with eighth sternite; internal margins weakly sclerotised and remainder membranous; gonapophyses densely covered with microtrichiae (Fig. 567). Cercus subrectangular, covered with brown setae; paraproct subquadrangular, twice length of cercus, weakly sclerotised on basal half and membranous apically; paraproct densely covered with prominent brown hairs (Fig. 626). Genital fork stout and sclerotised; termination of lateral arms with anterior margins weakly curved and well developed; anterior processes well developed and blunt apically, posterior processes well developed (Fig. 686). Spermatheca globular, without external sculpturing and lines of single spicules on internal surface; area of insertion of spermathecal membranous.

MALE. General body colour dark brown to black. Body length (specimens pinned, n = 2) 2.5-2.7 mm, wing length 1.8-2.1 mm, wing width 0.9-1.0 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark brown covered with recumbent white hairs. Scutal pattern, irrespective of light incidence, dark brown with 1+1 submedian white pruinose bands that arise on anterior third of scutum and diverge on posterior margin; single dark brown line on central region of thorax extending from anterior to posterior margins; humeri weakly silver pruinose; lateral and posterior margins dark brown to black (Figs. 791, 792). Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: tergites I-III pale brown; tergites IV-IX dark brown. Genitalia dark brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle subrectangular with dorsal and ventral margins sinuous, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 872). Ventral plate weakly sclerotised, subrectangular with anterior median process weakly developed, concave apically, and small flap-like process on ventral margin; ventral plate with shoulders underdeveloped and distinctly concave, and basal arms developed and subparallel; main body of ventral plate covered by small hairs on central region (Fig. 933). Median sclerite not examined. Paramere with well developed and sclerotised basal process with numerous long spines apically, central membranous area covered with fine spicules (Fig. 993).

PUPA. Cocoon length dorsally 2.7-3.0 mm (mean = 2.8 mm, s.d. = 0.13, n = 8), ventrally 3.2-4.2 mm (mean = 3.6 mm, s.d. = 0.35, n = 8); pupa length 2.7-3.7 mm (mean = 3.1 mm, s.d. = 0.32, n = 8); gill length 0.7-1.0 mm (mean = 0.8 mm, s.d. = 0.10, n = 8).

Cocoon: shoe-shaped as in Fig. 66, brown to dark brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture strongly elevated.

Gill: light brown with ten upwardly directed filaments arranged in bunch in vertical plane (Fig. 1057). Gill configuration with filaments branching basally at different heights; main trunk short, giving rise to three sets of primary branches; one dorsal and one median with four secondary branches each, and one ventral with two secondary branches. Filaments stout, pointed distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (frontoclypeus): with 2+2 frontal small, simple and 1+1 small, simple facial trichomes.Frontoclypeus with group of platelets mesally, 1+1 groups dorsolaterally and two platelets in two groups laterally in frontal region; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region. Small carina extends across facial region.

Thorax: 2-3 long, simple trichomes on dorsal cleft; 2-33 simple trichomes centrally near base of gills, 2+2 simple trichomes on ventral region; and one long, simple trichome on posterior region of thorax; tubercles rounded only visible at base of gill and postero-lateral margin of dorsal cleft.

Abdomen: abdominal tergite I with 1+ 1 submedian simple short setae and pointed tubercles on posterior margin; tergite II with 3+3 submedian spiniform setae in longitudinal row, 3+3 simple setae lateral to outer most of spiniform seta, one simple setae anterior to outermost spiniform setae, and 1+1 simple setae on lateral margin; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, 3+3 small setae anterior to outermost hooks, and 1+1 small, simple setae on lateral margin; tergites V-

VIII with 3+3 or 2+2 small simple setae in row on central region; tergite IX without setae, tergite IX weakly sclerotised without terminal spines. Spine combs on anterior margins of tergites II-IX. Sternite III, IV without setae or trichomes, though sometimes with 2+2 small sublateral simple setae; sternite V with 2+2 close simple hooks and 1+1 small sublateral setae; sternites VI, VII with 4+4 well separated simple hooks along posterior margins, and 2+2 small simple setae outermost to lateral hooks; sternite VIII without setae or trichomes; sternite IX weakly sclerotised. Spine combs on anterior margins of sternites III, IV, and VIII, IX, and anterolateral margin of sternite VIII.

LARVA (Final instar). Body length 5.2-6.0 mm (mean = 5.7 mm; s.d. = 0.27, n = 6); length of head capsule 0.5-1.3 mm (mean = 0.7 mm, s.d. = 0.33, n = 6); width of head capsule 0.5-1.1 mm (mean = 0.7 mm, s.d. = 0.27, n = 6). [I was unable to obtain fresh material of this species, therefore, the coloration here described has been derived from IBÁÑEZ-BERNAL (1992) and material fixed in alcohol housed at INDRE: Body colour dark grey to white]. General body form as in Fig. 1106

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft small and dome-shaped, and rounded apically; postgenal bridge nearly as long as hypostomium (Fig. 1159). Hypostomium strongly pigmented on anterior margin, with nine to 10 apical teeth weakly protruding in central region; median tooth sharp, sometimes more developed than sublateral teeth but smaller than lateral teeth; 3+3 sublateral teeth all of same length; 1+1 lateral teeth, more prominent than remainder; 3+3 small, lateral serrations; 1+1 lines of eight hypostomial setae parallel to lateral margin; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1214). Sub-esophageal ganglion lightly pigmented. Antenna nearly same length as labral fan stalk, segments light brown; length of antennal segments I-III excluding the sensillum 0.1:0.06-0.1:0.07-0.98 mm (n = 6). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately seven teeth, first, second and third more prominent than remainder; single prominent mandibular serration (Fig. 1268). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with more than 47 rays each with fine, single line of spines in a row.

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 30-40 processes (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 10 filaments, all branching basally.

Abdomen: whitish. Ventral nerve cord greyish. Ventral papillae absent. Cuticle without setae in all specimens examined. However IBÁÑEZ-BERNAL (1992) stated that small setae are found near the anal sclerite. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 111-134 rows of 28-34 simple hooks (n = 2). Rectal gills with three lobes each with six small, finger-like lobules (n = 4).

Taxonomic Discussion. VARGAS & DÍAZ NÁJERA (1956) discussed in detail the taxonomic confusion surrounding the material collected by VARGAS (1943a) and VARGAS *et al.* (1946) from Ayutla, Guerrero State, Mexico, which they previously identified as *S. pulverulentum.* They concluded that the material from Ayutla was morphologically different from the type material and other specimens identified as *S. pulverulentum* from other localities in Mexico, especially in the morphology of the ventral plate, and erected the name *S. guerrerense.*

Simulium guerrerense was described by VARGAS & DÍAZ NÁJERA in 1956 from a male holotype, a female (allotype), 15 adults (of both sexes), and numerous larvae and pupae collected in Guerrero State, Mexico. I have examined the male holotype, which is deposited in INDRE. The specimen is in good condition and it has been glued to a card point by the ventral side of the thorax. It appears to have been stored in alcohol and had lost all setae from the central region of the thorax (**Material Examined**). I have also examined the female allotype, and numerous adults and immature stages labelled as paratypes housed at INDRE (see **Material Examined)**.

In Mexico , the female of *S. guerrerense* is externally most similar to that of *S. pulverulentum* and *S. yepocapense* in that the thorax is brown with a median and 1+1 sublateral silver pruinose vittae (Figs. 376, 377). They cannot be easily separated without examination of link-reared males collected at the same locality. The best character to identify *S. guerrerense* is the morphology of the male ventral plate. In *S. guerrerense* the ventral plate is subquadrangular without the median process prominently expanded and the shoulders are not distinctly pronounced (Figs. 933). In *S. pulverulentum* the ventral plate has the median process prominently expanded and the lateral shoulders are produced (Fig. 942). *Simulium yepocapense* is recognized by the absence of a median process in the ventral plate (Fig. 949).

The pupal gill configuration and number of gill filaments (10) of *S. guerrerense* is very similar to that of *S. pulverulentum* (Figs. 1057, 1067), and I have been unable to find morphological differences to separate these species. However, VARGAS & DÍAZ NÁJERA (1956) stated that the striations on the surface of the gill filaments in *S. guerrerense* were more widely distributed than in *S. pulverulentum*. I considered that this character might vary intraspecifically, thus it cannot be used to separate these taxa.

The larva of *S. guerrerense* cannot be easily separated from *S. pulverulentum*. Nonetheless, in S. *pulverulentum* the median tooth of the hypostomium is relatively more prominent than in *S. guerrerense* (Figs. 1214, 1229). IBÁÑEZ-BERNAL (2002) stated that the larva of *S. guerrerense* can be identified by the positive head pattern, but this character has been shown to vary within populations of some species in the Neotropical Region (CHARALAMBOUS *et al.*, 1997).

Description of life stages of *S. guerrerense* may be found in IBÁÑEZ-BERNAL (2002) and COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium guerrerense was placed in the subgenus *Hemicnetha*, PAYNEI species group by ADLER & CROSSKEY (2008, 2009, 2010), which have been followed by COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008). More recently, SHELLEY *et al.* (2010) placed *S. guerrerense* in the TARSATUM species group of the subgenus *Trichodagmia* because of their synonymy of *Hemicnetha* under *Trichodagmia*, and this is accepted in the current work.

Distribution. *Simulium guerrerense* has only been recorded from the state of Guerrero in Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; **Material Examined**).

Biology and Medical Importance. The biology of *S. guerrerense* is poorly known. The immature stages are found in the same sorts of streams as some of the closely related species such as *S. pulverulentum* and *S. yepocapense* (IBÁÑEZ-BERNAL, 1992).

2.5.4.7. *Simulium* (*Trichodagmia*) *hieroglyphicum* PETERSON, VARGAS & RAMÍREZ PÉREZ (Figs. 72, 74, 84, 270, 511, 568, 627, 687, 793, 794, 873, 934, 994, 1058, 1107, 1160, 1215, 1269)

This is a zoophilic species only known from Costa Rica and Panamá. Several attempts to collect link-reared adults in its type locality were unsuccessful, with only one pharate pupa and a few mature larvae found. Therefore, the description provided here has been derived upon examination of the type material housed at NMNH, the description of PETERSON *et al.* (1988), and identified specimens deposited at BMNH, CUAC and MZUCR collections.

Simulium (Hemicnetha) hieroglyphicum PETERSON *et al.*, 1988: 76. HOLOTYPE male (reared), COSTA RICA: Provincia Alajuela, Cantón Poás, Rio Poasito, stream 34, upstream from bridge, at 23.5 km from Carrizal on the road to Poás Volcano; 4.xi.1986, (*Solano, A.V. & González, W.*) (NMNH) [Examined.]

FEMALE. [The description of the female has been derived from the examination of specimens on slides – see **Material Examined**, and the original description of PETERSON *et al.* (1988). The coloration of the thorax in the females was described from a pharate female in ethanol as in PETERSON *et al.* (1988); the number of specimens examined was not given in the latter paper]. General body colour blackish brown. Body 4.0 mm, wing length 4.0-4.5 mm [wing width was not given in the original description].

Head: dichoptic with dark red eyes and nudiocular area well developed. Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and 45 minute setulae in membrane centrally (Fig. 270).

Thorax: Scutum densely covered with short recumbent golden setae grouped in small clusters; lateral margins slightly more pale brownish and silver pollinose border extending around margins, posterior margin silver pollinose; humeri without silver pollinosity; scutum in posterior view with three slender dark vittae extending from anterior to near posterior margins. Scutellum dark brown with short, adpressed golden setae intermixed with long, black setae. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length except apical fifth which is bare. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 511. Fore leg with coxa, trochanter, and basal 1/3 of femur, basal 2/3 of tibia, and basal 5/7 to ½ of tarsal segment 1 yellow, remainder of leg black. Mid leg with coxa, trochanter, basal 1/3 of femur, basal 2/3 of tarsal segment I yellow, remainder of leg black. Hind leg with coxa, trochanter, basal 1/3 of femur, about basal ½ of tibia, and basal 5/6 to ½ of tarsal segment I yellow, remainder of leg black. Hind leg claw evenly curving with small but conspicuous basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites blackish brown with darker posterior margins. Tergal plates well developed. Sternites and genitalia heavily sclerotised. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, almost square with curved internal margin, weakly sclerotised, densely covered with long hairs apically and microtrichiae basally (Fig. 568). Cercus subrectangular, covered with brown setae; ventral extension of paraproct subrectangular, nearly two times longer than cercus, weakly sclerotised on basal half and membranous apically; paraproct densely covered microsetae hairs (Fig. 627). Genital fork stout and sclerotised; termination of lateral arms with anterior margin nearly straight and well developed; anterior processes well developed and pointed apically, posterior processes weakly developed (Fig. 687). Spermatheca globular, without external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. [Description provided here is based upon examination of the male holotype and one pharate male preserved in ethanol]. Body length 5.2 mm; wing length 3.9 mm; wing width (specimen in alcohol, n = 1). General body colour velvety brown to black.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum covered by short, recumbent, golden, yellow setae grouped into small clusters. Scutum brownish black, with margins slightly paler, narrowly silver pruinose along anterior margin [In the two specimens examined in spirit, the thorax was black independently of light source] (Figs. 793, 794 specimens in alcohol). Scutellum yellow covered by long, semi-erect golden yellow setae interspersed with long, erect, black setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Subcosta with setae at base. Leg coloration as in female.

Abdomen: tergites velvet, brownish black dorsally, and brownish yellow laterally and ventrally. Gonocoxite subrectangular; gonostyle elongate, with sinuous margins, two times longer than gonocoxite and terminating in single stout spine apically (Fig. 873). Ventral plate sclerotised, with broadly rounded lip centrally in lateral view; main body of ventral plate slightly wider than long; lateral shoulders absent, basal arms developed, subparalelel and sclerotised apically (Fig. 934). Median sclerite long, about three times longer than wide at widest point, with large incision apically on central region (Fig. 934). Paramere with well developed and sclerotised basal process, numerous long spines along whole length and numerous spinules on internal membrane (Fig. 994).

PUPA. Cocoon length dorsally 3.9-4.7 mm (mean = 4.2 mm, s.d. = 0.2, n = 8), ventrally 3.7-3.8 mm (mean = 3.7 mm, s.d. = 0.07, n = 6); pupa length 3.7-5.6 mm (mean = 4.7 mm, s.d. = 0.66, n = 8); gill length 1.1-2.3 mm (mean = 1.9 mm, s.d. = 0.54, n = 5).

Cocoon: shoe-shaped as in Fig. 66, light brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, and sometimes apparently with openings on anterior margin [three specimens I have examined from Panamá did not have the openings on anterior margin].

Gill: light brown with branches on the vertical plane and upwardly directed filaments (Figs. 84, 1058). Gill with two distinctly swollen primary branches, one anterior and one posterior. The posterior primary branch gives rise to 60-90 short white secondary filaments, all upwardly directed and extending from base of gill along its length; anterior primary branch dividing into two secondary filaments, the anterior finer than the posterior. Filaments generally stout, rounded distally, with spicules on surface, edges weakly crenate; filaments on dorsal branch longer than remainder filaments.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes [in the specimens I have examined the frontal trichomes were not seen]. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in two or three groups laterally in frontal region; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region. Frontoclypeus covered by prominent loose rugosities over entire surface (Fig. 72)

Thorax: with 1-2 simple trichomes near margin of dorsal cleft and 2-3 simple trichomes on posterior region; tubercles mostly rounded only visible posterior region extending from dorsal margin up to mid point of thorax; thorax covered by prominent loose rugosities over entire surface (Fig. 74).

Abdomen: abdominal tergite I with two small simple setae and 1+1 submedian groups of spinules on posterior margin; tergite II with 3+3 submedian spiniform setae in longitudinal row, 3+3 simple, short setae anterior to outermost spiniform setae, 1+1 lateral, small simple setae, and pointed tubercles on anterior and posterior margins; tergites III and IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to most lateral of the hooks; tergites V-VIII without setae; tergite IX without terminal spines. Spine combs distribution as follows: anterior margin of tergite II and 1+1 submedian groups on tergites III, IV, and VI. Sternites III, IV with 3+3 small simple setae; sternite V with 2+2 closed simple hooks; sternites VI, VII with 4+4 well separated simple hooks along posterior margins; sternites VIII, IX without visible setae. Spine combs on anterior margins of sternites III-IX.

LARVA (Final instar). Body length 8.8-9.1 mm (mean = 9.0 mm; s.d.= 0.17, n = 3); length of head capsule 0.9-1.8 mm (mean = 1.2 mm; s.d. = 0.39, n = 4); width of head capsule 0.9-1.9 mm (mean = 1.1 mm, s.d. = 0.5, n = 4). [PETERSON *et al.* (1988) gave larval measurements as follows, but they did not provide the number of specimens he examined: Body length 13.0-13.5 mm; length of head capsule 1.8 mm (n = 1), width of head capsule 1.9 mm (n = 1)]. Body colour dark grey (specimens in alcohol and in Carnoy's) (Fig. 1107)

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Cervical sclerites small, elliptical, free in membrane. Postgenal bridge deep, bell-shaped, triangular apically; postgenal bridge nearly one and half time length of hypostomium (Fig. 1160). Hypostomium strongly pigmented on anterior margin, with nine apical teeth distinctly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with pair adjacent to base of median tooth longer than remainder; 1+1 lateral teeth; 2+2 small, lateral serrations; 1+1 lines of approximately 13 hypostomial setae parallel to lateral margins; 2+2 long, simple setae in posterior half of hypostomium (Figs. 1215). Sub-esophageal ganglion unpigmented. Antenna slightly longer than labral fan stalk, segment I, apex of segment II and segment III dark brown, remainder of segment II pale brown; length of antennal segments I-III excluding the sensillum 0.08-0.1:0.2:0.08-0.09 mm (n = 3). Mandible with three apical teeth nearly of same length; mandibular comb with approximately seven to eight teeth, second, third and fourth longer than remainder of teeth; one prominent mandibular serration (Fig. 1269). Lateral mandibular process absent. Maxillary palps heavily pigmented; two and half times as long as wide at base. Labral fan with 64-69 rays (n = 3) each with single line of long spinules in a row.

Thorax: grey dorsally. Cuticle without setae. Proleg with plate heavily sclerotised with band of 45-63 row of sclerotised processes of 18-21 simple hooks (n = 3). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with two swollen primary branches and 60-90 secondary filaments, all branching from common trunk and pointed apically.

Abdomen: usually grey dorsally. Ventral nerve cord not examined. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending two thirds of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 201-287 rows of sclerotised processes of 38-59 simple hooks (n = 3) [PETERSON *et al.* (1988) examined larvae with 50-55 hooks in 500-550 rows]. Rectal gills with three lobes of approximately 22, 24 and 41 small, finger-like lobules [after PETERSON *et al.* (1988), number of specimens examined not given in this publication].

Taxonomic Discussion. *Simulium hieroglyphicum* was described by PETERSON *et al.* (1988) from a reared male holotype, and numerous females, males, pupae and larvae collected in Costa Rica. In the same paper, the authors also provided a key to separate all *Hemicnetha* species in the New World. I have examined three vials containing several larvae and pupae preserved in alcohol, and a single vial containing a single reared male housed at the NMNH. None of the specimens were labelled as type material. However, I have compared the locality information on their label as well as their preservation against the information given in the original description of *S. hieroglyphicum.* I am confident that these larvae and pupa are paratypes, while the single reared male is the holotype of *S. hieroglyphicum*, and therefore I have labelled them accordingly (**Material Examined**). Digital images have been taken of the male holotype, which are now held at the BMNH Simuliidae Digital Archive (Fig. 793). In addition, I have also examined two reared males, two reared females and larvae mounted on slides also housed at NMNH. All slides agreed with the data given in the original description, and they have also been labelled as paratypes (**Material Examined**). PETERSON *et al.* (1988) stated in the original description of *S. hieroglyphicum* that paratypes specimens were deposited in the MZUCR. However, this material was not found in the Simuliidae holdings at this institution. There are numeous slides housed at the MZUCR with identification labels as "*S. hieroglyphicum*", but the information on the label is incomplete, therefore I have been unable to determine their provenance or their type status.

The adults of *S. hieroglyphicum* still remain poorly described. Based on the original description of PETERSON *et al.* (1988), adults cannot be externally separated from other species within the TARSATUM species group (*sensu* SHELLEY *et al.*, 2010) without examination of the pupal gill filaments. *Simulium hieroglyphicum* is only readily recognized by the unique configuration of the pupal gill filaments, which have two swollen primary branches one anterior and one posterior. The anterior primary branches have two long secondary filaments and the posterior primary branch has between 60-90 secondary filaments (Figs. 84, 1058). The pupa can also be further recognized by the frontoclypeus and thorax with conspicuous rugosities arranged in a loose reticulated fashion (Figs. 72, 74). This is the only species of the TARSATUM species group with such a number of gill filaments and morphology of the pupal frontoclypeus and thorax.

The larva of *S. hieroglyphicum* may be distinguished by the well developed and forwardly protruded hypostomial teeth (Fig. 1160). In this respect, the larva of *S. hieroglyphicum* resembles that of *S. lobatoi.* However, *S. hieroglyphicum* is best identified by the dissected gill histoblast with the anterior and posterior primary branches distinctly swollen and the posterior primary branch with 60-90 secondary filaments. The dissected gill histoblast of *S. lobatoi* has a different configuration and number of filaments.

Descriptions of life stages of *S. hieroglyphicum* may be found in COSCARÓN & COSCARÓN-ARIAS (2007) and PETERSON *et al.* (1988).

Simulium hieroglyphicum was placed in the subgenus *Hemicnetha* by PETERSON *et al.* (1988). This wasn followed by CROSSKEY & HOWARD (1997, 2004) and ADLER & CROSSKEY (2008, 2009), who placed this species in the TARSATUM species group. More recently, SHELLEY *et al.* (2010) also included it in the TARSATUM species group of the subgenus *Trichodagmia*, and this classification has been followed in the current work.

Distribution. *Simulium hieroglyphicum* has been recorded from Costa Rica (PETERSON *et al.*, 1988) and Panama (ADLER & CROSSKEY, 2008, 2009, 2010; **Material Examined**).

Biology and Medical Importance. PETERSON *et al.* (1988) collected the immature stages of *S. hieroglyphicum* on rocks and trailing vegetation upstream from the bridge over the Rio Poasito in Costa Rica. The stream comes from slopes with abundant vegetation passing through pasture land at about 1940 m. The stream is about 3 m wide, 0.3 m in depth and has moderate to fast cascading flow over large boulders and smaller stones. The females appear to not be attracted to bite humans (PETERSON *et al.*, 1988).

I have visited the Rio Poasito and surrounding areas four times during a countrywide survey of the Simuliidae of Costa Rica (L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data). The stream is located in the rainforest on the slopes of the Poás Volcano. Several collections were made at 100 m from the bridge in a stretch of the stream of 2 m wide and 40-50 cm deep. The stream is fast flowing with clear water, water temperature of 14.5ºC and pH 7.5. The riverbed consists of rocks and boulders, where numerous rapids are seen. Only few larvae and a single pupa of *S. hieroglyphicum* were found attached to rocks together with *S. chiriquiense* and *S. tarsatum*.

2.5.4.8. ***Simulium* (*Trichodagmia*) *hinmani*** **VARGAS, MARTÍNEZ PALACIOS & DÍAZ NÁJERA** (Figs. 217, 271, 378, 379, 512, 569, 628, 688, 795, 796, 874, 935, 995, 1059, 1108, 1161, 1216, 1270)

This is an uncommon species only recorded from Mexico, morphologically similar to *S. earlei*. I have been unable to obtain pupae and larvae of *S. hinmani*, therefore the descriptions here provided for these life stages have been derived from the reviews of IBÁÑEZ-BERNAL (1992) and COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium hinmani VARGAS *et al.* 1946: 120. HOLOTYPE male. MEXICO: Mexico State, Los Remedios, no. 3848; 19.x.1944, (*A.Díaz Nájera*) (INDRE, 3848) [Examined.]

FEMALE. General body colour black. Body length (specimen in spirit, n = 1) 3.2 mm, wing length 3.4, wing width 1.6 mm.

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 217). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts parts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed sclerotised cornuae and teeth in the central trough and at the base of the cornuae (Fig. 271).

Thorax: scutum dark brown with evenly arranged, recumbent, whitish setae. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown with 1+1 median, white vittae, and 1+1 submedian white vittae beginning near anterior border of scutum and reaching to posterior margin; humeri silver pruinose; lateral margins weakly silver pruinose; posterior margin dark brown (Fig. 378). With posterior illumination, thorax dark brown, with 1+1 submedian comma-shaped, silver pruinose vittae divided by median dark brown to black line, and 1+1 subtriangular dark brown vittae; humeri and lateral margins silver pruinose; posterior margin black (Fig. 379). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta bare in the allotype, but with a line of setae except apical third of vein in other specimens examined from the type locality. Radius with setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 512. Fore leg with femur, basal third and apical third of femur, tibia and tarsal segments I-IV dark brown to black; coxa and trochanter pale yellow, mid region of tibia whitish with dark tinges on ventral surface. Mid leg with coxa, apical third of femur, basal and apical third of tibia, apical third of tarsal segment I, apical half of tarsal segment II, and tarsal segment II-IV dark brown; trochanter and remainder of tibia pale yellow; basal third of tarsal segment I and basal half of tarsal segment II white. Hind leg with coxa, apical half of femur, whole tibia except small rings at base and central region, apical half of tarsal segment I and apical third of tarsal segment II, and tarsal segments III-IV dark brown; trochanter, basal third of femur, and rings at base and mid region of femur pale yellow; basal half of tarsal segment I and basal third of tarsal segment II white. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX black with silver pruinosity on segment II. Tergal plates well developed. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with approximately 12 irregularly distributed setae on posterior margin; gonapophyses twice as long as length of eighth sternite at mid point, subtriangular, largely membranous except internal margins which are weakly sclerotised; gonapophyses densely covered with long hairs (Fig. 569). Cerci subrectangular, covered with brown setae; paraproct subquadrangular, twice as long as cercus, weakly sclerotised on basal half and strongly sclerotised apically; paraproct densely covered with prominent brown hairs basally and small setae apically (Fig. 628). Genital fork stout and sclerotised; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed and blunt apically; posterior processes weakly developed (Fig. 688). Spermatheca globular, without external sculpturing and small groups of 2-3 spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour dark brown. Body length (specimen in spirit, n = 1) 4.3 mm, wing length 3.1 mm, wing width 1.2 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark with evenly distributed yellowish hairs interspersed with recumbent and semi-erect brown hairs especially on posterior margin. Scutal pattern varies slightly with light incidence: with light source anterior thorax dark brown, with 1+1 pear-shaped median and 1+1 wide sublateral vittae extending from anterior margin to posterior region thorax, black median line extending length of thorax; humeri weakly pruinose; lateral and posterior margins black (Fig. 795). With posterior illumination, thorax dark brown, with 1+1 median, pruinose, pear-shaped vittae near anterior margin divided by median brown line running from anterior to posterior margins; humeri, lateral and posterior margins weakly pruinose (Fig. 796). Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare in the holotype and one other topotype specimen. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites III to VII [best seen in some specimens when tilted and viewed laterally]. Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle subrectangular with dorsal and ventral margins sinuous; gonocoxite and gonostyle covered by long brown hairs; gonostyle with microtrichiae basally (Fig. 874). Ventral plate weakly sclerotised, subquadrangular; main body with anterior margin concave centrally, without antero-median process; anterior margin with distinct depression centrally and small central keel; lateral shoulders undeveloped, basal arms well developed and subparallel (Fig. 935). Median sclerite about three times longer than wide at widest point, with small incision apically (Fig. 935). Paramere with well developed and sclerotised basal processes and short spines in central region (Fig. 995).

PUPA. [IBÁÑEZ-BERNAL (1992) provided the following measurements, n = 3: length of cocoon base 3.6-3.7 mm, height of cocoon anterior wall 1.5-1.9 mm, length of aperture 2.3-2.4 mm; width of the aperture 1.8-1.9 mm. COSCARÓN & COSCARÓN-ARIAS (2007) provided the following measurements, though the number of specimens examined was not given: cocoon basal length 3.6-3.7 mm, height of anterior portion 1.6-1.9 mm].

Cocoon: shoe-shaped as in Figs. 66, 68, dark brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture strongly elevated.

Gill: light brown with 10 upwardly directed filaments arranged in bunch in vertical plane (Fig. 1059). Gill configuration with filaments branching basally at different heights; main trunk short, giving rise to two sets of primary branches, one internal and one external: external branch with four secondary branches, internal branch with six secondary branches (Fig. 1059). Filaments stout, pointed distally, with spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in single group in frontal region; frontoclypeus without tubercles.

Thorax: with 4+4 long simple trichomes near margin of dorsal cleft, single simple trichome in posterior region and 2-3 simple trichomes in alar region; tubercles prominently spiniform, pointed and well distributed on antero-lateral region of thorax, few tubercles are found in posterior and alar regions.

Abdomen: abdominal tergite I with 1+1 median simple setae and 1+1 submedian long simple seta; tergite II with 3+3 submedian spiniform setae and 3+3 small simple setae lateral to outermost spiniform setae; tergites III, IV with 4+4 simple hooks in row, 1+1 small simple setae anterior to outermost hooks, and 1+1 small simple setae on lateral margins; tergites V-IX without visible trichomes or setae; tergite IX without terminal spines. Spine combs on posterior margin of tergite I, anterior and posterior margins of tergite II and antero-lateral margin of tergites III-VIII. Sternite III with 1+1 small simple setae and 3+3 small simple setae on lateral margins; sternite IV with 3+3 small simple setae in row and 1+1 small simple setae on lateral margins; sternite V with 2+2 close simple hooks; sternite VI, VII with 4+4 well separated simple hooks in row; sternites VIII, IX without setae. Spine combs on anterior margin of sternites III-VIII.

LARVA (Final instar). [IBÁÑEZ-BERNAL (1992) did not provide measurements for the larva. COSCARÓN & COSCARÓN-ARIAS (2007) gave only body length, but the number of specimens examined was not given: Body length 8.0 mm]. Body colour greenish grey (specimens fixed in alcohol). General body form as in Fig. 1108.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft small, subquadrangular, rounded apically postgenal bridge twice length of hypostomium (Fig. 1161). Hypostomium strongly pigmented on anterior margin, with nine apical teeth relatively evenly distributed on anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth; 1+1 lateral teeth, longer than sublateral teeth; 4+4 small, lateral serrations; 1+1 lines of nine hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Figs. 1216). Sub-esophageal ganglion not examined. Antennal segments longer than labral stalk, segments pale brown; ratio of length of antennal segments I-III excluding the sensillum 0.1:1.4:0.8 mm [after COSCARÓN & COSCARÓN-ARIAS, 2007]. Mandible with three apical teeth all of same length; mandibular comb with approximately nine teeth, third and fourth teeth more prominent than remainder, two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1270). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 45 rays each with fine, single line of spines in a row.

Thorax: grey dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 41-50 processes. Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 10 filaments.

Abdomen: usually grey dorsally. Ventral nerve cord not examined. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 225 rows of 50 simple hooks. Rectal gills with three lobes each with 15 small, finger-like lobules.

Taxonomic Discussion. *Simulium hinmani* was described by VARGAS *et al.* (1946) from a male holotype, one female allotype, and 20 females and males collected in Mexico. The larva was also described in the same paper from a single mature larva and 20 larvae of the sixth instar collected from Mariscal, Chiapas State, Mexico. VARGAS *et al.* (1946) stated that the male holotype was partially pinned and mounted on a slide and housed at INDRE. I have examined the male holotype from INDRE and it is in good condition. The specimen is mounted on a card, while three legs, one wing and its genitalia are mounted on a slide (**Material Examined**). I have also examined the female allotype (no. 3649), which is mounted on a card triangle; one wing, three legs and its genitalia are mounted on a slide (**Material Examined**).

The thoracic pattern of the adults of *S. hinmani* is most similar to that of *S. earlei* in that the thorax is dark brown with an indistinct pattern (Figs. 378, 379, 795, 796). The general morphology of the adult's genitalia, especially the female paraproct (Fig. 628) and genital fork (Fig. 688), and the male gonostyle (Fig. 874) and ventral plate (Fig. 935) fall within the variation found in *S. earlei* suggesting a possible synonymy. However, they may be separated by the configuration and number of pupal gill filaments in link-reared adults.

The pupa of *S. hinmani* has been recorded as having 10 filaments (Fig. 1059), which separates it from *S. earlei*, which commonly has 16 filaments (Fig. 1054). Other species with a 10-filamented pupa are *S. guerrerense*, *S. pulverulentum* and *S. yepocapense* (Figs. 1057, 1067, 1073) and they might not be able to be separated from *S. hinmani* in the absence of link-reared adults.

The larva of *S. hinmani* has a ten filaments in the dissected gill histoblast, which it shared *S. guerrerense*, *S. pulverulentum*, and *S. yepocapense*. However, *S. hinmani* can be separated from. *guerrerense* and *S. yepocapense* by the subquadrangular and short postgenal cleft and a prominent postgenal bridge, which is nearly twice as long as the length of the hypostomium (Fig. 1216; see also Figs. 1214, 1220, 1226). In this respect, *S. hinmani* is similar to *S. pulverulentum*, but in the latter species the 1+1 lateral teeth of the hypostomium are relatively more prominent (Fig. 1220), and the first three teeth of the mandibular comb are equal in length and more prominent than the remainder teeth (Fig. 1274). In *S. hinmani* the hypostomial and mandibular teeth have a different morphology (see Figs. 1216, 1270).

Descriptions of the life stages of *S. hinmani* may be found in IBÁÑEZ-BERNAL (1992), COSCARÓN & COSCARÓN-ARIAS (2007) and VARGAS *et al.* (1946).

PETERSON *et al.* (1988) placed *S. hinmani* in the subgenus *Hemicnetha*. In the World Inventory of Blackflies CROSSKEY & HOWARD (1997, 2004) placed *S. hinmani* in the MEXICANUM species group of the subgenus *Hemicnetha*, and ADLER *et al.* (2004) allocated this species to their PAYNEI species group. However, COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) still maintained it in the MEXICANUM species group, because they did not recognize the synonymy of *S. mexicanum* under *S. tarsatum* proposed in HERNÁNDEZ & SHELLEY (2005). This synonymy has been accepted by ADLER & CROSSKEY (2008, 2009, 2010), and more recently. This synonymy has been accepted by SHELLEY *et al.* (2010) subsumed all species previously placed in the PAYNEI species group under the TARSATUM species group in the subgenus *Trichodagmia*, where *S. hinmani* is now placed.

Distribution. *Simulium hinmani* has only been recorded from Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; IBÁÑEZ-BERNAL, 1992; **Material Examined**).

Biology and medical importance. Nothing is known on the biology of *S. hinmani* (COSCARÓN & COSCARÓN-ARIAS, 2007; IBÁÑEZ-BERNAL, 1992).

2.5.4.9. *Simulium (Trichodagmia) hippovorum* MALLOCH (Figs. 218, 272, 380-383, 513, 570, 629, 689, 797, 798, 875, 936, 996, 1060, 1109, 1162, 1217, 1271)

This a newly revalidated name for simuliid populations externally similar to *S. virgatum s.l.* that occur from Vancouver Island south through the Pacific States in the USA.

Simulium hippovorum MALLOCH, 1914: 28. HOLOTYPE female, MEXICO: Sierra Madre, Head of River Piedras Verdes, [July.27] (*C.H.T.Townsend*) (NMNH, cat. no. 15407) [Examined.] [Synonymy with *S. virgatum s.l.* by DYAR & SHANNON, 1927: 39; revalidation by ADLER *et al.*, 2004: 371; still considered as a synonym of *S. virgatum s.l.* by COSCARÓN & COSCARÓN ARIAS, 2007: 537 and COSCARÓN *et al.*, 2008: 32; regarded as a valid species by ADLER & CROSSKEY, 2008: 57, 2009: 47, 2010: 48, SHELLEY *et al.*, 2010: 64, and the current work.]

FEMALE. General body colour dark brown. Body length (specimen in spirit, n = 1) 5.5 mm, wing length 3.8 mm, wing width 1.9 mm.

Head: dichoptic with red eyes; nudiocular area well developed (Fig. 218). Frons, clypeus and occiput dark brown with silver pruinosity; frons with numerous, irregularly arranged, stout hairs predominantly on margins. Mouthparts parts dark brown. Antennae brown with scape, pedicel and basal third of first flagellomere yellow. Cibarium unarmed with lightly sclerotised margin of trough and highly sclerotised cornuae (Fig. 272).

Thorax: scutum predominantly dark brown with numerous recumbent white hairs interspersed with recumbent black setae. Scutal pattern varying in appearance with illumination. With anterior illumination, thorax dark brown with 1+1 pear-shaped silver pruinose and 1+1 subtriangular silver pruinose vittae extending from anterior to posterior margins; fine central dark brown line extending from anterior to posterior margins; humeri pale yellow; lateral and posterior margins dark brown to black (Figs. 380, 382) [thoracic pattern not well distinguished in figures]. With posterior illumination, thorax dark brown with 1+1 submedian silver pruinose vittae arising on anterior third of scutum and reaching posterior margins, both vittae diverging towards post-lateral margins at mid point; fine dark brown line extending from anterior to posterior margins; humeri pale yellow; lateral margin dark brown; posterior margin black (Fig. 381, 383). Scutellum mid brown recumbent white hairs interspersed with long erect brown hairs on posterior margin. Postnotum dark brown with grey pruinosity. Costa wing vein with setae interspersed with spines. Subcostal wing vein with row of four setae in basal half. Radius wing vein with line of setae interspersed with spines, basal sector of Radius bare. Basal tuft of dark hairs. Colour and proportions of legs as in Fig. 513. Fore leg with coxa, trochanter, femur and mid tibia brown; basal and apical third of tibia and tarsal segment dark brown to black. Mid and hind legs with trochanters, basal two thirds of femora and mid tibiae brown; coxae, apical third of femora, basal and apical thirds of tibiae, apical third of tarsal segments I, and apical two thirds of tarsal segments II, and tarsal segment III, IV dark brown; basal two thirds of tarsal segment I and basal third of tarsal segments II white. Claws curved with large basal tooth. Halteres pale yellow with slightly darkened stems.

Abdomen: tergites dark brown. Tergal plates sclerotised. Sternites mid brown. Genitalia brown. Eighth sternite with well sclerotised central plate and line of 8-10 well developed setae; gonapophyses well developed, subtriangular, covered in setae with some sclerotisation on lower surface (Fig. 570). Cercus subhemispherical, covered by long brown setae; paraprocts subrectangular, twice length of cercus largely membranous with some sclerotisation, covered with long setae basally and microtrichiae at apex (Fig. 629). Genital fork highly sclerotised, with termination of stem expanded apically and lateral arms straight; anterior processes well developed; posterior processes well developed with well developed anterior and posterior angles (Fig. 689). Spermatheca oval, strongly sclerotised with weak external sculpturing and spicules in rows; area of insertion of spermathecal duct membranous.

MALE. General body colour mottled orange-brown and black. Body length (specimens in spirit, n = 2) 5.3-6.0 mm, wing length 3.3-3.6 mm, wing width 1.3 mm.

Head: holoptic with facets red. Rest of head coloration as in female.

Thorax: scutum dark brown to black covered golden recumbent setae. Thoracic pattern varying with light illumination. With anterior light thorax dark brown to black with 1+1 median pear-shaped and 1+1 submedian triangular vittae on anterior third of scutum; humeri pruinose; lateral and posterior margins black (Fig. 797). With posterior illumination, thorax dark brown to black with 1+1 submedian silver pruinose bands extending from anterior to posterior margins; humeri weakly pruinose; lateral and posterior margins black (Fig. 798). Coloration and setation of pleural region, scutellum and postnotum as in female. Wing venation as in female except Sc bare. Leg and halteres coloration as in female.

Abdomen: tergites lightly mottled dark brown to black, genitalia light brown. Sternites pale brown with developed sternal plates. Gonocoxite subquadrangular; gonostyle elongate, over twice as long as wide, and slightly 'S' shaped with terminal spine (Fig. 875). Ventral plate subrectangular with well developed and large, wide median process arising from central region of ventral plate, length of median process one and a half times width at base; main body with anterior margin straight at base of median process, without developed shoulders, and basal arms diverging outwards and weakly sclerotised (Fig. 936). Median sclerite long, subtriangular, narrow at base without apparent apical incision (Fig. 936). Paramere with large basal processes and two distinct clusters of stout spines; central membrane densely covered with spinules (Fig. 996).

PUPA. Cocoon length dorsally 5.3-6.6 mm (mean = 5.8 mm, s.d. = 0.49, n = 5); ventrally 5.8-7.3 mm (mean = 6.4 mm, s.d. = 0.55, n = 5); pupa length 4.5-6.5 mm (mean = 5.6 mm, s.d. = 0.74, n = 5); gill length 2.8-3.2 mm (mean = 3.0 mm, s.d. = 0.15, n = 6).

Cocoon: shoe-shaped as in Fig. 69, mid to pale brown with obvious collar and long, slender fenestrations joined to form a loose lattice. Cocoon surface smooth and translucent, with no individual fibres visible.

Gill: light brown, protruding slightly beyond fenestrations, with eight upwardly-directed filaments (Fig. 1060). Main trunk small with all filaments dividing basally and arranged in a palmate-like configuration, with six filaments arising from a common trunk and two filaments slightly separated from remainder filaments. All filaments arise in basal quarter of gill, slender with only faintly crenate margins and rounded distally, their surfaces densely covered with fine spicules.

Head (*frontoclypeus*): with 1+1 long, simple, frontal trichomes and 2+2 small, simple facial trichomes. Frontal area with groups of platelets but devoid of tubercles; facial area with pointed and rounded tubercles.

Thorax: with 1-2 simple setae on dorsal cleft, and single simple trichome on posterior region; thorax with rounded and pointed tubercles distributed on posterior region near dorsal cleft and alar region and base of gill.

Abdomen: tergite I with 1+1 long sublateral simple trichomes and prominent pointed tubercles well distributed along central region and posterior margin; tergite II with 3+3 sclerotised spiniform simple trichomes in row interspersed with pointed tubercles that are well distributed all over tergites surface; tergites III, IV with 4+4 simple hooks in row on posterior and 1+1 or 2+2 small simple trichomes anterior to outermost hooks; tergite V with 3+3 submedian simple trichomes; tergites VI-VIII with 1+1 submedian simple trichomes; tergite IX weakly sclerotised without terminal spines. Spine combs on anterior margins of tergites III-IX. Sternite III, IV with 1+1 or 2+2 submedian small simple trichomes; sternite V with 2+2 close simple hooks; sternites VI, VII with 2+2 well separated simple hooks; sternite VIII weakly sclerotised. Spine combs on anterior margins of sternites III-VIII.

LARVA (Final instar). Body length 9.0-12.0 mm (mean = 10.1 mm, s.d. = 1.2, n = 4); width head capsule 0.8-1.1 mm (mean = 0.8 mm, s.d. = 0.09, n = 4); length of head capsule 0.7-0.8 mm (mean = 0.7 mm, s.d. = 0.05, n = 4). Body colour greyish (specimens preserved in ethanol). Body form as in Fig. 1109.

Head: mainly dark brown, anterior region of cephalic apotome yellow. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Postgenal cleft narrow, bell-shaped with subtriangular extension at apex; postgenal bridge as long as hypostomium (Fig. 1162). Hypostomium with margin straight and strongly pigmented anterior margin, having nine apical teeth; median tooth sharp, well developed and most prominent; 3+3 weakly developed sublateral teeth, sometimes the pair adjacent to median tooth longer; 1+1 lateral teeth; 3-4 lateral serrations; 1 + 1 lines of 10 hypostomial setae parallel to lateral margins (Fig. 1217). Antennal segments slightly passing apex of labral fans, segment I, base and apex of segment II, and segment three pale brown, remainder of segment II whitish; length of antennal segments excluding the sensillum 0.1:0.1-0.2:0.05-0.1 mm (n = 5). Mandible with three apical teeth the last two more developed than first teeth; mandibular comb with 10 teeth, second tooth more developed than remainder of tooth; two mandibular serrations, anterior more prominent than posterior (Fig. 1271). Maxillary palps heavily pigmented nearly twice as long as width at base. Labral fan with 47-68 rays each with fine, single line of spines in a row interspersed with finer microspinules (n = 5).

Thorax: grey dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with 30-54 row of sclerotised processes of 13-17 simples hooks (n = 3). Pupal respiratory gill histoblast dark brown with eight filaments.

Abdomen: usually completely grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord grey. Ventral papillae absent. Cuticle mainly lacking setae except area around anal sclerite. Anal sclerite well sclerotised with posterior arms extending to 70-90th row of posterior circlet hooks, no sclerotised areas between arms. Posterior circlet with 174-199 rows of sclerotised process of 26-38 simple hooks (n = 5). Anal gill with three lobes, each having 7-8 finger-like lobules (n = 1).

Taxonomic Discussion. *Simulium hippovorum* was described by MALLOCH (1914) from a single female collected in Sierra Madre, Mexico. In the same paper, MALLOCH doubted that this species was conspecific with *S. cinereum* described by BELLARDI in 1883. DYAR & SHANNON (1927) examined the female holotype of *S. hippovorum* and synonimized it with *S. virgatum s.l.*, an action that has been accepted by several authors, *e.g.* STONE (1948, 1969), CROSSKEY & HOWARD (1997, 2004), COSCARÓN (1987), COSCARÓN & COSCARÓN-ARIAS (2007), SHELLEY *et al.* (2002b), and COSCARÓN *et al.* (2008). However, ADLER *et al.* (2004) reviewed the taxonomy of this species within the context of the North American blackflies and revalidated the name *S. hippovorum* to apply to populations extending from Vancouver Island south through the Pacific States in North America. This action was taken because the holotype and the specimens from the Pacific region are greyer and black than the coloration recorded in *S. paynei* and the holotype of *S. virgatum s.l.*, which is more fuscous and reddish. The same authors also gave an historical account on the mis-identifications of previous workers and the most relevant literature dealing with *S. hippovorum*. I have examined the female holotype of *S. hippovorum*, which is housed at the NMNH (catalogue no. 15407) (**Material Examined**). The specimen has been pinned by the posterior region of thorax and its left side has a drop of grease, which is slightly obscuring the thoracic pattern. Its abdomen and the right hind leg are on two slides (**Material Examined**). I have taken digital images of the holotype of *S. hippovorum*, which are held in the Simuliidae Digital Imaging Archive at the BMNH. In addition, I have also examined several adults, and numerous pupal exuviae housed at BMNH, CUAC and NMNH simuliid collections and larvae identified as *S. hippovorum* by P.H. ADLER (**Material Examined**).

The general morphology of the adults and pupal exuviae of *S. hippovorum* is very similar to that of *S. virgatum s.l.* The females of both species cannot be easily separated in the absence of link-reared specimens. *Simulium hippovorum* may be separated from *S. virgatum s.l.* by the structure of the male genitalia and the pattern of the pupal gill filaments. In *S. hippovorum* the median process of the ventral plate is relatively more stout and the anterior margin is not concave at the base of the median process (Fig. 936). In addition, the pupal gill filaments are arranged in a palmate-like fashion with six filaments arising from a common trunk and two filaments slightly separated (Fig. 1060). The median process of the male ventral plate in *S. virgatum s.l.* is three times longer than its basal width, much thinner and the anterior margin is concave at the base of the median process (Fig. 948). The pupal gill filaments in *S. virgatum s.l.* all arise from a common trunk and divide into two upwardly directed branches, each branch having four secondary filaments (Fig. 1072).

The larva of *S. hippovorum* may be separated with difficulty from that of *S. virgatum s.l.* by the sublateral teeth adjacent to the median tooth being relatively more prominent and pointed (Fig. 1217). In *S. virgatum s.l.* the sublateral teeth adjacent to the median tooth are dome-shaped (Fig. 1225). The latter species cannot be separated from other closely related taxa, such as *S. bricenoi* and *S. paynei* in the absence of link-reared adults collected in the same locality as the larvae.

Description of the life stages of *S. hippovorum* may be found in MALLOCH (1914) and ADLER *et al.* (2004).

ADLER & CROSSKEY (2008, 2009, 2010), CROSSKEY & HOWARD (1997, 2004), COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) placed *S. hippovorum* in the PAYNEI species group in the subgenus *Hemicnetha*. However, this group has been subsumed under the TARSATUM species group in the subgenus *Trichodagmia* by SHELLEY *et al.* (2010), where *S. hippovorum* is now placed, and the this classification has been followed in the current work.

Distribution. *Simulium hippovorum* has only been found from Vancouver Island and British Columbia (Canada) southward the Pacific Coastal states of the USA into Sierra Madre, Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. ADLER *et al.* (2004) stated that immature stages of *S. hippovorum* are found in swift rocky flows. They readily colonised natural substrates including those coated with periphyton, but they anchor themselves to rocks, where they are often found together with *Hydropsyche* caddisflies. All life stages of *S. hippovorum* are present year-round in southern California. The females are zoophilic feeding on horses' ears, especially in the morning.

Larvae of *S. hippovorum* have been found to be attacked by the mermithid nematode *Neornesornermis flumenalis* (WELSH) (ADLER *et al.*, 2004).

2.5.4.10. *Simulium* (*Trichodagmia*) *lobatoi* LUNA DIAS, HERNÁNDEZ, MAIA-HERZOG & SHELLEY (Figs. 25, 60, 95, 218, 273, 384, 385, 514, 571, 630, 690, 799, 800, 876, 937, 997, 1061-1063, 1110, 1163, 1218, 1272)

This is a zoophilic species described by LUNA DIAS *et al.* (2004) from Brazil, which is externally similar to *S. rubrithorax*.

Simulium lobatoi LUNA DIAS *et al.*, 2004: 37. HOLOTYPE female (reared), BRAZIL: Mato Grosso State, Tangará da Serra, Estância Primavera, Cachoeira I, (site 1053); 26.v.1995, (*A.P.A.Luna Dias*, *P.R.Garritano*, *M.M.Elázaro* & *M.Leila*) (IOC). [Examined.]

FEMALE. General body colour dark brown. Body length (specimens pinned) 2.6-3.6 mm (mean= 3.1 mm, s.d. = 0.28, n = 14), wing length 2.4-2.9 mm (mean = 2.7 mm, s.d. = 0.16, n = 14), wing width 1.0-1.4 mm (mean = 1.2 mm, s.d. = 0.14, n = 14).

Head: dichoptic with dark red eyes and nudiocular area well developed. Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 273).

Thorax: scutum dark brown with evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent brown setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown with 1+1 submedian, white vittae, beginning near anterior border of scutum and curving towards mid line in anterior fourth of scutum from where they diverge towards lateral margins, terminating at a point two thirds of length of scutum; 1 median, fine, vitta beginning on anterior margin and running in a straight line for two thirds length of scutum; area between vittae and lateral margins dark brown, humeri brown with silver pruinose reflections (Fig. 384). With posterior illumination, thorax dark brown, with 1+1 longitudinal, wide, silver pruinose, median vittae divided by median dark brown line, 1+1 rounded, submedian, pruinose areas near anterior margin, and lateral margins silver pruinose in anterior half of scutum (Fig. 385). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length or bare. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 514. Fore and mid leg with coxae, femora, trochanters and tibiae of fore and mid legs brown, apex of femora and tibiae darker brown; fore tarsal segments and apex of tarsal segments I, II, and III of mid leg dark brown to black, base of tarsal segments I, II, and III of mid legs whitish; basal articulation of mid tibia yellowish. Hind leg with coxa, femur and tibia brown, trochanter, and basal articulation of femur yellow; half of tarsal segment I and base of segment II whitish, remaining of segments dark brown. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown to black and brown mottled in middle without silver pruinosity, except tergite II silver pruinose on posterior and lateral margins. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, almost square with curved internal margin, weakly sclerotised, densely covered with long hairs (Fig. 571). Cerci hemispherical, covered with brown setae; paraproct small, subtriangular, almost same length as cercus, weakly sclerotised on basal half and membranous apically; paraproct densely covered with prominent brown hairs and few basal setae (Fig. 630). Genital fork stout and sclerotised; termination of lateral arms with anterior margin curved and well developed; anterior processes well developed and blunt apically, posterior processes weakly developed (Fig. 690). Spermatheca globular, with weak external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct weakly sclerotised.

MALE. General body colour dark brown to black. Body length (specimens pinned) 2.7-3.6 mm (mean = 3.2 mm, s.d. = 0.32, n = 10), wing length 2.0-2.7 mm (mean = 2.4 mm, s.d. = 0.21, n = 10), wing width 1.1-1.3 mm (mean = 1.2 mm; s.d. = 0.21, n = 10).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark in posterior two thirds and orange in anterior one third with evenly distributed yellowish hairs interspersed with recumbent and semi-erect brown hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax dark brown, with single median and

1+1 submedian, white vittae, beginning near anterior border of scutum and diverging to lateral margins; vittae running nearly to mid point of thorax (Fig. 799). With posterior illumination, thorax dark brown, with 1+1 median, pruinose, pear-shaped vittae near anterior margin divided by median brown line running from anterior to posterior margins (pruinose areas can be observed on antero-lateral margins under certain lights); posterior margin dark brown to black (Fig. 800). Humeri and lateral margins dark brown with pruinose area. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Subcosta bare in two specimens examined. Leg coloration as in female.

Abdomen: tergites dark brown to black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites III to VIII (best seen in some specimens when tilted and viewed laterally). Genitalia brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle subrectangular with dorsal and ventral margins sinuous, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 876). Ventral plate weakly sclerotised, subrectangular, covered with long hair; anterior median process well developed with distinct depression apically and keel well developed; lateral shoulders slightly developed and basal arms well developed and subparallel (Fig. 937). Median sclerite long, about three times longer than wide at widest point, with small incision (appears curled up in all specimens examined) and small spines at apex (Fig. 937). Paramere with well developed and sclerotised basal process and numerous long spines along whole length (Fig. 997).

PUPA. Cocoon length dorsally 2.5-3.6 mm (mean = 3.1 mm, s.d = 0.28, n = 27), ventrally 3.9-6.0 mm (mean = 5.0 mm, s.d. = 0.53, n = 26); pupa length 3.6-5.1 mm (mean = 4.3 mm, s.d. = 0.44, n = 14); gill length 0.9-1.8 mm (mean = 1.3 mm, s.d. = 0.18, n = 32).

Cocoon: shoe-shaped as in Figs. 66, 68, brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated.

Gill: light brown with eight upwardly directed filaments arranged in bunch in vertical plane (Fig. 1061-1063). Gill configuration with filaments branching basally at different heights; main trunk short, giving rise to two sets of primary branches, one internal and one external: the more external consists of one dorsal branch with four secondary branches that bifurcate at different heights and one single ventral; the internal branch consists of three secondary branches that bifurcate at different heights. Gill filament variation was found in one specimen, in which the filaments of the dorsal branch of the external set were much smaller than those of the internal one (Figs. 1062-1063). Filaments stout, pointed distally, without spicules on surface, edges weakly crenate; all filaments usually approximately of same length, except ventral filament which is longer.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes, and 1+1 small, sublateral, simple trichomes between frontal and facial trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in two or three groups laterally in frontal region, respectively; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region.

Thorax: with 1-4 simple trichomes near margin of dorsal cleft and 1-4 simple trichomes on alar region; tubercles mostly rounded only visible at base of gill and postero-lateral margin of dorsal cleft.

Abdomen: tergite I with 1+1 simple, short setae laterally and rounded tubercles densely distributed on anterior margin, and entire area of posterior margin; tergite II with 3+3 submedian spines in longitudinal row, 3+3 simple, short setae lateral to outermost spine and rounded tubercles densely distributed mesally; tergites III and IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to most lateral of the hooks; tergites V-VIII without setae; tergite IX without terminal spines, weakly sclerotised. Spine combs distribution as follows: 1+1 groups on antero-lateral margin and 1 group on central portion of anterior margin of tergites III-VII. Sternite IV with 2+2 simple, small setae sublaterally; sternite V with two sublateral, simple setae, 1+1 close, simple hooks laterally and spine combs on anterior margin; sternite VI with 2+2 separated, simple, median hooks, 1+1 simple setae on posterior margin, and group of spine combs on anterior margin; sternites VII with 2+2 well separated hooks, and groups of spine combs on antero-lateral margin; sternite IX with spine combs on anterior margin.

LARVA (Last instar). Body length 8.7-10.6 mm (n = 4); length of head capsule 0.9-1.0 mm (n = 4); width of head capsule 0.7-0.8 mm (n = 4). Body colour dark grey dorso-laterally, whitish ventrally (specimens fixed in Carnoy's solution and/or ethanol). General body form as in Fig. 1110.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Figs. 1163). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth distinctly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with the pair adjacent to base of median tooth longer than remainder; 1+1 lateral teeth, longer than basal sublateral tooth; 2+2 small, lateral serrations; 1+1 lines of approximately 14 hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1218). Sub-esophageal ganglion lightly pigmented. Antenna longer than head fan stalk, segment I, apex of segment II and segment III dark brown, two thirds of segment II pale whitish; length of antennal segments I-III excluding the sensillum 0.1:0.1-0.2:0.1 mm (n = 6). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately 11 teeth, first four more prominent than remainder teeth; third, fourth and fifth mandibular comb teeth longer and more prominent than first, and sixth to eleventh mandibular comb teeth; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1272). Lateral mandibular process not seen. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with 49 rays each with fine, single line of spines in a row (n = 4).

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 41-50 processes (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with 8 filaments, all branching from common trunk and pointed apically.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 251-290 rows of 45-46 simple hooks (n = 3). A rectal gill with two lobes with approximately 24 small, finger-like lobules was observed (n = 1). However, this number of rectal gill branches does not fall within the variation found in species of *Trichodagmia*, which normally have three branches.

Taxonomic Discussion. *Simulium lobatoi* was described by LUNA DIAS *et al.* (2004) from six biting females, and 30 females and seven males (all reared), collected in the states of Mato Grosso and Goiás, Brazil. I have examined the female holotype which is housed at the IOC Simuliidae collection and it is in good condition (**Material Examined**). The larva of *S. lobatoi* was described for the first time by HERNÁNDEZ *et al.* (2008), and more recently SHELLEY *et al.* (2010) reviewed the taxonomy of this species.

Simulium lobatoi is morphologically similar to several species. It is most similar in coloration to *S. rubrithorax* in the TARSATUM species group [see MAIA-HERZOG *et al.*, 1984; SHELLEY *et al.* 1989b, 1997, 2002b for descriptions and taxonomic discussions]. The female of *S. rubrithorax* has a scutal pattern of the same basic design consisting of 1+1 submedian bowed vittae that converge posteriorly (Figs. 400, 401) [also see SHELLEY *et al.*, 2002b; SHELLEY *et al.*, 2010], while *S. lobatoi* (Figs. 384, 385) has the submedian vittae diverging posteriorly. In addition to coloration, the female of *S. lobatoi* can be distinguished from *S. virgatum s.l.* and *S. brachycladum* by its short, subtriangular highly setose gonapophyses (Fig. 571), which are elongated with fine setae in the latter two species (Figs. 562, 580). However, *S. lobatoi* (Figs. 25, 630) is more similar to species in the ORBITALE species group in its small, subrectangular paraprocts, which are covered only with prominent setae, compared to other Brazilian species in the TARSATUM species group that have well developed paraprocts covered with fine setae.

The male scutal pattern of *S. lobatoi* (Figs. 799, 800) is different to those of brown-coloured *S. rubrithorax* and *S. paynei* (Figs. 811, 812, 801-808) in that the posteriorly diverging submedian vittae in *S. rubrithorax* are reduced to submedian anterior cunae in *S. lobatoi*. In this respect, it is similar to *S.*

brachycladum (Figs. 777, 778) and *S. cristalinum* (Figs. 783, 784), except that these species are dark brown to black and have a broader median vitta with an anterior light source. Males of *S. lobatoi* (Figs. 60, 937) are distinguished by the less developed antero-median process of the ventral plate, which has a distinct depression apically. This distinct depression is lacking or relatively less prominent in *S. brachycladum* (Fig. 927), *S. cristalinum* (Fig. 930) and *S. virgatum s.l.* (Fig. 948).

Simulium lobatoi and *S. rubrithorax* have an eight-filamented pupa, which immediately separates them from other *Trichodagmia* species found in Brazil, for example *S. brachycladum* and *S. cristalinum*, which have six filaments. The length of gill filaments and form of the cocoon further distinguish *S. rubrithorax* from *S. lobatoi*. In populations of *S. rubrithorax* the mean pupal gill length is 3.2 mm (range 2.5-5.4 mm) (SHELLEY *et al.*, 1997) and in *S. virgatum s.l.* 2.6 mm (range 1.8-3.1 mm) (SHELLEY *et al.*, 2002b) compared to *S. lobatoi* where the mean is 1.3 mm (range 0.9-1.8 mm). In *S. rubrithorax* all filaments are slightly pointed distally and forwardly directed and the cocoon has prominent fenestrations (SHELLEY *et al.* 1997, 2002b), whereas in *S. lobatoi* gill filaments are strongly pointed distally and upwardly directed (Figs. 1061-1063)., and the cocoon does not have fenestrations.

The larva of *S. lobatoi* can be readily distinguished from other species of the TARSATUM species group by the dissected gill histoblast with eight filaments, all branching basally. In this respect, *S. lobatoi* is very similar to *S. rubrithorax*, but in the latter species the gill histoblast filaments are rounded apically (Simuliidae Digital Image Archives, BMNH; SHELLEY *et al.*, 1997), while in *S. lobatoi* they are pointed. The best character that distinguishes the larva of *S. lobatoi* from that of *S. rubrithorax* is the structure of the hypostomial teeth. In *S. lobatoi* the teeth of the hypostomium are forwardly protruding in the central region, with the median tooth longer than the remaining teeth, only three sublateral teeth and 1+1 lateral teeth that are slightly longer than the posterior sublateral teeth; the hypostomium has 1+1 lines of 14 hypostomial setae (Figs. 1218). The hypostomium of *S. rubrithorax* has all teeth at the same level, except that the median tooth is longer, and there are only 2+2 sublateral teeth and 1+1 lateral teeth all nearly at the same level in the central region; the hypostomium only has nine hypostomial setae (SHELLEY *et al.*, 1997). HERNÁNDEZ *et al.* (2008) recorded only two lobes in the rectal gill of *S. lobatoi*, but they were only able to examine a single specimen of this species with the rectal gill everted. Thus, the latter number of lobules might not be a correct and more material is needed in order to assess this problem.

HERNÁNDEZ *et al.* (2008) placed *S. lobatoi* in the subgenus *Hemicnetha*, PAYNEI species group because of its morphological similarity with the larva of *S. rubrithorax*. In the recent World Inventory of Blackflies (ADLER & CROSSKEY, 2008, 2009, 2010) *S. lobatoi* was maintained in this subgenus as well as by COSCARÓN & COSCARÓN-ARIAS (2008) and COSCARÓN *et al.* (2008). However, SHELLEY *et al.* (2010) placed this species in the TARSATUM species group of the subgenus *Trichodagmia,* which is followed in this work.

Distribution. *Simulium lobatoi* has a limited distribution around its type locality Tangará da Serra, Brazil. It has also been found in Cachoeira da Lageado, Cachoeira de Pequizeiro (Mato Grosso) and in the Planalto highland area of Goiás (Salto de Itiquira) together with *S. rubrithorax* and *S. spinibranchium* Lutz (ADLER & CROSSKEY, 2010; HERNÁNDEZ *et al.*, 2008; SHELLEY *et al.*, 2010; see also **Material Examined** in LUNA DIAS *et al.*, 2008).

Biology and Medical Importance. The blood-feeding habits of *S. lobatoi* are not well known, although a few specimens were collected biting man in Cachoeira do Pequizeiro. Adults were reared from immature stages that were collected from small to medium (50 cm to 10 m wide), clear, fast flowing rivers, with pupae attached to rocks and dead leaves in parts of the river where the current is faster (LUNA DIAS *et al.*, 2004; SHELLEY *et al.*, 2010).

2.5.4.11. *Simulium (Trichodagmia) paynei* VARGAS (Figs. 26, 38, 59, 69, 86, 91, 92, 219, 274, 386-393, 515, 572-573, 631-633, 691, 692, 801-808, 877-880, 938-941, 998-1001, 1064-1066, 1111, 1164, 1219, 1273)

This is a widespread species, which is suspected of being a species complex that still requires further taxonomic study. The description that follows is based upon examination of type material and identified specimens housed in the AMNH, BMNH, CUAC, INDRE, MZUCR and NMNH collections.

Simulium paynei VARGAS, 1942: 229. LECTOTYPE female, MEXICO: [Without further information.]; 1883, (*Bilimek*) (NM) [Examined.] [Substitute name for *Hemicnetha mexicana* ENDERLEIN, 1934b: 190].

Simulium mathesoni VARGAS, 1943b: 360. HOLOTYPE male, MEXICO: Estado de Morelos, Temixco; [No date] (*A. Martínez Palácios*) (INDRE, 3588) [Examined.] [Synonymised with *S. virgatum s.l.* by STONE, 1948: 400; synonymised with *S. paynei* by VARGAS & DÍAZ NÁJERA, 1953: 146; treated as a valid species by DALMAT, 1955: 164, but considered synonymous with *S. paynei* by most authors, *e.g.* WYGODZINSKY, 1958: 134; COSCARÓN, 1987: 36; COSCARÓN & COSCARÓN-ARIAS, 2007: 531; ADLER & CROSSKEY, 2008: 45, 2009: 47, 2010: 46; SHELLEY *et al.*, 2010: 65.]

Simulium bilimekae SMART, 1944: 132. [Unnecessary substitute name for *mexicanum* ENDERLEIN; misspelling as *S. bilimakae* in MAIA-HERZOG *et al.*, 1984: 353.]

Simulium (Dyarella) acatenangoensis DALMAT, 1951: 31. HOLOTYPE male (reared), GUATEMALA: Chimaltenango, Acatenango, Finca La Esperanza Pérez, Rio Ladrillera; 25.xi.1946, (*José H. Rosales & Daniel Luch*) (NMNH, acc. no. 409-27) [Examined.][The collectors' names on the slide do not agree with the names given in DALMATS' original description, see **Material Examined**.] [Synonymy with *S. paynei* by VARGAS & DÍAZ NÁJERA, 1954: 61; synonymy accepted by WYGODZINSKY, 1958: 134; COSCARÓN, 1987: 36; COSCARÓN & COSCARÓN-ARIAS, 2007: 531; COSCARÓN *et al.*, 2008: 32; ADLER & CROSSKEY, 2008: 45, 2009: 47, 2010: 46; SHELLEY *et al.*, 2002b: 148; SHELLEY *et al.*, 2010: 65, and the current work; synonymy also accepted by MAIA-HERZOG *et al.* (1983), but wrongly attributed to VARGAS & DIAZ NÁJERA (1953).]

Simulium conviti RAMÍREZ PÉREZ & VULCANO, 1973: 376. HOLOTYPE female, VENEZUELA: Bolívar State, Cabanayén (Gran Sabana); [Without date or collectors' name, but presumably collected by the authors.] [Holotype said to be housed at DERM, but it is not found in this collection and it is presumed to be lost, H. FRONTADO, pers. comm. to L.M. HERNÁNDEZ). [Synonymised with *S. paynei* by MAIA-HERZOG *et al.*, 1984: 353; synonymy followed by ADLER & CROSSkey, 2010: 48, COSCARÓN & COSCARÓN-ARIAS, 2007: 531, and SHELLEY *et al.*, 2010: 65.]

Simulium biuxinisa COSCARÓN & IBÁÑEZ-BERNAL, 1995: 61]. HOLOTYPE female (reared), MEXICO : Oaxaca, Arroyo Coladiente, km 205 Carretera 175 Tuxtepec-Oaxaca, Rio El Estudiante; 12.vi.1992, (*S. Coscarón & S. Ibañez-Bernal*) [Holotype said to be deposited at INDRE, but it was not found at this institution, H. HUERTAS, pers. comm. to L.M. HERNÁNDEZ] [Note from CROSSKEY & HOWARD (2004): "The title page of the article containing the description bears the date '1993' but the last page states 'Acceptado [= Accepted]: 3 Junio 1994' making it evident that the species must be dated after 1993, the work was apparently issued in 1995"] **New synonymy.**

FEMALE. General body colour dark brown to black. Body length (specimens pinned) 2.5-4.0 mm (mean = 3.1 mm, s.d. = 0.53, n = 8); wing length 2.3-3.1 mm (mean = 2.7 mm, s.d. = 0.27, n = 8), wing width 1.1-1.7 mm (mean = 1.3 mm, s.d. = 0.21, n = 8).

Head: dichoptic with red; nudiocular area well developed (Fig. 219). Frons, clypeus and occiput dark brown with silver pruinosity; frons with numerous, irregularly arranged, stout hairs predominantly on margins. Mouthparts black. Antennae brown with scape, pedicel and basal third of first flagellomere yellow. Cibarium unarmed with lightly sclerotised margin of trough and highly sclerotised cornuae (Fig. 274).

Thorax: scutum predominantly dark brown with numerous recumbent white hairs. Scutal pattern varying in appearance with illumination. With anterior illumination, thorax dark brown with 1+1 median, pear shaped median vittae and 1+1 sublateral wide silver pruinose vittae extending from anterior to posterior margin, leaving a dark brown, lyre-shaped mark on submedian region of thorax; humeri weakly pruinose; lateral and posterior margins dark brown to black (Figs. 386, 388, 390, 392). With posterior illumination, thorax dark brown with 1+1 submedian subtriangular silver pruinose vittae extending from anterior margin to mid region of thorax, fine dark brown line on central region of thorax; humeri and lateral margin weakly pruinose; posterior margin black (Figs. 387, 389, 391, 393). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura dark brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with few setae (at least three) setae on median region of vein. Radius with line of setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 515. Fore leg with coxa, trochanter, femur, and internal surface of tibia pale brown; external surface of tibia silver pruinose; apical third of tibia and tarsal segments black. Mid and hind legs with trochanters, two thirds of femora and mid part of tibiae pale brown; coxae, apical third of femora, apical and basal thirds of tibiae, and apical third of tarsal segment I and tarsal segments II-IV dark brown to black; basal third of tarsal segment I white. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I pale brown; tergites II-V velvet black; tergites VI, VII shiny black; tergites VIII, IX dark brown to black. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with two to three irregularly distributed setae on posterior margin; gonapophyses 1.5 times longer than length of eighth sternite at mid point, subtriangular, weakly sclerotised, densely covered with short hairs on central region (Figs. 38, 572, 573). Cercus ovoid; paraproct suboval, 1.5 times longer than cercus, weakly sclerotised on basal half and membranous apically; cercus and paraproct densely covered with prominent brown hairs (Figs. 2, 26, 631-633). Genital fork stout and sclerotised with apical region of stem expanded; termination of lateral arms with anterior margins straight and well developed; anterior processes well developed and pointed apically; posterior processes well developed and directed backwards to middle region of lateral arms (Fig. 691, 692). Spermatheca globular, without external sculpturing and with small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour dark brown to black. Body length (specimens pinned) 3.6-4.2 mm (mean = 3.7 mm, s.d. = 0.25, n = 3), wing length 2.0-3.6 mm (mean = 2.7 mm, s.d. = 0.54, n = 6), wing width 1.1-1.6 mm (mean = 1.2 mm; s.d.= 0.18, n = 6).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark brown to black covered by recumbent golden hairs; Scutal pattern varies slightly with light incidence: with light source anterior thorax dark brown, with single 1+1 submedian weakly pruinose vittae extending from anterior to posterior margins; humeri weakly pruinose; lateral and posterior margins dark brown to black (Figs. 801, 803, 805, 807). With posterior illumination, thorax dark brown, with 1+1 submedian, silver pruinose, posteriorly diverging lines extending from anterior to near posterior margin; humeri, lateral and posterior margins dark brown. (Figs. 802, 804, 806, 808). Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare. Leg coloration as in female though darker brown.

Abdomen: tergites black, basal fringe with long, golden hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites III to VI (best seen in some specimens when tilted and viewed laterally). Genitalia brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle elongate, twice longer than gonocoxite, with external margin usually straight and internal margin weakly sinous terminating in stout spine; gonocoxite and gonostyle covered with long setae (Figs. 877-880).Ventral plate sclerotised, subrectangular, with prominent median process on anterior region, anterior margin of ventral plate straight at junction with anterior process; anterior process with depression apically, 1 to 1.5 times longer than height of ventral plate at mid point; lateral shoulders slightly developed covered with long hair, basal arms well developed, sclerotised and curved inwards (Figs. 59, 938-941). Median sclerite about three times longer than wide at widest point, without apparent small incision apically (Figs. 938-941). Paramere with well developed and sclerotised basal processes and numerous spines along whole length, and central membrane covered by spinules (Figs. 998-1001).

PUPA. Cocoon length dorsally 4.2-6.4 mm (mean = 5.1 mm, s.d = 0.78, n = 12), ventrally 5.0-7.3 mm (mean = 6.0 mm, s.d. = 0.76, n = 10); pupa length 4.0-6.3 mm (mean = 4.5 mm, s.d. = 0.99, n = 10); gill length 2.2-3.3 mm (mean = 2.5 mm, s.d. = 0.31, n = 12).

Cocoon: shoe-shaped as in Fig. 69, brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly to strongly elevated with numerous prominent fenestrations.

Gill: light brown with eight upwardly directed filaments arranged in bunch in vertical plane (Figs. 1064-1066). Main trunk short dividing basally into two primary branches each with four filaments; all gill filaments arising from gill base. Filaments stout, rounded distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes, and 1+1 small, sublateral, simple trichomes between frontal and facial trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 6-7 in group in frontal region; tubercles absent over entire surface.

Thorax: with 3+3 simple trichomes near dorsal cleft, one simple trichome on central region, and six trichomes in pair in alar region; tubercles mostly rounded distributed over entire surface.

Abdomen: tergite I with 1+1 simple submedian trichome and 1+1 small simple trichomes on lateral margin, and rounded tubercles along posterior margin; tergite II with 3+3 submedian spines in longitudinal row, 1+1 simple trichomes lateral to outermost trichomes, and 2+2 small simple trichomes on lateral margins; tergites III-IV with 4+4 submedian simple hooks in longitudinal row, 1+1 simple, short setae anterior to outermost hooks, and 1+1 small simple trichomes laterally; tergite V with 4+4 small simple trichomes in longitudinal row, and 1+1 simple small trichomes laterally; tergites VI, VII with 2+2 submedian simple trichomes and 1+1 small simple trichomes laterally; tergites VIII, IX without visible trichomes, tergite IX without terminal spines Spine combs on anterior margins of tergites II-VIII. Sternite III with 1+1 submedian trichomes and 2+2 small simple trichomes on lateral margins; sternite IV with 2+2 submedian simple trichomes and 2+2 small simple trichomes laterally; sternite V with 2+2 close simple hook in row, 1+1 simple trichome anterior to outer hook, and 1+1 small simple trichomes on lateral margins; sternites VI, VII with 2+2 well separated hooks in row, and 1+1 small simple trichomes anterior to outermost hooks; sternite VIII without trichomes; sternite IX weakly sclerotised without visible trichomes. Spine combs on anterior margins of sternites III-IX.

LARVA (Last instar). Body length 9.0-10.4 mm (mean = 9.7 mm, s.d. = 0.57, n = 7); length of head capsule 0.9-1.0 mm (mean = 0.9 mm, s.d. = 0.05, n = 8); width of head capsule 0.7-0.8 mm (mean = 0.7 mm, s.d. = 0.04, n = 8). Body colour dark grey dorso-laterally, whitish ventrally (specimens fixed in alcohol and Carnoy's). General body form as in Figs. 86, 1111.

Head: mainly brown, sometimes with anterior region of cephalic apotome paler to dark brown. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive (Figs. 91). Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, subtriangular with indistinct small tube-like incision apically; postgenal bridge nearly as long as hypostomium (Figs. 1164). Hypostomium strongly pigmented on anterior margin, with nine apical teeth distinctly weakly protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with pair adjacent to base of median tooth longer than remainder; 1+1 lateral teeth, longer than sublateral tooth; 6+6 small, lateral serrations; 1+1 lines of approximately eight hypostomial setae parallel to lateral margins; 1+1 or 2+2 long, simple setae in posterior half of hypostomium (Figs. 1219). Sub-esophageal ganglion unpigmented. Antennal segments longer than labral fan stalk, segment I, apex of segment II and segment III dark brown, two thirds of segment II pale; length of antennal segments I-III excluding the sensillum 0.1:0.1:0.04-0.1 mm (n = 3). Mandible with three apical teeth, first one longer than second and third; mandibular comb with 11 teeth, first and second teeth more prominent than remainder; two mandibular serrations, anterior more prominent and longer than posterior (Fig. 1273). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with 47-50 rays each with fine, single line of spines in a row (n = 3).

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 27 rows of sclerotised processes of 17 hooks (n = 1). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with eight filaments, all branching from common trunk and rounded apically.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 132-151 rows of sclerotised processes of 30-49 simple hooks (n = 3). Rectal gills with three lobes each with 5-10 finger-like lobules; dorsal lobule on each branch more prominent than remaining lobules (n = 3).

Taxonomic Discussion. The complicated taxonomy surrounding *S. paynei*, its synonymies and the closely related species *S. rubrithorax* and *S. virgatum s.l.* has been reviewed by MAIA-HERZOG *et al.* (1984) and discussed also by SHELLEY *et al.* (2002b; 2010). In addition, ADLER *et al.* (2004) detailed the taxonomy of *S. paynei* and hinted at the existence of a lectotype at the ZMUH, but argued that this was not listed as such in WERNER (1996a,b). I have reviewed in detail the taxonomy of *S. paynei* in the light of the current work and have the following comments to make:

ENDERLEIN (1934a) described *Hemicnetha mexicana* based on two syntype females collected in Mexico by Bilimek, which were deposited in the NM and ZMHU collections. In the same paper, ENDERLEIN also described a male collected in Mexico by DEPPE and housed at the ZMHU that he believed was conspecific with the two females. In 1942, VARGAS noted that as *Simulium mexicanum* BELLARDI and *Hemicnetha mexicana* were placed in the same genus *Simulium*, the name *H. mexicana* will fall into homonymy with *S. mexicanum.* In order to avoid this homonym, he (VARGAS, 1942) erected the name *S. paynei* for the ENDERLEIN species. Eleven years later, VARGAS & DÍAZ NÁJERA (1953) examined the male and female deposited at the ZMUH and made preparations of both specimens (see **Material Examined**). The authors also compared the general morphology of these two specimens with that of *S. mathesoni*, which had been described by VARGAS in 1943b. VARGAS & DÍAZ NÁJERA (1953) stated that both male and female were conspecific, and argued that the morphology of *S. mathesoni* falls within the variation found in *S. paynei*, and considered both species as synonymous. It is difficult to understand how VARGAS & DÍAZ NÁJERA (1953) reached their conclusion because adults of *S. paynei* are very difficult to identify if they are not link-reared and collected at the same locality as the immature stages.

In 1984 MAIA-HERZOG *et al.* examined both females and the single male without type status of *H. mexicana*, and designated the female housed at the NM as a lectotype and the other female deposited at ZMHU as paralectotype (**Material Examined**). In the same paper, the authors agreed with the synonymies of previous authors (*S. mathesoni*, *S. bilimekae* and *S. acatenangoense*) with *S. paynei*, and also considered *S. conviti* as conspecific with *S. paynei*. They also agreed with VARGAS & DÍAZ NÁJERA (1953) in that both females and the male described as *H. mexicana* by ENDERLEIN (1934b) were conspecific. MAIA-HERZOG *et al.* (1984) attributed the synonymy of *S. acatenangoense* with *S. paynei* to VARGAS DÍAZ NÁJERA (1953), when it should be attributed to VARGAS & DÍAZ NÁJERA (1954). I have examined the type material of *H. mexicana.* The female lectotype is in relatively good condition being pinned through the posterior region of the thorax. Its antennal segments are missing, and two legs, one wing and the abdomen are said to have been mounted on a slide apparently by MAIA-HERZOG *et al.* (1984), but I have been unable to examine it. The female paralectotype (no. 4) is also in relatively good condition; it has also been pinned through the posterior region of the thorax, and one wing, one leg and its genitalia are on a slide. The single male is in poor condition being glued by the left side of its thorax, which is obscuring most of its pattern. The thorax is partially devoid of hairs in this specimen. I have taken digital images of the main salient taxonomic characters of these specimens, which are now housed at the Simuliidae Digital Images Archive held at the BMNH (Figs. 386-388, 573, 692, 801-802, 880, 941, 1001). There are some morphological differences in the anterior margin of the male ventral plate of *H. mexicana* and that of *S. mathesoni* (see Figs. 938, 939), but this might be due to the position of this structure on the slide as is discussed by SHELLEY *et al.* (2010). Therefore, I here consider that these species are synonymous for taxonomic stability.

In addition, I have also examined the type material of *S. mathesoni* and *S. acatenangoense*, and studied the original description of these species together with that of *S. conviti* and agree with the synonymies proposed by MAIA-HERZOG *et al.* (1984). The male holotype of *S. mathesoni* is deposited in the INDRE Simuliidae collection. The adult is in poor condition as it has been stored in ethanol. Four legs and one wing are missing, while its head has become detached from the thorax. The genitalia have been dissected and are now on a slide (**Material Examined**). I have taken digital images of key diagnostic characters of the holotype of *S. mathesoni* (Figs. 878, 939, 999), which are now in the Simuliidae Digital Image Archive at the BMNH (see also **Material Examined**). The male holotype of *S. acatenangoense* is housed at the NMNH (accession number 409-27). The specimen is on three slides only containing the genitalia, two wings and three legs; the remainder of the adult, and the cocoon and pupal exuviae were not found at the NMNH Simuliidae holdings. The collectors' names given in the original description as Alfonso Calí and Juan Marroquín do not agree with the names that appeared on the slide with labels in H.T. DALMAT'S hand [see synonomic list]. I have taken digital images of this specimen, which are held at the BMNH (Figs. 879, 940, 1000). I have also examined the pupal exuviae of the female allotype preserved in alcohol (the remainder of the adult is missing) together with five pinned females and males (their pupal exuviae in ethanol), all labelled as paratypes and housed in the NMNH (**Material Examined**).

I have examined in the INDRE Simuliidae collection one slide containing a male genitalia that bears a collection label in VARGAS' hand "Texmico, Morelos, 3.vii.1945, col. A. Díaz N.". The slide also bear labels with numbers "3703", "CAIMSimTip-00141" and a red label as "Holotype" added by an unknown reviser. It is evident that this specimen is not the holotype of *S. paynei* and I have labelled it accordingly (**Material Examined**). I have also informed H. HUERTAS in INDRE of this problem.

Another species previously considered as a synonym of *S. paynei* is *S. falculatum*. This species was treated by COSCARÓN (1987) as a "probable synonym" of *S. paynei*, but ADLER *et al.* (2004) considered it a valid species within the subgenus *Hemicnetha*. The taxonomic problem involving *S. falculatum* was reviewed by HERNÁNDEZ & SHELLEY (2005), who also provided details of the type material, and commented on the morphological similarities of this species with those of taxa placed in *Hearlea* [now the CANADENSE species group] and *Hemicnetha* [now the TARSATUM species group]. HERNÁNDEZ & SHELLEY (2005), however, treated *S. falculatum* as a valid species within the subgenus *Hemicnetha*, and this has been followed by ADLER & CROSSKEY (2009, 2010) and SHELLEY *et al.* (2010). I have re-examined the taxonomy of *S. falculatum* in the current work and placed it in the CANADENSE species group of the subgenus *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010) [see **Taxonomic Discussion** under *S. falculatum*].

Simulium biuxinisa was described by COSCARÓN & IBÁÑEZ-BERNAL in 1955 from two pharate females, five pupal exuviae and numerous larvae collected in Oaxaca State, Mexico by the authors. A pharate female with its pupal exuviae was designated as holotype and said to be housed in INDRE, but the holotype was not found in the Simuliidae holdings at this institution and is now presumed to be lost (H. HUERTAS pers. comm. to L.M. HERNÁNDEZ). Nonetheless, I have studied the original description of this species and examined one pharate female labelled as paratype deposited in INDRE. The female thoracic pattern and the general morphology of the female genitalia (Fig. 632), the gill configuration (Fig. 1065) and larval hypostomium fall within the morphological variation found in *S. paynei*, especially the distinct oval paraproct (Fig. 632; COSCARÓN & IBÁÑEZ-BERNAL, 1993, Fig. 5). Therefore, I consider these species to be conspecific. Variation in gonapophyses morphology was found between specimens of *S. paynei* from Ecuador and those from Mexico (see also COSCARÓN & IBÁÑEZ-BERNAL, 1993), but further study is necessary to assess this variation.

The female of *S. paynei* is externally most similar to that of *S. rubrithorax* and *S. virgatum s.l.* However, *S. paynei* may be separated by the dark brown coloration of the thorax (Figs. 386-393) compared to that of *S. rubrithorax*, which is a reddish brown (Figs. 398-401). *Simulium paynei* is separated from *S. virgatum s.l.* by the more oval cercus and paraproct (Figs. 26, 631-633). In *S. virgatum s.l.* the cercus is subrectangular, while the paraproct is subquadrangular (Figs. 11, 640). The males can only be separated from those of *S. rubrithorax*, *S. solarii* and *S. virgatum s.l.* by the structure of the ventral plate, especially the length of the anterior process and the morphology of the anterior margin (Figs. 59, 938-941).

The number of gill filaments (eight) and the gill configuration of *S. paynei* (Figs. 1064-1066) is very similar to that of *S. freemani*, *S. bricenoi*, *S. rubrithorax* and *S. virgatum s.l.* However, the pupa of *S. freemani* can be easily separated from that of *S. paynei* by the absence of prominent fenestrations on the anterior margin of the cocoon. The pupa of *S. bricenoi* is easily recognized by the prominently rugose thorax with raised, irregularly distributed reticulate markings over its entire surface. Based on the pupal gill configuration alone *S. paynei* cannot be separated from *S. rubrithorax* and *S. virgatum s.l.*

The larva of *S. paynei* cannot be easily separated from other morphologically related species such as *S. hippovorum*, *S. rubrithorax* and *S. virgatum s.l.* in the absence of link-reared adult's collected in the same locality (see **Key to larvae** in **section 2.4.9**).

The cytology of *S. paynei* was reviewed by CHUBAREVA *et al.* (1976) and MUHAMMAD (1988), and CHUBAREVA *et al.* (1976) also illustrated the male and female genitalia. MUHAMMAD (1988) identified specimens of *S. paynei* as *S. virgatum* "B". ADLER *et al.* (2004) found their specimens of *S. paynei* and the material identified by MUHAMMAD (1988) as *S. virgatum* "B" differed by about three fixed inversions suggesting that *S. paynei* is a species complex. They also discussed and illustrated morphological differences in the male genitalia between specimens collected in Murray County, Oklahoma State and southern Arizona in the USA. They advocated for an integrated chromosomal-morphological study throughout the distribution range of *S. paynei* to resolve this problem.

Descriptions of life stages of *S. paynei* can be found in COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955) [as *S. acatenangoense* and *S. mathesoni*], VARGAS (1943b) [as *S. mathesoni*] and VARGAS & DÍAZ (1953; 1957b).

ADLER *et al.* (2004) placed *S. paynei* in the PAYNEI species group of the subgenus *Hemicnetha*, and this has been followed by ADLER & CROSSKEY (2008, 2009, 2010), COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008). However, SHELLEY *et al.* (2010) subsumed this species group under the TARSATUM species group of the subgenus *Hemicnetha*, where *S. paynei* is now placed.

Distribution. *Simulium paynei* has been recorded from Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panamá, Perú, Venezuela and the USA (ADLER *et al.*, 2004; CROSSKEY & HOWARD, 1997, 2004; MAIA-HERZOG, *et al.* 1984; SHELLEY *et al.* 2010; **Material Examined**). It is likely that records of *S. virgatum s.l.* from Central America (for example Belize, El Salvador, Guatemala, Mexico, and Panamá) abstracted by ADLER & CROSSKEY (2008, 2009, 2010) and COSCARÓN & COSCARÓN-ARIAS (2007) represent *S. paynei.*

Biology and Medical Importance. The biology of *S. paynei* was reviewed in detail in ADLER *et al.* (2004). These authors collected pupae and larvae of this species in swift rocky sections of lowland rivers typically with stretches of flat sedimentary rocks and travertines in the USA. Most larvae can be found in depths of less than 10 cm. In Costa Rica, immature stages of *S. paynei* have been found in fast to medium flowing, clear water streams with water temperatures varying between 15-28ºC and pH 7-7.5. Most of the streams run through secondary forest (gallery forest) with rocky riverbeds, sometimes with sand and/or sediments at altitudes between 144 to 2056 m. In most cases, larvae and pupae were found in huge numbers attached to rocks in rapids and waterfalls (L.M. HERNANDEZ & L.G. GUILLERMO, unpublished).

In Guatemala the larvae occupy smaller streams from less than a meter to 2 m wide that pass over volcanic flows (see also DALMAT, 1955). IBÁÑEZ-BERNAL (1992) recorded *S. paynei* between 600 and 2000 m and stated that it apparently prefered rivers with 10 to 25ºC and pH 6.5-7.5. The females have been collected biting cats, cattle, dogs, donkey, goats, sheep and were found on the bellies and ears of horses in Guatemala by DALMAT (1955) [as *S. virgatum s.l.*].

The microsporidium *Polydisperenia simulii* (LUTZ & SPLENDORE) has been recorded infecting *S. paynei* by ADLER *et al.* (2004).

2.5.4.12. ***Simulium (Trichodagmia) pulverulentum*** **KNAB** (Figs. 220, 275, 394-397, 516, 574, 634, 693, 809, 810, 881, 942, 1002, 1067, 1112, 1165, 1220, 1274)

A common zoophilic species externally similar to *S. yepocapense* and *S. guerrerense*. The following description has been based upon examination of type material, and identified specimens housed in the BMNH and NMNH collections, and numerous specimens I have recently collected in Costa Rica.

Simulium pulverulentum KNAB, 1915: 177. LECTOTYPE female, BELIZE [as British Honduras]: Stann Creek District Punta Gorda, [No collection date.] (*J.D.Norton*) (NMNH, cat. no. 19111) [Examined.] [Several papers cite the publication year of *S. pulverulentum* as KNAB, 1914, but the actual publication date is 1915]. **New type designation.**

FEMALE. General body colour black. Body length (pinned specimens) 1.9-3.4 mm (mean = 2.3 mm, s.d. = 0.45, n = 10), wing length 2.0-2.9 mm (mean = 2.4 mm, s.d. = 0.27, n = 10), wing width 0.5-1.1 mm (mean = 1.0 mm, s.d. = 0.17, n = 10).

Head: dichoptic with red eyes; nudiocular area well developed (Fig. 220). Frons, clypeus and occiput black with grey pruinosity, covered in numerous fine golden hairs that are denser on margins. Proboscis and maxillary palps dark brown. Antennae dark brown with scape and pedicel orange. Cibarium with margin of central trough and well developed cornuae sclerotised. Central trough with several rows of small, mainly blunt but some sharp teeth, which extend on margin of trough to base of cornuae (Fig. 275).

Thorax: black (but fading to dark brown in old specimens) with grey pruinose pattern that varies with direction of light source. With light source anterior most of scutum grey pruinose with median black line, 1+1 narrow, curved submedian vittae beginning in anterior fourth of scutum and extending to posterior margin, 1+1 black ovoid areas lateral to anterior parts of vittae (Figs. 394, 396). Lateral and posterior margins black and paranotal folds and a circular area posterior to these velvet black. With posterior light source scutum greyish black with 1+1 submedian grey pruinose triangular areas joined at anterior scutal margin (Figs. 395, 397). Scutum with numerous, adpressed, short, golden setae. Pleural region black with grey pruinosity. Scutellum dark brown with dense covering of fine, long brass-coloured hairs. Postnotum black with grey pruinosity. Subcostal wing vein bare or with 1- 4 setae in middle part; basal section of Radius bare. Costal base tuft of dark brown setae. Legs coloration pattern and proportions as in Fig. 516. Fore leg coxa and basal half of trochanters light brown, coxae with grey pruinosity, femora and tibiae mottled light and dark brown with basal articulation of tibia cream, tarsi brownish black. Mid and hind leg coxae dark brown with grey pruinosity, trochanters mottled, light brown, femora dark brown with basal articulation cream, tibiae dark brown to black with basal articulation and a ring in basal quarter cream, basal two-thirds of basitarsi cream, rest dark brown to black, other tarsal segments black with articulation of second tarsal segment cream. Claws curved with large basal tooth. Halteres white with black stems.

Abdomen: tergite I dark brown with light brown central portion and long, brass-coloured basal fringe; tergite II dark brown with light brown central portion; tergites III-V velvet black, tergites VI-IX shiny black. Tergal plates highly sclerotised. Sternites and genitalia black. Eighth sternite well sclerotised with 1+1 groups of about 16 medium size setae; gonapophyses well developed, triangular, totally membranous except for inner sclerotised margin and covered with fine setae (Fig. 574). Cerci hemispherical and sclerotised; paraprocts large, membranous and subrectangular covered with long and short setae (Fig. 634). Genital fork short, strongly sclerotised and with highly developed lateral arms and anterior processes (Fig. 693). Spermatheca oval, strongly sclerotised with no external sculpturing and with spicules on inner surface randomly distributed; width of membranous area of insertion of spermathecal duct large, about half maximum width of spermatheca.

MALE. General body colour black. Body length (specimens preserved in alcohol) 2.6-3.7 mm (mean = 3.2 mm, s.d. = 0.35, n = 19), wing length 1.7-2.7 mm (mean = 2.1 mm, s.d. = 0.26, n = 19), wing width 0.7-1.5 mm (mean = 1.0 mm, s.d. = 0.22, n = 19).

Head: holoptic with red eyes. Rest of head as in female but less setose.

Thorax: with anterior light source scutum dark black with 1+1 small, grey pruinose median cunae that coalesce and 1+1 submedian, smaller cunae lateral to these on anterior margin (Fig. 809). With light source posterior 1+1 grey pruinose posteriorly diverging median bands in place of median cunae seen with anterior light source (Fig. 810). Scutum with dense covering of short, adpressed, golden setae. Scutellum dark black with short, adpressed, golden setae and long dark setae on posterior margin, postnotum dark black with grey pruinosity. Pleural region as in female. Subcostal wing vein and basal section of Radius bare. Leg coloration as in female, except basal half of mid and hind basitarsi cream and rings on mid and hind tibiae not so apparent. Halteres as in female.

Abdomen: tergite I velvet-black with basal tuft of long yellowish hairs. Tergites II-IX velvet black with following silver pruinose ornamentation: tergite II covering whole segment, all of tergite VI except central part of segment, VII- VIII with small lateral areas. Sternites mottled brown and black with poorly developed sternal plates. Genitalia black. Gonocoxite subrectangular, wider than long, gonostyle large, elongate with weakly developed terminal spine [DALMAT (1955) recorded two spines] (Fig. 881). Ventral plate rectangular with sclerotised, poorly developed basal arms and large keel forming tube; ventral plate densely covered with fine setae and small spines (Fig. 942). Median sclerite subrectangular (Fig. 942). Paramere (Fig. 1002) with enlarged base plate and numerous, similarly sized spines with convex sides.

PUPA. Cocoon length dorsally (specimens in alcohol or glycerine) 1.9-3.3 mm (mean = 2.8 mm, s.d. = 0.31, n = 29), ventrally 2.9-5.5 mm (mean = 3.8 mm, s.d. = 0.51, n = 30); pupa length 2.5-4.1 mm (mean = 3.3 mm, s.d. = 0.37, n = 30); gill length 0.6-1.3 mm (mean = 0.9 mm, s.d. = 0.16, n = 30).

Cocoon: shoe-shaped as in Fig. 66, mid brown; rim of aperture mid brown, reinforced and without fenestrations as seen in *S. virgatum s.l.* Cocoon surface of thin, amorphous, translucent, elastic substance in which thick, interwoven fibres are sometimes visible.

Gill: light to dark brown, generally protruding beyond collar of cocoon, with ten short, forwardly-directed filaments arranged in a bunch. Main trunk of gill giving rise to a ventral primary branch, which immediately bifurcates and a dorsal primary branch, which bifurcates basally to form an inner and outer secondary branch each with four filaments. Filaments arise basally on gill, are slender with crenate margins and pointed distally, their surfaces covered with fine spicules (Fig. 1067).

Head (*frontoclypeus*): with 2 + 2 frontal and 1 + 1 facial trichomes, all poorly developed and unbranched; surface of head with some platelets and no tubercles, except a patch of small tubercles in area of facial trichomes.

Thorax: with 5+5 poorly developed, unbranched trichomes in anterior half. Thorax usually without tubercles, except in a band either side of dorsal cleft, in a patch ventrally below gill and posteriorly. In some specimens the surface of anterior region of thorax covered in well developed highly sclerotised tubercles, which usually extend to posterior border of thorax either side of cleft and in pair of submedian and lateral bands to posterior thoracic border, which is densely covered by normal size tubercles.

Abdomen: Abdominal tergite I with 2+2 submedian, simple setae; tergite II with 3 + 3 well developed simple hooks and 3+3 fine setae anterior to these, one between the outer two and the others between these and lateral margin; III-IV with 4 + 4 simple hooks; IX with no spines; II-IX with 1+1 well developed areas of spine combs in submedian to lateral position on anterior margins. Sternite IV with no hooks or hairs; V-VII with 2 + 2 simple hooks; I + I patches of spine combs on anterior borders of sternites IV-VIII and over most of sternite IX.

LARVA (Final instar). Body length 4.0-5.1 mm (mean = 4.0 mm, s.d. = 0.46, n = 4); width head capsule 1.1-1.2 mm (mean = 1.1 mm, s.d. = 0.05, n = 4); length of head capsule 0.9-1.1 mm (mean = 0.9 mm, s.d. = 0.05, n = 4). Body colour greenish (in specimens preserved in alcohol and Carnoy's). Body form as in Fig. 1112

Head: mainly pale dark brown, anterior region of cephalic apotome pale yellow. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Postgenal cleft broadly bell-shaped and rounded apically; postgenal bridge nearly as long as hypostomium (Fig. 1165). Hypostomium with strongly pigmented anterior margin and nine apical teeth; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth; 1+1 lateral teeth more prominent than sublateral teeth; 1 + 1 lines of eight hypostomial setae parallel to lateral margin; 2 + 2 setae in posterior half of hypostomium (Fig. 1220). Antennal segments longer than labral fans stalk, all segments light brown; length of antennal segments 0.06-0.1:0.07:0.1:0.05-0.07 mm (n = 4). Mandible with two apical teeth of same length; mandibular comb with 10 teeth, the first four teeth more prominent than remainder; 1 + 1 mandibular serrations (Fig. 1274). Maxillary palps heavily pigmented; three times as long as wide at base. Labral fan with 33-45 rays each with fine, single line of spines in a row interspersed with finer microspinules (n = 4).

Thorax: grey dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with a band of 27-49 rows of sclerotised processes with 15-18 simple hooks (n = 4). Pupal respiratory gill histoblast dark brown, claviform; dissected gill histoblast with 10 filaments.

Abdomen: usually completely grey dorsally with tinge of brown. Ventral nerve cord grey. Ventral papillae absent. Cuticle mainly lacking setae except area around anal sclerite, where fine spines can be seen. Anal sclerite well sclerotised with posterior arms extending to 70-90th row of posterior circlet hooks; no sclerotised areas between arms. Posterior circlet with 103-113 rows of sclerotised processes with 23-36 simple hooks (n = 4). Rectal gills with three lobes, each with six to eight finger-like lobules (n = 3).

Taxonomic Discussion. *Simulium pulverulentum* was described in the female from a series of 35 specimens collected at Punta Gorda in southern Belize by KNAB (1915). In this publication KNAB stated that the a "type with catalogue no. 19111" was deposited at the NMNH. SHELLEY *et al.* (2002b) provided a re-description of *S. pulverulentum* and stated that a holotype had been selected and housed at the NMNH, and two paratypes had been sent to the BMNH. However, no records of specimens of *S. pulverulentum* in KNAB (1915) or any species in KNAB (1913, 1914a-c) being sent to the BMNH is mentioned. I have examined the type series of *S. pulverulentum*, of which 31 pinned females and one female on slide are housed at the NMNH, and two pinned females are deposited in the BMNH Simuliidae collections (see **Material Examined**). All 35 specimens bear a red label as "Cotype 19111 U.S.N.M.". An additional specimen housed at the NMNH agrees with the type locality information given in KNAB (1915), but it does not bear a red label as cotype (see **Material Examined**). Because all specimens bear the same information and accession number, they are syntypes following ICZN (1999). Therefore, I have selected a female as lectotype and labelled it accordingly. The female is in good condition being glued by the left side to a card point, and its thorax is partially devoid of hairs. I have taken digital images of its thoracic pattern (Figs. 394, 395) and abdomen, which are now held at the Simuliidae Digital Archives, BMNH. The remaining 34 specimens are here designated as paralectotypes and they have been labelled accordingly (**Material Examined**).

Simulium pulverulentum is similar to *S. guerrerense* described by VARGAS & DÍAZ NÁjera (1956) from Mexico. The first of these authors had included the latter species in a previous description of *S. pulverulentum*, but then distinguished the two species by the form of the ventral plate in the male (Figs. 933, 942). The differences cited for the female – in the genital fork, pilosity of the Subcostal vein in the wing and in the eighth sternite are here regarded as intraspecific variations, but differences in the size of the nudiocular triangle are probably interspecific. Their characters for separating pupae are, as they themselves noted, imprecise. IBÁÑEZ-BERNAL (1992) recorded the absence of spines on sternite V of the pupa of *S. pulverulentum* as diagnostic for this species compared to other *Hemicnetha* species in the area. The figure of the gill of *S. guerrerense* in IBÁÑEZ-BERNAL (1992) shows the gill tips as rounded, whereas VARGAS & DÍAZ NÁjera (1956) figured them as pointed for *S. pulverulentum*. PETERSON *et al.* (1988) in their key to pupae of species of New World *Hemicnetha* separated *S. guerrerense* (from Mexico) from *S. pulverulentum* (from Belize, Guatemala, Mexico, Panamá, El Salvador and Venezuela) on differences in the inclination of the cocoon aperture and the shorter gill of the latter species. They based their comparison on specimens of *S. pulverulentum* that they had examined and figured, and the key of VARGAS & DÍAZ NÁjera (1957b) for *S. guerrerense.* I can see no difference in gill length between the two species figured by VARGAS & DÍAZ NÁjera (1957b) and I am not convinced by the minor differences in cocoon aperture, which could be artefactual or an intraspecific variation. In addition, this is contrary to the observations of other authors. DALMAT (1955) recorded a maximum gill length of 0.9 mm on material that appears to be *S. pulverulentum* judging by the ventral plate; specimens from Belize measured 0.6-1.3 mm; LEWIS' (1963) material in the BMNH from northern Venezuela shows gill lengths varying from 1.0-1.4 mm (mean = 1.1 mm, s.d. = 0.09, n = 15); and RAMÍREZ PÉREZ (1983) recorded the length as 1.1 mm in specimens from the same area. VARGAS & DÍAZ NÁjera (1956) recorded the maximum gill length for *S. guerrerense* as 1.0 mm. A closer study of these species linking

DNA and chromosomal variation to morphological differences is required in order to establish the taxonomic status of *S. guerrerense*.

The dissected gill histoblast of the larva of *S. pulverulentum* has 10 filaments, as in *S. guerrerense*. However, these species may be separated by the morphology of the hypostomium. In *S. guerrerense* the hypostomium is relatively more pointed centrally and it is weakly expanded at mid length. Moreover, the 1+1 lateral teeth of the hypostomium are more prominent than the median and sublateral teeth, which are often strongly reduced (Figs. 1214). In *S. pulverulentum* (Fig. 1220) the hypostomium is dome-like, not pointed centrally, and the median tooth of the hypostomium is at the same height and longer than the 1+1 lateral teeth, all teeth are well developed in comparison with those of *S. guerrerense*.

Descriptions of the life stages of *S. pulverulentum* may be found in COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955), FAIRCHILD (1940), IBÁÑEZ-BERNAL (1992) and SHELLEY *et al.* (2002).

VARGAS & DÍAZ NÁJERA (1957b) and IBÁÑEZ-BERNAL (1992) included *S. pulverulentum* in the subgenus *Hemicnetha* in their overviews of Mexican simuliid species. ADLER & CROSSKEY (2008, 2009, 2010), COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) placed *S. pulverulentum* in the PAYNEI species group within the subgenus *Hemicnetha*. However, SHELLEY *et al.* (2010) placed it in the TARSATUM species group of the subgenus *Trichodagmia*, which is accepted in the current work

Distribution. SHELLEY *et al.* (2002b) stated that *S. pulverulentum* was a relatively common species in the mountainous areas of Belize where it was found sympatric with other species of *Hemicnetha* and *S. callidum*, *S. gonzalezi*, *S. haematopotum*, *S. metallicum s.l.* and *S. samboni*. Elsewhere, it occurs in Costa Rica, El Salvador, Guatemala, Honduras, Mexico , Nicaragua, Panamá, and Venezuela (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; DALMAT, 1955; IBÁÑEZ-BERNAL, 1992; **Material Examined**). CROSSKEY & HOWARD (1997) also included Guyana based on the record in VULCANO (1981). However, SHELLEY *et al.* (2002b) considered it unlikely that this species occurs in Guyana because it was not recorded there by SMART (1940), is not present in southern Venezuela contiguous with Guyana (RAMÍREZ-PÉREZ, 1983) nor in the contiguous eastern Roraima State in northern Brazil (M. MAIA-HERZOG, pers. comm. to A.J. SHELLEY). The record of CROSSKEY & HOWARD (1997, 2004) of *S. pulverulentum* in Colombia was ommitted by COSCARÓN & COSCARÓN-ARIAS (2007), probably because they have not found this species so far south in South America, and I agree with this view.

Biology and Medical Importance. In Belize and Costa Rica, the immature stages of *S. pulverulentum* were collected in large (5 to 30 m wide) and fast flowing rivers, with pupae and larvae attached to fallen leaves, submerged vegetation and rocks in parts of the river where the current is faster. The females are recorded as zoophilic (SHELLEY *et al.*, 2002b; L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data). In other Central American countries *S. pulverulentum* is found from sea level to 1600 m and larvae breed in rivers up to 25m wide (IBÁÑEZ-BERNAL, 1992). He considered *S. pulverulentum* of veterinary importance in Mexico, because it feeds on horses and cattle.

DALMAT (1955) considered *S. pulverulentum* as a coastal species with the females being zoophilic biting horses, mules and cattle. However, he (DALMAT, 1955, pp: 343) also mentioned that the female of *S. pulverulentum* does attack man, and also argued that *S. pulverulentum* in combination with *S. exiguum* may serve as the only vectors of the disease in areas where the main anthropophilic species (*S. callidum*, *S. metallicum s.l.* and *S. ochraceum s.l.*) does not occur.

2.5.4.13. ***Simulium* (*Trichodagmia*) *rubrithorax*** **LUTZ** (Figs. 10, 12, 27, 39, 221, 276, 398, 399, 400, 401, 517, 575, 635, 694, 811, 812, 882, 943, 1003, 1068, 1113, 1166, 1221, 1275)

This is a common species in Brazil that is closely related to *S. paynei* and *S. virgatum s.l.* The description here has been based on material collected in Brazil housed at IOC and BMNH, and examination of type material.

Simulium rubrithorax LUTZ, 1909: 132. NEOTYPE female, BRAZIL: Minas Gerais State, Juiz de Fora, 43°22'W 21°47'S, 10.x.1909 (*C.Chagas*) (IOC) [Neotype designation by MAIA-HERZOG *et al.*, 1984: 352.] [Lectotype female designation by VULCANO, 1958: 236 invalid as not from syntype series (see MAIA-HERZOG *et al*., 1984)]. [Examined.]

Simulium magnum LANE & PORTO in PORTO, 1940: 383. HOLOTYPE female, BRAZIL: Mato Grosso State, Chapada, Ponce, 600m, viii. 1934 (*J.Lane*) (FSP, as FSPUSP in SHELLEY *et al*., 1997) [Synonymy (as *S. major*) by PY-DANIEL, 1989: 255.]

Simulium major: LANE & PORTO, 1940: 192 incorrect subsequent spelling (of *S. magnum*) [See SHELLEY *et al*., 1997.]

Simulium mutucuna NUNES DE MELLO & VIEIRA DA SILVA, 1974: 69. HOLOTYPE female (Register No. 5042), BRAZIL: Roraima State, Road BR 174 (BV8), Campinho at Venezuelan Border. (No date) (*J.A.Nunes de Mello & Eduardo Vieira da Silva*) (INPA). [Probable synonym of *S. paynei* by COSCARÓN, 1987: 36; listed as a valid species by PY-DANIEL & MOREIRA-SAMPAIO, 1995; synonymised with *S. rubrithorax* by HERNÁNDEZ *et al*., 2007a: 12; still regarded as a probable synonym of *S. paynei* by COSCARÓN & COSCARÓN-ARIAS, 2007: 531; treated as synonym of *S. rubrithorax* by ADLER & CROSSKEY, 2008: 45, 2009: 48, 2010: 48, COSCARÓN *et al*., 2008: 32, and SHELLEY *et al*., 2010: 460.]

FEMALE. General body colour orange/brown and black. Body length (specimens pinned) 2.9-3.9 mm (mean = 3.5 mm, s.d. = 0.29, n = 10); wing length 3.2-4.6 mm (mean = 3.8 mm, s.d. = 0.4, n = 18), wing width 1.4-1.9 mm (mean = 1.7 mm, s.d. = 0.4, n = 16).

Head: dichoptic with red eyes showing golden highlights; nudiocular area well developed (Fig. 221). Frons, clypeus and occiput dark brown with silver pruinosity; frons with numerous, irregularly arranged, stout hairs predominantly on margins. Antennae brown with scape, pedicel and basal third of first flagellomere yellow. Mouthparts dark brown. Cibarium unarmed with lightly sclerotised margin of trough and highly sclerotised cornuae (Fig. 276).

Thorax: scutum predominantly orange-brown with numerous, recumbent, golden hairs. Scutal pattern varying in appearance with illumination. With anterior illumination, thorax dark brown with following areas grey-silver pruinose: wide median vitta originating as triangle with base on anterior margin, expanding to drop-shaped extending for nine tenths of scutum, divided longitudinally by fine, dark brown line; pair of lateral vittae beginning at anterior fifth of scutum and extending for nine tenths of its length; lateral border of scutum grey pruinose (Fig. 398, 400). With posterior illumination grey pruinose and brown areas become reversed, previously pruinose vittae appear dark brown and dark brown background silver-grey pruinose; posterior margin greyish black (Fig. 399, 401). Humeri orange-brown. Paranotal folds dark brown with silver pruinosity. Pleural region dark, mottled orange-brown with grey pruinosity; prominent patch of long, golden hairs on pronotum; pleural tuft of prominent, golden hairs. Scutellum mid brown with light pruinosity and numerous, long, recumbent, golden hairs and long, dark hairs on outer margins. Postnotum dark brown with grey pruinosity. Subcostal wing vein with row of 4-6 setae in basal half; many sensilla in basal area. Basal quarter of Radius bare; following quarter with irregular row of predominantly (or solely) fine setae; next quarter with irregular row of both fine and stout setae; distal quarter with regular row of mainly stout setae (total of 40-48 fine setae and 22-25 stout setae). Basal tuft of dark hairs. Colour and proportions of legs as in Fig. 517. Legs yellow with following dark areas: fore leg with distal sixth of femur, basal quarter and distal fifth and outer margin of tibia, basitarsus and tarsi dark brown; mid leg with coxa, distal sixth of femur, distal fourth, subbasal spot and outer margin of tibia black; distal two fifths of basitarsus and other tarsal segments dark brown; hind leg coxa black, distal quarter of femur, all of tibia except basal articulation and median quarter, distal half of basitarsus black; distal half of first tarsomere and remaining tarsi dark brown. Claw of hind leg curved with large basal tooth. Halteres pale yellow with slightly darkened stems.

Abdomen: tergites predominantly black, but mottled orange-brown; tergite I velvet yellow/black with fringe of long golden hairs; tergite II velvet black with anterior half mottled with rust coloured patches; tergites III, IV velvet-black; tergites V-IX shiny black. Tergal plates sclerotised as in *S. exiguum*. Sternites mid to pale brown. Genitalia brown. Eighth sternite with well sclerotised central plate and 1+1 groups of 11-13 well developed setae; gonapophyses large and well developed, subtriangular, covered in setae with some sclerotisation on lower surface (Figs. 10, 39, 575). Cercus hemispherical, but slightly flattened on outer surface; paraproct subrectangular, membranous and setose, ventral extension one and a half times longer than cercus, ovoid, and covered in fine setae (Figs. 27, 635). Genital fork (Figs. 12, 694) highly sclerotised with well developed anterior and posterior processes, end of stem spatulate. Spermatheca oval, strongly sclerotised without external sculpturing and with spicules in rows; width of membranous area of insertion of spermathecal duct small, about quarter maximum width of spermatheca.

MALE. General body colour mottled orange-brown and black. Body length 3.7-4.4 mm (mean = 4.0 mm, s.d. = 0.32, n = 4); wing length 2.6-3.8 mm (mean = 3.4 mm, s.d. = 0.4, n = 9); wing width 1.3-1.9 mm (mean = 1.6 mm, s.d. = 0.2, n = 9).

Head: holoptic with upper eye facets red and lower eye facets dark red (appearing black in dried specimens). Rest of head coloration as in female.

Thorax: scutum orange-brown with some black areas and silver pruinosity; numerous recumbent, golden hairs. Scutum with median, indistinct, white cuna and 1+1 submedian, indistinct, white cunae on anterior half and 1+1 light brown, submedian vittae in median half diverging posteriorly with anterior illumination (Fig. 811). Lateral margins and posterior quarter of scutum silver pruinose. With posterior lighting, scutum with 1+1 submedian, narrow, silver vittae in middle third of scutum diverging posteriorly (Fig. 812). Black areas around humeri and central third of scutum. Humeri orange-brown Coloration and setation of paranotal folds, pleural region, scutellum and postnotum as in female. Subcostal wing vein as female. Basal quarter of Radius bare, remainder with irregular row of 22-25 stout setae interspersed with several fine setae. Leg and halteres coloration as in female.

Abdomen: tergites mainly velvet black, slightly mottled, genitalia light brown. Tergite I mottled yellow and black with fringe of long, pale hairs. Silver ornamentation as follows: tergite II with anterior border silver pruinose and 1+1 large, silver, pruinose spots occupying five sixths of lateral area; tergites VI, VII with 1+1 relatively large, distinct, lateral, pruinose spots; remaining tergites with 1+1 small, pruinose, antero-lateral spots. Sternites pale brown with poorly developed sternal plates. Gonocoxite rectangular, one and a half times as wide as long; gonostyle elongate, over twice as long as wide, and slightly 'S' shaped with weakly developed, subterminal spine (Fig. 882). Ventral plate well developed with large, wide, median anterior process densely covered with long setae and well developed keel; lateral shoulders absent and basal arms well developed and almost parallel (Fig. 943). Median sclerite median sclerite pyriform with apical incision (Fig. 943). Paramere with large basal process and two distinct clusters of stout spines, submedian with about 20 spines, lateral with slightly fewer spines and extending to basal process (Fig. 1003).

PUPA. Cocoon length dorsally 3.4-5.2 mm (mean = 4.3 mm, s.d. = 0.6, n = 25); ventrally 4.1-6.1 mm (mean = 4.9 mm, s.d. = 0.5, n = 25); pupa length 3.1-4.9 mm (mean = 4.0 mm, s.d. = 0.4, n = 25); gill length 2.5-5.4 mm (mean = 3.2 mm, s.d. = 0.6, n = 25).

Cocoon: shoe-shaped as Figs. 66, 68, mid to pale brown with obvious collar and long, slender fenestrations joined to form loose lattice. Cocoon surface smooth and translucent, with no individual fibres visible. In many localities balls of white amorphous material of unknown origin occur, sometimes attached to pupa and gills.

Gill: light brown, protruding slightly beyond fenestrations, with eight forwardly-directed filaments (Fig. 1068). Main trunk dividing basally into two primary branches each with four filaments. All filaments arise in basal quarter of gill, are slender with only faintly crenate margins and rounded distally, their surfaces densely covered with fine spicules.

Head (Frontoclypeus): with 1+1 small, simple, frontal trichomes and 1+1 poorly developed, simple facial trichomes; frons with thickened margin at junction with clypeus. Frontal area with groups of platelets, but devoid of tubercles; facial area with regular rows of pointed and rounded tubercles.

Thorax: well sclerotised with faint ring of small platelets loosely arranged around gill base (predominantly on dorsal side). Antero-dorsal surface with 5+5 (or 6+6) weakly developed, simple trichomes, three of which usually lie in line midway between gill base and dorsal margin. Central antero-dorsal region with trichomes but no tubercles, which are present only in patches on lateral and ventral areas and along mid line.

Abdomen: tergite I completely sclerotised with numerous spine combs occupying most of posterior third to half of tergite; tergite II sclerotised in anterior half, often with small plates, 1+1 rows of 2-3 coarse hairs centrally, 1+1 hairs at outer end of row (often absent), anterior third with spine combs interspersed with hairs; tergite III with 4+4 simple hooks centrally, 1+1 simple hairs antero-lateral to them (frequently absent) and 1+1 anterior patches of spine combs; tergites IV, V with 1+1 rows of 1-4 hooks usually present and 1+1 anterior patches of spine combs; tergites VI-VIII with 1+1 anterior patches of spine combs (extending to lateral margins in tergites VII, VIII); tergite IX with rounded, apical tubercles not spines. Abdominal sternites III, IV with anterior band of spine combs; sternite V with 2+2 close, simple hooks and anterior band of spine combs, most prominent above hooks; sternites VI, VII with four evenly-spaced, simple hooks and anterior band of spine combs; sternites VIII, IX with central band of spine combs, often weakly defined in sternite IX.

LARVA (Final instar). Body length 10.9-15.2 mm (mean = 12.7 mm, s.d. = 1.0, n = 30); width head capsule 0.8-1.2 mm (mean = 1.0 mm, s.d. = 0.1, n = 30); length of head capsule 0.9-1.3 mm (mean = 1.1 mm, s.d. = 0.1, n = 30). Body colour grey in specimens preserved in alcohol. Body form as in Fig. 1113.

Head: mainly dark brown, anterior region of cephalic apotome yellow. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Postgenal cleft narrow, bell-shaped with subtriangular extension at apex; postgenal bridge as wide as hypostomium (Fig. 1166). Hypostomium rounded anteriorly with strongly pigmented anterior margin and nine apical teeth; median tooth sharp, well developed and most prominent; lateral and sublateral teeth directly adjacent to median tooth smaller and sharp, remaining sublateral teeth less well developed; 3-6 lateral serrations; 1 + 1 lines of 13 hypostomial setae parallel to lateral margins [this is the most common pattern, but a few specimens with nine setae have been examined]; 2 + 2 (rarely 3 + 3) setae in posterior half of hypostomium (Fig. 1221). Antennae long and pigmented; length of antennal segments excluding the sensillum 0.05-0.1:0.1:0.7-0.1 mm (n = 6). Mandible with three apical teeth, first and third longer than second; mandibular comb with 15 well developed teeth, first seven more prominent than remainder teeth; two mandibular serrations, posterior smaller than anterior; mandibular combs teeth (Fig. 1275). Maxillary palps heavily pigmented; three times as long as wide at base. Labral fan with 60-80 rays (n = 6).

Thorax: grey dorsally and ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of over 60 processes. Pupal respiratory gill histoblast dark brown, claviform.

Abdomen: usually completely grey dorsally, progressively paler ventrally, especially towards posterior where last segments white; faint segmental banding visible ventrally. Ventral nerve cord grey. Ventral papillae absent. Cuticle mainly lacking setae except area around anal sclerite. Anal sclerite well sclerotised with posterior arms extending to 70-90th row of posterior circlet hooks, anterior arms bifid at apex; no sclerotised areas between arms. Posterior circlet with over 350 rows of up to 55 hooks (n = 6). Anal gill trilobed, each lobe with 15-22 fine finger-like lobules of which one is slightly larger than remainder (n = 6).

Taxonomic Discussion. The taxonomic problems with *S. rubrithorax* were discussed by MAIA-HERZOG *et al.* (1984), who designated a neotype for this species. The closest species to *S. rubrithorax* were considered to be *S. bricenoi*, *S. conviti*, *S. paynei* and *S. virgatum s.l.* Taxonomic complications involving *S. paynei* were discussed in detail and the authors cited *S. acatenangoense*, *S. bilimekae*, and *S. mathesoni* as synonyms of *S. paynei* and added *S. conviti* as a new synonym. These synonyms were accepted in the World Inventory of the Blackflies (CROSSKEY & HOWARD, 1997, 2004; ADLER & CROSSKEY, 2008, 2009, 2010). SHELLEY *et al.* (2002b) in a survey of the Simuliidae of Belize provided a comprehensive revision of the closely related *S. virgatum s.l.* and agreed with the synonyms recorded in the world inventory of CROSSKEY & HOWARD (1997). SHELLEY *et al.* (2002b) also concluded that *S. virgatum s.s.* from the USA was possibly different to *S. virgatum s.l.* in which they included specimens from Belize with varying scutal coloration, *S. paynei* and *S. rubrithorax*. They suggested future work on *S. virgatum s.l.* using cytological and molecular techniques to resolve the validity of the constituent species before any firm synonymies could be made. More recent editions of the world inventory (CROSSKEY &

HOWARD, 2004; ADLER & CROSSKEY, 2008, 2009, 2010) followed ADLER *et al.* (2004), who revalidated *S. hippovorum* from its synonymy with *S. virgatum s.s.* ADLER *et al.* (2004) also listed the various misidentifications of *S. paynei* and provided cytological information that suggests that it is a complex of sibling species.

More recently, SHELLEY *et al.* (2010) re-examined their findings in SHELLEY *et al.* (2002b) and studied further specimens of *S. virgatum s.l.* They concluded that the black form from Belize is *S. paynei*; while the brown form from Belize could be the same species as *S. paynei* (Ecuador), and that these populations might possibly be conspecific with *S. rubrithorax*. I re-examined all specimens of *S. paynei* and *S. rubrithorax* in the course of the current work and I agree with SHELLEY *et al.* (2010), though the suggested possible synonymy of *S. rubrithorax* with *S. paynei* is not accepted in this work. This is because of morphological differences found in populations identified as *S. rubrithorax* [see relevant figures]. Thus, I treated them as valid taxa in this work. *Simulium mutucuna* has been synonymised under *S. rubrithorax* by HERNÁNDEZ *et al.* (2007a), but this species has been regarded as a probable synonym of *S. paynei* by several authors [see synonomic list]. *Simulium mutucuna* was collected in Roraima State, Brazil near the border with Venezuela, a country where *S. paynei* also occurs. The black coloration of the holotype puts it closer to *S. paynei*, but here I follow HERNÁNDEZ *et al.* (2007a) until a re-examination of the holotype of *S. mutucuna*, especially its genitalia, can be carried out.

In Brazil, the *S. rubrithorax* female is similar in scutal pattern and coloration to *S. brachycladum*, *S. cristalinum* and *S. lobatoi*, but they can be distinguished using other morphological characters [see also **Taxonomic Discussion** of *S. lobatoi*]. The gonapophyses of *S. rubrithorax* (Figs. 10, 39, 575) are well developed and triangular and less pointed apically than in *S. brachycladum* and *S. cristalinum*; the gonapophyses of *S. lobatoi* are more oval and highly setose (Fig. 571). The ventral extension of the female paraproct of *S. rubrithorax* is suboval and membranous and broader with no posterior tails compared to *S. brachycladum* and *S. cristalinum* (Figs. 621, 623, 635); in *S. lobatoi* (Fig. 630) the paraproct is less developed and highly setose (In the *S. rubrithorax* male the scutal pattern is most similar to that of *S. lobatoi* and both are brown (Figs. 799, 800, 811, 812). They are easily distinguished by the ventral plate with no lateral shoulders, median process well developed with median depression, twice as long as the main body of the ventral plate and with a well developed keel with a ventral invagination in *S. rubrithorax* (Fig. 943). In *S. lobatoi* the ventral plate has small lateral shoulders, a well developed median process which is distinctly concave centrally forming a bilobed structure, and a well developed keel with no invagination (Fig. 937).

In the pupa *S. rubrithorax* is easily distinguished from other Brazilean species of *Trichodagmia*, for example *S. brachycladum*, *S. cristalinum* and *S. lobatoi*, by the form and number of the gill filaments (Figs. 1049, 1052, 1053, 1061-1063). *Simulium rubrithorax* cannot be distinguished from the closely related species *S. paynei* and *S. virgatum s.l.*, as these species have the same configuration and number of pupal gill filaments (Figs. 1065, 1066, 1068, 1072)

In Brazil, the larva of *S. rubrithorax* can be easily distinguished from other *Trichodagmia* species by the dissected gill histoblast with eight filaments. However, elsewhere the larvae of *S. paynei*, *S. bricenoi* and *S. virgatum s.l.* also have a gill histoblast with eight filaments and they cannot be easily separated solely on this life stage [see **Key to larvae** in section **2.5.4**].

CROSSKEY & HOWARD (1997, 2004) placed *S. rubrithorax* in the PAYNEI species group of the subgenus *Hemicnetha*, which has been followed by ADLER *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), and ADLER & CROSSKEY (2008, 2009, 2010). More recently, SHELLEY *et al.* (2010) placed *S. rubrithorax* in the TARSATUM species group within the subgenus *Trichodagmia*, which is accepted in the current work.

Distribution: *Simulium rubrithorax* only occur in Brazil, where it has been recorded from the states of Bahía, Goiás, Mato Grosso, Minas Gerais, Rio de Janeiro, Rio Grande do Sul, Roraima and São Paulo (ADLER & CROSSKEY, 2008, 2009,s 2010; COSCARÓN, 1991; CROSSKEY & HOWARD, 1997, 2004; MAIA-HERZOG, *et al.* 1984; PY-DANIEL, 1989; SHELLEY *et al.*, 1997, 2010; **Material Examined**). A record of *S. rubrithorax* in Venezuela from LUTZ (1928), is regarded by RAMÍREZ PÉREZ (1987) as a misidentification of *S. paynei*, having compared LUTZ's material in the IOC with reared material collected at the same localities. COSCARÓN (1991) and CROSSKEY & HOWARD (2004) recorded *S.*

rubrithorax from Guyana, presumably based on SMART (1940). Two slide preparations in the BMNH collection (details of labels in **Material Examined** by SHELLEY *et al.*, 1997) that were used for the 1940 description of *S. rubrithorax* by SMART have been examined. One contains three males (without terminalia) dissected from their pupae and the other the terminalia of these males. These have now been identified as *S. maroniense s.l.* (SHELLEY *et al.*, 2004).

Biology and Medical Importance: *Simulium rubrithorax* breeds in fast-flowing water (particularly in waterfalls), where larvae and pupae can be found attached to rocks, often in enormous numbers (MAIA-HERZOG *et al.*, 1984). In the Amazônia onchocerciasis focus *S. rubrithorax* is probably zoophilic as in other parts of Brazil where it bites horses and most probably cattle. Yanomami Indians in the focus use larvae collected from a local waterfall as food (SHELLEY & LUNA DIAS, 1989). ANDRADE & PY-DANIEL (2000) [as *Hemicnetha rubrithorax*] cited predation of larvae by fish species of the families Characidae and Poecilidae in north eastern Brazil.

2.5.4.14. ***Simulium (Trichodagmia) smarti*** **VARGAS** (Figs. 9, 222, 277, 402, 403, 518, 576, 636, 695, 813, 814, 883, 944, 1004, 1069, 1114, 1167, 1222, 1276)

This is a zoophilic species originally described from Mexico and Guatemala and externally similar to *S. tarsatum*. I have been unable to obtain pupal exuviae and larvae of this species. Therefore, the description provided here for these life stages has been derived from the original description of VARGAS (1946), and the revisions of COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955) and IBÁÑEZ-BERNAL (1992).

Simulium (Eusimulium) smarti VARGAS, 1946: 327. HOLOTYPE female, MEXICO: Chiapas state, El Rubí stream, Finca El Vergel, 1000m; 27.i.1943, (*Vargas-Díaz*) (INDRE, no. 3684) [Examined.]

FEMALE. General body colour black. Body length (specimens pinned, n = 2) 3.4-4.3 mm, wing length 3.6-3.8 mm, wing width 1.8-1.9 mm.

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 222). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts dark brown to black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed and sclerotised cornuae, with fine teeth in central trough and lateral margin of cornuae [best seen at higher magnification] (Fig. 277).

Thorax: scutum black with numerous, adpressed, short, black setae becoming longer and upright on posterior border, interspersed with clumps of adpressed, brass-coloured, scale-like setae. Scutal pattern only varying slightly with illumination. With light anterior scutum weakly pruinose on anterior margin, humeri, anterior and posterior margins black (Fig. 402). With light posterior, thorax black and distinctly silver pruinose on anterior margin (Fig. 403). Scutellum dark brown to black with grey pruinosity and with scattered, upright, black bristles on whole surface except anterior border and brass-coloured, adpressed, scale-like setae over whole surface. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae along its length. Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 518. Fore leg with coxa, trochanter and femur brown; tibia and tarsal segments dark brown. Mid leg coxa, trochanter, femur, tibia, apex of tarsal segment I, and tarsal segment II-IV dark brown; remainder of tarsal segment I white. Hind leg with coxa and trochanter missing in the holotype; femur, tibia, apical half of tarsal segment I and tarsal segments II-IV dark brown; basal half of tarsal segment I pale yellow. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown to black, tergite I with pale brown areas laterally. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subquadrangular, with weakly curved internal margins, poorly sclerotised and densely covered with long hairs and microtrichiae (Figs. 576). Cercus hemispherical, covered with long black setae; paraproct small, subquadrangular, one and half time longer than cercus, weakly sclerotised on basal half and membranous apically; paraproct densely covered with brown hairs and few basal setae (Fig. 636). Genital fork stout and sclerotised; termination of lateral arms with anterior margins straight and well developed; anterior processes developed, blunt apically; posteroir processes round apically (Fig. 695). Spermatheca globular, with weak external sculpturing and groups of single or two-three spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body black. Body length (specimens pinned, n = 2) 4.0-4.3 mm; wing length 2.7-3.2 mm, wing width 1.2-1.8 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: coloration and setation of scutum, humeri, paranotal folds, pleural region, scutellum and postnotum as in female, except that it does have a distinct pruinose area on anterior margin with anterior and posterior illumination (Figs. 813, 814). Scutellum brown to black with clumps of adpressed, brass-coloured, scale-like setae interspersed with long black erect hairs. Postnotum black with silvery grey pruinosity. Wing setation as in female, except Sc and basal section of Radius bare in the single specimen examined. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites VI-VII (best seen in some specimens when tilted and viewed laterally). Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle elongate with lateral margins weakly sinuous, terminating in single, stout spine; gonocoxite and gonostyle covered with long brown setae (Fig. 883). Ventral plate sclerotised, subrectangular, covered with long hair; main body of ventral plate widely expanded centrally [best seen in lateral view], without antero-median process; lateral shoulders undeveloped, basal arms well developed, subparallel, distinctly expanded apically (Fig. 944). Median sclerite long, with apical incision (Fig. 944). Paramere with well developed and sclerotised basal process and numerous long spines along whole length (Fig. 1004).

PUPA. Gill length 2.6 mm [Other measurements and the number of specimens examined were not given in the original description].

Cocoon: shoe-shaped as in Figs. 66, 68, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture strongly elevated.

Gill: light brown with 18 upwardly directed filaments arranged in loose bunch in vertical plane (Fig. 1069). Gill configuration with filaments branching basally at different heights; main trunk short, giving rise to two sets of primary branches, one internal and one external: the more external consists of nine splayed-out secondary filaments; the internal branch has nine secondary filaments arranged in bunch (Fig. 1069). Filaments stout, rounded distally, with spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 small simple facial trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 4-5 platelets in two to three groups laterally in frontal region, respectively; tubercles rounded scarcely distributed over entire surface.

Thorax: with 2+2 simple trichomes near margin of dorsal cleft, 2+2 small simple trichomes on central region, one simple trichome posteriorly, and 3+3 simple small trichomes on alar region; tubercles mostly rounded well distributed over entire region.

Abdomen: abdominal tergite I with 1+1 submedian simple setae and 1+1 small simple setae on lateral margins; tergite II with 3+3 submedian spiniform setae in row, 2+2 small simple setae anterior to outermost spiniform setae, and 1+1 small simple setae on lateral margins; tergites III, IV with 4+4 submedian simple hooks in row, 1+1 small simple setae anterior to outermost hooks, and 1+1 small simple setae on lateral margins; tergite V with 4+4 submedian small simple setae in row and 1+1 small simple setae on lateral margins; tergite VI with 2+2 submedian small simple setae and 1+1 small simple seta laterally; tergite VII with 1+1 small simple setae on lateral margins; tergite VIII without setae; tergite IX without setae or spine combs. Spine combs on posterior margins of tergites I, II, and anterior margins of tergites III-VIII. Sternite III with 2+2 submedian small simple setae and 2+2 small simple setae laterally; sternite IV with 3+3 submedian small simple setae in row, and 2+2 small simple setae on lateral margins; sternite V with 2+2 close simple hooks, 2+2 small simple setae anterior to outermost hooks, and 2+2 small simple setae on lateral margins; sternites VI, VII with 4+4 well separated simple hooks in row and 2+2 small simple setae anterior to outermost hooks; sternites VIII, IX without trichomes or setae; sternite IX weakly sclerotised. Spine combs on anterolateral margins of sternites III-VIII.

LARVA (Last instar). [DALMAT (1955) gave the following measurements for the body length 8.2-8.9 mm (n = 2); length of head capsule 0.9 mm (n = 4); other measurements were not provided IBÁÑEZ-BERNAL (1992) gave only measurements for the body length 10.9-11.2 mm (n = 2); head length 1.2 mm (n = 2)]. Body colour yellow with no dark patches on ventrolateral regions of segments VI, VII [preservation of specimens not stated but probably in ethanol] (Fig. 1114).

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Fig. 1167). Hypostomium strongly pigmented on anterior margin, with approximately seven apical teeth arranged on central region and forwardly protruding; median tooth sharp, well developed and more prominent than remainder; 3+3 sublateral teeth, the pair adjacent to base of median tooth longer than remainder; lateral tooth reduced to 2+2 small teeth; 7+7 lateral serrations; 1+1 lines of ten hypostomial setae parallel to lateral margins; 1+1 long, simple setae in posterior half of hypostomium (Fig. 1222). Sub-esophageal ganglion not examined. Antenna slightly longer than labral fans stalk, segment I with small patch at its base, remainder dark brown, segment II nearly transparent except for two dark brown patches in the middle, segment III dark brown; length of antennal segments I-III not given because of lack of material. Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately eight teeth, second, third and fourth longer than remaining teeth; one prominent mandibular serration (Fig. 1276). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with 43-59 rays each with fine, single line of spines in row.

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 65-74 processes. Pupal respiratory gill histoblast not examined.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord not examined. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills where six to seven rows of single, bifid or trifid anal scales are seen. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 450-460 rows of simple hooks. Rectal gills with three lobes, each lobe with approximately 19 small, finger-like lobes.

Taxonomic Discussion. *Simulium smarti* was described by VARGAS in 1946 based on a female holotype, one male allotype, and one male and three females (all as paratypes) collected in Chiapas State, Mexico. He referred to larvae in the same paper, although he did not provide a description only stating "larvae live in large quantities in fast running streams, attached to stones". The larval stage was fully described later by VARGAS *et al.* (1946). In the same paper VARGAS (1946) also mentioned he had examined numerous specimens from Guatemala, although he did not indicate their exact provenance. I have examined the female holotype, which is housed in INDRE. The female holotype has the thorax glued to a card and the pleura are fairly damaged; its head, wings, legs (two legs are partially damaged), abdomen and genitalia are on a slide (**Material Examined**). I have also examined a male on a slide labelled as allotype at INDRE. The slide only contains the wings, legs and the genitalia; the remainder of the specimen was not found within the INDRE Simuliidae holdings. In addition, I examined two males and two females labelled as paratypes deposited at INDRE and a further male at NMNH (**Material Examined**).

The female of *S. smarti* is externally indistinguishable from that of *S. tarsale* and *S. tarsatum* in which the thorax is black covered with clusters of recumbent yellow hairs (Figs. 402, 403, 406-409, 410, 411). However, VARGAS (1946) stated that *S. smarti* can be separated by the coloration of fore tibia. In

S. tarsatum the fore tibia is bicoloured, pale yellow in its basal half (Fig. 521), while in *S. smarti* it is completely black (Fig. 518). In this respect, *S. smarti* is more similar to *S. tarsale* from which it cannot be easily separated [see **Taxonomic Discussion** under *S. tarsale*]. The thoracic patterns of the male of *S. smarti* and *S. tarsatum* are also similar (Figs. 813, 814, 819, 820), but they can be distinguished by the general morphology of the ventral plate. In *S. smarti*, the anterior margin is prominently bulbous centrally [when examined in lateral view] (Fig. 944), while in *S. tarsatum* is not bulbous centrally (Fig. 947). The male, pupa and larva of the closely related species *S. tarsale* remain unknown, thus comparisons cannot be made.

The best character to recognise *S. smarti* is the configuration and number of the pupal gill filaments. The pupa has 18 gill filaments with some filaments appearing to be more splayed-out and dividing at some distance from the base of the gill (Fig. 1069). The pupa of *S. tarsatum* has 12 filaments, all arranged in a bunch basally (Figs. 83, 1071). Another species with a similar number of gill filaments is *S. earlei* (15 to 17 filaments, most common number 16), but the filaments are not splayed out and some filaments divide at their apical third (Fig. 1054).

The larva of *S. smarti* is best identified by the configuration of the dissected gill histoblast of mature larvae with 18 filaments and the hypostomium with only seven teeth arranged on the central region and protruding forward (Figs. 1222). Other closely related species with a similar number of filaments in the gill histoblast is *S. earlei*, but the gill histoblast of *S. earlei* commonly have 16 filaments and *S. smarti* has 15 filaments. In addition, the morphology of the hypostomial teeth of *S. earlei* is rather different (Figs. 1212) from that of *S. smarti* (Fig. 1222).

Full descriptions of adults, pupae and larvae of *S. smarti* can be found in VARGAS (1946), VARGAS & DIAZ NÁJERA (1957b), IBÁÑEZ-BERNAL (1992) and COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium smarti was placed in the MEXICANUM species group of the subgenus *Hemicnetha* by CROSSKEY & HOWARD (1997, 2004), COSCARÓN & COSCARÓN-ARIAS as (2007) and COSCARÓN *et al.* (2008). ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010) placed *S. smarti* in the TARSATUM species group of the subgenus *Trichodagmia*, which is also followed in this work.

Distribution. *Simulium smarti* has only been recorded from Mexico (Chiapas State) and Guatemala (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; IBÁÑEZ-BERNAL, 1992); VARGAS, 1946; **Material Examined**).

Biology and Medical Importance. DALMAT (1955) and IBÁÑEZ-BERNAL (1992) stated that pupae and larvae of *S. tarsatum* (as *S. mexicanum*) are commonly found in streams between 300-2.200 m attached to rocks, although they can also attached to leaves and stems. COSCARÓN & COSCARÓN-ARIAS (2007) stated that *S. smarti* breeds in small waterfalls and torrential streams of clear water (0-23°C), attached to rocks and aquatic vegetation. In Guatemala, the females are zoophilic biting horses, cows and sheep (DALMAT, 1955).

2.5.4.15. ***Simulium* (*Trichodagmia*) *solarii*** **STONE** (Figs. 58, 223, 278, 404, 405, 519, 577, 637, 696, 815, 816, 884, 945, 1005, 1070, 1115, 1116, 1168, 1223, 1277)

This is a zoophilic species externally very similar to *S. virgatum s.l.* and known from Mexico and southern Unites States of America.

Simulium (Dryarella) solarii STONE, 1948: 402. HOLOTYPE male (reared), UNITED STATES OF AMERICA: Texas State. Menard County; 23.iv.1923, (*A.Stone*) (NMNH, no. 58956) [Examined.] [The pinned holotype male does not have on the label the name of the river, but STONE (1948) stated that it is was collected in the "San Saba River". The latter appears on the label of the slide that contain the male genitalia of the holotype.]

FEMALE. General body colour dark brown. Body length (specimens pinned) 2.9-3.7 mm (mean = 3.3 mm, s.d. = 0.25, n = 10), wing length 2.2-2.9 mm (mean = 2.5 mm, s.d. = 0.24, n = 10), wing width 1.0-1.5 mm (mean = 1.2 mm, s.d. = 0.17, n = 10).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 223). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts black. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed sclerotised cornuae and minute serrations on base of cornuae and pointed teeth on membrane of hypopharynx (Fig. 278).

Thorax: scutum dark brown to black with evenly arranged, recumbent, whitish setae, interspersed with fine, semi-recumbent brown setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown to black with 1+1 submedian, pear-shaped pruinose and 1+1 sublateral wide pruinose vittae extending from anterior to posterior margins; dark brown lyre-shaped on submedian region of thorax, and fine line on central region extending from anterior to posterior margins; humeri pale brown; lateral and posterior margins dark brown (Fig. 404). With posterior illumination pattern similar to that with anterior light source but 1+1 silver pruinose comma-shaped vittae on anterior third of scutum (Fig. 405). Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta bare. Radius with numerous setae intermixed with few spines towards apex, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 519. Fore leg with coxa, half of femur, two thirds of tibia, apical third of tarsal segment I and tarsal segments II-III dark brown; trochanter, basal half of femur, basal third of tibia pale brown; basal two thirds of tarsal segment I white. Fore and hind legs with coxae, trochanters, femora, most of tibiae, apical third of tarsal segments I, and tarsal segments II-IV dark brown; basal third of tibiae pale to brown; two thirds of tarsal segment I white. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I, II pale brown, tergites III-IX dark brown. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly two and half times longer than eighth sternite at mid point, almost subtriangular with weakly curved internal margins, weakly sclerotised, and densely covered with long hairs (Fig. 577). Cercus hemispherical, covered with brown setae; paraproct 1.5 times longer than cercus, broadly subrectangular, weakly sclerotised on basal half and membranous apically; paraproct densely covered with prominent brown hairs basally and smaller setae apically (Fig. 637). Genital fork stout and sclerotised; termination of lateral arms with anterior margins curved and well developed; anterior processes developed apically; posterior processes undeveloped (Fig. 696). Spermatheca globular, with weak external sculpturing and with small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour dark brown. Body length (specimens pinned) 2.7-3.4 mm (mean = 3.0 mm, s.d. = 0.31, n = 4), wing length 2.0-2.9 mm (mean = 2.4 mm, s.d. = 0.37, n = 4), wing width 0.7-1.3 mm (mean = 0.9 mm, s.d. = 0.26, n = 4).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark covered by white recumbent hairs. Scutal pattern varies slightly with light incidence: with light source anterior thorax dark brown to black, with faint pruinose area on anterior third of scutum; fine dark brown line on central region of thorax extending from anterior to posterior margins; humeri silver pruinose; anterior to posterior margins dark brown (Fig. 815). With posterior illumination, thorax similar to anterior light incidence but pruinose area more distinct (Fig. 816). Scutellum dark brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female. Leg coloration as in female.

Abdomen: tergites dark brown to black, basal fringe with long, brown hairs. Pruinose ornamentation on lateral margin of tergite V, VI [best seen in some specimens when tilted and viewed laterally]. Genitalia brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle subrectangular with dorsal and ventral margins sinuous, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 884). Ventral plate sclerotised, subrectangular, covered with short hair; anterior median process prominently developed, nearly two and a half times longer than its basal and distinctly covered by long hairs; anterior margin of ventral plate distinctly concave at both sides of median process; lateral shoulders well developed, and basal arms well developed and subparallel (Fig. 58, 945). Median sclerite long, about three times longer than wide at widest point, with small incision (Fig. 945). Paramere with well developed and sclerotised basal process and numerous long spines along whole length; central membrane covered by multibranched spicules (Fig. 1005).

PUPA. Cocoon length dorsally 3.6-4.8 mm (mean = 4.0 mm, s.d = 0.40, n = 10), ventrally 4.3-6.0 mm (mean = 5.6 mm, s.d. = 0.78, n = 10); pupa length 4.0-5.1 mm (mean = 4.5 mm, s.d. = 0.31, n = 10); gill length 1.2-1.8 mm (mean = 1.4 mm, s.d. = 0.21, n = 10).

Cocoon: shoe-shaped as in Fig. 66, brown to black, composed of thick, coalesced fibres with reinforced rim to anterior aperture, without fenestrations and margin of aperture elevated.

Gill: light brown with 15 upwardly directed filaments arranged in bunch in vertical plane (Fig. 1070). Gill with main trunk short, with 14 bunched together and branching basally at different heights, and asingle filament separated from the remainder. Filaments stout, rounded distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 2+2 frontal and 1+1 facial small, simple trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and single group with 2 platelets laterally in frontal region; tubercles absent.

Thorax: with 3+3 simple long trichomes near margin of dorsal cleft, 2-3 simple trichomes on central region, one simple trichome on posterior region, and four simple trichomes in alar region; tubercles rounded, only visible on anterior margin posteriorly and near alar region.

Abdomen: abdominal tergite I with 1+1 median simple short setae, 4+4 submedian small simple setae and 1+1 small simple setae laterally; tergite II with 4+4 spiniform setae in row, 2+2 simple setae between mid spiniform setae, 2+2 small setae anterior to outermost spiniform setae, and 1+1 small setae laterally; tergites III, IV with 4+4 simple hooks in row on posterior margin, 2+2 small simple setae anterior to outermost hook, and 1+1 small simple setae laterally; tergite V with 2+2 submedian simple setae and 1+1 small simple setae laterally; tergites VI-VII with 1+1 submedian small simple setae; tergite VIII apparently without setae; tergite IX weakly sclerotised without terminal spines. Spine combs distribution as follows: central region tergite I, and anterolateral margins of tergites II-VIII. Sternite III with 2+2 well separated submedian simple setae; sternite IV with 2+2 close submedian simple setae; sternite V with 2+2 close simple hooks in row, and 1+1 simple setae lateral to outermost hook; sternites VI, VII with well spaced simple hooks in row; sternite VIII with 1+1 simple setae; sternite IX weakly sclerotised. Spine combs on anterolateral margins of sternites III-VIII.

LARVA (Final instar). Body length 8.0-11.5 mm (mean = 9.6 mm, s.d. = 1.2, n = 7); length of head capsule 0.8-1.0 mm (mean = 0.9mm, s.d. = 0.07, n = 7); width of head capsule 0.7-0.8 (mean 0.7, s.d. = 0.04, n =7). Body colour dark grey dorso-laterally, whitish ventrally (specimens fixed in spirit). General body form as in Figs. 1115, 1116.

Head: varying from pale yellow with brown head spots to dark brown with yellowish head spots, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive or negative. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge 1.5 times length of hypostomium (Fig. 1168). Hypostomium strongly pigmented on anterior margin, with approximately nine often reduced teeth, evenly distributed on anterior region [sometimes the teeth they can be concentrated on central region] with median and 1+1 adjacent sublateral teeth weakly protruding forward; median tooth sharper and more developed; 3+3 sublateral teeth; 1+1 reduced lateral teeth; lateral serrations absent; 1+1 lines of approximately nine hypostomial setae parallel to lateral margins; 2+2 long, simple setae in posterior half of hypostomium (Fig. 1223) [VARGAS *et al.* (1946) and IBÁÑEZ-BERNAL (1992) stated that larvae can have seven or 10 teeth]. Sub-esophageal ganglion pigmented. Antennal segments slightly longer than labral fan stalk, segment I and two thirds of segment II pale brown, apex of segment II and segment III dark brown; length of antennal segments I-III excluding the sensillum 0.09-0.1:0.1:0.08-0.09 mm (n = 5). Mandible with three apical teeth, first one longer than second and third apical teeth; mandibular comb with approximately six teeth, first three shorter than the last three; one prominent mandibular serration (Fig. 1277). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 45-66 rays each with fine, single line of spines in a row (n = 5).

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 34-48 sclerotised processes of 14-19 simple hooks (n = 4). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with eight filaments, all branching from a common trunk and pointed apically.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments are white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 164-208 rows of sclerotised processess of 38-49 simple hooks (n = 5). Rectal gills with three swollen lobes of 6-7 small, finger-like lobules, one dorsal filament more swollen than remainder (n = 1).

Taxonomic Discussion. *Simulium solarii* was described by STONE in 1948 from numerous adults and pupal exuviae collected in the state of Texas, USA and Mexico. In the same paper, he discussed the taxonomic confusion of *S. solarii* with *S. virgatum s.l.* and the misidentifications made by previous authors. He did not describe the larva at this time because of "his insufficient knowledge of simuliid larvae". The larva was later described (as *S. virgatum*) for the first time by VARGAS *et al.* (1946), but it was IBÁÑEZ-BERNAL (1992) and ADLER *et al.* (2004) who gave a detailed description and full illustrations of the larva of this species. I have examined the male holotype of *S. solarii*, which is deposited at the NMNH. The pinned male holotype is in good condition and it has been glued to a card point by the ventral side of the thorax; its genitalia are on a slide. The pupal pelt has been glued to a separate card together with the pinned adult (**Material Examined**). In addition, I have also examined several adults, pupae and larvae labelled as paratypes, and other identified material deposited at the BMNH, NMNH and CNC collections (see **Material Examined**).

The taxonomy of *S. solarii* has been recently reviewed in detail by ADLER *et al.* (2004), who also provided all relevant literature and pointed out the mis-identifications made by previous authors. In the USA, females of *S. solarii* resemble externally the brown form of *S. virgatum s.l.* from which they can only be separated by the morphology of the genital fork. In *S. solarii* the posterior processes of the genital fork are absent (Fig. 696), while they are prominent in *S. virgatum s.l.* (Fig. 699). The male is also externally similar to that of *S. virgatum s.l.* However, both species can be reliably separated by the structure of the ventral plate. In *S. solarii* the ventral plate has the main body with a prominent median process, the shoulders are well developed and the anterior margin is distinctly concave at the base of the median process (Fig. 945). On the contrary, the ventral plate in *S. virgatum s.l.* has the median process relatively less prominent than in *S. solarii*, the lateral shoulders are less developed and the anterior margin is straight on both sides of the median process (Fig. 948). The adults of *S. solarii* may only be separated from other externally similar and sympatric species such as *S. paynei* by the configuration and number of the pupal gill filaments in link-reared specimens.

In the pupal stage, *S. solarii* can be easily recognized from other species of the TARSATUM species group in having 15 gill filaments, all branching near the base of the gill (Fig. 1070). The pupae of *S. paynei*, *S. rubrithorax* and *S. virgatum s.l.* may be distinguished by their eight-filamented gill (Figs. 1064, 1065, 1068, 1072) and the cocoon having prominent fenestrations on the anterior margin The cocoon of *S. solarii* does not bear fenestrations on the anterior margin.

The larva of *S. solarii* can only be reliably separated from other species in the TARSATUM species-group by the dissected gill histoblast with 15 filaments. The larvae of similar species, for example *S. virgatum s.l.* and *S. paynei*, both have a dissected gill histoblast with eight filaments. The different morphology of the hypostomial teeth also readily separates these species (Figs. 1219, 1225) from that of *S. solarii* (Fig. 1223).

ADLER *et al.* (2004) recorded a head colour variation in the larvae of *S. solarii* inhabiting the same stream. The head coloration can vary from dark brown with yellowish head spots to yellowish with brown head spots (Figs. 1115, 1116). ADLER *et al.* (2004) also noted that in both these coloured forms the chromosomes have a Y-linked inversion at the base of chromosome arm IIIL. However, ADLER *et* *al.* (2004) advocated a band by band comparison of both colour variants in order to elucidate if they represent a single species or not.

Simulium solarii was placed in the BRACHYCLADUM species group in the subgenus *Hemicnetha* by CROSSKEY & HOWARD (1997, 2004), COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008). However, ADLER *et al.* (2004) and ADLER & CROSSKEY (2008, 2009, 2010) placed it in the PAYNEI species group within *Hemicnetha.* More recently, SHELLEY *et al.* (2010) placed *S. solarii* in the TARSATUM species group of the subgenus *Trichodagmia*, this classification is accepted in this paper.

Distribution. *Simulium solarii* is a very common species in the Balcones Escarpments, Texas, west to southern New Mexico, USA where it is sympatric with *S. paynei.* In Mexico it is found south to San Luis de Potosí, Mexico State (ADLER & CROSSKEY, 2008, 2009, 2010; ADLER *et al.*, 2004; **Material Examined**).

Biology and Medical Importance. The immature stages of *S. solarii* are found in rocky streams and rivers up to 30 m wide. Larvae have been collected throughout the year, while adults were captured from February into August (ADLER *et al.*, 2004). STONE (1948) recorded a female taken from the underside of a horse.

ADLER *et al.* (2004) recorded larvae hosting the microsporidian *Polydispyrenia simulii* (LUTZ & SPLENDORE) and adults attacked by the water mite *Sperchon texanai* DAVIS & COOK.

2.5.4.16. *Simulium* (*Trichodagmia*) *tarsale* WILLISTON (Figs. 224, 279, 406-409, 520, 578, 638, 697, 817, 818, 885, 946, 1006)

This is a poorly known species only recorded from the West Indies and still considered as *species inquirendae* by some authors. The description here provided has been based on examination of type and other identified adults deposited at BMNH and NMNH, the original descriptions of WILLISTON (1896) and MALLOCH (1914), and the revision of STONE (1969).

Simulium tarsale WILLISTON, 1896: 269. LECTOTYPE female, WEST INDIES, SAINT VINCENT: March [Without date or year.], (*H.H.Smith*) (BMNH, BM 1907-66) [Examined.] [Lectotype designation by SMART, 1942: 49; still considered as a *species inquirendae* by COSCARÓN & COSCARÓN-ARIAS, 2007: 560; treated as a valid species in the subgenus *Hemicnetha* by ADLER *et al.*, 2008: 46, 2009: 48; treated as a valid species in the TARSATUM species group of the subgenus *Trichodagmia* by SHELLEY *et al.*, 2010: 65 and the current work.]

Simulium clavipes MALLOCH, 1914: 41. HOLOTYPE female, WEST INDIES, GUADELOUPE: 30.vii.[Without year.], (NMNH, type no. 15411) [Examined.] [Synonymy by SMART, 1942: 49.] [Still considered as a *species inquirendae* by COSCARÓN & COSCARÓN-ARIAS, 2007: 560; treated as a valid species in the subgenus *Hemicnetha* by ADLER *et al.*, 2008: 46, 2009: 48, 2010: 48; treated as a valid species in the TARSATUM species group of the subgenus *Trichodagmia* by SHELLEY *et al.*, 2010: 65 and the current work.]

FEMALE. General body colour black. Body length (specimens in spirit) 2.3-2.7 mm (mean = 2.4 mm, s.d. = 0.11, n =10), wing length 2.4-2.9 mm (mean = 2.7 mm, s.d. = 0.16, n = 10), wing width 1.0-1.4 mm (mean = 1.2 mm, s.d. = 0.10, n = 10).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 224). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts parts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and without teeth (Fig. 279).

Thorax: Scutum black covered with evenly arranged, recumbent, yellowish setae, interspersed with fine, semi-recumbent brown setae; posterior margin with long dark hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black; humeri, lateral and posterior margins black (Figs. 406, 408). With posterior illumination, thorax black with 1+1 submedian wide pruinose area on anterior third of scutum; humeri weakly silver; lateral and posterior margins black (Figs. 407, 409).

Scutellum dark brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae extending to apical third of vein. Radius with line of setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 520. Fore leg with coxa, trochanter, femur and basal two thirds of tibia brown to pale brown; apical third of tibia and tarsal segment dark brown. Mid and hind legs with coxa, trochanter and basal two thirds of femur brown; tibia, apical two thirds of tarsal segment I, apical three thirds of tarsal segment II, and remainder of tarsal segments dark brown; basal two thirds of tarsal segment I and basal one third of tarsal segment II white. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX black. Tergal plates well developed in pinned specimens examined. Sternites and genitalia black. Eighth sternite sclerotised with 7-10 long, irregularly distributed setae on posterior margin; gonapophyses 1.5 time longer than length of eighth sternite at mid point, subtriangular, weakly sclerotised, densely covered with short hairs on central region (Fig. 578). Cercus subrectangular, covered with brown setae; paraproct long, subquadrangular, two and half time longer than cercus, sclerotised on basal half and membranous apically; paraproct densely covered with prominent brown hairs (Fig. 638). Genital fork stout and sclerotised; termination of lateral arms with anterior margins curved and well developed; anterior processes well developed and rounded apically; posterior processes absent (Fig. 697). Spermatheca globular, with external sculpturing and small groups of spicules on internal surface; area of insertion of spermathecal duct membranous.

MALE. General body colour black. Wing length (n = 1) 2.6 mm, wing width 1.2 mm [Body length not avialable as single male examined had been dissected].

Head: holoptic with red eyes. Clypeus black with grey pruinosity. Rest of head coloration as in female.

Thorax: scutum black covered by irregularly distributed recumbent golden setae interspersed with thin erect black setae, especially on posterior region. Scutal pattern varies slightly with light incidence: with light anterior scutum black with median, faint silver pruinose area on anterior third of scutum (Fig. 817). With posterior illumination scutum black with silver pruinose reflections on anterior third [best seen when specimen is slightly tilted laterally] (Fig. 818). Humeri brownish sometimes with silver reflections; lateral and posterior margins black. Scutellum dark brown to black with golden, recumbent hairs and long, erect, dark brown setae. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare. Leg coloration as in female. Halteres as in female.

Abdomen: tergites I-VI black with silver pruinose ornamentations on anterior and lateral margins of tergite II and lateral margin of tergite VI, [other segments dissected]. Sternites I-VI black with developed sternal plates. Genitalia probably black. Gonocoxite subquadrangular; gonostyle elongate and flattened, with lateral margins sinuous, narrower apically without terminal spine (Fig. 885). Ventral plate subtriangular with blunt process and keel on central region covered by hairs; lateral shoulder rectangular, basal arms stout (Fig. 946). Median sclerite long and slender as in Fig. 946. Paramere with enlarged basal processes and few stout spines mesally (Fig. 1006).

PUPA. [Based upon STONE (1969): Dorsal length 2.9 mm. Other measurements and number of specimens examined not given].

Cocoon: closely woven with dorsal aperture elevated.

Gill: dark brown with eight clumped filaments, shorter than cephalothorax.

Head (*frontoclypeus*): with short peg-like setal bases.

Thorax: with small simple trichomes.

Abdomen: tergites III, IV and sternites IV to VI with hooks; tergites and sternites without terminal spines.

LARVA (Final instar). [Based upon STONE (1969): Total length 6.00 mm. Other measurements and number of specimens examined not given].

Head: Cephalic apotome yellow, darkened posteriorly with weak positive head pattern. Antennal segments pale yellow, scarcely exceeding the cephalic stem. Postgenal cleft reaching base of hypostomium; hypostomium with anterior margin curved, central tooth slender, rather small, all other teeth smaller. Anal sclerite slender. Rectal gill not everted [recorded as "absent" by Stone (1969)].

Taxonomic Discussion. *Simulium tarsale* was described by WILLISTON (1896) based on three specimens collected in the West Indies (St. Vincent) by H. H. Smith and deposited in the BMNH. SMART (1940) in a paper dealing with the Simuliidae of British Guiana and the Lesser Antilles referred to the name of *S. tarsale* and mentioned that "no trace of the types of this species can be found in the British Museum". Two years later, he stated that the three specimens of the type series of *S. tarsale* were discovered in the museum and designated a female as lectotype (SMART, 1942). In the same paper, he also discussed additional morphological characters that were not included in WILLISTON'S (1896) original description of *S. tarsale*, examined type material of *S. clavipe*s described by MALLOCH in 1914 from Guadeloupe, and concluded that these species were synonymous. This synonymy was later confirmed by STONE (1969), while describing the simuliid fauna of Dominica. STONE also suggested that *S. tarsale* resembled species of the subgenus *Hemicnetha*, but refrained to include it in this subgenus because the fore tarsal segments II, III are flattened and the claws lacked teeth. Both COSCARÓN (1987) and CROSSKEY & HOWARD (1997, 2004) were unable to place this species to subgenus.

The taxonomy of *S. tarsale* has been recently reviewed by HERNÁNDEZ & SHELLEY (2005), who also examined the type material of this species and compared it with the type of *S. clavipes*. The same authors noted the close similarity of *S. tarsale* with *S. tarsatum* (formerly *S. mexicanum*). In the same paper HERNÁNDEZ & SHELLEY (2005) also discussed the general morphology of *S. tarsale* and *S. clavipes* and agreed with SMART'S (1942) synonymy.

In his revision of the Simuliidae of Dominica STONE (1969) described two pupal exuviae and one larva collected in Springfield Estate on 26.July.1926 by Flint. Stone identified these specimens as *Simulium* sp., but he hinted the possibility that they could represent the pupa and the larva of *S. tarsale*. He stated that one of the pharate pupa showed an indication of the slender black stripes on the thorax, which are found in *S. tarsale*. I have studied the description and figures given in STONE (1969) and tried to locate this material in the NMNH Simuliidae holdings. Unfortunately, I was unable to find the aforementioned material at the NMNH. The description given by STONE (1969), especially the male gonostyle and ventral plate, agree with the variation found in species now placed in the TARSATUM species group of the subgenus *Trichodagmia* (*sensu* SHELLEY *et al*., 2010). As no other species of *Hemicnetha* (*sensu* ADLER *et al.* 2004) has been recorded in Dominica, I agree with STONES' (1969) identification and regard these specimens as the immature stages of *S. tarsale* until further material is available to further assess its taxonomic status.

Simulium tarsale, *S. tarsatum* and *S. smarti* are very closely related species based on the external coloration of the adult's thorax. The female of *S. tarsale* externally resembles *S. smarti* and *S. tarsatum* in having a dark brown to black thorax covered with yellowish to golden hairs (Figs. 402, 403, 406-411) [even though the two type specimens of *S. tarsale* have most of the thorax devoid of hairs, a few yellow hairs are still present in these specimens and also in the female collected in Dominica]. However, *S. tarsale* may be distinguished by the presence of 1+1 submedian black or silver pruinose areas [depending on light source] (Figs. 406-409), which are not present in *S. smarti* and *S. tarsatum* (Figs. 402, 403, 410, 411). In addition, the genital fork of *S. tarsale* lacks the distinct triangular internal posterior processes (Fig. 697) that are present in *S. tarsatum* (Fig. 698; see also SHELLEY *et al*., 2002b, Fig. 138, as *S. mexicanum*). This character is also shared with *S. smarti* (Fig. 695). Moreover, the Sc wing vein in *S. tarsale* has a single line of short brown setae varying from only nine setae in the holotype to approximately 17 setae in the paratype of *S. clavipes*, while the basal section of the R wing vein is bare. In *S. smarti* the Sc and basal section of the R wing veins have a double line of prominent long dark brown setae.

In the male *S. tarsale* is easily separated from that of *S. tarsatum* and *S. smarti* by the morphology of the ventral plate. In *S. tarsale* the ventral plate has a prominent median process forwardly produced (Fig. 946), which is absent in *S. tarsatum* and *S. smarti* (Figs. 56, 944, 947). The ventral plate of *S. smarti* is prominently produced centrally and the basal arms are distictly expanded apically (Fig. 944). In *S.*

tarsatum the ventral plate is relatively less produced centrally and the basal arms are pointed apically (Figs. 56, 947).

The pupa of *S. tarsale* has a gill with eight filaments following STONE (1969). This character readily separate it from *S. tarsatum* (12 filaments) and *S. smarti* (15 filaments) (Figs. 83, 1069, 1071). The larva of *S. tarsale* remains poorly described, hence it cannot be readily separated from that of *S. tarsatum* and *S. smarti*. Further material is needed in order to provide a more complete description of the immature stages of *S. tarsale* to assess its taxonomic status.

HERNÁNDEZ & SHELLEY (2005) stated that the general morphology of *S. tarsale* falls within the morphological variation found in species of the subgenus *Hemicnetha* and, consequently, they assigned this species to this subgenus in the TARSATUM species group [formerly known as the MEXICANUM species group of CROSSKEY & HOWARD (1997, 2004)]. COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008) treated *S. tarsale* as *species inquirendae* within the subgenus *Hemicnetha*, where the TARSATUM species group was not recognized. However, ADLER & CROSSKEY (2008, 2009, 2010) agreed with the taxonomic changes proposed by HERNÁNDEZ & SHELLEY (2005), and this classification which has also been followed by SHELLEY *et al.* (2010), except that they *S. tarsale* in the TARSATUM species group of the subgenus *Trichodagmia* (which is also followed in the current work).

Distribution. *Simulium tarsale* has only been found on the West Indies in the islands of Dominica, Guadeloupe and Saint Vincent (ADLER & CROSSKEY, 2008, 2009, 2010; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. The biology of this *S. tarsale* is relatively unknown. P.H. ADLER has collected specimens of this species on "waterfalls" in Dominica (P.H. ADLER, pers. comm. to L.M. HERNÁNDEZ).

2.5.4.17. *Simulium (Trichodagmia) tarsatum* MACQUART (Figs. 6, 28, 46, 56, 68, 70, 73, 83, 225, 280, 410, 411, 521, 579, 639, 698, 819, 820, 886, 947, 1007, 1071, 1117, 1169, 1224, 1278)

A common, zoophilic species in South America that has a wide distribution range, indicating that it might be a species complex. This species still requires further taxanomic studies because species currently considered as synonyms of *S. tarsatum* are treated by other authors as valid species.

Simulium tarsatum MACQUART, 1846 [1844]: 20. HOLOTYPE female [Not male as published.], COLOMBIA (as "Nouvelle-Grenade" in description, "Nova Granata" on label): [Handwritten label, *S. tarsatum*, n.sp.] [Collection date and collector unknown.] (BMNH, ex. Bigot Collection, B.M. 1960-1539) [Examined.] [Considered as *species inquirendae* by COSCARÓN & COSCARÓN-ARIAS, 2007: 560 and COSCARÓN *et al.*, 2008: 33; regarded as a valid species by ADLER & CROSSKEY, 2008: 46, 2009: 48, 2010: 49, SHELLEY *et al.*, 2010: 65, and the current work.]

Simulium mexicanum BELLARDI, 1862 (appendix to part 2): 6. LECTOTYPE female, MEXICO: Veracruz State, Tuxpango, near Orizaba; [Collection date and collector unknown.] (DBAT) [Examined.] [Lectotype designation in SHELLEY *et al.*, 1989: 103.] [Synonymy by HERNÁNDEZ & SHELLEY, 2005: 6; considered a valid species by COSCARÓN & COSCARÓN-ARIAS, 2007: 560 and COSCARÓN *et al.*, 2008: 33, but still regarded as conspecific with *S. tarsatum* by ADLER & CROSSKEY, 2008: 46, 2009: 58, 2010: 49, SHELLEY *et al.*, 2010: 65, and the current work.]

Simulium seriatum KNAB, 1914a: 84. HOLOTYPE female, PERÚ: Sta Eulalia, 12091; 5.vii.1913, (*C.H.T.Townsend*) (NMNH, type no. 18349) [Examined.] [Synonymy by HERNÁNDEZ & SHELLEY, 2005: 6; considered as a valid species by COSCARÓN & COSCARÓN-ARIAS, 2007: 549 and COSCARÓN *et al.*, 2008: 31, but regarded as conspecific with *S. tarsatum* by ADLER & CROSSKEY, 2008: 46, 2009: 48, 2010: 49, SHELLEY *et al.*, 2010: 65, and the current work.]

Simulium aureopunctatum MALLOCH, 1914: 27. HOLOTYPE female, GUATEMALA: Livingston; 6.v. or 5.vi. [Year not given.], (*Barber & Schwarz*) (NMNH, cat. no. 15406) [Examined.] [The adult has been lost; only a hind leng and one wing remain glued to a card point - see **Material Examined**] [Previous synonymy with *S. mexicanum* by BEQUAERT, 1934: 208; synonymy by

Hernández & Shelley, 2005: 6; regarded as a synonym of *S. mexicanum* by Coscarón & Coscarón-Arias, 2007: 548 and Coscarón *et al.*, 2007: 31, but considered a synonym of *S. tarsatum* by Adler & Crosskey, 2008: 46, 2009: 48, 2010: 49, Shelley *et al.*, 2010: 65, and the current work.]

Simulium placidum Knab, 1915: 281. HOLOTYPE female, TRINIDAD: Arima river; 31.xii.1913, (*F.W.Urich*) (BMNH) [Examined.] [Previous synonymy with *S. mexicanum* by Vargas & Díaz Nájera, 1951: 133; synonymy by Hernández & Shelley, 2005: 6; regarded as a synonym of *S. mexicanum* by Coscarón & Coscarón-Arias, 2007: 548 and Coscarón *et al.*, 2007: 31, but considered a synonym of *S. tarsatum* by Adler & Crosskey, 2008: 46, 2009: 48, 2010: 49, Shelley *et al.*, 2010: 65, and the current work.]

Simulium lugubre Lutz & Nuñez Továr in Lutz, 1928: 46. SYNTYPES female and male, VENEZUELA: Aragua, Rio de Maracay, La Trinidad; 28.xii.1915, (*A.Lutz & Nuñez Továr*) (IOC) [Examined.] [Previous synonymy with *mexicanum* by Fairchild, 1940: 708; synonymy by Hernández & Shelley, 2005: 6; regarded as a synonym of *S. mexicanum* by Coscarón & Coscarón-Arias, 2007: 548 and Coscarón *et al.*, 2007: 31, but considered a synonym of *S. tarsatum* by Adler & Crosskey, 2008: 46, 2009: 48, 2010: 49, Shelley *et al.*, 2010: 65, and the current work.]

Simulium turgidum Hoffmann, 1930: 298. SYNTYPES females, MEXICO: Chiapas State, Soconusco District, Finca Santa Anita; vii.1930, [Collector and depository unknown.] [Previous synonymy with *S. mexicanum* by Bequaert, 1934: 208; synonymy by Hernández & Shelley, 2005: 7; still regarded as a synonym of *S. mexicanum* by Coscarón & Coscarón-Arias, 2007: 548 and Coscarón *et al.*, 2007: 31, but sconsidered a synonym of *S. tarsatum* by Adler & Crosskey, 2008: 46, 2009: 48, 2010: 49, Shelley *et al.*, 2010: 65, and the current work.]

Trichodagmia laticalx Enderlein, 1934a: 291. LECTOTYPE female, PERU: Challanga; [Without date or collector.] (NMHU) [Examined.] [Previous synonymy with *S. seriatum* by Coscarón, 1987: 36; synonymy and lectotype designation by Hernández & Shelley, 2005: 7; regarded as a synonym of *S. seriatum* by Coscarón & Coscarón-Arias, 2007: 549 and Coscarón *et al.*, 2008: 31, but sregarded as conspecific with *S. tarsatum* by Adler & Crosskey, 2008: 46, 2009: 48, 2010: 49, Shelley *et al.*, 2010: 65, and the current work.]

Trichodagmia latidigitus Enderlein, 1936: 129. LECTOTYPE female, COLOMBIA: Muzo terr. aol; [Without date.], (*O. Thieme S.*) (NMHU) [Examined.] [Previous synonymy with *S. seriatum* by Coscarón, 1987: 36; synonymy and lectotype designation by Hernández & Shelley, 2005: 7; regarded as a synonym of *S. seriatum* by Coscarón & Coscarón-Arias, 2007: 549 and Coscarón *et al.*, 2008: 31, but regarded conspecific with *S. tarsatum* by Adler & Crosskey, 2008: 46, 2009: 48, 2010: 49, Shelley *et al.*, 2010: 65, and the current work.]

Simulium bellardii Py-Daniel & Moreira Sampaio, 1994b: 149. [Unnecessary replacement name for *mexicanum* Bellardi proposed by these authors on upgrading the subgenus *Hemicnetha* to genus – see Crosskey & Howard, 1997: 85; synonymy by Hernández & Shelley, 2005: 7.]

FEMALE. General body colour black. Body length (specimens preserved in alcohol) 2.6–3.7 mm (mean = 3.1 mm, s.d. = 0.35, n = 7), wing length 2.5 – 2.9 mm (mean = 2.7 mm, s.d. = 0.15, n = 7), wing width 1.3 –1.5 mm (mean = 1.3 mm, s.d. = 0.14, n = 7).

Head: dichoptic with red eyes; nudiocular area well developed (Fig. 225). Frons, clypeus and occiput black with grey pruinosity, covered in numerous black bristles that are longer and denser on upper margin of clypeus and occiput. Mouthparts black. Antennae dark brown with scape, pedicel and first flagellomere orange. Cibarium with large, unarmed central trough, cornuae well developed and sclerotised (Fig. 280).

Thorax: scutum, humeri and paranotal folds black with grey pruinosity irrespective of light direction (Figs. 410-411). Scutum with numerous, adpressed, short, black setae becoming longer and upright on posterior border, interspersed with clumps of adpressed, brass-coloured, scale-like setae. Scutellum dark brown to black with grey pruinosity and with scattered, upright, black bristles on whole surface except anterior border and brass-coloured, adpressed, scale-like setae over whole surface. Postnotum black with grey pruinosity. Pleural region dark brown with grey pruinosity. Costal wing vein with setae interspersed with spines. Subcostal wing vein with irregular row of setae over entire length; basal section of R with three irregular rows of setae along entire length. Costal base tuft of dark brown setae. Colour and proportions of legs as in Fig. 521. Fore legs with coxae, trochanters, and femora light brown, tibiae white pruinose with apical third and inner margin black, tarsi black. Mid leg coxae dark brown with grey pruinosity, trochanters and femora black, tibiae black with up to basal third light brown, basal two-thirds of basitarsus light brown, rest black, other tarsal segments black. Hind leg coxae dark brown with grey pruinosity, trochanters light brown, femora black, basal third of tibiae white merging to black on apical two-thirds, basal half of basitarsi white distal half black, rest of tarsi black. Claws curved with basal tooth. Halteres white with black stems.

Abdomen: tergite I velvet-black with long, brass-coloured basal fringe, tergite II mottled brown and black with grey pruinosity, tergites III-V velvet black, tergites VI-IX shiny black. Tergal plates highly sclerotised especially on tergite II. Sternites II and I light brown, remainder black. Genitalia black. Eighth sternite well sclerotised with 4-6 setae on each side; gonapophyses well developed, subtriangular, totally membranous and covered with fine setae (Fig. 579). Cerci hemispherical; paraprocts large and subquadrangular with long bristles and short thick setae (Figs. 28, 639). Genital fork short, strongly sclerotised and with highly developed lateral arms and anterior processes (Fig. 698). Spermatheca oval, strongly sclerotised with no external sculpturing and spicules on inner surface randomly distributed; width of membranous area of insertion of spermathecal duct large, about half maximum width of spermatheca.

MALE. General body colour black. Body length (specimens preserved in alcohol) 3.3–3.7 mm (mean = 3.5mm, s.d. = 0.14, n = 5), wing length 2.6–3.1 mm (mean = 2.8mm, s.d. = 0.21, n = 5), wing width 1.2–1.5 mm (mean = 1.4 mm, s.d. = 0.10, n = 5).

Head: holoptic with red eyes. Clypeus black with grey pruinosity. Rest of head coloration as in female.

Thorax: coloration and setation of scutum, humeri, paranotal folds, pleural region, scutellum and postnotum as in female, except scale-like setae golden and thin dark median line running whole length of scutum, free of these scales (Figs. 819, 820). Subcostal wing vein and basal section of Radius bare. Leg coloration and form as in female, except white area of hind tibia reduced to point of articulation with femur. Halteres as in female.

Abdomen: tergite I velvet-black with basal tuft of long black hairs. Tergites II-IX velvet-black with the following silver pruinose ornamentation: tergite II covering whole segment, tergite IV covering anterior border, except for median portion, tergites V-VII completely covered except for median triangle on posterior border of each tergite; tergite VIII with small lateral area on anterior margin. Sternites mottled brown and black with poorly developed sternal plates. Genitalia velvet-black. Gonocoxite rectangular, wider than long, gonostyle elongate with margins sinuous and weakly developed subterminal spine (Fig. 886). Ventral plate subrectangular with sclerotised, poorly developed basal arms and large keel; mian body of ventral plate densely covered with fine setae and small spines (Fig. 947). Median sclerite elongate with apical depression (Fig. 947). Paramere with enlarged basal process and few stout spines apically (Fig. 1007).

PUPA. Cocoon length dorsally 2.8–3.8 mm (mean = 3.2 mm, s.d. = 0.24, n = 12), ventrally 3.5–5.4 mm (mean = 4.4 mm, s.d. = 0.52, n = 12); pupa length 4.1–5.4 mm (mean = 4.7 mm, s.d. = 0.46, n = 10); gill length 1.2–1.9 mm (mean = 1.6 mm, s.d. = 0.17, n = 12).

Cocoon: shoe-shaped (Fig. 68), mid brown; rim of aperture mid brown, reinforced and without fenestrations as seen in *S. virgatum s.l.* Cocoon surface of thin, amorphous, translucent, elastic substance in which thick, interwoven fibres are sometimes visible.

Gill: light to dark brown, generally protruding beyond collar of cocoon, with 12 short, forwardly-directed filaments often arranged in a bunch. Main trunk of gill short giving rise to an inner primary branch bearing five filaments and an outer branch with seven filaments. Filaments arise basally on gill (Figs. 83, 1071), are slender with crenate margins and rounded distally, their surfaces covered with fine spicules; all filaments relatively of same length.

Head (*frontoclypeus*): with 2 + 2 frontal and 1+ 1 facial trichomes, all poorly developed and unbranched; surface of head with platelets, which in frontal region are scattered, enlarged and highly sclerotised and in facial region are dense and of normal size, and usually with scattered, rounded tubercles (Fig. 70).

Thorax: with 5 + 5 antero-dorsal, poorly developed, unbranched trichomes. Surface of anterior region of thorax covered in well developed highly sclerotised tubercles, which usually extend to posterior border of thorax, and in a pair of submedian and lateral bands to posterior thoracic border which is densely covered by normal size tubercles. Ventral surface of thorax without tubercles (Fig. 73).

Abdomen: tergite II with 3 + 3 well developed simple hooks and 1+1 simple fine hairs external to these; III-IV with 4 + 4 simple hooks; IX with no spines; II-IX with 1+1 well developed areas of spine combs on anterior margins and I and II with groups of spine combs on posterior margins. Sternite IV with no hooks or hairs; V-VII with 2 + 2 simple hooks; I + I patches of spine combs on anterior borders of sternites IV-VIII.

LARVA (Last instar). Body length 5.6-7.6 mm (mean = 6.5 mm, s.d. = 0.90, n = 7); length of head capsule 0.5-1.0 mm (mean = 0.7 mm, s.d. = 0.16, n =7), width of head capsule 0.5-0.8 mm (mean = 0.6 mm, s.d. = 0.1, n = 7). Body colour grey with faint greenish lateral (in specimens preserved in alcohol and/or Carnoy's). Body form as in Fig. 1117

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive surrounded by dark pigmentation; occasionally the 1+1 lateral group of head spots is negative in relation to the dark pigmentation of the cephalic apotome in this region. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft bell-shaped and rounded anteriorly; postgenal bridge nearly as long as hypostomium (Fig. 1169). Hypostomium strongly pigmented on anterior margin, with approximately nine poorly developed apical teeth; median tooth more developed than remaining teeth; 3+3 sublateral teeth; 1+1 lateral teeth; 1+1 lines of approximately nine hypostomial setae parallel to lateral margins; 2+2 simple setae centrally and 1+1 long, simple setae in posterior half of hypostomium (Figs. 1224). Sub-esophageal ganglion lightly pigmented. Antennal longer than labral fans; all segments lightly pigmented; length of antennal segments I-III excluding the sensillum 0.07-0.1:0.2-0.6:0.1 mm (n = 6). Mandible with two apical teeth, the external more prominent than the internal; mandibular comb with six teeth, third and fourth teeth more prominent than remainder; single prominent lateral serration (Fig. 1278). Lateral mandibular process absent. Maxillary palps heavily pigmented, about twice as long as width at base. Labral fan with more 48-60 rays with fine, single line of spines in a row.

Thorax: grey dorsally and whitish ventrally, with a large grey brown patch occupying ventral surface of proleg and median patch posterior to this. Cuticle without setae. Proleg with plate heavily sclerotised band of 30-46 sclerotised processes of 17- 21 simple hooks (n = 7). Pupal respiratory gill histoblast dark brown, claviform, with 12 filaments, all branching from common trunk at different levels.

Abdomen: usually greyish brown, though in some specimens indistinct bands in anterior constricted abdominal segments; ventrally whitish with irregular white patches. Ventral nerve cord greyish. Ventral papillae absent. Cuticle with occasional fine hairs on dorsal and ventral surfaces. Anal sclerite well sclerotised with posterior arms extending to about 65th row of posterior circle hooks. Posterior circlet with 121-156 rows of sclerotised processes of 25-42 simple hooks (n = 7). Rectal gills with three lobes, each lobe with 12-14 finger-like lobules giving a total of 37-45 lobules; at least one lobule on each branch is larger than remainder lobules (n = 3).

Taxonomic Discussion. The taxonomy of *S. tarsatum* has been thoroughly reviewed by SHELLEY *et al.* (1989, 2002b) [as *S. mexicanum*] and, more recently by HERNÁNDEZ & SHELLEY (2005), who commented on the condition of the type material of all synonymies under *S. tarsatum*, designated two lectotypes and proposed nine new synonymies (see synonymic list). In the recent revision of Neotropical Simuliidae COSCARÓN & COSCARÓN-Arias (2007) [followed also in COSCARÓN *et al.*, 2008] did not accept the synonymy of *S. seriatum* and *S. tarsatum* with *S. mexicanum* because of "lack of other life cycle stages". However, ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010) accepted all synonymies proposed in HERNÁNDEZ & SHELLEY (2005), and this has also been followed in the current work.

The thoracic pattern and vestiture of the female of *S. tarsatum* resembles that of *S. smarti* and *S. tarsale* (Figs. 410, 411), but *S. tarsatum* can be separated from *S. tarsale* by the presence of posterior processes in the genital fork (Figs. 698). *Simulium smarti* can only be reliably separated by the examination of the pupal gill filaments in link-reared females. The male of *S. tarsatum* has a similar thoracic pattern to that of the female, and they can only be distinguished from other species in the TARSATUM species group by the number of the pupal gill filaments and the morphology of the ventral plate, especially the absence of an antero-median process (Figs. 56, 947). The male of *S. tarsale* may be distinguished by the presence of an antero-median process in the ventral plate (Fig. 946).

The pupa of *S. tarsatum* can be readily separated from all other species in the TARSATUM species group by the 12 short, forwardly-directed gill filaments arranged in a bunch and dividing basally (Fig. 1071). In *S. smarti* the pupa has 18-filaments (Fig. 1069). The pupal gill filamentas of *S. tarsale* reportedly has eight filaments (STONE, 1969).

The larva of *S. tarsatum* can only be readily identified from other species by the dissected gill histoblast with 12 short filaments and the morphology of the teeth in the mandibles, especially the prominent teeth of the mandibular comb and the presence of a prominent, single anterior serration (1278).

Full descriptions of adults and immature stages of *S. tarsatum* may be found in COSCARÓN & COSCARÓN-ARIAS (2007), IBÁÑEZ-BERNAL (1992) and SHELLEY *et al.* (1989, 2002b).

CROSSKEY & HOWARD (1997, 2004) placed *S. tarsatum* [as *S. mexicanum*], in the MEXICANUM species group of the subgenus *Hemicnetha*. HERNÁNDEZ & SHELLEY (2006) replaced the name of the latter species group with TARSATUM to reflect the new synonymy of *S. mexicanum* under *S. tarsatum*. The latter taxonomic changes have not been accepted by COSCARÓN & COSCARÓN-ARIAS (2007) and COSCARÓN *et al.* (2008), who still maintained the MEXICANUM species group. However, ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010) recognized the TARSATUM species group inwhich *S. tarsatum* has been placed.

Distribution. *Simulium tarsatum* is a common species in South America. SHELLEY *et al.* (2010) stated that this species is relatively common in Belize, where it was found sympatrically with *S. pulverulentum*, *S. paynei* (as *S. virgatum s.l.*), *S. callidum*, *S. gonzalezi* and *S. samboni*. It is very common in Costa Rica where it has been found from 56 sites (L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished data). Elsewhere, it has also been recorded from Argentina, Bolivia, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Panamá, Perú, Tobago, Trinidad and Venezuela (ADLER & CROSSKEY, 2008 2009, 2010; COSCARÓN & COSCARÓN-Arias, 2007; **Material Examined** [see also **Material Examined** in SHELLEY *et al.* (200b) and HERNÁNDEZ & SHELLEY (2005)].

Biology and Medical Importance. The immature stages of *S. tarsatum* are often found in small, fast flowing streams at both low and high altitudes usually in, or in close proximity to waterfalls; it is a common species in Costa Rica (SHELLEY *et al.*, 2002b; L.M. HERNÁNDEZ & L.G. CHAVERRI, unpublished). The females are zoophilic, though it has been reported occasionally biting man in Colombia, Ecuador and Venezuela (SHELLEY *et al.*, 2002b). In Trinidad the females bite mules and donkeys. *Simulium tarsatum* together with *S. metallicum s.l.* were originally thought to be associated with the regular transmission of Venezuelan Equine Encephalitis in Colombia, but recent evidence suggests that at most they only occasionally transmit the virus mechanically (HOMAN *et al.*, 1985; WEAVER *et al.*, 2004). In Guatemala, *S. tarsatum* bites horses, mules, cattle, sheep, goats, pigs, dogs, chickens (DALMAT, 1955).

2.5.4.18. *Simulium (Trichodagmia) virgatum* COQUILLETT (complex) (Figs. 11, 29, 64, 226, 281, 412-415, 522, 580, 640, 699, 700, 821-824, 887, 948, 1008, 1072, 1118, 1170, 1225, 1279)

This is a widespread, zoophilic species that still requires a considerable amount of study using molecular and cytogenetic techniques and probable status as a species complex are finally clarified. I refer to *S.*

virgatum as *sensu lato* following SHELLEY *et al.* (2002b, 2010) because several names have been included whose validity at the species level is still uncertain.

Simulium virgatum COQUILLETT, 1902: 97. HOLOTYPE male, UNITED STATES OF AMERICA: New Mexico State, Las Vegas Hot Springs, 4.viii.[Without year.] (*H.S.Barber*) (NMNH, cat. no. 6183). [Examined.]

Simulium cinereum BELLARDI, 1859: 13. SYNTYPES female and male, MEXICO: Morelia. [Collection date not specified] (*Henri de Saussure*) (DBAT) [Preoccupied; location of the holotype unknown.]

Simulium tephrodes SPEISER, 1904: 148. [Replacement name for *S. cinereum* BELLARDI.]

Simulium rubicundulum KNAB, 1915: 178. HOLOTYPE female, MEXICO: Córdoba, 17.xii.1907 (*F. Knab*) (NMNH, cat. no. 19112) [Examined.] [Synonymy with *S. virgatum* by DYAR & SHANNON, 1927: 39].

Simulium chiapanense HOFFMANN, 1930: 293. SYNTYPES females, MEXICO: Chiapas State, Soconusco District, Finca Santa Anita, vii.1930, (*C.C.Hoffmann*) [Type depositary not cited, specimens numbered as 18006] [Synonymy by DAMPF in BEQUAERT, 1934: 214.]

FEMALE. Generally dark brown to black. Body length (specimens pinned) 2.8-4.7 mm (mean = 3.6 mm, s.d. = 0.51, n = 14); wing length 2.3-3.8 mm (mean = 3.0 mm, s.d. = 0.47, n = 14), wing width 1.3-2.1 mm (mean = 1.5 mm, s.d. = 0.25, n = 14).

Head: dichoptic with red eyes and nudiocular area well developed (Fig. 226). Frons, clypeus and occiput dark black with silver pruinosity; frons with numerous, irregularly arranged, stout hairs predominantly on margins. Mouthparts black. Antennae brown with scape, pedicel and basal third of first flagellomere yellow. Cibarium unarmed with lightly sclerotised margin of trough and highly sclerotised cornuae (Fig. 281).

Thorax: scutum black covered with recumbent white hairs interspersed with erect brown setae on posterior margin. Scutal pattern varying in appearance with illumination. With anterior illumination, thorax black [most common pattern] with 1+1 median pear-shaped and 1+1 sublateral triangular vittae extending from anterior to posterior margins, 1+1 wider anteriorly triangular black cunae that arise on anterior third of scutum extending into thinner lines that reach posterior margin; 1 fine dark brown to black line on central region po thorax; humeri faintly pruinose; anterior and posterior margins black (Figs. 412, 414) [in some specimens the thorax can be brown to dark brown]. With posterior illumination, thorax dark brown to black with 1+1 submedian silver pruinose vittae that arise on anterior third extending to posterior margins [in some specimens the pruinose cunae only reach mid of thorax]; humeri silver pruinose; lateral margins weakly pruinose; posterior margin black (Figs. 413, 415). Pleural region black with grey pruinosity. Scutellum dark brown to black with white hairs interspersed with long, dark hairs on posterior margin. Postnotum dark brown to black with grey pruinosity. Costal wing vein with setae and spines. Subcostal wing vein with row of 4-6 setae at mid point. Radius of wing with setae interspersed with spines; basal section of radius bare. Basal tuft of dark hairs. Colour and proportions of legs as in Fig. 522. Leg I with coxa dark brown to black; trochanter and basal two thirds of femur dark brown; apical third of femur, apical and basal thirds and internal surface of tibia at mid point, and tarsal segment I-IV black; external surface of tibia whitish. Leg II-III with coxa, apical thirds of femora, tibia; apical half of tarsal segments I-II, and tarsal segments III-IV black; trochanters, basal half of femora and in mid tibia [only in few specimens] brown; basal half of tarsal segments I-II white. Claws curved with large basal tooth. Halteres pale yellow with slightly darkened stems.

Abdomen: tergites predominantly black. Tergal plates developed. Sternites and genitalia black. Eighth sternite with well sclerotised central plate and 1+1 groups of 11-13 well developed setae; gonapophyses large and well developed, subtriangular, nearly twice length of eighth sclerite at mid point (Fig. 580). Cerci subrectangular; paraprocts large, subquadrangular, three times longer than cercus; paraproct covered with long brown setae basally and microtrichiae apically (Figs. 11, 29, 640). Genital fork highly sclerotised with stem weakly expanded, and lateral arms straight; anterior process well developed, subtriangular; posterior process well developed and directed toward mid region of space between lateral arms (Figs. 699, 700). Spermatheca oval, strongly sclerotised without external sculpturing and with groups of three internal spicules in rows; area of insertion of spermathecal duct membranous.

MALE. Generall body black. Body length (specimens pinned) 3.5-4.7 mm (mean = 4.0 mm, s.d. = 0.35, n = 14); wing length 2.6-3.7 mm (mean = 3.2 mm, s.d. = 0.35, n = 14), wing width 1.2-2.0 mm (mean = 1.6 mm, s.d. = 0.23, n = 14).

Head: holoptic with upper eye facets red and lower eye facets dark red (appearing black in dried specimens). Rest of head coloration as in female.

Thorax: scutum dark brown to black covered with white recumbent hairs. Thorax pattern varying with light illumination. With light anterior scutum with 1+1 median silver pruinose and 1+1 laterally prominent wide silver pruinose vittae reaching near posterior margin; fine brown line on central region of thorax extending from anterior to posterior margins; humeri silver pruinose; lateral and posterior margins black (Figs. 821, 823). With light posterior scutum dark brown to black with median silver pruinose band, fine brown line on central region of thorax extending from anterior to posterior margins (Figs. 822, 824); humeri and lateral margins weakly pruinose; posterior margins black. Paranotal folds, pleural region, scutellum and postnotum as in female. Subcostal wing vein as female. Legs and halteres coloration as in female.

Abdomen: tergites velvet black; silver pruinose ornamentation in anterior margin of tergite I, ventral and lateral margins of tergite II, lateral margin of tergites IV-VI, and ventral margin of tergite VII [best seen when specimens tilted laterally]. Gonocoxite subquadrangular; gonostyle elongate, over twice length of gonocoxite, with margins weakly sinuous terminating in stout apical spine (Fig. 887). Ventral plate well developed with large, wide median anterior process nearly three times longer than width at base; main body of ventral plate with anterior margin is slightly concave at base of median process, shoulders weakly developed, and basal arms short, sclerotised and curved inwards; ventral plate covered by hairs (Fig. 948). Median sclerite elongate, subtriangular, narrow at base (Fig. 948). Paramere with large basal process and cluster of stout spines centrally; membranous covered by small spinules (Fig. 64, 1008).

PUPA. Cocoon length dorsally 4.5-5.2 mm (mean = 4.8 mm, s.d. = 0.24, n = 6); ventrally 4.8-5.9 mm (mean = 5.1 mm, s.d. = 0.45, n = 6); pupa length 3.5-5.9 mm (mean = 3.8 mm, s.d. = 0.24, n = 6); gill length 2.3-2.9 mm (mean = 2.4 mm, s.d. = 0.27, n = 6).

Cocoon: shoe-shaped as in Fig. 69, mid to pale brown with obvious collar and long, slender fenestrations joined to form a loose lattice; cocoon surface smooth and translucent, with no individual fibres visible.

Gill: light brown, protruding slightly beyond fenestrations, with eight upwardly-directed filaments (Fig. 1072). Main trunk dividing basally into two primary branches each with four filaments. All filaments arise in basal quarter of gill, are slender with only faintly crenate margins and rounded distally, their surfaces densely covered with fine spicules.

Head (*frontoclypeus*): with 1 + 1 small, simple or bifid, frontal trichomes and 2 + 2 poorly developed, simple facial trichomes. Frontal area with groups of platelets but devoid of tubercles, facial area with rounded tubercles.

Thorax: well sclerotised with 4 + 4 small simple setae on dorsal cleft, 2+2 simple setae at base of gill, one small simple seta posteriorly, and 4+4 simple setae in alar region; tubercles pointed and only visible in alar region

Abdomen: tergite I with 1+1 sublateral long simple setae and small rugosities on posterior margin; tergite II with 3+3 submedian spiniform setae in row, 2+2 sublateral simple setae and 1+1 simple setae on lateral margin; tergites III-IV with 4+4 simple hooks in row, tergite III with 1+1 small simple setae between outermost hooks and 1+1 small setae anterior to outermost hooks, tergite IV with 1+1 small simple setae on lateral margin; tergite V with 2+2 median simple setae and 1+1 small setae laterally; tergites VI-VII with 1+1 submedian small simple setae; tergite VIII and IX without setae, tergite IX weakly sclerotised without visible terminal spines. Spine combs on anterolateral margin of tergites II-VIII. Sternites III-IV without visible setae or trichomes; sternite V with 2+2 close simple hooks, and 1+1 small simple setae anterior to outermost hook; sternite VI-VII 2+2 well separated simple hooks;

sternite VIII-IX without visible setae; sternite IX weakly sclerotised. Spine combs distribution on anterolateral margins of sternite III-VIII.

LARVA (Final instar). Body length 9.6-10 mm (mean = 9.8 mm, s.d. = 0.20, n = 3), width head capsule 0.9–1.2 mm (mean = 1.2 mm, s.d. = 0.55, n = 3), length of head capsule 0.8- 1.6 mm (mean = 1.0 mm, s.d. = 0.46, n = 3). Body colour grey in specimens preserved in alcohol. Body form as in Fig. 1118.

Head: mainly dark brown, anterior region of cephalic apotome yellow. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern negative. Postgenal cleft narrow, bell-shaped with subtriangular extension at apex; postgenal bridge as long as hypostomium (Fig. 1170). Hypostomium rounded anteriorly with strongly pigmented anterior margin and nine apical teeth evenly distributed along anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, the pair adjacent to median tooth more prominent than 2+2 outermost sublateral teeth, which are strongly reduced; 1+1 prominent lateral teeth; 5-6+5-6 lateral serrations; 1+1 line of nine hypostomial setae parallel to lateral margin; 1+1 long simple trichomes on posterior half of hypostomium (Fig. 1225). Antennal segment as long as labral fan stalk, all segments dark brown except basal and apical thirds of segment II which is whitish; length of antennal segments excluding the sensillum 0.09-0.1:0.1:0.1 mm (n = 3). Mandibles with three apical teeth first and third of same length; mandibular comb with 10 teeth, first four teeth more prominent than remainder; one prominent anterior mandibular serration, the posterior very reduced and only visible at higher magnification (Fig. 1279). Maxillary palps heavily pigmented; three times as long as wide at base. Labral fan with 58-67 rays with single line of longer spinules interspersed with finer microspinules (n = 3).

Thorax: dark grey dorsally and pale grey ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with a band of over 38-46 rows of sclerotised processes of 16-17 simple hooks (n = 3). Pupal respiratory gill histoblast dark brown, claviform.

Abdomen: usually completely grey dorsally, progressively paler ventrally especially the last two segments. Ventral nerve cord grey. Ventral papillae absent. Cuticle mainly lacking setae except area around anal sclerite. Anal sclerite well sclerotised with posterior arms extending to 70-90th row of posterior circlet hooks, no sclerotised areas between arms. Posterior circlet with 135-166 rows of sclerotised process of 40-57 hooks (n = 3). Rectal gill with three lobes, each with 7-8 finger-like lobules (n = 1).

Taxonomic Discussion. The complicated taxonomy of *S. virgatum s.l.* has been reviewed by ADLER *et al.* (2004) and SHELLEY *et al.* (2002b), who also quoted the most relevant publications dealing with the taxonomy of this species, and discussed its synonymies and the mis-identifications by other authors. More recently, SHELLEY *et al.* (2010) have also dealt with the status of *S. virgatum s.l.*, with regards to its most closely related species, *S. hippovorum*, *S. paynei* and *S. rubrithorax*. These authors agree with the taxonomic arrangements proposed in ADLER *et al.* (2004) and these have also been accepted in the current work. SHELLEY *et al.* (2010) also pointed out the taxonomic confusion involving *S. paynei* from Mexico with the material that they have identified as "*S. virgatum s.l.* black and brown forms" from Belize. I have re-examined this material, along with the type material of *S. virgatum s.l.*, and its synonym *S. rubicundulum* within the context of the current work, and I agree with the taxonomic arrangement in SHELLEY *et al.* (2010) [see also **Taxonomic Discussion** under *S. paynei* in this work].

The thorax in females of *S. virgatum s.l.* is commonly black with 1+1 submedian, pear-shaped and 1+1 sublateral, wide silver pruinose cunae (specimens from USA and Mexico) (Figs. 412-415). However, specimens identified as *S. virgatum s.l.* with a brown to dark brown thorax have been recorded in New Mexico and Texas [same pattern as in Figs. 414, 415 as *S. rubicundulum* in **Material Examined**], and these are also within the distribution range of *S. paynei* and *S. solarii*, species of which females cannot be easily identified based only on their scutal pattern. Thus, some of the records as the brown form of *S. virgatum s.l.* might be of *S. paynei* and/or *S. solarii.* Other species with a similar thoracic pattern to that of *S. virgatum s.l.* are *S. bricenoi*, *S. freemani* and *S. hinmani* (Figs. 364, 365, 372-375, 378, 379). When link-reared specimens are available, the female of *S. bricenoi* is easily separated by the rugosities and markings found on the pupal thorax. The other species cannot be easily separated from

S. virgatum s.l. based on the thoracic pattern.Variation in females of *S. virgatum s.l.* has been reported by ADLER *et al.* (2004), who stated that the scutum in this species varies from reddish orange (as in the type material of *S. rubicundulum,* Figs. 414, 415) to chestnut. They argued that this variation might be related to temperature and therefore might vary from season and latitude, or it might be associated with sibling species.

The male of *S. virgatum s.l.* can only be separated from other species in the TARSATUM species group (especially *S. hippovorum*, *S. paynei* and *S. rubrithorax*) by the morphology of the ventral plate. In the holotype and other specimens examined from the USA of *S. virgatum s.l.*, the median process is relatively thinner and approximately three times longer than its basal width, and the anterior margin is slightly concave at the base of the median process (Fig. 948). In *S. hippovorum*, *S. paynei.* and *S. rubrithorax* the morphology of the antero-median process and the main body of the ventral plate is different from that of *S. virgatum s.l.* (Figs. 59, 936, 938-941, 943). Other species with similar thoracic patterns are *S. bricenoi*, *S. freemani*, *S. hinmani* and *S. solarii* but they all can be separated by the different length and width of the antero-median process of the ventral plate (see Figs. 57, 58, 928, 932, 935, 945).

The pupa of *S. virgatum s.l.* has eight gill filaments (Figs. 1072). a character that it also shares with *S. bricenoi*, *S. freemani*, *S. hippovorum*, *S. paynei* and *S. rubrithorax*. *Simulium freemani* can be separated by the absence of fenestrations in the cocoon and *S. bricenoi* by the rhomboid-like makings on the pupal thorax. The pupa of *S. hippovorum* can be separated by the palmate-like gill configuration (Fig. 1060). *Simulium paynei* and *S. rubrithorax* pupae (Figs. 1064-1066, 1068) cannot be separated from that of *S. virgatum s.l.* in the absence of link-reared adults.

The larva of *S. virgatum s.l.* similar to other closely related member of the TARSATUM species group which have a dissected gill histoblast with eight filaments, for example *S. bricenoi*, *S. freemani*, *S. hippovorum*, *S. lobatoi*, *S. paynei* and *S. rubrithorax*. These species can only be separated with some difficulty by the combination of characters given in the key to larvae, especially the different number of hypostomial setae, shape of the hypostomial teeth and postgenal cleft, and the number and morphology of the mandibular teeth [see **section 2.4.9**].

MUHAMMAD (1988) showed through cytological analyses of larvae collected mainly from southwestern USA and Guatemala that *S. virgatum s.l.* is a sibling species complex of four cytotypes, denominated A-D. His main emphasis was on descriptions of polytene chromosomes and the relationships between the different cytotaxa studied, rather than correlating cytological and morphological variation in the complex. Later, PETERSON & KONDRATIEFF (1995), in their review of the black flies of Colorado State in the USA, recommended a review of the taxonomy of this species complex because collections made in the same and other localities collected by MUHAMMAD in Texas suggested to these authors that he may have mis-identified some of his specimens and he was dealing with morphologically different species and not just *S. virgatum s.s.* ADLER *et al.* (2004) also suggested that *S. virgatum s.l.* is a species complex and P.H. ADLER has also mentioned this problem to L.M. HERNÁNDEZ and A.J. SHELLEY (pers. comm.).

Full descriptions of the adults, pupa and larva of *S. virgatum s.l.* may be found in ADLER *et al.* (2004), DALMAT (1955), IBÁÑEZ-BERNAL (1992) and SHELLEY *et al.* (2002).

ADLER & CROSSKEY (2008, 2009, 2010), CROSSKEY & HOWARD (1997, 2004), COSCARÓN & COSCARÓN-ARIAS (2007), and COSCARÓN *et al.* (20008) placed *S. virgatum s.l.* in the PAYNEI species group. However, this species group has been subsumed under the TARSATUM species group by SHELLEY *et al.* (2010), where *S. virgatum s.l.* is now placed.

Distribution. *Simulium virgatum s.l.* is a fairly common species, where it occurs in the southernmost parts of North America, for example Texas and New Mexico (ADLER *et al.*, 2010; **Material Examined**). Based on the material examined and the literature reviewed for the current work, the records *S. virgatum s.l.* from certain Central American countries (for example Belize, El Salvador, Guatemala, Mexico, and Panamá) abstracted by ADLER & CROSSKEY (2008, 2009, 2010), CROSSKEY & HOWARD (1997, 2004) and SHELLEY *et al.* (200b) might correspond to *S. paynei.*

Biology and Medical Importance. ADLER *et al.* (2004) stated that immature stages of *S. virgatum s.l.* live in rocky streams 1-8 m wide, with temperatures sometimes exceeding 25°C. They can be collected attached to bedrock and stones. In North America, the larva can be found from March through August and in southern Arizona, reared adults were collected in early February. The females are zoophilic.

ADLER *et al.* (2004) recorded the fungus *Harpella leptosa* LICHTW. & S.T. MOSS from the larval midgut.

2.5.4.19. *Simulium (Trichodagmia) yepocapense* DALMAT (Figs. 227, 282, 416, 417, 523, 581, 641, 701, 825, 826, 888, 949, 1009, 1073, 1119, 1171, 1226, 1280)

A zoophilic species only recorded from Guatemala and Mexico. I have been unable to obtain material of pupae and larvae of *S. yepocapense*. Hence, the description here provided for these life stages has been derived from COSCARÓN & COSCARÓN-ARIAS (2007), DALMAT (1955) and IBÁÑEZ-BERNAL (1992).

Simulium (*Dyarella*) *yepocapense* DALMAT, 1949: 548. HOLOTYPE female (reared), GUATEMALA: Chimaltenango Department, San Pedro de Yepocapa, Finca Niágara, Rio Sacayá; 4.x.1948, (*Jorge Aleman & Miguel Xinic*) (NMNH) [Examined.]

Simulium (*Dyarella*) *ardeni* DALMAT, 1953: 35. HOLOTYPE male (reared). GUATEMALA, San Pedro Carcha, Altaverapaz, Rio Tzunutz; 16.xi.1944, (*G.B.Fairchild*) (NMNH, acc. no Fair 5-24A) [Examined.] [Synonymy by VARGAS & DÍAZ NÁJERA, 1954: 61.]

FEMALE. General body colour dark brown. Body length (specimens pinned) 2.3-3.8 mm (mean = 3.7 mm, s.d. = 0.43, n = 9), wing length 2.3-2.7 mm (mean = 2.4 mm, s.d. = 0.13, n = 9), wing width 1.2-1.8 mm (mean = 1.4 mm, s.d. = 0.21, n = 9).

Head: dichoptic with dark red eyes and nudiocular area well developed (Fig. 227). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed, sclerotised cornuae and with teeth at base of cornuae and central trough (Fig. 282).

Thorax: scutum dark brown with evenly arranged, recumbent, golden setae. Scutal pattern varying slightly with illumination. With anterior illumination, thorax dark brown with 1+1 median, pear-shaped and 1+1 sublateral, wide grey pruinose vittae extending from anterior to posterior margins, leaving a lyre-shaped band on mid region of thorax; fine dark brown line on central region of thorax extending from anterior to posterior margins; humeri faint pruinose; lateral and posterior margins dark brown to black (Fig. 416). With posterior illumination, thorax dark brown, with distinct silver pruinose area on anterior third of scutum; humeri and lateral margins silver pruinose; posterior margin dark brown to black (Fig. 417). Scutellum dark brown with recumbent yellow hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta varying from pilose (holotype) to bare (paratypes). Radius with numerous setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 523. Fore leg with coxa, trochanter, femur, and mid part of tibia pale yellow; remainder of leg dark brown. Fore and hind legs with trochanters, basal two thirds of femora, areas on basal third of tibiae, and basal two thirds of tarsal segment I whitish to pale yellow; remainder of legs dark brown. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX dark brown to black; segments I-II with feint pruinosity on anterior margin. Tergal plates well developed in pinned specimens examined. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with long, irregularly distributed setae on posterior margin; gonapophyses nearly twice as long as length of eighth sternite at mid point, subtriangular; internal margins of gonapophyses curved at junction with eighth sternite and weakly sclerotised, remainder of gonapophyses membranous (Fig. 581). Cercus subrectangular, covered with brown setae; paraproct subquadrangular, twice as long as cercus and weakly sclerotised; paraproct densely covered with prominent brown hairs and few basal setae (Fig. 641). Genital fork stout and sclerotised; termination of lateral arms with anterior margins straight and well developed; anterior processes poorly developed and rounded apically; posterior processes well developed (Fig. 701). Spermatheca globular, without external sculpturing and apparently with fine single spicules; area of insertion of spermathecal duct membranous.

MALE. General body colour dark brown to black. Body length (specimens pinned) 2.4-2.8 mm (mean = 2.6 mm, s.d. = 0.51, n = 7), wing length 1.2-2.6 mm (mean = 2.2 mm, s.d. = 0.51, n = 7), wing width 1.1-1.4 mm (mean = 1.2 mm; s.d. = 0.11, n = 7).

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum dark brown covered by recumbent golden hairs. Scutum, irrespective of light incidence, dark brown with faint pruinosity extending across anterior third of thorax (Figs. 825-826). Humeri weakly pruinose; lateral and posterior margins dark brown. Scutellum brown with golden, recumbent hairs and long, erect, dark brown setae. Postnotum dark brown to black with silvery grey pruinosity. Wing setation as in female, Leg coloration as in female.

Abdomen: tergites dark brown, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II, III and VII [best seen in some specimens when tilted and viewed laterally]. Genitalia brown; sternal plates developed. Gonocoxite subquadrangular; gonostyle elongate, subrectangular with dorsal and ventral margins prominently sinuous, terminating in single, stout spine; gonocoxite and gonostyle covered with long setae (Fig. 888). Ventral plate weakly sclerotised, subquadrangular, without developed shoulders or anterior median process; and basal arms well developed and subparallel (Fig. 949). Median sclerite long, about three times longer than wide at widest point, with small incision (Fig. 949). Paramere with well developed and sclerotised basal processes and numerous long spines centrally; median membrane covered by small spinules (Fig. 1009).

PUPA. [DALMAT (1955) and IBÁÑEZ-BERNAL (1992) did not state the number of specimens they examined, but provided measurements for the cocoon length dorsally as 3.4-4.0 mm (n = 4). Other measurements were not provided]; gill length 0.5 mm (n = 1); other measurements are not given because of the poor condition of available specimens].

Cocoon: shoe-shaped as in Fig. 66, dark brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture strongly elevated.

Gill: light brown with ten upwardly directed filaments arranged in bunch in vertical plane (Fig. 1073). Gill with filaments branching basally at different heights; main trunk short, giving rise to three sets of primary branches; one dorsal and one median with four secondary branches each, and one ventral with two secondary branches. Filaments stout, pointed distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (frontoclypeus): with 2+2 small, simple frontal and 1+1 small, simple facial trichomes Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and two platelets in groups of two laterally in frontal region; tubercles absent in frontal region, but rounded and well distributed over entire surface in facial region. Small carina extends across facial region.

Thorax: [IBAÑEZ-BERNAL (1992) stated that five long trifid trichomes are found in this region; two long, simple trichomes near base of gills, and one long, simple trichome on central region, posteriorly]; tubercles rounded only visible at base of gill and postero-lateral margins of dorsal cleft.

Abdomen: abdominal tergite I with 1+ 1 submedian simple short setae and pointed tubercles on posterior margin; tergite II with 3+3 submedian spiniform setae in longitudinal row, 1+1 or 2+2 spiniform setae on lateral margins, and pointed tubercles on posterior margins; tergites III, IV with 4+4 submedian simple hooks in longitudinal row, and 1+1 small setae on lateral margins; tergites V-VIII apparently without setae or trichomes; tergite IX weakly sclerotised without terminal spines. Spine combs on anterior margins of tergites II-IX. Sternites III, IV without setae or trichomes; sternite V with 2+2 close simple hooks; sternites VI, VII with 4+4 well separated simple hooks along posterior margin; sternite VIII without setae or trichomes; sternite IX weakly sclerotised. Spine combs on anterior margins of sternites III, IV, and VIII, IX, and anterolateral margins of sternites V-VII.

LARVA (Last instar). [DALMAT (1955) and IBÁÑEZ-BERNAL (1992) provided the following measurements: Body length 8.7-10.6 mm (n = 4); length of head capsule 0.9-1.0 mm (n = 4); width of head capsule 0.7-0.8 mm (n = 4). COSCARÓN & COSCARÓN-ARIAS (200) gave measurements for the body maximum length 7.0-8.0 mm]. Body colour dark grey dorso-laterally, whitish ventrally (specimens preserved in Carnoy's solution and/or alcohol). General body form as in Fig. 1119.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, bell-shaped, subtriangular apically; postgenal bridge nearly as long as hypostomium (Fig. 1171). Hypostomium strongly pigmented on anterior margin, with approximately nine apical teeth protruding in central region; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, with pair adjacent to median tooth longer than remainder; 1+1 lateral teeth as long as first sublateral teeth; 5+5 or 6+6 small, lateral serrations; 1+1 lines of nine hypostomial setae parallel to lateral margins; 2+2 long, simple setae in posterior half of hypostomium (Figs. 1226). Sub-esophageal ganglion lightly pigmented. Antennal segments longer than labral fan stalk, all segments slightly pigmented; length of antennal segments I-III not given in original description. Mandible with three apical teeth, first one longer than second and third; mandibular comb with ten teeth, first four more prominent than remainder; two mandibular serrations, anterior more prominent than posterior (Fig. 1280). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fans with 43-48 rays each with fine, single line of spines in a row.

Thorax: grey dorsally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 48 processes. Pupal respiratory gill histoblast not examined.

Abdomen: [coloration of thorax and ventral nerve cord not given]. Ventral papillae absent. Cuticle lacking setae. Anal sclerite well sclerotised with anterior arms extending one third of diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 220-222 rows (n= 3). Rectal gills with three lobes, each with approximately 11 small, finger-like lobules.

Taxonomic Discussion. *Simulium yepocapense* was described by DALMAT (1949) based on a reared female holotype, and 11 females and five males (as paratypes and all reared) collected from Chimaltenango Department, Guatemala. The larva was described for the first time by DALMAT (1955) together with a redescription of the adults. An error appeared in this paper as DALMAT stated that the pupa of *S. yepocapense* has eight gill filaments (pp: 207), while figure 300 (Plate 37) illustrates a pupa with 10 gill filaments, which is the correct number of filaments for this species. DALMAT (1949) also incorrectly stated that the cocoon of *S. yepocapense* was slipper-shaped, but it is evident from his figure that the cocoon is shoe-shaped (see Plate VII, Fig. 27; see also DALMAT, 1955, Pl. 39, Fig. 340). I have examined the female holotype and nine paratypes, which are deposited at the NMNH (accession no. Yepo. 570-578). The holotype has been dissected and it is mounted on seven slides (**Material Examined**). Its cocoon is said to have been preserved in alcohol, but I was unable to find it in the NMNH holdings.

VARGAS & DÍAZ NÁJERA (1954) reviewed the taxonomy of several simuliid species in Mexico and synonymised *S. ardeni* with *S. yepocapense*. I have studied the original description of the former species and have the following comments to make. *Simulium ardeni* was described by DALMAT (1953) based on a reared male holotype, and two reared males and four pupal exuviae (all as paratypes, one male as allotype) collected in Rio Tzunutz, Guatemala. I have examined the male holotype with accession number (Fair. 5-24A), which is housed at NMNH. The specimen is mounted on seven slides contaning the adult, its pupal exuviae and gill filaments. The cocoon wassaid to be preserved in alcohol but was not found at the NMNH (**Material Examined**). No other specimens from the type series of *S. ardeni* were found at this institution. In addition, I have also examined two slides containing the gill filaments of both sides of a pupa and the male genitalia (labelled as paratypes) deposited at INDRE (see **Material Examined**). I have taken digital images of key taxonomic character of the latter material, which are now stored at the Digital Archive at the NMNH. The general morphology of *S. ardeni*, especially the structure of the male ventral plate and the configuration and number of the gill filaments fall within the variation found in *S. yepocapense*, hence I agree with the synonymy of VARGAS & DÍAZ NÁJERA (1954).

The female of *S. yepocapense* is externally similar to that of *S. guerrerense* and *S. pulverulentum* from which it is very difficult to separate in the absence of link-reared specimens. The male of *S. yepocapense* is easy to separate from the latter two species by the morphology of the ventral plate, especially the absence of developed lateral shoulder and an antero-median process (Fig. 949).

The pupa of *S. yepocapense* has 10 filaments (Fig. 1073) and its configuration is very similar to that of *S. guerrerense*, *S. pulverulentum* (Figs. 1057, 1067). In the pupa *S. yepocapense* cannot be easily separated from the latter two species in the absence of link reared males, on which dissection of the genitalia is paramount. Another species with a 10-filamented pupa is *S. hinmani* (Fig. 1059), but the configuration of the pupal gill filament is different in the latter species.

The dissected gill histoblast of the mature of larva of *S. yepocapense* has ten filaments, a character that it also shares with *S. guerrerense* and *S. pulverulentum*. However, *S. yepocapense* may be separated by the hypostomial teeth forwardly protruded and the median tooth more prominent than the remainder teeth (Figs. 1171, 1226). The morphology of the hypostomial teeth in the latter two species is different (Figs. 1159, 1165, 1214, 1220).

Distribution. *Simulium yepocapense* has a discontinuous distribution in Guatemala and Mexico (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; IBÁÑEZ-BERNAL, 1992; **Material Examined**).

Biology and Medical Importance. DALMAT (1955) stated that the larvae and pupae of *S. yepocapense* can be collected mainly attached to rocks, but also on leaves in rapids in small streams. In Guatemala, the females have been reported as zoophilic biting cats, cows, horses, and sheep (DALMAT, 1955; IBÁÑEZ-BERNAL, 1992). *Simulium yepocapense* has a wide altitudinal distribution from sea level up to 2.400 m according IBÁÑEZ-BERNAL (1992).

2.6. Species transferred from the subgenus *Trichodagmia* to the subgenus *Psilopelmia*.

In the recent classification of SHELLEY *et al.* (2010) *S. oviedoi* and *S. rivasi* were placed in the ORBITALE species group in the subgenus *Trichodagmia*. I have now allotted both species to the subgenus *Psilopelmia*, BICOLORATUM species group based on the morphology of the male gonostyle and the ventral plate, and the female cibarium (see **Taxonomic Discussion**).

2.6.1. *Simulium (Psilopelmia) oviedoi* RAMÍREZ-PÉREZ, 1971 (Figs. 228, 283, 524, 582, 642, 702, 889, 950, 1074, 1076, 1120, 1172, 1227, 1281)

This is a poorly known species that still requires more study. It is only known from Mérida State, Venezuela and morphologically similar to *S. rivasi*. The description here provided have been derived from the original description of RAMÍREZ PÉREZ (1971), examination of identified material housed at the AMNH, BMNH and MLP, and the recent book of the Neotropical Simuliidae by COSCARÓN & COSCARÓN-ARIAS (2007).

Simulium oviedoi RAMÍREZ-PÉREZ, 1971: 363. HOLOTYPE [Life stage not indicated in original description.], VENEZUELA: Mérida State, Nacimiento del Rio Motatán, entre el Páramo, El Águila y Chachopo, at 3330 m; [No date or collector's name given in the original description, but probable collected by Ramírez-Pérez.] (DERM) [Location of the holotype unknown - see *Notes on Ramírez Pérez' Simuliidae collection* in SHELLEY *et al.*, 2010.]

FEMALE. General body colour black. Body length (specimen pinned, n = 1) 3.8 mm; wing length 3.6 mm; wing width 1.7 mm.

Head: dichoptic with dark red eyes and nudiocular area poorly developed (Fig. 228). Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi-recumbent brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum dark brown. Cibarium with well developed sclerotised cornuae, without teeth (Fig. 283).

Thorax: scutum black covered with recumbent white hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black median silver pruinose line and 1+1 pruinose vittae extending from anterior to posterior margins; humeri silver pruinose; lateral and posterior margins black. With posterior illumination, thorax black with 1+1 faint submedian pruinose areas on anterior third of scutum, and single faint pruinose line on central region of thorax; humeri and lateral margins faintly silver pruinose; posterior margin black. Scutellum brown with recumbent white hairs intermixed with long, brown bristles. Postnotum dark brown with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta with line of setae towards apex. Radius with setae intermixed with distinct spines, basal section of radius bare. Basal tuft of long, dark setae. Leg coloration and proportions as in Fig. 524 (pharate female). Fore leg with mid part of femur and tibia pale brown; coxa, trochanter, femur and tibia basally and apically, and tarsal segments I-IV dark brown. Mid leg with basal two thirds of femur and basal third of tibia pale brown; coxa, trochanter, apical third of femur, apical third of tibia and tarsal segments I-IV dark brown. Hind leg with basal two thirds of femur and basal third of tibia pale brown; coxa, trochanter, apical third of femur, apical third of tibia and tarsal segments II-IV dark brown; tarsal segment I mostly white with brown tinges apically. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX black with silver pruinosity on segments VI-VIII. Tergal plates well developed. Sternites and genitalia dark brown to black. Eighth sternite sclerotised with approximately 14 irregularly distributed setae on posterior margin; gonapophyses nearly as long as length of eighth sternite at mid point, subtriangular, largely membranous except internal margins which are weakly sclerotised; gonapophyses densely covered with long hairs (Fig. 582). Cercus suboval, covered with brown setae; paraproct subrectangular, twice longer than cercus, weakly sclerotised on basal half and strongly sclerotised apically; paraproct densely covered with prominent brown hairs basally and small setae apically (Fig. 642). Genital fork stout, sclerotised with stem expanded apically; termination of lateral arms with anterior margin straight and well developed; anterior processes well developed and blunt apically; posterior processes developed (Fig. 702). Spermatheca globular, without external sculpturing or visible internal spicules; area of insertion of spermathecal duct membranous.

MALE. General body black. [COSCARÓN & COSCARÓN-ARIAS (2007) provided measurements for the Wing width 2.6 mm. Other measurements and the number of specimens examined were not indicated in this publication.]

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black. Scutal pattern, scutellum and postnotum apparently as in female following COSCARÓN & COSCARÓN-ARIAS (2007). Wing setation as in female, except Sc bare in two specimens examined. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergites II, V-VII (best seen in some specimens when tilted and viewed laterally). Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle subtrapezoidal with dorsal and ventral margins weakly sinuous, and terminating in stout apical spine; gonocoxite and gonostyle covered by long brown hears; gonostyle covered with microtrichiae basally (Fig. 889). Ventral plate weakly sclerotised, subtriangular and main body broadly developed mesally; lateral shoulders undeveloped and basal arms small and subparallel (Fig. 950). Median sclerite and parameres not examined because of lack of material

PUPA. [COSCARÓN & COSCARÓN-ARIAS (2007) provided measurements for the cocoon length dorsally 3.0-3.4 mm, ventrally 3.2 mm; pupa length 4.0-4.4 mm; gill length 1.4-1.7 mm. The number of specimens examined was not given in this publication]; gill length 0.7 mm (n = 2); [other measurements not provided because of lack of material.

Cocoon: shoe-shaped as Fig. 66, brown composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: dark brown with six forwardly directed filaments arranged in bunch in vertical plane. Gill configuration with filaments branching basally at different heights; main trunk short and wider, giving rise to three primary branches each giving rise to two secondary filaments (Fig. 1074). Gill variation occurs in this species, where secondary filaments of middle branch much shorter than other filaments.

Filaments stout, rounded distally, with small spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): without visible facial or frontal trichomes. Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in groups of two or three laterally in frontal region, respectively; tubercles prominently spiny and well distributed over entire surface.

Thorax: with simple trichomes interspersed with trifid trichomes; tubercles prominently spiny and well distributed over entire surface (Fig. 1076).

Abdomen: abdominal tergite I with 1+1 simple long setae on anterolateral margins; tergite II with 3+3 close and 1+1 separate submedian spiniform setae in row, 2+2 simple setae anterior to outermost spiniform setae, and 1+1 or 2+2 small simple trichome; tergites III-IV with 4+4 simple hooks in row, 2+2 small simple setae anterior to outermost of hooks, and 1+1 small simple setae on lateral margins; tergite V submedian, 1+1 submedian and 1+1 simple setae on lateral margins in row; tergites VI-IX without visible setae; tergite IX weakly sclerotised without terminal spines. Spine combs on anterior margin of tergite VIII. Sternite III with 1+1 sublateral long simple trichomes and 3+3 simple or bifid long trichomes on lateral margins; sternite IV with 1+1 submedian spiniform trichome, 1+1 submedian simple trichomes, and 2+2 simple trichomes on lateral margins; sternite V with 2+2 submedian close bifid hooks, and 1+1 simple setae on lateral margins; sternites VI, VII with 4+4 simple or bifid hooks in row; sternites VIII, IX without visible setae; sternite IX weakly sclerotised. Spine combs on anterior margins of sternites III-VIII.

LARVA (Final instar). [COSCARÓN & COSCARÓN-ARIAS (2007) gave measurements only for the body length 7.0-8.0 mm. Other measurements and number of specimens examined not given in this publication]. General boyd form as in Fig. 1120.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft small, bell-shaped, subtriangular apically; postgenal bridge as long as hypostomium (Fig. 1172). Hypostomium strongly pigmented on anterior margin, with 11 apical teeth evenly distributed on anterior margin; median tooth sharp, well developed and most prominent; 3+3 sublateral teeth, the outermost pair more prominent than remainder of teeth; 1+1 lateral teeth more prominent than sublateral teeth and same length as median tooth, and 1+1 paralateral teeth; 2+2 small lateral serrations; 1+1 line of approximately 23 long hypostomial setae parallel to lateral margin; 1+1 small bifid seta in central region of half of hypostomium (Fig. 1227). Sub-oesophageal ganglion unpigmented. Antennal segments longer than labral stalk; length of antennal segments I-III excluding the sensillum 1:1.8-2.4:2-2.4 mm (n = 2). Mandible with three apical teeth, first one longer than second and third; mandibular comb with approximately 15 teeth, the first two longer than remainder; 3+3 mandibular serrations, third serration relatively more prominent than middle one, and first serration very reduced (Fig. 1281). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with 19-22 rays each with fine, single line of spines in a row (n = 2).

Thorax: Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 24 processes with 111 simple hooks (n = 2). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with six filaments, all branching from wide common trunk.

Abdomen: Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with posterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with approximately 106 rows of 17 simple hooks (n = 1). Rectal gill not everted in single specimens examined.

Taxonomic Discussion. *Simulium oviedoi* was described by RAMÍREZ-PÉREZ in 1971 from specimens collected in Venezuela. He did not state which life stage he designated as the holotype, although he figured and described the female, and provided illustrations of the male genitalia, pupal gill filaments, pupal cephalic and thoracic trichomes, larval head capsule and hypostomium. In the original description RAMÍREZ-PÉREZ (1971) stated that the holotype and paratypes were deposited in DERM, but I have been unable to obtain this material for study [see *Note on Ramírez Pérez' Simuliidae collection* in **Materials and Methods** of SHELLEY *et al.*, 2010].

The adults of *S. oviedoi* are very difficult to identify without examination of the pupal gill. The pupal gill in *S. oviedoi* has six filaments, which easily separates it from other simuliid species allotted to the subgenus *Trichodagmia*, except *S. brachycladum*, *S. cristalinum* and *S. rivasi*, which all have the same number of gill filaments (Figs. 1049, 1052, 1053, 1074). *Simulium oviedoi* is most closely similar to *S. rivasi* along its distribution range because all primary branches arise from a short and wide common trunk (Figs. 1074, 1075), but they can be separated by the morphology of the tubercles on the frontoclypeus and thorax of the pupa. In *S. oviedoi* the frontoclypeus and the thorax of the pupa are densely covered with prominent spiny tubercles (Figs. 1076), whereas in *S. rivasi* they are densely covered with rounded tubercles (Fig. 1077). *Simulium cristalinum* can be recognized by the dorsal set of primary branches dividing at some distance from the base of the gill, and the frontoclypeus and the thorax of the pupa with sparsely distributed, rounded tubercles (see COSCARÓN & PY-DANIEL, 1989). *Simulium brachycladum* may be recognized by having all filaments of the same girth and pointed apically (Fig. 1049).

In Venezuela the larva of *S. oviedoi* can be separated from that of *S. rivasi* by the presence of 1+1 lines of approximately 23 hypostomial setae (Fig. 1227) and the mandibles often with a third mandibular serration (Fig. 1281). In *S. rivasi* the hypostomium only has 1+1 lines of 11 hypostomial setae (Fig. 1228) and the mandible only has two mandibular serrations (Fig. 1282).

The taxonomic position of *S. oviedoi* and its closest relative, *S. rivasi*, has been problematic within the genus *Simulium*. COSCARÓN (1987) included it in the OVIEDOI species-group, which he regarded as equivalent to a subgenus very close to *Hemicnetha* and *Grenieriella*, based on the general aspect of adults and the larva. Nonetheless, he stated that the morphology of the genitalia of the OVIEDOI group was similar to that of *Ectemnaspis* [now a synonym of *Psilopelmia*, see SHELLEY *et al.* (2010)] and related groups. In this paper, he emphasized that the larval morphology precluded the placing of these two taxa in any known subgenus. This was based on the type of the labral fans, the presence of robust marginal teeth on the mandible and an intermediate number of rows of hooks in the anal ring [= posterior circlet]. Later, CROSSKEY (1988) placed *S. oviedoi* and *S. rivasi* as "Unplaced to species group" within the genus *Simulium*, but PETERSON *et al.* (1988) included both taxa in their key to the New World species of *Hemicnetha*. The latter was not followed in the World Inventory of Blackflies by CROSSKEY & HOWARD (1997, 2004), who still regarded *S. oviedoi* and *S. rivasi* as "Species unplaced to subgenus".

More recently, COSCARÓN & COSCARÓN-ARIAS (2007) reviewed the taxonomy of *S. oviedoi* and *S. rivasi* and placed both species in the OVIEDOI species group within the subgenus *Hemicnetha* because this subgenus offered the best closest fit, even though characters of the male genitalia were similar to species in the subgenus *Ectemnaspis*. The latter assumption was based on the common characters with species in the subgenus *Hemicnetha* such as smooth cibarium, deep nudiocular triangle, absence of hairs on the basal section of the Radius, shape of the pupal cocoon and gill, reinforcement of frontoclypeal base, which are also similar in species of *Hearlea*. The authors also argued that important taxonomic characters in the OVIEDOI species group differ from the known *Hemicnetha* species groups, such as the gonapophyses acute apically and about as long as wide at base, subtriangular paraprocts, gonostyles shorter than the gonocoxite with slight distal curvature, ventral plate subtriangular without a median carina (similar to *Ectemnaspis*), and larval body with dorsal curvature subterminally. HERNÁNDEZ *et al.* (2007a) reviewed COSCARÓN & COSCARÓN-ARIAS' (2004) findings and considered *S. oviedoi* and *S. rivasi* as a member of the TARSATUM species group, which was followed in the World Inventory of Blackflies (ADLER & CROSSKEY, 2008, 2009, 2010). HERNÁNDEZ *et al.* (2007a) based their conclusion upon the examination of the adult general morphology, wing venation, the morphology of the larval hypostomium given in RAMÍREZ-PÉREZ (1971) and the morphology of the frontoclypeus and gill filaments of the pupa (see Figs. 211, 212 in HERNÁNDEZ *et al.*, 2007a).

I have re-examined all material identified as *S. oviedoi* in HERNÁNDEZ *et al.* (2007a) and made new dissections of the female genitalia (**Material Examined**), reviewed the original description and illustrations in RAMÍREZ-PÉREZ (1971, 1983), and compared the morphology of this species with other Neotropical species allotted to the subgenera *Trichodagmia* and *Psilopelmia* (and its synonym *Ectemnaspis*). Although externally similar to species of *Trichodagmia*, I have found that the general morphology of the adults' genitalia (Figs. 642, 643, 702, 703, 889, 890, 950, 951, 1010) in *S. oviedoi* and *S. rivasi*, especially the male ventral plate and gonostyle (Figs. 889, 890), does not agree completely with the illustrations given in RAMÍREZ-PÉREZ (1971) nor with current morphological concept of species groups in *Trichodagmia* as defined by SHELLEY *et al.* (2010). They are most closely related to species of *Psilopelmia* because the ventral plate is subtriangular, broadly expanded centrally, without defined shoulders and central keel (Figs. 950, 951). In addition, the gonostyles are subtrapezoidal in shape and much shorter than the gonostyle (Fig. 889, 890). The presence of a prominent median and 1+1 lateral teeth, 1+1 paralateral teeth and numerous lateral serrations in the larval hypostomium also does not fall within the variation found in species of *Trichodagmia* (Figs. 1127, 1228). The latter characters are most commonly found in species of the subgenus *Psilopelmia.* Therefore, I here assign *S. oviedoi* and *S. rivasi* to the BICOLORATUM species group in subgenus *Psilopelmia*, because of the unarmed female cibarium without prominences at the base of the cornuae [see SHELLEY *et al.* (2010) for details on species group delineation within *Psilopelmia*].

Description of the life stages of *S. oviedoi* may be found in RAMÍREZ-PÉREZ (1971) and COSCARÓN & COSCARÓN-ARIAS (2007).

Distribution. *Simulium oviedoi* has only been recorded from Venezuela (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; CROSSKEY & HOWARD, 1997, 2004; **Material Examined**).

Biology and Medical Importance. Nothing is known on the biology and female feeding habits of *S. oviedoi.*

2.6.2. *Simulium (Psilopelmia) rivasi* RAMÍREZ-PÉREZ, 1971 (Figs. 284, 418, 419, 525, 583, 643, 703, 827, 828, 890, 951, 1010, 1075, 1077, 1121, 1173, 1228, 1282)

This is a poorly known species that still requires more study. It is only known from Mérida state, Venezuela and is morphologically similar to *S. oviedoi.* The description provided here has been derived from the original description of RAMÍREZ-PÉREZ (1971), the review of COSCARÓN & COSCARÓN-ARIAS (2007) and examination of identified material housed at the AMNH, BMNH and MLP.

Simulium rivasi RAMÍREZ-PÉREZ, 1971: 359. HOLOTYPE [Life stage not indicated in original description.], VENEZUELA: Mérida State, Nacimiento del Rio Chama, entre el Páramo El Aguila y Apartaderos; [No date or collector's name given in the original description, but probably by Ramírez-Pérez] (DERM) [Location of the holotype unknown-see *Note on Ramírez Pérez' Simuliidae collection* in SHELLEY *et al.*, 2010.]

FEMALE. General body colour black [COSCARÓN & COSCARÓN-ARIAS (2007) stated that the size and coloration for *S. oviedoi* is the same as in *S. rivasi*].

Head: dichoptic with dark red eyes and nudiocular area well developed. Frons, clypeus and occiput black, with silvery grey pruinosity; clypeus and frons covered with semi erect brown hairs. Mouthparts dark brown. Antennae with scape and pedicel yellowish brown, rest of flagellum black. Cibarium with well developed sclerotised cornuae and without teeth (Fig. 284).

Thorax: scutum black with evenly arranged, recumbent, whitish setae interspersed with black hairs. Scutal pattern varying slightly with illumination. With anterior illumination, thorax black with silver pruinose line on median region of thorax, and 1+1 wide faint silver pruinose vittae extending from anterior posterior margin, 1+1 pear-shaped black bands on central region of thorax [with certain lights prominent silver pruinosity is seen anterior to lateral vittae]; humeri silver pruinose; lateral and posterior margins black, weakly pruinose (Fig. 418). With light posterior thorax black with one median and 1+1 submedian faint silver pruinose lines arising from mid length of thorax and extending near posterior margin thorax; humeri black; lateral and posterior margins faintly pruinose (Fig. 419). Scutellum dark brown with long, brown bristles. Postnotum dark brown to black with silver pruinosity. Pleura brown with silver pruinosity. Costa of wing with dense distribution of spines and setae. Subcosta, Radius, basal section of radius, and basal tuft not examined. Leg coloration and proportions as in Fig. 525 [only single pharate female available; mid leng not figured]. Fore leg with coxa, apical third of trochanter, apical third of femur, basal and apical third of tibia, and tarsal segments I-IV dark brown; remainder of legs pale brown. Mid leg with coxa, apical two thirds of trochanter, basal and apical thirds of femur and tibia, apical third of tarsal segment I, and tarsal segments II-IV dark brown; remainder of trochanter, femur and tibia pale brown; remainder of tarsal segment I white. Hind leg with mid part of femur and tibia white; coxa, trochanter, remainder of femur and tibia, and tarsal segments dark brown, except white basal half of tarsal segment I. Hind leg claw with prominent basal tooth. Halteres cream yellow with brown base.

Abdomen: tergites I-IX black with silver pruinosity on posterior margins of tergites I, II, and anterolateral margins of tergites V-VII. Tergal plates well developed. Sternites and genitalia black. Eighth sternite sclerotised with numerous and irregularly distributed setae on posterior margin; gonapophyses nearly same length as eighth sternite at mid point, subtriangular, largely membranous; gonapophyses densely covered with microtrichiae (Fig. 583). Cercus subrectangular, covered with brown setae; paraproct subquadrangular, twice as long as cercus, largely sclerotised; paraproct densely covered with brown hairs basally and small setae apically (Fig. 643). Genital fork stout, sclerotised, stem expanded apically; termination of lateral arms with anterior margin weakly straight and well developed; anterior processes well developed and blunt apically; posterior processes weakly developed (Fig. 703). Spermatheca globular, without external sculpturing and apparently without internal spicules; area of insertion of spermathecal duct membranous.

MALE. General body colour black. Body length (specimens pinned, n = 1) 3.5 mm, wing length 2.9 mm, wing width 1.7 mm.

Head: holoptic with dark red eyes. Rest of head coloration as in female.

Thorax: scutum black with evenly distributed yellowish hairs with weak green reflections with certain light interspersed with recumbent and semi-erect brown erect hairs especially on anterior margin. Scutal pattern varies slightly with light incidence: with light source anterior thorax black, with silver pruinose areas on anterior margin; humeri silver pruinose; lateral and posterior margins black (Fig. 827). With posterior illumination, thorax dark black (Fig. 828). Scutellum dark brown covered with recumbent golden hairs interspersed with erect brown hair on posterior margin. Postnotum brown with silvery grey pruinosity. Wing setation as in female, except Sc bare in two specimens examined. Leg coloration as in female.

Abdomen: tergites black, basal fringe with long, brown hairs. Pruinose ornamentation on antero-lateral margins of tergite II and lateral margins of tergites V, VI (best seen in some specimens when tilted and viewed laterally). Genitalia black; sternal plates developed. Gonocoxite subquadrangular; gonostyle subtrapezodial with dorsal and ventral margins sinuous; gonocoxite and gonostyle covered by long brown hears; gonostyle with microtrichiae basally (Fig. 890). Ventral plate sclerotised, subtriangular; main body of ventral plate with anterior margin prominent anteriorly, without median process; shoulders undeveloped and basal arms subparallel (Fig. 951). Median sclerite three times longer than wide at widest point, with incision apically (Fig. 951). Paramere with well developed and sclerotised basal processes and short spines in central region; central membranous densely covered by spinules (Fig. 1010).

PUPA. Cocoon length dorsally 3.4-4.2 mm (mean = 3.7 mm, s.d = 0.38, n = 4), ventrally 4.5-5.0 mm (mean n = 3); pupa length 4.2-4.5 mm (n = 3); gill length 1.5-1.8 mm (n = 3).

Cocoon: shoe-shaped as in Fig. 66, brown, composed of thick, coalesced fibres with reinforced rim to anterior aperture, margin of aperture weakly elevated.

Gill: light brown with six forwardly and upwardly directed filaments arranged in bunch in vertical plane. Gill with filaments branching basally at different heights; main trunk short and wider, giving rise to two sets of primary branches, one internal and one external; external branch consists of two branches one anterior and one posterior with two secondary filaments each; internal branch with two secondary filaments (Fig. 1075). Filaments stout, rounded distally, without spicules on surface, edges weakly crenate; all filaments approximately same length.

Head (*frontoclypeus*): with 1+1 frontal simple or trifid long trichomes, facial trichomes absent in all specimens I have examined (see **Material Examined**). Frontoclypeus with group of platelets mesally, 1+1 groups dorso-laterally and 2-3 platelets in groups of two or three laterally in frontal region, respectively; tubercles rounded and well distributed over entire surface.

Thorax: without visible trichomes on dorsal cleft and 2+2 simple or trifid long trichomes on alar region; tubercles rounded and well distributed over entire surface (Fig. 1077).

Abdomen: abdominal tergite I with 1+1 simple long setae on anterolateral margins; tergite II with 3+3 close and 1+1 separate submedian spiniform setae in row, 2+2 simple setae anterior to outermost spiniform setae, and 1+1 small simple trichomes; tergites III, IV with 4+4 simple hooks in row, 2+2 small simple setae anterior to outermost of hooks, and 1+1 small simple setae on lateral margins; tergite V submedian, 1+1 submedian and 1+1 simple setae on lateral margin in row; sternites VI-VIII without visible setae; sternite IX weakly sclerotised without terminal spines. Spine combs on anterior margin of tergites VI-IX, some well developed and resembling teeth, especially on tergites VII, VIII. Sternite III with 1+1 small median simple setae, and 3+3 spiniform setae on lateral margins; sternite IV with 1+1 submedian sclerotised spiniform setae and 2+2 simple setae in row, and 1+1 simple sclerotised setae and 2+2 simple setae on lateral margins; sternite V with 2+2 submedian close bifid hooks, and 1+1 or 3+3 simple setae on lateral margins; sternites VI, VII with 3+3 or 4+4 simple, bifid or trifid hooks in row; sternites VIII, IX without visible setae; sternite IX weakly sclerotised. Spine combs on anterior margins of sternites III-VIII.

LARVA (Final instar). Body length 7.4-8.5 mm (n = 2); length of head capsule 0.9-1.0 mm (n = 2); width of head capsule 0.8-0.9 mm (n = 2). Body colour whitish (specimens fixed in ethanoll). General body form as in Fig. 1121.

Head: mainly dark brown, anterior region of cephalic apotome yellowish. Numerous small setae present on all surfaces and head capsule slightly wrinkled. Head pattern positive. Cervical sclerites small, elliptical, free in membrane. Postgenal cleft deep, triangular and pointed apically; postgenal bridge as long as hypostomium (Fig. 1173). Hypostomium strongly pigmented anteriorly, with 11 apical teeth evenly distributed on anterior margin and forwardly protruded; median tooth sharp, well developed and as prominent as lateral teeth; 3+3 sublateral teeth, with pair adjacent to base of lateral tooth longer than remainder; 1+1 lateral prominent teeth and 1+1 paralateral teeth; 1+1 lines of seven hypostomial setae parallel to lateral margins; 1+1 long bifid and 2+2 or 1+2 small bifid small setae in posterior half of hypostomium; 1+1 lines of approximately 18 lateral serrations (Fig. 1228). Sub-oesophageal ganglion lightly unpigmented. Antennal segments longer than labral fan stalk, all segment brown; length of antennal segments I-III excluding the sensillum 0.04-0.08:0.1:0.1mm (n = 3). Mandible with three apical teeth, first one longer than second and third; mandibular comb with 18 teeth, first and second more prominent than remainder; two prominent mandibular serrations nearly of same length; anterior more prominent and longer than posterior (Fig. 1282). Lateral mandibular process absent. Maxillary palps heavily pigmented; one and a half times as long as wide at base. Labral fan with more 22-23 rays each with fine, single line of spines in a row (n = 2).

Thorax: grey dorsally and whitish ventrally. Cuticle without setae. Proleg with plate heavily sclerotised with band of approximately 27-37 processes (n = 2). Pupal respiratory gill histoblast dark brown; dissected gill histoblast with six filaments, all branching from common trunk.

Abdomen: usually grey dorsally, progressively paler ventrally, especially towards posterior where last segments white. Ventral nerve cord greyish. Ventral papillae absent. Cuticle lacking setae except area around anal sclerite and rectal gills. Anal sclerite well sclerotised with anterior arms extending one third diameter of posterior circlet anteriorly; no sclerotised areas between arms. Posterior circlet with 251-290 rows of 45-46 simple hooks (n = 2). Rectal gills apparently with two lobes of approximately 24 small, finger-like lobules [material at hand in poor condition]

Taxonomic Discussion. *Simulium rivasi* was described by RAMÍREZ-PÉREZ in 1971 from an unspecified number of adults and immature stages collected in Venezuela, but he did not state which life stage had been designated as the holotype. Sub-sequent mis-spellings of *S. rivasi* as *rivai* and *ribai* may be found in RAMÍREZ-PÉREZ (1971). The latter author figured and described the female, and provided illustrations of the male genitalia, the morphology of the gill filaments, cephalic and thoracic trichomes of the pupa, head capsule and hypostomium of the larva. In the original description RAMÍREZ-PÉREZ (1971) indicated that the holotype and paratypes were deposited in DERM, but I have been unable to locate this material in DERM holdings (see *Notes on Ramírez Pérez' Simuliidae* in SHELLEY *et al.*, 2010).

The adults, pupa and larva of *S. rivasi* are morphologically similar to those of *S. oviedoi*, but both species can be separated by the different morphology of tubercles on the frontoclypeus and thorax on the pupa (Figs. 1076, 1077). The larva of *S. rivasi* may be separated from that of *S. oviedoi* by the different number of hypostomial setae and mandibular serrations (Figs. 1228, 1282) [see **Taxonomic Discussion** under *S. oviedoi*].

The same taxonomic problem surrounding *S. oviedoi* also applies to *S. rivasi* [see **Taxonomic Discussion** under *S. oviedoi*]. *Simulium rivasi* is here placed in the BICOLORATUM species group of the subgenus *Psilopelmia* together with *S. oviedoi* because of the unarmed female cibarium without prominences at the base of the cornuae (SHELLEY *et al.*, 2010)

Description of the life stages of *S. oviedoi* may be found in RAMÍREZ-PÉREZ (1971) and Coscarón & COSCARÓN-ARIAS (2007).

Distribution. *Simulium rivasi* has only been recorded in Venezuela (ADLER & CROSSKEY, 2008, 2009, 2010; COSCARÓN & COSCARÓN-ARIAS, 2007; **Material Examined**).

Biology and Medical Importance. Little is known about the biology of *S. rivasi*. RAMÍREZ-PÉREZ (1971) stated that he reared adults from pupae collected in a small stream with a temperature of 13°C at 3,700 m. Nothing is known about the female feeding behaviour of this species.

2.7. APPENDIX 1. FIGURES.

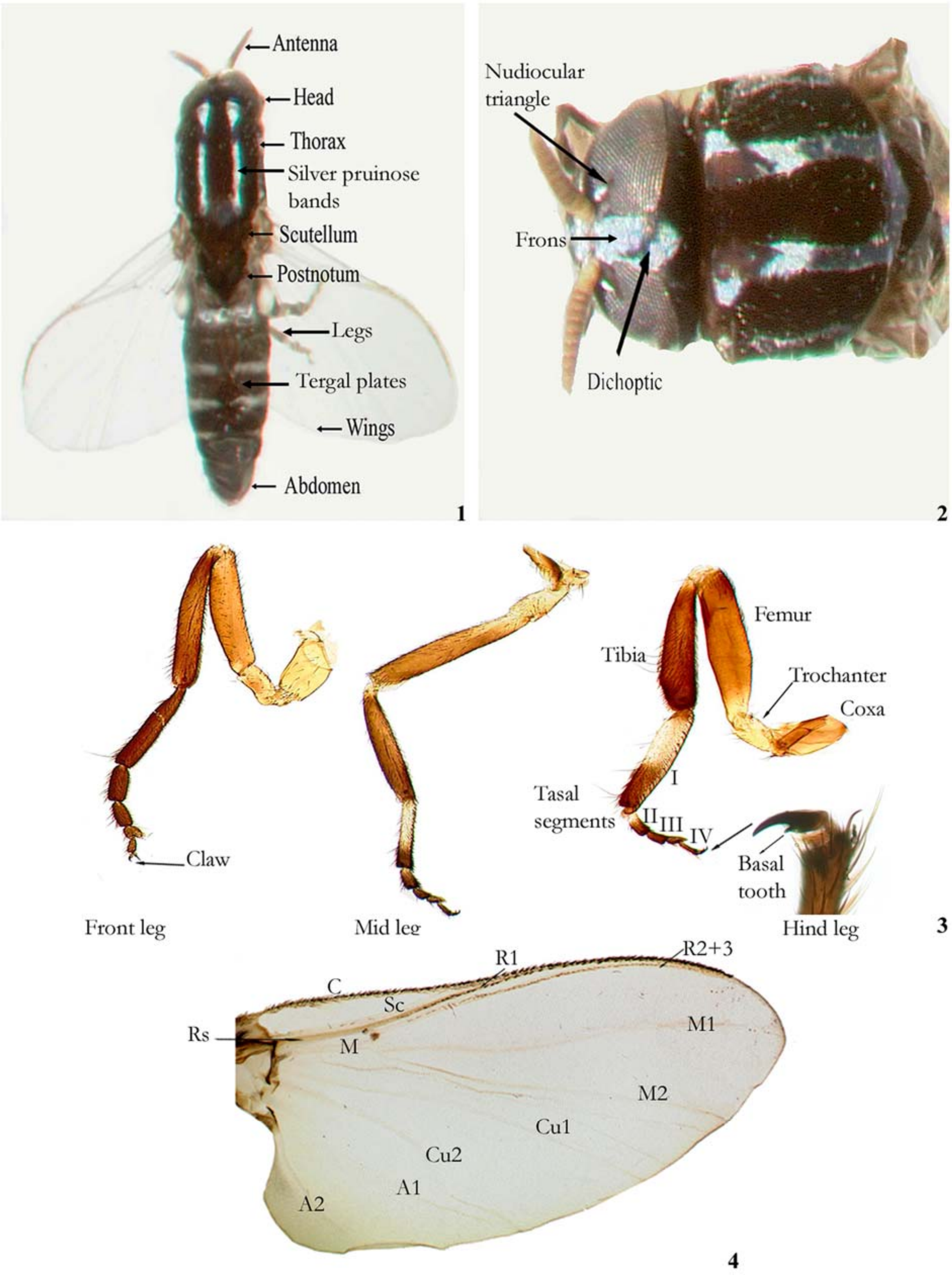

PLATE 1. Figs. 1-4. External morphology of adult female. 1- Female of *Simulium* (*S. quadrivittatum*); 2- Head of *Simulium* (*S. quadrivittatum*). 3- Leg coloration pattern (*S. nigrimanum*), inset high magnification of the hind claw showing the basal tooth; 4- Wing (*S. nigrimanum*). C, Costa vein, Sc, Subcosta; R, Radius vein; Rs, Basal sector of Radius; M, Median vein; Cu, Cubital vein; A, Anal vein.

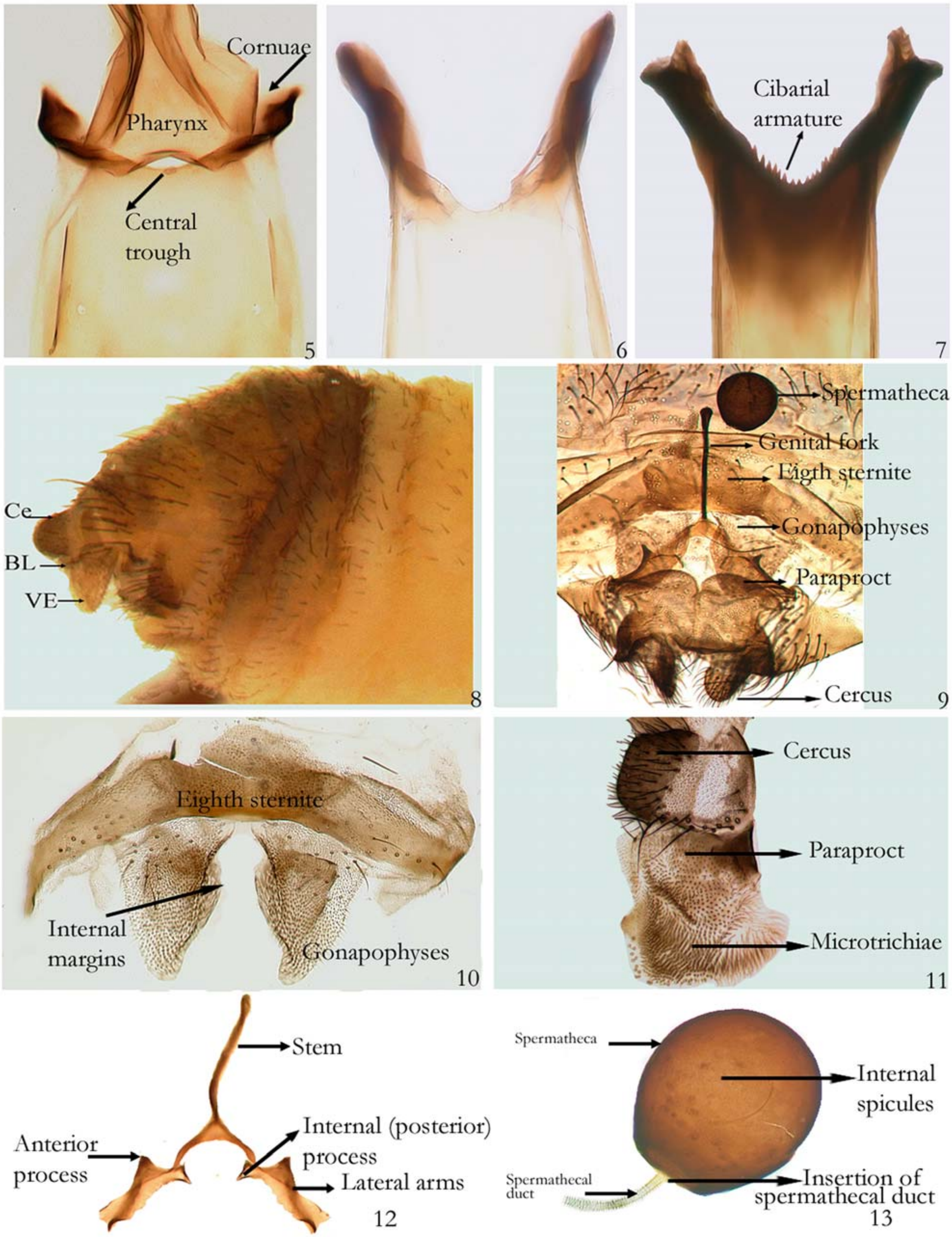

PLATE 2. Figs. 5-13. Internal morphology of female. 5- Structure of the cibarium; 6- Cibarium without teeth (*S. tarsatum*); 7- Cibarium with teeth (*S. nigrimanum*); 8- Lateral view of paraproct of *Simulium* sp.: Ce- Cercus, BL- Basal lobe of paraproct, VE- ventral extension of paraproct.; 9- Genitalia *in situ* (*S. smarti*); 10- Eighth sternite and gonapophyses (*S. rubrithorax*); 11- Cercus and paraproct (*S. virgatum s.l.*); 12- Genital fork (*S. rubrithorax*); 13- Spermatheca and spermathecal duct (*S. itaunense*).

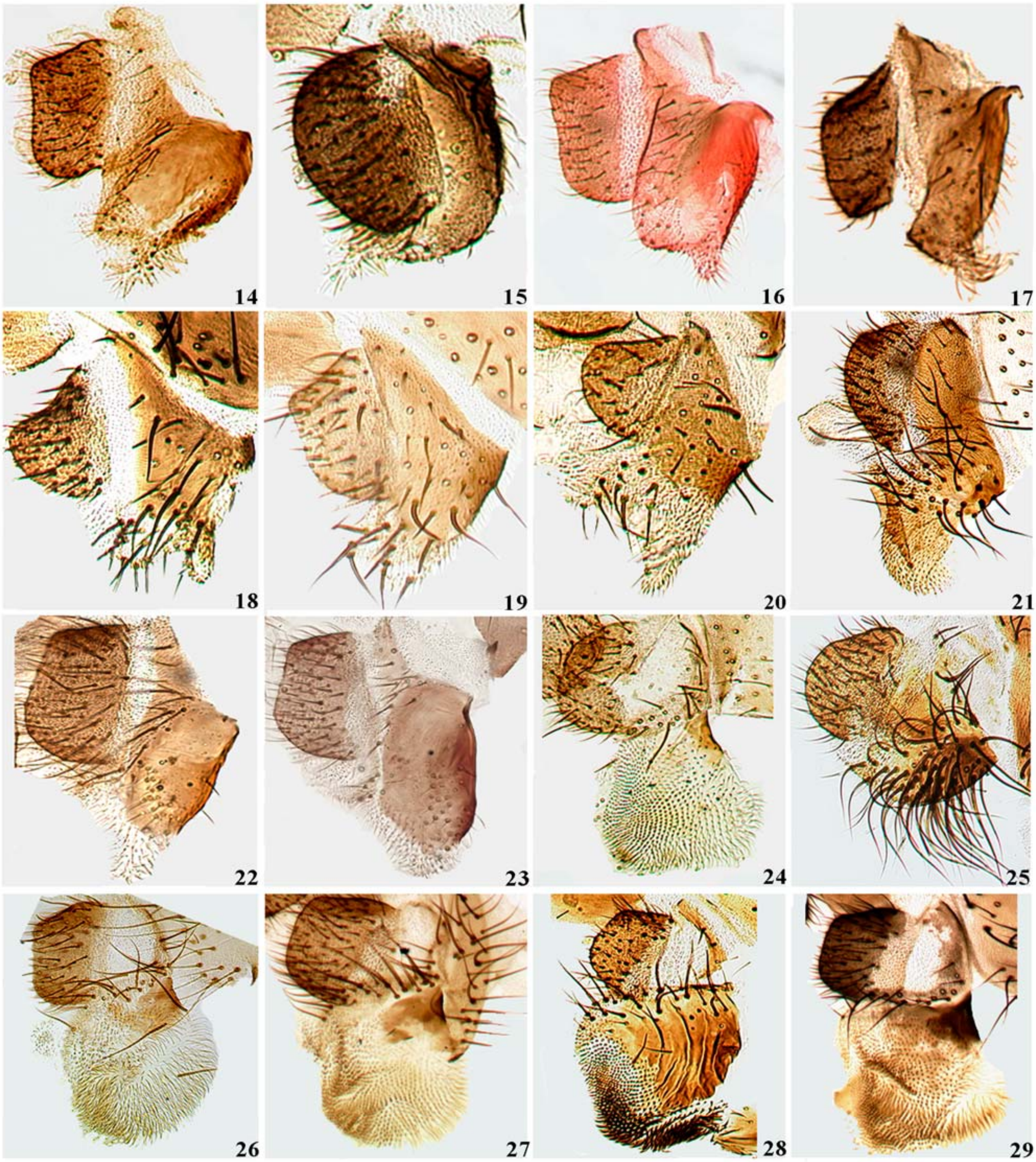

PLATE 3. Figs. 14-29. Female cercus and paraproct morphological variation. 14-17. CANADENSE species group: 14- *S. ayrozai*; 15- *S. canadense*; 16- *S. dalmati*; 17- *S. capricorne*. 18-21. ORBITALE species group: 18- *S. duodenicornium*; 19- *S. guianense s.l.*; 20- *S. orbitale* (neotype); 21- *S. townsendi* (as *S. chalcocoma*). 22-23. PICTIPES species group: 22- *S. claricentrum*; 23- *S. pictipes*. 24-29. TARSATUM species group: 24- *S. bricenoi* (as *S. wirthi*, paratype); 25- *S. lobatoi* (paratype); 26- *S. paynei*; 27- *S. rubrithorax*; 28- *S. tarsatum* (as *S. seriatum*, holotype); 29- *S. virgatum s.l.*

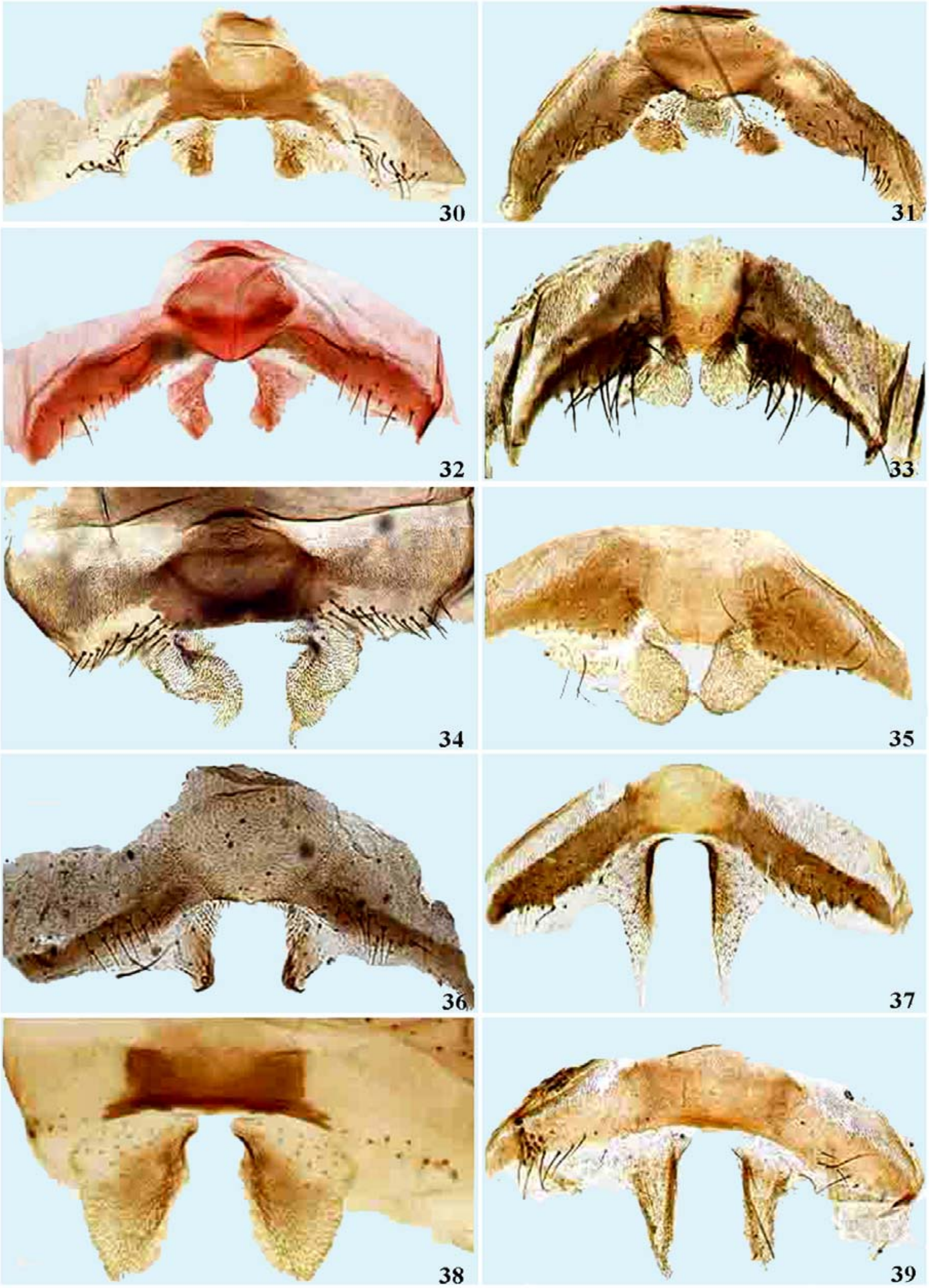

PLATE 4. Figs. 30-39. Female gonapophyses morphological variation. 30-32. CANADENSE species group: 30- *S. ayrozai*; 31- *S. canadense*; 32- *S. dalmati*. 33-35. ORBITALE species group: 33- *S. duodenicornium*; 34- *S. townsendi* (as *S. chalcocoma*); 35- *S. orbitale* (neotype). 36. PICTIPES species group: 36- *S. claricentrum*. 37-39. TARSATUM species group: 37- *S. brachycladum*; 38- *S. paynei*; 39- *S. rubrithorax*.

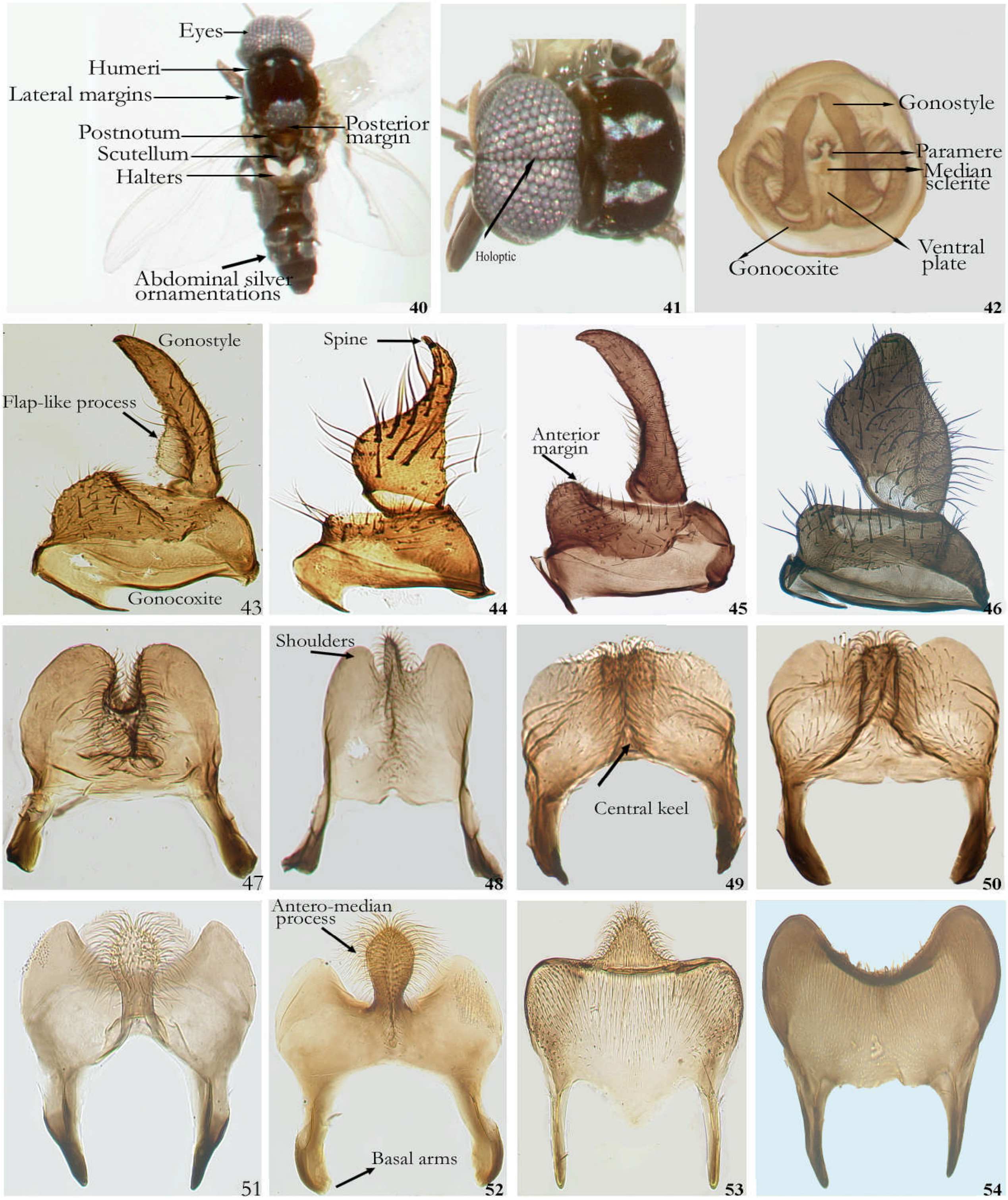

PLATE 5. Figs. 40-54. External and internal morphology of adult male. 40- Male of *Simulium* (*S. quadrivittatum*); 41- Head of *Simulium* (*S. quadrivittatum*); 42- Male genitalia *in situ* (*S. canadense*); 43-46. Male gonocoxite and gonostyle variation: 43- CANADENSE species group: *S. canadense*; 44- ORBITALE species group: *S. orbitale*; 45- PICTIPES species group: *S. pictipes*; 46- TARSATUM species group: *S. tarsatum*. 47-54. Ventral plate variation. 47-50. CANADENSE species group: 47- *S. canadense*; 48- *S. ayrozai*; 49- *S. ethelae*; 50- *S. microbranchium*. 51-54. ORBITALE species group: 51- *S. orbitale*; 52- *S. itaunense*; 53- *S. lahillei*; 54- *S. perplexum*.

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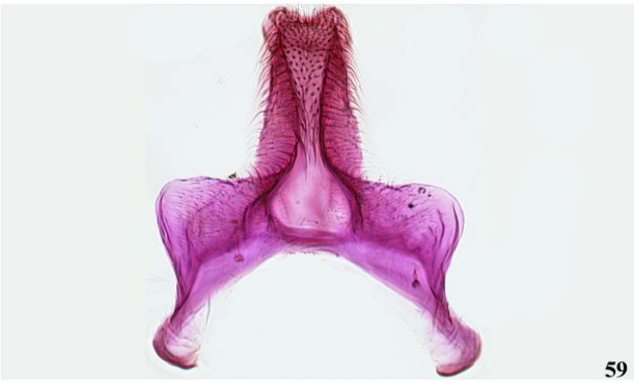

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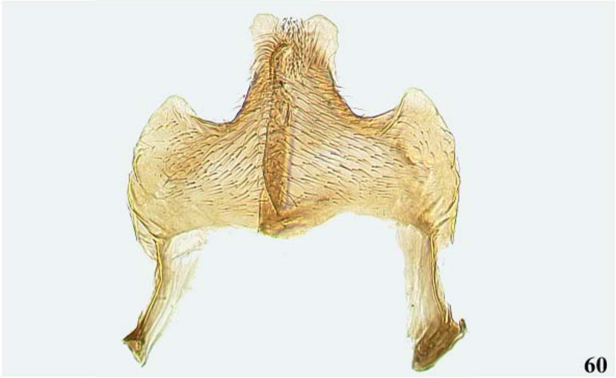

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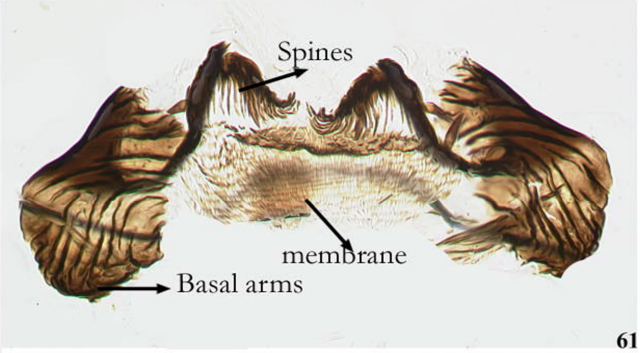

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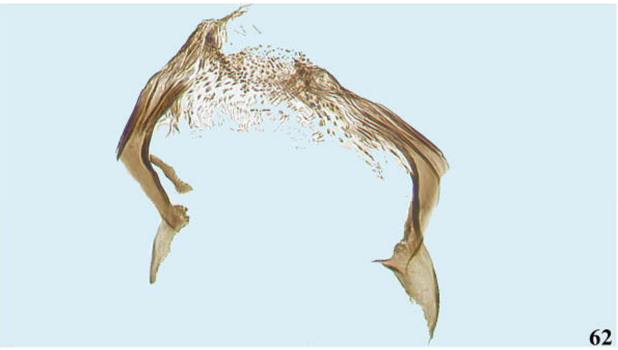

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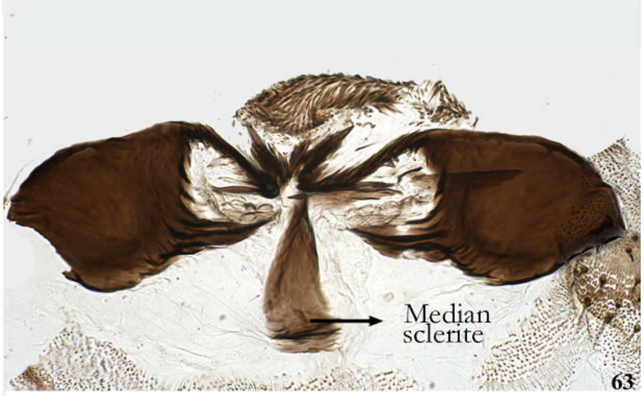

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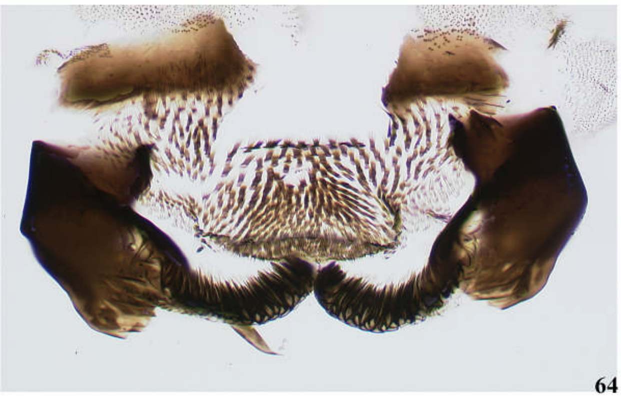

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PLATE 6. Figs. 55-64. Internal morphology of adult male. 55-58. Male ventral plate variation. 55- PICTIPES species group: *S. pictipes*; 56-60. TARSATUM species group: 56- *S. tarsatum*; 57- *S. freemani* (paratype); 58- *S. solarii* (holotype); 59- *S. paynei* (as *Hemicnetha mexicana*); 60- *S. lobatoi* (paratype). 61-64. Male paramere variation: 61- CANADENSE species group: *S. canadense*; 62- ORBITALE species group: *S. orbitale*; 63- PICTIPES species group: *S. pictipes*; 64- TARSATUM species group: *S. virgatum s.l.*

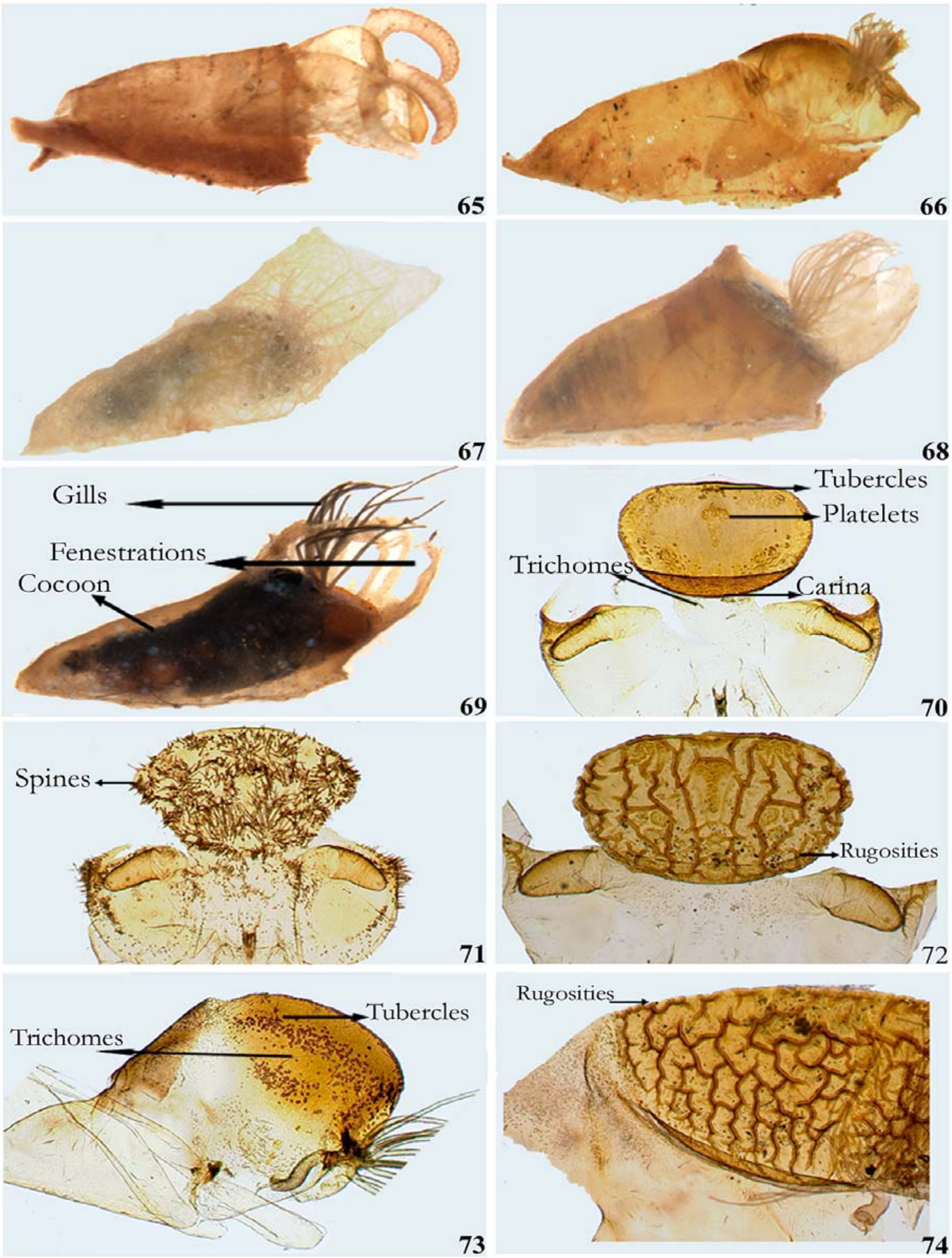


PLATE 7. Figs. 65-74. Morphology of the pupa. 65-69. Variation in cocoon shape: 65- Slipper-shaped (*S. ethelae*, as *S. chiriquiense*); 66- Shoe-shaped (*S. nigrimanum*); 67- Boot-shaped (*S. pictipes*); 68- Shoe-shaped without fenestrations and raised anterior margin (*S. tarsatum*); 69- Shoe-shaped with fenestrations (*S. paynei*). 70-72. Variation of the integument and sculpturing of the frontoclypeus: 70- *S. tarsatum*; 71- *S. hirtipupa*; 72- *S. hieroglyphicum*. 73-74. Variation of the integument and sculpturing of the thorax: 73- *S. tarsatum*; 74- *S. hieroglyphicum*.

PLATE 8. Figs. 75-84. Variation in number and configuration pattern of gill filaments: 75- *S. canadense*; 76- *S. contrerense* (holotype); 77- *S. larvispinosum*; 78- *S. menchacai*; 79- *S. guianense s.l.*; 80- *S. duodenicornium*; 81- *S. nigrimanum*; 82- *S. pictipes*; 83- *S. tarsatum*; 84- *S. hieroglyphicum* (topotype).

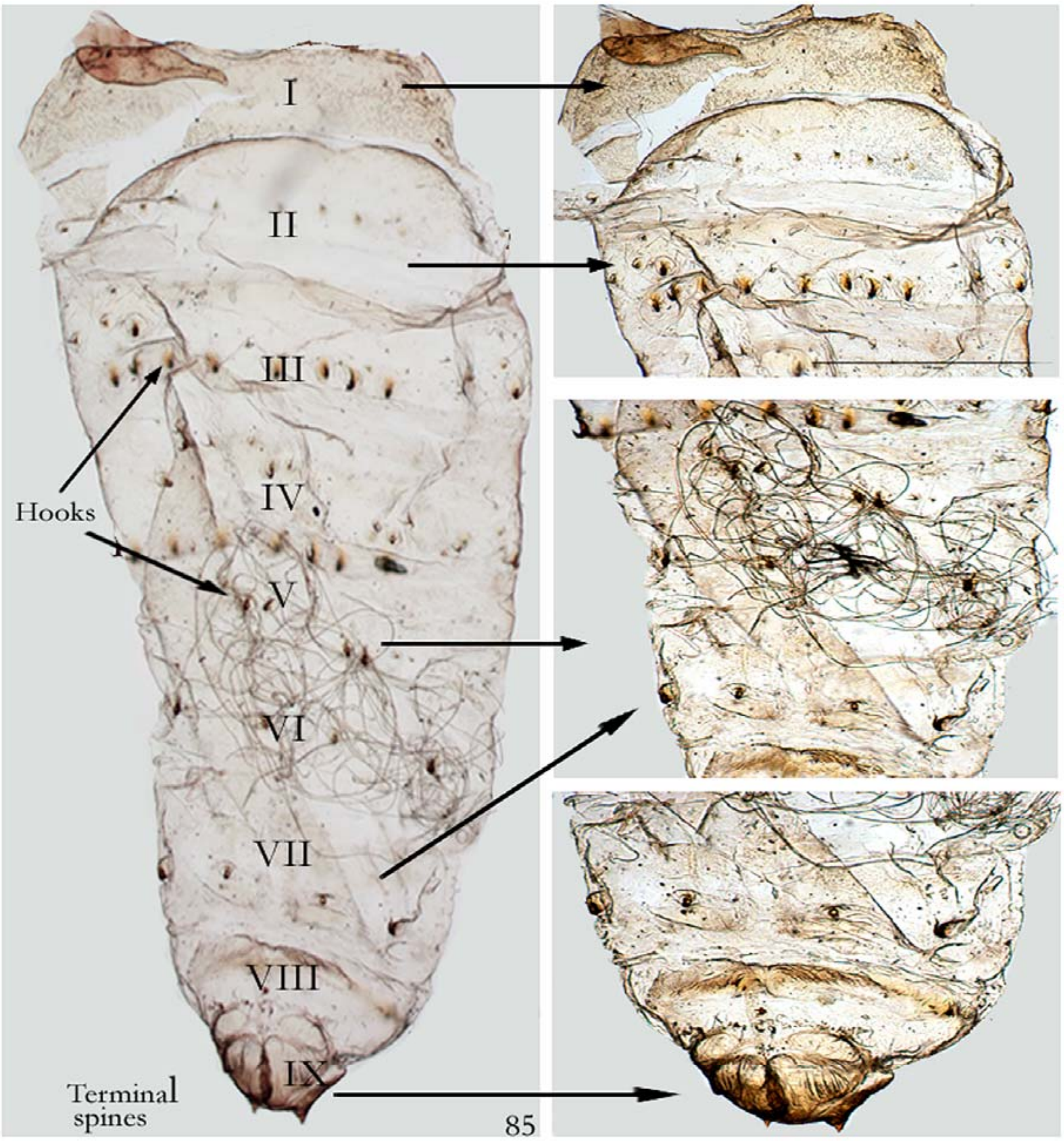
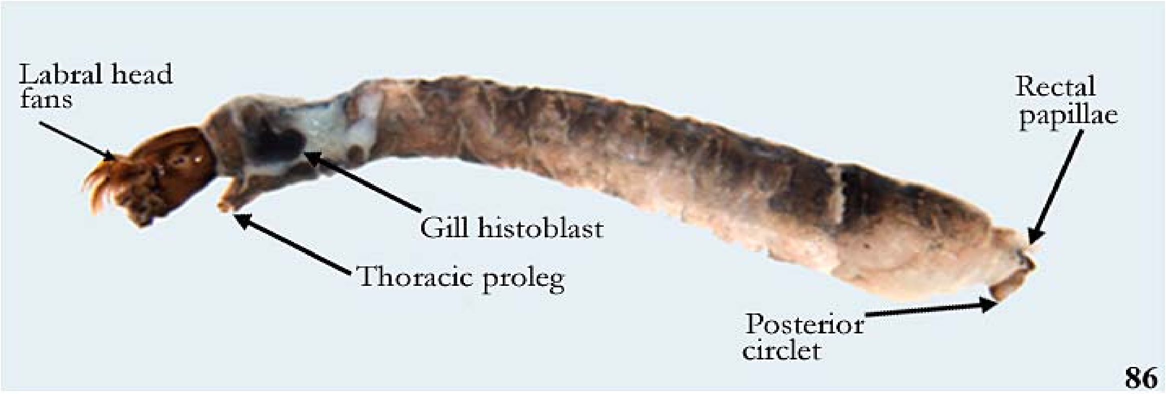


PLATE 9. Fig. 85. Pupal abdominal onchotaxy (*S. canadense*); inset higher magnification of selected abdominal segments showing hooks and trichomes.



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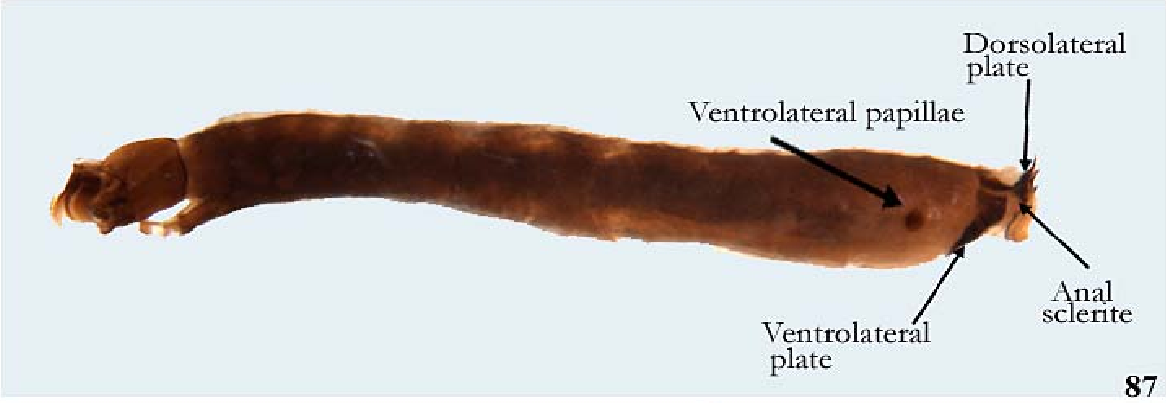

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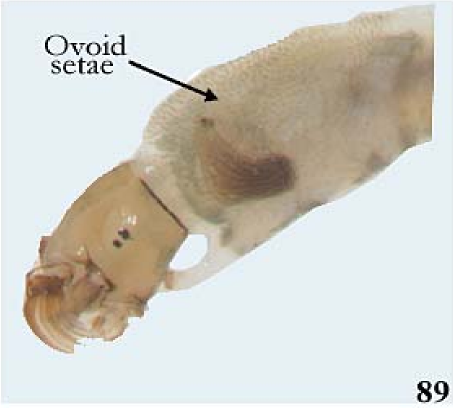

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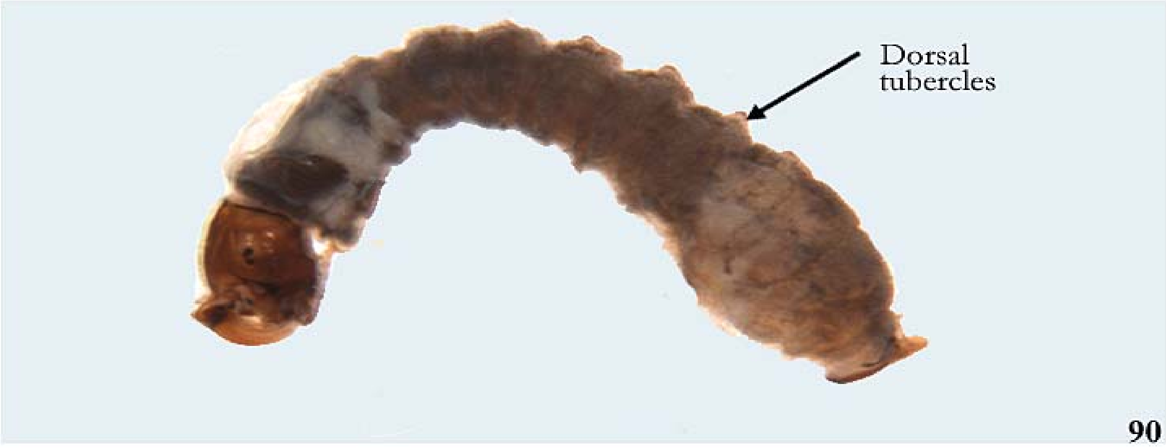

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PLATE 10. Figs. 86-90. Morphology of the larva in lateral view. 86- *S. paynei*; 87- *S. gorirossiae* showing the accessory secondary sclerotised and the ventral papillae on segment VIII; 88- *S. orbitale*; 89- Head and thorax of *S. orbitale* showing the ovoid setae on the integument; 90- *S. lithobranchium* showing the dorsolateral tubercles.

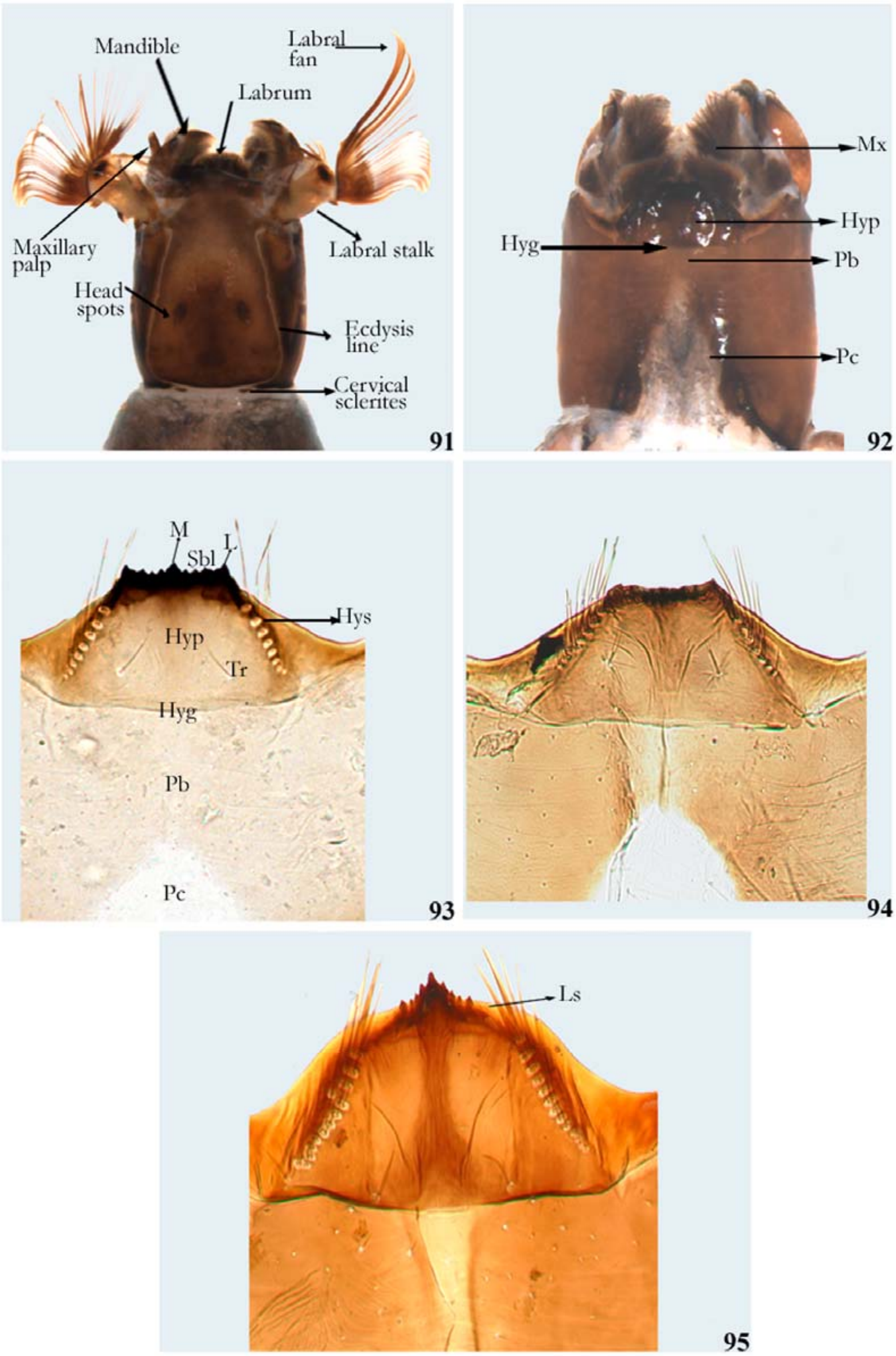

PLATE 11. Figs. 91-95. Morphology of the larva. 91- Head in dorsal view (*S. paynei*); 92- Head in ventral view (*S. paynei*): Mx, maxilla; Hyp, hypostomium; Pb, postgenal bridge; Pc, postgenal cleft; Hyg, hypostomal groove; 93- Hypostomium of *Simulium* (*Trichodagmia*) sp. (teeth evenly distributed along anterior margin): M, M, median tooth; Sbl, sublateral teeth; L, lateral teeth; Hyp, hypostomium; Tr, trichomes; Hyg, hypostomial groove; Pb, postgenal bridge; Pc, postgenal cleft; 94- Hypostomium of *S. nigrimanum* (teeth reduced); 95- Hypostomium of *S. lobatoi* (teeth centrally arranged and protruded forward), Ls, lateral serrations.

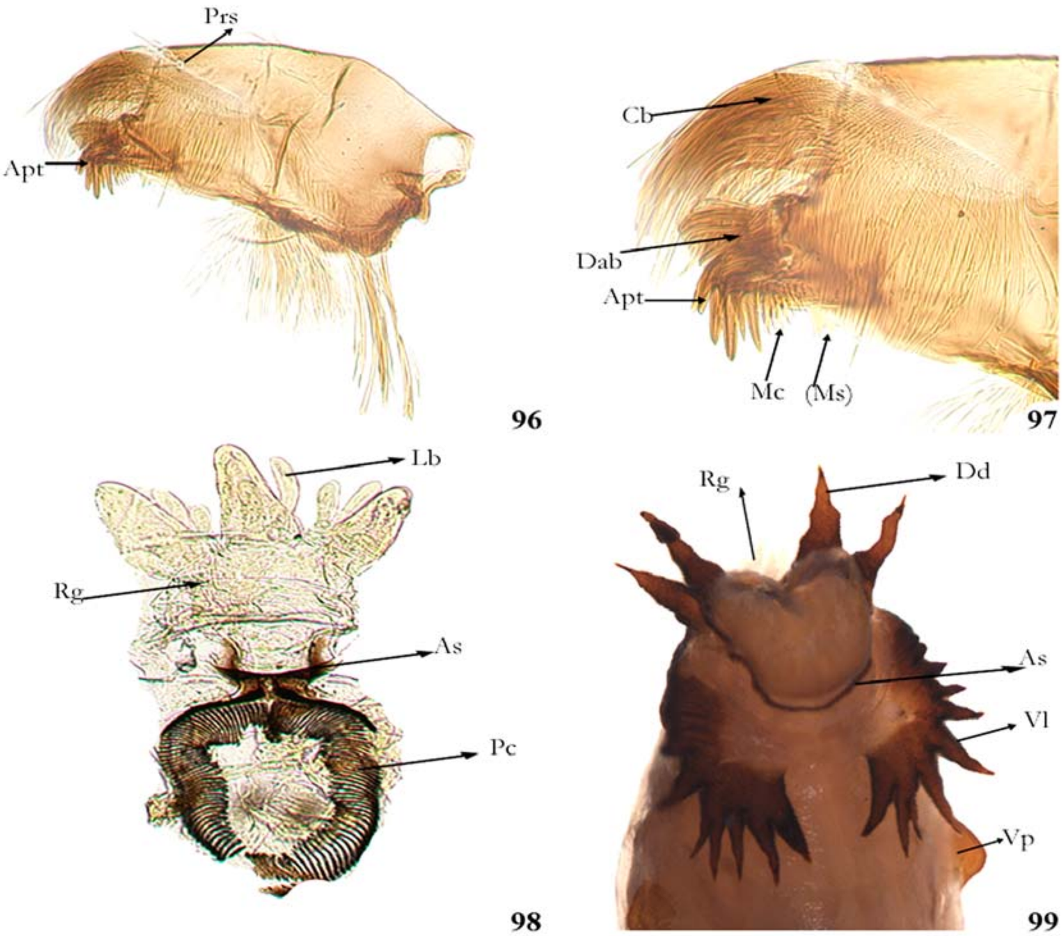

PLATE 12. Figs. 96-99. Morphology of the larva. 96-97: Mandible: 96- *S. bricenoi*, Apt, apical teeth; Prs, preapical sensilla; 97- Mandible at higher magnification (*S. bricenoi*): Cb, covering brush; Dab, distal adoral brush; At, apical teeth; Mc, mandibular comb; (Ms), mandibular serrations. 98-99. Distal region of the abdomen: 98- *S. canadense*: Rg, rectal gill; Lb, lobules; As, anal sclerite; Pc, posterior circlet; 99- *S. gorirossiae*: Rg, rectal gill; Dd, dorsolateral accessory sclerotised plates; Vl, ventrolateral accessory sclerotised plates; Vp, ventral papillae.

PLATE 13. Figs. 100-115. Female scutum and abdominal coloration, ALBELLUM species group. The first figure for each species shows anterior light direction and the second posterior light direction. 100-101- *S. albellum*; 102, 103- *S. auricoma*; 104, 105- *S. galloprovinciale*; 106, 107- *S. margaritae*; 108, 109- *S. popowae*; 110, 111- *S. transcaspicum*. 112-115. Coloration of the abdomen: 112- *S. albellum*, dorsal view; 113- *S. auricoma*, dorsal view; 114- *S. galloprovinciale*, dorsal view; 115- *S. popowae*, dorsolateral view.

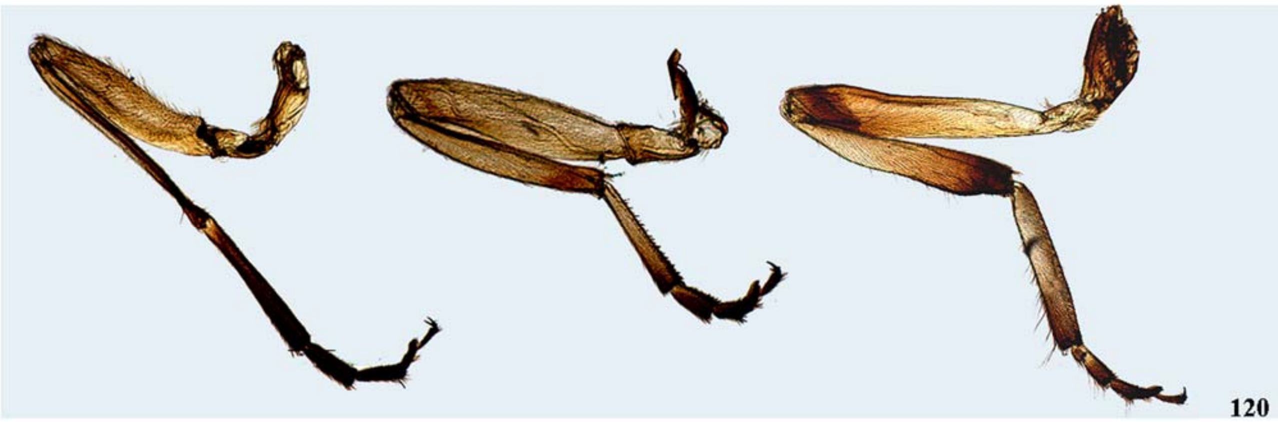

PLATE 14. Figs. 116-120. Female nudiocular triangle and leg coloration, ALBELLUM species group. 116, 117. Nudiocular triangle: 116- *S. galloprovinciale*; 117- *S. margaritae*. 118-120. Coloration of the legs: 118- *S. auricoma*; 119- *S. galloprovinciale*; 120- *S. margaritae*.

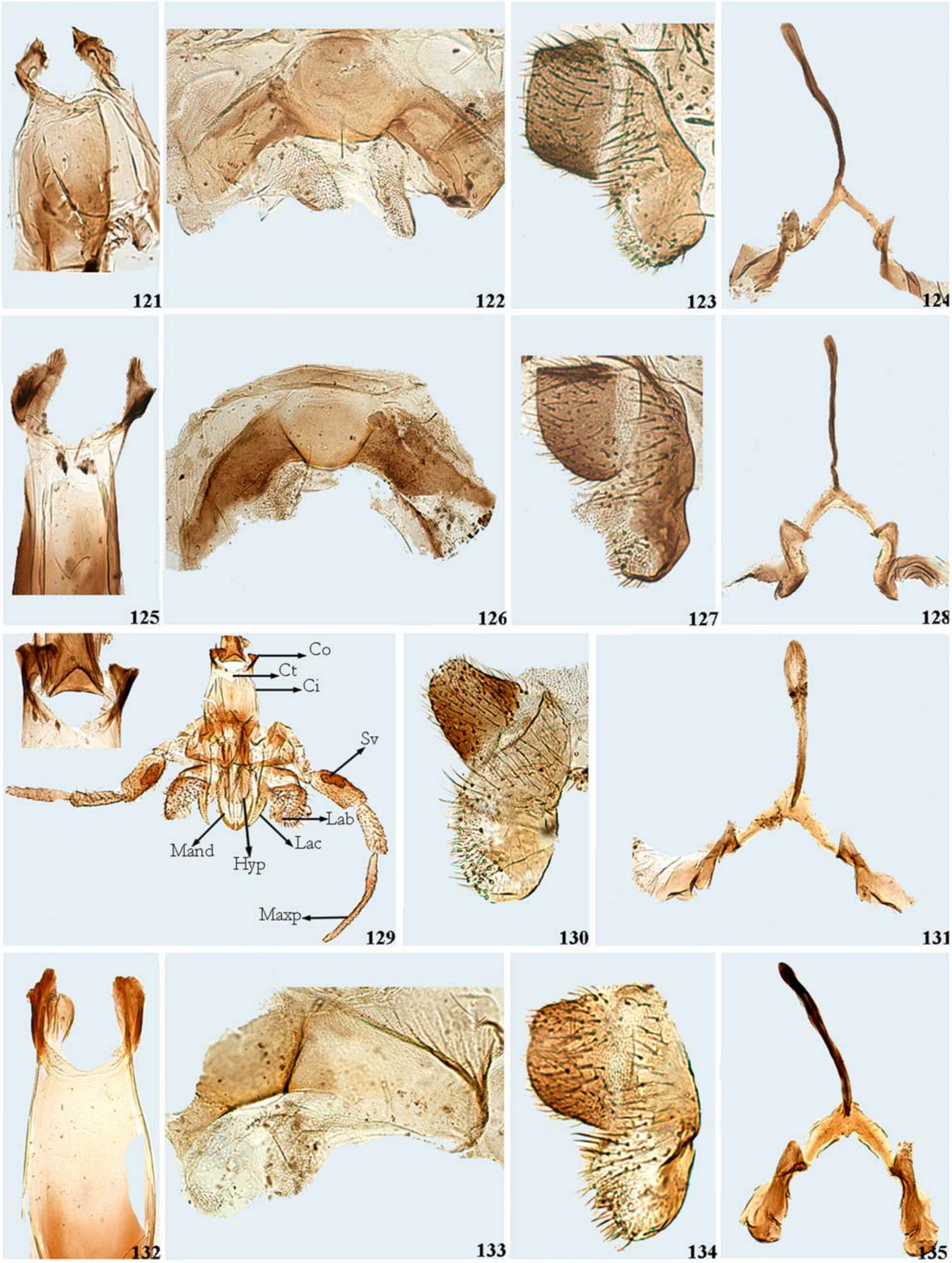

PLATE 15. Figs. 121-135. Internal morphology of female, ALBELLUM species group, from left to right: cibarium, gonapophyses, cercus and paraproct, genital fork. 121-124: *S. auricoma*; 125-128: *S. galloprovinciale*; 129-131: *S. margaritae*; inset in Fig. 129 shows the cibarium at higher magnification; 132-135: *S. transcaspicum*;. Co, cornuae; Ct, central trough; Ci, cibarium; Sv, sensory vesicle (Lutz' organ); Lab, labellum; Lac, lacinia; Maxp, maxillary palps; Mand, mandible; Hyp, hypopharynx.

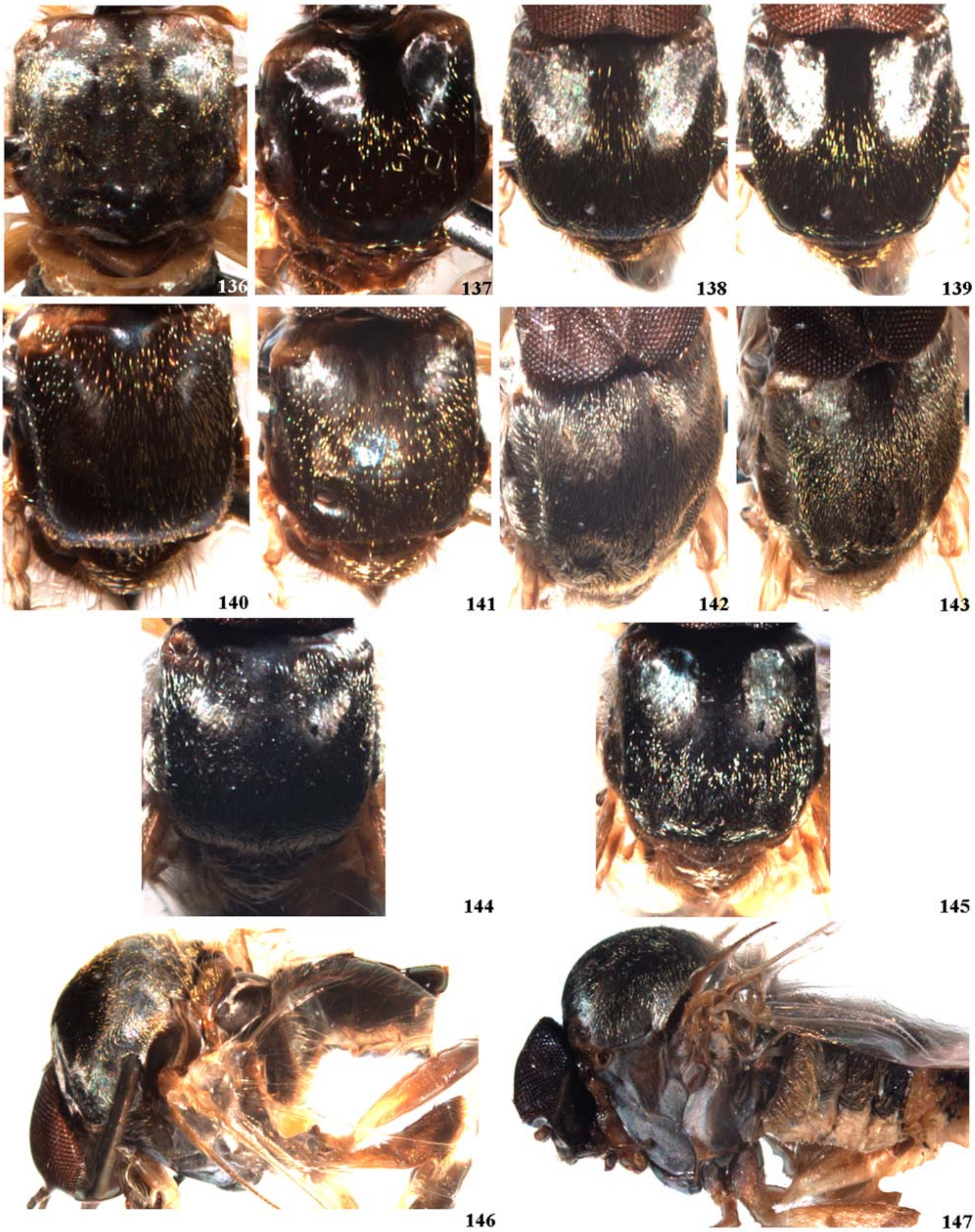

PLATE 16. Figs. 136-147. Male scutum and abdominal coloration, ALBELLUM species group. The first figure for each species shows anterior light direction and the second posterior light direction. 136, 137- *S. auricoma*; 138, 139- *S. galloprovinciale*; 140, 141- *S. ibericum*, holotype; 142, 143- *S. margaritae*; 144-, 145- *S. transcaspicum*. 146-147. Coloration of the abdomen, dorsolateral view: 146- *S. galloprovinciale*; 147- *S. transcaspicum*.

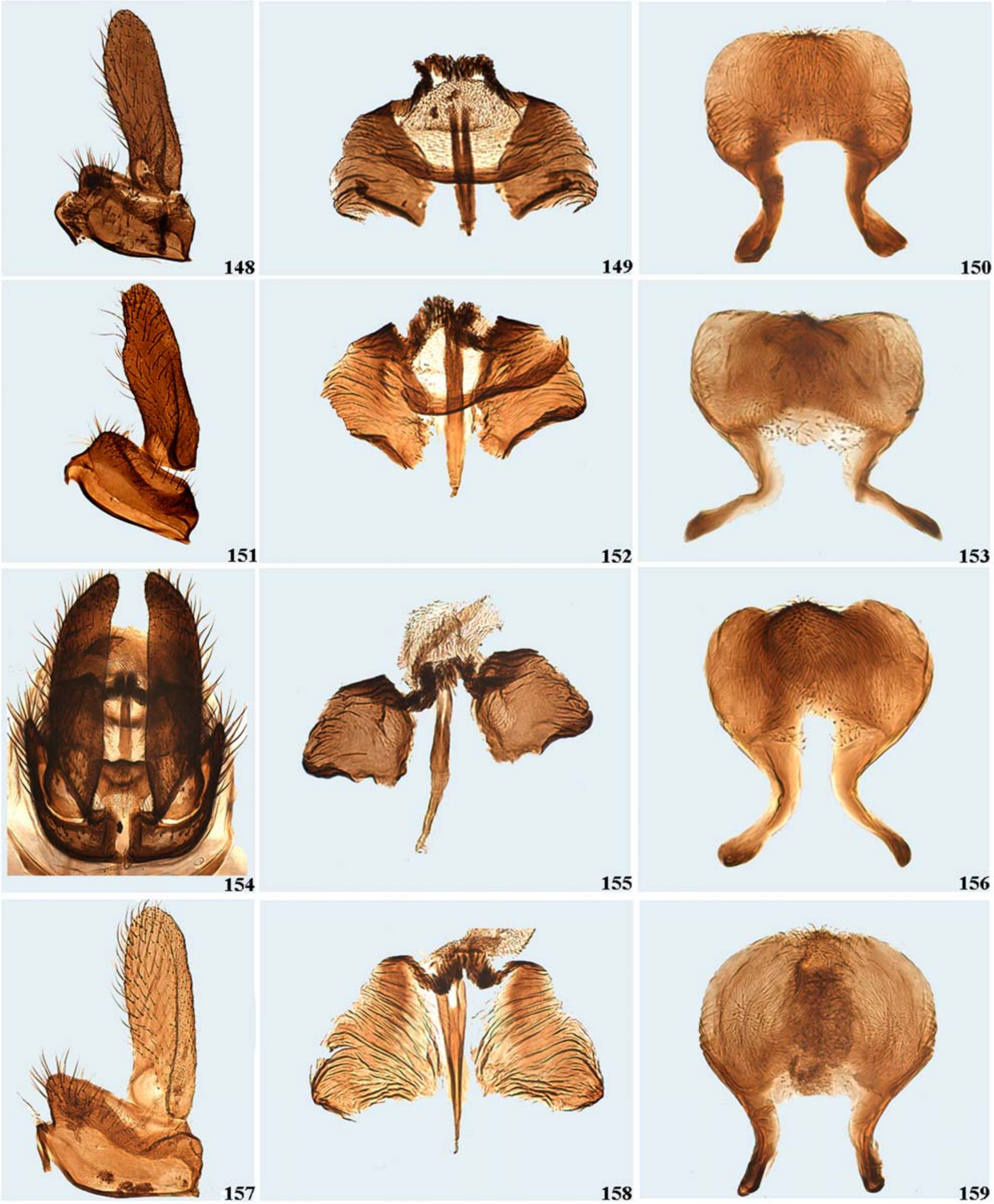

PLATE 17. Figs. 148-159. Internal morphology of male, ALBELLUM species group, from left to right: gonocoxite and gonostyle; parameres and median sclerite; ventral plate. 148-150: *S. auricoma*; 151-153: *S. galloprovinciale*; 154-156: *S. ibericum* (paratype), Figs. 154 shows the gonostyle and remainder of genitalia *in situ*; 157-159: *S. margaritae*.

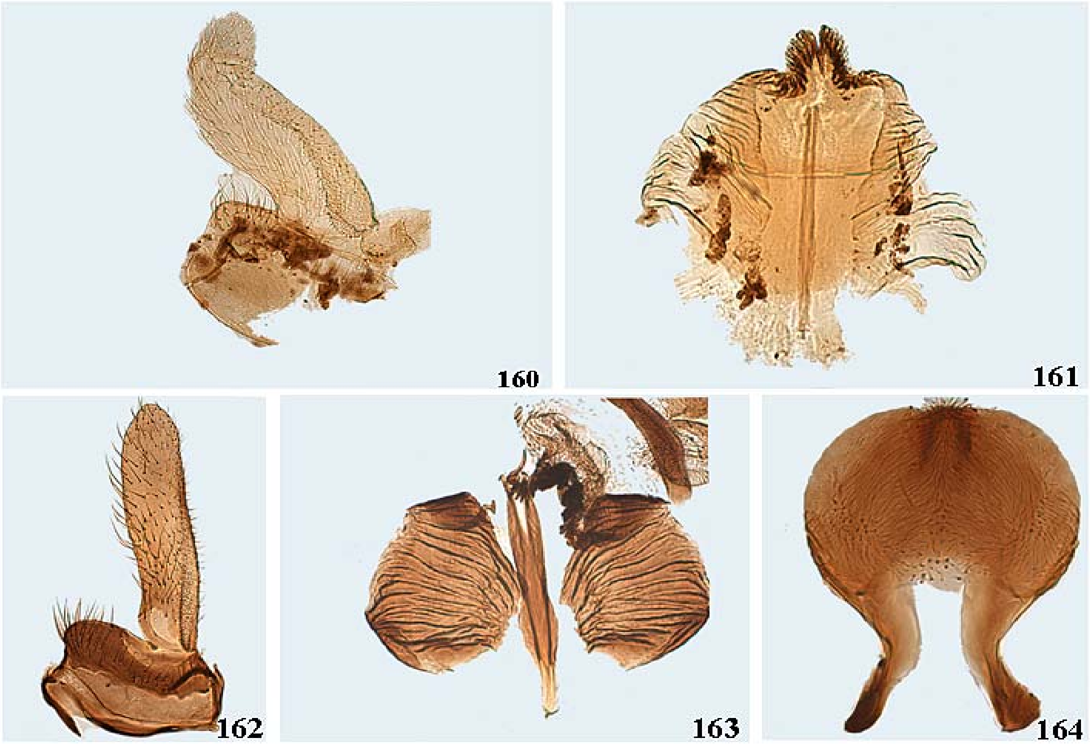

PLATE 18. Figs. 160-164. Internal morphology of male, ALBELLUM species group, from left to right: gonocoxite and gonostyle; parameres and median sclerite; ventral plate. 160-161 *S. marocanum*; 162-164: *S. transcaspicum*.

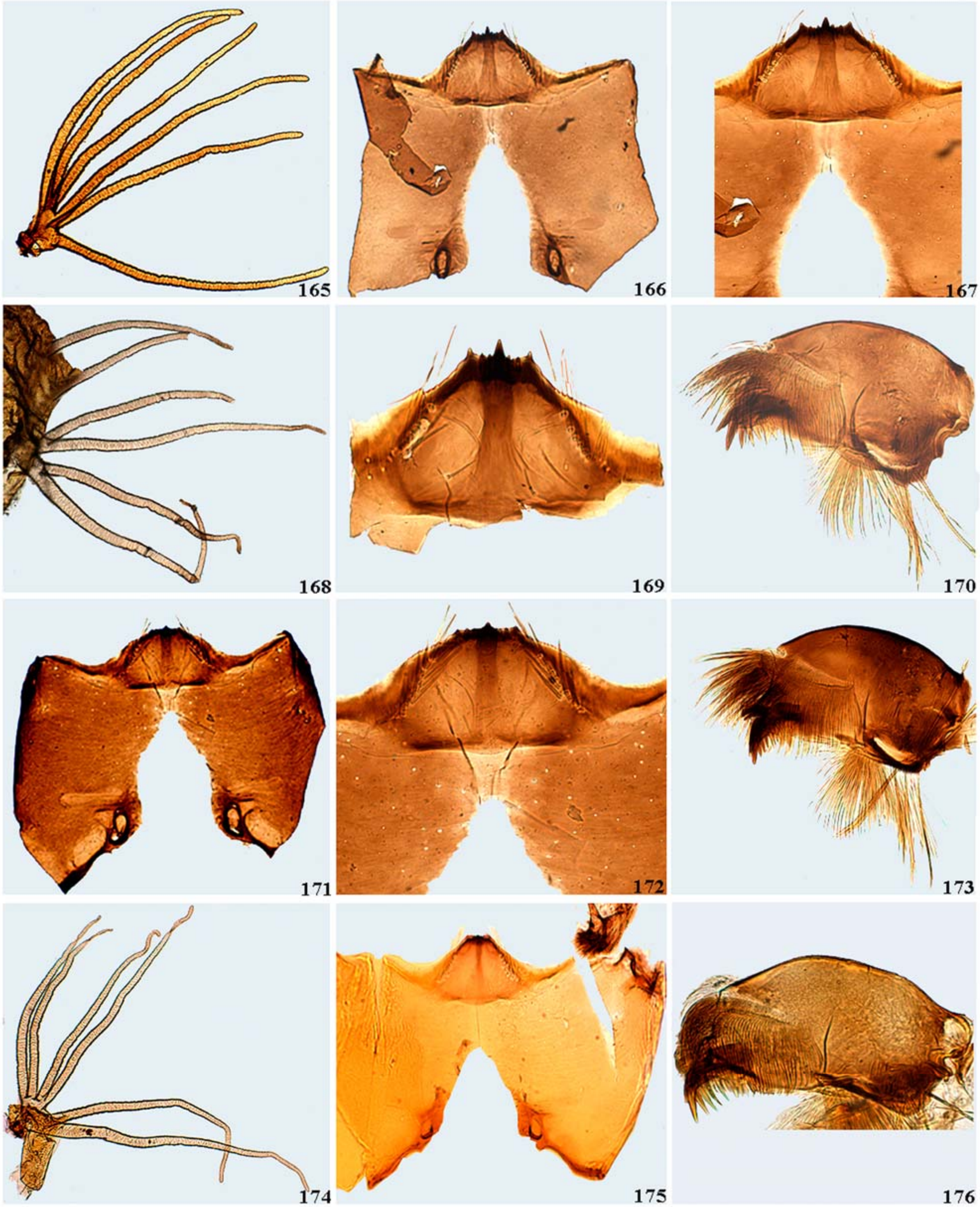

PLATE 19. Figs. 165-176. Pupal gill and larval morphology, ALBELLUM species group. 165, 168, 174. Pupal gill configuration: 165- *S. auricoma*; 168- *S. galloprovinciale*; 17- *S. marocanum*. 166-167, 169-170, 171-173, 175-176. Morphology of the hypostomium, hypostomial teeth and/or mandible. 166, 167: Hypostomium and hypostomial teeth of *S. auricoma*; 169, 170: Hypostomium and mandible of *S. galloprovinciale*; 171-173: Hypostomium, hypostomial teeth and mandible of *S. ibericum* (paratype); 175-176: Hypostomium and mandible of *S. popowae*.

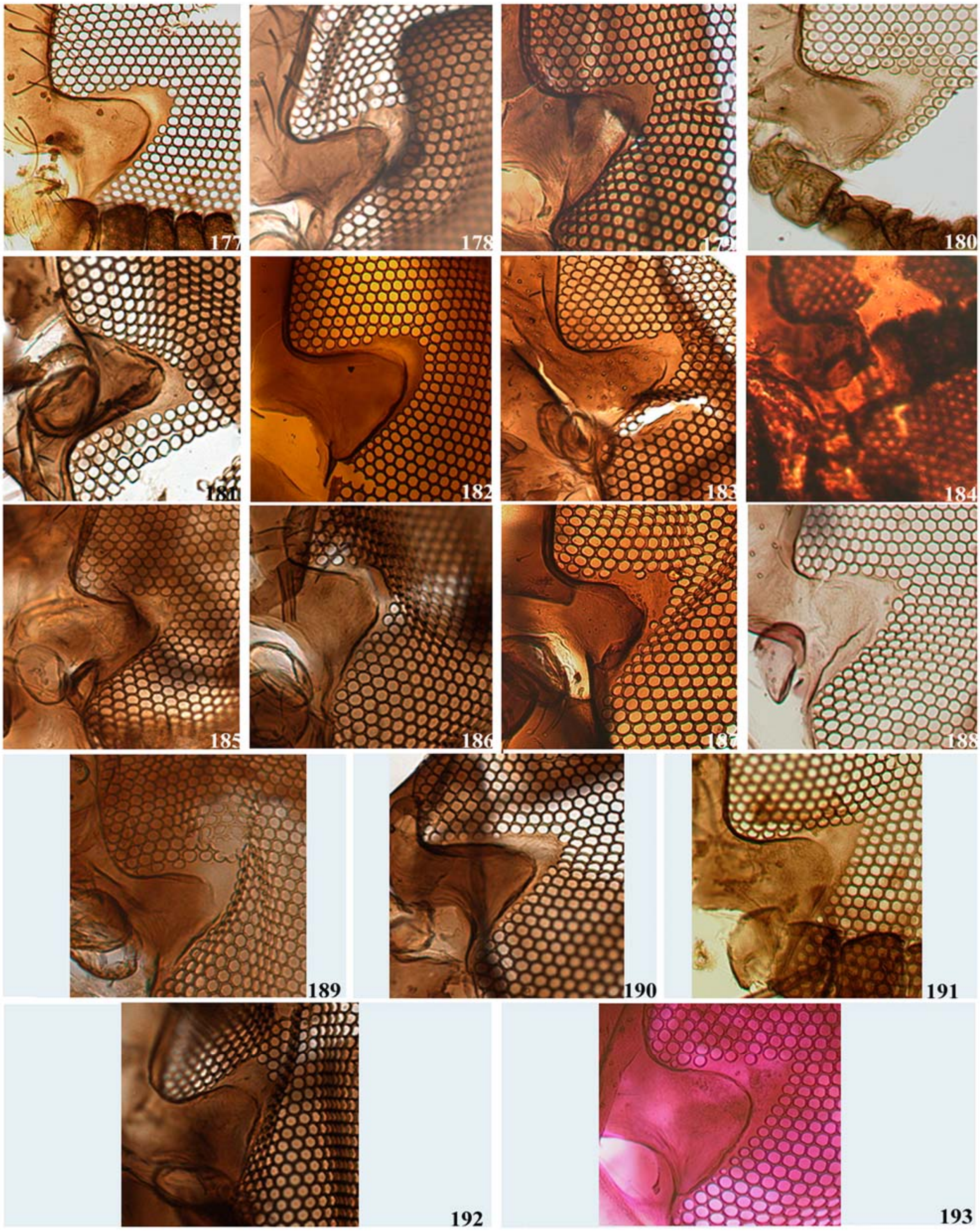

PLATE 20. Figs. 177-193. Nudiocular triangular, CANADENSE species group: 177- *S. ayrozai*; 178- *S. burchi*, paratype; 179, *S. canadense*; 180- *S. capricorne*; 181- *S. carolinae*; 182- *S. contrerense*, allotype; 183- *S. dalmati*, paratype; 184- *S. delatorrei*, holotype; 185- *S. estevezi*, paratype; 186- *S. ethelae*; 187- *S. falculatum*, holotype; 188- *S. gorirossiae*, paratype; 189- *S. johnsoni*, paratype; 190- *S. larvispinosum*; 191- *S. menchacai*; 192- *S. microbranchium*; 193- *S. temascalense*, holotype.

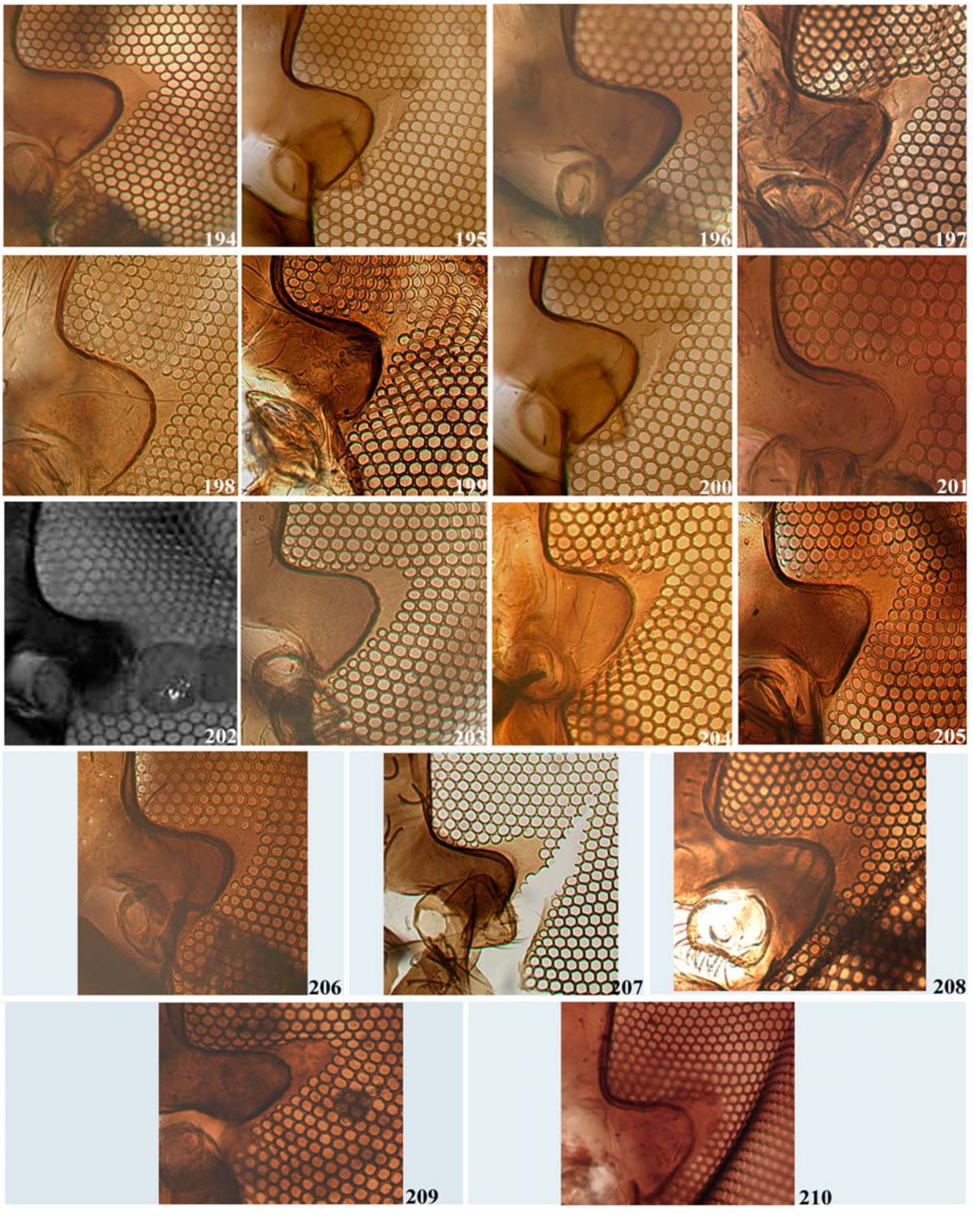

PLATE 21. Figs 194-210. Nudiocular area of female, ORBITALE and PICTIPES species groups. ORBITALE species groups: 194- *S. duodenicornium*; 195- *S. guianense s.l.*; 196- *S. hirtipupa*; 197- *S. huairayacu*, paratype; 198- *S. itaunense*; 199- *S. lahillei*; 200- *S. lithobranchium*, topotype; 201- *S. nigrimanum*; 202- *S. nunesdemelloi* (HAMADA *et al*., 2010); 203- *S. orbitale*; 204- *S. perplexum*, paratype; 205- *S. scutistriatum*; 206- *S. townsendi*, paratype; 207- *S. wygodzinskyorum*, holotype. PICTIPES species group: 208- *S. claricentrum*; 209- *S. innoxium*; 210- *S. pictipes*

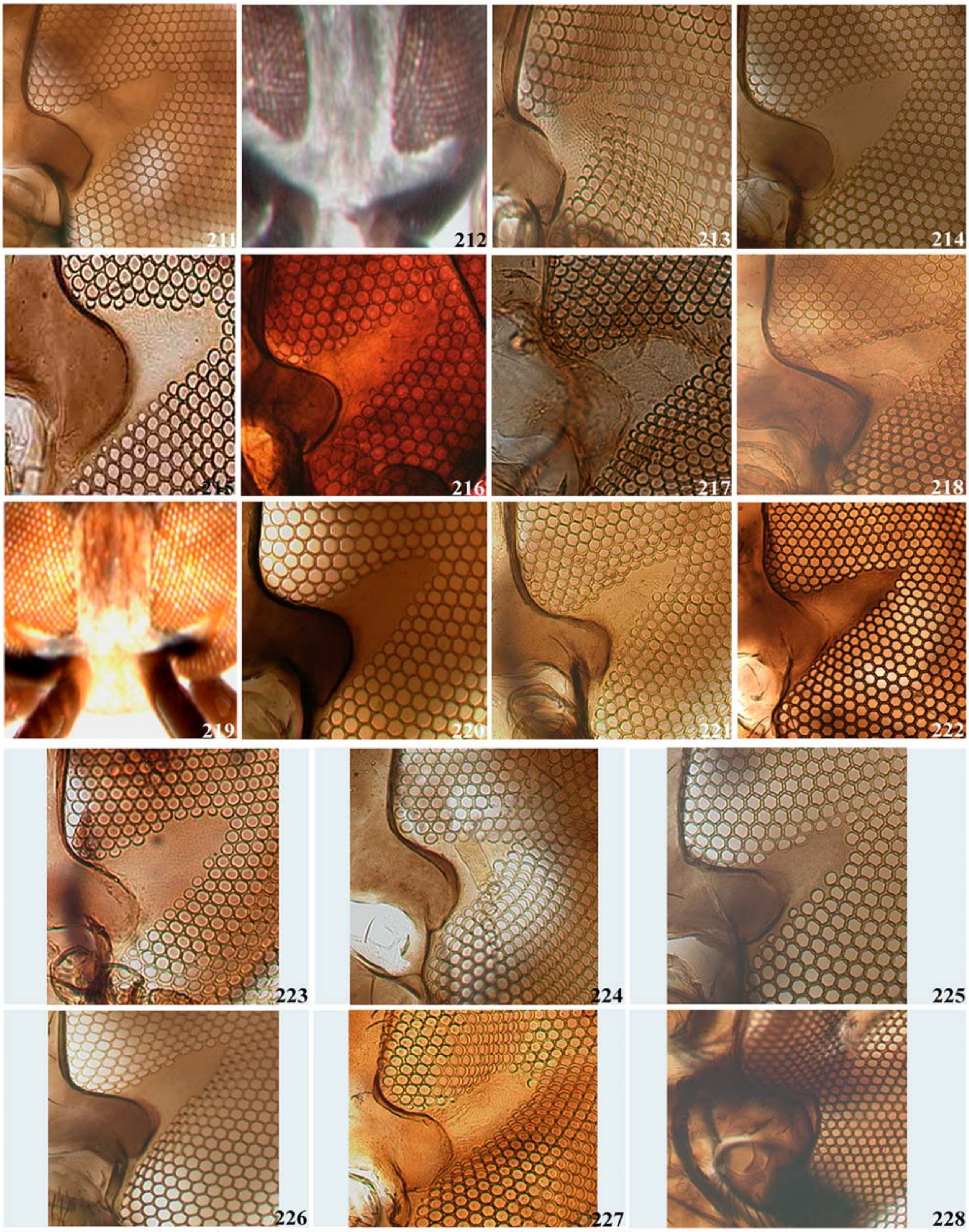

PLATE 22. Figs. 211-228. Nudiocular area of female, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species groups. TARSATUM species group: 211- *S. brachycladum*; 212- *S. bricenoi* (as *S. wirthi* paratype); 213- *S. cristalinum*; 214- *S. earlei*; 215- *S. freemani*; 216- *S. guerrerense*, paratype; 217- *S. hinmani*, paratype; 218- *S. hippovorum*; 219- *S. paynei*; 220- *S. pulverulentum*; 221- *S. rubrithorax*; 222- *S. smarti*, paratype; 223- *S. solarii*; 224- *S. tarsale* (as *S. clavipes*, paratype); 225- *S. tarsatum* (as *S. mexicanum*); 226- *S. virgatum s.l.*; 227- *S. yepocapense*, paratype. Subgenus *Psilopelmia*, BICOLORATUM species group: 228- *S. oviedoi*.

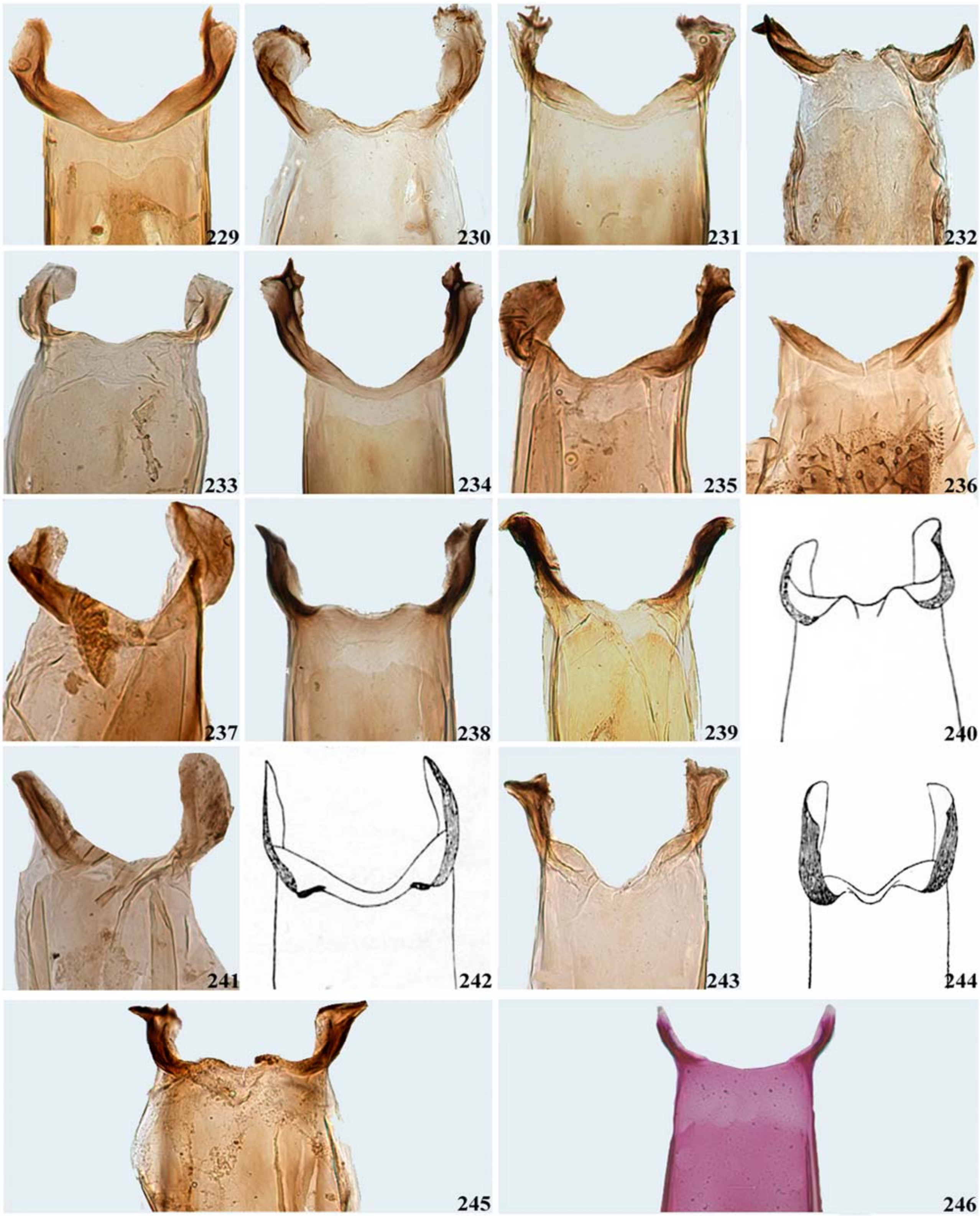

PLATE 23. Figs 229-246. Cibarium of female, CANADENSE species group: 229- *S. ayrozai*; 230- *S. burchi*, paratype; 231- *S. canadense*; 232- *S. capricorne*; 233- *S. carolinae*; 234- *S. contrerense*, allotype; 235- *S. dalmati*; 236- *S. delatorrei*, paratype; 237- *S. estevezi*, paratype; 238- *S. ethelae* (as *S. chiriquiense*); 239- *S. falculatum*, holotype; 240- *S. gorirossiae* (after VARGAS & DÍAZ NÁJERA, 1957b); 241- *S. johnsoni*, paratype; 242- *S. juarezi* (after VARGAS & DÍAZ NÁJERA, 1957b); 243- *S. larvispinosum*; 244- *S. menchacai* (after VARGAS & DÍAZ NÁJERA, 1957b); 245- *S. microbranchium*; 246- *S. temascalense*, holotype.

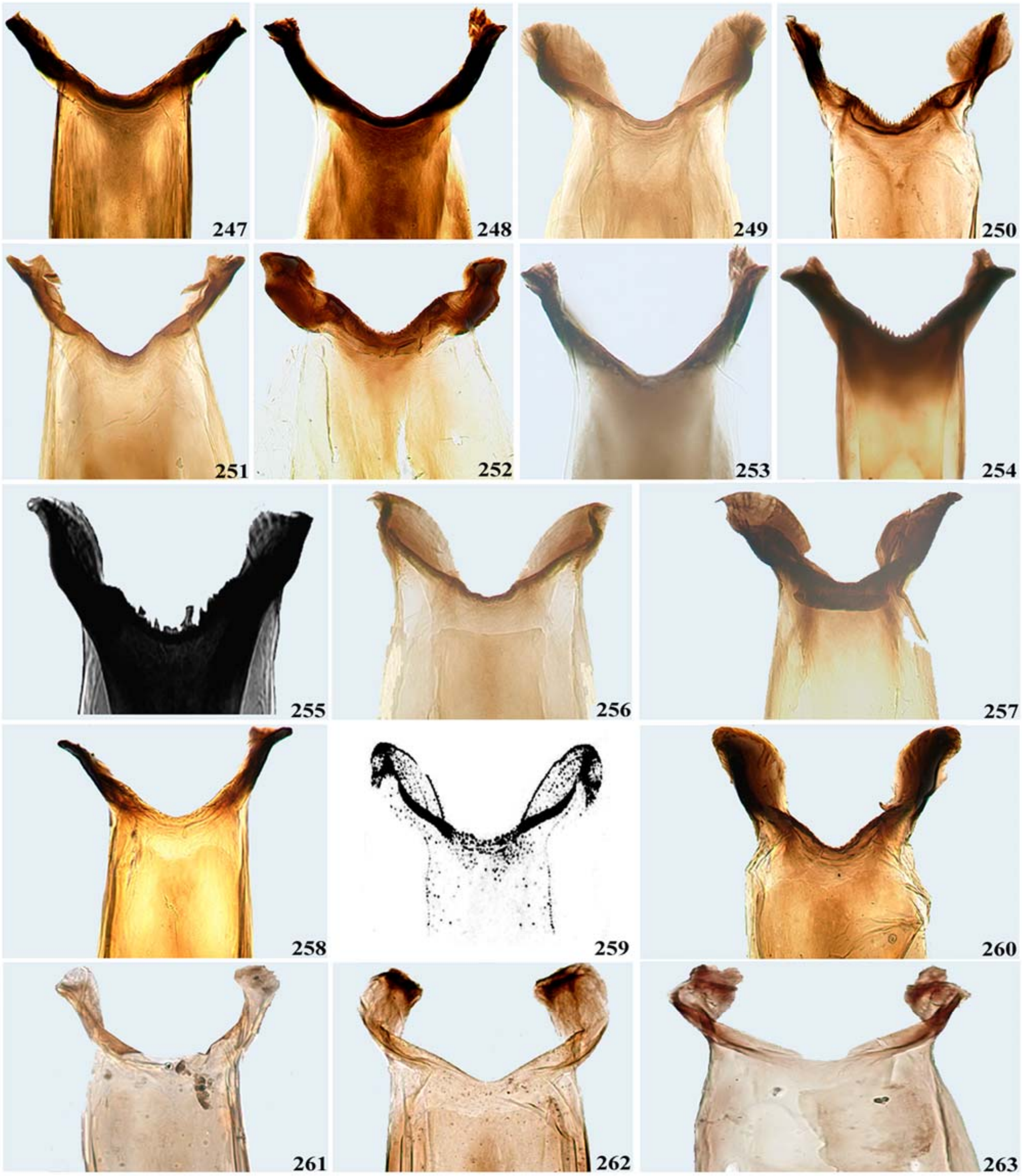

PLATE 24. Figs 247-263. Cibarium of female, ORBITALE and PICTIPES species groups. ORBITALE species groups: 247- *S. duodenicornium*, topotype; 248- *S. guianense s.l.*; 249- *S. hirtipupa*; 250- *S. huairayacu*, paratype; 251- *S. itaunense*; 252- *S. lahillei*; 253- *S. lithobranchium*, topotype; 254- *S. nigrimanum*; 255- *S. nunesdemelloi* (after HAMADA *et al.*, 2006); 256- *S. orbitale*; 257- *S. perplexum*, paratype; 258- *S. scutistriatum*; 259- *S. sumapazense* (after MUÑOZ DE HOYOS, 1996); 260- *S. townsendi*, holotype. PICTIPES species group: 261- *S. claricentrum*; 262- *S. innoxium*; 263- *S. pictipes*.

PLATE 25. Figs 264-274. Cibarium of female, TARSATUM species group: 264- *S. brachycladum*; 265- *S. bricenoi* (as *S. wirthi*, paratype); 266- *S. cristalinum*; 267- *S. earlei*; 268- *S. freemani*; 269- *S. guerrerense* (after Vargas & Díaz Nájera, 1956); 270- *S. hieroglyphicum*, paratype; 271- *S. hinmani*; 272- *S. hippovorum*; 273- *S. lobatoi*, paratype; 274- *S. paynei*.

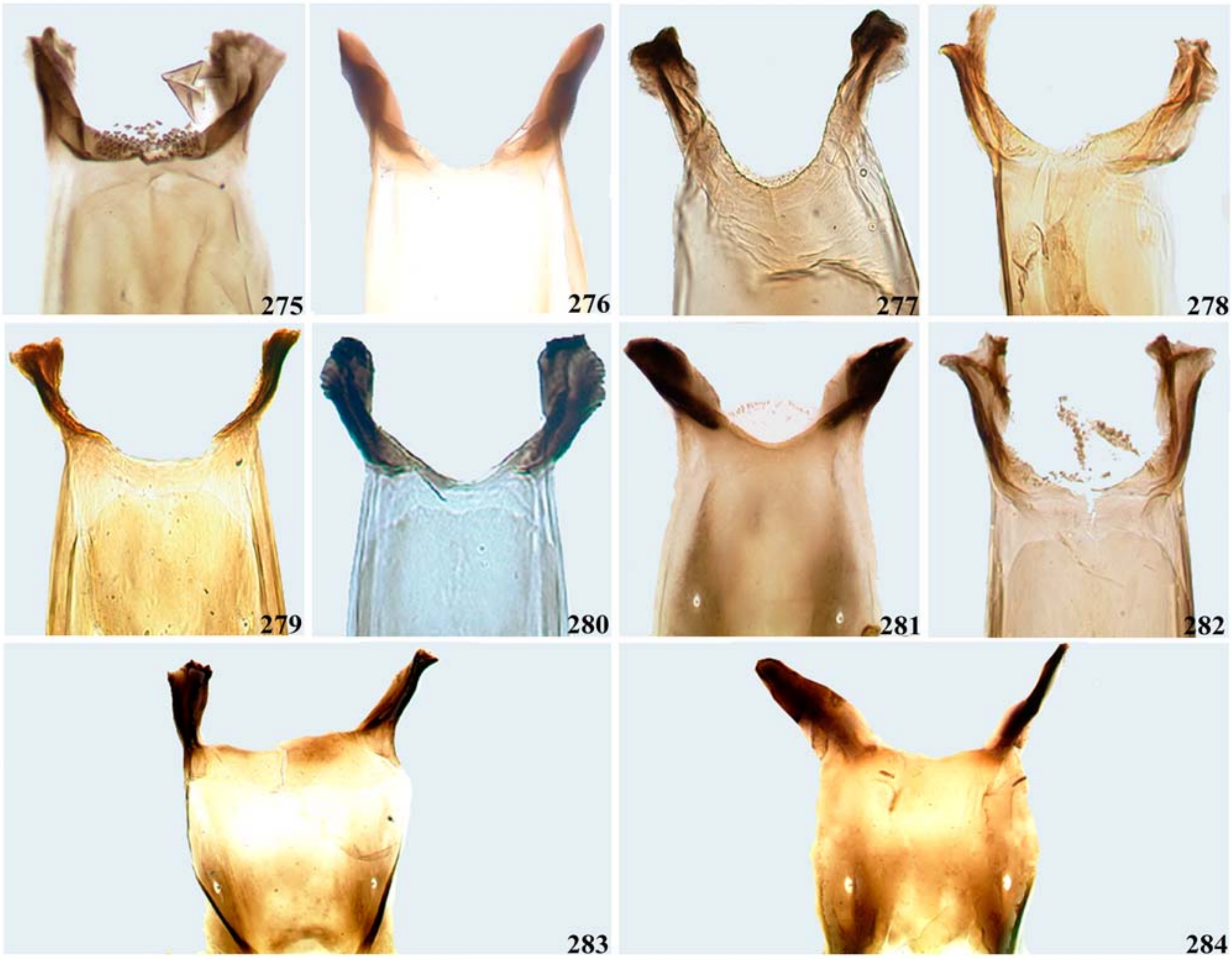

PLATE 26. Figs. 275-284. Cibarium of female, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 275- *S. pulverulentum*; 276- *S. rubrithorax*; 277- *S. smarti*, paratype; 278- *S. solarii*, paratype; 279- *S. tarsale*, paralectotype; 280- *S. tarsatum* (as *S. mexicanum*); 281- *S. virgatum s.l.*; 282- *S. yepocapense*, holotype. Subgenus *Psilopelmia*, BICOLORATUM species group: 283- *S. oviedoi*; 284- *S. rivasi*

PLATE 27. Figs. 285-300. Scutal coloration of female. The first figure for each specimen shows anterior light direction and the second posterior light direction, CANADENSE species group: 285, 286- *S. ayrozai*, paratype; 287, 288- *S. burchi*, holotype; 289, 290- *S. canadense*, allotype; 291, 292- *S. canadense*, paratype; 293, 294- *S. capricorne*; 295, 296- *S. carolinae*; 297, 298- *S. dalmati*, allotype; 299, 300- *S. delatorrei*.

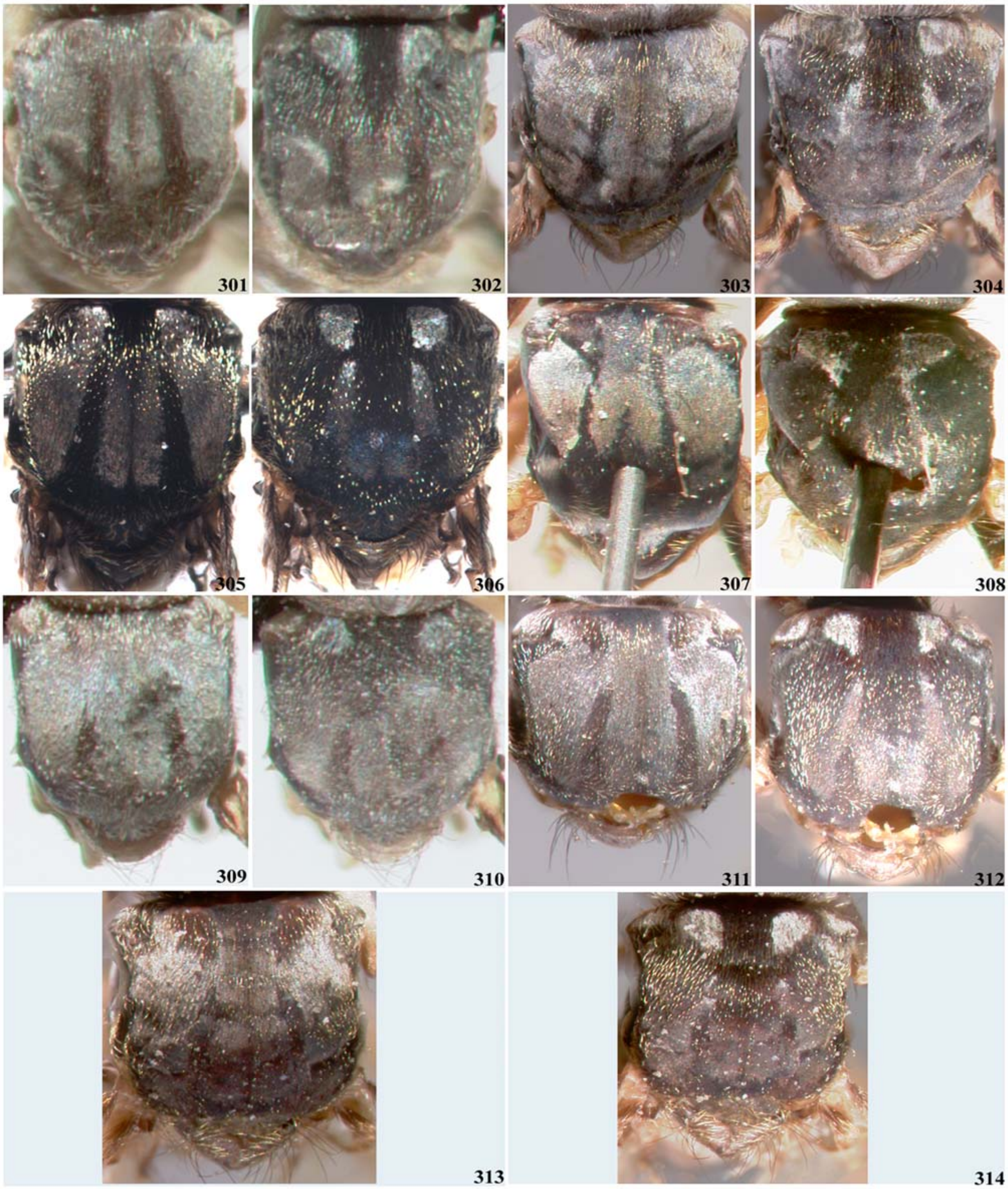

PLATE 28. Figs. 301-314. Scutal coloration of female. The first figure for each specimen shows anterior light direction and the second posterior light direction, CANADENSE species group: 301, 302- *S. estevezi*, allotype; 303, 304- *S. ethelae*, holotype; 305, 306- *S. ethelae* (as *S. chiriquiense*, Costa Rica); 307, 308- *S. falculatum*, holotype; 309, 310- *S. johnsoni*, paratype; 311, 312- *S. larvispinosum*; 313, 314- *S. microbranchium*.

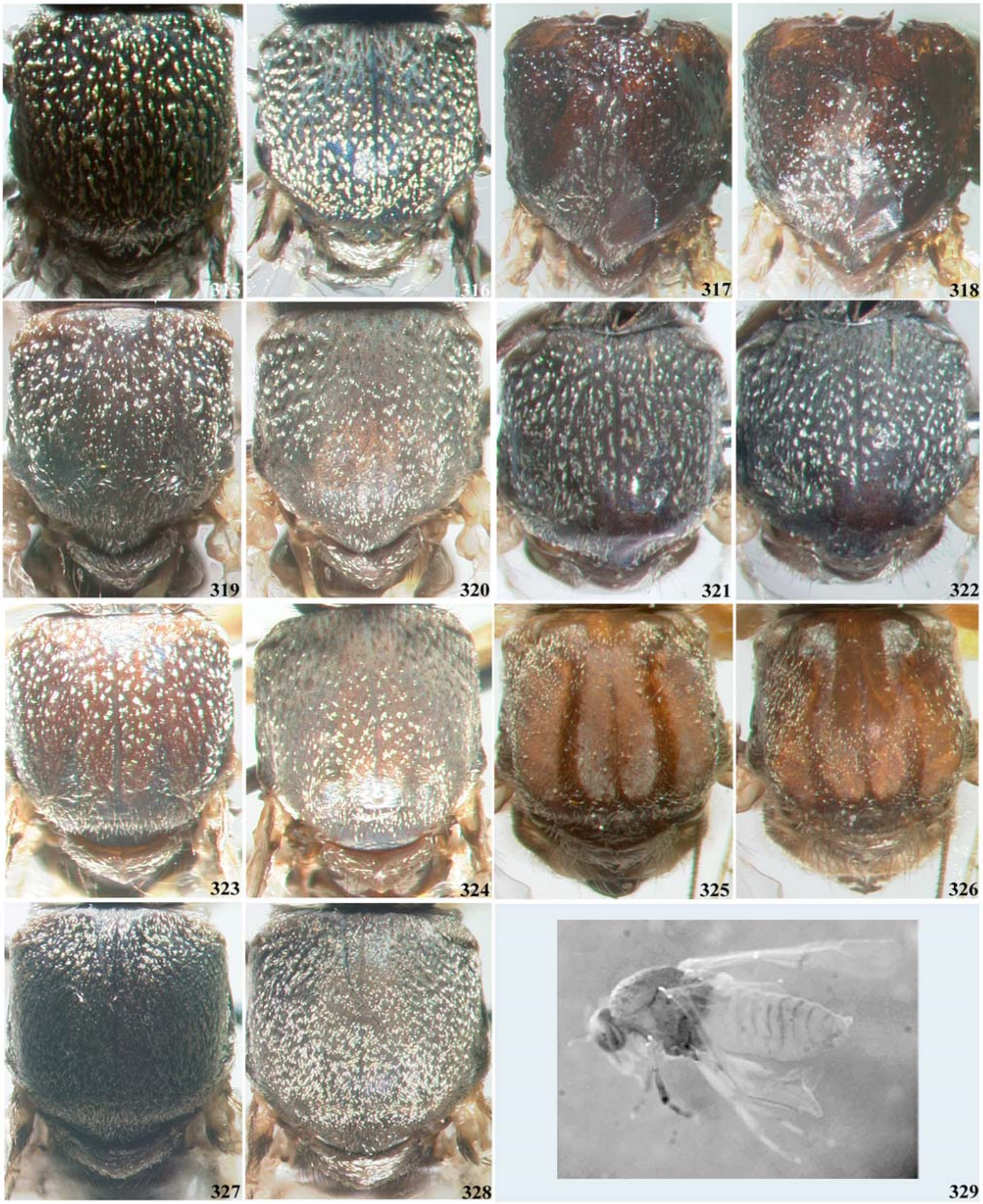

PLATE 29. Figs. 315-329. Scutal coloration of female, except for figure 329 for which a dorsolateral view of the whole adult is given. The first figure for each specimen shows anterior light direction and the second posterior light direction, ORBITALE species group: 315, 316- *S. duodenicornium*, topotype; 317, 318- *S. guianense s.l.*, lectotype (British Guiana); 319, 320, *S. guianense s.l.*, Brazil; 321, 322- *S. hirtipupa* (specimens labelled as neotype – this work); 323, 324- *S. hirtipupa* (variation); 325, 326- *S. huairayacu*; 327, 328- *S. itaunense*; 329- *S. jeteri* (after PY-DANIEL *et al.*, 2005).

PLATE 30. Figs. 330-345. Scutal coloration of female. The first figure for each specimen shows anterior light direction and the second posterior light direction, ORBITALE species group: 330, 331- *S. lahillei*, neotype; 332, 333- *S. lahillei*; 334, 335, *S. lithobranchium*, topotype; 336, 337- *S. nigrimanum*; 338, 339- *S. nunesdemelloi* (after HAMADA *et al.*, 2006); 340, 341- *S. orbitale*, neotype; 342, 343- *S. perplexum*, holotype; 344, 345- *S. scutistriatum*, holotype.

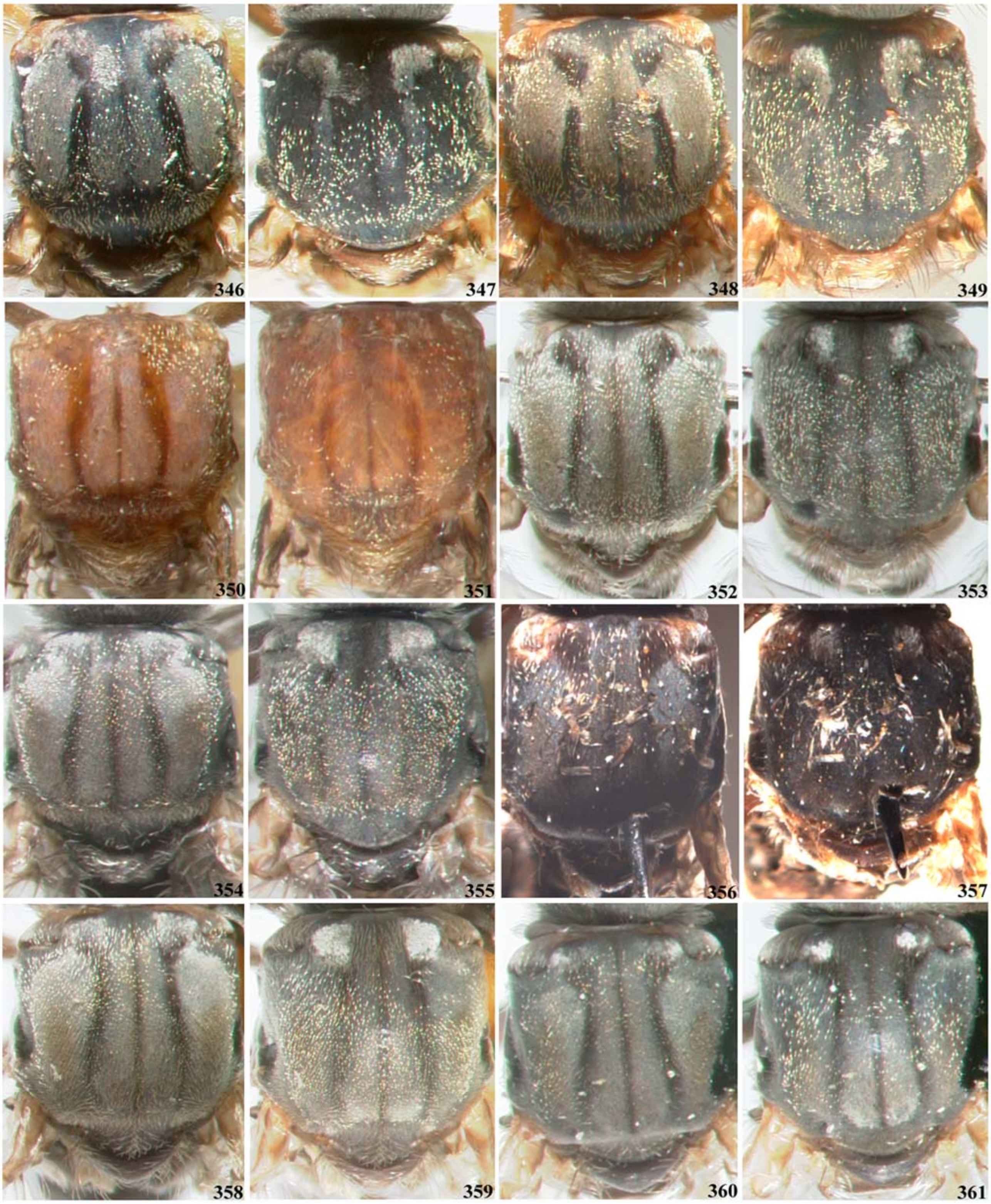

PLATE 31. Figs. 346-361. Scutal coloration of female. The first figure for each specimen shows anterior light direction and the second posterior light direction, ORBITALE and PICTIPES species groups. ORBITALE species group: 346, 347- *S. townsendi*, holotype; 348, 349- *S. townsendi*, paratype; 350, 351, *S. wygodzinskyorum*, holotype. PICTIPES species group: 352, 353- *S. claricentrum*, paratype; 354, 355- *S. innoxium*; 356, 357- *S. innoxium* (as *S. aldrichianum*, holotype); 358, 359- *S. pictipes*; 360, 361- *S. pictipes* (as *S. longistylatum*, allotype).

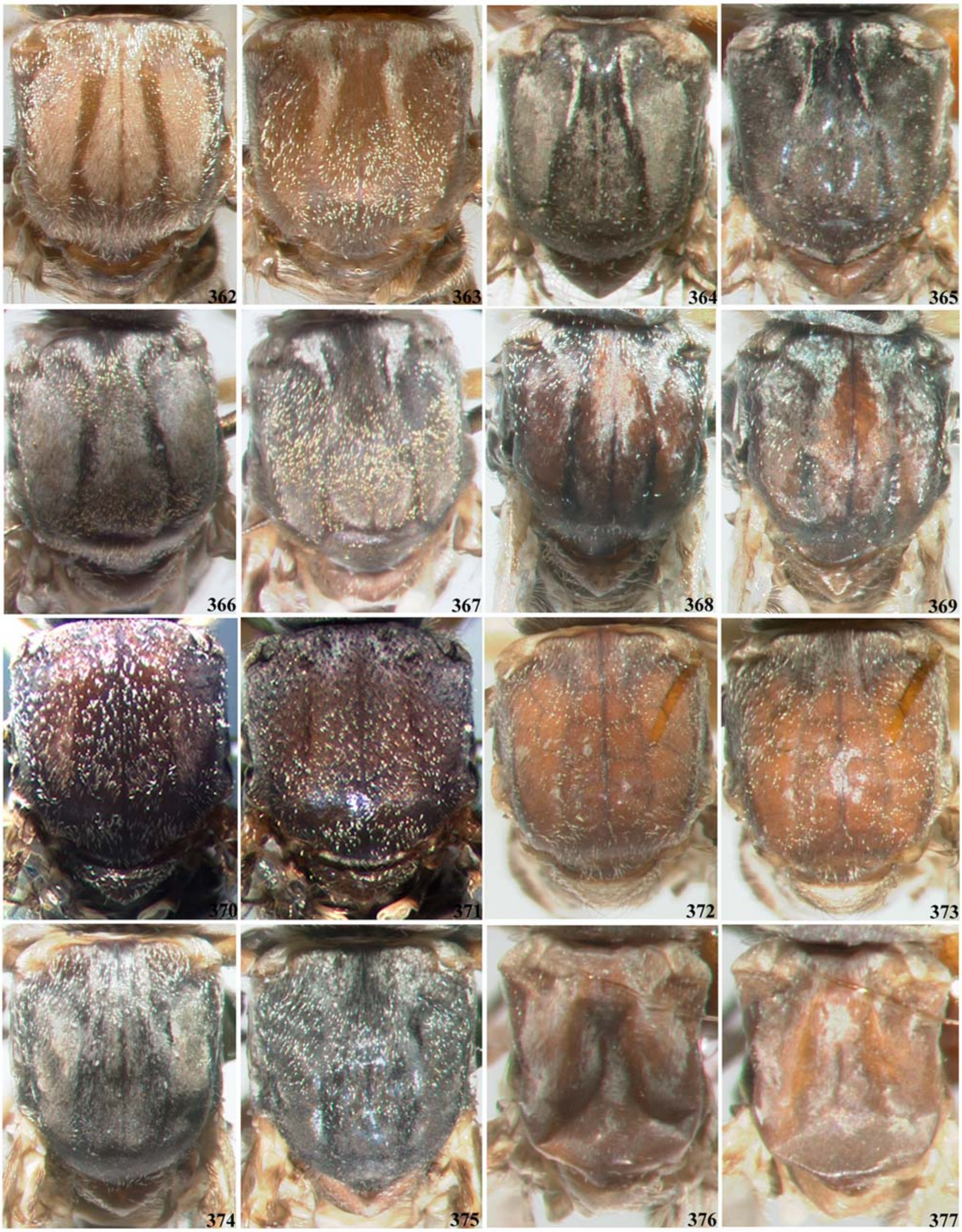

PLATE 32. Figs. 362-377. Scutal coloration of female. The first figure for each specimen shows anterior light direction and the second posterior light direction, TARSATUM species group: 362, 363- *S. brachycladum*; 364, 365- *S. bricenoi*, paratype; 366, 367- *S. bricenoi* (as *S. wirthi*, paratype); 368, 369- *S. cristalinum*; 370, 371- *S. earlei*; 372, 373- *S. freemani*, allotype; 374, 375- *S.* near *freemani*, USA; 376, 377- *S. guerrerense*, allotype.

PLATE 33. Figs. 378-393. Scutal coloration of female unless stated otherwise. The first figure for each specimen shows anterior light direction and the second posterior light direction, TARSATUM species group: 378, 379- *S. hinmani*, paratype; 380, 381- *S. hippovorum*, holotype; 382, 383, *S. hippovorum*, paratype; 384, 385- *S. lobatoi*, paratype; 386, 387- *S. paynei* (as *Hemicnetha mexicana*, lectotype); 388, 389- *S. paynei* (as *S. mathesoni*, Mexico); 390, 391- *S. paynei* (as *S. acatenangoensis*, Guatemala); 392, 393- *S. paynei*, Ecuador.


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PLATE 34. Figs. 394-409. Scutal coloration of female. The first figure for each specimen shows anterior light direction and the second posterior light direction, TARSATUM species group: 394, 395- *S. pulverulentum*, lectotype; 396, 397- *S. pulverulentum*, Belize; 398, 399, *S. rubrithorax*, neotype; 400, 401- *S. rubrithorax*, Brazil; 402, 403- *S. smarti*, holotype; 404, 405- *S. solarii*, paratype; 406, 407- *S. tarsale*, lectotype; 408, 409- *S. tarsale* (as *S. clavipes*, holotype).

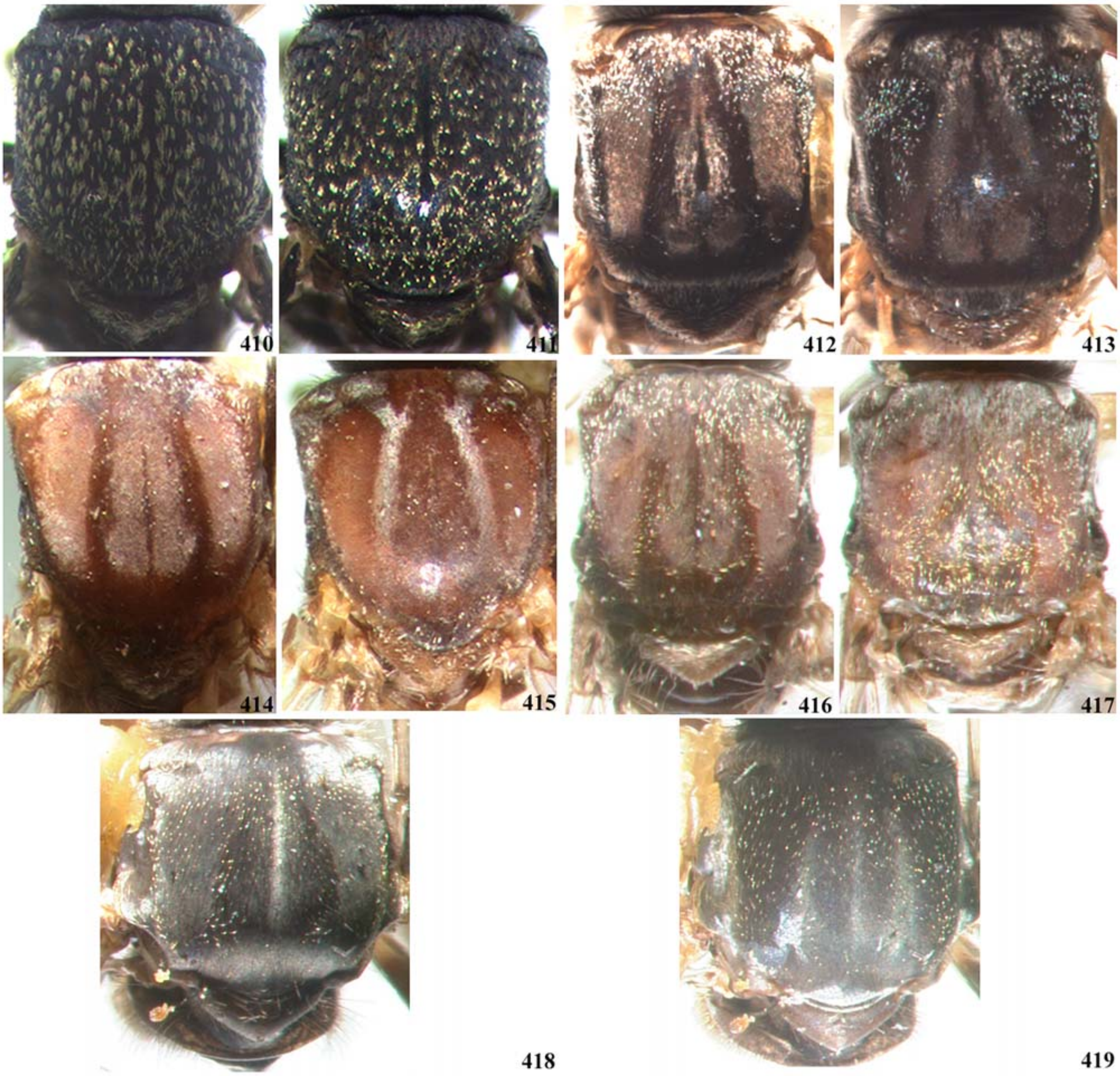

PLATE 35. Figs. 410-419. Scutal coloration of female. The first figure for each specimen shows anterior light direction and the second posterior light direction, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 410, 411- *S. tarsatum* (as *S. mexicanum*); 412, 413- *S. virgatum s.l.*, USA; 414, 415, *S. virgatum s.l.* (as *S. rubicundulum*, holotype); 416, 417- *S. yepocapense*, paratype. Subgenus *Psilopelmia*, BICOLORATUM species group: 418, 419- *S. rivasi.*

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PLATE 36. Figs. 420-427. Fore, mid and hind legs of female, CANADENSE species group: 420- *S. ayrozai*; 421- *S. burchi*, paratype; 422, *S. canadense*; 423- *S. capricorne*; 424- *S. carolinae*; 425- *S. contrerense*, allotype; 426- *S. dalmati*, allotype; 427- *S. delatorrei*, holotype.

PLATE 37. Figs. 428-436. Fore, mid and hind legs of female, CANADENSE species group: 428- *S. estevezi*, allotype [mid leg not illustrated]; 429- *S. ethelae*; 430, *S. falculatum*, holotype; 431- *S. gorirossiae*; 432- *S. johnsoni*, paratype; 433- *S. larvispinosum*; 434- *S. menchacai*; 435- *S. microbranchium*; 436- *S. temascalense*, holotype.

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PLATE 38. Figs. 437-444. Fore, mid and hind legs of female, ORBITALE species group: 437- *S. duodenicornium*, topotype; 438- *S. guianense s.l.*; 439- *S. hirtipupa*; 440- *S. huairayacu*, paratype; 441- *S. itaunense*; 442- *S. lahillei*; 443- *S. lithobranchium* (modified after HAMADA *et al.*, 2010); 444- *S. nigrimanum*.

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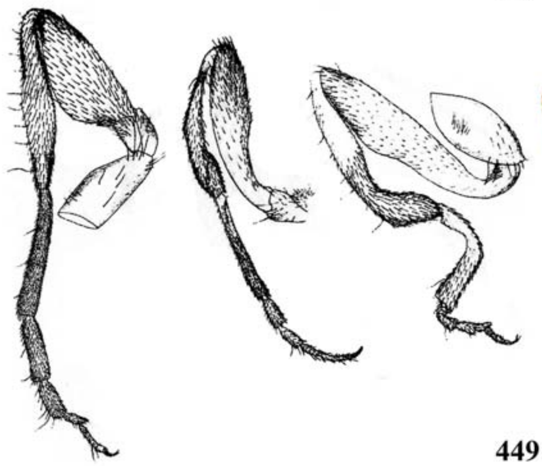

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PLATE 39. Figs. 445-501. Fore, mid and hind legs of female, ORBITALE species group: 445- *S. nunesdemelloi* (after HAMADA *et al*., 2006); 446- *S. orbitale*; 447, *S. perplexum*, paratype; 448- *S. scutistriatum*; 449- *S. sumapazense* (after MUÑOZ DE HOYOS, 1996); 500- *S. townsendi* (as *S. muiscorum*); 501- *S. wygodzinskyorum*, holotype.


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PLATE 40. Figs. 502-509. Fore, mid and hind legs of female, PICTIPES and TARSATUM species groups. PICTIPES species group: 502- *S. claricentrum*; 503- *S. innoxium*; 504- *S. pictipes*. TARSATUM species group: 505- *S. brachycladum*; 506- *S. bricenoi* (as *S. wirthi*, paratype); 507- *S. cristalinum*; 508- *S. earlei*; 509- *S. freemani*.

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PLATE 41. Figs. 510-517. Fore, mid and hind legs of female, TARSATUM species group: 510- *S. guerrerense*, paratype; 511- *S. hieroglyphicum*, paratype; 512, *S. hinmani*, allotype; 513- *S. hippovorum*; 514- *S. lobatoi*, paratype; 515- *S. paynei*; 516- *S. pulverulentum*; 517- *S. rubrithorax*.

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PLATE 42. Figs. 518-525. Fore, mid and hind legs of female, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species groups. TARSATUM species group: 518- *S. smarti*, paratype; 519- *S. solarii*; 520- *S. tarsale* (as *S. clavipes*, paratype); 521- *S. tarsatum* (as *S. mexicanum*); 522- *S. virgatum s.l.*; 523- *S. yepocapense*, holotype. Subgenus *Psilopelmia*, BICOLORATUM species group: 524- *S. oviedoi*; 525- *S. rivasi* [mid leg not illustrated].

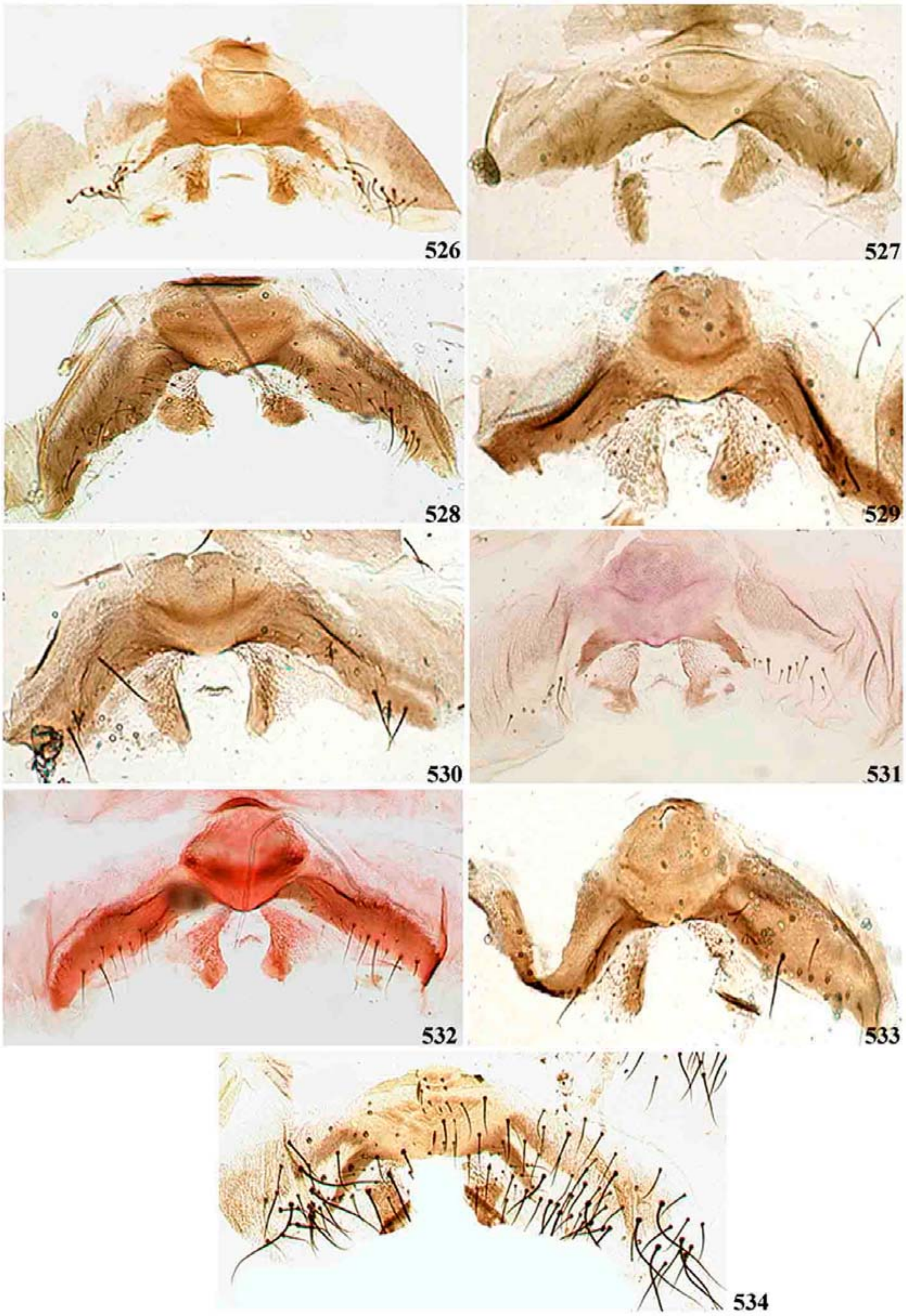


PLATE 43. Figs. 526-534. Eighth sternite and gonapophyses of female, CANADENSE species group: 526- *S. ayrozai*; 527- *S. burchi*; 528- *S. canadense*; 529- *S. capricorne*; 530- *S. carolinae*; 531- *S. contrerense*, allotype; 532- *S. dalmati*, allotype; 533- *S. delatorrei*; 534- *S. estevezi*, allotype.

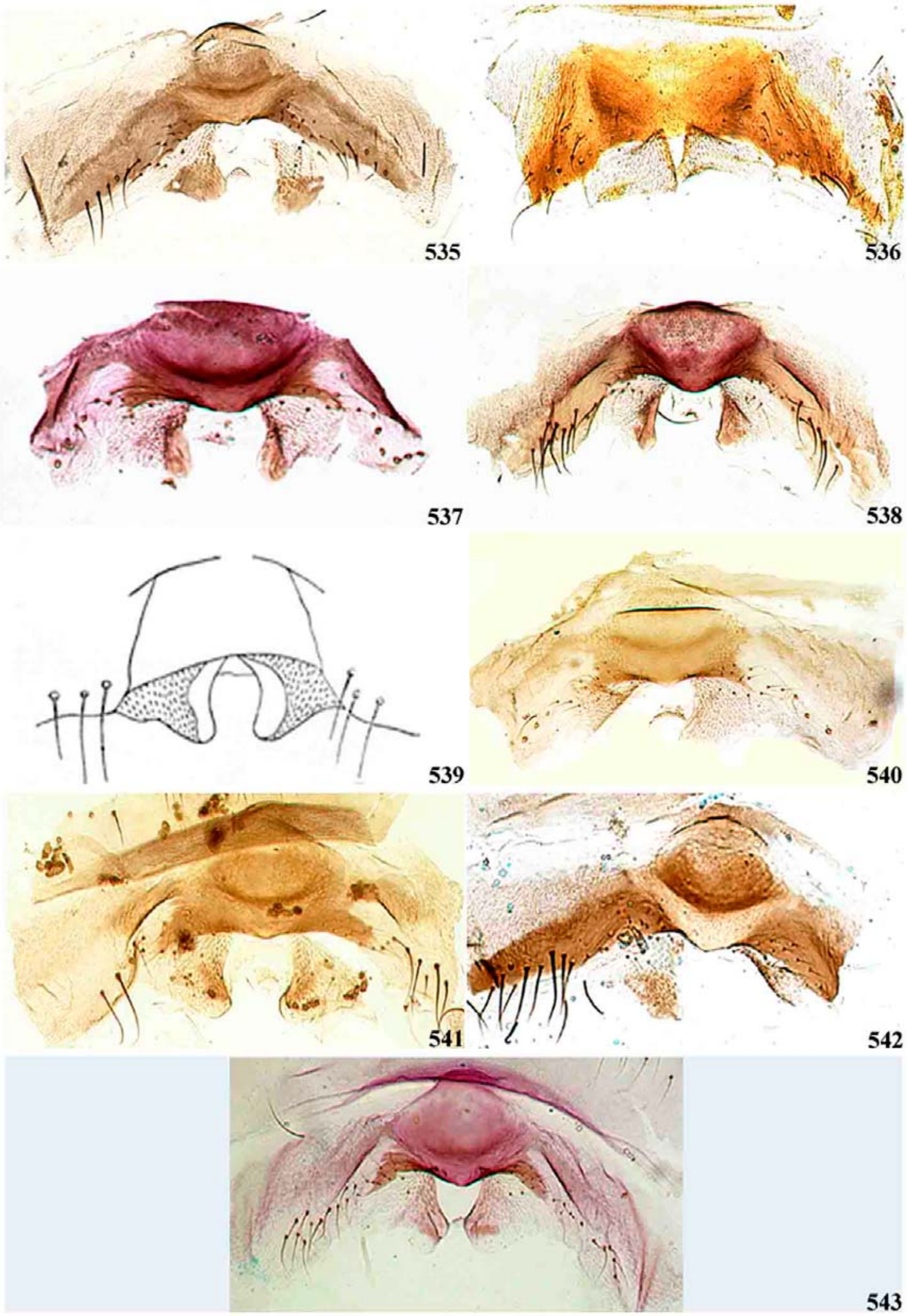


PLATE 44. Figs. 535-543. Eighth sternite and gonapophyses of female, CANADENSE species group: 535- *S. ethelae* (as *S. chiriquiense*); 536- *S. falculatum*, holotype; 537- *S. gorirossiae*, paratype; 538- *S. johnsoni*, paratype; 539- *S. juarezi* (VARGAS & DÍAZ NÁJERA, 1957b); 540- *S. larvispinosum*; 541- *S. menchacai*; 542- *S. microbranchium*; 543- *S. temascalense*, holotype.

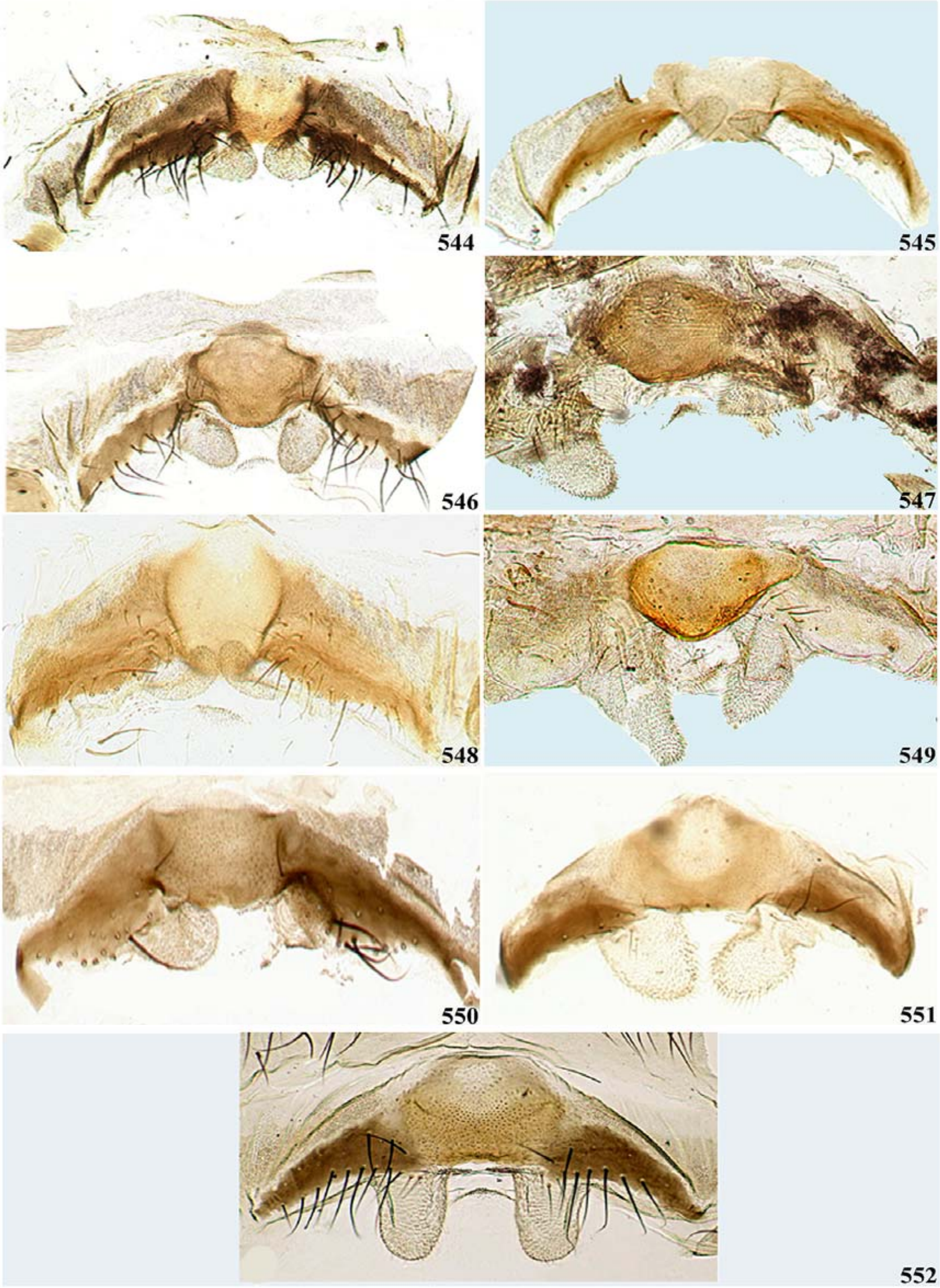


PLATE 45. Figs. 544-552. Eighth sternite and gonapophyses of female, ORBITALE species group: 544- *S. duodenicornium*, topotype; 545- *S. guianense s.l.*; 546- *S. hirtipupa*; 547- *S. huairayacu*; 548- *S. itaunense*; 549- *S. lahillei*; 550- *S. lithobranchium*, topotype; 551- *S. nigrimanum*; 552- *S. nunesdemelloi* (after HAMADA *et al.*, 2006).

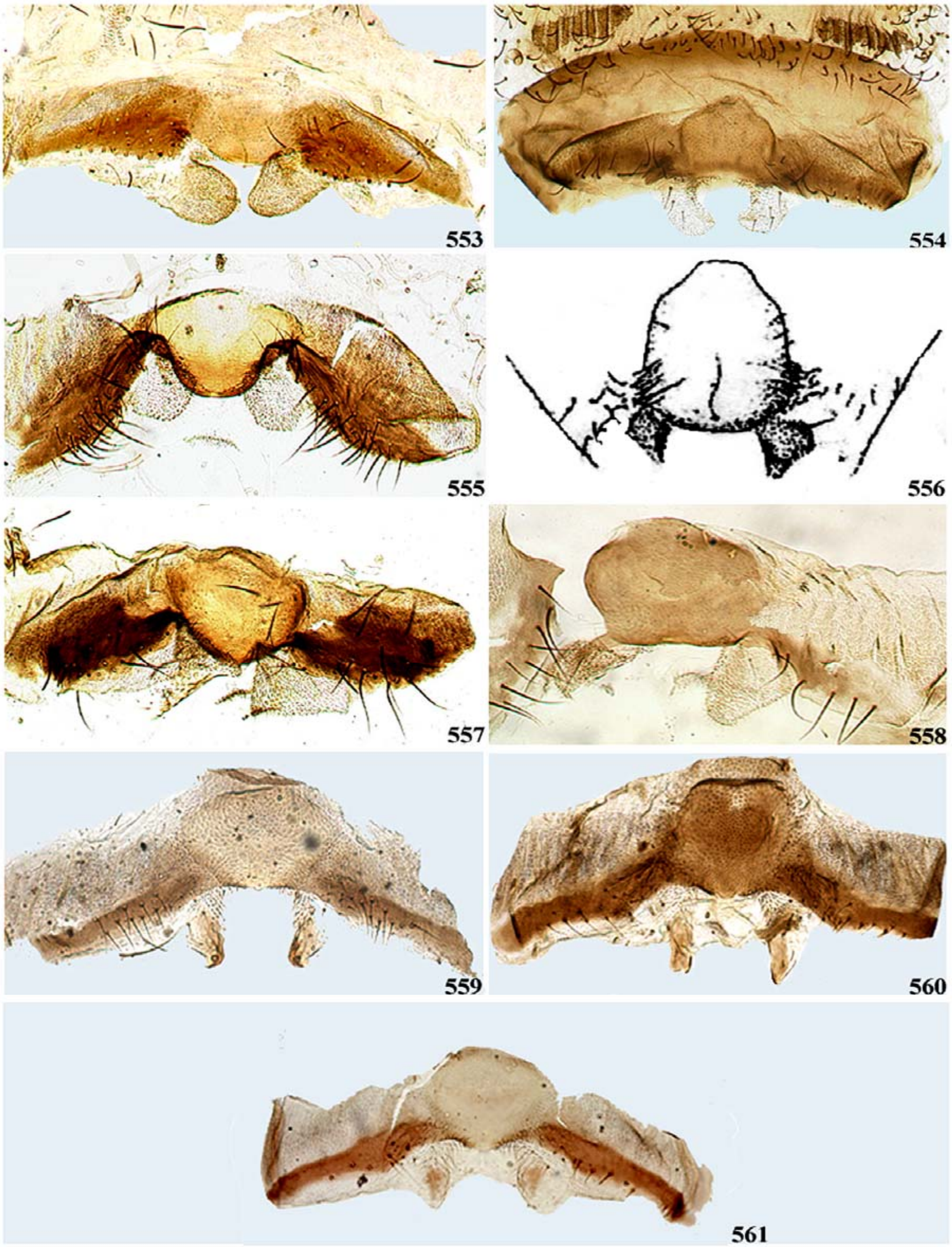


PLATE 46. Figs. 553-561. Eighth sternite and gonapophyses of female, ORBITALE and PICTIPES species groups. ORBITALE species groups: 553- *S. orbitale*, neotype; 554- *S. perplexum*, paratype; 555- *S. scutistriatum*; 556- *S. sumapazense* (after MUÑOZ DE HOYOS, 1996); 557- *S. townsendi*, holotype; 558- *S. wygodzinskyorum*, holotype. PICTIPES species group: 559- *S. claricentrum*; 560- *S. innoxium*; 561- *S. pictipes*.

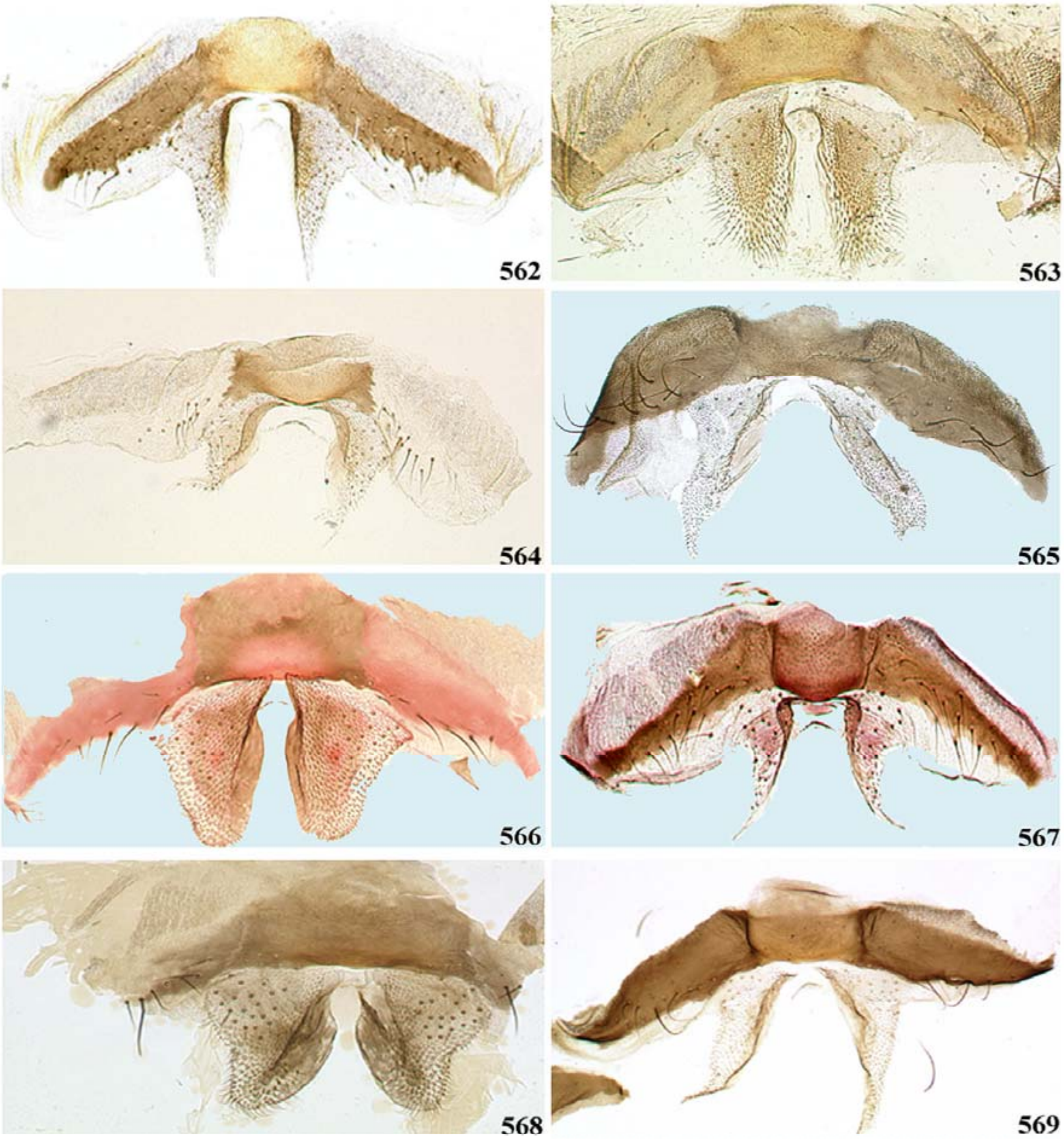


PLATE 47. Figs. 562-569. Eighth sternite and gonapophyses of female, TARSATUM species group: 562- *S. brachycladum*; 563- *S. bricenoi* (as *S. wirthi*, paratype); 564- *S. cristalinum*, paratype; 565- *S. earlei*; 566- *S. freemani*, allotype; 567- *S. guerrerense*, allotype; 568- *S. hieroglyphicum*, paratype; 569- *S. hinmani*, paratype.

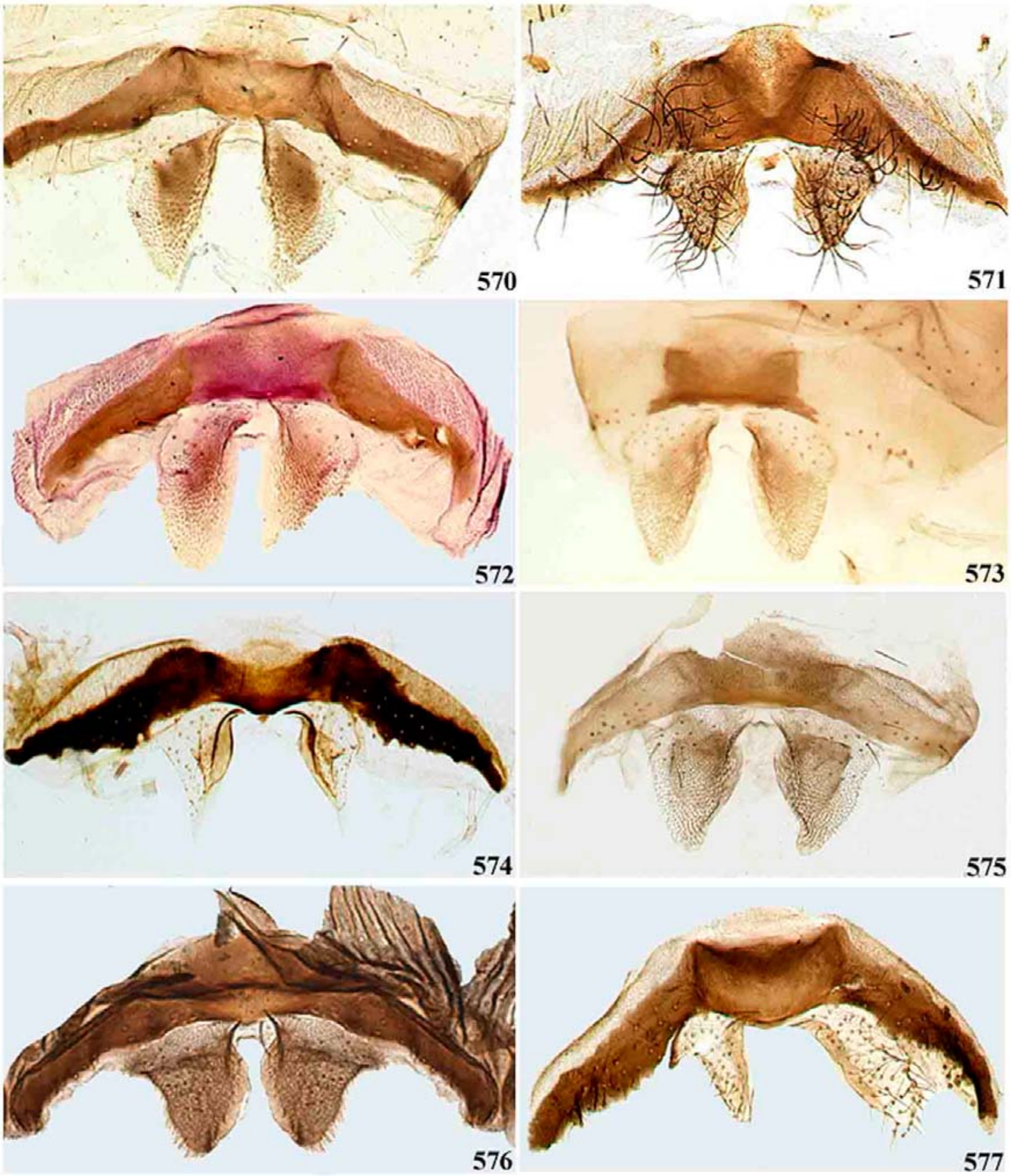


PLATE 48. Figs. 570-577. Eighth sternite and gonapophyses of female, TARSATUM species group: 570- *S. hippovorum*; 571- *S. lobatoi*, paratype; 572- *S. paynei* (as *Hemicnetha mexicana*, lectotype); 573- *S. paynei*, Ecuador; 574- *S. pulverulentum*; 575- *S. rubrithorax*; 576- *S. smarti*, paratype (modified – left side of gonapophyses broken in the slide); 577- *S. solarii*, paratype.

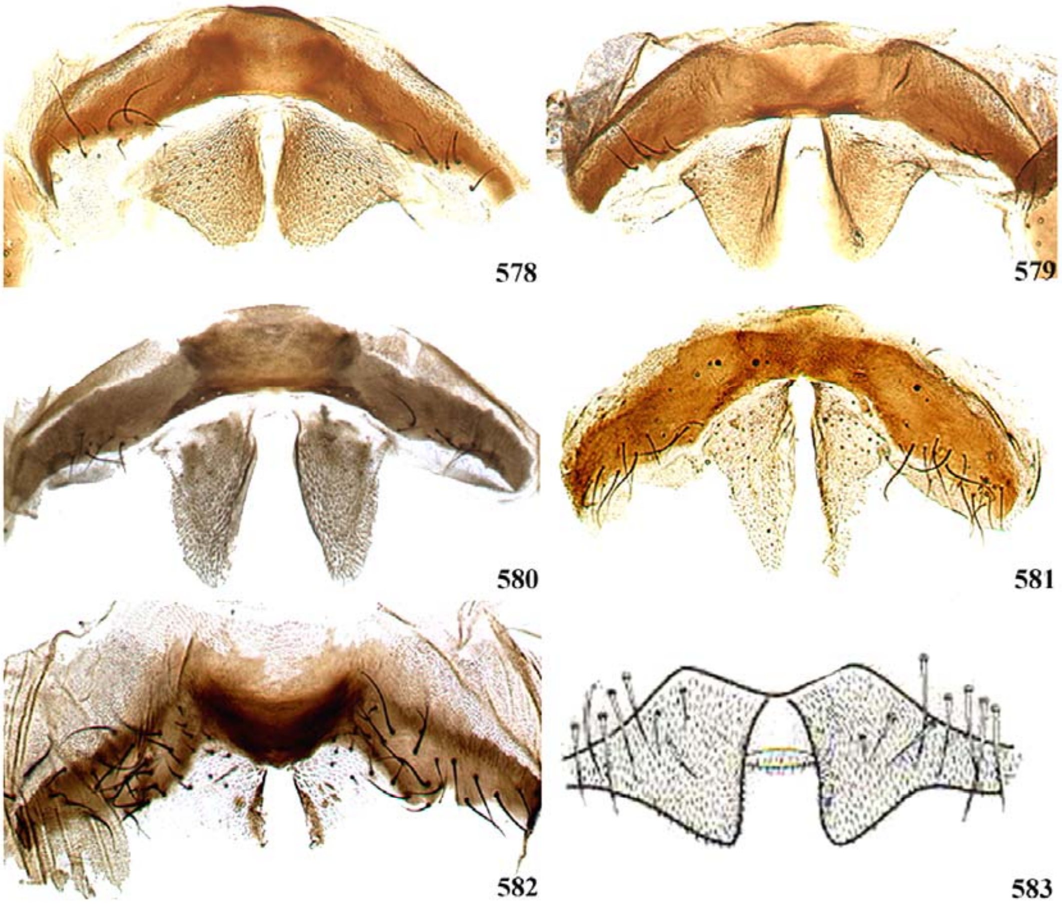


PLATE 49. Figs. 578-583. Eighth sternite and gonapophyses of female, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 578- *S. tarsale*, lectotype; 579- *S. tarsatum*, lectotype; 580- *S. virgatum s.l.*; 581- *S. yepocapense*. Subgenus *Psilopelmia*, BICOLORATUM species group: 582- *S. oviedoi*; 583- *S. rivasi* (after RAMÍREZ-PÉREZ, 1971).

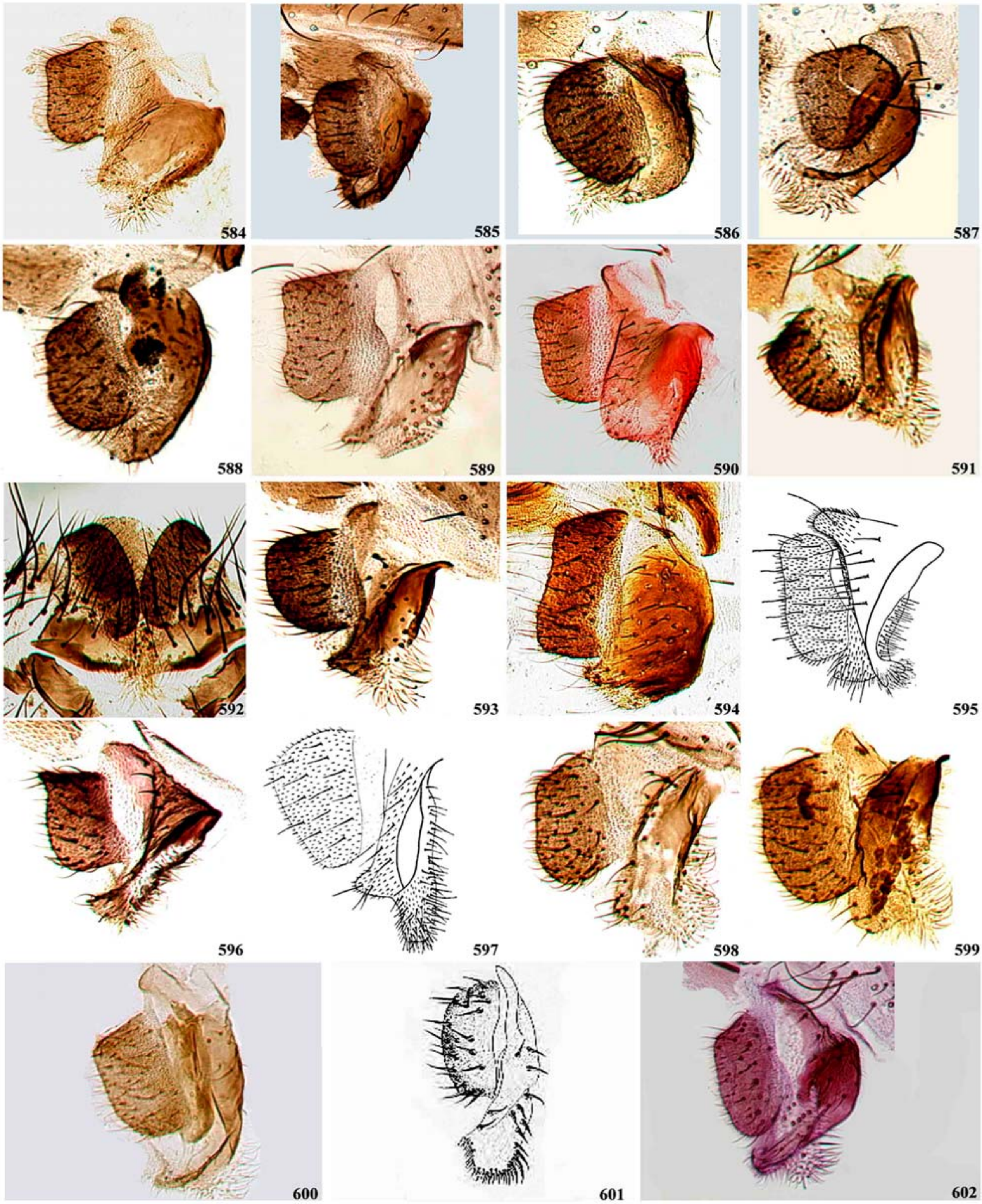


PLATE 50. Figs. 584-602. Cercus and paraproct of female, CANADENSE species group: 584- *S. ayrozai*; 585- *S. burchi*, paratype; 586- *S. canadense*; 587- *S. capricorne*; 588- *S. carolinae*; 589- *S. contrerense*, allotype; 590- *S. dalmati*, allotype; 591- *S. delatorrei*, holotype; 592- *S. estevezi*, allotype (both cercus and paraprocts *in situ*); 593- *S. ethelae* (as *S. chiriquiense*); 594- *S. falculatum*; 595- *S. gorirossiae* (after VARGAS & DÍAZ NÁJERA, 1957b); 596- *S. johnsoni*, paratype; 597- *S. juarezi* (after VARGAS & DÍAZ NÁJERA, 1957b); 598- *S. larvispinosum*; 599- *S. menchacai*; 600- *S. microbranchium*, paratype; 601- *S. nigricorne* (after DALMAT, 1950); 602- *S. temascalense*, holotype.

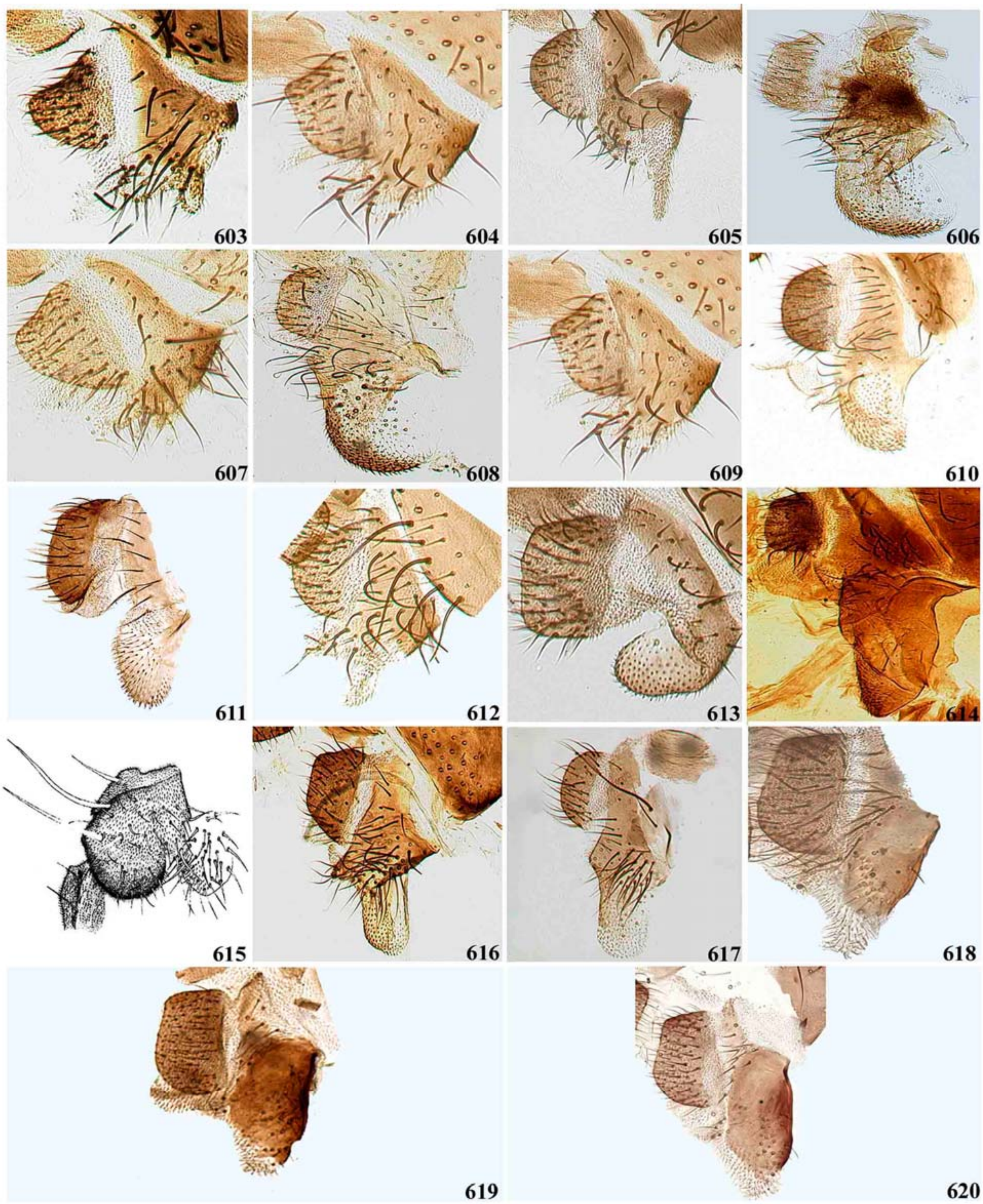


PLATE 51. Figs. 603-620. Cercus and paraproct of female, ORBITALE and PICTIPES species groups. ORBITALE species group: 603- *S. duodenicornium*, topotype; 604- *S. guianense s.l.*; 605- *S. hirtipupa*; 606- *S. huairayacu*; 607- *S. itaunense*; 608- *S. lahillei*; 609- *S. lithobranchium*, topotype; 610- *S. nigrimanum*; 611- *S. nunesdemelloi* (after HAMADA *et al.*, 2006); 612- *S. orbitale*, neotype; 613- *S. perplexum*, paratype; 614- *S. scutistriatum*, holotype; 615- *S. sumapazense* (after MUÑOZ DE HOYOS, 1996); 616- *S. townsendi*, holotype; 617- *S. wygodzinskyorum*, holotype. PICTIPES species group: 618- *S. claricentrum*; 619- *S. innoxium*; 620- *S. pictipes*.

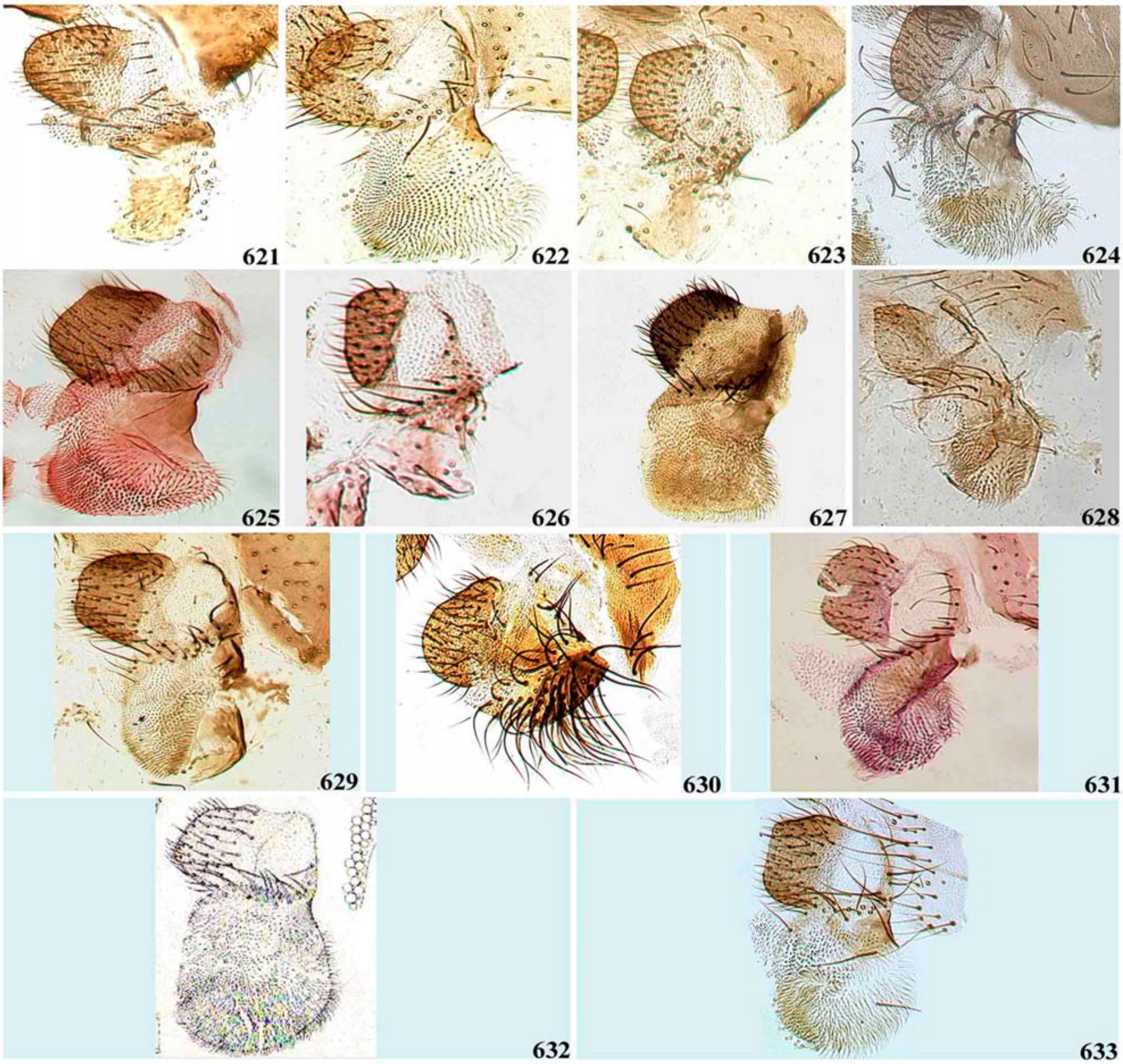


PLATE 52. Figs. 621-633. Cercus and paraproct of female, TARSATUM species group: 621- *S. brachycladum*; 622- *S. bricenoi* (as *S. wirthi*, paratype); 623- *S. cristalinum*; 624- *S. earlei*; 625- *S. freemani*, allotype; 626- *S. guerrerense*, allotype; 627- *S. hieroglyphicum*, paratype; 628- *S. hinmani*; 629- *S. hippovorum*; 630- *S. lobatoi*, paratype; 631- *S. paynei* (as *Hemicnetha mexicana,* lectotype); 632- *S. paynei* (as *S. biuxinisa* after COSCARÓN & IBÁÑEZ-BERNAL, 1995); 633- *S. paynei*, Ecuador.

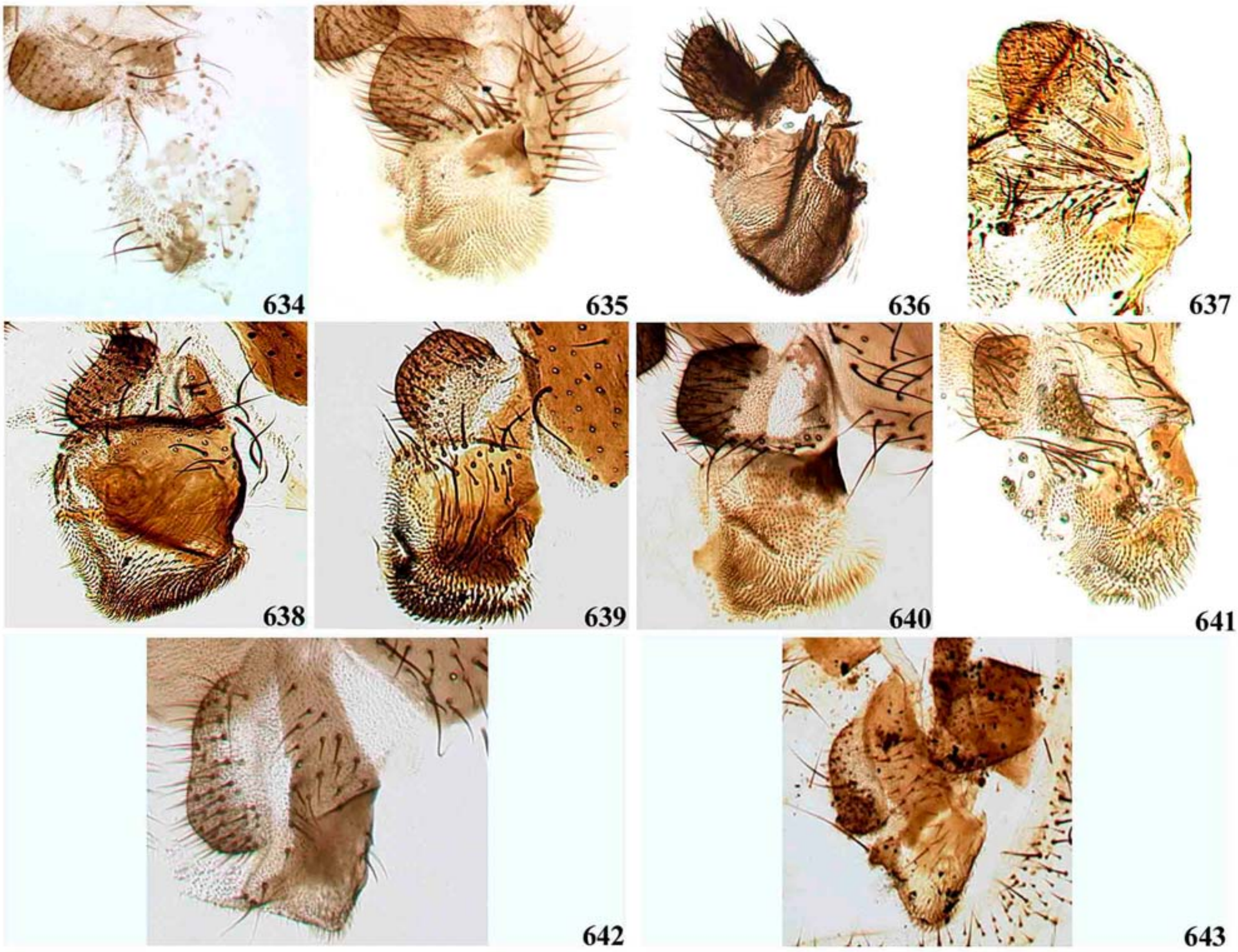


PLATE 53. Figs. 634-643. Cercus and paraproct of female, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 634- *S. pulverulentum*; 635- *S. rubrithorax*; 636- *S. smarti,* paratype; 637- *S. solarii*, paratype; 638- *S. tarsale*, lectotype; 639- *S. tarsatum*, lectotype; 640- *S. virgatum s.l.*; 641- *S. yepocapense*, paratype. Subgenus *Psilopelmia*, BICOLORATUM species group: 642- *S. oviedoi*; 643- *S. rivasi*.

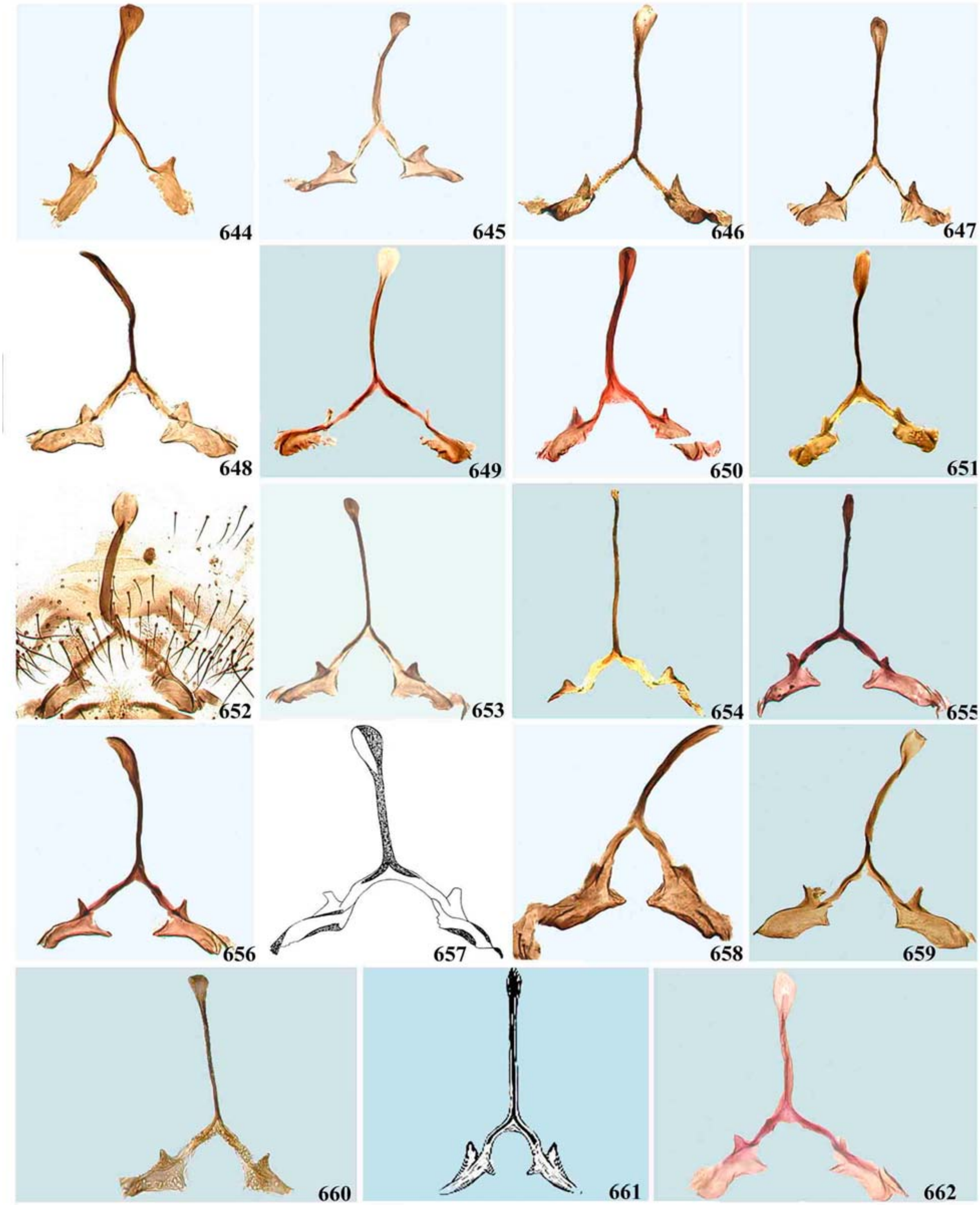


PLATE 54. Figs. 644-662. Genital fork of female, CANADENSE species group. 644- *S. ayrozai*; 645- *S. burchi*; 646- *S. canadense*; 647- *S. capricorne*; 648- *S. carolinae*; 649- *S. contrerense*, allotype; 650- *S. dalmati*, allotype; 651- *S. delatorrei*, holotype; 652- *S. estevezi*, allotype; 653- *S. ethelae* as *S. chiriquiense*); 654- *S. falculatum*, holotype; 655- *S. gorirossiae*, paratype; 656- *S. johnsoni*, paratype; 657- *S. juarezi* (after VARGAS & DÍAZ NÁJERA, 1957b); 658- *S. larvispinosum*; 659- *S. menchacai*; 660- *S. microbranchium*, paratype; 661- *S. nigricorne* (after DALMAT, 1949); 662- *S. temascalense*, holotype.

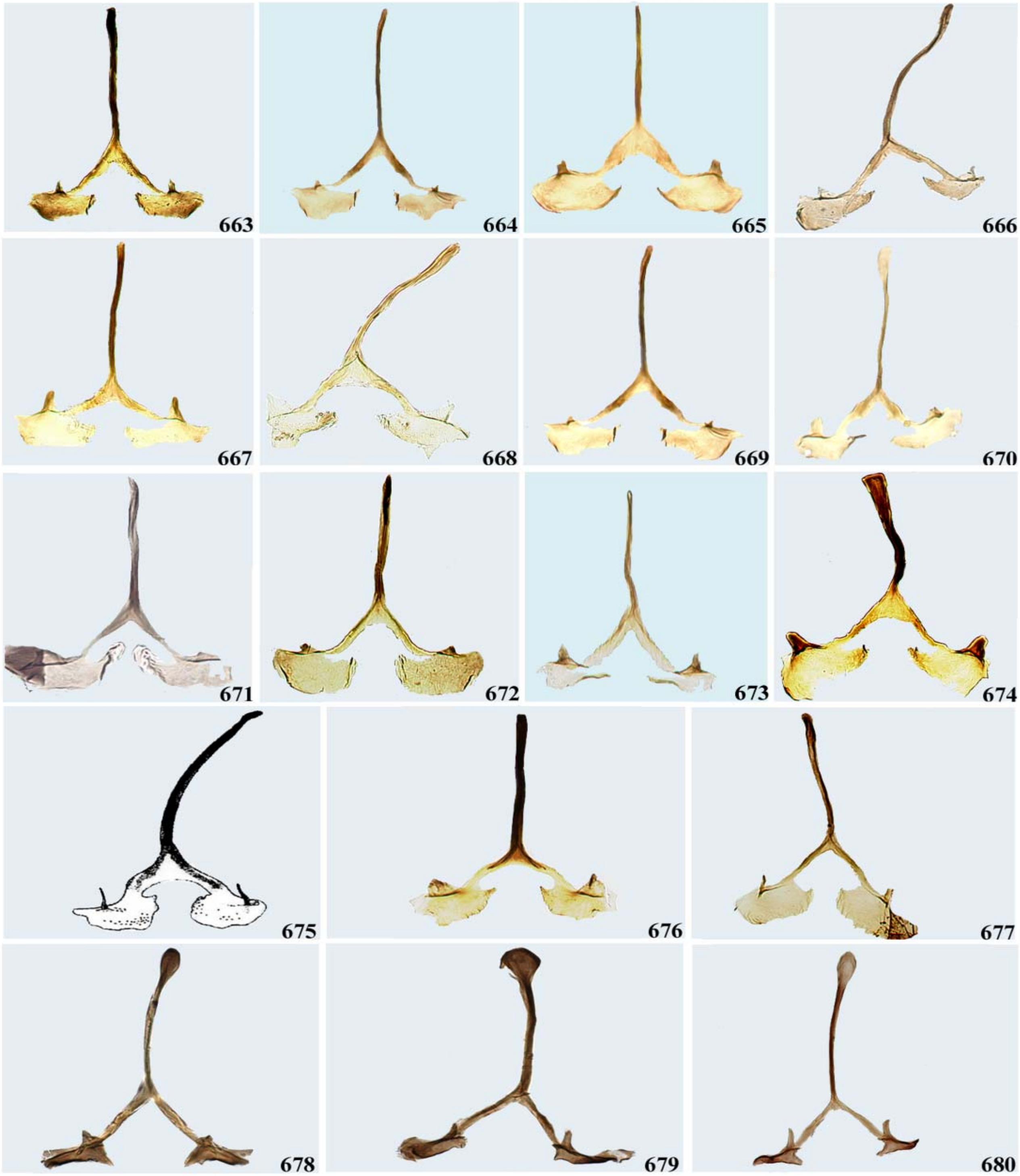
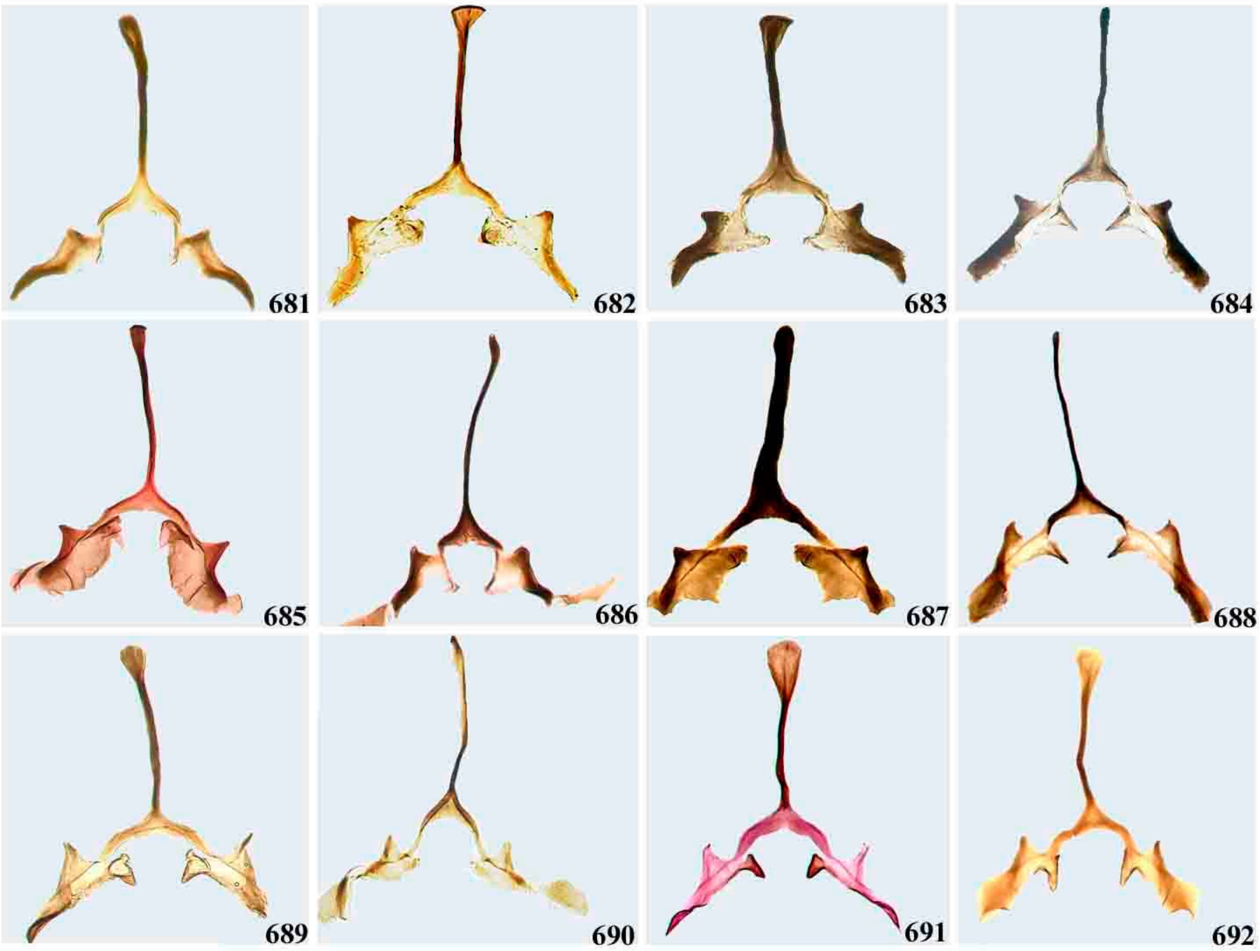


PLATE 55. Figs. 663-680. Genital fork of female, ORBITALE and PICTIPES species groups. ORBITALE species group: 663- *S. duodenicornium*, topotype; 664- *S. guianense s.l.*; 665- *S. hirtipupa*; 666- *S. huairayacu*; 667- *S. itaunense*; 668- *S. lahillei*; 669- *S. lithobranchium*, topotype; 670- *S. nigrimanum*; 671- *S. nunesdemelloi* (after Hamada *et al.*, 2006); 672- *S. orbitale*; 673- *S. perplexum*, paratype; 674- *S. scutistriatum*; 675- *S. sumapazense* (after Muñoz de Hoyos, 1996); 676- *S. townsendi*, holotype; 677- *S. wygodzinskyorum*, holotype. PICTIPES species group: 678- *S. claricentrum*; 679- *S. innoxium*; 680- *S. pictipes*.



LATE 56. Figs. 681-692. Genital fork of female, TARSATUM species group: 681- *S. brachycladum*; 682- *S. bricenoi* (as *S. wirthi*, paratype); 683- *S. cristalinum*; 684- *S. earlei*; 685- *S. freemani*, allotype; 686- *S. guerrerense,* allotype; 687- *S. hieroglyphicum*, paratype (modified – left side broken in the specimen); 688- *S. hinmani*, allotype; 689- *S. hippovorum*; 690- *S. lobatoi*, paratype; 691- *S. paynei* (as *Hemicnetha mexicana,* lectotype); 692- *S. paynei*, Ecuador.

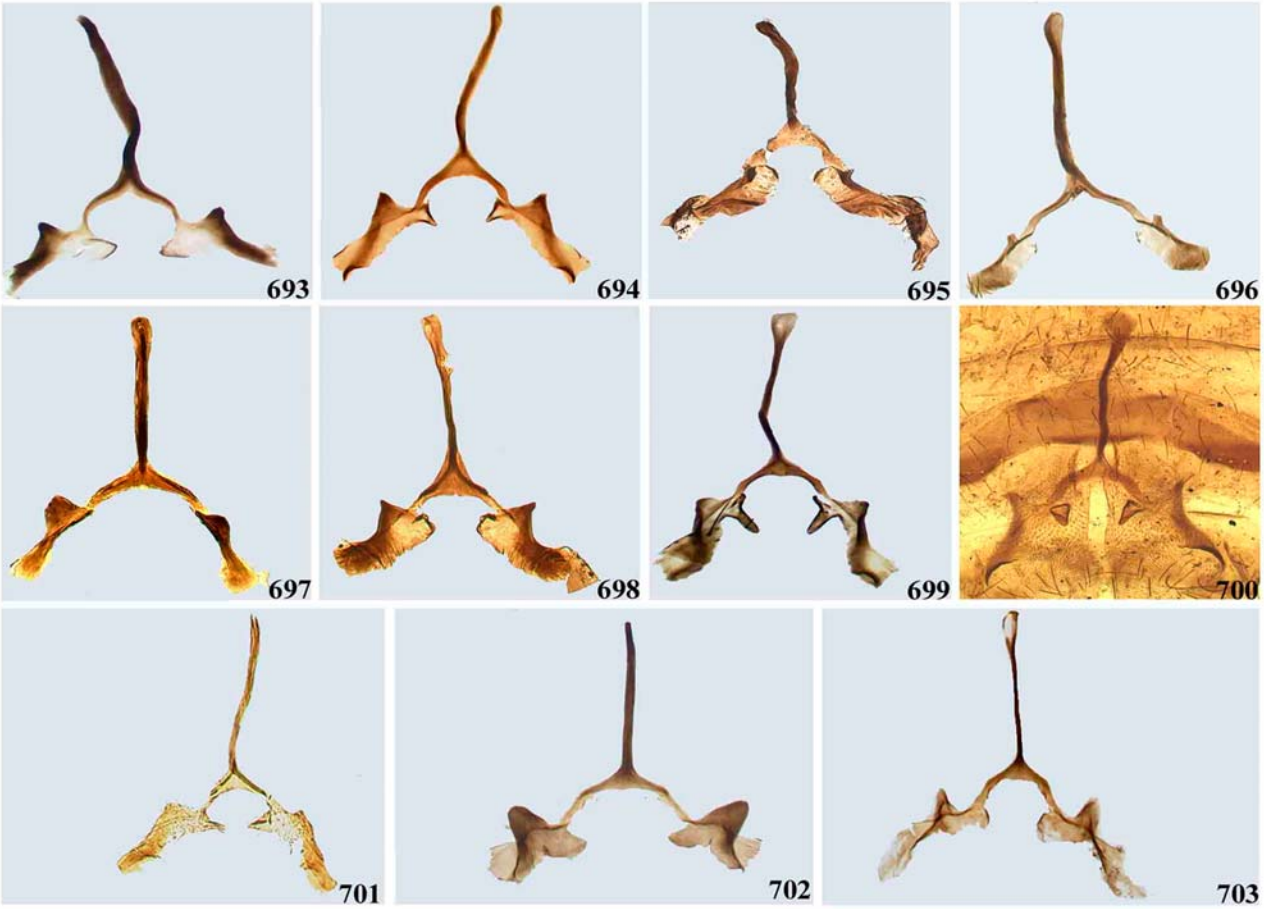


PLATE 57. Figs. 693-703. Genital fork of female, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 693- *S. pulverulentum*; 694- *S. rubrithorax*; 695- *S. smarti*, paratype; 696- *S. solarii*, paratype; 697- *S. tarsale*, lectotype; 698- *S. tarsatum*, lectotype; 699- *S. virgatum s.l.*; 700- *S. virgatum s.l.* (as *S. rubicundulum*, holotype, *in situ*); 701- *S. yepocapense*, paratype. Subgenus *Psilopelmia*, BICOLORATUM species group: 702- *S. oviedoi*; 703- *S. rivasi*.

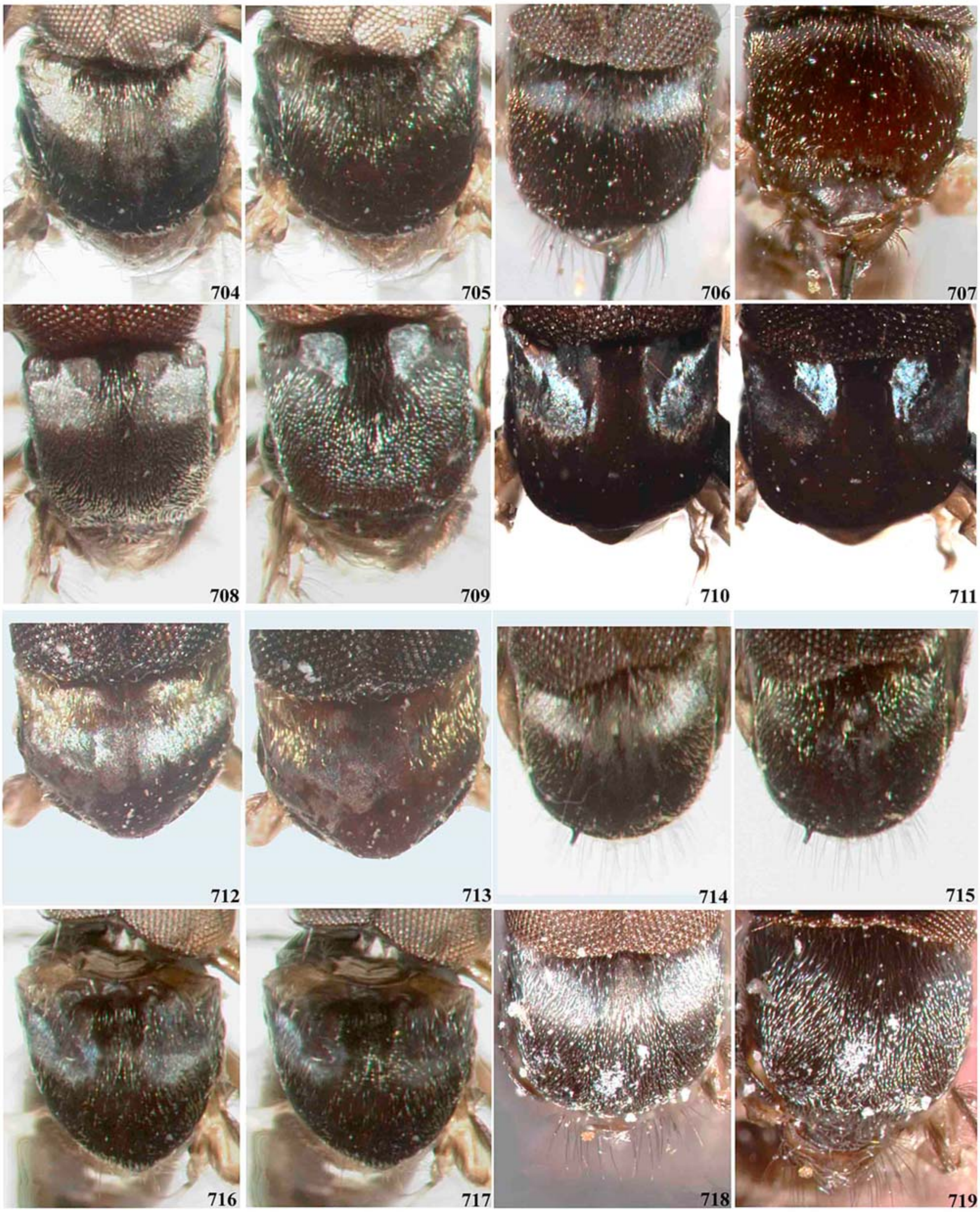


PLATE 58. Figs. 704-719. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction. CANADENSE species group: 704, 705- *S. ayrozai*, paratype; 706, 707- *S. burchi*, paratype; 708, 709- *S. canadense*, holotype; 710, 711- *S. canadense* (as *S. fraternum*, holotype); 712, 713- *S. capricorne*; 714, 715- *S. carolinae*; 716, 717- *S. dalmati*, holotype; 718, 719- *S. delatorrei*, allotype.

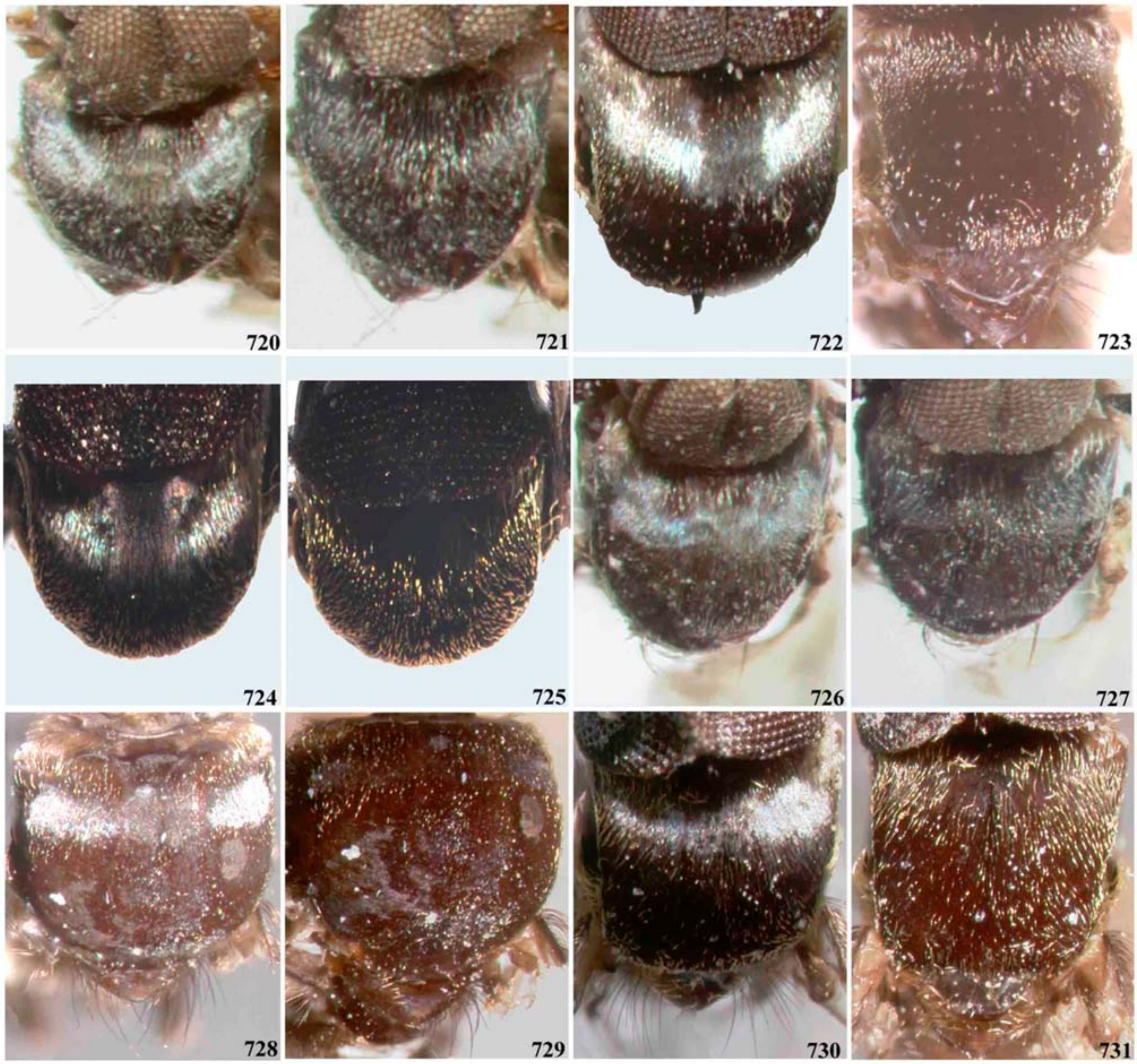


PLATE 59. Figs 720-731. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction. CANADENSE species group: 720, 721- *S. estevezi*, holotype; 722, 723- *S. ethelae*, holotype; 724, 725- *S. ethelae* (as *S. chiriquiense*, Costa Rica); 726, 727- *S. johnsoni*, paratype; 728, 729- *S. larvispinosum*; 730, 731- *S. microbranchium*.

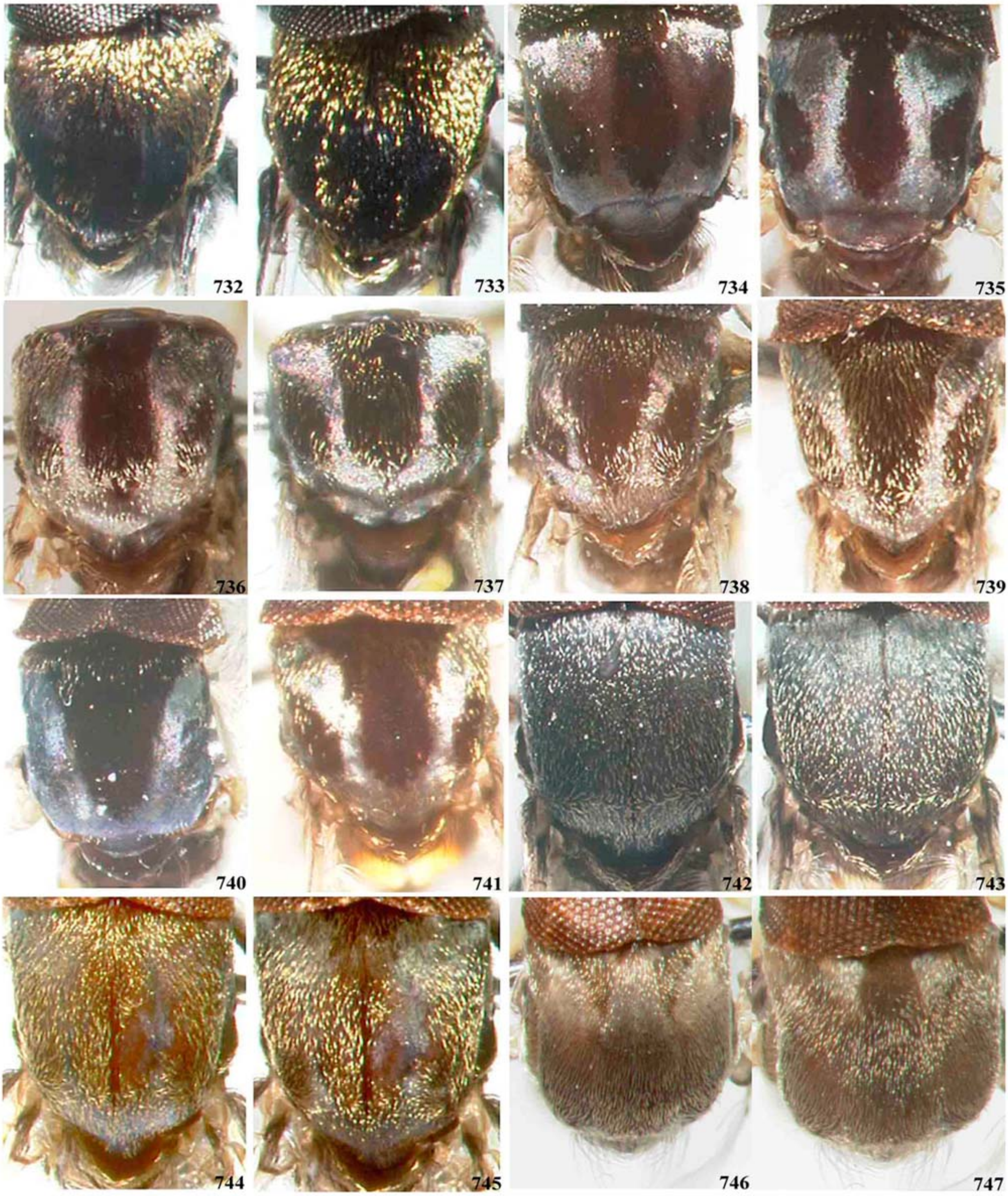


PLATE 60. Figs 732-747. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction unless stated otherwise. ORBITALE species group: 732, 733- *S. duodenicornium*, topotype; 734, 735- *S. guianense s.l.*; 736- *S. guianense s.l.*, Rio Mau, posterior illumination; 737- *S. guianense s.l.*, Rio Tocantins, posterior illumination; 738- *S. guianense s.l.*, Rio Mucajai, posterior illumination; 739- *S. guianense s.l.*, Rio Surumu, posterior illumination; 740- *S. guianense s.l.*, Rio Tapajós; 741- *S. guianense s.l.*, Rio Surumu, posterior illumination; 742, 743- *S. hirtipupa*; 744, 745- *S. hirtipupa* (variation); 746, 747- *S. huairayacu*.

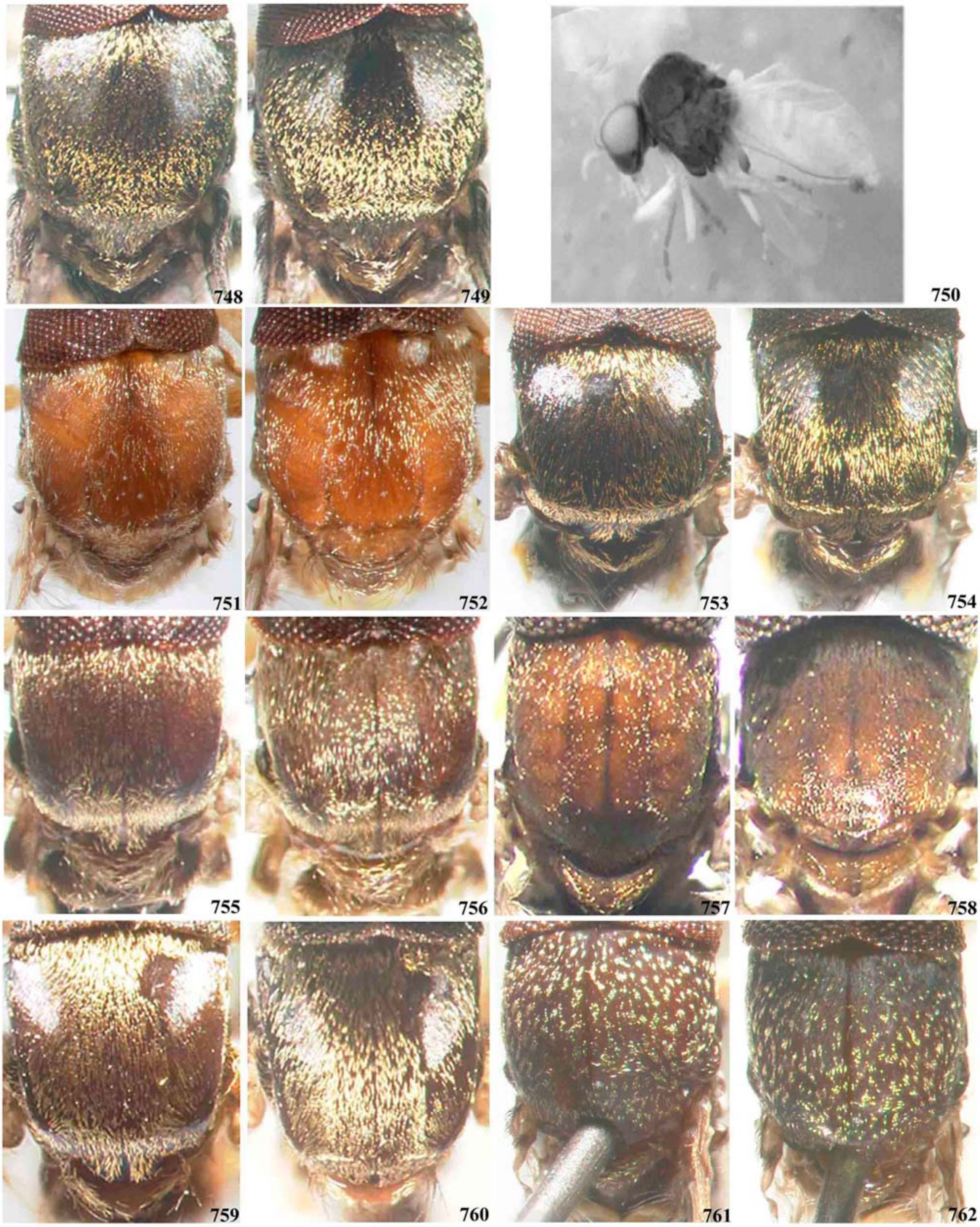


PLATE 61. Figs 748-762. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction unless stated otherwise. ORBITALE species group: 748, 749- *S. itaunense*; 750- *S. jeteri* (after PY-DANIEL *et al.*, 2005, lateral view); 751, 752- *S. lahillei*; 753, 754- *S. lithobranchium*, topotype; 755, 756- *S. nigrimanum*; 757, 758- *S. nunesdemelloi* (after HAMADA *et al.*, 2006); 759, 760- *S. orbitale* (labelled as neoallotype); 761, 762- *S. perplexum*, paratype.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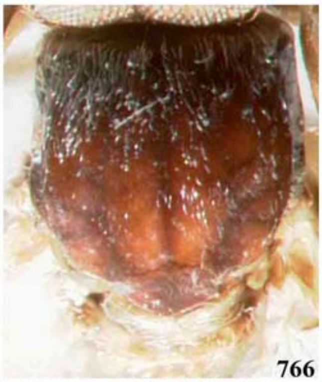
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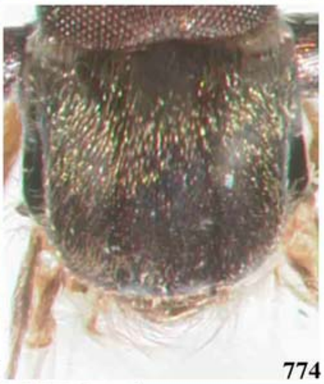
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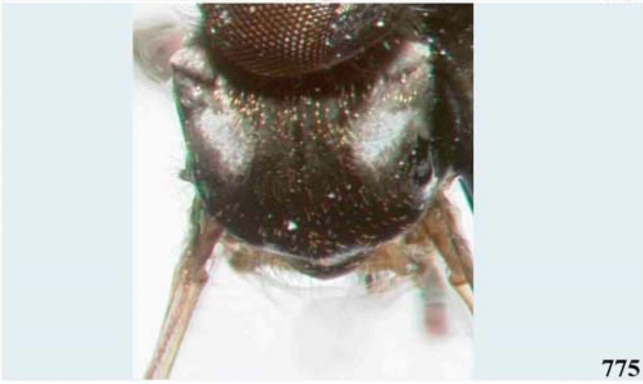
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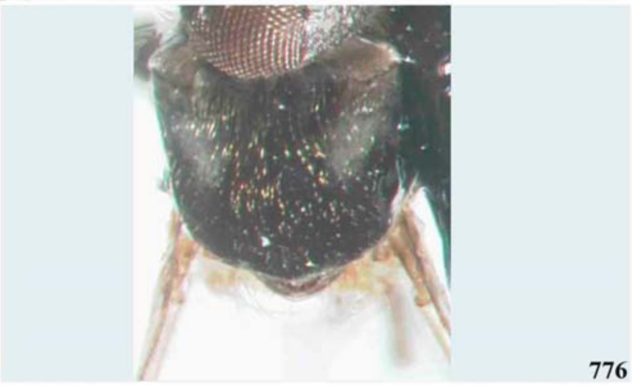
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PLATE 62. Figs 763-776. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction. ORBITALE and PICTIPES species groups: 763, 764- *S. scutistriatum*; 765, 766- *S. townsendi* (as *S. muiscorum*) [specimen pinned from ethanol]; 767, 768- *S. wygodzinskyorum*. PICTIPES species group: 769, 770- *S. claricentrum*, holotype; 771, 772- *S. innoxium*; 773, 774- *S. pictipes*; 775, 776- *S. pictipes* (as *S. longistylatum*, holotype).

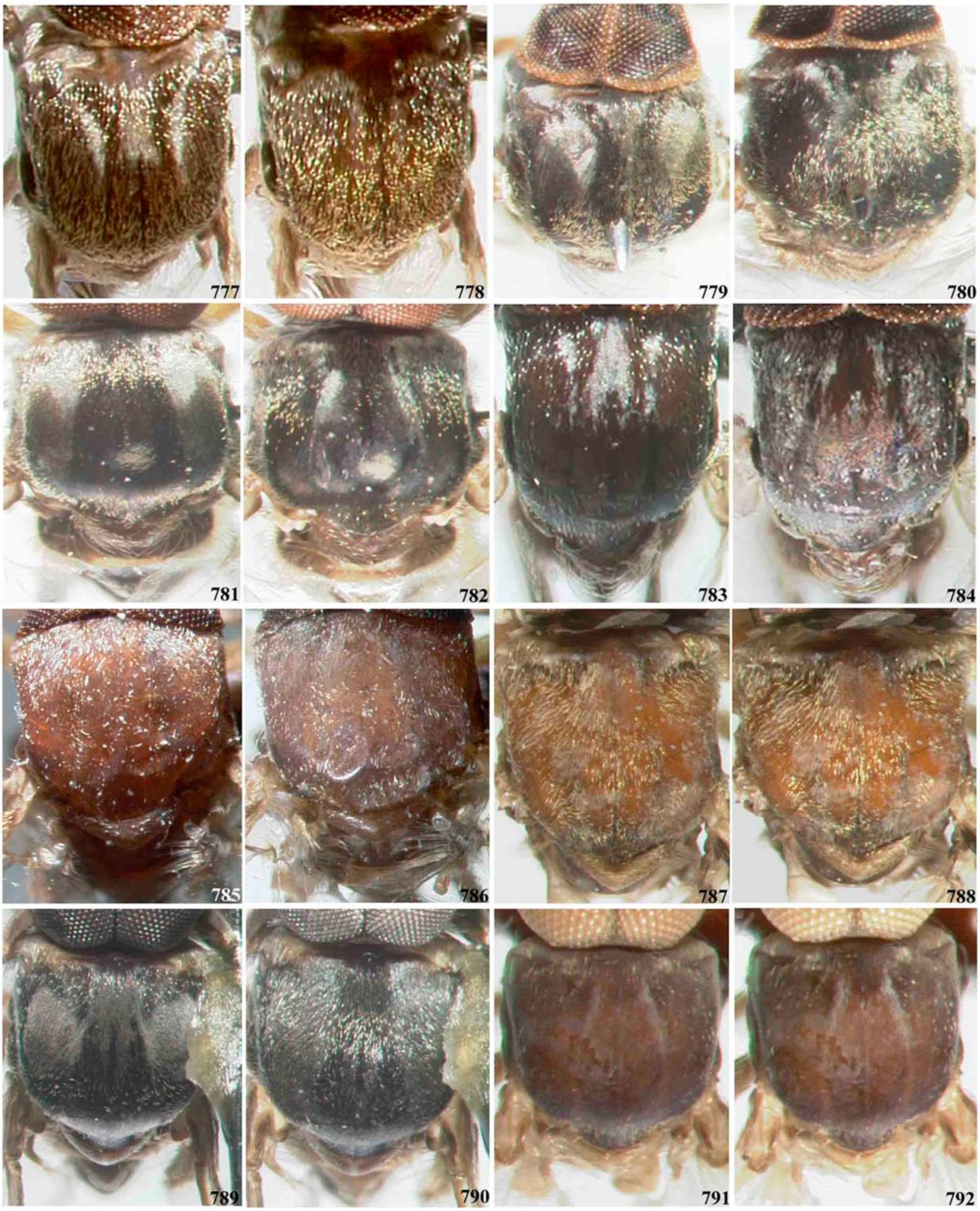

PLATE 63. Figs. 777-792. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction. TARSATUM species group: 777, 778- *S. brachycladum*; 779, 780- *S. bricenoi*, paratype; 781, 782- *S. bricenoi* (as *S. wirthi*, holotype); 783, 784- *S. cristalinum*; 785, 786- *S. earlei*, paratype; 787, 788- *S. freemani*, holotype; 789, 790- *S.* near *freemani,* USA (variation); 791, 792- *S. guerrerense*, holotype.

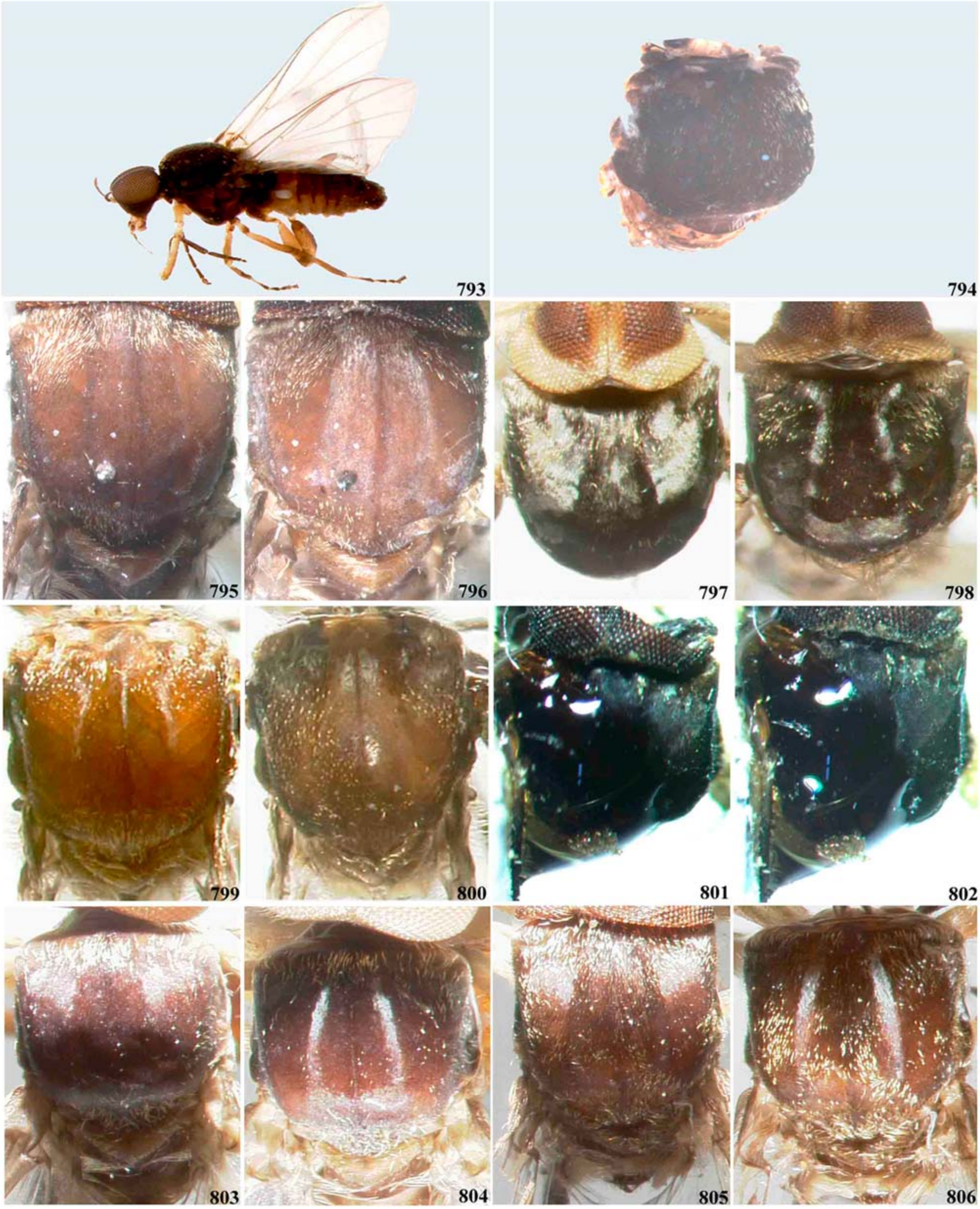

PLATE 64. Figs. 793-806. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction unless stated otherwise. TARSATUM species group: 793- *S. hieroglyphicum*, holotype (in spirit, lateral view); 794- *S. hieroglyphicum* (pharate male in spirit); 795, 796- *S. hinmani*, holotype; 797, 798- *S. hippovorum*; 799, 800- *S. lobatoi*; 801, 802- *S. paynei* (as *Hemicnetha mexicana*); 803, 804- *S. paynei* (as *S. mathesoni*, Mexico); 805, 806- *S. paynei* (as *S. acatenangoensis*, Guatemala).

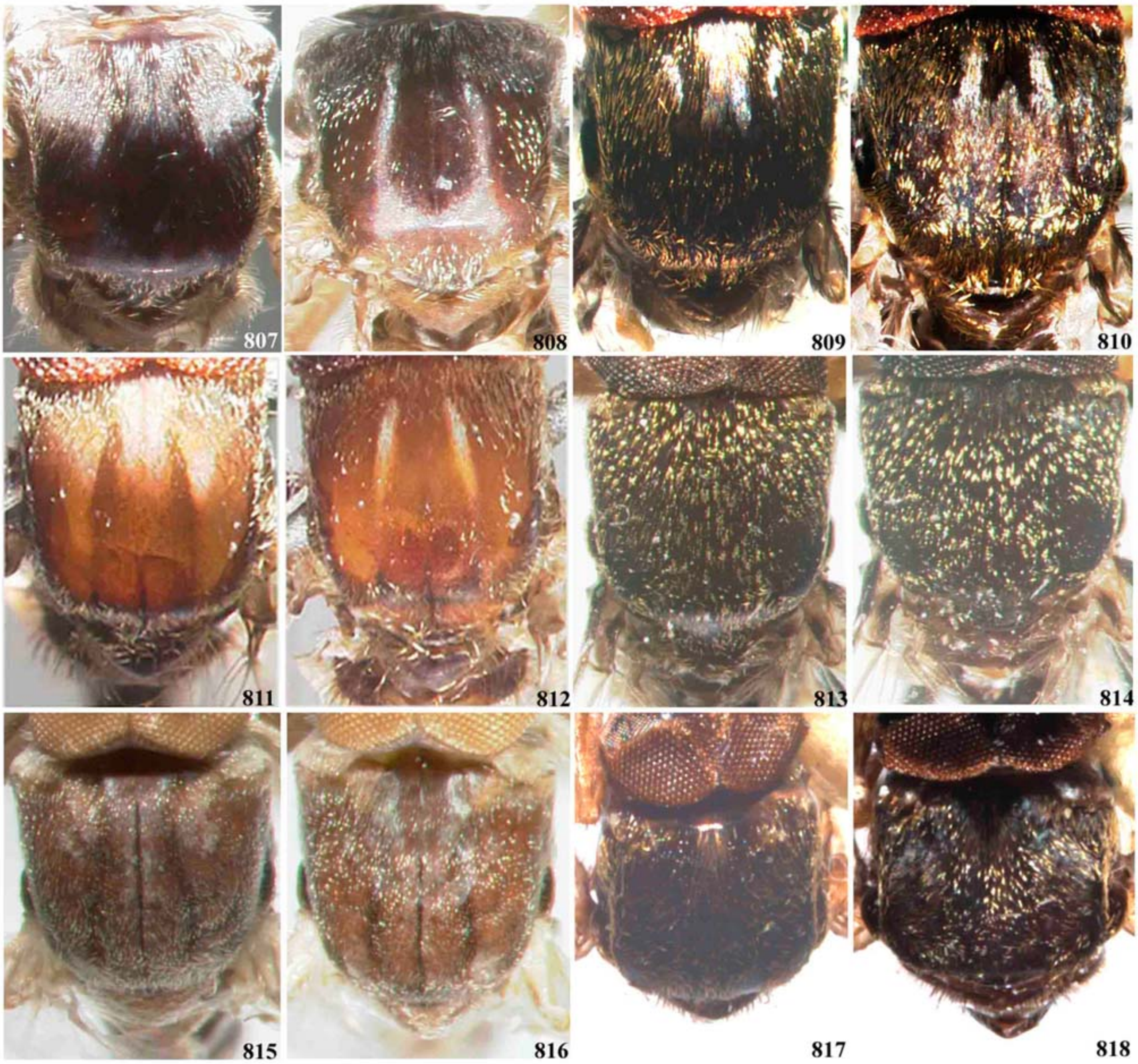

PLATE 65. Figs. 807-818. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction. TARSATUM species group: 807, 808- *S. paynei*, Ecuador; 809, 810- *S. pulverulentum*; 811, 812- *S. rubrithorax*; 813, 814- *S. smarti*, paratype; 815, 816- *S. solarii*, holotype; 817, 818- *S. tarsale*.

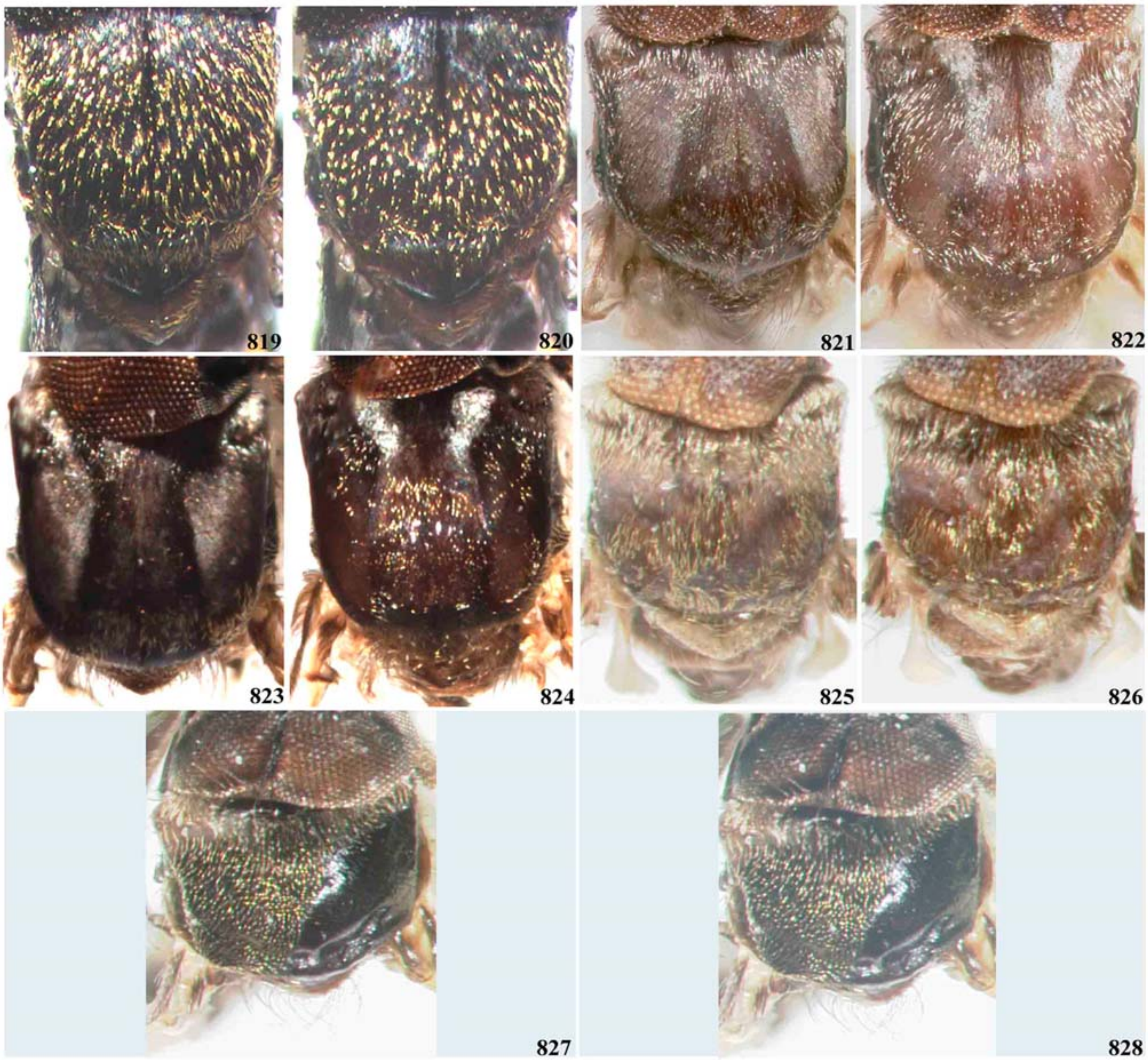

PLATE 66. Figs. 819-828. Scutal coloration of male. The first figure for each specimen shows anterior light direction and the second posterior light direction, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 819, 820- *S. tarsatum* (as *S. mexicanum*); 821, 822- *S. virgatum s.l.*, holotype; 823, 824- *S. virgatum s.l.*, black form, USA; 825, 826- *S. yepocapense*, paratype. Subgenus *Psilopelmia*, BICOLORATUM: 827, 828- *S. rivasi*.


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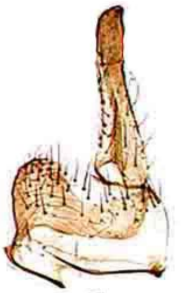
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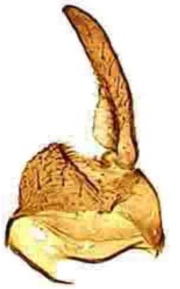
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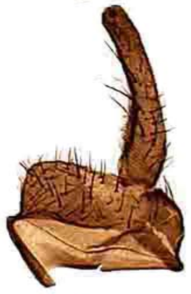
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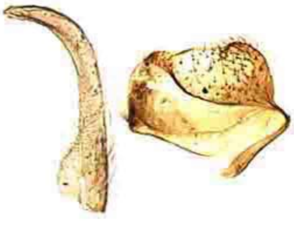
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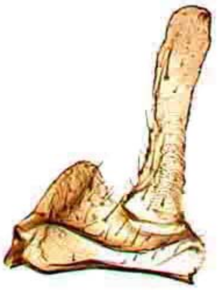
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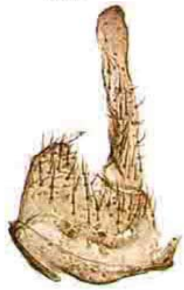
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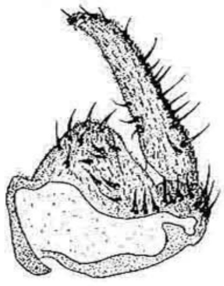
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PLATE 67. Figs. 829-846. Gonocoxite and gonostyle of male, CANADENSE species group: 829- *S. ayrozai*, holotype; 830- *S. burchi*, paratype; 831- *S. canadense*; 832- *S. canadense* (as *S. fraternum*, holotype); 833- *S. capricorne*; 834- *S. carolinae*; 835- *S. contrerense*, holotype; 836- *S. contrerense*, paratype; 837- *S. dalmati*, holotype; 838- *S. delatorrei*, paratype; 839- *S. estevezi*, holotype; 840- *S. ethelae*; 841- *S. gorirossiae*, holotype; 841a- *S. johnsoni* (after VARGAS & DÍAZ NÁJERA, 1957b); 842- *S. juarezi* (after VARGAS & DÍAZ NÁJERA, 1957b); 843- *S. larvispinosum*; 844- *S. menchacai*, paratype; 845- *S. microbranchium*, allotype; 846- *S. nigricorne* (after DALMAT, 1950).

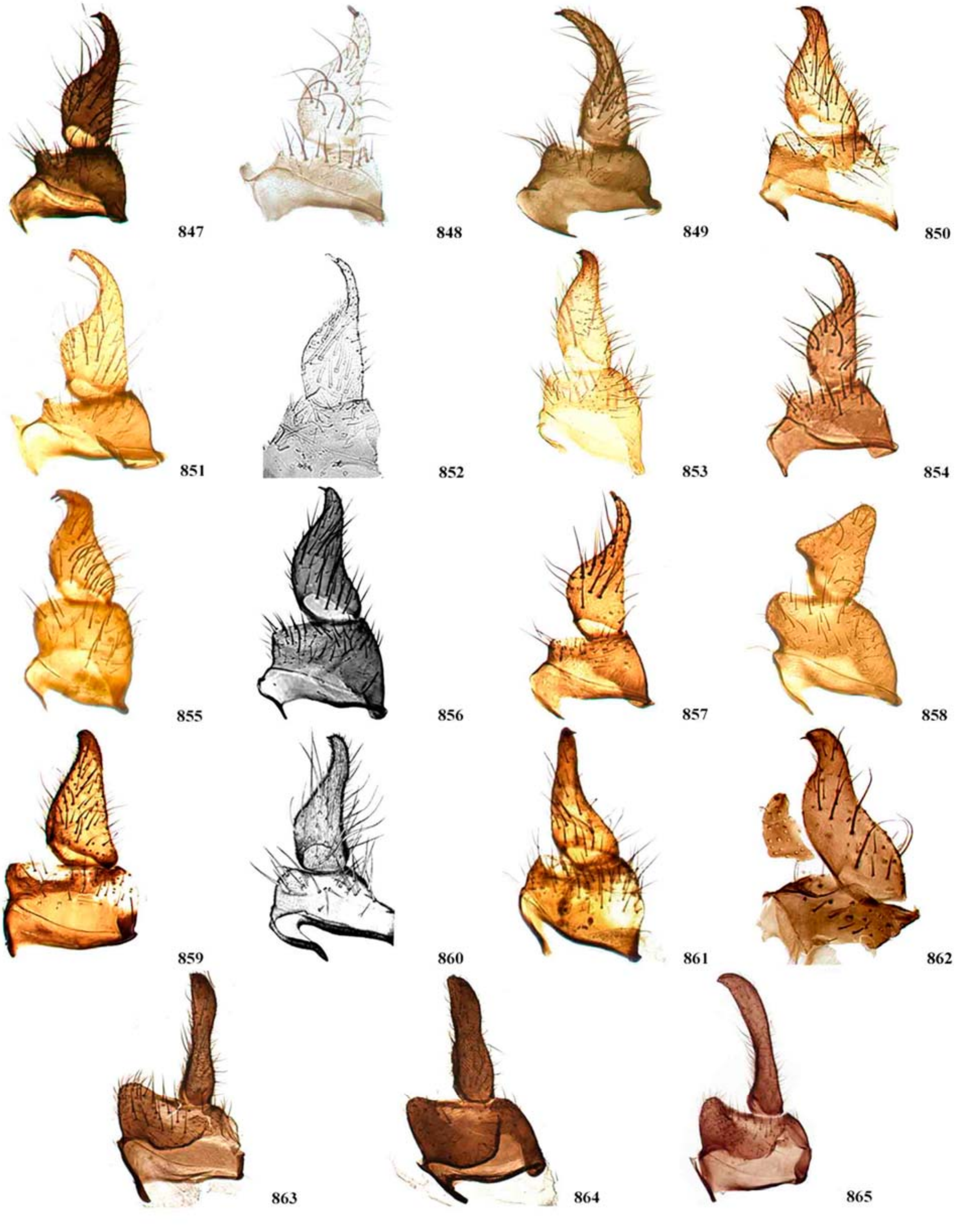

PLATE 68. Figs. 847-865. Gonocoxite and gonostyle of male, ORBITALE and PICTIPES species groups. ORBITALE species group: 847- *S. duodenicornium*, topotype; 848- *S. guianense s.l.*; 849- *S. hirtipupa*; 850- *S. huairayacu*; 851- *S. itaunense*; 852- *S. jeteri* (after Py-Daniel *et al.,* 2005); 853- *S. lahillei*; 854- *S. lithobranchium*, topotype; 855- *S. nigrimanum*; 856- *S. nunesdemelloi* (after Hamada *et al*., 2006); 857- *S. orbitale*; 858- *S. perplexum*, paratype; 859- *S. scutistriatum*; 860- *S. sumapazense* (after Muñoz de Hoyos, 1996); 861- *S. townsendi* (as *S. muiscorum*); 862- *S. wygodzinskyorum*. PICTIPES species group: 863- *S. claricentrum*; 864- *S. innoxium*; 865- *S. pictipes.*

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PLATE 69. Figs. 866-880. Gonocoxite and gonostyle of male, TARSATUM species group: 866- *S. brachycladum*; 867- *S. bricenoi*, holotype; 868- *S. bricenoi* (as *S. wirthi*, paratype); 869- *S. cristalinum*; 870- *S. earlei*, holotype; 871- *S. freemani*, holotype; 872- *S. guerrerense*, paratype; 873- *S. hieroglyphicum*, paratype; 874- *S. hinmani*, holotype; 875- *S. hippovorum*; 876- *S. lobatoi*; 877- *S. paynei* (as *Hemicnetha mexicana*); 878- *S. paynei* (as *S. mathesoni*, holotype); 879- *S. paynei* (as *S. acatenangoensis*, holotype); 880- *S. paynei*, Ecuador.


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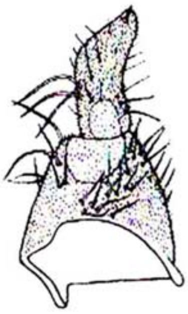
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PLATE 70. Figs. 881-890. Gonocoxite and gonostyle of male, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 881- *S. pulverulentum*; 882- *S. rubrithorax*; 883- *S. smarti*, allotype; 884- *S. solarii*, holotype; 885- *S. tarsale*; 886- *S. tarsatum* (as *S. mexicanum*); 887- *S. virgatum s.l.*, holotype; 888- *S. yepocapense*. Subgenus *Psilopelmia*, BICOLORATUM species group: 889- *S. oviedoi* (after RAMÍREZ-PÉREZ, 1971); 890- *S. rivasi*.

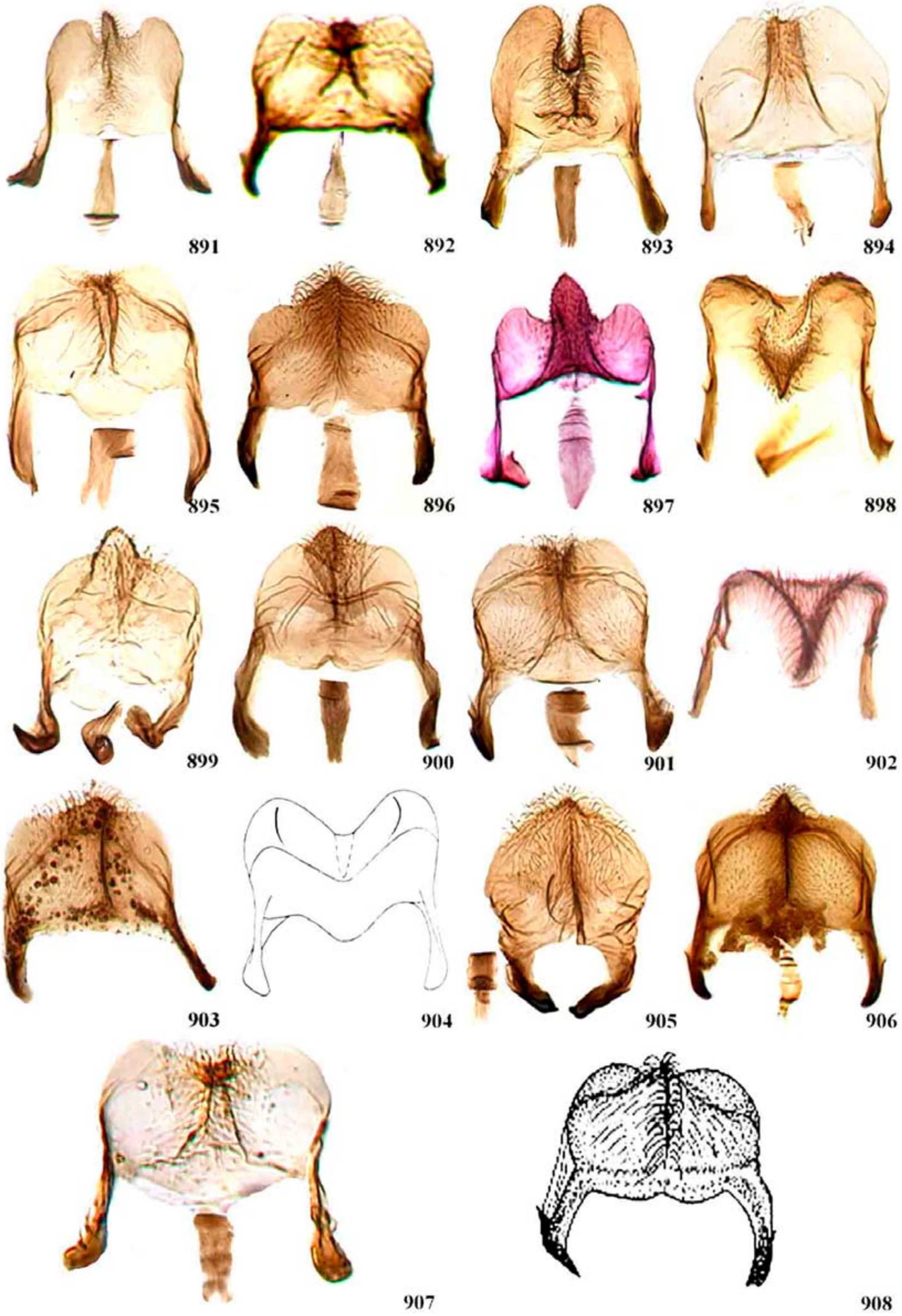

PLATE 71. Figs. 891-908. Ventral plate and median sclerite of male, CANADENSE species group: 891- *S. ayrozai*, holotype; 892- *S. burchi*, allotype; 893- *S. canadense*; 894- *S. canadense* (as *S. fraternum*, holotype); 895- *S. capricorne*; 896- *S. carolinae*; 897- *S. contrerense*, holotype; 898- *S. dalmati*, holotype; 899- *S. delatorrei*, paratype; 900- *S. estevezi*, holotype; 901- *S. ethelae*; 902- *S. gorirossiae*, holotype; 903- *S. johnsoni*; 904- *S. juarezi* (after VARGAS & DÍAZ NÁJERA, 1957b) [anterior margin distorted]; 905- *S. larvispinosum*; 906- *S. menchacai* [median sclerite of a paratype]; 907- *S. microbranchium*, allotype; 908- *S. nigricorne* (after DALMAT, 1950).

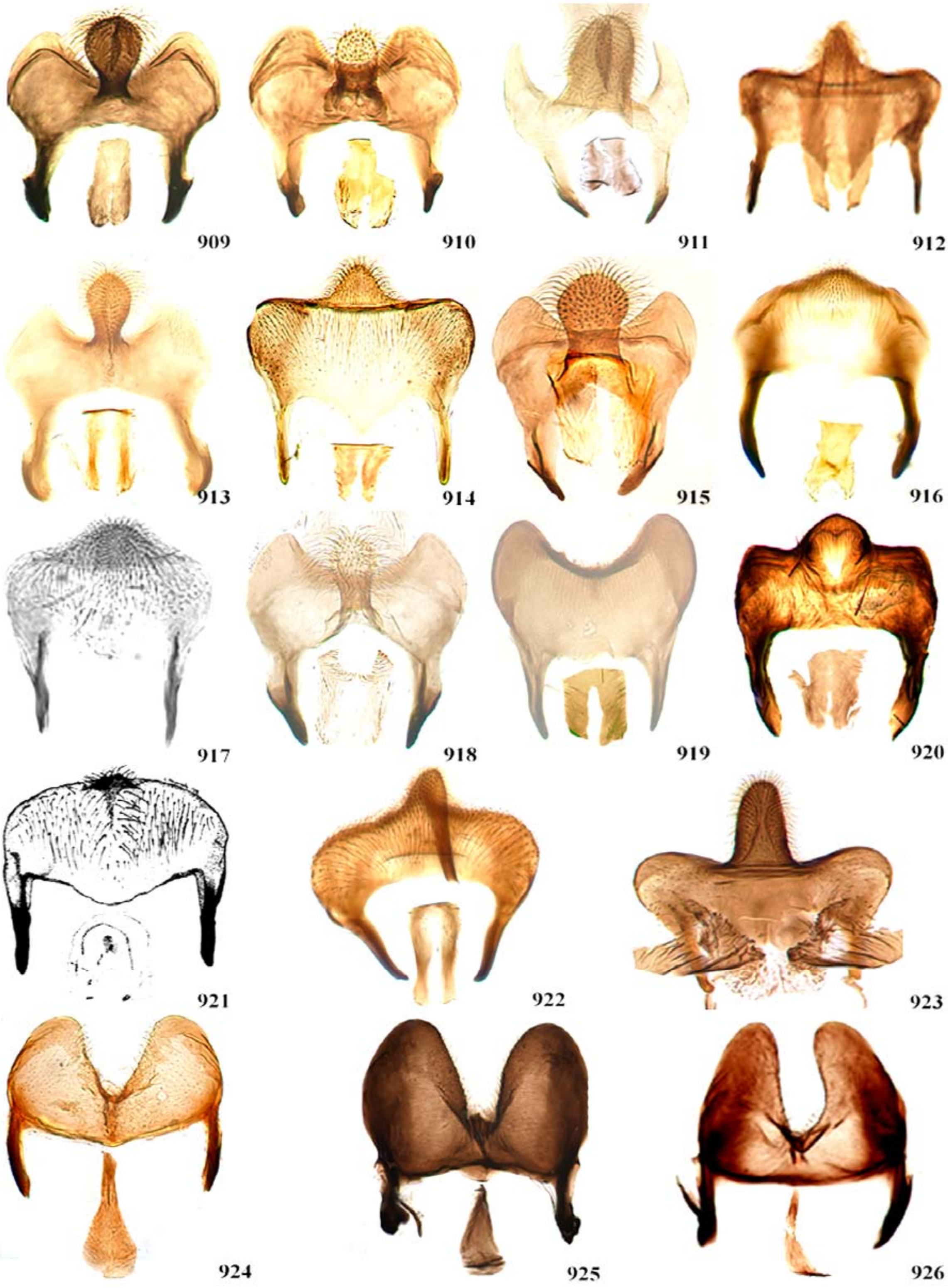

PLATE 72. Figs. 909-926. Ventral plate and median sclerite of male, ORBITALE and PICTIPES species groups. ORBITALE species group: 909- *S. duodenicornium*, topotype; 910- *S. guianense s.l.*; 911- *S. hirtipupa*; 912- *S. huairayacu*; 913- *S. itaunense*; 914- *S. lahillei*; 915- *S. lithobranchium*, topotype; 916- *S. nigrimanum*; 917- *S. nunesdemelloi* (after HAMADA *et al.*, 2006); 918- *S. orbitale*; 919- *S. perplexum*, paratype; 920- *S. scutistriatum*; 921- *S. sumapazense* (after MUÑOZ DE HOYOS, 1996); 922- *S. townsendi* (as *S. muiscorum*); 923- *S. wygodzinskyorum*, paratype. PICTIPES species group: 924- *S. claricentrum*; 925- *S. innoxium*; 926- *S. pictipes.*


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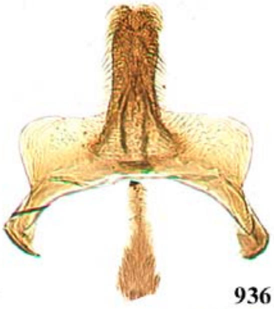
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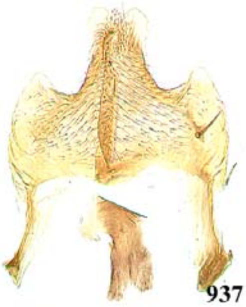
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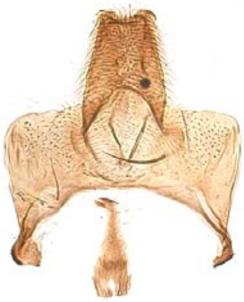
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PLATE 73. Figs. 927-941. Ventral plate and median sclerite of male, TARSATUM species group: 927- *S. brachycladum*; 928- *S. bricenoi*, holotype; 929- *S. bricenoi* (as *S. wirthi*, paratype); 930- *S. cristalinum*; 931- *S. earlei*, holotype; 932- *S. freemani*, holotype; 933- *S. guerrerense*, paratype; 934- *S. hieroglyphicum*, pharate male; 935- *S. hinmani*, holotype; 936- *S. hippovorum*; 937- *S. lobatoi*, paratype; 938- *S. paynei* (as *Hemicnetha mexicana*); 939- *S. paynei* (as *S. mathesoni*, holotype); 940- *S. paynei* (as *S. acatenangoensis*, holotype); 941- *S. paynei*, Ecuador.


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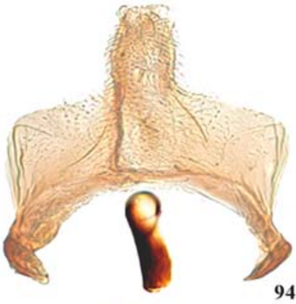
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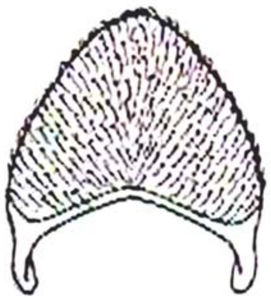
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PLATE 74. Figs. 942-951. Ventral plate and median sclerite of male, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 942- *S. pulverulentum*; 943- *S. rubrithorax*; 944- *S. smarti*, allotype; 945- *S. solarii* (ventral plate, holotype; median sclerite, paratype); 946- *S. tarsale*, Dominica (ventral plate *in situ*; median sclerite not well defined in the slide of the single specimens examined); 947- *S. tarsatum* (as *S. mexicanum*); 948- *S. virgatum s.l.*, holotype; 949- *S. yepocapense*, paratype. Subgenus *Psilopelmia*, BICOLORATUM: 950- *S. oviedoi* (after RAMÍREZ-PÉREZ, 1971); 951- *S. rivasi.*

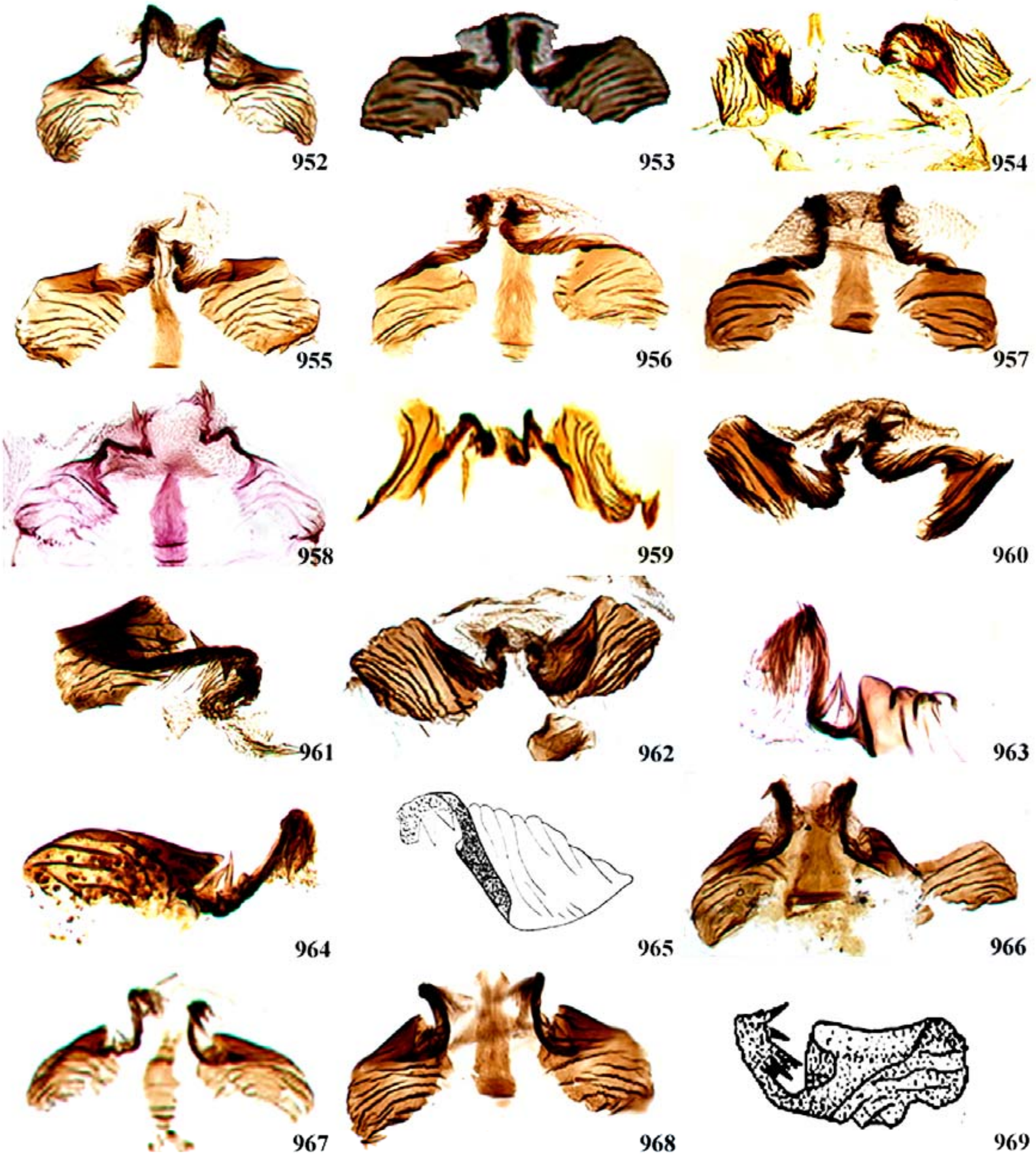

PLATE 75. Figs. 952-969. Male paramere, CANADENSE species group: 952- *S. ayrozai*, holotype; 953- *S. burchi*, allotype; 954- *S. canadense*; 955- *S. canadense* (as *S. fraternum*, holotype); 956- *S. capricorne*; 957- *S. carolinae*; 958- *S. contrerense*, holotype; 959- *S. dalmati*, holotype; 960- *S. delatorrei*, paratype; 961- *S. estevezi*, holotype; 962- *S. ethelae*; 963- *S. gorirossiae*, holotype; 964- *S. johnsoni*, holotype; 965- *S. juarezi* (after VARGAS & DÍAZ NÁJERA, 1957b); 966- *S. larvispinosum*; 967- *S. menchacai*, paratype; 968- *S. microbranchium*; 969- *S. nigricorne* (after DALMAT, 1950).

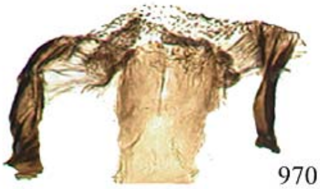
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PLATE 76. Figs. 970-986. Male paramere, ORBITALE and PICTIPES species groups. ORBITALE species group: 970- *S. duodenicornium*, topotype; 971- *S. guianense s.l.*; 972- *S. hirtipupa*; 973- *S. huairayacu*, paratype; 974- *S. itaunense*; 975- *S. lahillei*; 976- *S. lithobranchium*, topotype; 977- *S. nigrimanum*; 978- *S. nunesdemelloi* (after HAMADA *et al.*, 2006); 979- *S. orbitale*; 980- *S. perplexum*, paratype; 981- *S. scutistriatum*; 982- *S. sumapazense* (after MUÑOZ DE HOYOS (1996); 983- *S. townsendi* (as *S. muiscorum*). PICTIPES species group: 984- *S. claricentrum*; 985- *S. innoxium*; 986- *S. pictipes*.

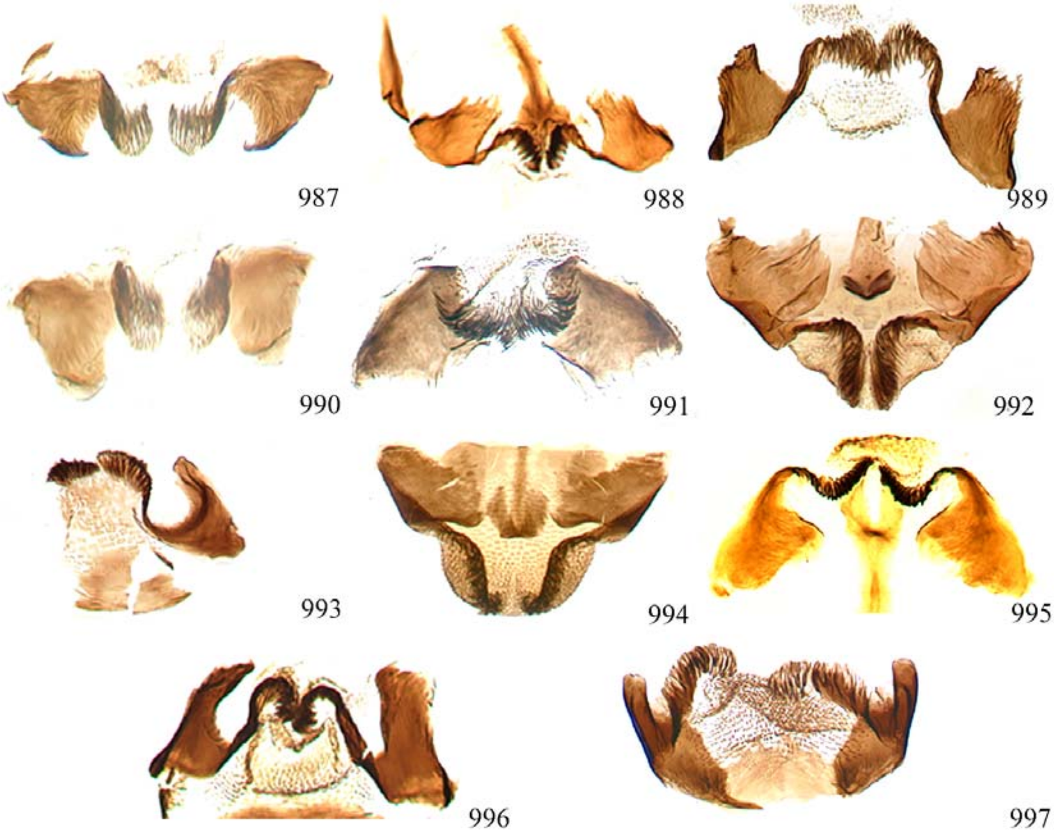

PLATE 77. Figs. 987-997. Male paramere, TARSATUM species group: 987- *S. brachycladum*; 988- *S. bricenoi*, holotype; 989- *S. bricenoi* (as *S. wirthi*, paratype); 990- *S. cristalinum*; 991- *S. earlei*; 992- *S. freemani*, holotype; 993- *S. guerrerense*, paratype; 994- *S. hieroglyphicum*, paratype; 995- *S. hinmani*, holotype; 996- *S. hippovorum*; 997- *S. lobatoi*, paratype.

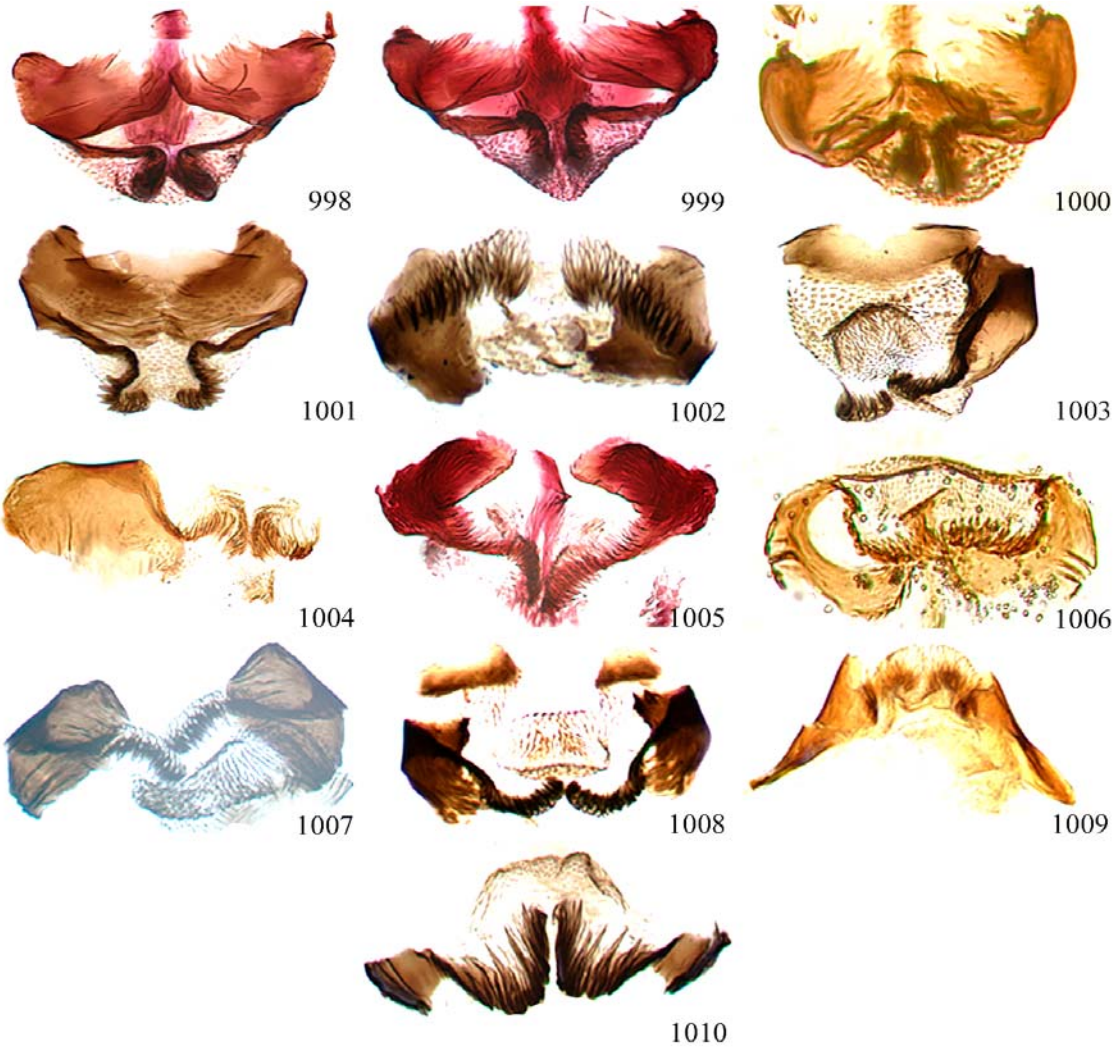

PLATE 78. Figs. 998-1010. Male paramere, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 998- *S. paynei* (as *Hemicnetha mexicana*); 999- *S. paynei* (as *S. mathesoni*, holotype); 1000- *S. paynei* (as *S. acatenangoensis*, holotype); 1001- *S. paynei*, Ecuador; 1002- *S. pulverulentum*; 1003- *S. rubrithorax*; 1004- *S. smarti*, paratype; 1005- *S. solarii*, paratype; 1006- *S. tarsale*, Dominica; 1007- *S. tarsatum* (as *S. mexicanum*); 1008- *S. virgatum s.l.*, holotype; 1009- *S. yepocapense*, paratype. Subgenus *Psilopelmia*, BICOLORATUM: 1010- *S. rivasi*.


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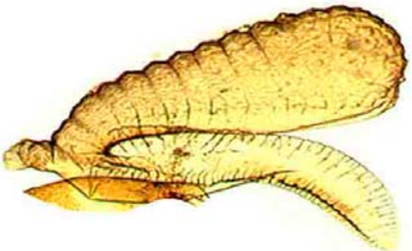
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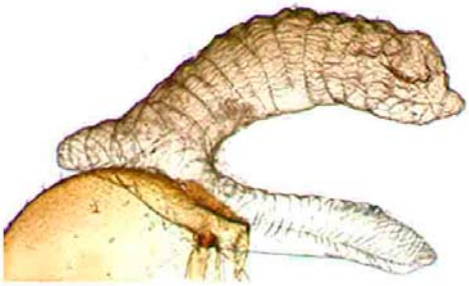
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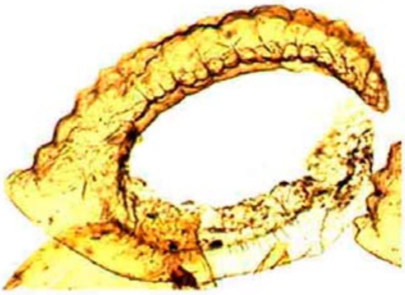
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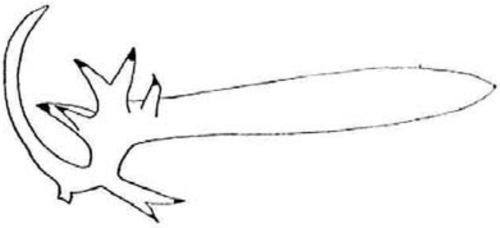
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PLATE 79. Figs. 1011-1020. Pupal gill, CANADENSE species group: 1011- *S. ayrozai*; 1012- *S. burchi*; 1013- *S. canadense*; 1014- *S. capricorne*; 1015- *S. capricorne* (as *S. deleoni*, holotype); 1016- *S. carolinae*; 1017- *S. contrerense*, holotype; 1018- *S. dalmati*; 1019- *S. delatorrei*, paratype; 1020- *S. estevezi*.

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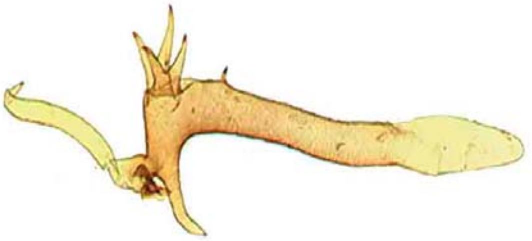

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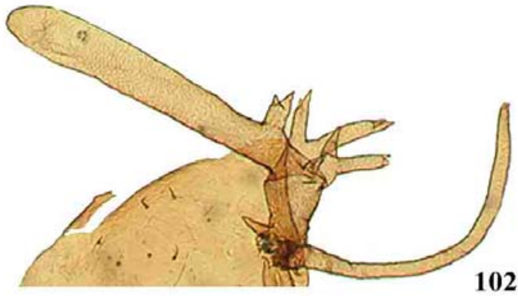

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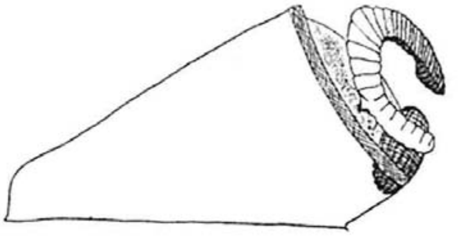

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PLATE 80. Figs. 1021-1029. Pupal gill, CANADENSE species group: 1021- *S. ethelae* (as *S. chiriquiense*); 1022- *S. gorirossiae*; 1023- *S. johnsoni*, holotype; 1024- *S. juarezi*; 1025- *S. larvispinosum*; 1026- *S. menchacai*; 1027- *S. microbranchium*; 1028- *S. nigricorne* (after Dalmat, 1950); 1029- *S. temascalense*, holotype.

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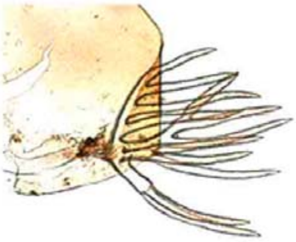

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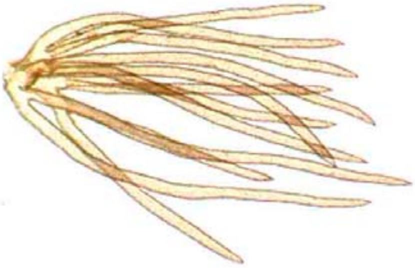

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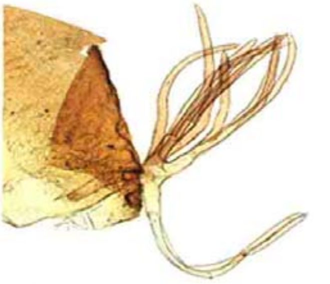

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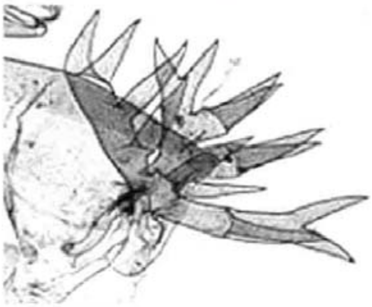

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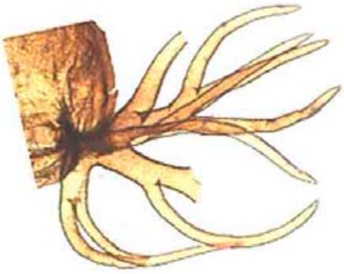

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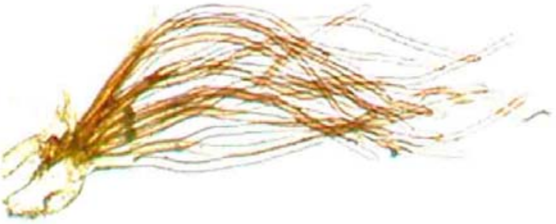

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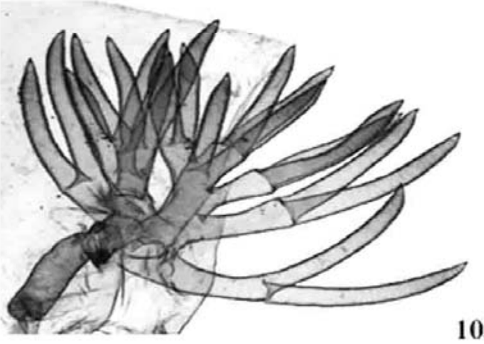

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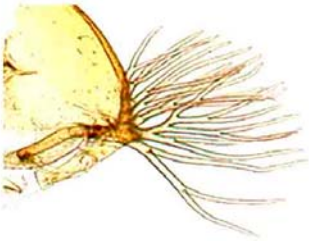
PLATE 81. Figs. 1030-1039. Pupal gill, ORBITALE species group: 1030- *S. duodenicornium*, topotype; 1031- *S. guianense s.l.*; 1032- *S. hirtipupa*; 1033- *S. huairayacu*; 1034- *S. itaunense*; 1035- *S. jeteri* (after PY-DANIEL *et al.*, 2005); 1036- *S. lahillei;* 1037- *S. lithobranchium,* topotype; 1038- *S. nigrimanum;* 1039- *S. nunesdemelloi* (after HAMADA *et al.*, 2006).



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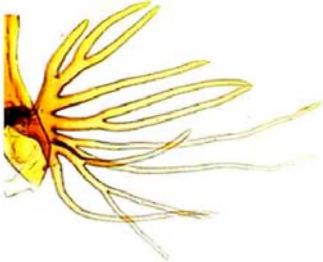

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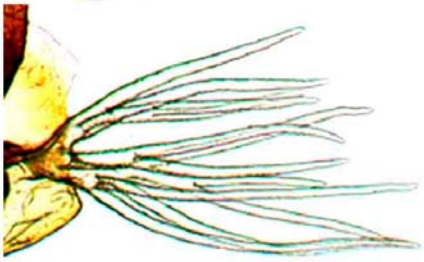

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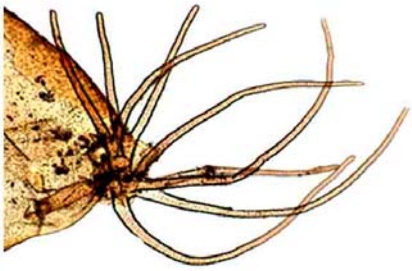

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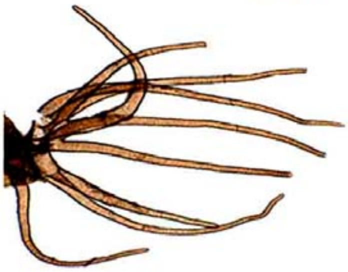

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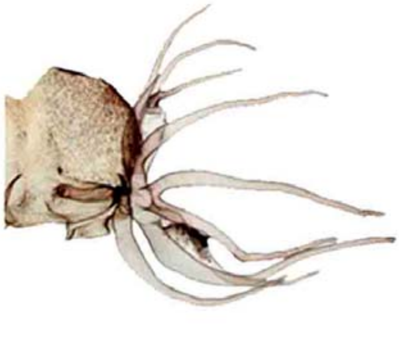

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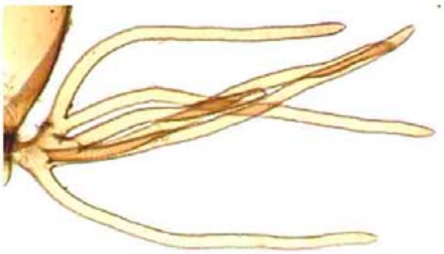
PLATE 82. Figs. 1040-1048. Pupal gill, ORBITALE and PICTIPES species group. ORBITALE species group: 1040- *S. orbitale*; 1041- *S. perplexum*; 1042- *S. scutistriatum*; 1043- *S. sumapazense*, holotype; 1044- *S. townsendi* (as *S. muiscorum*); 1045- *S. wygodzinskyorum*, paratype. PICTIPES species group: 1046- *S. claricentrum*; 1047- *S. innoxium*; 1048- *S. pictipes*.



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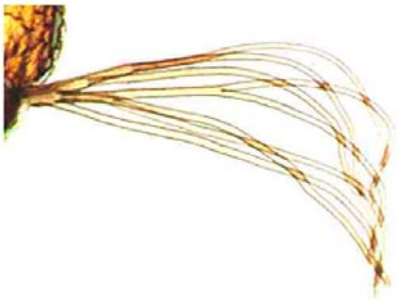

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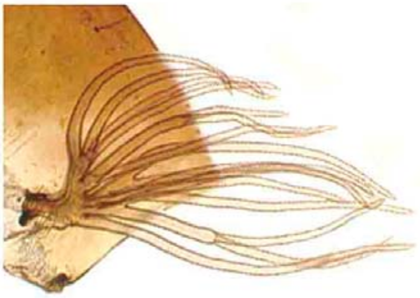

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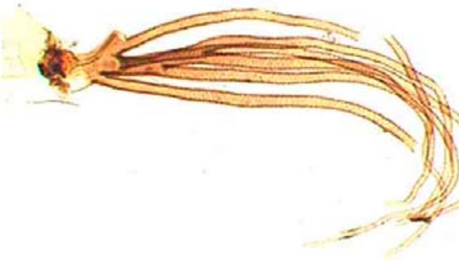

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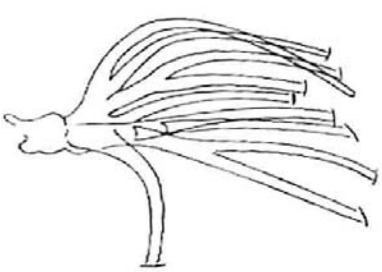
PLATE 83. Figs. 1049-1058. Pupal gill, TARSATUM species group: 1049- *S. brachycladum*; 1050- *S. bricenoi*, allotype; 1051- *S. bricenoi* (as *S. wirthi*, paratype); 1052- *S. cristalinum*; 1053- *S. cristalinum*, variation; 1054- *S. earlei*; 1055- *S. freemani*, holotype (gill filaments in *situ*); 1056- *S. freemani*, paratype [only specimen available with some broken filaments]; 1057- *S. guerrerense* (after VARGAS & DÍAZ NÁJERA, 1956); 1058- *S. hieroglyphicum*, paratype.



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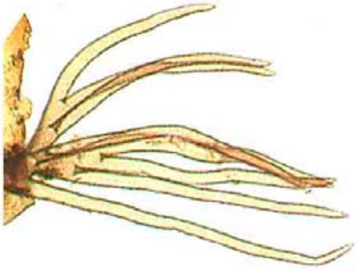

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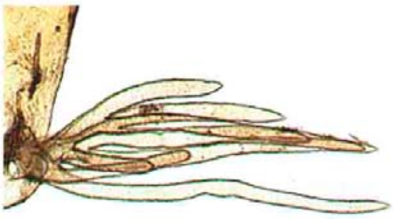

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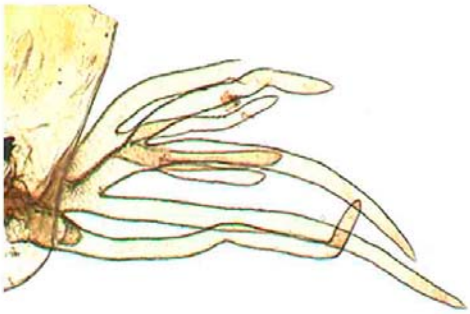

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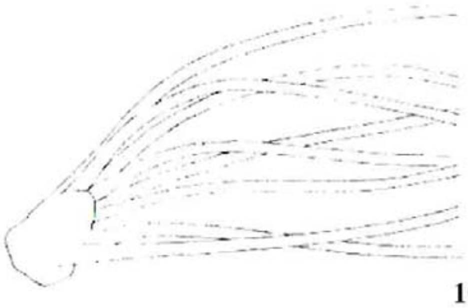

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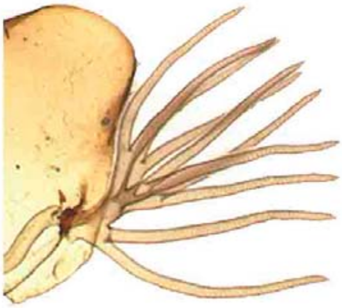

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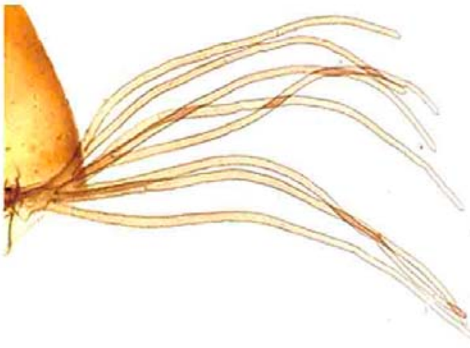

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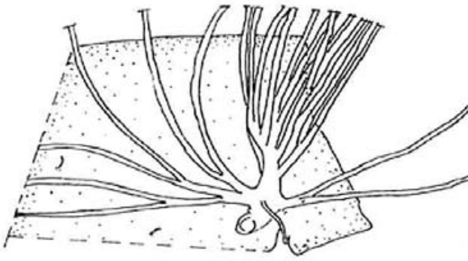
PLATE 84. Figs. 1059-1068 Pupal gill, TARSATUM species group: 1059- *S. hinmani* (after IBÁÑEZ-BERNAL, 1992); 1060- *S. hippovorum*; 1061- *S. lobatoi*, paratype; 1062- *S. lobatoi*, variation; 1063- *S. lobatoi*, variation; 1064- *S. paynei* (as *S. mathesoni* after VARGAS, 1943b); 1065- *S. paynei* (as *S. bricenoi*, paratype); 1066- *S. paynei*, Costa Rica; 1067- *S. pulverulentum*; 1068- *S. rubrithorax*.



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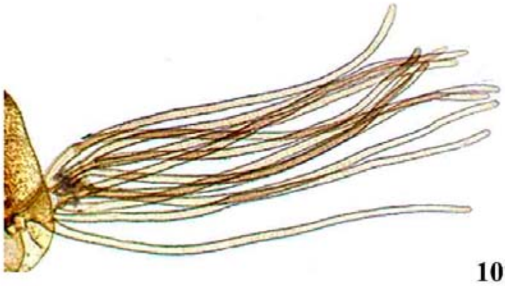

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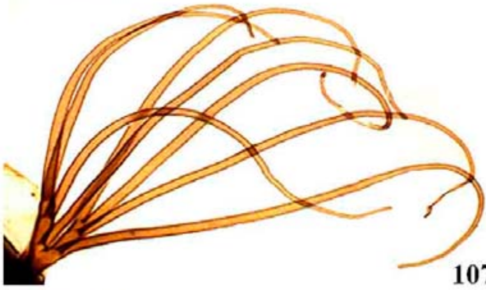

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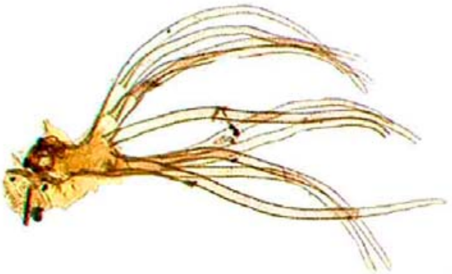

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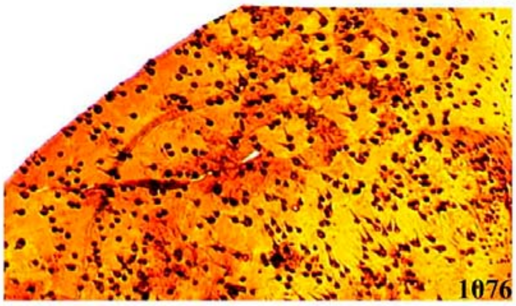

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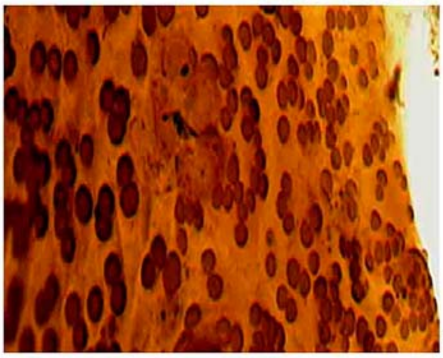

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PLATE 85. Figs. 1069-1077. Pupal gill, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 1069- *S. smarti* (after COSCARÓN & COSCARÓN-ARIAS, 2007); 1070- *S. solarii* (gill filaments *in situ*); 1071- *S. tarsatum* (as *S. mexicanum*); 1072- *S. virgatum s.l.*; 1073- *S. yepocapense*, holotype. Subgenus *Psilopelmia*, BICOLORATUM: 1074- *S. oviedoi*; 1075- *S. rivasi*. Tubercles on pupal thorax integument: 1076- *S. oviedoi*; 1077- *S. rivasi*.

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PLATE 86. Figs. 1078-1084. Larva, lateral view, CANADENSE species group: 1078- *S. burchi*; 1079- *S. canadense*, 1080- *S. capricorne*; 1081- *S. carolinae*; 1082- *S. delatorrei*; 1083- *S. ethelae* (as *S. chiriquiense*); 1084- *S. gorirossiae*.


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PLATE 87. Figs. 1085-1092. Larva, lateral view, ORBITALE species group: 1085- *S. duodenicornium*, topotype; 1086- *S. guianense s.l.*; 1087- *S. hirtipupa*; 1088- *S. huairayacu*; 1089- *S. itaunense* (photos Mateus Pepinelli); 1090- *S. jeteri* (after Py-Daniel *et al.*, 2005); 1091- *S. lahillei;* 1092- *S. lithobranchium,* topotype (arrow indicate the presence of tubercles on the abdomen).

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PLATE 88. Figs. 1093-1098. Larva, lateral view, ORBITALE species group: 1093- *S. nigrimanum;* 1094- *S. nunesdemelloi* (after Hamada *et al.*, 2006); 1095- *S. orbitale*; 1096- *S. scutistriatum*; 1097- *S. sumapazense* (after Muñoz de Hoyos, 1996); 1098- *S. townsendi* (as *S. muiscorum*).

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PLATE 89. Figs. 1099-1106. Larva, lateral view, PICTIPES and TARSATUM species group. PICTIPES species group: 1099- *S. claricentrum*; 1100- *S. innoxium*; 1101- *S. pictipes*. TARSATUM species group: 1102- *S. brachycladum*; 1103- *S. bricenoi*; 1104- *S. earlei*; 1105- *S. freemani*; 1106- *S. guerrerense*.

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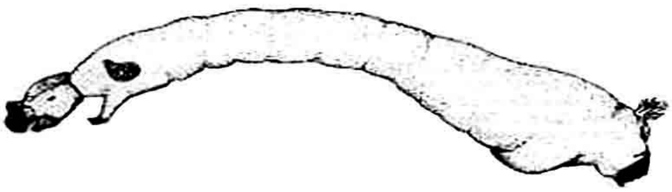

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PLATE 90. Figs. 1107-1114. Larva, lateral view, TARSATUM species group: 1107- *S. hieroglyphicum*; 1108- *S. hinmani* (after IBÁÑEZ-BERNAL, 1992); 1109- *S. hippovorum*; 1110- *S. lobatoi*; 1111- *S. paynei*, Costa Rica; 1112- *S. pulverulentum*; 1113- *S. rubrithorax*; 1114- *S. smarti* (after IBÁÑEZ-BERNAL, 1992).

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PLATE 91. Figs. 1115-1121. Larva, lateral view, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 1115- *S. solarii*, head brown; 1116-*S. solarii*, head yellow; 1117- *S. tarsatum* (as *S. mexicanum*); 1118- *S. virgatum s.l.*; 1119- *S. yepocapense*, (after IBÁÑEZ-BERNAL, 1992). Subgenus *Psilopelmia*, BICOLORATUM: 1120- *S. oviedoi* (photo MATEUS PEPINELLI); 1121- *S. rivasi* (photo MATEUS PEPINELLI).


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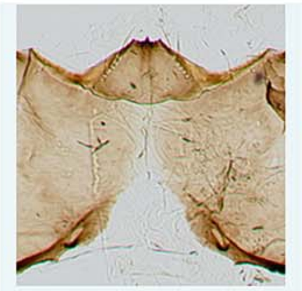
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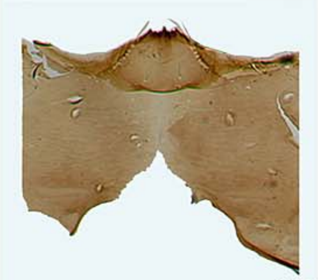
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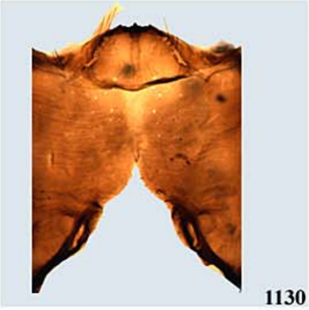
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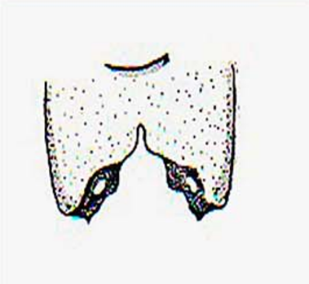
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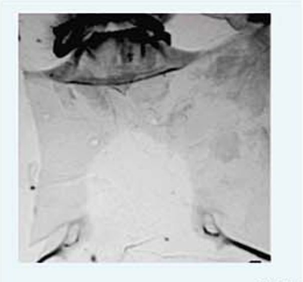
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PLATE 92. Figs. 1122-1141. Postgenal cleft of larva, CANADENSE and ORBITALE species groups. CANADENSE species group: 1122- *S. ayrozai*, 1123- *S. burchi*, 1124- *S. canadense*, 1125- *S. capricorne*; 1126- *S. carolinae*; 1127- *S. dalmati*; 1128- *S. delatorrei*; 1129- *S. estevezi*; 1130- *S. ethelae*; 1131- *S. gorirossiae*; 1132- *S. johnsoni*; 1133- *S. larvispinosum*; 1134- *S. microbranchium* (after Dalmat, 1955); 1135- *S. paracarolinae*. ORBITALE species group: 1136- *S. duodenicornium*, topotype; 1137- *S. guianense s.l.*; 1138- *S. hirtipupa*; 1139- *S. huairayacu*; 1140- *S. itaunense*; 1141- *S. jeteri* (after Py-Daniel *et al.*, 2005).

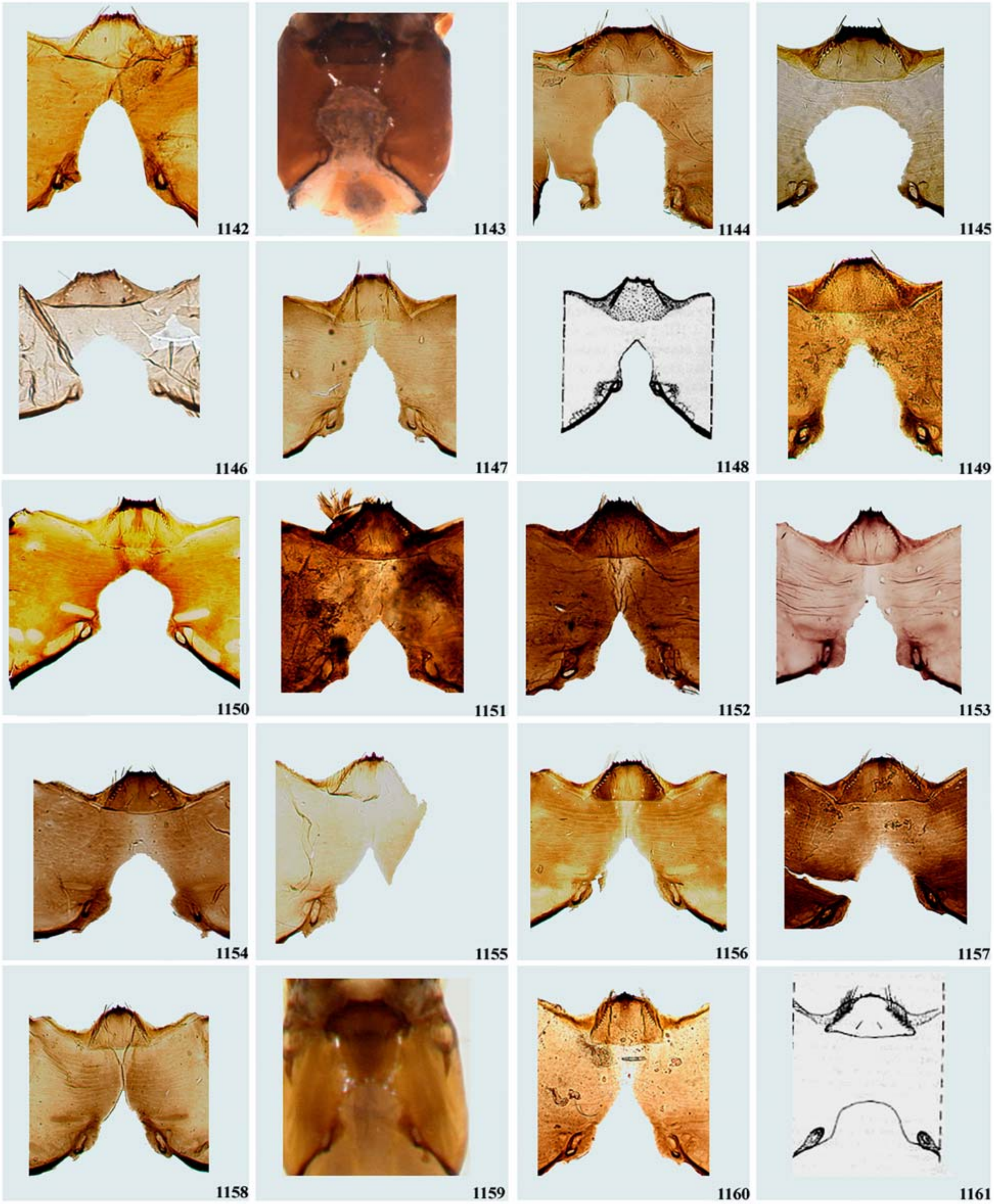

PLATE 93. Figs. 1142-1161. Postgenal cleft of larva, ORBITALE, PICTIPES and TARSATUM species groups. ORBITALE species group: 1142- *S. lahillei*; 1143- *S. lithobranchium*, topotype; 1144- *S. nigrimanum*; 1145- *S. nunesdemelloi* (after HAMADA *et al*., 2006); 1146- *S. orbitale*; 1147 *S. scutistriatum*; 1148- *S. sumapazense* (after MUÑOZ DE HOYOS, 1996); 1149- *S. townsendi* (as *S. muiscorum*); 1150- *S. wygodzinskyorum*, paratype. PICTIPES species group: 1151- *S. claricentrum*; 1152- *S. innoxium*; 1153- *S. pictipes*. TARSATUM species group: 1154- *S. brachycladum*; 1155- *S. bricenoi*; 1156- *S. cristalinum*, paratype; 1157- *S. earlei*; 1158- *S. freemani*; 1159- *S. guerrerense*; 1160- *S. hieroglyphicum*; 1161- *S. hinmani* (after IBÁÑEZ-BERNAL, 1992).

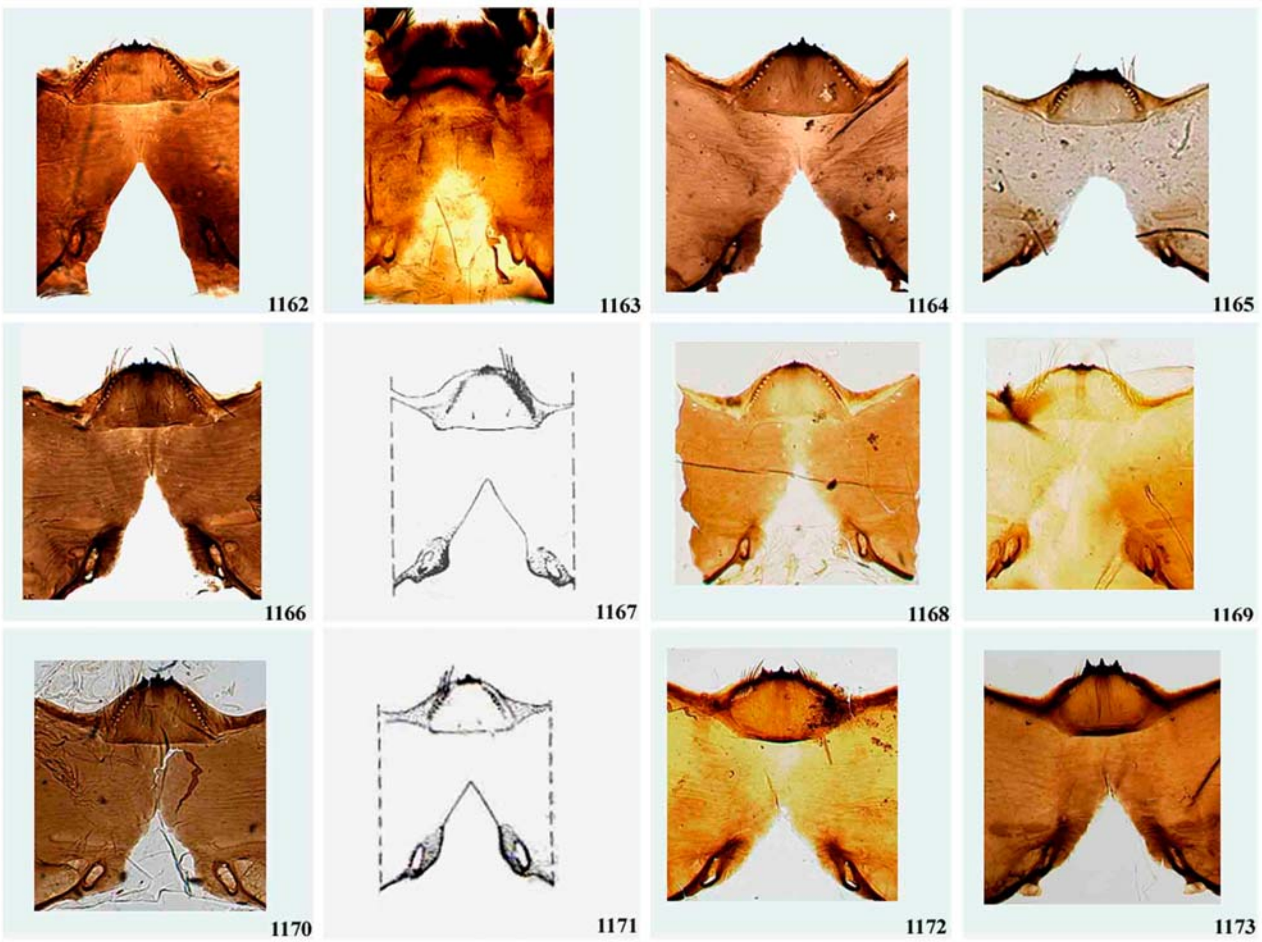

PLATE 94. Figs. 1162-1173. Postgenal cleft of larva, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 1162- *S. hippovorum*; 1163- *S. lobatoi*; 1164- *S. paynei*; 1165- *S. pulverulentum*; 1166- *S. rubrithorax*; 1167- *S. smarti* (after Ibáñez-Bernal, 1992); 1168- *S. solarii*; 1169- *S. tarsatum* (as *S. mexicanum*); 1170- *S. virgatum s.l.*; 1171 *S. yepocapense* (after Ibáñez-Bernal, 1992). Subgenus *Psilopelmia*, BICOLORATUM: 1172- *S. oviedoi*; 1173- *S. rivasi*.

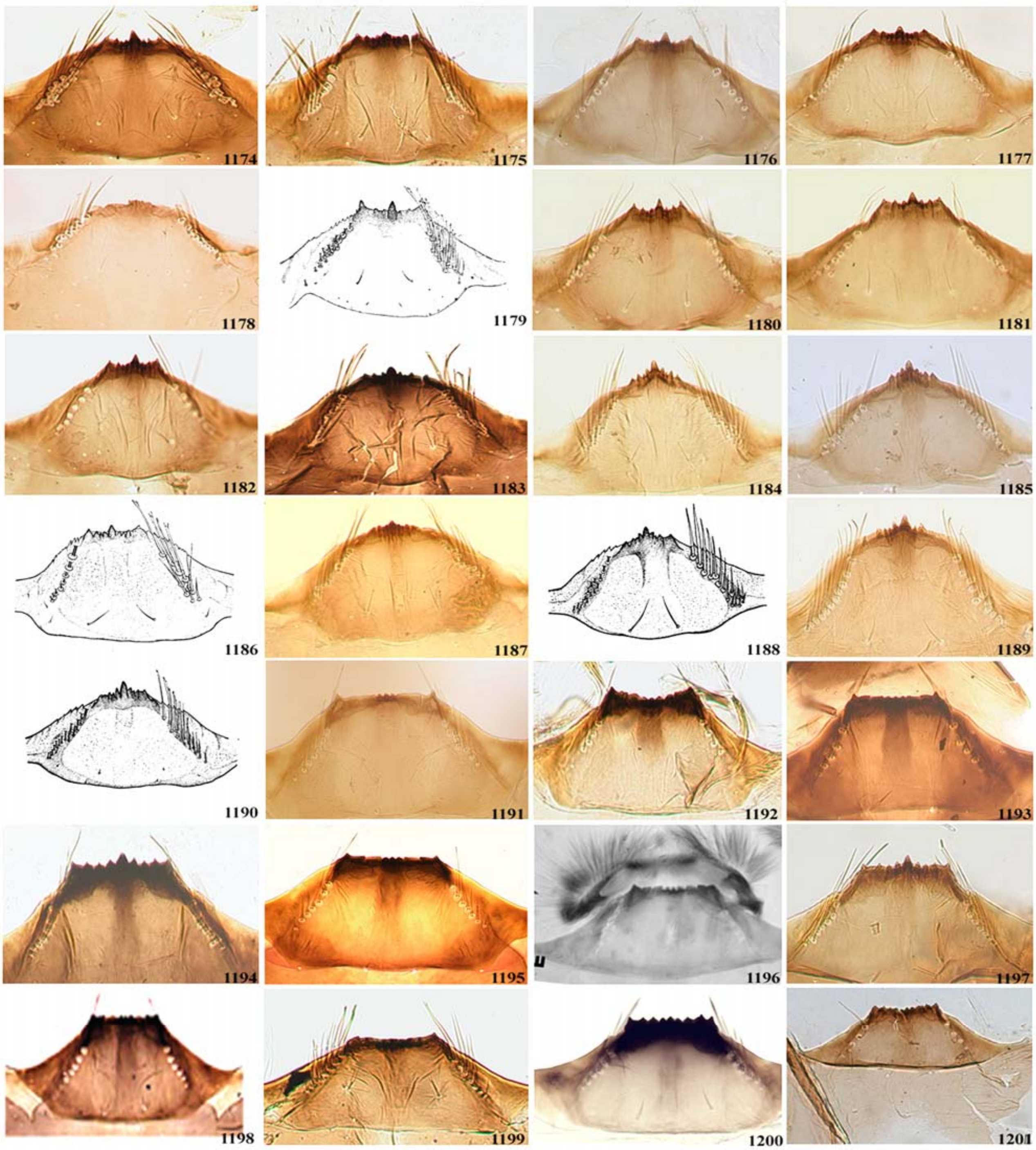

PLATE 95. Figs. 1174-1201. Hypostomial teeth of larva, CANADENSE and ORBITALE species groups. CANADENSE species group: 1174- *S. ayrozai*; 1175- *S. burchi*; 1176- *S. canadense*; 1177- *S. capricorne*; 1178- *S. carolinae*; 1179- *S. contrerense* (after Díaz Nájera & Vulcano, 1962a); 1180- *S. dalmati*; 1181- *S. delatorrei*; 1182- *S. estevezi*; 1183- *S. ethelae* (as *S. chiriquiense*); 1184- *S. gorirossiae*; 1185- *S. johnsoni*; 1186- *S. juarezi* (after Díaz Nájera & Vulcano, 1962a); 1187- *S. larvispinosum*; 1188- *S. menchacai* (after Díaz Nájera & Vulcano, 1962a); 1189- *S. paracarolinae*; 1190- *S. temascalense* (after Díaz Nájera & Vulcano, 1962a). ORBITALE species group: 1191- *S. duodenicornium*, topotype; 1192- *S. guianense s.l.*; 1193- *S. hirtipupa*; 1194- *S. huairayacu*; 1195- *S. itaunense*; 1196- *S. jeteri* (after Py-Daniel *et al.*, 2005); 1197- *S. lahillei*; 1198- *S. lithobranchium* (after Hamada *et al.* 2006); 1199- *S. nigrimanum*; 1200- *S. nunesdemelloi* (after Hamada *et al.*, 2006); 1201- *S. orbitale*.

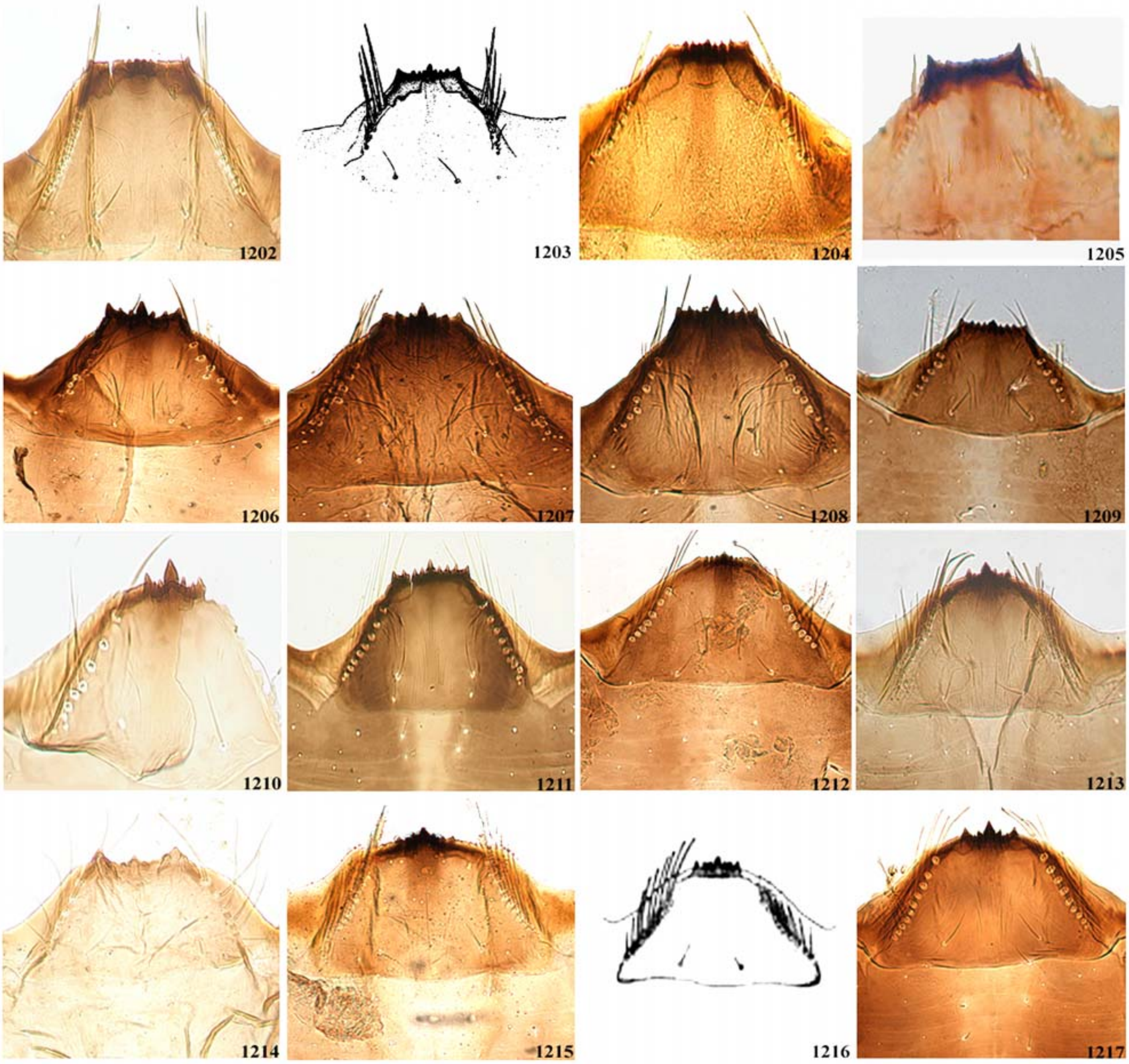

PLATE 96. Figs. 1202-1217. Hypostomial teeth of larva, ORBITALE, PICTIPES and TARSATUM species groups. ORBITALE species group: 1202- *S. scutistriatum*; 1203- *S. sumapazense* (after Muñoz de Hoyos, 1996); 1204- *S. townsendi* (as *S. muiscorum*); 1205- *S. wygodzinskyorum*. PICTIPES species group: 1206- *S. claricentrum*; 1207- *S. innoxium*; 1208- *S. pictipes*. TARSATUM species group: 1209- *S. brachycladum*; 1210- *S. bricenoi*; 1211- *S. cristalinum*; 1212- *S. earlei*; 1213- *S. freemani*; 1214- *S. guerrerense*; 1215- *S. hieroglyphicum*; 1216- *S. hinmani* (after Ibáñez-Bernal, 1992); 1217- *S. hippovorum*.

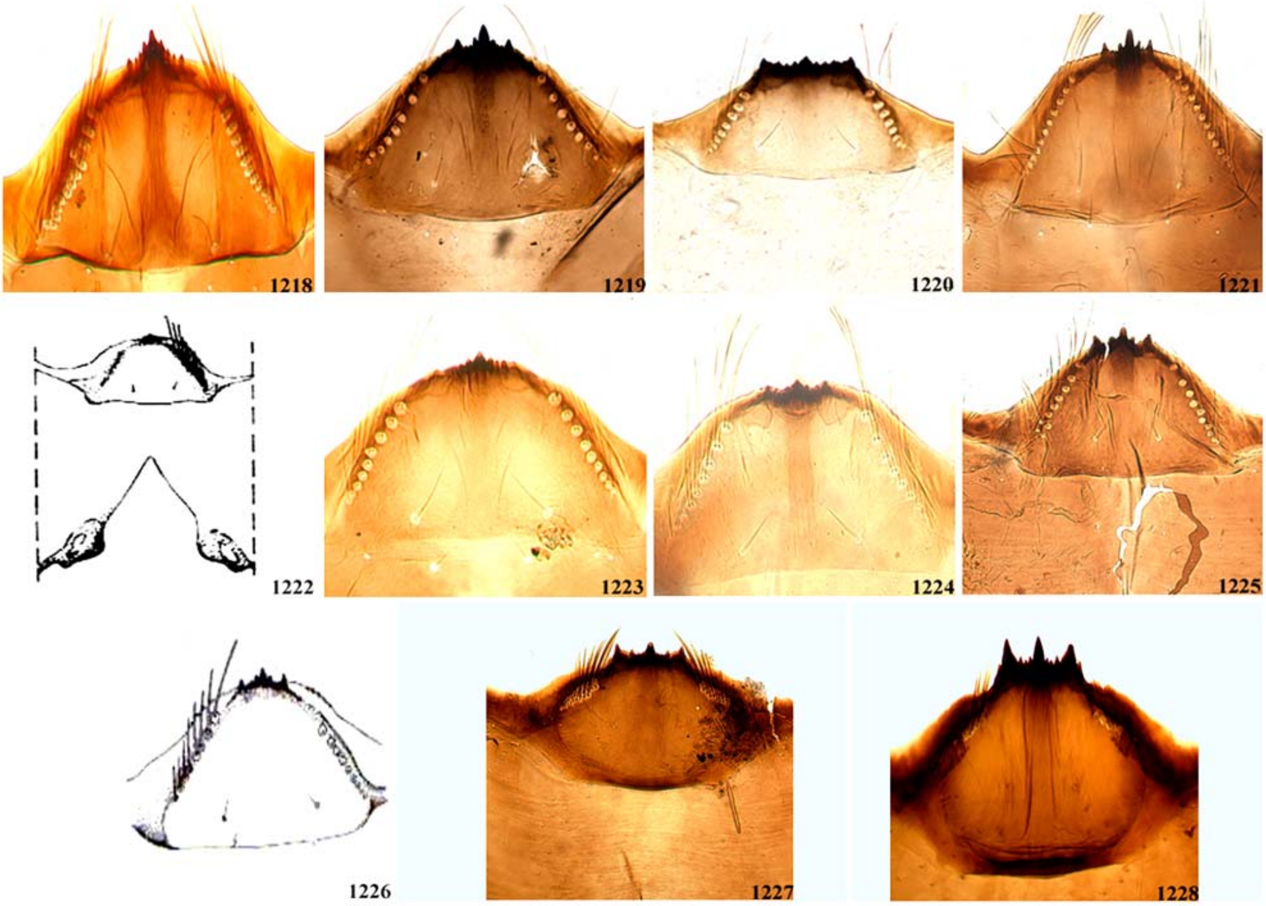

PLATE 97. Figs. 1218-1228. Hypostomial teeth of larva, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 1218- *S. lobatoi*; 1219- *S. paynei*; 1220- *S. pulverulentum*; 1221- *S. rubrithorax*; 1222- *S. smarti* (after IBÁÑEZ-BERNAL, 1992); 1223- *S. solarii*; 1224- *S. tarsatum* (as *S. mexicanum*); 1225- *S. virgatum s.l.*; 1226- *S. yepocapense* (after IBÁÑEZ-BERNAL, 1992). Subgenus *Psilopelmia*, BICOLORATUM: 1227- *S. oviedoi*; 1228- *S. rivasi*.


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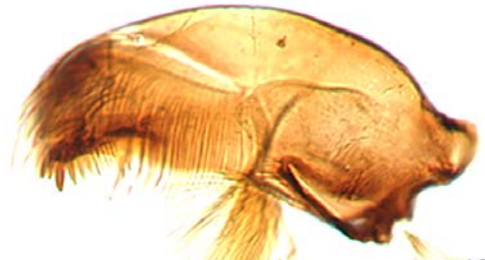
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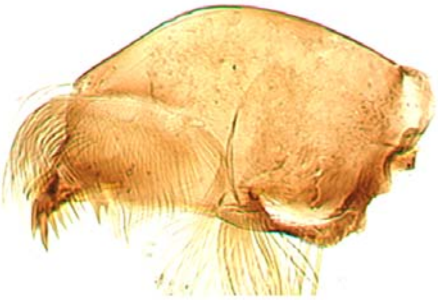
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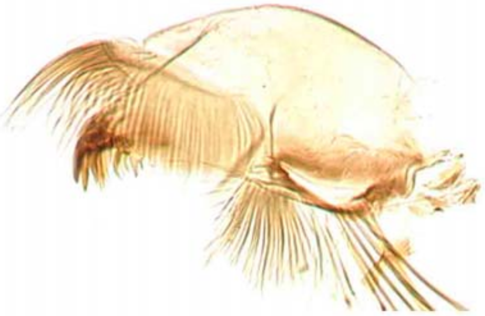
PLATE 98. Figs. 1229-1238. Mandible of larva, CANADENSE species group: 1229- *S. ayrozai*; 1230- *S. burchi*; 1231- *S. canadense*; 1232- *S. capricorne*; 1233- *S. carolinae*; 1234- *S. contrerense* (after DÍAZ NÁJERA & VULCANO, 1962a); 1235- *S. dalmati*; 1236- *S. delatorrei*; 1237- *S. estevezi*; 1238- *S. ethelae* (as *S. chiriquiense*).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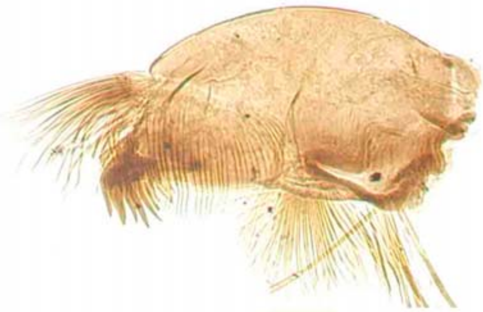
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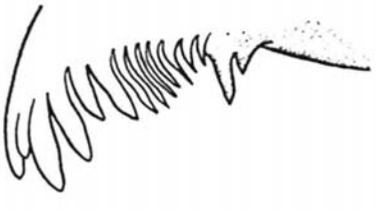
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PLATE 99. Figs. 1239-1245. Mandible of larva, CANADENSE species group: 1239- *S. gorirossiae*; 1240- *S. johnsoni*; 1241- *S. juarezi* (after DÍAZ NÁJERA & VULCANO, 1962a); 1242- *S. larvispinosum*; 1243- *S. menchacai* (after DÍAZ NÁJERA & VULCANO, 1962a); 1244- *S. paracarolinae*; 1245- *S. temascalense* (after DÍAZ NÁJERA & VULCANO, 1962a).

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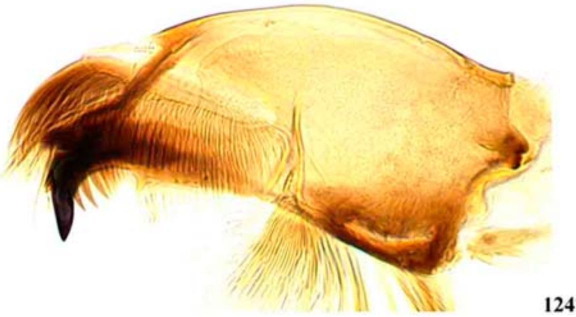

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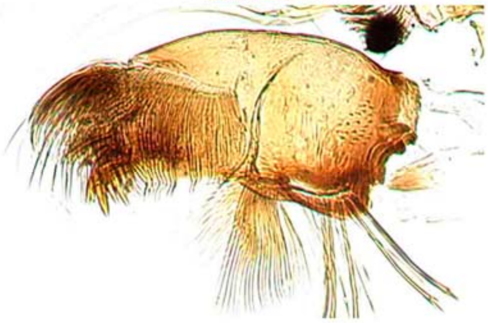

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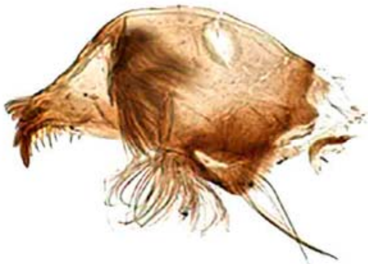

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PLATE 100. Figs. 1246-1255. Mandible of larva, ORBITALE species group: 1246- *S. duodenicornium*, topotype; 1247- *S. guianense s.l.*; 1248- *S. hirtipupa*; 1249- *S. huairayacu*; 1250- *S. itaunense*; 1251- *S. jeteri* (modified from PY-DANIEL *et al.*, 2005); 1252- *S. lahillei*; 1253- *S. lithobranchium*, topotype; 1254- *S. nigrimanum*; 1255- *S. orbitale*.

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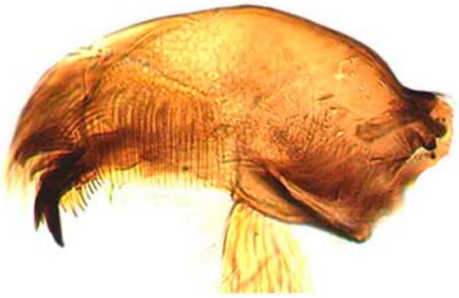

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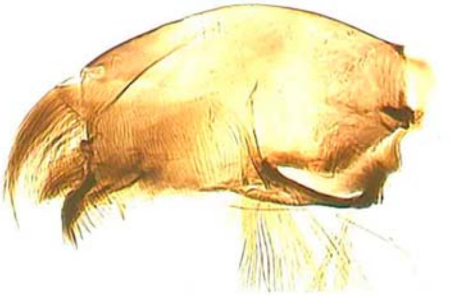

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PLATE 101. Figs. 1256-1265. Mandible of larva, ORBITALE, PICTIPES and TARSATUM species groups. ORBITALE species group: 1256- *S. scutistriatum*; 1257- *S. sumapazense* (after Muñoz de Hoyos, 1996); 1258- *S. townsendi* (as *S. muiscorum*); 1259- *S. wygodzinskyorum*. PICTIPES species group: 1260- *S. claricentrum*; 1261- *S. innoxium*; 1262- *S. pictipes*. TARSATUM species group: 1263- *S. brachycladum*; 1264- *S. bricenoi*; 1265- *S. cristalinum*, paratype.

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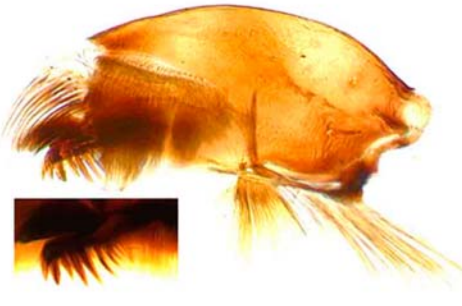

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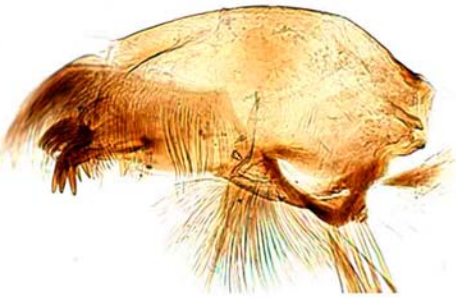

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PLATE 102. Figs. 1266-1275. Mandible of larva, TARSATUM species: 1266- *S. earlei*; 1267- *S. freemani*; 1268- *S. guerrerense*; 1269- *S. hieroglyphicum*, paratype; 1270- *S. hinmani* (after IBÁÑEZ-BERNAL, 1992); 1271- *S. hippovorum*; 1272- *S. lobatoi*; 1273- *S. paynei*, Costa Rica; 1274- *S. pulverulentum*; 1275- *S. rubrithorax*.

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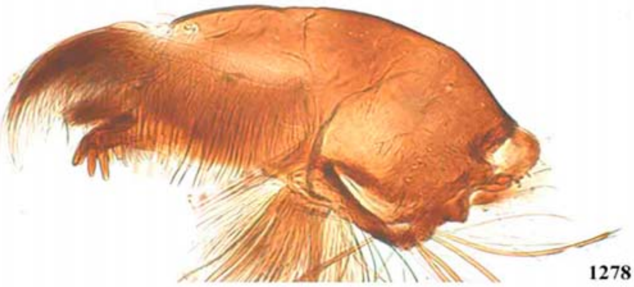

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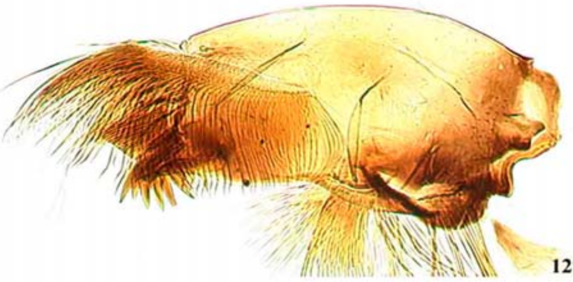

1279

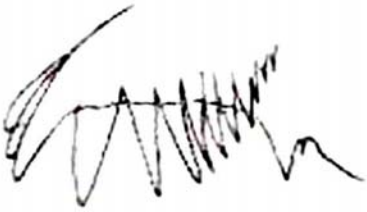

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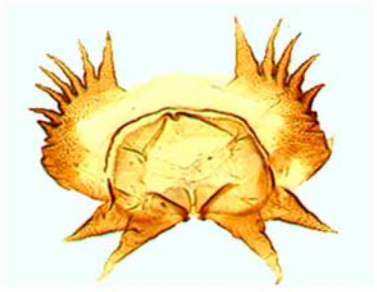
PLATE 103. Figs. 1276-1282. Mandible of larva, TARSATUM species group and subgenus *Psilopelmia*, BICOLORATUM species group. TARSATUM species group: 1276- *S. smarti* (after IBÁÑEZ-BERNAL, 1992); 1277- *S. solarii*; 1278- *S. tarsatum* (as *S. mexicanum*); 1279- *S. virgatum s.l.*; 1280- *S. yepocapense* (after IBÁÑEZ-BERNAL, 1992). Subgenus *Psilopelmia*, BICOLORATUM: 1281- *S. oviedoi*; 1282- *S. rivasi*.


1283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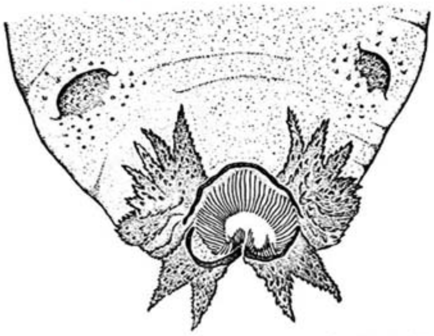
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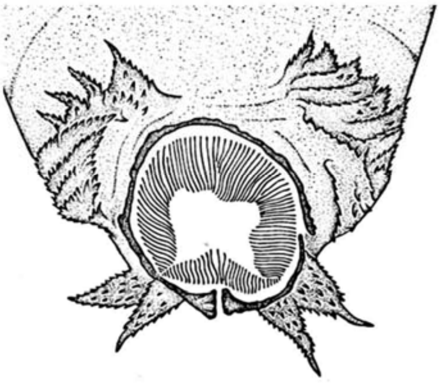
1289

PLATE 104. Figs. 1283-1289. Anal sclerite and sclerotized accessory plates of the larva, CANADENSE species group: 1283- *S. carolinae*; 1284- *S. gorirossiae*; 1285- *S. johnsoni*; 1286- *S. larvispinosum*; 1287- *S. menchacai* (after DÍAZ NÁJERA & VULCANO, 1962a); 1288- *S. paracarolinae*; 1289- *S. temascalense* (after DÍAZ NÁJERA & VULCANO, 1962a).

2.8. APPENDIX 2. DIAGNOSIS OF *TRICHODAGMIA* ENDERLEIN BY OTHER AUTHORS.

The diagnosis of the subgenus *Trichodagmia,* its synonyms *Dyarella*, *Grenieriella*, *Hemicnetha*, and *Thyrsopelma* and its recognized species groups by various authors was given in SHELLEY *et al.* (2010). I have reproduced them in here together with SHELLEY *et al.* (2010) expanded diagnosis for the subgenus *Trichodagmia*. In additionI have also included the diagnosis of the subgenera *Hearlea*, *Obuchovia*, and *Shewellomyia* now considered junior synonyms of *Trichodagmia.* All names are arranged in alphabetical order.

Dyarella VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA, 1946 (as subgenus)

VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA (1946).

Adults: Large, male gonostyle conical with sinuous edges and rounded apex with one spine, not more than three times as long as wide and with no basal processes and 1 ½ times longer than gonostyle. Female with large, pointed gonapophyses pointing towards cerci.

Larvae: Large with 7th abdominal segment 1 1/2 times bigger than first. In lateral view regular dorsal profile and ventral at level of 6th and 7th segments strongly convex up to anal sucker. Second antennal segment with 2 clear areas appearing to divide segment. Distal borders of hypostomium (as submentum) and cephalic apotome (as dorsal plate) convex, teeth of hypostomium small, 9-11 lateral hypostomial setae, fan with more than 50 rays (except *S. earlei* and *S. pulverulentum*), anterior arms of anal sclerite not flattened, posterior sucker with 160-500 hooks, rectal scales absent (except *S. pulverulentum*).

VARGAS & DÍAZ NÁJERA (1948a).

Female: Posterior basitarsus with well developed calcipala with its inferior border reaching or passing pedisulcus. Claws of hind leg with tooth. Postnotum not pilose. Paraproct just passes ventral border of cercus, gonapophyses long.

VARGAS & DÍAZ NÁJERA (1948b).

Female: Scutum with faint or well marked lines or bands, or only lines.

VARGAS & DÍAZ NÁJERA (1949).

Pupa: Cocoon shoe-shaped (as sandal), pupae without spine combs on dorsal abdominal segments VI-VIII, dorsal segment II generally with 3+3 well developed spines and other smaller ones, ventral abdominal segments V-VII with 2+2 large, simple curved hooks (except *S. pulverulentum* only on two of segments).

Grenieriella VARGAS & DÍAZ NÁJERA, 1951

VARGAS & DÍAZ NÁJERA (1951b).

Adults: Medium to large, dark mesonotum with pattern. Thorax with propleural and post spiracular setae. Wings with basal section of R setose and Sc setose or bare. Female hind leg claws with or without tooth. Gonocoxite wider than long, gonostyle twice as long as gonocoxite wider in basal two thirds then getting thinner and ending in point with terminal and subterminal spine. Ventral plate wider than long with well developed keel. Paraprocts wide with rounded ends. Gonapophyses strong, lobular covered in small setae. Lateral ends to genital fork very typical.

Pupa: Highly sclerotised with small, thickened, shoe-shaped cocoon, gills pointed distally.

STONE (1963) (As *Chirostilbia*).

Adults: Frons rather pollinose, usually distinctly so; cibarium without teeth; first and second fore tarsomeres broad and flattened; tarsal claw with small subbasal tooth; anal lobe [= paraproct] elongate, ventrally produced, often somewhat shiny triangle; distimere [=gonostyle] of male shorter than basimere [=gonocoxite], tapering apically.

Pupa: Respiratory organ with eight or more slender filaments, branching variously; cocoon with broad antero-ventral band, the aperture opening antero-dorsally.

COSCARÓN (1987, 1991).

Female: Large species (wing length 2.9-4.4 mm). Scutum general colour brown with scutum from orange- brown to violet brown or blackish, generally ornamented with 1+1 submedian longitudinal greyish stripe joined posteriorly showing like lyre shape; pilosity generally homogeneous, but can be grouped simulating scales. Abdomen generally dark brown to black. Frons relatively wide and fronto-ocular triangle relatively deep. Cibarium with basal portion well sclerotised with small and smooth teeth. Basal section of R with hairs. Legs with filiform hairs. Claw with well developed subbasal process. Eighth sternite well sclerotised with median portion depressed; gonapophyses subovoid to subtriangle shape. Paraprocts higher than long [longer than wide?], with slight anterior concavity or with distal border sinuous. Genital fork with paired arms expanded distally.

Male: General colour as in female from brown yellowish to black. Distimere [=gonostyle] longer than basimere [=gonocoxite], subtriangular with slightly convex internal margin and no more than four spines. Ventral plate body wide relatively short and median protuberance in form of lobule. Endoparameres with robust base but branches without hooks.

Pupa: Cocoon resistant, with anterior border elevated protecting the base of the gills. Gill with 11-20 branches relatively thick and apically pointed. Trichomes of head and thorax small multibranched. Abdomen with spine com on penultimate tergite, rest very reduced or absent and terminal spur very reduced.

Larva: Body shape like *(Hemicnetha).* Cephalic apotome dark brown mostly homogeneous, darkened on basal margin. Hypostomium with normal teeth and anterior border in form of small table [=straight]. Postgenal bridge shorter than hypostomium. Antenna relatively thick, with median article longer than proximal and distal. Mandible with several internal teeth rows. Anal sclerite with simple hairs. Anal disc with 200-360 rows of hooks. Anal gills with elongated diverticles in number of 10-22 on each lobe.

COSCARÓN & COSCARÓN-ARIAS (2007).

These authors regarded *Grenieriella* as a synonym of *Trichodagmia.*

Hearlea **VARGAS, MARTÍNEZ PALACIOS & DÍAZ NÁJERA**

VARGAS *et al.* (1946) [Based on characters of the male genitalia included in key to separate the subgenera of *Simulium*].

Male: Gonostyle long, well developed with single spine. Gonostyle more than four times longer than wide without basal processes; ventral plate semicircular in shape, with or without median emargination; gonostyle with single spine.

VARGAS & DÍAZ NÁJERA (1957b) [Based on the identification key to separate the subgenera of *Simulium*].

Female: Basitarsus of the hid leg narrow or widened with calcipala well developed, the inferior border of the calcipala very close to pedisulcus or extending beyond it. Claw of hind leg weakly curved with or without basal tooth. Gonapophyses so small that they do not reach the ventral border of cercus. Paraprocts extending beyond the ventral margin of cercus, with or without emarginations.

Male: Scutum with lines or bands that might surround the mesoscutum by its margins, the transversal band on anterior region can be continuous or interrupted. Gonostyles with single apical spine. Gonostyles much longer than the height of gonocoxites. Gonostyle cylindrical, more than four times longer than wide, with or without basal process.

Pupa: Gill very wide. Tergite II with 6 strong spines, 3 at each side of median line, though sometimes 2 finer spines and irregularly distributed can be seen.

COSCARÓN (1987).

Female: Species of medium size. Scutum with two distinct bands resembling a lyre-shaped with certain lights. Nudiocular triangular as long as high. Basal region of cibarium unarmed or with small denticules. Basal region of Radius bare. Claws with small basal tooth. Gonapophyses not well developed only extending margin of sternite VIII but to reaching ventral margin of cercus. Paraprocts with external surface largely bare and bright, with a distal depression and lobed margin. Genital fork with median stem strongly curved.

Male: Scutum with a pair of silver band anteriorly. Gonocoxite smaller than gonostyle. Gonostyle more or less cylindrical, four times longer than wide with or without basal lobe and with single apical spine. Ventral plate approximately as long as wide; in ventral view ventral plate with distal margin developed; median keel and sometimes a median process extending beyond the anterior magi. Parameres with widened basal arms and strong spines.

Pupa: Cocoon with fine fibres, parchment-like, transparent, without visible interlaced fibres or anterior projections. Gills not filamentous but wide and asymmetric. Frontoclypeal and thoracic trichomes simple and robust. Abdominal distal tergites without spine combs and without terminal spines.

Larva: Body flattened at the distal region of abdomen, with truncate border. Antennal segments longer than apex of labral fan stalk; second antennal segments longer than first. Cephalic apotome without visible primitive punctuations. Anal sclerite with distinct spiny sclerotised plates that could form a ring. Anal sclerite with more than 200 rows of hooks. Anal gill with numerous lobules. Postgenal cleft deep. Hypostomial bridge shorter than the height of hypostomium; median tooth longer than lateral teeth; border of the hypostomium weakly curved. Mandible with two rows of internal teeth; first internal teeth longer than the apical and preapical.

COSCARÓN *et al.* (2004).

Female: Wing length 2.5-5.0 mm. General coloration blackish brown; scutum blackish with 1+1 silvery vittae sometimes joining 1+1 anterior submedian subtriangular or subquadrate spots, and bordered laterally and posteriorly by silver pruinose areas. Legs yellowish to greyish brown, with apical portions dark brown to black. Frons convergent below, fronto-ocular triangle deep, about as long as wide; maxillary palpus with sensory vesicle elongate, nearly 1/2 length of basal palpomere. Cibarium broadly U-shaped, with basal portion often thickened, medially cleft, and without strong teeth, although often with wrinkles or small serrations on pair of sublateral subovoidal prominences. Basal sector of R bare. Sc with 6-18 setae. Hind basitarsus with length/width ratio 5.7-6.0; claw with small, subbasal tooth. Gonapophysis surpassing edge of sternite VIII, subtriangular, with blunt apex and gradually concave internal margins; cerci generally subquadrate. Paraprocts low, sparsely haired, truncate distally, with abundant short hair; genital fork with stout rods, apically expanded arms bearing strong anteriorly directed apodemes; spermatheca ovoid, with internal spicules.

Male: Wing length 2.6-5.0 mm. General coloration similar to that of female, differing as follows: scutum generally velvety black with anterior 1/3 with whitish pruinosity. Sc frequently bare; hind basitarsus with length/width ratio of 2.7-3.6. Gonocoxite subquadrate, with small protuberance on external margin; gonostylus thin, elongate, 1/3 longer than gonocoxite, with small haired subbasal carina posteriorly, and 1 subapical spine; ventral plate generally subquadrate, with narrow median carina; endoparameres with wide base and numerous strong hooks; median sclerite subrectangular.

Pupa: Cocoon slipper or shoe shaped, typically coarsely woven, no threads evident, with or without reinforced anterior edge; length basally 3.5-4.5 mm (range = 2.4-7.0 mm). Gill inflated, gradually flattened, pseudosegmented, and lacking secondary branches to cylindrical, smooth, with secondary branches. Frontoclypeus gradually swollen basally. Frontoclypeus and anterodorsum of thorax smooth or covered with abundant impressed platelets or rounded or pointed elevated granules. Frontoclypeus with 2+2 frontal and 1+1 facial setae; thorax with 3(4)+3(4) dorsocentral and 2+2 dorsolateral stout trichomes. Abdominal chaetotaxy as in figure 125. Setae of abdominal tergite I relatively short, hair-like, and with small platelets along anterior edge; setae of abdominal tergites II-VI short and slender. Tergites II-IV with 4+4 retrorse hooks, those of tergite II smaller; tergites V-VIII with minute spine-combs. Tergite X with or without terminal hooks. Sternites IV-VII with small, wrinkled areas.

Larva: Body length 6.5-12.0 mm. Distal portion of body typically flattened dorsally and gradually swollen ventrally (Fig. 127 G); body without evident setae. Cervical sclerites free or adjoining posterior edge of postgena. Antenna longer than stalk of cephalic fan, with proximal article elongate and deeply incised, creating segmented appearance; medial article longer than proximal and distal. Cephalic apotome faintly darkened basally, typically lacking discernible head spots. Cephalic fan with 39-54 primary rays. Mandible with strong lateral process, robust intermediate and internal teeth, and 2 thin marginal teeth. Postgenal cleft bluntly to acutely tapered apically; hypostomial bridge generally shorter than hypostomium height, ratio of hypostomium/hypostomial bridge = 0.7-1.5:1.0; anterior margin of hypostomium curved or straight, with median tooth longer than corner teeth. Anal sclerite sometimes encircling posterior circlet, and distal portion of abdomen with accessory plates. Anal papillae of 3 lobes, with 15-78 secondary lobules. Posterior circlet with 102-400 rows of 16-27 hooks.

COSCARÓN & COSCARÓN–ARIAS (2007).
The authors employed the same diagnosis as the paper of COSCARÓN *et al.* (2004).

Hemicnetha ENDERLEIN, 1934

STONE (1963).

Adults: Rather large species; frons pollinose, cibarium unarmed or with many rather irregularly placed teeth; scutum of female usually slightly reddish with pollinose vittae; posterior terga of female shiny; no hairs on basal section of radius dorsally; calcipala well developed; claws of female with distinct subbasal tooth; ovipositor lobe a long triangle reaching to or surpassing base of cercus; anal lobe large produced ventrally but not posteriorly, without ventral notch in profile; distimeres [= gonostyles] of male longer than basimere [= gonocoxite], flattened with single apical tooth and with lateral margins often sinuous; ventral plate broad, often with long median projection.

Pupa: Cocoon with aperture well raised above surface and nearly horizontal in profile. Respiratory filaments usually 8-15 mostly arising near base.

Larva: Hypostomium with central tooth longer than corner teeth; hypostomial setae in strong, closely set row, eight or more on each side, apex often obliquely truncate ventrally in profile.

COSCARÓN (1987, 1991).

Female: Species medium sized to large, wing length 2.6-4.5 mm. Frons relatively wide, convergent, with grey pollinosity. Fronto-ocular triangle [= nudiocular area] deep. Scutum brown to blackish, pollinose, frequently with 1+1 submedian, longitudinal, greyish stripes appearing as light lyre shape; pilosity homogeneous to grouped and simulating scales. Abdomen brownish. Cibarium basally smooth, medially with well sclerotised cornuae, with or without small spiculae. Sc with hair, sometimes reduced only to basal area. Basal sector of R generally without hair. Legs without petaloid hair. Calcipala well developed; claws with big subbasal tooth. Eighth sternite with median depression and few hairs laterally, gonapophyses well developed extending to ventral margin of cercus or beyond, subtriangular with many microtrichiae. Gonapophysis well developed extending to or beyond cercus, subtriangular with abundant microtrichiae; paraprocts large, generally longer than wide, rounded distally with depressions and slight curvature in profile. Genital fork robust with anterior conical acuminate apodemes on lateral branches.

Male: Coloration as in female, but darker. Basimere [= gonocoxite] generally wider than high [= long]. Distimere [= gonostyle] flattened with sinuous form and longer than basimere, generally twice as long as wide with small subapical spur. Ventral plate wider than high with keel or median process. Endoparameres with big bases and strong teeth.

Pupa: Cocoon with compact weave, generally with anterior edge elevated, sometimes with festoons protecting the gills. Gills relatively thick, branching close to base with short basal trunk, filaments in number 6-50 with rounded to acute apices. Frontoclypeus very wide in males with basal reinforcement over facial trichomes not able to separate from females. Frontoclypeus and thorax with simple or branched and generally short. Distal abdominal tergites without spine combs and no terminal spur.

Larva: Body wider distally and flattened postero-dorsally and distal portion truncated. Cephalic apotome with median and sublateral punctiform spots not very evident. Hypostomium generally with frontal edge curved with median tooth longer than lateral teeth. Mandible with first internal and first marginal teeth well developed and presence of various rows of internal teeth. Anal ring with 200-300 rows of 30-60 hooks. Anal gills with 20-50 diverticula on each branch.

BRACHYCLADUM species group [as subgroup].

Female: Scutum with lyre design and scales not arranged in groups or lines. Cibarium well sclerotised and with lightly sclerotised denticles on median portion of base [=central trough], and laterally with spicules. Basal section of R bare. Gonapophyses subtriangular, twice as long as basal width, pointed apically and with well sclerotised internal basal margin. Paraprocts subrectangular, with anterior border unsclerotised and not concave, distally rounded and without distal spicules.

Male: Wing without setae on basal section of R. Ventral plate with median process and relatively fine distally.

Pupa: Cocoon highly elevated anteriorly [= shoe shaped], not protecting gills, with no fenestrations [as festoons]. Gill with 6-15 [as 6-10 in key, *S. solarii* omitted], relatively stout, filiform, laterally uncurved, symmetrical, apically rounded, unsclerotised filaments. Frontoclypeus and thorax with no tubercles.

Larva: Integument without setae. Hypostomium with median and intermediary teeth generally well differentiated, anterior borders in form of plateau. Cervical sclerites narrow, less than twice as wide as long. Anal sclerite without chitinous strengthening and in form of X Posterior sucker [as anal ring] with more than 150 rows of hooks [190 rows with 31-35 hooks per row for *S. brachycladum* in COSCARÓN (1991)].

MEXICANUM species group [as sub group].

Female: Black species with totally black abdomen. Scutum usually with lyre pattern and setae distributed homogeneously, not arranged in lines. Cibarium unarmed. Setae on basal section of Radius. Gonapophysis about as long as wide, usually blunt apex (except *S. guerrerense* and *S. yepocapense*) and internal margin well sclerotised. Paraproct subrectangular, wider than long without depression, distal border with no lobules, truncated and rounded, never pointed, and with microtrichiae.

Male: Wing without setae on basal section of R. Ventral plate widened with slight median keel, slight lateral shoulders [as projections] and no median process.

Pupa: Cocoon smooth without festoons [= fenestrations], shoe-shaped and made of strong material, covering most of gill. Gill with around 12 almost parallel, relatively thick, filiform, uncurved, symmetrical filaments with no terminal spine or sclerotisation. Frontoclypeus and exposed portion of thorax with abundant, obvious tubercles.

Larva: Integument without setae. Hypostomium with median and intermediate teeth generally well differentiated, lateral borders descending slightly from the angle tooth, thereby giving a slight curve. Cervical sclerites narrow, less than twice as wide as long. Mandible with pre-apical and first internal teeth larger than apical teeth. Anal sclerite without chitinous strengthening and in form of X. Anal ring [= posterior sucker] with more than 150 rows of hooks.

PAYNEI species group [as sub group].

Female: Black with totally black abdomen. Scutum with lyre pattern and setae distributed homogeneously and not arranged in lines. Cibarium unarmed with little sclerotisation of median depression [= central trough]. Basal section of R without setae. Gonapophyses twice as long as wide with blunt ends, internal margin not sclerotised. Paraproct subrectangular, wider than long without depression, distal border with no lobules, truncated and rounded, never pointed, no sclerotisation on anterior border and with microtrichiae.

Male: Wing without setae on basal section of R. Ventral plate with median process and relatively fine distally.

Pupa: Cocoon material compact and with festoons [= fenestrations] anteriorly, covering most of gill. Gill with eight filiform, uncurved laterally, symmetrical filaments, resistant and with rounded, unsclerotised ends. Frontoclypeus reinforced at base and widened, being identical in female and male.

Larva: Integument without setae. Hypostomium with median and intermediary teeth generally well differentiated, anterior border of hypostomium arched, intermediate teeth and those on the angle reduced [=lateral teeth]. Lateral borders descending slightly from the angle tooth, thereby giving a slight curve. Mandible with pre-apical tooth as long as or longer than apical tooth. Cervical sclerites narrow, less than twice as wide as long. Anal sclerite without chitinous strengthening and in form of X. Posterior sucker [as anal ring] with more than 150 rows of hooks [320 rows with 40-60 hooks in each in COSCARÓN (1991)].

COSCARÓN & COSCARÓN-ARIAS (2007).

As COSCARÓN (1987), except for the following additions or omissions:

Female: Tonality of vittae changing with different light direction. Cibarium basally smooth, medially with well sclerotised cornuae, with or without small spiculae, as also central area which sometimes appear over pharyngeal membrane. Sensory vesicle of maxillary palps big, frequently half of palpomere length. Description of eighth sternite omitted. Gonapophysis frequently two times longer than wide, subtriangular to subtrapezoidal and internal edge well sclerotised. Paraprocts subquadrangular, with distal edge straight to slightly curved or rounded; cerci mostly with distal edge flattened. Spermatheca subtrapezoidal with light neck connecting with spermathecal duct.

Male: Gonostyle with median lateral protuberances, generally two times longer than gonocoxite. Ventral plate with. keel projected apically as median process to about as long as wide or flattened laterally.

Pupa: Cocoon shoe shaped, sometimes with festoons protecting the gills. Gills with 6-90 filaments, externally frequently with striated annulations and spiculae. Frontoclypeus and exposed portion of thorax generally without tubercles, but present and very small on facial area and posterior edge of thorax. Frontoclypeus with 2+2 frontal, 1+1 facial and thorax with 5+5 or 6 + 6 thoracic trichomes.

Larva: Body wider distally and flattened postero-dorsally. Cephalic apotome with punctiform spots median and sublateral generally not evident. Mandible with anterior internal teeth big and showing several rows of teeth; marginal teeth in number of 1-2 with second tooth very small. Antenna with median article bigger than proximal and distal. Anal ring with 200-500 rows with 22-73 hooks each. Rectal papillae with 5-41 diverticulae on each lobe.

BRACHYCLADUM species group.

Female: Gonapophysis subtriangle shape, acute apex, near two times longer than width with sparse microtrichiae, moderate number of hair and well sclerotised along inner margin; paraprocts membranous without microtrichiae and low number of hair, apex rounded with small concavity posteriorly. Cibarium with median area bearing small teeth.

Male: Gonostylus relatively short with lateral protuberances, ratio length/width about 1.5.

Pupa: Cocoon with aperture elevated, without festoons; frontoclypeus and thorax without tubercles, except on facial area; gill with 6-15 branches.

Larva: Hypostomium anterior edge straight with median teeth generally with same length or longer than lateral teeth. Postgenal bridge longer than hypostomium. Anal ring with 134- 190 rows with 25-28 hooks each.

MEXICANUM species group.

Female: Gonapophysis about as long as wide at base up to two times longer than wide, distally acute to blunt. Paraproct subrectangular, with abundant microtrichiae and no anterior concavity.

Male: Gonostylus about three times longer than width with slight lateral protuberances; ventral plate about as long as wide, without median process but flattened laterally and with high keel.

Pupa: Cocoon with aperture moderately to well elevated, no festoons; frontoclypeus and thorax with or without tubercles. Gill with 8-90 branches.

Larva: Postgenal bridge frequently shorter than hypostomium; hypostomium front slightly curved with median teeth higher than lateral teeth. Postgenal cleft apex sharp. Anal ring with 200-550 rows with 27-55 hooks.

OVIEDOI species group.

Female: Eighth sternite well sclerotised on the centre; gonapophyses subtriangle shape, relatively short with acute, apex ratio length/width at base = 0.7-0.9. Paraprocts subtriangular, slightly shorter than wide at base. Genital fork with antero-lateral process strong and well sclerotised.

Male: Ratio of length/width of hind basitarsus = 4. Gonostylus shorter than gonocoxite subcylindrical with slight distal curvature and apical spur; ventral plate about as long as wide at base without any keel or lateral entrances; endoparameres with strong teeth.

Pupa: Cocoon shoe shaped relatively low anteriorly with reinforced anterior edge. Frontoclypeus reinforced basally and very wide in males nearly same shape as female, frontoclypeus and thorax with abundant granulose tubercles, frequently very acute and multibranched trichomes. Gills with six thick relatively short branches emerging form short and thick trunk. Abdomen with apical spur small.

Larva: Body with soft dorsal subterminal curvature and without ventro-lateral tubercles. Cephalic apotome with positive spots. Antennae short and robust, only reaching half length of cephalic fan stem; medial article longer than others. Cephalic fan with 20-25 rays with thick teeth all of similar length. Mandible with two marginal teeth of similar size. Postgenal bridge as long as hypostomium length. Lateral sclerite of thoracic proleg with 32-45 teeth. Anal sclerite with abundant hair, but no scales. Anal ring with 100-120 rows with 17-18 hooks each. Rectal papillae with 20-26 diverticula on each lobe.

PAYNEI species group.

Female: Gonapophysis two times longer than wide, blunt apex with abundant microtrichiae and not sclerotised internally; paraproct subrectangular, with anterior edge not concave.

Male: Gonostylus 2.1-2.2 times longer than wide at base, lateral sides with scarce protuberances; ventral plate with moderate body length and thick median process with abundant hair.

Pupa: Cocoon well elevated anteriorly with collar of festoons; frontoclypeus and exposed portion of thorax without tubercles, only diminutive tubercles on facial area; thorax dorsally generally with gelatinous cover of variable disposition in according to species. Gills with eight branches.

Larva:. Postgenal bridge about as long as hypostomium. Hypostomium frontal edge curved. Anal ring with about 220-360 rows of 40 hook each.

Obuchovia RUBTZOV, 1947

RUBTZOV (1947). [As group VI with species *albellum* probably as type species].
In page 105 it reads as follows:

This species differs from other species by the combination of the followings characters: a wide leaf-like admiculum resembling that of *Eusimulium*; styli and coxites like *Simulium*; 10 antennal segments instead of 11; long, simple claws as like in *Simulium* or rather like in *Wilhelmia*. And in total opposite to *Wilhelmia* membrane with hairs like in *Odagmia*, *Wilhelmia*; absence of silver spots like *Eusimulium*; long and dense pubescence like in mountain species. In addition, very peculiar abdominal coloration of yellow with black spots; six-filamented pupa; very peculiar abdominal chaetotaxy of pupa, more or less row or even teeth at the end of mandibles in larva and very wide submentum like in *Wilhelmia*. Species with a Transcaucasia, and show a peculiar combination of characters related to species found in high mountains.

In page 116 the author stated the following in English:

18. *Simulium (Obuchovia) albellum*, subgen. et sp. n.

Very isolated species. *S. popovaoe* Rubz. And possibly *Simulium auricoma* described before belong possibly to this group. Larval submentum much elongated in transverse direction and bears 15-20 lateral setae forming 2-3 series. On the posterior sucker about 200 rows of hooks, the total number of the latter being 6000-7500. Cocoon boot-shaped. Pupa with 6+6 short respiratory filaments. Dorsum of the male grey. Silver colored markings absent in both sexes. Admiculum broad, leaf-shaped. Pleural membrane hairy.

Abdomen of the female yellow with black spots. Claws simple and relatively long. Distribution Tadjikistan, Hisar Mountains range 1500-2000, Uzbekistan, Karjantau.

RUBTZOV (1951).

Most similar to species of *Simulium s.str.* in the following characters: Simple claws. Silver spots on fore tibia, sometimes silver spots on notum. Presence of heels on hind tarsal segment and a cleft on second tarsi. It differs in the following characters: Membrane with dense patch of hairs. First tarsal segment of fore leg flat, moderately widened. Basal hairs of Radius vein bare. Genital plates lengthened, covered very short thin hairs. Legs mostly yellow. Female abdomen yellow with distinctive pattern of dark spots. Admiculum of males extremely wide, leaf-shaped with triangular and obtuse processes; width of admiculum margin in the middle exceeding its length almost two times. Coxite and styli as in group *Odagmia* End. Pupa with six filaments in all species. Cocoon boot-shaped; segment VI-VIII for dorsal side without spines, the ventral side with more spines and/or spine combs in several rows.

Larva: Submentum very wide in basal half; ration of distance between lateral teeth and height of submentum 1 to 2; 15-2- setae along side of submentum distributed in 1 to 2 rows. Mandibles with short apical tooth. Posterior sucker with numerous rows of hooks, more than 2000, altogether about 5 to 7 thousands.

Four species can be attributed to this subgenus, *S. albellum*, *S. popovaoe* Rubz., an undescribed species from Caucasus, and probably the European *S. auricoma* Mg. from Crimea. The distribution of those species mostly Mediterranean. The first collection of this species was made by Obuchova, who tragically died in the expedition in the mountain of Central Asia. The subgenus is named after her.

CROSSKEY (1967).

Female and Male: Basal sector of Radius bare. Pleural membrane haired. Katepisternum bare. Fore tarsi broadly dilated or narrow and slender. Hind basitarsus slightly enlarged, more or less parallel-sided in female but broader and slightly convex in male. *Female*: Tarsal claws simple or at most with trace of very small blunt basal tooth. Scutum with or without silver-grey anterior pattern. Abdomen with fine plate hair and without scale covering; abdominal ground colour yellow, row of large paired spots on either side of tergites black or darkened. Gonapophyses broadly elongate and truncate, somewhat tongue-shaped, short haired. Spermatheca without internal hairs. *Male*: Genitalia very enlarged and elongate styles and relatively small coxites; style parallel-side and at least 21/2 times as long as coxite; coxite not produced beyond base of style; ventral plate with small basal arms and rounded or subcordate body, body of plate not toothed and with short fine inconspicuous hair, plate narrow in profile with only slight curvature; median sclerite long and narrow, deeply cleft. Parameres large and subtriangular, parameral hooks small and numerous, subequal in size.

Pupa: Gill with six filaments arising from base and directed forwards; gill much shorter than body of pupa and concealed completely or almost so within cocoon. Abdomen, in addition to normal armature, with 4 small hooks dorsally on each side of segment. Abdominal segments 6-8 without spine-combs. Cocoon closely woven, shoe-shaped and with very long neck.

Larva: Hypostomium with short teeth, corner teeth not strongly prominent; rows of hypostomial setae irregular and divergent posteriorly from lateral margins of hypostomium. Head-capsule strongly infuscate yellow-brown to dark with areas of head spots slightly paler, head-spots therefore negative. Postgenal cleft large and subtriangular, broadly sagitate or subcordate, much longer than postgenal bridge. Antennae short, third segment much shorter than second. Thoracic and abdominal cuticle bare. Abdomen broadest just anterior to posterior circlet. Ventral papillae absent. Rectal scale present. Rectal gills with secondary lobules. Posterior circlet with about 100-200 rows of 17-36 hooks.

CROSSKEY & SANTOS GRÁCIO (1985).

A entirely Palaearctic group that forms an element among Eurasian blackflies characterized by a combination of a 6-filamented pupal gills, the pupa deeply sunken within a very large shoe-shaped cocoon, the adult pleural membrane haired, and the male genitalia with an unusual form of rather flattened and rounded ventral plate.

CROSSKEY (2002b).

Adults females in species of the subgenus *Obuchovia* are unusual among blackfly females in having a pattern of dark brown or black marks on a pale yellow ground colour variably developed on the adominal segments.

Thyrsopelma ENDERLEIN, 1934

STONE (1963) (As *Chirostilbia*).

Adults: Frons rather pollinose, usually distinctly so; cibarium without teeth; first and second fore tarsomeres broad and flattened; tarsal claw with small subbasal tooth; anal lobe [= paraproct] elongate, ventrally produced, often somewhat shiny triangle; distimere [= gonostyle] of male shorter than basimere [=gonocoxite], tapering apically.

Pupa: Respiratory organ with eight or more slender filaments, branching variously; cocoon with broad antero-ventral band, the aperture opening antero-dorsally.

COSCARÓN (1987, 1991).

Female: Species relatively big, wing length 2.0-3.5 mm [3.6 mm in COSCARÓN, 1991]. General coloration blackish. Scutum brown-reddish with gray pollinosity and hair yellow to silvery grouped simulating scales. Abdomen black. Fronto-ocular triangle about as high as wide. Basal portion of cibarium smooth, slightly concave and well sclerotised branches [= cornuae] and sometimes also the border of the median area. Basal sector of R haired; Sc with or without hair. Claw without subbasal tooth. Eighth sternite with abundant hair; gonapophyses subovoidal generally wider than long. Paraprocts longer than wide [as más alto que largos] with distal margin rounded to shorter than wide [as "menos altos que largos"] with distal margin sinuous and membranous. Genital fork with thickened lateral arms and median relatively short (approximately one third longer than each of the pair of [lateral] arms); spermatheca with few internal spines.

Male: Coloration similar to female, showing in some cases black silvery lateral margin and 1+1 anterior spots as wide longitudinal stripes; abdomen blackish with 1+1 lateral silvery spot on segments II and smaller on V-VII. Basimere [= gonocoxite] subtrapezoidal; distimere [= gonostyle] at least twice as long as basimere, subtriangular shape, curved on third apical and getting thinner distally with one apical spur. Ventral plate body wider than high with median projection varying from a short lobule to a long, robust process very conspicuous in profile. Median sclerite subrectangular shape with deep median incision. Endoparameres without hooks or hooks reduced to simple spines.

Pupa: Cocoon with strong, parchment like consistency, extended ventrally, [anterior] border lightly reinforced, very resistant, rough and projecting anteriorly in form of collar protecting the gills. Cephalic trichomes (2+2 frontal, 1+1 facial) and thoracic (5-8) single and small.

Frontoclypeus and exposed portion of thorax with rounded tubercles only on base of frontoclypeus and in ventro-lateral area of thorax or with acute apex or transformed in spines. Gill branches relatively thick, smooth, with apex acute and well sclerotised in number of 12-50.

Larva: Body cuticle with simple hairs, generally lanceolate. Cephalic apotome weakly darkened basally. Antenna longer than apex of cephalic fan stem, with median article about two times longer than the proximal or distal. Cephalic fan rays teeth with similar length and arranged divergent at sides distally, forming two rows. Mandible with big pre-apical teeth nearly as long as the apical tooth; marginal teeth big. Postgenal cleft subovoidal, postgenal bridge a little shorter the hypostomium length. Hypostomium median tooth lower than lateral teeth, and intermediate lateral teeth very wide. Cervical sclerite enlarged. Anal disc with 150-300 rows with 25-40 hooks each. Anal gill diverticles in number of 10-15 on each lobe.

COSCARÓN & COSCARÓN-ARIAS (2007).

As COSCARÓN (1987) with the following additions.

Female: Species relatively big, wing length 2-3.6 mm. Frons relatively wide. Fronto-ocular triangle about as high as wide to higher than wide. Sensorial vesicle of maxillary palp smaller than half of palpomere. Details of leg setation omitted. Gonapophysis with borders sclerotised. Details of paraproct, genital fork and spermatheca omitted.

Male: Gonostylus from 1.5-2 times longer than gonocoxite. Ventral plate body with big median process. Endoparameres [= parameres]without teeth.

Pupa: Cocoon shoe shaped with no reference to weave; 5-6 thoracic trichomes.

Larva: Body cuticle with simple hairs, generally as racket shape. Details of cervical sclerite omitted. Anal sclerite without scales, anal ring with 120-300 rows with 17-35 hooks each. Rectal papillae diverticles in number of 5-30 on each lobe.

Shewellomyia **SHEWELL, 1959**

SHEWELL (1959).

Large species; thoracic dorsum trivittate; mesopleural membrane bare; basal section of radius bare; tibiae without bright niveous patches; for tarsal segments not much dilatated.

Female: Head and thoracic thickly cinereous-pollinose; mouth part adapted for biting; tarsal claws simple; posterior margin of seven abdominal sternite with conspicuous fringe of long hairs, paraprocts (anal lobe) with large highly polished ventral prolongation; ovipositor lobes very widely separated.

Male: Style without apical tooth; ventral plate broadly cleft almost to base.

Pupa: Respiratory organ with nine uniformly radiating, somewhat inflated, rather shorts filaments; abdominal armature lacking on fifth to seventh tergites; cocoon fabric loosely reticulate, porous, with greatly elevated opening.

Larva: Exceptionally long and slender, evenly expanding posteriorly, seventh abdominal segment strongly bulbous ventrally; antenna six-segmented; submentum with eight to 11 hairs on each side.

ADLER *et al.* (2004) (as PICTIPES species group)

Female: Cibarium without armature between cornuae. Tibia without bright white patches; claws toothless. Sternite VII with fringe of long hairs posteriorsly. Hypogynial valve short, with inner margins concave. Genital fork with lateral plates of each arm lacking ventrally directed tubercle. Anal lobe subquadrate , with large polished sclerotised area.

Male: Gonostylus nearly 4 times as long as wide, without apical spinule. Ventral plate in ventral view with deep medial cleft posteriorsly.

Pupa: Gill with 9 rather swollen filaments. Cocoon boot shaped. Cribriform.

Chromosomes: Standard banding sequence as given in BEDO (1975)

Trichodagmia **ENDERLEIN, 1934**

STONE (1963) *(*As *Chirostilbia).*

Adults: Frons rather pollinose, usually distinctly so; cibarium without teeth; first and second fore tarsomeres broad and flattened; tarsal claw with small subbasal tooth; anal lobe [= paraproct] elongate, ventrally produced, often somewhat shiny triangle; distimere [= gonostyle] of male shorter than basimere [= gonocoxite], tapering apically.

Pupa: Respiratory organ with eight or more slender filaments, branching variously; cocoon with broad antero-ventral band, the aperture opening antero-dorsally.

COSCARÓN (1987, 1991).

Trichodagmia regarded as a possible synonym of *Grenieriella* and so has the same diagnosis.

COSCARÓN & COSCARÓN-ARIAS (2007).

Grenieriella accepted as synonym of *Trichodagmia.* Diagnosis follows that of *Grenieriella* of COSCARÓN (1987) with the following changes:

Female: Scutum coloration brown orange, dark brown to blackish. Abdomen with 1+1 greyish spots on tergite II. Fronto-ocular triangle about as long as wide. Cibarium well sclerotised with small teeth generally like spiculae on median depressed area. Details of wing venation and leg hairing omitted. Eighth sternite well sclerotised with median portion depressed; gonapophysis subovoidal to subtriangle shape with blunt apex and small anterior depression. Details of paraproct omitted. Genital fork with wide anterior branches and strong, well sclerotised apodemes.

Male: Gonostylus near 1,5 times longer than gonocoxite, subcylindrical, acuminated distally and about twice as long as wide at base, generally with one apical spur. Ventral plate body wide about twice as wide as long with a short median process. Endoparamere [= paramere]branches without hooks.

Pupa: Cocoon shoe shaped, weave thick. Frontoclypeus reinforced basally. Gill with 12-20 branches generally moderate thick and relatively short.

Larva: Mandible with several internal teeth rows and thin marginal teeth. Postgenal cleft deep. Anal sclerite with abundant hair, not scales. Anal ring with 150-360 rows with 23-40 hooks each. Rectal papillae with elongated diverticles in number of 10-45 on each lobe.

SHELLEY *et al.* (2010) (as Subgenus)

Adults: Medium to large brown to black flies (up to 5.0 mm) with or without scutal.

Female: Nudiocular area partially to well developed. Cibarium variable, ranging from generally unarmed [including membrane with denticles attached to unarmed central trough – this character is probably more commonly found in species than has been described because the membrane may be lost during dissection), to armed with large pointed teeth. Wing venation variable with Subcosta either bare or with setae, basal section of Radius usually with setae and often with more than one row. Claws generally with basal tooth. Gonapophyses membranous, setose and either triangular pointing posteriorly or ovoid and pointing to median line of abdomen, exceptionally with coarse hairs. Paraproct varying from subtriangular to subrectangular with ventral extension from less than half to more than length of cercus often with membranous processes, with fine setae and coarse hairs. Genital fork variable with ends of lateral arms either arranged obliquely or parallel to transverse axis of abdomen, and anterior and posterior processes to lateral arms developed to greater or lesser extent.

Male: Gonostyle either subrectangular and rounded distally with sinuous lateral margins and a distal spine or spindle-shaped with one or more distal spines; gonostyle same length or longer than gonocoxite. Ventral plate varying from rectangular with no lateral shoulders on main body and an underdeveloped median process to well developed lateral shoulders, and a keel and or fissure on the median process and main body and median process or rarely heart shaped (*S. oviedoi*, *S. rivasi*). Paramere with well developed spines or no spines.

Pupa: With shoe-shaped cocoon (exceptionally slipper-shaped) and thick filaments of variable length, but shorter than pupa and with rounded or pointed tips.

Larva: [The referred to the diagnostic characters of other authors in their Appendix 8].

2.9. APPENDIX 3. TABLES.

TABLE 1. Previous and current classification of the subgenus *Trichodagmia*.

Previous classification	Current classification
Subgenus *Obuchovia* As valid subgenus – CROSSKEY & HOWARD (1997) As new subgeneric synonymy of the subgenus *Hemicnetha* – ADLER *et al.* (2004) As valid subgenus – ADLER & CROSSKEY (2008, 2009, 2010), SHELLEY *et al.* (2010)	Subgenus considered here the ALBELLUM species group [New subgeneric synonymy under subgenus *Trichodagmia* – this work]
Subgenus *Hearlea* As valid subgenus *Hearlea* - COSCARÓN & COSCARÓN-ARIAS (2007) As the CANADENSE species group of the valid subgenus *Hemicnetha* – ADLER *et al.* (2004) and ADLER & CROSSKEY (2008, 2009, 2010) As the CANADENSE species group of the subgenus *Trichodagmia* – SHELLEY *et al.* (2010)	Subgenus considered here the CANADENSE species group
Subgenera *Thyrsopelma* and *Trichodagmia* As the valid subgenera *Thyrsopelma* and *Trichodagmia* – COSCARÓN & COSCARÓN-ARIAS (2007) As the ORBITALE species group of the subgenus *Trichodagmia* – ADLER & CROSSKEY (2008, 2009, 2010) As the ORBITALE species group of the subgenus *Trichodagmia* – SHELLEY *et al.* (2010)	Subgenera considered here the ORBITALE species group
Subgenus *Shewellomyia* As new subgeneric synonymy of subgenus *Shewellomyia* under the valid subgenus *Hemicnetha* (ADLER *et al.*, 2004) As the PICTIPES species group of the valid subgenus *Hemicnetha* – ADLER *et al.* (2004) and ADLER & CROSSKEY (2008, 2009, 2010) As the PICTIPES species group of the subgenus *Trichodagmia* – SHELLEY *et al.* (2010)	Subgenus considered here the PICTIPES species group
Subgenus *Hemicnetha* As valid subgenus *Hemicnetha* – CROSSKEY & HOWARD (1997), COSCARÓN & COSCARÓN-ARIAS (2007), ADLER *et al.* (2004) and ADLER & CROSSKEY (2008, 2009, 2010) As new subgeneric synonymy under the subgenus *Trichodagmia* to represent the TARSATUM species group – SHELLEY *et al.* (2010)	Subgenus considered here the TARSATUM species group

2.10. Appendix 4. Material Examined.

The information on data labels of the taxa examined in this paper is here provided. The classification given in **Chapter 2** for *Trichodagmia* and that of Shelley *et al.* (2010) for this and other subgenera, for example *Aspathia*, is followed. Subgenera, species group and valid species are listed alphabetically, and synonyms in order of date of species publication. See **Chapter 2** in section **"2.3.7 Acronyms Used for Depositaries of Simuliidae"** for explanation of abbreviations for names of depositories. For each species, specimens examined are listed in the following order: TYPE MATERIAL- this includes information on types of the valid species and its synonyms; OTHER MATERIAL- it refers to species of the valid species that are not types. Within these two sections specimes are listed by country, province or state in alphabetical order. Within each country specimens are divided into the categories PINNED, SLIDE or SPIRIT [= 80% ethanol at the BMNH; probably 70%-80% in other institutions].

Genus *Simulium* Latreille, 1802

Subgenus *Aspathia* Enderlein, 1935

Simulium (Aspathia) anduzei Vargas & Díaz Nájera, 1948b

TYPE MATERIAL

MÉXICO

Federal District

SLIDES

Guayotla, Sn Mateo, Tlatenango; iii.1949, (*A.Díaz*)— 1female (only wings) (INDRE, no. 1962) [ALLOTYPE] [The specimens bear several labels: White label with red edges in Vargas's hand with locality information, date and collector's name; Yellow label "Alotipo"; White label "CAIMSimTp-00118". Others label here added: White label "Digitially photographed wings INDRE Allotype female Examined: L.M.Hernández 2009".]

Simulium (Aspathia) covagarciai Ramírez Pérez, Yárzabal, Takaoka, Tada & Ramírez, 1984

The material listed in Shelley *et al.* (2010) was examined for the current work.

Simulium (*Aspathia*) *hechti* Vargas, Martínes-Palacios & Díaz-Nájera, 1946

OTHER MATERIAL

MEXICO

Federal District

SPIRIT

Cascada de Alferres; 25.iii.1945, (*A.Diaz N.*)— 3pupal exuviae (NMNH).

UNITED STATES OF AMERICA

New Mexico State

SPIRIT

W. Emory Post, Hwy 90, 754º21; 21.x.1988, (*M.Craig*)— 2pharate pupal exuviae (NMNH).

Simulium (*Aspathia*) *jacumbae* Dyar & Shannon, 1927

TYPE MATERIAL

UNITED STATES OF AMERICA

SLIDES

Jacumba Spg. Col.; [Without date], (*E.A.McGregor*)— male (not associated with pupal exuviae) [HOLOTYPE] (NMNH, acc. no., 28348) [The specimen is in good condition with the adult mounted on a slide in full] [The specimen bear a White label with blue lines around the edges with the locality and collector's name handwritten in brown ink. It has handwritten in pencil "*jacumbae*"; Red Label with the top left handside corner handwritten in black "Type 28348 U.S.N.M.". Other labels here added:

White label "Digitally photographed adult thorax, genitalia L.M.Hernández 2010"; White label "*Simulium jacumbae* Dyar & Shannon, 1927 Examined: L.M.Hernández 2010"].

Simulium* (*Aspathia*) *jobbinsi **VARGAS, MARTÍNEZ PALACIOS & DÍAZ NÁJERA, 1946**

OTHER MATERIAL

GUATEMALA

Chimaltenago Department

PINNED

Acatenango, Finca Armenia, Rio Lojas; 2.x.1948, (*H.T.Dalmat*)— 1male (BMNH; (acc. no. 401.1). Acatenango, Finca Quisache, Rio Pocitos; 8.xi., 18.xi.1948, (*H.T.Dalmat*)— 1female (BMNH; acc. no. 414.20, 414.29, 414.64, 419.9).

SLIDES

Acatenango, Finca Quisache, Rio Pocitos; 16.xi., 18.xi.1948, (*H.T.Dalmat*)— 1female1male (BMNH; acc. no. 414-51, 414-56).

Simulium* (*Aspathia*) *kompi **DALMAT, 1951**

TYPE MATERIAL

GUATEMALA

Chimaltenango Department

SLIDES

Acatenango, Aldea Los Pajales, Rio Ciprés; 15.vi.1949, (*Roberto Marroquin*)— male (not associated with pupal exuviae) (NMNH) [HOLOTYPE] [The specimen is in three slides containig the wings, legs and genitalia; the remainder of the holotype is missing] [The slides bear several labels: Red label with black line around the edges and handwritten by DALMAt in black ink "HOLOTYPE male, *Simulium (S.) kompi*, n.sp. H.T.Dalmat", and in black ink and also in DALMAT'S hand "acc. Acat. 697-9" and the body part each slide contains; White label with lines around edges and in Dalmats' handwriting with locality information, date and collector's name. Other labels here added on the back of the slides: White label "*Simulium kompi* Dalmat Examined: L.M.Hernández 2010"; White label "Digitally photographed wing, legs and genitalia L.M.Hernández 2010"].

Simulium (Aspathia) metallicum **BELLARDI, 1859 (complex)**

All material listed in SHELLEY *et al.* (2002b, 2010) was examined for the current work. Further material examined where new labels have been added is as follows:

Synonym of *S. metallicum s.l.* as *Simulium nitidum* MALLOCH, 1912

TYPE MATERIAL

PERU

PINNED

Huancabamba; 6.ix.1911, (*C.H.T.Townsend*)— female (not associated with pupal exuviae) [HOLOTYPE] (USNM, cat. no. 15307) [The specimen is glued to a card point by the ventrolateral right side; it has lost three legs from the left side, but otherwise is in good condition] [The holotype bears several labels: White label with locality and collection date handwritten in black ink; White label with collectors' name printed in black ink; White label handwritten in black ink "Small tooth"; Red label "15307 U.S.N.M."; White label with black lines around the edges and handwritten in black ink "*Simulium nitidum* Malloch"; White label, handwritten in pencil "Syn. of *metallicum* Luz ?1925 Shelley 1982". Other labels here added: White label "Digitally photographed Thorax ant+post; abdomen, lateral view L.M.Hernández 2010"; White label "*Simulium nitidum* Malloch syn. of *S. metallicum* Bellardi in SHELLEY *et al.*, 1984".]

Synonym of *S. metallicum* as *Simulium violascens* ENDERLEIN, 1934

TYPE MATERIAL

MEXICO

PINNED
[Without locality, date or collector's name, but in original description the collector is said to be *Deppe*]— 1female (not associated with pupal exuviae) [HOLOTYPE] (NMHU) [The specimen is in relatively good condition though both antennae and wings, and five legs are missing] [The specimen have several labels: White label and handwritten in black ink "Mexico"; White label in ENDERLEIN'S hand *Odagmia violascens* and printed Dr. Enderlein det. 1934"; Red label "TYPUS"; White label "Zool. Mus. Berlin"; White label in COSCARCÓN'S hand "*Simulium metallicum* Bellardi Det. Coscarón, 1997"; White and yellow labels "Zool. Mus. Berlin". Other labels here added: "Digitally photographed Th. ant.+post, abdomen L.M.Hernández"; White label "*Simulium violascens* Enderlein syn. of *S. metallicum* Bellardi by COSCARÓN *et al.*, 1999 Examined: L.M.Hernández"].

OTHER MATERIAL

COSTA RICA

[WITHOUT PROVINCE]

PINNED
San Ramón, vi.1954, 200ft; (*P.A.Buxton*)— 1female (not associated with pupal exuviae) (BMNH). Rincón; 20.iv.1985, (*J. Memucu*)— 7females (man-biting) (BMNH) [All identified as near *S. metallicum s.l.* by L.M.Hernández]. [Without locality]; iii.1984, (*J.Lane*)— 6females (not associated with pupal exuviae) (BMNH) [All identified as near *S. metallicum* by L.M.Hernández].

MEXICO

Veracruz State

SLIDES
Veracruz; iii.1946, (*J.Parra*)— 3larvae (BMNH, B.M. 1848-401).

***Simulium* (*Aspathia*) *puigi* VARGAS, MARTÍNEZ & DÍAZ NÁJERA, 1946**

TYPE MATERIAL

MÉXICO

Chiapas State

PINNED
Mariscal, Aldea El Oriente, no. 671; 19.xi.1944, (*José Parra*)— male (not associated with pupal exuviae; only head, thorax, right wing, legs of right side; one antennae, left wing, legs of left side and genitalia on a slide] [HOLOTYPE] (INDRE, 3816) [The specimen is in good condition. It has been glued to a card point by the ventral side of thorax. One antennal segment, the left wing, the legs of left side and genitalia are on a slide; one gonostyle is missing] [The specimen bear several labels: Red label "Holotipo"; White label "CAIMSimTp-00218"; Pale green label "HOLOTIPO"; White label "*S. puigi*"; White label with locality information, date and collector's name; White label "3816"; White label "male". Other labels here added: White label "Digitally photographed Thorax ant.+post, abdomen L.M.Hernández"; White label "*Simulium puigi* Vargas *et al.* 1946 Holotype male INDRE Examined: L.M.Hernández 2008"]. Same data as holotype— 1female (not associated with pupal exuviae; one antennae, right wing, left side legs, and genitalia on a slide] [ALLOTYPE] (INDRE, 3816). Same data as holotype— 4females1male (not associated with pupal exuviae; the male have the abdomen missing) [PARATYPES] (INDRE) [All specimens have a blue label "Paratipo"].

SLIDES
Same data as pinned adult— male (only one antenna, left wing, left side legs, and genitalia on slide] [HOLOTYPE] (INDRE, 3816) [The slide have a White label with red borders with locality information, date and collector's name handwritten in black ink, a Red label "HOLOTIPO", and a White label "CAIMSimTp-00075". Other labels here added: White label "Digitally photographed genitalia, legs and wing L.M.Hernández 2009"; White label "*Simulium puigi* VARGAS *et al.* 1946 Examined: L.M.Hernández 2009"; White label in L.M. HERNÁNDEZ'S hand "Only wing, legs and genitalia; one gonostyle missing; remainder pinned Ex. L.M.Hernández 2009"]. Same data as holotype— 1female (not associated with pupal exuviae; only one antennal segment, right wing, left side

legs, and genitalia; remainder pinned] [ALLOTYPE] (INDRE, 3816) [The slide bear several labels: White label with red edges and in VARGAS'S hand with locality information, date and collectors' name; Yellow label "ALOTIPO"; White label "CAIMSimTp-00074". The slide have written directly onto it in red pencil "foto horquilla" [= photo, genital fork]". Other labels here added: White label "Digitally photographed "Wing, legs, genitalia INDRE Allotype Female L.M.Hernández 2009"; White label "*Simulium puigi* VARGAS *et al.*, 1946 Examined L.M.Hernández 2009"; White label in L.M. HERNÁNDEZ' hand "Only wing, legs, antennal segment and genitalia. Remainder pinned Det. L.M.Hernández 2009.]

OTHER MATERIAL

COSTA RICA

Punta Arenas Province

PINNED

Monteverde Res. Cloud For., 1500m; ii.1980, (*Manson*)—3females (not associated with pupal exuviae) (CNC). Monteverde Estación Biológica, 1540-1800m; 21-24.vii.1995, (*J.M.Cummings*)— 15females (not associated with pupal exuviae) (CNC). Monteverde; 25.vii.1980, (*D.M.Wood*)— 8females (not associated with pupal exuviae) (CNC). Monteverde; 18.25.v., 25-31.v.1988, (*B.Hubbley*)— 4females (not associated with pupal exuviae) (ROM). Monteverde Res. Cloud For., 1500m; 23.viii.1996, (*C.Condy*)— 4females (malaise trap, forest edge/field) (ROM). Monteverde, 1700m; 1.v.1980, (*B.V.Brown*)— 2females (malaise trap, stunted forest) (ROM) [All material identified with doubt as *S. puigi* by L.M. HERNÁNDEZ, 2008].

***Simulium* (*Aspathia*) *racenisi* RAMÍREZ PÉREZ, 1971**

All specimens listed as *S. racenisis* in SHELLEY *et al.* (2010) were examined in this paper.

***Simulum (Aspathia) spilmani* STONE, 1969**

TYPE MATERIAL

WEST INDIES, DOMINICA

PINNED

Clark Hall; 8-10.i.1965, (*W.W.Wirth*)— 1female (Malaise trap) [PARATYPES] (NMNH). Clarke Hal, 11-20.i..1965 (*W.W.Wirth*)-4 females (light trap) [PARATYPES] (NMNH). Clarke Hal, 21-31.i.1965 (*W.W.Wirth*)— 7females6males (Malaise trap) [PARATYPES] (NMNH). Clarke Hal, 1-10.ii.1965 (*W.W.Wirth*)— 3females1male (light trap) [PARATYPES] (NMNH). Clarke Hall; 21-28.ii.1965m (*W.W.Wirth*)— 1female3males (light trap) [PARATYPES] (NMNH). Clarke Hall; 1-10.iii.1965, (*W.W.Wirth*)— 6males (light trap) [PARATYPES] (NMNH). Clarke Hall. vii.1964, (*T.F.Spilman*)— 1female2males (light trap) [PARATYPES] (NMNH). Fresh Water I; 21.ii.1964, (*Dale F.Bray*)— 3females [PARATYPES] (NMNH, no. 70735). S. Chiltern Est.; 20.ii.1965, (*W.W.Wirth*)— 2females1male (light trap) (NMNH). Cabrits Swamp; 23.ii.1965, (*W.W.Wirth*)— 2females (light trap). Antrhim, 1000'; 17.iii.1965, (*J.F.G.Clarke*)— 1female3males [PARATYPES] (NMNH). C'leauGommier; 17.iii.1956, (*J.F.G.Clarke*)— 1male [PARATYPE] (NMNH) [All specimens bear several labels: White label with locality, date and collector's name; White label " Bredin-Archbold Smithosnian Bio. Surv. Dominica"; White label with blue border "Paratype *Simulium spilmani* Stone NMNH 70735. I have added other label: White label "*Simulium spilmani* Stone Examined L.M.Hernández]. Clarke Hall; 21-31.i.1965, (*W.W.Wirth*)— 1female (light trap) (Brendin-Archbold Smithsonian Institution Survey-Dominica) (NMNH) [The specimen have a White label with red lines around the edges and added by an unknown reviser "Holotype, *Simulium spilmani*, USNM 70735". It also has a White label in red ink with R.W. CROSSKEY'S hand "This is not the holotype (which is the male on slide in the slide collection) R.W.C. 28.x.1982". I agree with R.W. CROSSKEY that this is not the holotype of *S. spilmani*, but a paratype. I have added other labels to this effect: White label "Paratype"; White label "This is not the holotype; holotype in slide collection Exam: L.M.Hernández 2010"].

SLIDES

Clarke Hall, 1-8.viii.1964, (*T.J.Spilman*)— male (in light trap) [HOLOTYPE] (USNM, 70735) [The specimen bear a White label with black lines around the edges and handwritten in black ink with the locality information, date, collector's name and collecting method; also handwritten "*Simulium male*". On the same label it has been crossed out in pencil the name "*metallicum*" and have been added also in pencil "Holotype"; Red label with black edges and handwritten in black ink "Holotype *Simulium spilmani* Stone, USNM 70735". Other labels here added on the back of the slide: White label "Digitally photographed genitalia, thorax L.M.Hernández 2010"; White label "*Simulium spilmani* Stone Holotype male Exam: L.M.Hernández 2010"]. Clarke Hall; 1-10.iii.1965, (*W.W.Wirth*)— 1male [PARATYPE] (NMNH, 70735). Clarke Hall; 11-8.viii.1964, (*T.J.Spilman*)— 2females [PARATYPES] (NMNH, 70735). [Without locality, date of collector's name.])— 1male [PARATYPE] (NMNH, 70735) [I have added a White label to all the specimens labelled as paratypes "*Simulium spilmani* Stone Exam: L.M.Hernández 2010"].

OTHER MATERIAL

WEST INDIES, DOMINICA

PINNED

Clarke Hall, 21-31.i.1965 (*W.W.Wirth*)— 17females (malaise trap) (NMNH). Clarke Hall, 1-10.ii.1965 (*W.W.Wirth*)— 1female (light trap) (NMNH). S. Chilterns Est.; 20.ii.1965, (*W.W.Wirth*)— 2females (light trap).

SLIDES

Layo River, *ca.* 50'elev., 15°24.23'N 61°24.8'W; 16.ii.2005, (*P.H.Adler*)— 2females (not associated with pupal exuviae), 4pupal exuviae (BMNH). Doneky Road, Pont-Casse, Castle bruce Rd; 19.iv.1959, (*R.F.Darsie*)— 3larvae (NMNH).

SPIRIT

Layo River, ca 50'elev., 15°24.23'N 61°24.8'W; 16.ii.2005, (*P.H.Adler*)— 5pupal exuviae (BMNH).

Simulium (Aspathia) tricorne DE LEÓN, 1945

GUATEMALA

Acatenango Department

PINNED

Finca Los Pajales, Rio Cipres; 3.vii.1950, (*H.T.Dalmat*)— 1female1male (NMNH, acc. no. 128-10; 777-13).

Subgenus *Psilopelmia* ENDERLEIN, 1934

BICOLORATUM species group

Simulium (Psilopelmia) oviedoi RAMÍREZ-PÉREZ, 1971

The material listed in HERNÁNDEZ *et al.* (2007a) was examined in this paper. Further material examined where new labels haven added is as follows:

OTHER MATERIAL

VENEZUELA

Mérida State

PINNED

Aguilera-Apartadero, 3500 m; [Without date.], (*Jaime Ramirez*)— 1female (reared; only thorax, and two legs; head, wing, three legs, abdomen and genitalia on slide) (AMNH) [Identified by RAMÍREZ PÉREZ.]

SLIDE

Aguilera-Apartadero, 3500 m; [Without date.], (*Jaime Ramirez*)— 1female (reared; only thorax, and two legs; head, wing, three legs, abdomen and genitalia on slide) (AMNH) [Identified by RAMÍREZ PÉREZ]. Road Apartaderos, Sto Domingo, 3500m; 16/26.ii.1968, (*P. & B. Wygodzinsky*)— 1female1male (reared), 2 larvae (MLP).

[WHITOUT COUNTRY BUT PROBABY VENEZUELA]

SLIDE
[Without locality data or collector's name.]; v.11, [Without collector's name]— 1male (reared), 1pupal exuviae, 2larvae (AMNH).

Simulium (Psilopelmia) rivasi RAMÍREZ PÉREZ, 1971

The material listed in HERNÁNDEZ *et al.* (2007a) was examined in this paper. Further material examined where new labels haven added is as follows:

OTHER MATERIAL

VENEZUELA

Mérida State

PINNED
Road Apartaderos–Sto Domingo, 3500 m; 16-26.ii1968, (*P. & B. Wygodzinsky*, *M. Coronos*)— 1male (reared; only head, one wing and legs; one wing, abdomen and genitalia on slide) (AMNH) [Identified by S. COSCARÓN].

SLIDE
Mérida, Apartaderos, 3850 m; 13.ii.1968, [Without collector's name.]— 1female (reared), 2pupal exuviae, 3larvae (AMNH). Road Apartaderos–Sto. Domingo, 3500 m; 16-26.ii1968, (*P. & B. Wygodzinsky*, *M. Coronos*)— 1male (reared; only one wing, abdomen and genitalia on slide; head, one wing and legs pinned) (AMNH) [Identified by S. COSCARÓN]. N. de Apartaderos, 3850m; 3.ii.1968, (*R. Pérez*)— 1female, 1male, 2larvae (reared) (MLP). Páramo, 4100m; 6.x.1980, [Without collector's name.]— 1female (reared) (MLP).

SPIRIT
Merida, (v.14), rd Mucubaji-Sto. Domingo, 3400 m; 20-26.xi.68, (*Wygodzinsky*)— 4larvae (two mature), 3pupal exuviae (AMNH) [Identified by S. COSCARÓN].

Subgenus *Simulium* LATRILLE

ORNATUM species group

Simulium (Simulium) ornatum (MIEGEN, 1818) (complex)

OTHER MATERIAL

UNITED KINGDOM

Surrey County

Carnoy's fluid
Un-named stream 500m west of Thursley Village, (National Grid References: SU897398); 11.x.2009, (*R. Post*)— several larvae and pupal exuviae (BMNH) [Identified by R.J. POST].

TUBEROSUM species group

Simulium (Simulium) appalachiense ADLER, CURRIE & WOOD, 2004

TYPE MATERIAL

UNITED STATES OF AMERICA

South Carolina State

PINNED
Oconoee Co, Chauga River, Chau Ram Co. Park, 34°40.88'N 83°08.80'W; 6.iii.1988, (*P.H & C.R.L. Adler*)— 1female1male (reared; female only thorax and pupal exuviae and cocoon, remainder on a slide; male only head, thorax, three legs, pupal exuviae and cocoon, remainder on a slide) [PARATYPES] (BMNH) [The specimens bear a Blue label "PARATYPE *Simulium appalachiense* Adler, Currie, Wood 2004". Other labels here added: White label "Material in slide collection; White label "Digitally photographed Th. ant+post, abdomen in lateral view L.M.Hernández'10].

SLIDES
Oconoee Co, Chauga River, Chau Ram Co. Park, 34°40.88'N 83°08.80'W; 6.iii.1988, (*P.H & C.R.L. Adler*)— 1female1male (reared; female only head, wings, legs and genitalia; thorax, pupal exuviae and cocoon pinned; male only both wings, abdomen, genitalia, one wing and three legs, remainder pinned), 3pupal exuviae, 3larvae [PARATYPES] (BMNH)

SPIRIT
Oconoee Co, Chauga River, Chau Ram Co. Park, 34°40.88'N 83°08.80'W; 6.iii.1988, (*P.H & C.R.L. Adler*)— numerous pupal exuviae and larvae [PARATYPES] (BMNH).

VENUSTUM species group

Simulium (Simulium) posticatum **MEIGEN, 1838**

OTHER MATERIAL

UNITED KINGDOM
SLIDES
Oxon, River Evenlode at Combe, SP4 20148; 13.v.2004, (*D.Werner*)— 3females3males (not associated with pupal exuviae) (BMNH). Oxon, River Cherwell at Enslow, SP 477 184; 29.iv.2004, (*D.Werner*)— 3pupal exuviae, 3larvae (BMNH).

SPIRIT
Oxon, River Evenlode at Combe, SP4 20148; 13.v.2004, (*D.Werner*)— numerous females and males (not associated with pupal exuviae) (BMNH). Oxon, River Cherwell at Enslow, SP 477 184; 29.iv.2004, (*D.Werner*)— numerous females and males (not associated with pupal exuviae) (BMNH).

Subgenus *Trichodagmia* ENDERLEIN, 1934

ALBELLUM species group

Simulium (Trichodagmia) albellum **Rubtzov, 1947**

OTHER MATERIAL

RUSSIA
PINNED
[Illegible]— 2females (not associated with pupal exuviae) [Identified by R.W. CROSSKEY; the specimen bear a White label "Part of exchange with I.A. RUBTZOV (his letter of 28.ii.1965 to R.W.C. refers)"].

Simulium (Trichodagmia) auricoma **MEIGEN, 1818**

OTHER MATERIAL

CYPRUS
PINNED
Troodos Mts, str. at Agios Nikolaos, 2 km NW of Kakopetria, 32°52'E34°68N, 900m; 11-12.v.1974, *(H.Malicky)*— 1male (not associated with pupal exuviae) [Identified by R.W. CROSSKEY, B.M. 1983-32]

FRANCE
PINNED
Honnek, Vosges, 200-4000ft; 8-28.viii.1936, (*P.A.Button*)— 2females (not associated with pupal exuviae; only thorax; remainder of body on a slide) (BMNH) [Identified by R.W. CROSSKEY].

SLIDES
Honnek, Vosges, 200-4000ft; 8-28.viii.1936, *(P.A.Button)*— 2females (only head, wings, legs and genitalia; thorax on slides) (BMNH) [Identified by R.W. CROSSKEY].

GREECE

PINNED

Paikon Mts, torrent in gorge below Kastanari, 800m, 40º58', 22º22'; 10.vi.1989, (*Malicky*)— 1female (BMNH) [Identified by R.W.CROSSKEY, 2000. It bears a White label "Specimen dried from alcohol"]. Greek islands, Lesbos, 4 km W of Agiassos, 400 m; 26.v.1975, (*Maliky*)— 1pupal exuviae, 1larva (BMNH).

MOROCCO

SLIDES

Rif Mts, Aarkob; 27.iv.1998, (*B.Belgat*)— 1larva (BMNH)

Simulium (Trichodagmia) galloprovinciale GIUDICELLI, 1963

OTHER MATERIAL

SPAIN

Jean Province

PINNED

Cazorla area, 3 km SW of Puente de las Herrerias, trib. of R. Guadalquivir, UTM Grid WC 049; 18.v.1986, (*R.W.Crosskey*)— 1female (reared; only thorax, remainder of body, and pupal exuviae and cocoon on several slides) (BMNH, B.M. 1986-228) [Identified by R.W. CROSSKEY]; 1female1male (reared) (BMNH).

SLIDES

Cazorla area, 3 km W of Puente de las Herrerias, trib. of R. Guadalquivir, UTM Grid WC 049; 18.v.1986, (*R.W.Crosskey*)— 1female (reared; only head, wings, lead genitalia, and pupal and cocoon; thorax pinned) (BMNH, B.M. 1986-228) [Identified by R.W. CROSSKEY].

MOROCCO

SLIDES

Rif Mts, Nakla; 3.v.1999,(*B. Belgat*)— 1larva (BMNH).

Simulium (Trichodagmia) ibericum CROSSKEY & SANTOS GRACIO, 1985

TYPE MATERIAL

PORTTUGAL

PINNED

Nr. Viseu, R. Dao; 13.viii.1971, (*R.W.Crosskey*)— male (reared) [HOLOTYPE] [In good condition; the pupa is glued to a card which is attached to the pinned adult][The specimen bear several labels: White round label with red edges "Holotype"; White label with locality information"; White label " *Simulium (Obuchovia) ibericum* sp.n. Det. R.W.Crosskey; White label "Holotype male" and in CROSSKEY'S hand "S*imulium (Obuchovia) ibericum* sp.n R.W.Crosskey". Other labels here added: White label "Digitally photographed Th. anterior+posterior, abdomen, lateral view L.M.Hernández"]. Same data as holotype-2males (reared) [PARATYPES][Identified by R.W. CROSSKEY].

SPAIN

Caceres Province

SLIDES

Rio Ruecas; 27.viii.1971 (*R.O.C.*)— 2larvae [PARATYPES] (BMNH).

Simulium (Trichodagmia) margaritae (RUBTZOV, 1956)

OTHER MATERIAL

ARMENIA

PINNED

R. Kosakh; 25.iv.1948, (*Rubtsov*)— 1female (not associated with pupal exuviae; only thorax; remainder of body on several slides) [Identified by R.W. CROSSKEY] [The specimen have several labels: White label "from type locality"; White label "received in exchange with I.A. RUTBSOV 1964]; 1female1male (not associated with pupal exuviae) (BMNH).

SLIDES
R. Kosakh; 25.iv.1948, (*Rubtsov*)— 1female (not associated with pupal exuviae; only head, wings, legs, genitalia; thorax pinned)[Identified by R.W. CROSSKey] [The specimen have a White label "from type locality"; White label "received in exchange with I.A. RUTBSOV 1964].

TURKEY
SLIDES
Tunceli Prov., 40 Km S of Pulumur; 18.v.1970, (*Heide Zwick*) — 1larva (BMNH).

Simulium (Trichodagmia) marocannum BOUZIDI & GIUDICELLI, 1988
OTHER MATERIAL

MOROCCO
SLIDES
High Atlas; 20.xi.1985, [Without collectots' name.]— 1male (not associated with pupal exuviae), 1pupa exuviae (only gill filaments) (BMNH).

Simulium (Trichodagmia) popowae RUBTZOV, 1940
OTHER MATERIAL

AZERBAIJAN
PINNED
Nakhitshevan Aut. Rep., Orduba district, Pazmari; 14.vii.1939, (*Gauzer*)— 2females (not associated with pupal exuviae) (BMNH) [Specimens identified by I.A. RUBTZOV; White label "Part of exchange with A.V. YANKOVSKY, received by R.W. CROSSKEY 28.ix.1983"].

SLIDES
R. Gyanjachaya near Khnlar and Zurnabad; 9.v.1952, (*Djafarov*)— 1larva (BMNH) [Specimen identified by RUBTZOV; White label "Part of exchange with A.V.YANKOVSKY, received by R.W.CROSSKEY 28.ix.1983"].

Simulium (Trichodagmia) transcapicum ENDERLEIN, 1921
OTHER MATERIAL

PERSIA
PINNED
Chalous; 5.[Illegible].1957, (*D.Giaquinto*)— 1female (not associated with pupal exuviae; only thorax; remainder Of body on slide) (BMNH) [Identified by R.W. CROSSKEY] [The specimen also have a label in blue ink "*Simulium ? transcapicum* Det. P.Freeman, det. 1953]; 7males (not associated with pupal exuviae) (BMNH) [Identified by R.W. CROSSKEY].

SLIDES
Chalous; 5.[illegible].1957, (*D.Giaquinto*)— 1female (not associated with pupal exuviae; only head, abdomen, legs and wings; thorax pinned) [Identified by R.W. CROSSKEY] [The specimen also have a label in blue ink "*Simulium ? transcapicum* Det. P.Freeman, det 1953].

CANADENSE species group

Simulium (Trichodagmia) ayrozai VARGAS, 1945
TYPE MATERIAL

MÉXICO
Federal District
PINNED

Desierto de los Leones; 5.iii.1944, (*Martínez-Díaz*)— 2females5males (not associated with pupal exuviae) [PARATYPES] (INDRE), 2males (not associated with pupal exuviae) (NMNH) [All specimens have a blue label as "PARATIPOS [=PARATYPES]"].

SLIDES
Desierto de los Leones; 5.iii.1944, (*Martínez & Díaz N.*)— male (only one wing, three legs, and genitalia; remaiNder of the adult missing) [HOLOTYPE] (INDRE, 3676) [The specimen is in relative good condition] [The slide bear several labels: White label with red borders with locality information, date and collector's name; White label "CAIMSimTp-0012". Other label here added: White label "Digitally Photographed wing, legs and genitalia L.M.Hernández"].

SPIRIT
Desierto de los Leones; 5.iii.1944, (*Martínez & Díaz N.*)— male (reared; only thorax, one wing and three legs, and pupal exuviae; one wing, three legs, and genitalia on a slide) [HOLOTYPE] (INDRE, 3676) [The specimen is in relative good condition, although it is slightly brittle] [The specimen bear several labels: White label with locality information, date and collector's name handwritten in black and "3676"; White label in black ink "(87-415)"; White label "1A, 1E"; White label "CAISimTp-0013". Other labels here added: Digitally photographed Thorax and pupal exuviae L.M.Hernández"]. Same data as holotype— 1female (reared) [INDRE, no. 3616] (genitalia said to be on a slide with no. "3613", but I was not able to locate this slide. The specimen bear several labels: White label with locality information, date and collector's name and number "3616"; White label "39(87-392)"; White label "CAIMSimTp-00015"].

OTHER MATERIAL

MÉXICO
Federal District
PINNED
Salazar; 23.iii.1994, (*A.Díaz N.*)— 1female (not associated with pupal exuviae) (BMNH, B.M. 1949-239)

SLIDES
Desierto de los Leones; 21.iii.1955, 21.v.1955, 26.iii1948, (*Díaz Nájera*)— 1pharate female, 1pharate female, 1larva (MLP).

SPIRIT
Same data as holotype— 1female1male (reared) [PARATYPES] (INDRE).

[WITHOUT STATE]
[Without locality, date or collector's name]— 1pupal exuviae, 1larva (MZUCR).

Simulium (Trichodagmia) burchi **DALMAT, 1951**

TYPE MATERIAL

GUATEMALA
El Quiché Department
PINNED
Finca Micovez, Rio Micovez; 15.xi.1949, (*Herbert, T. Dalmat*)— female (not associated with pupal exuviae) [HOLOTYPE] (NMNH, acc. no. 8X-3) [The specimen bear a Red label in DALMAT'S hand "Holotype *Simulium (Hearlea) burchi*, n.sp. H.T.Dalmat"; White label with locality information, date and collector's name; White label "8X-3". Other labels here added: White label "*Simulium burchi* Det. L.M.Hernández 2010"; White label "Digitally photographed Thorax ant.+post.; abdomen L.M.Hernández"]. Same data as holotype— 2females (not associated with pupal exuviae; only thorax, remainder on slide), 1male (reared; pupal exuviae in alcohol) [PARATYPES] (NMNH, females acc. no. 8X-1, 8X-2; male 8x-7) [All specimens have a green label in DALMAT'S hand "PARATYPE "*Simulium (Hearlea) burchi*, n.sp. H.T.Dalmat"].

SLIDES
Same data as holotype; [Without collector’s name.]— 1pharate male (MLP) [PARATYPE]. Same data as holotype— 1male (reared; pupal exuviae in alcohol; adult thorax lost) [ALLOTYPE] (NMNH, acc. no. 8X-10) [The slide bear a Red label in DALMAT’S hand “ALLOTYPE 8X-10 *Simulium (Hearlea) burchi*, n.sp. H.T.Dalmat”]. Same data as holotype— 2females (only head, wings, abdomen, genitalia and legs; thorax pinned) [PARATYPES] (NMNH, acc. nos. 8X-1, 8X-2) [The specimens bear a Green label handwritten in DALMAT’S hand ‘PARATYPE *Simulium (Hearlea) burchi*, n.sp. H.T.Dalmat”].

SPIRIT
Same data as holotype and adults on slide— 1male (only pupal exuviae; adult in three slides) [as ALLOTYPE] (NMNH, acc. no. 8X-10). Same data as holotype— nine pupal exuviae [PARATYPES] (NMNH, acc. no. 8X-1, 8X-2, 8X-7, 8X-8, 8X-12, 8X-13, 8X-14; 9I-1, 9I-12).

OTHER MATERIAL

GUATEMALA

El Quiché Department

PINNED
Finca Micovez, Rio Micovez; 15.xi.1949, 15.xi.1950, 28.vii., 30.vii, vii.1951, (*Herbert*, *T. Dalmat*)— 9males (reared; pupal exuviae in alcohol) (NMNH, acc. no. 11Y-1, 11Y-2, 11Y-6, 11Y-7, 11Y-22, 11Y-25, 11Y-26; 12-2; 13O-5).

SLIDES
Finca Micovez, Rio Micovez; 15.xi.1950, (*Herbert*, *T. Dalmat*)— 2males (reared; pupal exuviae in alcohol) (NMNH, acc. no. 11Y-1; 11Y-24)

[WITHOUT DEPARTMENT]

SLIDES
[Without locality, dare or collector’s name.]— 1larva (MLP, 123-2) [Identified by S. COSCARÓN 2000.]

[WITHOUT COUNTRY OR LOCALITY, BUT PROBALY GUATEMALA]

[Without locality, date or collector’s name.]— 1female (reared), 1larva, 1pupal exuviae (MLP) [Identified S. COSCARÓN as *S. burchi*]; several 17 mature larvae (in poor condition) (NMNH, acc. no.13I-2)

MÉXICO

SLIDES
Rio Frio; 6.ix.1969, (*P. & B. Wygodzinsky*)— 1larva (MLP).

Simulium (Trichodagmia) canadense **HEARLE, 1932**

TYPE MATERIAL

CANADA

British Columbia State

PINNED
Kamloops, Lanes Creek; 6.viii.1931, (*T.R.Molliet & R.T. Turner*) (CNC)— male [HOLOTYPE] (CNC) [The specimen bear several labels: White label with locality information, date and collector’s name, and handwritten in black ink “*S. virgatum*”; Blue label “67.b”; Red label and handwritten in black in “HOLOTYPE *Simulium virgatum race canadensis* Hearle CNC no.3454”; White label and handwritten in black ink “var. *canadensis*”; White label and printed in black ink “*Simulium virgatum* Coquillet”. Other labels here added: White label “Digitally photographed Th. ant.+.post, abdomen L.M.Hernández”; White label in L.M.HERNÁNDEZ’S hand “*Simulium canadense* Hearle Examined L.M.Hernádez 2008”; White label “Digitally photographed Th. ant.+post., abdomen L.M.Hernández 2009]. Kamloops; 29.v.1928, (*Eric Hearle*)— 1female (reared; pupal exuviae glued to a leaf attached to the specimen) [as

ALLOTYPE] (CNC, no. 3454) [The specimen bear several labels: White label with locality information, date and collector's name. The label have on the top "No. KS1-Bred"; Red label and handwritten in black ink "Allotype Sim. *virgatum* race *canadensis* Hearle CNC No. 3454"; White label and printed "Peterson Creek"; Blue label "96"; White label and handwritten in black ink "Reared from isolated pupa"; White label and printed in black ink "*Simulium variegatum*"; White label and handwritten in black ink "var. Canadensis Hearle". White label "Digitally photographed Th. ant.+.post, abdomen L.M.Hernández"; White label in L.M. HERNÁNDEZ'S hand "*Simulium canadense* Hearle Examined L.M.Hernádez 2008"]. Kamloops, Cold Creek; 11.vi., 14.vi.16.vi.1930, (*Eric Hearle*)— 2females2males (not associated with pupal exuviae) [PARATYPES] [The specimens bear several labels: White label with locality, date and collector's name; Blue label "10; Yellow label "Paratype 3454"; White label "*Simulium virgatum* Coquillet"; White label "*var. canadensis* Hearle";' White label "Hearle collection". Other labels here added: White label: "Digitally photographed Th. ant.+post.; abdomen L.M.Hernández CNC-male no.1"]; 3females3males (reared) [PARATYPES, no. 3454] (BMNH, B.M.1932-392); 2females1male [PARATYPES] (NMNH, acc. no. 3454). Lanes Cre, Kam.; 8.viii.1921, (*T.K.M. & R.T.T.*)— 2females (not associated with pupal exuviae) [PARATYPES] (CNC). Kamloops, Jamison Creek; 4.vii.1931, (*T.K.Moilliet*)— 2females (not associated with pupal exuviae) [PARATYPES] (CNC) [All paratypes have Yellow label "PARATYPES no. 3454"].

SLIDES
Kamloops, 12.vi.1930, (*Eric Hearle*)— 1male (only a male genitalia) (NMNH).

Synonymy of *S. canadense* as *Simulium fraternum* TWINN, 1938

TYPE MATERIAL

UNITED STATES OF AMERICA

Utah State

PINNED
Davis Co., Farmington; 4.ix.1934, (*G.F.Knowlton & C.F.Smith*)— male (only head, one wing, thorax, five legs, and part of abdomen; genitalia on slide) [HOLOTYPE] (CNC) [The specimen bear several labels: White label with locality information and date; White label with collector's name; Pale blue label: "SLIDE, no. male; and encircled in black ink "S.219"; Red label and handwritten in black ink "fraternum Twin Type 4452"; Red label and handwritten "Holotype *Simulium fraternum* Twinn CNC No. 4452"; White label "*canadense*". Other labels here added: White label "Material in slide collection genitalia White label "Digitally photographed Th. ant.+post Holotype Male L.M.Hernández; White label "*Simulium fraternum* Twinn 1938 syn. of *S. canadense* Examined: L.M.Hernández'10"].

SLIDES
Davis Co., Farmington; 4.ix.1934, (*G.F.Knowlton & C.F.Smith*)— male (only genitalia; head, wings, thorax, and legs and part of abdomen) [HOLOTYPE](CNC) [The slide bear a White label with locality information, date and collector's name handwritten in black ink. The label also bear on the top left hand side corner handwritten in red ink "Type 4452"; the species name is handwritten in black ink and below it is written in closed brackets "see pinned specimen". It also has "S.129" written and encircled in red ink and printed in black ink "Dom. Ent. Br. Ottawa". Other labels here added: White label "Digitally photographed genitalia Male (all) Holotype L.M.Hernández; White label "*Simulium fraternum* Twinn, 1938 syn. of *S. canadense* Examined: L.M.Hernández'10; White label in L.M.HERNÁNDEZ'S hand "Head, thorax, legs, one wing pinned Examined: L.M.Henrnández10"].

OTHER MATERIAL

CANADA

British Columbia

PINNED
Kamloops, Cold Creek; 7.vi.1930, (*Eric Hearle*)— 1male (not associated with pupal exuviae) (CNC). Bog R.R.trac stream; 4.vi.5.vi.1955, 4.vi.-7.vi.1955, 31.v.-2.vi.1955, (*G.E.Shewell*)— 3females2males (reared) (CNC).

MÉXICO
Federal District
PINNED
Contreras; 7.iv.1944, (*A.Díaz N.*)— 1female (not associated with pupal exuviae) (BMNH, B.M. 1949-236).

[WITHOUT STATE]
[Without locality, date or collector's name]— 1pupal exuviae (MZUCR).

UNITED STATES OF AMERICA
California State
PINNED
Andrea Canyon, Palm Springs, 13.iii.1955, (*W.R.M.Mason*)— 1male (reared) (CNC). Menducino Co., Univ. Cal. Hopland Field Stan.; 4.vi.1983, (*G. & M.Wood*)— 2females1male (reared; one male without pupal exuviae) (CNC).

SLIDES
[Without locality, date o collector's name.]— 1pupal exuviae (MLP).

SPIRIT
Menducino Co., Eel River aboe Rod Rios, 39°40'N 123°20'W; 8.v.1985, (*G.W.Courtney*)— several pupal exuviae and larvae (CUAC); 1pupal exuviae, 1larva (BMNH). Toulumme Co., Big Crek, just N. of Groveland, jnct. Rt. 120 and Big Cr. Shaff Rd.; 8.v.1992, (*P.H.Adler*)— numerous larvae and several pupal exuviae (CUAC). Sonoma Co., Santa Rosa Creek, Annadel Park; 8.iii.1990, (*P.H. & C.R.C.Adler*)— several larvae and pupal exuviae (CUAC).

Nevada State
SLIDES
Charslenton Mts; 25.v.1940, (*R.Cheer*)— 2males (reared), 1larva (MLP).

New Mexico State
SPIRIT
Doña Ana Co. Aquirre Springs Nat'l Rec. Site; 16.v.1992, (*M.E.Craig & B.V.Peterson*)— 21pupal exuviae, 42 larvae (NMNH). Sierra Co., Percha River, Hiollsboro, 5.480'; 16.v.1991, (*M.E.Craig & B.V.Peterson*)— 2females6males (reared) (NMNH).

Oregon State
PINNED
Oregon, Mt Vernon, Grant Co.; 11.vii.1963, (*G.C. & D.M.Wood*)— 1male (reared) (CNC), 1female1male (BMNH).

Simulium (Trichodagmia) capricorne DE LEÓN, 1945

Synonymy of *S. capricorne* as *Simulium deleoni* VARGAS, 1945

TYPE MATERIAl

MÉXICO
Federal District
SLIDES
Desierto de los Leones; 5.iii.1944, (*A.Díaz Nájera & A.Martínez Palacios*)— 1male (reared; only three legs, one wing and genitalia; remainder of adult and the pupal exuviae in spirit) [HOLOTYPE] (INDRE, no. 3619) [The male, cocoon and pupal exuviae are preserved in ethanol; three legs, one wing and the genitalia are on a slide. The slide is in good condition] [The slide bear several labels: White label with red edges and handwritten in black ink with locality information, date and collector's name and

“3619”; Red label “HOLOTIPO”; White label “CAIMSimTp-00096”; Other labels here added: Digitally photographed legs I-III, wing and genitalia INDRE HOLOTYPE L.M.Hernández”; White label in L.M. Hernández’s hand “MALE; remainder of adult, cocoon and pupal exuviae in alcohol Ex. L.M.Hernández’09”]. Same data as holotype— pharate female [ALLOTYPE] (INDRE, no. 36178) [The slide bear several labels: White label with red edges and handwritten in black ink with locality information, date and collector’s name and “3617”; Yellow label “PARATIPO”; White label “CAIMSimTp-00097”. Other labels here added: White label “Digitally photographed Leg I, genitalia ALLOTYPE Female INDRE L.M.Hernández”]. Same datas as holotype— 1male (reared; only one wing, three legs and gentialia, remainder of adult in ethanol) [PARATYPE] (INDRE, no.3670) [The specimen bear a Blue label “PARATIPO” and a White label “CAIMSimTp-00098”].

SPIRIT
Same data as specimen on slide— male (reared; only remainder of adult and the pupal exuviae; three legs, one wing and genitalia on slide; there is an extra pupal exuviae together with the holotype) [HOLOTYPE] (INDRE, no. 3619) [The specimen bear several label: White label with locality information, date and collector’s name and handwritten in black ink and “Holotipo”; White label “1A 1P”; White label “CAIMSimTp-00018”. Other labels here added: White label in L.M. Hernández’s hand “Digitally photographed pupal exuviae and adult Holotipo Ex. L.M.Hernández’09”]. Same data as specimen on slide and as the holotype— 1male (reared) [PARATYPE] (INDRE) [The specimen bear several labels: White label “CAISimTp-00024”; White label “Digitally photographed cocoon and gills L.M.Hernández”].

OTHER MATERIAL

GUATEMALA

Chimaltenango Department

PINNED
Acatenango, Finca Tohuyá, Rio Laguneta; 25.ix.1948, 26.v.1949, (*H.T.Dalmat*)— 1female1male (not associated with pupal exuviae) (MLP, female acc. no. 423-7; male no. 426-21), 3females2males (not associated with pupal exuviae) (BMNH, females acc. no. 603-1, 719-15, 423-23; males acc. no. 719-12, 719-39). Finca Torre, Rio Torre; 4.iv., 26.iii.1949, (*H.T.Dalmat*)— 1female1male (not associated with pupal exuviae) (BMNH; female 608-1, male 637-11). Miramar, Finca San José, Rio Chorrera; 23.xi.1948, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (BMNH, acc. no. 437-3). Finca Providencia, Rio Costita; 2.iv.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (BMNH, male 141-16) [All specimens identified by Dalmat 1948]. Acatenango, Finca Providencia, Rio Costita; 23.xii.1948; 2.xiv.1949, (*H.T.Dalmat*)— 1female1male (not associated with pupal exuviae) (NMNH, acc. no.153-1, 2). Rio Costita; 2.xiv.1949, (*H.T.Dalmat*)— 8females1male (NMNH, acc. no. 641-1, 641-5, 641-6, 641-9, 641-10, 641-13, 641-14, 641-17, 641-19). Yepocapa, Finca Quisaché, Rio Positos; 7.xii.1948, (*H.T.Dalmat*)— 4females1male (reared, but not associated with pupal exuviae) (NMNH, acc. nos. 414-12, 414-83, 414-84; 620-5; 903-21, 903-24). Acatenango, Finca Tehuyá; 15.xi.1949, 25.iii.1949, 26.v.1949, (*H.T.Dalmat*)— 6females20males (not associated with pupal exuviae) (NMNH, acc. nos. 426-4, 426-8; 603-6, 603-5; 719-3, 719-5, 719-9, 719-13, 719-14, 719-17, 719-18, 719-21, 719-22, 719-26, 719-27, 719-37, 719-38, 719-41, 719-48, 719-54, 719-61, 719-64, 719-65, 719-68). Acatenango, Finca San Diego, Rio San Diego; 6.xi.1948, (*H.T.Dalmat*)— 1female4males (not associated with pupal exuviae) (NMNH, acc. no. 416-19, 416-24, 416-25, 416-32, 416-35). Acatenango, Finca Esperanza, Rio Ladrillara; 21.iii.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae; adult missing) (NMNH, acc. no. 591-32). Acatenango, Finca S. Antonio, Rio Chajillo, Nejapa; 20.ix.1948, (*H.T.Dalmat*)— 1female (not associated with pupal exuviae) (NMNH, acc. no. 264-5) [All specimens with identification labels as *S. capricorne* by H.T. Dalmat].

SLIDES
Acatenango, Finca El Carmen, Rio Cocoyá; 26.xi.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (MLP, acc. no. 620-6) [Identified by H.T.Dalmat 1948]; 1male (NMNH, acc. no. 620-5). Finca Nueva Providencia, Rio Los Tablones; 5.vii.1948, [Without’s collector names.]— 1female (in

three slides), 1male (in three slides) (reared) (NMNH, acc. no. 236-7, 236-8, 236-9; 237-10). Rio Costita; 2.xiv.1949, (*H.T.Dalmat*)— 1female (NMNH, acc. no. 641-14). Yepocapa, Finca Quisaché, Rio Positos; 7.xii.1948, (*H.T.Dalmat*)— 1female (NMNH, 414-8). Acatenango, Finca Tehuyá; 26.v.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (NMNH, acc. nos. 719-50) [All specimens identifed as *S. capricorne* by H.T. DALMAT].

SPIRIT

Acatenango, Finca Tohuyá, Rio Laguneta; 2.iv.1948, (*José Rosales & Daniel Luch*)— 1pupal exuviae (NMNH, acc.no. Acate. 112-9) [The specimen bear a White label in red ink and DALMAT'S hand "PLESIOTYPE"] [White label in COSCARÓN'S hand "*Simulium capricorne* De León S. Coscarón 2000"].

Solalá Department

PINNED

Rio Patanatic, no. 3, Panajachel; 16.iii.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (NMNH, acc. no. 6C-1) [Specimen with identification labels as *S. capricorne* by H.T. DALMAT]. Solalá, Rio Catarata, Panachel; 7.viii.1949, (*H.T.Dalmat*)— 1female1male (not associated with pupal exuviae) (NMNH, acc. no. 817-4; 12K-16).

[WITHOUT STATE]

PINNED

iii., [Without locality, collecting year date or collector's name.]— 1female (reared) [Identifed by S. COSCARÓN 2000]. [Without locality or date] (*Dalmat*)— 1pupal exuviae (MLP, no. 377) [Identified by H.T.DALMAT]. [Without locality, date or collector's name.]— 1larva (MLP, 292-5) [Specimens with White label "Ex. Coleción Dalmat"].

MÉXICO

Distrito Federal

PINNED

Dept. Leones; 5.iii.1944, (*Martínez-Díaz*)— 1female1male(not associated with pupal exuviae) (BMNH, B.M. 1949-236). Rio Frio; 6.ix.1969, (*P & B. Wygodzinsky*)— 1larva (MLP) [Identified by S. COSCARÓN 2000].

Oaxaca State

SLIDES

[Without locality, date or collector's name]— 1pupal exuviae (MZUCR)

[WITHOUT COUNTRY OR STATE, BUT PROBABLY GUATEMALA]

SPIRIT

[Without locality, date of collector's name.]— numerous pupal exuviae and larvae (NMNH, acc. no. 2-6; 30-23; 136-14, 139-1, 139-4; 228-29; 231-25; 236-12, 236-13, 236-16A; 239-(2)-16A, 239-15; 242-5; 244-7; 250-13; 258(8)-8A; 265-15; 269-6; 277-12; 292-2, 292-5, 292-7; 294-4; 316-3, 317-5, 317-6, 317-2, 317-17; 331-19, 331-23, 331-24; 333-24; 347-10; 348-5, 348-16; 350-11, 373-19; 377-6, 377-7, 377-16, 377-20; 378-4, 378-6, 377-10; 414-7, 414-12, 414-17, 414-48, 414-84, 414-85, 414-89, 414-92C(6), P5-21); 1male (reared) (NMNH, acc. no. 236-11) [All specimens bear an indentification label in COSCARÓN'S hand "*Simulium carolinae* 2000"].

***Simulium (Trichodagmia) carolinae* DE LEÓN, 1945**

OTHER MATERIAL

GUATEMALA

Chimaltenango Department

PINNED

Pochuta, Finca La Torre, Rio Chorrera; 18.iii.1948, (*H.T.Dalmat*)— 1female (not associated with pupal exuviae) (NMNH, acc. no. 2C-10). Acatenango, Finca El Carmen, Rio Cocoyá; 19.v.50, (*H.T.Dalmat*)— 1female (NMNH, acc. no. 113-5).

Solalá Department

PINNED

Solalá, R. Catarata, campamento, RH1, kms. 24 y 25; 9.xii.1949, 4.xii.1949, (*H.T.Dalmat*)— several females (not associated with pupal exuviae) (BMNH, acc. no. 9T7); 1female (not associated with pupal exuviae) (NMNH, acc. no. 9T-I). Sololá, Puente Pananjachel, R. Catarata, 12.xii.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (BMNH, acc. no. 9L-4). Sololá, Puente Pananjachel, R. Catarata, 12.xii.1949, 11.iii.1951, 15.vi.1951, (*H.T.Dalmat*)— 4females3males (not associated with pupal exuviae) (NMNH, acc. no. 12R-2, 12R-3, 12R-5, 12R-6, 12R-7, 12R-8). Sololá, Otitlán, Finca Montes de Oro, Rio Catarata, Sta. Alicia, 11.viii.1951, 24.iii.1951, (*H.T.Dalmat*)— 13females5males (not associated with pupal exuviae) (NMNH, acc. no. 12K-1, 12K-2, 12K-7, 12K-8, 12K-9, 12K-14, 12K-17, 12K-19, 12K-21, 12K-22, 12K-26, 12K-27, 12K-28, 12K-30). Sololá, Panajachel, Rio Catarata; 2.ii.1948, 7.vii.1949, 11.viii.1951, (*H.T.Dalmat*)— 6females9males (not associated with pupal exuviae) (NMNH, acc. no. 8A-2; 13U-1, 13U-2, 13U-3, 13U-4, 13U-5, 13U-7, 13U-8, 13U-9, 13U-10, 13U-12, 13U-15, 13U-13, 13U-20, 13U-21, 13U-23, 13U-27; R-20).

SLIDES

Solalá, Rio Catarata, Sta. Alicia, 12R15; 2.iii.1951, (*H.T.Dalmat*)— 1male (reared) (MLP). Solalá, Rio Catarata, Sta. Alicia, R18; 3.ii.1948, (*H.T.Dalmat*)— 1female (not associated with pupal exuviae) (MLP). [Without locality, date or collector's name.]— 2larvae (MLP; one slide bear a White label with a note in blue ink apparently in COSCARÓN'S hand "head capsule and appendices does not correspond", acc. no. 331-24). Finca Monte de Oro, Sololá, R. Catarata, Sta. Alicia; 24.iii.1951, (*Dalmat, H.T.*)— 1female (no associated with pupal exuviae) (MLP, no. 12k-15; 12-18). [Without locality, date or collector's name.]— 2larvae (MLP, acc. no. 331-24). Acatenango, Finca Nueva Providencia, Rio Las Tablones; 5.vii.1948, [Without collector's name.]— 2females, 1pupal exuviae (NMNH, 236-9; 236-7) [Identified by H.T. DALMAT]. Sololá, Otitlán, Finca Montes de Oro, Rio Catarata, Sta. Alicia, 11.viii.1951, 24.iii.1951, (*H.T.Dalmat*)— 2females2males (not associated with pupal exuviae) (NMNH, acc. no. 12K-24, 12k-29), 2males (not associated with pupal exuviae) (NMNH, acc. nos. 12K-27; 13U-8).

Simulium (Trichodagmia) contrerense **DÍAZ NÁJERA & VULCANO, 1962**

TYPE MATERIAL

MÉXICO

Distrito Federal

SLIDES

Contreras, Los Dínamos; 20.v.1962, (*I.Córdova*)— male (reared) [HOLOTYPE] (INDRE, no. 6519) [The holotype is in relative good condition and it has been mounted on four slides; three legs are missing] [The slides bear several labels: White label with locality information, date and collector's name handwritten in black ink and number "6519"; Red label "HOLOTIPO"; White label "CAIMSimTp-00107-109". Other labels here added: White label "Digitally photographed pupal abdomen, gill, genitalia (all), palps, antenna, wing, legs INDRE HOLOTYPE L.M.Hernández"]. Same data as holotype— 1female (reared, in four slides) [as ALLOTYPE] (INDRE, no. 6520) [The specimen is in good condition, the spermatheca is missing] [The allotype bear similar labels as the holotype except: Yellow label "ALOTIPO"; White label "CAIMSimTp-000102-106". Other labels here added "White label "Digitally Photographed genitalia (all), palps, nud. area, legs I-III, wing, hind claw ALLOTYPE, INDRE L.M.Hernández"]; 1female (reared), 1male (only genitalia) [Both slides bear a Blue label "PARATIPO" and a White label "CAIMSimTp-00101, 102"] (INDRE).

Simulium (Trichodagmia) dalmati **VARGAS & DÍAZ NÁJERA, 1948b**

TYPE MATERIAL

MÉXICO
Veracruz State
PINNED
Cumb., Acultzingo; 31.viii.1948, (*I.Córdoba*)— male (not associated with pupal exuviae; gentalia, left wing and three left legs on slide) [HOLOTYPE] (INDRE, no. 3934) [The specimen is in good condition and it has been glued to a card point by the ventral side of thorax. The left three legs, left wing and genitalia is on a slide] [The specimen bear several labels: Red labels "HOLOTIPO"; White label "CAIMSimTp-00187"; Green label "HOLOTIPO"; White label "*dalmati* male"; White label with locality information, date and collector's name; White label "3934". Other labels here added: White label "Digitally photographed Thorax ant.+post.; abdomen L.M.Hernández"; White label *Simulium dalmati* Vargas & Díaz Nájera, 1948 Holotype male INDRE Examined: L.M.Hernández 2008"]. Same data as holotype— 2females2males (not associated with pupal exuviae; one female "CAISimTp-00191" with only thorax, remainder on slide) [PARATYPES, one female labelled as ALLOTYPE] [One female and two males bear a Blue label "PARATIPO"; one female has a Yellow label as ALOTIPO; the female allotype have its right wing, right three lengs and genitalia on a slide] (INDRE).

SLIDES
Same as the pinned adults— male (only wing and three legs of the left side, and genitalia; remainder pinned) [HOLOTYPE] [The slide have a White label with red border with locality, date and collector's name handwritten in black ink; there is also a Red label "HOLOTIPO" and a White label "CAIMSimTp-00100". Other labels here added: White label "Digitally photographed genitalia, legs, wings INDRE Holotype L.M.Hernández"; White label in L.M. HERNÁNDEZ'S hand "Remaining of male pinned L.M.Hernández"]. Same label as pinned adult— 1female (not associated with pupal exuviae) (only right wing and right side legs, and genitalia; the spermatheca is missing) [ALLOTYPE) (INDRE, 3935); 1female (only head, genitalia, legs and wings; thorax pinned) [The specimen have a White label "CAISimTp-00191" and a Blue lable "PARATYPE"].

OTHER MATERIAL

MÉXICO
SLIDES
Veracruz State
Cumbres de Acultzingo; 31.viii.1948, (*Córdoba*)— 1pharate male, 1larva (MLP).

Simulium (Trichodagmia) delatorrei **DALMAT, 1950**

TYPE MATERIAL

GUATEMALA
Chimaltenango Department
PINNED
Acatenango, 12.iv.1949, (*H.T.Dalmat*)— 1female (reared; only adult, pupal exuviae in spirit) [PARATYPE] (BMNH, female 652-3); 1male (reared; only head, thorax and three legs, remainder on slide, pupal exuviae probably in spirit) [PARATYPE] (NMNH [Both paratypes have a Green label in DALMAT'S hand "*Simulium delatorrei* n.sp. H.T.Dalmat PARATYPE female"].

SLIDES
Acatenango, 12.iv.1949, (*H.T.Dalmat*)— 1male (reared, but pupal exuviae probably in ethanol; only abdomen, genitalia and three legs; head, thorax and three legs pinned) [PARATYPE] (NMNH, acc. no. 652-4).

SPIRIT
Acatenango, 12.iv.1949, (*H.T.Dalmat*)— 1female (reared; only pupal exuviae) [PARATYPE] (NMNH).

Totonicapán Department
PINNED

R. Samalá; 15.iii.1949, (*H.T.Dalmat*)— 1male (reared; pupal exuviae in alcohol) [ALLOTYPE] (NMNH, 6T-2) [The specimen bear a red label in DALMAT'S hand "*Simulium delatorrei* n.sp. ALLOTYPE H.T.Dalmat". Other labels here added: *Simulium delatorrei* Dalmat Det. L.M.Hernádez 2010"; White label "Digitally photographed Thorax ant+post; abdomen, lateral view NMNH Male 6T-2 ALLOTYPE L.M.Hernández 2010"]. R. Catarata; 10.xii.1949, [Without collector's name.]— 1female (reared; pupal exuviae in alcohol) [PARATYPE] (NMNH, acc.no. F-10). R. Samala; 15..iii.1949, 5.x.1949, 6.iv.1948, 11.xii.1947, (*H.T.Dalmat*)— 1female3males (reared; pupal exuviae in alcohol) [PARATYPES] (NMNH, acc. no. LT-11; 4x-22; FF-2; I-18). Rio Ciprés, Finca Los Pajales; 13.iv.1949, (*H.T.Dalmay*)— 2males (reaed; pupal exuviae in alcohol) [PARATYPES] (NMNH, acc. no. L52-4, L52-5] [All paratypes bear a Green label in DALMAT'S hand "PARATYPE *Simulium delatorrei* n.sp. H.T.Dalmat].

SLIDES
Sololá, Catarata Panajochel; 24.ii.1949, (*H.T.Dalmat & Jaime Rosales*)— female (not associated with pupal exuviae) [The specimen is in five slides contaning the legs, wings genitalia, head and cibarium; remainder of adult, and pupal exuviae and cocoon was not found in the NMNH holdings and they presumably lost] [HOLOTYPE] (NMNH, acc. no. 6P-8) [The specimen bears several labels: White label with blue edges in red ink and in DALMAT'S hand "HOLOTYPE Female *Simulium delatorrei* n.sp. H.T.Dalmat"; each slide have in black ink at the top, right handside corner "acc. 6P-8"; White label with blue edges with locality information, date and collector's name. Other labels here added on the back of the slides: White label "*Simulium delatorrei* Dalmat Det. L.M.Hernández 2010"; White label "Digitally photographed head, wing, legs I-III, genitalia L.M.Hernández 2010"]. Rio Somalá; 11.xii.1947, [Without collector's name.]— 1pupal exuviae [PARATYPE] (MLP) [mounted in the same slide there is one larva, but this specimen is not a paratype].

SPIRIT
R. Samalá; 15.iii.1949, (*H.T.Dalmat*)— numerous pupae [PARATYPES] [All specimens in same vial with a White label and handwritten in red ink "Paratypes *S. delatorrei* H.T.Dalmat" and another White label "6T-20"].

OTHER MATERIAL

GUATEMALA

Chimaltenango Department

PINNED
Finca Pajales, Rio Ciprés; 18.viii.1949, 9.viii.1949, 26.xii.1949, (*H.T.Dalmat*)— 7females3males (reared; pupal exuviae in alcohol) (NMNH, acc no. 753-1, 753-4, 753-6, 753-7; 777-1, 777-4, 777-6, 777-7). Finca El Carmen, Rio Cocayá; 12.iv.1950, (*H.T.Dalmat*)— 5females3males (reared; pupal exuviae in alcohol) (NMNH, acc. no. 991-2, 991-3, 991-4, 991-5, 991-10, 991-13, 991-14, 991-15).

SLIDES
Finca El Carmen, Rio Cocayá; 12.iv.1950, (*H.T.Dalmat*)— 1male (reared; pupal exuviae in alcohol) (NMNH, acc. no. 991-10). Finca Pajales, Rio Ciprés; 18.viii.1949, 9.viii.1949, 26.xii.1949, (*H.T.Dalmat*)— 7females3males (reared; pupal exuviae in alcohol) (NMNH, acc. no. 778-4, 778-5).

[WITHOUT COUNTRY, BUT PROBABLY GUATEMALA]

SLIDES
[Without country, locality, date or collector's name.]— 1pharate female, 2pharate males (MLP).

SPIRIT
[Without country, locality, date or collector's name.]— 11larvae (5mature) (NMNH) [The vial have a White label and handwritten in black ink "*delatorrei* 7N-16").

Simulium (Trichodagmia) estevezi **VARGAS, 1945b**

TYPE MATERIAL

MÉXICO

Oaxaca State

PINNED

San Felipe del Agua; 12.xii.1943, (*A.Martinez*)— male (not associated with pupal exuviae; left wing, left legs, and genitalia on slide) [HOLOTYPE] (INDRE, no. 3554) [The specimen is in relatively good condition; one antenna, the left wing, the three legs of left side and its genitalia are on a slide. It has been glued to a card point by the ventral side of thorax] [The specimen bear several labels: Red label "HOLOTIPO"; White label "CAIMSimTp-00195"; White label "male"; White label "*estevezi*"; White label with locality data, date and collector's name; White label "3554". Other labels here added: White label "Digitally photographed Thorax ant.+post., abdomen L.M.Hernández"; White label "*Simulium estevezi* Vargas, 1945 Holotype male INDRE Examined: L.M.Hernández 2008"]. San Felipe del Agua, 1600m; 11.xii.1943, (*A. Martinez*)— 1female (teneral specimen not associated with pupal exuviae; only head, thorax, right wing, and part of the adoment; head, left wing, three legs and genitalia on a slide; remainder of legs and spermatheca missing) [ALLOTYPE] (INDRE, no. 3555) [The specimen bear several labeler: White label "CAISimTp-00194"; White label "Paratipo"; White label and handwritten in black ink "*S. estevezi* female"; White label with locality information, date and collector's name handwritten in black ink; White label and handwritten in pencil "3555"; Blue label with black edges "Paratipo". Other labels here added: White label " Digitally photographed Thorax ant.+post., abdomen L.M.Hernández"; White label "*Simulium estevezi* Vargas, 1945 PARATYPE (ALLOTYPE) female 3555 Examined: L.M.Hernández"; White label "*Simulium estevezi* This is the Allotype see slide no. 3555 Examined L.M.Hernández'10"; White label "Material in Slide Collection Slide 3555 L.M.Hernádez'10"].

SLIDES

Same data as pinned adult— male (only left wing, left legs and genitalia) [HOLOTYPE) (INDRE, 3554) [The slide have a white label with locality, date and colector's name; Red label "HOLOTIPO"; White CAIMSimTp-00095". Other labels here added: Digitally photographed antennae, legs, wing, genitalia INDRE HOLOTYPE Ex. L.M.Hernández'09"; White label in L.M. HERNÁNDEZ'S hand "Remainder of the adult pinned, Holotype Ex. L.M.Hernández'09"]. Same data as in pinned adult— 1 female (teneral specimen not associated with pupal exuviae; only head, left wing, three legs and genitalia, thorax pinned) [as ALLOTYPE] (INDRE, no. 3555) [The slide bear several labels: White label with red edges with locality information, date and collector's name; Yellow label "ALOTIPO"; White label "CAIMSimTp-000194". Other labels here added: White label "Digitally photographed Wing, legs, genitalia, cibarium, part of wing, claw hind leg L.M.Hernández"; White label in L.M. HERNÁNDEZ'S hand "Remainder of adult pinned ALLOTYPE female 3555 Examined. L.M.Hernández'09;].

OTHER MATERIAL

MÉXICO

Oaxaca State

SLIDES

San Felipe del Agua; 6.i.1955, (*P.Baustita*)— 1pupal exuviae (MLP).

Veracruz State

SLIDES

Tequiza; 5.viii.1948, (*Reyes & Cordova*)— 1larva (MLP).

[WITHOUT STATE]

[Wihtout locality, date or collector's name.]— 1pupal exuviae (MZUCR).

Simulium (Trichodagmia) ethelae **DALMAT, 1950**

TYPE MATERIAL

GUATEMALA
Sololá Department
PINNED
Solalá, Rio Los Arcos, near Los Encuentros; 4.xi.1948, [Without collector's name.]— female (reared, but not associated with pupal exuviae) [HOLOTYPE] (NMNH, acc. no. 30-1) [The specimen bear several labels: White label "30-1 female"; White label with locality information and date; Red label in DALMAT'S hand "HOLOTYPE Female *Simulium ethelae*, n.sp. H.T.Dalmat". Other labels here added: White label "*Simulium ethelae* Dalmat Det. L.MHernández 2010"; White label "Digitally photographed Thorax ant.+post., abdomen, one ant. segment and three legs missing, L.M.Hernández 2010"; White label "Examined: L.M.Hernández 2010"]. Same data as holotype— 1female (reared, but not associated with pupal exuviae) [PARATYPE] (NMNH, acc. no. 30-2).

SLIDES
Solalá, Los Arcos, near Los Encuentros; 4.xi.1948, [Without collector's name.]— 1female (reared), 1 pupal exuviae [PARATYPES] (MLP).

OTHER MATERIAL

COSTA RICA
Alajuelas Province
SPIRIT
Rio Chorreras, at km 198m, route 9, NW of Heredia, altitude 1780 m, (site 17-7); 9.x.1984, (*L.W.Lichtwardt*)— 2pupal exuviae, 1larva (BMNN) [Identified as *S. chiriquiense* by A.J. SHELLEY].

Cartago Province
Cordillera Talamanca, Cerro de la Muerte, Quebrada Cerro, first unnamed stream alter Las Georgina (right side of road), (site CR-234), 9°32'69"N 83°42'76"W, 2754m; 12.viii.2010, (*L.M.Hernández & L.G.Chaverri*)— 1male (reared) (BMNH) [Previously identified as *S. chiriquiense* by L.M.Hernández 2010].

Puntarenas Province
SPIRIT
Small stream near Rio Parrita, on Pacific side of Empalma, 1800 m, (site CR-22); 8.xi.1984, (*L.W.Lichtwardt*)— 1pupal exuviae, 2larvae (BMNH). Rio Parrita, Chiquito on Pacific side of Empalme, 1800 m, (site C.Rica 54-3); 8.xi.1984, (*L.W.Lichtwardt*)— 1pupal exuviae (BMNH) [All specimens identified as *S. chiriquiense* by A.J. SHELLEY].

San José Province
SLIDES
Rd from San Isidro del General to San José City, at km 105, unnamed stream, 9°32'68"N 83°42'41'W, 10020ft, (site CR-151); 28.i.2009, (*L.M.Hernández & L.G.Chaverri*)— 2females1male (reared), 4pupal exuviae, 4larvae (BMNH) [Previosuly identified as *S. chiriquiense* by L.M. HERNÁNDEZ 2010].

SPIRIT
S. Fork of Rio Humo at km 72 on route 2, altitude 2060 m, (site CR 51-6); 8.ix.1984, (*L.W.Lichtwardt*)— 7pupal exuviae, 2 larvae (BMNH) [Identified as *S. chiriquiense* by A.J. SHELLEY].

GUATEMALA
PINNED
Mixco, Rio Cataratas, El Campamento, R. no. 1 entre kms 24 y 25; 9.xi.1949, (*H.T.Dalmat*)— 2males (reared, but not associated with pupal exuviae; male acc. no 9T-3 only head, thorax, one wing and four legs; abdomen and genitalia on slide) (NMNH, acc. no. 9T-3, 9T-4) [Both specimens bear a green label in DALMAT'S hand "IDEOTYPES Male, *S. ethelae* Dalmat H.T.Dalmat"]. Rio Cascada, campamento R.N.1, kms 24 y 25; 9.xii.1949, (*H.T.Dalmat*)— 6females3males (reared, but not associated with pupal exuviae) (NMNH, males acc. no. 9T-5, 9T-9, 9T-10, 9T-14, 9T-21; females acc. no. 9T-2, 9T-8, 9T-17,

9P-2, 9P-3). Sololá, Rio Catarata, Puente Panajachel, 12.xii.1949, (*H.T.Dalmat*)— 1female (reared, but not associated with pupal exuviae) (NMNH, acc. no. 9L-7).

SLIDES

[Without locality, date or collector's name.]— 1pupal exuviae, 1larva (MLP) [The slide containing the larva have a label with "Collection Dalmat 12D-2"; the slide containing the pupal exuviae bear a label "Identified by COSCARÓN 2000]. [Without locality, date or collector's name.]— 1pupal exuviae (MZUCR). Rio Cascada, km 24 y 25, Campamento no.1, (site 9-7-22); 9.xii.1949, [Without collector's name.]— 2females (not associated with pupal exuviae) (one female only cibarium, gonapophyses and genital fork; another female only antennae and mouthparts); two males (only genitalia; one male "9T-16") (MZUCR) [Identified by H.T. DALMAT]. Rio Cascada, campamento R.N.1, kms 24 y 25; 9.xii.1949, (*H.T.Dalmat*)— 2females (reared, but not associated with pupal exuviae) (NMNH, acc. no. 9T-13, 9T-15). Mixco, Rio Cataratas, El Campamento, R. no. 1 entre kms 24 y 25; 9.xi.1949, (*H.T.Dalmat*)— 1male (reared, but not associated with pupal exuviae; only abdomen and genitalia; head, thorax, one wing and four legs pinned) (NMNH, acc. no. 9T-3). Rio Cascada, campamento R.N.1, kms 24 y 25; 9.xii.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (NMNH, acc. no. 9T-11)

MÉXICO

SLIDES

Rio Frio; 6.ix.1969, (*P. & B.Wygodzinsky*)— 1pupal exuviae (MLP).

PANAMA

Chiriqui Province

SPIRIT

Los Planes de Horruto, 19 km of Gualaca, 8°38'N 82°14'W; 25.iii.1979, (*J.L.Petersen*)— 2pupal exuviae, 1larva (BMNH) [The specimens have been identified by J.L. PETERSEN as "*Simulium chiriquiense*", and the vial bear a White label and printed in black ink "voucher specimens see: PETERSEN (1982) Population genetics of some New World Simuliidae; in Developments in the Genetics of Disease Vectors, pp: 628-641, Stipes Pub. Co. Champaign. Illinois, USA"].

[WITHOUT PROVINCE]

SLIDES

[Without locality, date or collector's name.]— 2pupal exuviae (MZUCR). Cerro Punta; 11.v.1954, [Without collector's name.]— 1female (reared) (NMNH) [Identified previously as *S. chiriquiense* by an unknown reviser].

Simulium (Trichodagmia) falculatum ENDERLEIN, 1929

All material listed in HERNÁNDEZ & SHELLEY (2005) was examined for the current work.

Simulium (Trichodagmia) gorirossiae VARGAS & DÍAZ NÁJERA, 1957

TYPE MATERIAL

MÉXICO

Chiapas State

SLIDES

Guadalupe Zajú; iii.1946, (*A.Díaz N.*)— male (not associated with pupal exuviae) (only genitalia) [HOLOTYPE] [The slide is in good condition. The slide bears a red label "HOLOTIPO", and White label with red edges with species's name, locality information, date and collector's name and "6427" handwritten in black ink; White label "HOLOTYPE, INDRE 6427, CAIMSimTp-00157". Other labels here added: White label "Digitally photographed Genitalia (all) L.M.Hernández INDRE Male]. Same data as holotype— 1female (reared) [as ALLOTYPE] (INDRE 6428, CAIMSimTp-00156) [The slide bear a Yellow label as "ALLOTYPE" and a White label with red edges and handwritten in black ink with species's name, locality, date and collector's name and "6428". Other labels here added: White label "Digitally photographed gen. fork, spermatheca, head, gill INDRE Female-1 L.M.Hernández"].

VERACRUZ STATE

SLIDES

Cas. Teocelo; 10.iv.1946, (*W.Lassman*)— 1female1male (not associated with pupal exuviae) (only three legs and one wing) [PARATYPES, the female labelled as ALLOTYPE] (INDRE; female with number "6429" and male with number "6430"] [The slides bear a White label with red edges, the locality information, date, collector's name and species identification handwritten in black ink; White label "CAIMSimTp-00155" for the slide with number "6429"; White label "CAIMSimTp-00154" for the slide with number "6430"]

OTHER MATERIAL

MEXICO

SLIDES

[Without country, locality, date or collector's name.]— 1pupal exuviae, 3larvae [Two slides containing two larvae have a red dot on the right hand side corner, which indicate that they were used by NELIDA CALAGARI for illustration of this species] (MLP, no. 22); 1pupal exuviae (MZUCR).

SPIRIT

Zaju, Finca Guadalupe; 11.i.1946, (*A.Diaz N.*)— 8larvae (all immature) (BMNH, B.M. 1948-401) [Previously identified as *S. carolinae* by DÍAZ NÁJERA; identified as *S. gorirrosiae* by L.M. HERNÁNDEZ'2010].

Simulium (Trichodagmia) johnsoni **VARGAS & DÍAZ NÁJERA, 1957**

TYPE MATERIAL

MÉXICO

Oaxaca State

PINNED

Cerro San Felipe; 36.i.1949, (*Córdoba*)— 1female (not associated with pupal exuviae; only thorax, remaider on slide) [PARATYPE] (INDRE, 6434) [The specimen have a Blue label "PARATIPO" and a White label "CAISimTp-000198". Other labels here added: White label "Digitally Photographed Th. ant.+post., abdomen L.M.Hernadez"; White label "Material in slide collection Paratype 6434 by L.M.Hernández'10]. Tepanzacoaleo; 25.xi.1948, (*I.Córdoba*)— 1female (not associated with pupal exuviae; only head, thorax, right wing, legs of right side, and abdomen; left wing and legs of left side on a slide) [PARATYPE] (INDRE, 6433).

SLIDES

Cerro San Felipe; 36.i.1949, (*Córdoba*)— 1female (not associated with pupal exuviae; only left wing, left side legs, and genitalia; head, thorax, right side wing and legs, and part of abdomen pinned) [PARATYPE] (INDRE, 6434) [The specimen bear a White label with red edges with locality information, date and collector's name; White label "CAIMSimTp-00150" and a Blue label "PARATIPO"]. Tepanzacoaleo; 25.xi.1948, (*I. Córdoba*)— 1male (not associated with pupal exuviae; only left wing, and legs of left side on sa lide; the head, thorax, right wing, legs of right side, and abdomen pinned) [PARATYPE] (INDRE, 6433) [The specimen bear a White label with red edges with locality information, date and collector's name; White label "CAIMSimTp-00151").

SPIRIT

Tepanzacoaleo; 25.xi.1948, (*I.Córdoba*)— 1pupal exuviae [PARATYPE] (INDRE).

Veracruz State

SLIDES

Cascada de Teocelo; v.1946, (*J.Parra*)— 1male (reared) [HOLOTYPE] (INDRE, 6431) [The slide is in relatively good condition; it only contains one side of the pupal thorax and gill, both gonostyles, the ventral plate and the parameres] [The slide bear several labels: White label with red edges with locality information, date and collector's name and "6431" handwritten in black ink; Red label "HOLOTIPO"; White label

"CAIMSimTp-00153". Other labels here added: White label genitalia (all), gills L.M.Hernández"]. Same data as holotype— 1female (reared) (only gill, partially cercus and paraprocts) [PARATYPE, as ALLOTYPE] (INDRE, 6432) [The slide bear similar labels as the holotype except Yellow label "ALOTIPO" and a White label "CAIMSimTp-00152"].

OTHER MATERIAL

MÉXICO

Oaxaca State

SLIDES

San Felipe del Agua; 10.1948, (*Díaz Nájera & Vulcano*)— 1larva (MLP) [Previoysly identified as *S. temascalense* by DÍAZ NÁJERA & VULCANO].

Veracruz State

SLIDES

Cascada de Teocelo; v.1946, (*J.Parra*)— 2 pupal exuviae (MLP).

***Simulium (Trichodagmia) juarezi* VARGAS & DÍAZ NÁJERA, 1957**

OTHER MATERIAL

MÉXICO

Federal District

PINNED

Rio Frio, 3000 m; 6.ix.1969, (*P. & B.Wygodzinsky*)— 1female1male (reared), 1pupal exuviae (MLP). [Without locality, date or collector's name.]— 1pupal exuviae (MZUCR).

SLIDES

Rio Frio, 3000 m; 6.ix.1969, (*P. & B.Wygodzinsky*)— 1pupal exuviae (MLP).

***Simulium (Trichodagmia) larvispinosum* DE LEÓN, 1948**

OTHER MATERIAL

GUATEMALA

Chimaltenango Department

PINNED

Acatenango; 19.viii.1948, (*H.T.Dalmat*)— 1female (not associated with pupal exuviae) (NMNH, acc. no. 254-1). Acatenango, Finca Sta Marta, Rio Manjón; 8.iii.1948, (*H.T.Dalmat*)— 2females (not associated with pupal exuviae) (NMNH, acc. no. 143-11).

Sololá Department

PINNED

Rio Santa Anita, Finca Montes de Oro, 250m; [Without date or collector's name.]— 1pharate female (MLP). Rio Santa Anita, Finca Montes de Oro; 24.iii.1941, (*H.T.Dalmat*)— 2females1male (not associated with pupal exuviae; one male lost; female 12K-5 with only thorax and three partially broken legs, remainder of the female in a slide) (NMNH, acc. no. 12K-3, 12K-5, 12K-33).

SLIDES

Finca Montes de Oro, Rio Santa Anita, 900m; [Without date or collector's name.]— 1female (reared) (MLP). [Without locality, date or collector's name.]— 1male (reared) (MLP). Rio Santa Anita, Finca Montes de Oro, Atitlán, R. Catarata; 24.iii.1941, (*H.T.Dalmat*)— 2females1male (not associated with pupal exuviae) (NMNH, acc. no. 12K-10, 12K-12, 12K-25). Rio Santa Anita, Finca Montes de Oro; 24.iii.1941, (*H.T.Dalmat*)— 1female (not associated with pupal exuviae; only head, genitalia and one leg; remainder pinned) (NMNH, acc. no. 12K-5).

[WITHOUT STATE]

[Without further locality information, or collector's name.]; XXII— 1male (MLP).

[WITHOUT COUNTRY]
SLIDES
[Without locality, date or collector's name.], XXII— 2females (not associated with pupal exuviae); 1male, 1larva (MLP).

Simulium (Trichodagmia) menchacai VARGAS & DÍAZ NÁJERA, 1957
TYPE MATERIAL

MÉXICO
Oaxaca
SLIDES
Cerro Sn. Felipe; 30.i.1948, (*I.Córdoba*)— 1male (not associated with pupal exuviae) (only genitalia) [PARATYPE] (INDRE, 3946) [The specimen bear several labels: White label with red edges with locality information, date and collector's name and "3946" handwritten in black ink; Blue label "Paratipo"; White label "CAIMSimTp-00149". Other labels here added: White label "Digitally photographed Genitalia INDRE Male-1 L.M.Hernández].

OTHER MATERIAL

MÉXICO
Oaxaca State
SLIDES
Cerro de San Felipe; 13.v.1962, (*Reyes & Vulcano*)— 2pharate females, 1pharate male (MLP).

Simulium (Trichodagmia) microbranchium DALMAT, 1949
TYPE MATERIAL

GUATEMALA
PINNED
Apojanol, entre Ouezenaltenango y Huehuetenago; 15.xii.1948 [Without collector's name]— 1female (not associated with pupal exuviae) [PARATYPE] (NMNH, acc. no. 5Y-6).

Solalá Department
SLIDES
Los Arcos, near Los Encuentros; 4.xi.1948, [Without collector's name.]— female (in five slides) [HOLOTYPE] (NHMNH, acc. no. 0004) [The slide bear several labels: White square label with blue edges and in red ink with DALMAT'S handwriting "Holotype *Simulium microbranchium* female n.s.p, H.T.Dalmat"; White label with blue edges in black and DALMAT'S hand with locality information, date and collector's name. Other labels here added on the back of the slide: White label "*Simulium microbranchium* Det. L.M.Hernández"; White label "Digitally photographed (all parts) L.M.Hernández"]. Totonicapan; 11.xii.1947, (*Onofre Ochoa & H.T.Dalmat*)— 1male [as ALLOTYPE] (NMNH, acc. no. I-23) [The specimen bear similar labels as the holotype except in DALMAT'S hand and in red ink "ALLOTYPE". Other labels here added on the back of the slide: White label "*Simulium microbranchium* Det. L.M.Hernández"; White label "Digitally photographed (all parts) L.M.Hernández"]. Same data as holotype— 1pharate female [PARATYPE] (MLP).

OTHER MATERIAL

GUATEMALA
El Quiché Department
PINNED
R. Micovez, Nebaj Quiché; 15.xi.1949, 28.iii., 20.ix, 25.ix., 30.viii.51, (*H.T.Dalmat*)— 1female1male (not associated with pupal exuviae) (MLP; female no. 130-15; male 130-760), 3males (not associated with pupal exuviae) (BMNH, acc. no. 13O-7, 130-9, 130-23). R. Micovez, Nebaj Quiché; 20.ix; 1951, (*H.T.Dalmat*)— 18females (not associated with pupal exuviae) (NMNH, acc. no. 8x-5; 9L-2; 12L-10; 130-y-7, 130-y-8, 130-y-21, 130-y-24, 130-y-27, 130-y-32; 13P-16, 13P-19, 13P-25; 11Y-3, 11Y-3, 11Y-6,

11Y-12, 11Y-17, 11Y-13, 11Y-18, 11Y-19, 11Y-20, 11Y-28) [All specimens bear an identification label by H.T. DALMAT], 13males (not associated with pupal exuviae) (NMNH, acc. no. 11Y-5, 11Y-10, 11Y-11, 11Y-15; nos.13P-2, 13P-6, 13P-7, 13P-8, 13P-9, 13P-10, 13P-15, 13P-16, 13P-26, 13P-22, 13P-32, 13P-33; 130-11, 130-28) [All specimens determined by H.T. DALMAT]. Sololá, Rio Catarata, El Puente, Panayochel; 1.xii.1949, (*H.T.Dalmat*)— 1female1male (not associated with pupal exuviae) (NMNH, no. 9L-2, 9L-6) [Identified by H.T. DALMAT]. Micovez, Nebaja, Quiche; 15.xi.1949, (*H.T.Dalmat*)— 2males (not associated with pupal exuviae; the male 8X-6 only with thorax, remainder of the adult on a slide) (NMNH, acc. no. 8X-6, 8X-9) [The specimens bear a Green label in DALMAT'S hand "IDEOTYPE"].

SLIDES
R. Micovez, Nebaj Quiché; 20.ix; 1951, (*H.T.Dalmat*)— 2females (not assoiated with pupal exuviae (NMNH, acc. no. 11Y-3, 11Y-18), 1male (only head, one wing and legs, thorax pinned) (NMMNH, acc. no. 13P-10). Micovez, Nebaja, Quiche; 15.xi.1949, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae; the male 8X-6 only with head, wings, legs, abdomen and genitalia, the thorax is pinned) (NMNH, acc. no. 8X-6) [The specimen bear a Green label in DALMAT'S hand "IDEOTYPE"].

Simulium (Trichodagmia) paracarolinae **COSCARÓN, 2004 [In COSCARÓN, MIRANDA-ESQUIVEL, MOULTON, COSCARÓN-ARIAS & IBÁÑEZ-BERNAL, 2004]**

OTHER MATERIAL

GUATEMALA
SLIDES
[Without locality, date or collector's name.], XXII— 2larvae (MLP).

[WITHOUT COUNTRY, BUT PROBABLY GUATEMALA]
SLIDES
[Without locality, date or collector's name.], XVII— 1larva (MLP) [The slide have on the label a red dot on the top right handside corner of the label indicating that it was used by NÉLIDA CALAGARI to illustrate this species].

Simulium (Trichodagmia) temascalense **DÍAZ NÁJERA & VULCANO, 1962**

TYPE MATERIAL

MÉXICO
SLIDES
Michoacán Department, Temascal, 2800 m; 3.xii.1961, (*I. Córdova Ruiz*)— female (reared, in two slides) [HOLOTYPE] (INDRE, no. 6518) [The specimen bear several labels: White label with red edges and handwritten in black ink with species' name, locality information, date and collector's name; also handwritten in pencil "female"; Red label "HOLOTIPO"; White label "CAIMSimTp-000147", "CAIMSimTp-000148". Other labels here added: White label "Digitally photographed (all parts) Holotype INDRE L.M.Hernández"].

ORBITALE species group

Simulium* (*Trichodagmia*) *duodenicornium **PEPINELLI, HAMADA & TRIVINHO-STRIXINO, 2005**

The material listed in SHELLEY *et al.* (2010) was examined in the current work.

Simulium (Trichodagmia) guianense **WISE, 1911 (complex)**

The material listed in SHELLEY *et al.* (1997, 2000, 2004, 2010) was examined for this work.

Simulium* (*Trichodagmi*a) *hirtipupa **LUTZ, 1910**

The material listed in SHELLEY *et al.* (2010) was examined for this work. Futher material is follows:

OTHER MATERIAL

BRAZIL
Mato Grosso do Sul
SLIDES
Municipio Bonito, at Ilha do Padre, 4 km from Fazenda Cachoeira, Rio Formoso 21º07'26"S 056º23'16"W, 871ft; 29.x.2002, (*A.J.Shelley*, *M.M.Herzog*, *A.P.A.Luna Dias* & *L.M.Hernández*)— 3larvae (BMNH).

Simulium (Trichodagmia) huairayacu **WYGODZINSKY, 1953**

TYPE MATERIAL

ARGENTINA
Rio de los Sosa, Tafi, Tucumán, 800 m; 22.vii.1951, (*Wygodzinsky*)— 1female1male (reared, on same pin, and not associated with pupal exuviae) [PARATYPES] (AMNH). Rio Sosa, RA Tucumán; 22.vii.1951, (*Wygodzinsky*)— 1female1male (on same pinned, not associated with pupal exuviae) [PARATYPE] (IML, acc. no. 924) [The specimens bear a White label in WYGODZINSKY'S hand "*Simulium huairayacu* Wygodz." and in red ink "Paratipo". It is printed on the label "Wygodzinsky det. INST. MED. REG.". The specimens bear other White labels "PARATIPO", "IMR 924" and "SIMULIIDAE *Simulium huairayacu*". Other labels here added: White label "Digitally photographed male, female Thorax ant.+post. L.M.Hernadez'09"]. [Without locality, date or collector's name but with no. "866" that referes to "Quebrada de los Sosa, Tafi, Tucumán, 1300 m; 23.v.1951, (*Wygodzinsky*)" in WYGODZINSKY (1951)]— 1female1male (both on same pinned, reared; only thorax and pupal exuviae, remainder of specimens on two slides) [PARATYPES] (INDRE) [The specimens bear several labels: Blue label "PARATIPO"; White label in WYGODZINSKY'S hand "*Simulium huairayacu* Wygod." and printed "INST. MED. REG.", on the right handside of the label it is handwritten in red ink "Paratipo"; White label "CAISimTp-00227"; White label "866"; White label "Male and Female". Other labels here added: *Simulium huairayacu* Wygodzinsky Examined: L.M.Hernández'10; White label "Material in slide collection Paratype female 866, male-866 By L.M.Hernández'10].

SLIDES
[Without locality, date or collector's name, but with no. "866" that referes to "Quebrada de los Sosa, Tafi, Tucumán, 1300 m; 23.v.1951, (*Wygodzinsky*)" in WYGODZINKSY (1951).]— 1female1male (head, genitalia, legs and wings; thorax and pupal exuviae pinned) [PARATYPES] (INDRE, CAISimTp-00227) [The information on these two slides agree with that of the pinned adults. Other labels here added: White label: "PARATYPE" *Simulium huairayacu* Wygodzinsky Examined: L.M.Hernández'10; White label "Only Female Paratype-866 and Male Paratype-866, remainder of the adult pinned L.M.Hernández'10].

OTHER MATERIAL

ARGENTINA
Córdoba Province
PINNED
Huerta Grande, Rio Suquia, 400mm from Cabañas del Monje, (site Arg-1); 23.x.2008, (*L.M.Hernández*)— 1male (reared) (BMNH).

SLIDES
Huerta Grande, Rio Suquia, complejo turístico Las Siete Cascadas, (site Arg-2); 23.x.2008, (*L.M.Hernández*)— 5pupal exuviae, 3larvae (BMNH). Huerta Grande, Rio Suquia, complejo turístico Las Siete Cascadas, (site Arg-2); 23.x.2008, (*L.M.Hernández*)— 2larvae (BMNH).

SPIRIT
Huerta Grande, Rio Sequia, 400mm from Cabañas del Monje, (site Arg-1); 23.x.2008, (*L.M.Hernández*)— several larvae and pupal exuviae (BMNH). Huerta Grande, Rio Suquia, complejo turístico Las Siete Cascadas, (site Arg-2); 23.x.2008, (*L.M.Hernández*)— numerous pharate pupae, larvae (BMNH).

Jujuy Province

Garganta del Diablo, Tiltala; 1.x.1962, (*Coscarón*)— 1female1male (not associated with pupal exuviae) (MLP).

Tucumán Province

SLIDES

Rio de los Soga, Tafi, Tucumán, 800 m; 22.vii.1951, (*Wygodzinsky*)— 1female1male (reared, but not associated with pupal exuviae; the male is dichoptic) (AMNH). Anaje Norte, Gda de las Cañas; 10.vi.1983, (*Coscarón*)— 1male (reared), 1pupal exuviae (MLP). Normenta, Rio Candelaria; 17.vi.1993, (*Coscarón*)— 2males (reared) (MLP).

SPIRIT

Santa Quebrada del Toro; 30.vii.1997, (*S.Coscarón*)— 3 pupal exuviae, several larvae (BMNH).

***Simulium* (*Trichodagmia*) *itaunense* D'ANDRETTA & GONZÁLEZ B, 1964**

All material listed as *S. itaunense* in HERNÁNDEZ *et al.* (2005) and SHELLEY *et al.* (2010) has been examined for this work.

***Simulium* (*Trichodagmia*) *lahillei* (PATERSON & SHANNON, 1927)**

TYPE MATERIAL

ARGENTINA

Tucumán Province

Famillá, (IMR 825); 18.ix.1949, (*Wygodzinsky*)— 1female (reared) [NEOTYPE] (NMHU) [The specimen is in good condition, though the central region of thorax is weakly collapsed; the female has been glued to a point card by its right side together with its pupal pelt] [The specimen bear several labels: White label "IMR 825"; White label with locality information; White label with black borders in WYGODZINSKY'S hand "*Simulium lahillei* Paterson & Shannon" and printed in black ink "Wygodzinksy det. INST. MED. REG"; White label "Zool. Mus. Berlin". Other labels here added: White, round label with purple edges "Neotype"; White label "Digitally photographed Th. ant.+post., abdomen L.M.Hernández; White label "*Simulium lahillei* (Paterson & Shannon) Neotype designated by L.M.Hernández, in preparation"].

OTHER MATERIAL

ARGENTINA

Córdoba Province

PINNED

Arrroyo Matadero, Siambón, Tucumán, IMR 807; 26.vi.1949, (*Wygodzinsky*)— 1female1male (reared, only thorax; wings, legs, abdomen and genitalia on slide) (BMNH, B.M. 1949-471) [The specimens bear a White label with black border in WYGODZINSKY'S hand "*Simulium lahillei* Paterson y Shannon Wygodzinsky det. INS. MED. REG." and a White "IMR 807"]. Raco, Tucumán, 800m; 4.vii.1959, (*Wygodzinsky*)— 1female (not associated with pupal exuviae; only thorax, head, wings, legs, abdomen and genitalia on slide) (AMNH). [Without locality information, date or collector's name.]— 1male (reared in the lab, but not associated with pupal exuviae) (MLP] [The specimen bear a White label "IMR 898" that agree with the locality given in WYGODZINSKY (1953) for *S. lahillei* "Argentina, Dep. Monteros, Tucumán, 800 m; 12.x.1950, (*Wygodzinsky*)". It also has a determination label in WYGODZINSKY'S hand "*Simulium lahillei* Wygodzinsky . INS. MED. REG."]. [Without locality information, date or collector's name.]— 1female (not associated with pupal exuviae) (MLP) [The specimen bear a White label "IMR 898". It also has a determination label in WYGODZINSKY'S hand "*Simulium lahillei* Wygodzinsky . INS. MED. REG La Cumbre; 7.xii.1991, (*Coscarón*)—1male (not associated with pupal exuviae) (MLP).

SLIDES

Arrroyo Matadero, Siambón, Tucumán, IMR 807; 26.vi.1949, (*Wygodzinsky*)— 1female1male (reared, only wings, legs, abdomen and genitalia, thorax pinned) (BMNH, B.M. 1949-471). Raco, Tucumán, 800m; 4.vii.195[Year illegible.], (*Wygodzinsky*)— 1female (not associated with pupal exuviae; only thorax, head, wings, legs, abdomen and genitalia on a slide) (AMNH). Córdoba, Rio Tarceró; 23.vi.1995, (*Coscarón*)— 1larva (BMNH).

SPIRIT

Córdoba, Rio Tarceró; 23.vi.1995, (*Coscarón*)— 3pharate pupal exuviae, 1larva (MLP), 1pharate pupal exuviae (BMNH).

Tucumán Province

PINNED

Same data as neotype— 1male (not associated with pupal exuviae) (MLP, IMR no. 898). Dept. Monteros, Rio de la Sosa, 800m; 12.x.1950, (*Wygodzinsky*)— 1male (not associated with pupal exuviae) (MLP; IMR no. 898) [The specimens have a White identification label in WYGODZINSKY'S hand "*Simulium lahillei* Paterson & Shannon]. Harco Halle, Cda de las Cañas; 10.vi.1983, (*Coscarón*)— 4female5males (not associated with pupal exuviae) (MLP). Harco Halle, Cda de las Cañas; 10.v.1983, (*Coscarón*)— 2males (not associated with pupal exuviae) (MLP). Los Rios, El Ciciliano, Cuesta de Miranda, 1950m; 2.xii.1971, (*Coscarón*)— 1male (reared) (MLP). Sierra, [Remainder of locality illegible]; 27.xii.1945, (*Wygodzinsky*)— 1male1female (reared, on same pin) (NMNH, acc. no IMR 858) [The specimen have a White label with lines around edges in black ink *"Simulium lahillei* Paterson & Shannon Wygodzinsky det. Int. Med. Reg."].

PERU

PINNED

Verrugas, Cañas, stream; 20.v.1925, 20.v.1928, (*R.C.Shannon*)— 2females1male (reared, but not associated with pupal exuviae) (NMNH) [Identified by S. COSCARON'82].

[WITHOUT COUNTRY, BUT LIKELY TO BE ARGENTINA]

PINNED

[Without locality, date or collector's name.]— 1female (not associated with pupal exuviae) (MLP, IMR no. 898) [The specimen have an identification label in WYGODZINSKY'S hand "*Simulium lahillei* Paterson & Shannon].

Simulium (Trichodagmia) lithobranchium **HAMADA, PEPINELLI, MATTOS-GLÓRIA & LUZ, 2010**

OTHER MATERIAL

Goiás State

PINNED

Near Montividiu, Rio Verdão, (site 1442), 17°26'S 51°10'W 2634 ft; 3.viii.2001, (*A.J.Shelley*, *M.Maia-Herzog & A.P.A.Luna Dias*)— 3females3males (reared; 1female and 1male on two slides), 2larvae (mounted on two SEM stubs] (BMNH). Near Aparecida do Rio Doce, Fazenda Tabatupã, Rio Doce, (site 1443), 18°17'S 51°7'W 1851 ft; 4.viii.2001, (*A.J.Shelley*, *M.Maia-Herzog & A.P.A.Luna Dias*) — 1male (reared) [All specimens previously identified as "*Simulium guianense s.l.* Atypical population with abdominal tubercles in SHELLEY *et al.*, 2002a"].

SLIDES

Near Montividiu, Rio Verdão, (site 1442), 17°26'S 51°10'W 2634 ft; 3.viii.2001, (*A.J.Shelley*, *M.Maia-Herzog & A.P.A.Luna Dias*)— 1female1male (reared), 2larvae (BMNH) [All specimens previously identified as "*Simulium guianense* Atypical population with abdominal tubercles in SHELLEY *et al.*, 2002a"].

SPIRIT

Near Aparecida do Rio Doce, Fazenda Tabatupã, Rio Doce (site 1443), 18º17'S 51º7'W 1851 ft; 4.viii.2001, (*A.J.Shelley*, *M.Maia-Herzog* & *A.P.A.Luna Dias*)— 4larvae (BMNH). Near Montividiu, Rio Verdão, (site 1442), 17º26'S 51º10'W 2634 ft; 3.viii.2001, (*A.J.Shelley*, *M.Maia-Herzog* & *A.P.A.Luna Dias*)— 9larvae (BMNH) [Eight larvae in Carnoy's sent to SERGIO LUZ, IOC, Manaus] [All specimens previously identified as "*Simulium guianense s.l.* Atypical population with abdominal tubercles in SHELLEY *et al.*, 2002a"].

Simulium **(*Trichodagmia*)** ***nigrimanum*** **MACQUART, 1838**

The material listed in SHELLEY *et al.* (2000, 2001) was examined for the current work.

Simulium (Trichodagmia) nunesdemelloi **HAMADA, PEPINELLI & HERNÁNDEZ, 2006**

TYPE MATERIAL

BRAZIL

Amazonas State

SPIRIT

São Gabriel da Cachoeira County 00º10'S 67º01'W, Rio Negro, 8.x.1998, (*N.Hamada*, *R.L.M.Ferreira* & *L.Aquino*)— 3pupal exuviae (BMNH) [PARATYPES].

Simulium **(*Trichodagmia*)** ***orbitale*** **LUTZ, 1910**

The material listed in SHELLEY *et al.* (2010) was examined for this paper.

Simulium (Trichodagmia) perplexum **SHELLEY, MAIA-HERZOG, LUNA DIAS & COUCH, 1989**

All material listed in SHELLEY *et al.* (1989, 2004) was examined for the current work.

Simulium **(*Trichodagmia*)** ***scutistriatum*** **LUTZ, 1909**

The material listed in SHELLEY *et al.* (2010) was examined for the current work.

Simulium **(*Trichodagmia*)** ***sumapazense*** **COSCARÓN & PY-DANIEL, 1979**

TYPE MATERIAL

COLOMBIA

SLIDE

Páramo de Sumapaz, 3.700 m; 30.vi.1965, (*P.* & *B.Wygodzinsky*)— pupal exuviae [HOLOTYPE] (MLP) [The specimen bear several labels: Red label "HOLOTIPO"; White label with locality, date and collector's name. At the bottom of the label it reads in COSCARON'S hand "*S. (Grenierella) sumapazense* n. sp. The slide have a red dot indicating that this species was figured by NÉLIDA CALAGARIS. It also reads in pencil "dibujo x pupa". Other labels here added: White label "Digitally photographed gill, frontoclypeus by L.M.Hernández 2005"; White label: *Simulium sumapazense* Coscarón & Py-Daniel, 1989 det. L.M.Hernández 2005"].

Simulium (Trichodagmia) townsendi **MALLOCH, 1912**

All material listed in HERNÁNDEZ & SHELLEY *et al.* (2005) was examined for the current work.

Simulium (Trichodagmia) wygodzinskyorum **COSCARÓN & PY-DANEIL, 1989**

TYPE MATERIAL

PERU

PINNED

1000M, Estancia El Naranjal, San Ramón, Junin; 20.vii.1965, (*P.* & *B.Wygodzinsky*)— 1female (reared) [HOLOTYPE] (AMNH) [The holotype is pinned and is in relatively good condition with the head, abdomen, genitalia and one hind leg in small plastic card attached to the pin; the pupa has been glued to another card and attached to the same pin] [The specimen bear several labels: Red label "HOLOTIPO"; White label with locality data and date; White label with collector's names' White label in COSCARÓN'S hand "*Simulium (Genierella) wygodzinskyorum* Det. Coscarón 1988". Other labels here added: White label "Digitally photographed Th. ant.+post; head; genitalia; hind leg L.M.Hernández"; White label in L.M. HERNÁNDEZ'S hand "*Simulium wygodzinskyorum* Coscarón & Py-Daniel, 1989 Examined L.M.Hernández 2008"]. Same data as holotype— 1male (not associated with pupal exuviae) (as ALLOTYPE) (AMNH).

SLIDES

June, Estancia El Naranjal, San Ramón; 20.vii.1965, (*P. & B.Wygodzynsky*)— 1pharate male [PARATYPE] (MLP).

OTHER MATERIAL

ECUADOR

SLIDE

Nigo; vii.2000, (*C.L.C.-Arias*)— 1larva (MLP).

PICTIPES species group

Simulium (Trichodagmia) claricentrum ADLER, 1990

TYPE MATERIAL

UNITED STATES OF AMERICA

Pennsylvania State

PINNED

Eerie Co., Sixteenmile Creek, junction of Washington Street and Shaduck Road, Northeast (town), 42º11'N 79º50'W; 10.viii.1988, (*P.H. & C.R.L.Adler*)— male (reared; pupal exuviae and one larval head in a vial with glycerine attached to the pin) [HOLOTYPE] (NMNH) [The specimen bears several labels: White label with locality information, date and collectors' name printed in black ink; Red label with black edges and printed in black ink "HOLOTYPE" and in P.H.ADLER'S hand "*Simulium claricentrum* male design. P.H.Adler 1989". Other labels here added: White label "*Simulium claricentrum* Adler 1990" Ex. L.M.Hernández 2010", White label "Digitally photographed Th. ant.+post.; abdomen, lateral; cocoon, gill filaments L.M.Hernández 2010"]. Eerie Co., Sixteenmile Creek, junction of Washington Street and Shaduck Road, Northeast (town), 42º11'N 79º50'W; 10.viii.1988, (*P.H. & C.R.L.Adler*)— 1male (reared) [HOLOTYPE] (NMNH), 3females2males (reared) (BMNH)) [One female only with thorax pinned, the remainder is on a slide; one male with only head and three legs, the remainder is on a slide], 11females7males (reared) (CNC), 7females8males (reared) (NMNH) [All labelled as PARATYPES]

SLIDES

Eerie Co., Sixteenmile Creek, junction of Washington Street and Shaduck Road, Northeast (town), 42º11'N79º50'W; 10.viii.1988, (*P.H. & C.R.L.Adler*)— 1female (reared; only head, abdomen, legs, wings and genitalia, thorax pinned), 1male (reared; only abdomen, wings, three legs and genitalia, the head and thorax are pinned) [PARATYPES] (BMNH).

OTHER MATERIAL

UNITED STATES OF AMERICA

Oklahoma State

SLIDES

Murray Co., Davis, Honey Creek, Bridal Veil Falls, Turner Falls Park; 19.i.1995, (*P.F.Wagner*)— 2pupal exuviae, 2pharate male, 5larvae (CUAC) [All identified as *S. claricentrum* by P.H. ADLER; two larvae identified as *Simulium near claricentrum* by L.M. HERNÁNDEZ].

SPIRIT

Murray Co., Davis, Honey Creek, Bridal Veil Falls, Turner Falls Park; 19.i.1995, (*P.F.Wagner*)— numerous pupal exuviae and larvae (CUAC) [All identified as *S. claricentrum* by P.H. ADLER].

Simulium (*Trichodagmia*) *innoxium* COMSTOCK & COMSTOCK, 1895

Synonymy of *S. innoxium* as *Schoenbaueria aldrichiana* ENDERLEIN, 1936

TYPE MATERIAL

UNITED STATES OF AMERICA

NEW YORK STATE

PINNED

Ithaca; 18.viii.1928, (*G.Enderlein*)— female (one wing on a microslide) (ZMUH) [HOLOTYPE] [The specimen is in good condition. It has been micropinned through the katespisternum with the end of pin visible in the posterior region of thorax; one wing is on a microslide; one leg is missing] [The specimen bear several labels: Gren label with locality information, date and collector's name printed in black ink; Orange label "TYPUS"; White label in ENDERLEIN'S hand "*Schoenbaueria aldrichiana* Type End." and printed in black ink "Dr. Enderlein det 193", "5" is written in black ink]; White label "Zool. Mus. Berl.". Other labels here added: White label "Digitally photographed Thorax ant.+post.; abdomen (dorso-lateral view) Female Holotype ZMUH Examined: L.M.Hernández'10"]; White label "*Schoenbaueria aldrichiana* ENDERLEIN syn of *S. innoxium* Examined L.M.Hernández'10; White label "Syn. by STONE, 1964: 42 Examined L.M.Hernández 2010"].

SLIDES

Same information as the pinned adult)— female (only one wing; remainder of adult pinned) (ZMUH) [HOLOTYPE] [The slide bear the locality information, date and collector's name in ENDERLERINS' hand written directly into the small carbox that protect the microslide. It has a signature at the bottom of the left handside corner. Other labels here added: White label "Digitally photographed Thorax ant.+post.; abdomen, lateral view L.M.Hernández 2010"; White label "*Schoenbaueria aldrichiana* ENDERLEIN syn of *S. innoxium* L.M.Hernández 2010"].

OTHER MATERIAL

UNITED STATES OFAMERICA

North Carolina State

SPIRIT

Macon Co., Culasaja Gorge; 18.viii.1985, (*P.H.Adler*)— numerous pupal exuviae (BMNH; CUAC) [All specimens identified as *S. innoxium* by P.H. ADLER].

South Carolina State

PINNED

Oconee Co., Little River, 34°50'23"N 82°58'86'W; 23.x.2008, (*C.E.Beard*)— 1female1male (not associated with pupal exuviae; the male with only head, thorax and two legs; remainder on a slide), 1 (BMNH) [All specimens identified as *S. innoxium* by P.H. ADLER].

SLIDES

Oconee Co., Little River, 34°50'23"N 82°58'86'W; 23.x.2008, (*C.E.Beard*)— 4females (not associated with pupal exuviae) (BMNH); 1male (not associated with pupal exuviae; only abdomen, one wing, four legs, and genitalia; head, thorax, one wing and two legs pinned) (BMNH) [Identified as *S. innoxium* by P.H. ADLER]. Oconee Cl., Little River; 18.iii.1989, (*S. Tedders*)— 4females (at light trap) (BMNH) [All specimens identified as *S. innoxium* by P.H. ADLER]. Oconee Co., Little River at Rt. 24; 2.iii.1984, (*M.A.McClure*)— 2pupal exuviae, 5larvae (BMNH; CUAC) [All specimens identified as *S. innoxium* by P.H. ADLER].

SPIRIT

Oconee Co., Little River at Rt. 24; 2.iii.1984, (*M.A.McClure*)— numerous larvae (CUAC) [All specimens identified as *S. innoxium* by P.H. ADLER]. Oconee Co., Little River, 34°50'23"N 82°58'86'W; 23.x.2008, *(C.E.Beard)*— 27females (not associated with pupal exuviae) (CUAC) [All specimens identified as *S. innoxium* by P.H. ADLER]. Oconee Cl., Little River; 18.iii.1989, (*S.Tedders*)— 12females (at light trap) (CUAC) [All specimens identified as *S. innoxium* by P.H. ADLER].

***Simulium* (*Trichodagmia*) *pictipes* HAGEN, 1880**

Synonym of *Simulium pictipes* as *Simulium longistylatum* SHEWELL, 1959

TYPE MATERIAL

CANADA

PINNED

Quebec, Baia Comeau, Outardes River; 21.vii.1955, (*L.S.Wolse*)— 1male (not associated with pupal exuviae) [HOLOTYPE] (CNC) [The specimen is in good condition and it has been glued to the pin by the right side. It has several labels: White label with locality information, date and collector's name; Red label: "HOLOTYPE, *S. (H.) longistylatum* Shew. CNC no. 6695". Other labels here added: White label "Digitally photographed Thorax anterior, posterior, abdomen Holotype CNC L.M.Hernández"; White label in L.M. HERNÁNDEZ'S hand "*Simulium* (*Hemicnetha*) *longistylatum* Shewell. Examined L.M.Hernández 2008"]. Same data as holotype— 1female (not associated with pupal exuviae) [PARATYPE] (CNC). Manic., Baie Comeau; 2.vii.1955, (*B.G.Blair*)— 2females (not associated with pupal exuviae) [PARATYPE] (CNC). Manic., Baie Comeau; 2.viii.1955, (*L.S.Wolfe*)— 1female (not associated with pupal exuviae) [PARATYPE] (CNC). Manic., Baie Comeau; 1.viii.1955, (*L.S.Wolfe*)— 1female (not associated with pupal exuviae) [PARATYPE] (CNC). Manic., Baie Comeau; 1.viii.1955, (*B.G.Blair*)— 1female (not associated with pupal exuviae) [PARATYPE] (CNC). Manic., Baie Comeau; 25.vii.1955, (*B.G.Blair*)— 4females (not associated with pupal exuviae) [PARATYPES] (CNC). Manic., Baie Comeau; 25.vii.1955, (*L.S.Wolfe*)— 4females (not associated with pupal exuviae) [PARATYPES] (CNC). Manic., Baie Comeau; 3.vii.1955, (*L.S.Wolfe*)— 1female (not associated with pupal exuviae) [PARATYPE] (CNC). Manic., Baie Comeau; 30.vii.1955, (*L.S.Wolfe*)— 2females (not associated with pupal exuviae) [PARATYPES] (CNC). Manic., Baie Comeau; 30.vii.1955, (*B.G.Blair*)— 4females (not associated with pupal exuviae) [PARATYPES, 1female as ALLOTYPE] (CNC). Outardes R., Baie Comeau; 2.vii.1955, (*B.G.Blair*)— 3males (not associated with pupal exuviae; 1male with genitalia on a slide) [PARATYPES] (CNC). Outardes R., Baie Comeau; 2.vii.1955, (*L.S.Wolfe*)— 1male (not associated with pupal exuviae; 1male with genitalia on slide) [PARATYPE] (CNC). Outardes R., Baie Comeau; 21.vii.1955, (*B.G.Blair*)— 14males (not associated with pupal exuviae) [PARATYPES] (CNC). Outardes R., Baie Comeau; 14.vii.1955, (*B.G.Blair*)— 1male (not associated with pupal exuviae) [PARATYPES] (CNC). Outardes R., Baie Comeau; 18.vii.1955, (*L.S.Wolfe*)— 5males (not associated with pupal exuviae) [PARATYPES] (CNC). Orille; 2.viii.1924, (*B.L.Viereck*)— 1male (not associated with pupal exuviae) [PARATYPE] (CNC). Ontario, Bala Falls; 14.ix.1925, (*G.S.Walley*)— 3males (not associated with pupal exuviae) [PARATYPES] (CNC). 7th Remblay R.; 20.vii.1955, (*B.G.Blair*)— 1male (not associated with pupal exuviae) [PARATYPE] (CNC). Moase R.; 10.viii.1955, (*B.G.Blair*)— 1female (not associated with pupal exuviae) [PARATYPE] (CNC).

SLIDES

Outardes R., Baie Comeau; 18.vii.1955, (*L.S.Wolfe*)— 1female (not associated with pupal exuviae) [PARATYPE, no. slide 14B].

OTHER MATERIAL

CANADA

Alabama

SPIRIT

Dekalb Co., Little River, Desoto Falls, Desoto State Park; 10.v.1995, (*C.A.Stoops*)— numerous pupal exuviae and larvae (CU).

British Columbia

PINNED

Royal Oak; 14.iv.1917, (*R.C.Tehemme*)— 1female (biting horse) (BMNH). Victoria; 15.iv.1917, (*A.E.Cameron*)— 6females (not associated with pupal exuviae) (BMNH).

Northwest Territories

SLIDES

Cameron River, Ingraham Trail, 46.0 km. E of Yellowknife; 30.vi.2001, (*P.H.Adler*)— 4males (not associated with pupal exuviae) (BMNH; CUAC).

SPIRIT
Cameron River, Ingraham Trail, 46.0 km. E of Yellowknife, 30.vi.2001, (*P.H.Adler*)— numerous males (collected from a spider web) (CUAC) [Identified as *S. longistylatum* Shewell by P.H. ADLER]. Cameron River, Ingraham Trail, 54.8 km E. km of Yellowknife, 62°29'31.9"N 13°32'51.4"W; 30.vi.2001, (*D.C.Currie & P.H.Adler*)— several pupal exuviae and larvae (CUAC) [Identified as *S. longistylatum* Shewell by P.H. ADLER].

Ontario State
PINNED
Fitzroy, Hbr., Ont., Ottawa; 11.ix.1936, (*C.R.Twinn*)— 1female1male (reared, but not associated with pupal exuviae) (BMNH) [Both specimens have a White identification label "*Simulium pictipes* Hgn. Det. C.R.Twinn" and White label "Press. by PROF. P.A. BUSTON B.M. 1936-695"]; 4females (reared, but not associated with pupal exuviae) (CNC) [Three specimens have identification labels "*Simulium pictipes* Hgn. Det. C.R.Twinn"; another specimen with an identification label "*S. pictipes* Det. Shewell 11.1919"]. Carlenton Place; 8.viii.1935, (*C.R.Twinn*)— 2females2males (reared, but not associated with pupal exuviae) (CNC) [All specimens have an identification label "*S. pictipes* Hgn. Det. C.R.Twinn"].

Saskatchewan
PINNED
Ferdetter Creek, El Dorado; 12.iv.1961, (*F.J.H.Freden*)— 3females2males (reared) (BMNH) [The specimens have a White label "Presented by F.J.H. FREDEN (Canada Agric.) B.M. 1983-188) and "*Simulium* (*Shewellomyia*) *longistyllatum* Shewell Det. R.W.Crosskey"].

UNITED STATES OFAMERICA
Alaska State
PINNED
Battle Bay, off Glacier Bay, Alaska; 10.vi.1907, (*D.H.Nelles*)— 2females (BMNH) [Identified as *S. pictipes* by an unknown reviser. P.H.ADLER regards this record as doubtful, pers. comm. to L.M. HERNÁNDEZ].

Maryland State
PINNED
Great Falls, Maryland; 30.v.1914, (*A.W.Pomeroy*)— 3males (BMNH; 1 male with White label "Ex. Wellcome Coll. B.M. 1990-107" and 2 males with a White label "Ex. London School of Hygiene and Tropical Medicine BMNH(E) 1995-264"].

New York State
PINNED
Ithaca; 1.vii.1901, 22.vii., 5.vii.1901; [Without collector's name]— 2females3males (not associated with pupal exuviae) (BMNH) [All specimens bear identification labels "*Simulium pictipes* Hagen Determined by E.Roubaud, 1906" and a White label "N. America Ex. Coll. Tyler Towsend. Puchrd. Fr. E.Brunetti 1903-16"].

South Carolina State
SLIDES
Pickens, Six Miles Creek, Rt 291; 10.ix.1997, (*C.L.Evans*)— 1female (not associated with pupal exuviae) (BMNH).

SPIRIT
Pickens, Six Mile Creek, Rt. 291; 10.ix.1997, (*C.L.Evans*)— several adults (not associated with pupal exuviae) (CUAC).

TARSATUM species group

Simulium (*Trichodagmia*) *brachycladum* Lutz & Pinto, 1932

The material listed in Maia-Herzog *et al.* (1984) and Shelley *et al.* (2010) was examined for the current work. Futher material examined is as follows:

OTHER MATERIAL

BRAZIL

São Paulo State

SPIRIT

Northern of Serra da Bocaina, locality 1/4; 15-18.v.1979, (*R.W.G.Crosskey & A.J.Shelley*)— 5larvae (BMNH, BM-1979-258).

Simulium (*Trichodagmia*) *bricenoi* Vargas, Martínez Palacios & Díaz Nájera, 1946

The material listed under *S. bricenoi* (and its synonym *S. wirthi*) in Shelley *et al.* (2010) was examined for the current work.

Simulium (*Trichodagmia*) *cristalinum* Coscarón & Py-Daniel, 1989

The material listed in Shelley *et al.* (2010) was examined for this work.

Simulium (*Trichodagmia*) *earlei* Vargas, Martínez Palacios & Díaz-Nájer, 1946

The material listed in Shelley *et al.* (2002b) was examined for this work. Futher material examined is as follows:

OTHER MATERIAL

BELIZE

[WITHOUT PROVINCE OR FURTHER DETAILS]

SLIDES

BE-96, [Without locality, dtae and collector's name]— 2larvae (BMNH).

COSTA RICA

Guanacaste Province

SLIDES

Quebrada Zapote, (site CR-8), 10°51'5"N 85°29'2"W, 393m; 16.i.2008, (*L.M.Hernández & L.G.Chaverri*)— 1larva (BMNH).

Simulium (Trichodagmia) freemani Vargas & Díaz Nájera, 1949

TYPE MATERIAL

MÉXICO

Oaxaca State

PINNED

Etla, San Pablo; 21.i.1949, (*F.Reyes*)— 1male (reared; pupal exuviae in alcohol; left wing, abdomen, genitalia and three legs of left side in a slide, remainder of the specimen pinned) [HOLOTYPE] (INDRE, No. 3964) [The specimen is in relatively good condition and it has been pinned on a card point by the left side. The specimen appear to be have been stored in alcohol and the thorax has weakly collapsed. Its left wing, left three legs, abdomen and genitalia are on a slide. The cocoon and pupal exuviae are stored in ethanol] [The specimen bear several labels: White label "CAIMSimTp-00200"; Red label and White label "HOLOTIPO"; White label "*freemani* male"; White label "3964"; White label with locality, date and collector's name. Other labels here added: White label "Digitally Photographed Thorax ant.+post. Holotype male L.M.Hernández"; White label "*Simulium freemani* Vargas & Díaz Nájera, 1949 Examined L.M.Hernández 2008"]. Same data as holotype— 1female (reared, but not associated with pupal exuviae; only thorax, one wing and three legs, the left wing, three legs, abdomen and genitalia are on a slide) [as ALLOTYPE] (INDRE, no. 3963) [The specimen bear several labels: White label "CAIMSimTp-00201"; White and Yellow label "ALOTIPO"; White label "3963". Other labels here added: White label "Digitally photographed Thorax ant.+post. L.M.Hernández"; White label "*Simulium freemani* Vargas & Díaz Nájera Examined. L.M.Hernández'08"].

SLIDES
Same data as pinned adult— 1male (reared, pupal exuviae in alcohol; only left wing, left three legs, abdomen and genitalia, remainder pinned) [HOLOTYPE] (INDRE, no. 3964) [The slide have a White label with red edges bearing the locality information, date and collector's name handwritten in black ink, and "male 3964" on the top right handside corner; Red label "HOLOTYPE"; White label "CAIMSimTp-00144". Other labels hear added: White label "Digitally photographed wing, legs, genitalia (all) INDRE Male Holotype L.M.Hernández'09"; White label "Male (only wing, legs and genitalia), Adult Pinned Ex.: L.M.Hernández'09"]. Same data as pinned adult— 1female (not associated with pupal exuviae; only one antennal segment, left wing, three legs, abdomen and genitalia, remainder pinned) [as ALLOTYPE] (INDRE, no. 3963) [The slide bear several labels: White label with locality information, date and collector's name, and "female 3963" handwritten in black ink; Yellow label "ALOTIPO"; White label "CAIMSimTp-00143". Other labels here added: White label "Digitally photographed wing, genitalia (all) INDRE FEMALE ALLOTYPE L.M.Hernández'09"; White label "Female (only wing, legs and genitalia). Adult Pinned Ex. L.M.Hernández'09".]. Comalte; x.1948, (*B.Luna*)— 1male (reared; only one wing, three legs, abdomen, genitalia and pupal gill filaments of one side) [The slide bear several labels: White label with red edges with locality information, date and collector's name, species name, a number "3961" and "male" handwritten in black ink; Blue label "Paratipo"; White label "CAIMSimTp-00142". Other label here added: White label "*Simulium freemani* Vargas & Díaz Nájera 1949 Ex. L.M.Hernández"].

SPIRIT
Same as pinned holotype— male (only pupal exuviae) [HOLOTYPE] (INDRE, 3964) [The vial bear several labels: White label with locality information, date and collector's name, and species identification handwritten in black ink; White label "CAIMSimTp-00012". Other label here added: White label "Digitally photographed cocoon and gill INDRE Holotype male Ex. L.M.Hernández"]. Etla, San Sebastian; 12.ii.1949, (*Reyes-Cordova*)— 1female (reared) [PARATYPE] (INDRE). Comaltepec; x.1948, (*B.Luna*)— 1pupal exuviae [PARATYPE] (INDRE). Etla, San Pablo; 21.i.1949, (*F.Reyes*)— 1male (not associated with pupal exuviae) [PARATYPE] (INDRE). Rancho Manuel Torres; 5.xii.1948, (*F.Reyes*)— 1pupal exuviae [PARATYPE] (INDRE).

OTHER MATERIAL

UNITED STATES OF AMERICA

Arizona State

PINNED
Oak Ck. Cn., Pine Falt Camp 5400'; 20-22.iv.1967, (*D.M.Wood*)— 1female1male (reared) (BMNH).

New Mexico State

SLIDES
Sierra Co., Percha Creek, at Kingston, 6150' elevation; 16.v.1991, (*B.V.Peterson & M.E.Craig*)— 2females2males (reared), 2 pupal exuviae (NMNH).

SPIRIT
Sierra Co., Percha Creek, at Kingston, 6150' elevation; 16.v.1991, (*B.V.Peterson & M.E.Craig*)— 2females3males (reared), numerous pupal exuviae, 3larvae (NMNH). Grant Co., Emery Pass, Hwy 152, 6210'; 15.v.1990, (*B.V.Peterson & M.E.Craig*)— numerous pupal exuviae (NMNH). Grant Co., stream in Railroad Canyo, Hwy. 152, 6210'; 15.v.1993, (*B.V.Peterson & M.E.Craig*)— 4males (reared) (NMNH).

Utah State
SLIDES
Box Older, Co. Rt. 89-91, ca 1 mi. N of junction of interstate 15 boundary, Cache Nat. For.; 27.iii.1997, (*P.H.Adler*)— 1larva (BMNH), 1larva (CUAC).

SPIRIT
Box Older, Co., Brigham City, Rt. 89; 6.vi.1992, (*P.H.Adler*)— 1pupal exuviae (CUAC). Box Older, Co Rt 89-91, ca 1mi. N of junction of interstate 15 boundary, Cache Nat. For.; 27.iii.1997, (*P.H.Adler*)— several larvae (CUAC).

Simulium (Trichodagmia) guerrerense VARGAS & DÍAZ NÁJERA, 1956

TYPE MATERIAL

MÉXICO
Guerrero State
PINNED
Ayutla; xii.1945, (A. Díaz N.)— male (not associated with pupal exuviae) [HOLOTYPE] [INDRE, no. 6412) [The pinned male holotype is in good condition and it has been glued by the ventral side of the thorax to a card point. It appears to have been stored in alcohol the central region of thorax is devoid of hairs] [The specimen bear several labels: Red and White labels "HOLOTIPO"; White label "CAIMSimTp-002002"; White label and handwritten in black ink "*S. guerrerense*"; White label with locality data, date and collector's name; White label and handwritten in blue ink "6412"; White label "male". Other labels here added: White label "Digitally photographed Thorax ant.+post, abdomen INDRE male holotype L.M.Hernádez"; White label "*Simulium guerrerense* Vargas & Díaz Nájera, 1956 Examined: L.M.Hernández 2008"]. Same data as holotype— 1female1male (not associated with pupal exuviae) [the female labelled as ALLOTYPE] (INDRE) [The female bear a Blue label "ALOTIPO", and White labels "no. 6413" and "CAISimTp- 00204"].

SLIDES
Same data as holotype— 1female (only genitalia) [as ALLOTYPE] [The information on the slide correspond with the pinned specimen. However, the pinned specimens is intact, therefore this is not a part of the allotype and it has been labelled accordingly by L.M. HERNÁNDEZ]; 2females (reared), 2pharate females, 2females (not associated with pupal exuviae), 1pharate male, 3males (not associated with pupal exuviae), 6pupal exuviae and 12larvae [All labelled as PARATYPES] (INDRE) [Most of the specimens have a White label with red borders with locality information handwritten in black ink. The female allotype bear a Yellow label "ALOTIPO"and White label CAISimTp-00070". Other labels here added to the Allotype: White label "Digitally photographed gen. fork, paraproct, gonapophyses L.M.Hernández'09].

SPIRIT
Same data as holotype— numerous pupal exuviae and larvae [PARATYPES] (INDRE).

OTHER MATERIAL

Guerrero State
SLIDES
Ayutla; xii.1942, (*A. Díaz N.*)— 5pupal exuviae, 9larvae (INDRE) [All specimens with White label "CAISimTp-0003].

SPIRIT
Ayutla; xii.1942, (*A. Díaz N.*)— numerous pupal exuviae (INDRE) [All specimens with White label "CAISimTp-0003].

Simulium (Trichodagmia) hieroglyphicum PETERSON, VARGAS & RAMÍREZ PÉREZ, 1988

TYPE MATERIAL

COSTA RICA

Alajuela Province

SLIDES

Poasito; 5.ix.1986, 8.ix.1986, 18.xii.1986, (*A.Solano & W.González*)— 1female (reared; in six slides with pupal exuviae in two slides, set 4), 1female (reared; in six slides with pupal exuviae in two slides, set 5), 1male (reared; in four slides with pupal exuviae in two slides, set 7), 1male reared in three slides with pupal exuviae in 2 slides, set 6), 3larvae (in five and six slides, sets 1-3) [All specimens have been labelled as PARATYPES] (NMNH).

SPIRIT

Poasito; 4.xi.1986, (*A.Solano & W.González*)— male (reared) [HOLOTYPE] (NMNH) [The male and its cocoon and pupal exuviae are in good condition] [The specimen bear a White label and handwriten in black ink "Simuliidae, *Simulium hieroglyphicum* (*H.*) R. PyV. V. Det.: J.Ramirez, V.Vargas", on the back of the slide White label and handwriten in black ink "Loc: Costa Rica, Prov: Alajuelas; Cols: A.S. y W.G.". Other labels here added: White label with red edges and handwritten in red ink "HOLOTYPE", and handwritten in L.M. HERNÁNDEZ'S hand "*Simulium hieroglyphicum* Peterson *et al.* 88 Ex. L.M.Hernández"; White label in L.M. HERNÁNDEZ'S hand "Digitally photographed Cocoon, pupal gill L.M.Hernández'2010"]. Poasito; 31.i.1970, (*G.Z.R.*, *M.V.V.*, *R.E.S.*)— several pupae (NMNH) [PARATYPES] [The vial bear a White label with locality data, date and collectors' name handwritten in black ink; printed at the top of the label "Universidad de Costa Rica, Facultad de Microbiologia, Dpto. de Parasitologia"; White label with species identification handwritten in black ink, printed at the top of the "Universidad de Costa Rica, Facultad de Microbiologia, Dpto. de Parasitologia". Other labels here added: White label with blue edges "Paratype *Simulium hieroglyphicum* Peterson *et al.* Ex.: L.M.Hernández"; White label "*Simulium hieroglyphicum* Peterson *et al.* '88 Ex. L.M.Hernández 2010"]. Poasito; viii-xi.1986, (*A.S.*, *W.G.*)— several larvae [PARATYPES] [The vial bear a White label with locality, date and collectors' initials handwritten in black ink; at the top of the label it is printed "Universidad de Costa Rica, Facultad de Microbiologia, Dpto de Parasitologia"; White label with species identification handwritten in black ink, and printed at the top of the label "Universidad de Costa Rica, Facultad de Microbiologia, Dpto de Parasitologia". Other labels here added: White label with blue edges "Paratype *Simulium hieroglyphicum* Peterson *et al.* Ex.: L.M.Hernández; White label "*Simulium hieroglyphicum* Peterson *et al.* '88 Ex. L.M.Hernández 2010"].

OTHER MATERIAL

COSTA RICA

Alajuela Province

SLIDES

Rd from S. José to Poasito, Rio Poasito, (site CR-173), 10º9'45.4"N 84º12'17"W, 2039m; 21.ii.2010, (*L.M.Hernández & M.Moraga*)— 1pharate male (BMNH). Rd from S. José to Poas Volcano, Rio Poas, (site CR-155), 10º9'45.4"N 84º17'12"W, 2039m; 17.ii.2010, (*L.M.Hernández, L.G.Chaverri & S.Avila*)— 1larva (BMNH).

PANAMA

Chirriqui Province

SPIRIT

Cerro Punta, 8°53'N 82°36'W; 23.vi.1999, (*W.K.Reeves*)— 2pupal exuviae, 1cocoon, 1larval head capsule (CUAC).

Simulium (Trichodagmia) hinmani VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA, 1946

TYPE MATERIAL

MÉXICO

México State

PINNED
Los Remedios; 19.x.1944, (*A.Diaz N.)*— male (only head, thorax, three legs and one wing; three legs and genitalia on slide) [HOLOTYPE] (INDRE, 3848). Same date as holotype— 1female (only head, one antennal segment, right wing, legs and thorax; one wing, three legs and genitalia on a slide) [as ALLOTYPE] (INDRE, 3849) [The slide bear a Yellow label as "ALLOTYPE"].

SLIDES
Los Remedios; 19.x.1944, (*A.Diaz N.*)— male (only parameres, median sclerite, both gonostyles, three legs and one wing; remainder pinned) [HOLOTYPE] (INDRE, 3848) [The material is in good condition] [The slide bear a White label with red border and handwritten in black ink with species' name, locality data, date and collector's name; Red label "HOLOTIPO"; White label "CAIMSimTp-00038". Other labels here added: White label "Body Part(2): Wing, legs, paramere, m. sclerite, gonostyle, gonocoxite Taken by L.M.Hernández (BMNH, 2002)"; White label "Male only three three legs, wing and genitalia; remainder pinned L.M.Hernández 2009"]. Same date as holotype— 1female (only genitalia, one wing and three legs; remainder of the specimen pinned) [as ALLOTYPE] (INDRE, 3849) [The slide bear a Yellow label as ALLOTYPE" and a White label "CAISimTp-00039"; White label "Only three three legs, wing and genitalia; remainder pinned L.M.Hernández 2009"].

OTHER MATERIAL

MEXICO

México State

SLIDES
Los Remedios; 19.x.1944, (*A. Díaz N.*)— 1female1male (not associated with pupal exuviae) (INDRE, 003(87-020) [The specimens have been dissected from alcohol; the vial had a White label "CAIMSimTp-000161"]; 1female (only one hind leg), 1male (only genitalia) (BMNH).

Simulium (Trichodagmia) hippovorum Malloch, 1914

TYPE MATERIAL

MEXICO

Chiapas Department

PINNED
Sierra Madre, Head of River Piedras Verdes, alt. 7300 ft; [July.27] (*C.H.T.Townsend*)— female (on a horse ear) [HOLOTYPE] (NMNH, cat. no.15407) [The specimen bear several labels: White label "7.27"; White label and handwritten in black ink "ear of horse"; White label with locality information printed in black ink"; White label with locality information and altitude printed in black ink; White label with collectors' name"; Red label "Type no. 15407 U.S.N.M."; White label and printed in black ink "SLIDES"; White label with black edges and in Malloch's hand "*Simulium hippovorum* Malloch". Other labels here added: White label "Digitally photographed Th. ant.+post.; abdomen, lateral L.M.Hernández 2010"; White label "*Simulium hippovorum* Malloch Examined L.M.Hernández 2010"].

SLIDES
Same as pinned holotype— female [HOLOTYPE] (NMNH, cat. no.15407) [The specimen is in two slides. One slide have a Red label and handwritten in black ink with the species's name, locality information, collector's name and type number. Other labels here added: White label "Digitally photographed Th. ant+post; abdomen, lateral L.M.Hernández 2010"; White label "*Simulium hippovorum* Malloch Examined L.M.Hernández 2010"] [The other slide have a White label with locality information handwritten in black ink. There is also a handwritten note "off type claws with very small tooth". Other labels here added: White label "Digitally photographed claw, genitalia of female and leg L.M.Hernández 2010; White label "Adult in pinned collection Ex. L.M.Hernández"; White label "*Simulium hippovorum* Malloch Examined L.M.Hernández 2010"].

OTHER MATERIAL

CANADA

Bristish Columbia

PINNED

Qualicum, Big Qualicum R.; 30.v.1955, (*G.E.Shewell*)— 5males (resting on bridge) (CNC) [Previously identified as *S. virgatum s.l.* Black form by L.M. HERNÁNDEZ 2008"]; 1female1male (resting on bridge) (NMNH).

UNITED STATES OF AMERICA

California State

PINNED

Sonoma Co., Russian Rive, below dam at Healdsburg Memorial Beach Co. Park, Healdsburg; 22.iii.1990, (*P.H. & C.R.L.Adler*)— 2females2males (not associated with pupal exuviae), 2pupal exuviae, 1larva (BMNH) [Identified as *S. hippovorum* by P.H. ADLER].

SLIDES

Sonoma Co., Russian Rive, below dam at Healdsburg Memorial Beach Co. Park, Healdsburg; 22.iii.1990, (*P.H. & C.R.L.Adler*)— 2females2males (not associated with pupal exuviae), 2pupal exuviae, 1larva (BMNH) [Identified as *S. hippovorum* by P.H. ADLER]. San Diego Mountain, Wier Historical Site; 8.vii.1997, (*T.Pachon*)— 3larvae (BMNH) [Identified as *S. hippovorum* by P.H. ADLER]. Sonoma Co., Russian Rive, below dam at Healdsburg Memorial Beach Co. Park, Healdsburg; 22.iii.1990, (*P.H. & C.R.L.Adler*)— 1larva (BMNH) [Identitied as *S. hippovorum* by P.H. ADLER].

SPIRIT

Sonoma Co., Russian Rive, below dam at Healdsburg Memorial Beach Co. Park, Healdsburg; 22.iii.1990, (*P.H. & C.R.L.Adler*)— numerours adults, pupal exuviae and larvae (CUAC) [Identified as *S. hippovorum* by P.H. ADLER]. San Diego Mountain, Wier Historical Site; 8.vii.1997, (*T. Pachon*)— numerous larvae and pupal exuviae (CUAC).

Simulium (Trichodagmia) lobatoi **LUNA DIAS, HERNÁNDEZ, MAIA-HERZOG & SHELLEY, 2004**

All material listed under LUNA DIAS *et al.* (2004) and HERNÁNDEZ *et al.* (2008) was examined for this paper. Reference to their material was also made by SHELLEY *et al.* (2010).

Simulium (Trichodagmia) paynei **VARGAS, 1942**

All material listed under *S. virgatum s.l.* and *S. paynei* in SHELLEY *et al.* (2002b, 2010) was re-examined within the context of the current work. Some specimens identitifed as *S. virgatum s.l.* by the latter authors might represent specimens which I have identified as *S. paynei*. The reader should consult the latter publications and this work for an up-to-date on the distribution of these two species.

TYPE MATERIAL

MEXICO

PINNED

[Without further locality information], 1883, (*Bilimek*)— 1female (not associated with pupal exuviae) [LECTOTYPE] (NM) [Two legs, one wing and the abdomen is said to be have been mounted on slide by MAIA-HERZOG *et al.*, 1984, but I have been unable to examine it] [The specimen bear several labels: White round label with purple edges "Lectotype"; White round label "410"; Orange label "TYPUS; White label with country, locality and year printed in black ink; White label in ENDERLEIN'S hand "*Hemicnetha mexicana* Type Enderl. female and printed "Dr. Enderlein det. 1934"; White label with printed information in black ink "LECTOTYPE designated by A.J.Shelley 1982" and in A.J. SHELLEY'S hand "*Simulium paynei*". I have here added other labels: White label "Digitally photographed Th. ant.+post L.M.Hernández"; White label "*Simulium paynei* Vargas n. name for *Hecminetha mexicana* Enderlein Examined: L.M.Hernández'09; White label "Lectotype designated by MAIA-HERZOG *et al.*, 1984: 352; the authors stated that two legs, one wing and abdomen are on a slide L.M.Hernández'09".].

[Without further locality information.]; 1883, (*Bilimek*)— 1female (not associated with pupal exuviae; only thorax, one wing and legs; wing, legs and genitalia on slide) [PARALECTOTYPE] (ZMUH) [The specimen bear several labels: White, round label with blue edges "PARALECTOTYPE; Orange label "Typus"; White round label "460"; White, rectangular label "4female"; White label "Mexico, Bilimek, 1883"; White label in ENDERLEIN'S hand "*Hemicnetha mexicana* Type Enderl" and printed "Dr. Enderlein det. 1934"; White label in VARGA'S hand "*S.(H.) paynei* Dr. L.Vargas det. V. 1953"; White label "Zool. Muse. Berlin". Other labels here added: White label "One wing, one leg and genitalia on slide"; *Simulium paynei* Vargas n.name for *Hemicnetha mexicana* End. Examined: L.M.Hernández'09"; White label "Genitalia on slide L.M.Hernández'09"].

SLIDES
Same as pinned adults— 1female (only one wing, leg and genitalia) [PARALECTOTYPE] (ZMHU, no.4) [The slide bear several label: White label with red edges in VARGAS'S hand "*Hemicnetha mexicana* End. 1934 Typus Mexico female 4"; White label in VARGAS'S "*S. (Hemicnetha) paynei* Vargas det. Dr. Vargas v.1953" and printed "Instituto de Enfermedades Tropicales, Mexico". Other labels here added: White label "Digitally photographed genitalia (all), leg, wing, ZMHU female L.M.Hernández'09"; White label "Female genitalia, leg, wing; adult pinned"].

Synonym of *S. paynei* as *Simulum mathesoni* VARGAS, 1943
TYPE MATERIAL

MÉXICO
Morelos Estate
SLIDES
Temixco; 21.xi.1943, (*A. Martínez Palácios*)— male (not associated with pupal exuviae) (INDRE, 3588) [HOLOTYPE] [The slide only contain one wing, three legs and the genitalia of the holotype; head, thorax, part of abdomen, two legs and one wing in spirit] [The slide bear several labels: White label with red edges with locality information, date and collector's name, species name, no. 3599 and male handwritten in black ink; Red label "HOLOTIPO", White label "CAISimTp-00086". Other labels here added: Digitally photographed Wing, legs; genitalia (all) INDRE HOLOTYPE male Ex.: L.M.Hernández'09; White label "Male only wing, legs, genitalia Ex.: L.M.Hernández'09.]

SPIRIT
Temixco; 21.xi.1943, (*A. Martínez Palácios*)— male (not associated with pupal exuviae) (INDRE, 3588) [HOLOTYPE] [Only head, thorax, part of abdomen, two legs and one wing; remainder on a slide] [The specimen bear several labels: White label with locality, date and identification label in VARGAS'S hand "HOLOTIPO"; White label "a-T (87-439)"; White label " CAISimTp-0008". Other label here added: White label "Digitally photographed Thorax INDRE HOLOTYPE Male Ex.: L.M.Hernández 2010"].

Synonym of *S. paynei* as *Simulium acatenangoense* DALMAT, 1951
TYPE MATERIAL

GUATEMALA
Chimaltenango Department
PINNED
Acatenango, Finca and Rio San Diego; 16.xii.1948, (*H.T.Dalmat*)— 3females3males (reared) [PARATYPES] (NMNH, acc. no. 516-1, 516-2, 514-6; 601-1, 606-2, 606-4, 606-7) [PARATYPES] [All specimens have a green label in DALMATS'S hand "Paratype *Simulium acantenangoensis* H.T.Dalmat. Other labels here added: White label "Digitally photographed L.M.Hernández 2010; White label "*Simulium acatenangoense* Dalmat syn. *S. paynei* Vargas Ex: L.M.Hernández'10 "].

SLIDES
Acatenango, Finca La Esperanza Pérez, Rio Ladrillera; 25.xi.1948, (*José H. Rosales & Daniel Luch*)— 1 male in three slides (only legs, genitalia and both wings; adult's thorax, head and pupal exuviae were not found at the NMNH holdings)[HOLOTYPE] (NMNH, acc. no. 409-27) [The slides bear a White label

with blue lines around edges with locality information, date and collector's name in DALMAT'S hand and in black ink; White label with blue lines around edges and written in red ink in DALMAT's hand "*Simulium (D.) acatenangoensis* n.sp. HOLOTYPE male H.T.Dalmat" and in black ink "acc. no. 409-27"; each slide have in red ink and in DALMAT'S hand the structure their contain. Other labels here added: White label "Digitally photographed genitalia, wing, and legs I-III L.M.Hernández 2010; White label "*Simulium acatenangoensis* Dalmat syn. *S. paynei* Vargas Ex: L.M.Hernández'10 "].

SPIRIT
Acatenango, Finca La Esperanza Pérez, Rio Ladrillera; 25.xi.1949, [Without collector's name]— 1female pupal exuviae [as ALLOTYPE] (NMHN, 409-3). Finca La Torry, Finca La Torre; 4.vii.1949, [Without collector's name.]— 1female pupal exuviae [PARATYPE] (NHMH, 748-383). Finca and Rio San Diego; 16.xii.1948, [Without collector's name.]— 3female pupal exuviae [PARATYPES] (NMNH, 516-1, 516-2, 516-4). Finca and Rio San Diego; 3.iii.1948, 16.xii.1948, 30.iii.1949, [Without collector's name.]— 3pupal exuviae (males) [PARATYPES] (NMNH, 516-1; 601-2, 601-4).

Synonym of *S. paynei* as *Simulium biuxinisia* COSCARÓN & IBÁÑEZ-BERNAL, 1995 [This work]

TYPE MATERIAL

MÉXICO

Oaxaca State

PINNED
Km 205, Carretera Tuextepec-Oaxaca, 1710 m; 12.vi.1992, (*S.Ibañez Bernal*)— 1female (reared) [PARATYPE] (INDRE, acc. no. E008) [The specimen bear several labels: White label "CAIMSimTp-00092"; White label with locality information, date and collector's name handwritten in black ink; White label with red edges "*Simulium* (*Hemicnetha*) *biuxinisa* n.sp. P4 female Coscarón & Ibáñez-Bernal". Other label here added: White label "Digitally photographed all parts L.M Hernández 2009".]

OTHER MATERIAL

COLOMBIA

Cundinamarca Dept.

Rio Dulce, 3 km N. of Alban, 1800,m, 42; 8.viii.1967, (*P. & B.Wygodzinsky*)— 1female1male (reared) (AMNH [Identified as *S. paynei* by COSCARÓN 1985]. Valle, N. of Degua, 1200; 26.viii.1967, (*P. & B.Wygodzinsky*)— 2males (reared) (MLP, nos. 53, 56) [All identified as *S. paynei* by A.J. SHELLEY].

Imbabura Province

SLIDES
4km from Ibarra, Tulca Rd on Salinas Rd, unnamed stream, (site E20); 9.ix.1983, (*M.Arzue & A.J.Shelley*)— 3larvae (BMNH) [All identified as *S. paynei* by A.J. SHELLEY].

COSTA RICA

Cártago Province

PINNED
Rd. from Turrialba to San José, unnamed stream after Rio Sereno, near bridge, (site CR-193), 9°57'39"N 83°46'8"W, 1615m; 25.ii.2010, (*L.M.Hernández & L.G.Chaverri*)— 3males (one male with genitalia and abdomen on slide), 1female (reared) (BMNH) [Identified as *S. paynei* by L.M. HERNÁNDEZ].

SLIDES
Rd. from Turrialba to San José, unnamed stream after Rio Sereno, near bridge, (site CR-193), 9°57'39"N83°46'8"W, 1615m; 25.ii.2010, (*L.M.Hernández & L.G.Chaverri*)— 1male (only genitalia and abdomen; remainder pinned), 3pharate males, 5larvae (BMNH) [Identified as *S. paynei* by L.M. HERNÁNDEZ].

San José Province

SPIRIT

Aseri, Mercedess, R. Parruas; v.1989, (*H.Nairema & H.Torres*)— 1females2males (reared), 2larvae (NMNH).

Puntarenas Province

PINNED

Monteverde, 1400m; ii-iii.1988, (*B.Hubley*)— 2females (malaise trap) (ROM). Monteverde, 1539m; 18-25.iii.1988, (*B.Hubley & D.Bell*)— 1female (malaise trap) (ROM). Monteverde, 1700m; 1-5.iii.1988, (*B.V.Brown*)— 1female (malaise trap, stunted forest) (ROM). Monteverde, 1700m; 7-12.v.1989, (*E.Fuller*)— 1female (malaise trap; prerains, forest edge), 11females (at light) (ROM).

GUATEMALA

Chimaltenango Department

PINNED

El Vergel; 15.vi.1944, (*A. Diaz N.*)— 1male (not associated with pupal exuviae) (NMNH) [Identified as *S. rubicundulum* probably by VARGAS]. Acatenango; 3.v.1949, (*Dalmat*)— 2females1male (no associated with pupal exuviae) (MLP, acc. no. 640-3; 717-15, 717-17). Acatenango, Finca S. José, R. Chorrera; 11.xi..1948, (*Dalmat*)— 1male (no associated with pupal exuviae) (MLP) [All previous specimens identified as *S. rubicundulun* by H.T. DALMAT]. Acatenango, Finca Tohuyá, Rio Laguneta; 15.ix.1948, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (NMNH, 444-6). Acatenango, Finca San Rafael, R. San Rafael; 18.xi.1948, (*Dalmat*)— 2females2males (not associated with pupal exuviae (NMNH, acc. no. 411-3, 411-16, 411-18, 411-58). Paraxaj, R.Paraxaj; 8.xi.1948, (*H.T.Dalmat*)— 1female (no associated with pupal exuviae (NMNH, no. 390). Acatenango, Finca Esperanza, R. Lochille; 30.x.1948, (*H.T.Dalmat*)— 1female (not associated with pupal exuviae) (NMNH, no. 362-19). Acatenango, Finca Providencia, R. Tablón; 6.x.1948, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae (NMNH, no. 348-12). Acatenango, Finca Quisache, Rio Posasito, 8.xi.1948, (*H.T.Dalmat*)— 1female (no associated with pupal exuviae) (NMNH, no. 419-1) [All specimens bear an identification label as "*Simulium acatenangoensis* by H.T. DALMAT" and a White identification label in S. COSCARÓN'S hand "*Simulium paynei* Vargas det. Coscarón 05"].

MEXICO

Morelos State

SLIDES

Temixco, Morelos; 3.vii.1945, (*A.Días N.*)— 1male (not associated with pupal exuviae; only both gonostyles, parameres and ventral plate; the median sclerite is missing; remainder of adult presumably lost) [The slide bear a white label with red edges, with locality information, date and collector's name and "3703" handwritten in black ink; handwritten in blue ink at the top of the label "HOLOTIPO"; Red label "HOLOTIPO"; White label "CAISimTp-00141". Other labels here added: White label "Digitally photographed genitalia (all) INDRE male L.M.Hernández'09"; White label "This is not the holotype of *S. paynei*; see MAIA-HERZOG *et al.* 1984 L.M.Hernández'09"; White label "Slide mislabelled L.M.Hernández'09".]

Oaxaca State

PINNED

Km 205, Carretera Tuextepec-Oaxaca, 1710 m; 12.vi.1992, (*S.Ibañez Bernal*)— 1larva (INDRE, E008; CAIMSimTp-00093) [The slide bear a Blue label as PARATIPO [=PARATYPE], but this is not a paratype according to the original description, L.M.Hernández 2009"].

SLIDES

Oaxaca, Ao. Coladiante, s/ruta 175; 12.vi.1992, (*Coscarón*)— 1female (reared), 1pupal exuviae, 1larva (MLP) [The slides have a red dot that means they were used for illustration by NELIDA CALAGARI]. Km 205, Carretera Tuextepec-Oaxaca, 1710 m; 12.vi.1992, (*S.Ibañez Bernal*)— 1larva (INDRE, E008) [The slide bear a White label "CAIMSimTp-00093" and also a Blue label "PARATYPE". However, this specimen is not a partype based on the original description and it has labelled accordingly by L.M. HERNÁNDEZ].

Veracruz State
PINNED
Cordova, 107 Reyes; 10.vii.1948 (*Reyes & Cordova*)— 1female1male (not associated with pupal exuviae) (NMNH) [Both specimens bear an identification label in A. STONE'S hand as "*Simulium mathesoni* Vargas" and written on the label "Slide 48-9-30a; 48-9-30b; the female have a White label with "3" printed in black ink]. Fortin de las Flores, Sumidero, Planta de la Cervecera, 2500-3000ft; 22-23.v.1965, (*H.V.Weems*)— one female (at black light) [Identified as *S. virgatum* Coq. Brown Form by L.M. HERNÁNDEZ 2010].

[Without State]
SLIDES
[Without further locality information.], (*Deppe*)— 1male (not associated with pupal exuviae) [The specimen bear several labels: White label "5 male"; Orange label "Typus"; Green label "Mexico, Deppe"; White label in ENDERLEIN'S hand "*Hemicnetha mexicana* Type male Enderl." and printed "Dr. Enderlein det. 1934"; White label in VARGAS'S hand "*S. (H.) paynei* Dr. L.Vargas det. V. 1953"; White label "Zool. Muse. Berlin". Other labels here added: White label "Digitally photographed Th. anterior, posterior ZMHU male L.M.Hernández; White label "*Simulium paynei* Vargas n. name for *Hemicnetha mexicana* End. Examined: L.M.Hernández'09"; White label "Genitalia on slide L.M.Hernández'09".]

UNITED STATES OF AMERICA
New Mexico Department
SPIRIT
Grant Co., Emery Pass, Rd. 152, 6200'; 15.v.1990, (*M.E.Craig & B.V.Peterson*)— 3pupal exuviae (NMNH).

Texas Department
SPIRIT
Bandera Co., Duncan Creek Ranch, Road no 337 west of Medina; 11.v.1990, (*B.V.Peterson*)— 6pupal exuviae, numerous larvae (NMNH). Bandera Co., Medina River; 9-12.v.1992, (*O.E.Rowles*)— 3females, 13males (reared) (NMNH). Bandera Co., 3 mi. n.w. Medina River; 2.iii.1991, (*D.W.Bowles*)— 3pupal exuviae (NMNH). Hidalgo Co, Coronado N.F., Rock Dam side of Geronimo Trail; 9.viii.1991, (*M.E.Craig*)— several males (reared) (NMNH). Zavala Co.; 20.iv.1954, (*A. Stone*)— 2males (reared) (NMNH) [One specimens bear a label in P.H. ADLER'S hand "*Simulium paynei* Vargas P.H.Adler 1999"].

VENEZUELA
Mérida State
PINNED
Rangel Department, Murucumba; [Without date or collector's name.]— 1female (reared) (MLP). [Without further locality information or collector's name.]— 1female (reared) (MLP) [Identified as *S. paynei*].

Tachira State
S. Cristobal Department, El Corazo; [Without date or collector's name.]— 1female (reared) (MLP).

Simulium (Trichodagmia) pulverulentum KNAB, 1915

All material listed under in the paper of SHELLEY *et al.* (2002a) was examined for this paper. Further material examined where new labels have been added is as follows:

TYPE MATERIAL

BELIZE [As BRITISH HONDURAS]

PINNED

Punta Gorda; [Without date], (*J.D.Norton*)— female (not associated with pupal exuviae) (NMNH; cotype no. 19111) [LECTOTYPE] [The specimen bear several labes: White label with locality information; White label with collector's name; Red label "Cotype 19111 U.S.N.M.". Other labels here added: White label in L.M. HERNÁNDEZ'S hand "LECTOTYPE *Simulium pulverulentum* Designated: L.M.Hernández 2010"; White label "Digitally photographed Thorax ant.+post.; abdomen, lateral L.M.Hernández"]. Same information as lectotype— 31females (not associated with pupal exuviae) [PARALECTOTYPES] [All specimens bear a Red label "Cotype 19111". Other labels here added: White label "PARALECTOTYPE *Simulium pulverulentum* Designated: L.M.Hernández 2010] (NMNH); 2females (not associated with pupal exuviae) [PARALECTOTYPES] (BMNH, B.M. 1952-404) [The specimens bear several labels: Red label "Cotype no. 19111 U.S.N.M"; White label and handwrittien in blue ink "*Simulium pulverulentum* Knab". Other labels here added: White label "*Simulium pulverulentum* PARALECTOTYPE Designated: L.M.Hernández 2010"].

OTHER MATERIAL

BELIZE [As British Honduras]

PINNED

Punta Gorda; [Without date.], (*J.D.Norton*)— female (not associated with pupal exuviae) (NMNH) [Identified as *S. pulverulentum* by L.M. HERNÁNDEZ 2010].

COSTA RICA

Limón Province

PINNED

Rio Guacimo, at 500m from main road (site 34), 10°12'29"N 83°41'19"W, 125m; 20.i.2008, (*L.M.Hernández & L.G.Chaverri*)— one male (reared) (only thorax, four legs and one wing; genitalia and one wing on slide; head missing) (BMNH).

SLIDES

Rio Guacimo, at 500m from main road (site 34), 10°12'29"N 83°41'19"W, 125m; 20.i.2008, (*L.M.Hernández & L.G.Chaverri*)— 1male (reared) (only genitalia and one wing, head missing; remainder of adult pinned) (BMNH) [The specimen have a White label "CR-34 photos BMNH 626019"].

Punta Arenas Province

SLIDES

Rio Platanarez, 33°87'07" 545°24'29", 181m; 14.viii.2009, (*L.G.Chaverri & M.Monagas*)— 3larvae (BMNH) [Identified as *S. pulverulentum* by L.M. HERNÁNDEZ 2009]. Osa, Punta Areas, Cortes, Rio Balzar, 32°74'29"51°51'40, 57m; 19.viii.2009, *L.G.Chaverri & M.Monagas*)— 1larva (BMNH) [Identified as *S. pulverulentum* by L.M.HERNÁNDEZ 2009].

***Simulium* (*Trichodagmia*) *rubrithorax* LUTZ, 1909**

All material listed under SHELLEY *et al.* (1997, 2010) were examined for this paper. Further material examined as follows:

OTHER MATERIAL

BRAZIL

Goiãs State

SLIDES

Belem-Brasilia Highway, km 146; 26.v.1976, (*A.J.Shelley*)— 1male (reared) (BMNH) [Identified by A.J. SHELLEY].

Minas Gerais State

SLIDES

Pedralva, Fazenda Santo Antonio; 19.ii.2010, (*A.P.A.Luna Dias*)— 3larvae (BMNH) [Identified *S. rubrithorax* by A.J. SHELLEY]. Pedralva Fazenda Sto Antonio; 15.v.1979, (*A.J.Shelley & A.P.A.Luna Dias*)— 1larva (BMNH) [Identified *S. rubrithorax* by A.J. SHELLEY].

SPIRIT
Pedralva, Fazenda Santo Antonio (stream); 15.vi.1979 (*A.J.Shelley*)— 1female (not associated with pupa), 2pupal exuviae, 1larva (BMNH) [Identified *S. rubrithorax* by A.J. SHELLEY]. Pedralva, Faz. Sto Antonio da Baixa, (site 487-15); 16.x.1970, (*A.J.Shelley & A.P.A.Luna Dias*)— 1male (reared) (BMNH) [Identified *S. rubrithorax* by A.J. SHELLEY]. Pedralva, Fazenda Santo Antonio, watwerfall near swimming pool; 25.ix.2007, (*A.J.Shelley & A.P.A.Luna Dias*)— 1pupal exuviae, several larvae [specimen transferred to alcohol 100% and housed at BMNH] (BMNH) [Identified *S. rubrithorax* by A.J. SHELLEY]. Pedralva, Fazenda Santo Antonio; 19.ii.2010, (*A.P.A.Luna Dias*)— several larvae (BMNH) [Identified *S. rubrithorax* by A.P.A.LUNA DIAS]. Pedralva, Fazenda Santo Antonio; 8.vi.2010, (*A.P.A.Luna Dias*)— several pharate pupal exuviae and larvae (BMNH) [Identified *S. rubrithorax* by A.P.A.LUNA DIAS].

São Paulo State
SLIDES
Fazenda Barro Tarro; 15-18.v.1979, (*R.W.Crosskey & A.J.Shelley*)— 1male (reared) (BMNH, B.M. 1979-258).

***Simulium* (*Trichodagmia*) *smarti* VARGAS, 1946**

TYPE MATERIAL

MÉXICO
Chiapas State
El Rubí, Finca El Vergel; 27.i.1943, (*Vargas-Díaz*)— 1female (not ssociated with pupal exuviae; only thorax, the head, wings, legs, abdomen and genitalia are on a slide) [HOLOTYPE] (INDRE, no. 3684) [The female holotype appeared to have been pinned by the pleura and it is showing a hole on both side. However, it has now been dissected and only the thorax remained glued to a card point. The remainder of the adults is on slide] [The specimen bear several labels: Red and White labels "HOLOTIPO"; White label "*smarti* female"; White label with locality data, date and collector's name; White label "3684". Other labels here added: Digitally photographed Thorax ant.+post. Holotype female L.M.Hernández"; White label "*Simulium smarti* Vargas, 1946 Examined: L.M.Hernández 2008"]. Same data as holotype— 1female (not associated with pupal exuviae) [PARATYPE] (INDRE). El Rubí, Finca El Vergel; 23.i.1945, (*Vargas-Díaz*)— 1male (not associated with pupal exuviae) [PARATYPE] (NMNH) [The specimen have a Pale green label "PARATIPO"; White label in VARGAS'S hand "*Simulium smarti* Det. L.Vargas; White label probably in COSCARÓN'S hand "*Simulium (Hemicnetha) smarti* Vargas"]. Cas. Belem; 25.i.1945, (*Vargas-Díaz N.*)— 2females2males (not associated with pupal exuviae) [1 female only thorax, remainder on slide; one female only thorax, wing and one leg, remainder on a slide; one male only thorax, remainder on slide;; White label "CAISimTp-00206"; the females bear a White label "CAISimTp-00209", CAISimTp-00207] [PARATYPES] (INDRE) [All specimens have a Blue label as "PARATIPO"].

SLIDES
Same data as pinned adult— 1female (only head, wings, legs, abdomen and genitalia; thorax pinned) [HOLOTYPE] (INDRE, no. 3684) [The slide bear several labels: White label with red edges with locality data, date, collector's name, species identification and "3684" handwritten in black ink; Red label "Holotipo"; White label "CAIMSimTp-00140". Other labels here added: White label "Digitally Photographed wing, cibarium, Lutz organ, legs, hind claw, genitalia INDRE HOLOTYPE Female Ex. L.M.Hernández'09]; White label "Female (only wings, head, legs, genitalia) Adult Pinned Ex. L.M.Hernández'09"]. Same locality and collector as holotype; 23.i.1945— 1male (not associated with pupal exuviae; only wings, legs and genitalia) [as ALLOTYPE] (INDRE, no. 3685) [The slide bear several labels: White label with red edges with locality data, date, collector's name, species identification and "3685" handwritten in black ink; Red label "ALLOTYPE"; White label "CAIMSimTp-00139".

Other labels here added: White label "Digitally Photographed genitalia (all) INDRE ALLOTYPE Male Ex. L.M.Hernández'09"]. Cas. Belem; 25.i.1945, (*Vargas-Díaz N.*)— 1male (not associated with pupal exuviae; only head, abdomen, genitalia, legs and wings; reaminder of body pinned) [The slide bears a White label no. "CAISimTp-00206"; female (only head, wings, legs and genitalia on slide; thorax pinned, slide with a White label "CAISimTp-00209"; female (only head, genitalia and five legs; remainder pinned, specimen with White label "CAISimT-p00207) [All with a Blue label "PARATYPES"] (INDRE).

OTHER MATERIAL

GUATEMALA

SLIDES

Finca Barretal, camino a San Vicente; 18.vi.1945, [Without collector's name.]— 1female1male (reared) (MLP).

Simulium (Trichodagmia) solarii **STONE, 1948**

TYPE MATERIAL

UNITED STATES OF AMERICA

TEXAS STATE

PINNED

Menard Co., 23.iv.1941, (*Stone*, *A.*)— male (reared; genitalia on slide) [HOLOTYPE] (NMNH, acc. no. 58956) [The pinned male holotype is in good and it has been glued to a card point by the thorax, ventrally, together with its pupal pelt. Its genitalia is on a slide only containing the ventral plate and both gonostyles] [The specimen bear several labels: White label with locality information, date and collector' name; Pink label "Slide 68-5"; Red label "Type 58956 U.S.N.M.". Other labels here added: White label "Digitally photographed Thorax ant.+post.; abdomen, cocoon L.M.Hernández"; White label "*Simulium solarii* Stone, 1948 Holotype male; [gen. on slide] Examined: L.M.Hernández 2008-2009"]. Uvalde; 21.iv.1941, (*Stone*, *A.*)— 2females2males (reared) [one female and one male with genitalia probably on slides with no. 60-2) [PARATYPES] (CNC) [All specimens have a Red label "PARATYPE NMNH no. 58956", and a Yellow label "PARATYPE *S. solarii* no. 74553"]. Menard Co.; 23.iv.1941, (*Stone*, *A.*)— 2males (reared) [All specimens have a Red label "PARATYPE NMNH no. 58956", and a Yellow label "PARATYPE *S. solarii* no. 74553"; one male have a handwritten label in blue ink and probably in STONE'S hand *"Simulium solarii* Stone" and printed "Det. A. Stone"]. Menard; 23.iv.1939, (*A. Stone*)— 1female (reared) [PARATYPES] (NMNH, no. 58956). Menard; 21.vi.1939, (*Roy Melvin*)— 5females1male (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 58956). Los Moros Creek, w. of Menard County; 22.v.1950 (*Roy Melvin*)— 9females (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 58956). Los Moros Creek, Menard; 12.iv., 14.iv.1943, (*C.L.Smith)*— 2females1male (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 5896). Los Moros Creek, Menard; 10.viii.1942, (*Roy Melvi*)— 2females1male (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 58956). Con Con; 29.viii.14, [Without collector's name.]— 17females (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 58956) [All the specimens have a White label "Bishop 3617"]. Junction, Texas; 21.ii.1939, (*F.C.Bishop*)— 2females (reared) [PARATYPES] (NMNH, no. 5896; one specimen with a White label "Slides no. 39.iii.27"]. Upper Little Walnut Creek, Austin; 1936, (*A.B.Griffen*)— 4females1male (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 58956). Kerr County, Kerrville; 4.vi.1948, (*C.W.Sabrosky*)— 1female (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 58956). Burnet County, Showel Mt; iv.1912, [Without collector's name.]— 3females (not associated with pupal exuviae) [PARATYPES] (NMNH, no. 58956). Uvalde; 21.iv.1941, (*A. Stone*)— 9females (reared) [PARATYPES] (NMNH, no. 58956), 1female (reared), 1pupal exuviae (adult lost) [PARATYPES, no. 58956] (BMNH). Uvalde; 6.vii.1938, (*W.L.Barret*)— 4males (not associated with pupal exuviae) [PARATYPES, no. 58956] [All specimens have a White label "Bishop 20.192"].

SLIDES

Same data as pinned adult— male (only both gonostyles and the ventral plate; parameres and median sclerite are missing, remainder of adult and its pupal pelt pinned) [HOLOTYPE, no. 68-5] (NMNH, 58956) [The slide is partially broken in one corner. It bears several labels: White label with locality information, date and collector's name; the species name is handwritten in pencil and the name is underlined in red ink; Red label "TYPE 58956 NMNH"; White round with red edges "Holotype". Other labels here added: Digitally Photographed both gonostyles, ventral plate NMNH HOLOTYPE Male Ex.: L.M.Hernández'09; White label "Male only both gonotyles and ventral plate Ex. L.M.Hernández'09"; White label "Adult Pinned L.M.Hernández'09"]. Menard; 22.vi.1922, [Whitout collectors' name.]— 1male (only genitalia), 1 slide containg the genital capsule of five females [all labelled as PARATYPES] (NMNH) [The slide have handwritten on the label *S. virgatum* Coq., but this has been crossed out in pencil and added: "*solarii* Stone". The slide have a red label "PARATYPE"]. Uvalde; 13.iv.1939, (*Deonier & Barret*)— 1female1male (not associated with pupal exuviae) [PARATYPES] (NMNH) [The slide have handwritten on the label *S. virgatum* Coq., but this has been crossed out in pencil and added: "*solarii* Stone". The slide have a red label "PARATYPE"]. Uvalde; 21.iv.1941, (*A. Stone*)— 1female (only head) [PARATYPE] (NMNH) [The slide have handwritten on the label "*Simulium* sp. no.15", but this has been crossed out in pencil and added: "*solarii* Stone female". It also has in black ink "SI.48.8.24a". The slide also have a Red label "PARATYPE"]. Nueces R. Uvalde; 7.vi.1938, (*W.L.Barret Jr.*)— 1male (only genitalia) [PARATYPES] (NMNH) [The slide have handwritten on the label in pencil: "*solarii* Stone"; it also has in black ink at the bottom of the right handside corner "Slide 38.vi.30a". The slide also have a Red label "PARATYPE"]. Frio River, Concan; 21.iv.1941, (*A.Stone*)— 1female (only genitalia) [PARATYPE] (NMNH, acc. no. 60-2) [The slide have handwritten on the label "*Simulium* sp. no.15", but this has been crossed out in pencil and added: "*solarii* Stone female". The slide also have a red label "PARATYPE"]. Junction, Texas; 21.ii.1939, (*F.C.Bishop*)— 1male (reared; only genitalia, remainder pinned) [PARATYPE] (NMNH) [The slide have handwritten on the label "*Simulium virgatum* Coq.", but this has been crossed out in pencil and added: "*solarii* Stone". It also in black ink "Slide 39.ii.22" and a Red label "PARATYPE"]. Taxa, Uvalde Co; [Without date or collector's name.]— 1male (only genitalia) (BMNH).

MÉXICO
San Luis de Potosí State
SLIDES
Las Cascadas; Micos, 22.xii.1943, (*A.Díaz N.*)— 1female (only legs, wings and genitalia), 1male (only four legs, wings and genitalia) [PARATYPE] (NMNH) [The slide have handwritten in black ink "*S. (D.) virgatum* female, male", but this has been crossed out in pencil and added: "*solarii* Stone female, male". The slide also have hadwritten in black ink "Slide 48.8.19a" and a Red label "PARATYPE"], 1female 1male (not associated with pupal exuviae) [PARATYPES] (INDRE) [The slides have a White label with red edges and handwritten in black ink the locality information, date and collector's name; *S. (D.) virgatum* has been crossed out and written in blue colored pencil "*solarii*"; the slide also have a White label with red edge "*Simulium solarii* Stone Paratype female and male. Bboth slides have a blue label "PARATIPO"; the slide containing the female bear a White label "CAIMSimTp-00091" and the male "CAIMSimTp-00050"].

Tamaulipas Department
PINNED
Xicotencatl; v.1944, (*M. Macias*)— 1female1male (not associated with pupal exuviae; the genitalia of the male is on a slide) [PARATYPES] (NMNH, no. 58956; the male have a White label "Slide 48.8.19a"] [Previously identified as *S. virgatum*]; 1female1male [PARATYPES] (INDRE, no. 3777 for the slide containing the female and 3976 for the slide containing the male) [The slides bear a White label with red edges with locality information, date and collector's name and "*S. (D.) virgatum"* crossed out and written in blue colored pencil "*solarii*"; the slides also have a White label with red edges "*Simulium solarii* Stone Paratype female and male. Both slides have a blue label "PARATIPO". The slide containing the female bear a White label "CAIMSimTp-00048" and the male "CAIMSimTip00049"].

SLIDES
Xicotencatl; v.1944, (*M. Macias*)— 1male (not associated with pupal exuviae; only genitalia, remainder pinned [PARATYPE] (NMNH) [The slide have handwritten on the label "*Simulium* sp. no. 15", but this has been crossed out in pencil and added: "*solarii* Stone". The slide also have handwritten in black ink "Slide 48.8.19a". The slide also have a red label "PARATYPE"].

OTHER MATERAL

UNITED STATES OF AMERICA

TEXAS STATE

SLIDES

Uvalde; 9.ix.1941, (*W.L.Barret Jr. & F.C.Bishopp*)— 2females3males (not associated with pupal exuviae) (NMNH, Lot 41-16806, in Balsam viii.57). Uvalde; 21.vi.1941, [Without collector's name.]— 5larvae (NMNH; in Balsam viii.57). Uvalde; 21.vi.1941, (*A.Stone*)— 1larva (NMNH no.59). Edwards Co.; 22.iv.1941, (*A.Stone*)— 1larva (NMNH, no. 64). Austin, 18.x.1922, (*Painter*)— 1male (only hing leg and genitalia) (NMNH no. 60) [The slide have a White label and printed in black "Simuliidae" "Det. G.S.Stains 194", and handwritten in black ink "*Simulium virgatum* Coq. male". The latter has been crossed out in pencil and added: "*solarii* Stone". I have added a White label: *S. solarii* Stone Ex: L.M.Hernández'09; see STONE, 1948: 404]. Bandera Co., Medina River, 1 mi. NW Medina, RT. 16; 8.iii.1997, (*D.E.Bowles*)— 1male, 1pupal exuviae (CUAC). Sattler, River Road, Pondo Rosa, Guadalupe River; 19.ii.2000, (*Simmons*)— 6larvae (3 larvae with brown head and 3 larvae with yellow head) (CUAC) [Specimens identified by P.H. ADLER].

SPIRIT

Bandera Co., Medina River, 1 mi. NW Medina, RT. 16; 8.iii.1997, (*D.E.Bowles*)— several pupal exuviae, larvae, and reared adults (CUAC). Sattler, River Road, Pondo Rosa, Guadalupe River; 19.ii.2000, (*Simmons*)— numerous larvae and pupal exuviaer (CUAC) [All specimens identified by P.H. ADLER]..

New Mexico State

SPIRIT

Eddy Co, Black River ford near Black River village; 3,340'; 14.v.1991, (*M.E.Craig & B.V.Peterson*)— numerous females and males (reared) (NMNH).

***Simulium* (*Trichodagmia*) *tarsale* WILLISTON, 1896**

All material listed in HERNÁNDEZ & SHELLEY (2005) was examined in the current work. Further material examined where new labels have been added is as follows:

TYPE MATERIAL

WEST INDIES, SAINT-VINCENT

PINNED

1000 ft; [Without date.], (*H.H.Smith*)— female (only thorax and one left front leg; one wing, abdomen and genitalia and five legs on a slide; head and one wing missing) [LECTOTYPE] (BMNH, BM 1907-66]. [The lectotype bear several labels: White label with locality data and collector's name; White label "1000 ft"; White handwritten label "harvest by stream"; White label and printed "W. Indies 1907-66"; White re-bordered, and handwritten label "*Simulium tarsale*". At the bottom of the label of the right-hand side corner "Williston"; White label "LECTOTYPE female of *Simulium tarsale* Williston R.W.Crosskey det 1981". Other labels added: White label "Scutal pattern digitally photographed Taken by L.M.Hernández BMNH(E) 2004"; White label "Material in slide collection"; White label "Digitally photographed BMNH(E) 625454"]. Same data as the lectotype— 1female (only thorax, one wing and three legs on the right side; head, abdomen, one wing and one hind leg on slide) [PARALECTOTYPE] (BMNH, B.M. 1907-66) [The paralectotype have similar labels as the lectotype except one label "Paralectotype female of *Simulium tarsale* Williston R.W.Crosskey det 1981" and another label in SHELLEY'S hand "Head, abdomen, wing and leg 3 on slide"].

SLIDES

1000 ft; [Without date.], (*H.H.Smith*)— female (only wing, abdomen and genitalia and five legs; thorax and one front leg pinned] [LECTOTYPE] (BMNH, B.M. 1907-66). Same data as lectotype— 1female (only head, abdomen, one wing and one hind leg; thorax, right wing and three legs on the right side pinned]

[PARALECTOTYPE] (BMNH). Guadaloupe, 4000ft; 20.vii. [Without date.]— 1female (not associated with pupal exuviae) [PARATYPE, no. 15411] (CNC) [With identification label as *S. clavipes*].

Synonymy of *S. tarsale* as *Simulium clavipes* MALLOCH, 1914

TYPE MATERIAL

WEST INDIES, DOMINICA

PINNED

Dominica; viii.1965, (*A.Busk*)— 1female [PARATYPE, no.15411] (NMNH) [This specimen is labelled as paratype but it was not included in the original description of *S. clavipes* by MALLOCH; see also STONE (1969)].

WEST INDIES, GUADALOUPE

PINNED

Guadeloupe, 4000ft; 30.vii.[Without year.], (*August Busck*)— female (not associated with pupal exuviae) [HOLOTYPE] (NMNH, accession number Type 15411) [The specimen bear several labels: White label "4000ft"; White label with locality information and date printed in black ink; White label with collectors' name"; Red label "Type no. 15411 U.S.N.M.". Other labels here added: White label "*Simulium clavipes* Malloch syn. of *S. tarsale* Williston Ex.: L.M.Hernández 2010"; White label "Digitally photographed Th. ant.+post.; abdomen, lateral L.M.Hernández 2010"]. Same data as holotype— 2females (not associated with pupal exuviae) [PARATYPES] (BMNH, B.M. 1952-404, presented by NMNH, no. 15411). Guadeloupe, 4000ft; 30.vii. [Without year]— 21females [Four specimens with head, wings, legs, abdomen and genitalia on slide] [PARATYPES] (NMNH, no. 15411).

SLIDES

Guadeloupe, 4000ft; 30.vii.[Without year.], (*August Busck*)— 1female (only head, abdomen, one wing and one hind leg) [PARATYPES] (BMNH, B.M. 1952-404, presented by NMNH acc. no. 15411). Guadeloupe, 4000ft; 30.vii.[Without year.]— 4females (only head, wings, legs, abdomen and genitalia on slide; thorax pinned] (NMNH, no. 1511) [PARATYPES].

OTHER MATERIAL

WEST INDIES, DOMINICA

PINNED

Clarke Hall; 8-10.i.1965, (*W.W.Wirth*)— 12females (collected on malaise trap, Bredin-Archbold Smithsonian Bio Surv. Exp.) (NMNH). Clarke Hall; 11-20.i.1965, (*W.W.Wirth*)— 10females (collected on malaise trap, Bredin-Archbold Smithsonian Bio. Surv. Exp.) (NMNH). Clarke Hall; 21-31.i.1965.i.1965, (*W.W.Wirth*)— 40females collected on malaise trap, Bredin-Archbold Smithsonian Bio. Surv. Exp.) (NMNH). Clarke Hall; 12-18.x.1964, (*P.J.Spangler*)— 1female (Bredin-Archbold Smithsonian Bio. Surv. Exp.) (NMNH). Freshwater Lake; 2400 ft.; 22.ii.1964, (*Dale F. Bray*)—1female (collected at light) (NMNH). Antrim, 1000 ft; 17.iii.1956, (*J.F.G.Clarke*)— 1male (only thorax, legs, wings and part of abdomen; genitalia on slide with no. 69-3) (NMNH).

SLIDES

Parish at St. Joseph Springfield Estate; 15.iii.2003, (*M.E.Irwin*, *M.B.*,[Illegible], *B. Bensen*, *G. Carner*)— 5females (malaise trap) (BMNH) [Identified as *S. tarsale* by P.H.ADLER 2004.]. Clarke Hall; x.1964, (*P.J.Spangler*)— 1female (not associated with pupal exuviae). Antrim, 1000 ft; 17.iii.1956, (*J.F.G.Clarke*)— 1male (only genitalia; thorax, legs, wings and part of abdomen pinned) (NMNH, slide no. 69-3).

SPIRIT

Parish at St. Joseph Springfield Estate; 15.iii.2003, (*M.E.Irwin*, *M.B.*[Illegible], *B.Bensen*, *G.Carner*)— 24females (malaise trap) (CUAC) [Identified as *S. tarsale* by P.H. ADLER 2004.]

WEST INDIES, GUADELOUPE

PINNED

Guadeloupe; vii-viii.1957, (*W.B.Heed*)— 1female (NMNH).

***Simulium* (*Trichodagmia*) *tarsatum* MACQUART, 1846**

All material listed under *S. mexicanum* in SHELLEY *et al.* (2002b) and under *S. tarsatum* in HERNÁNDEZ & SHELLEY (2005) was examined for this paper. Further material examined where new labels have been added is as follows:

Synonymyy of *S. tarsatum* as *Simulium aureopunctatum* MALLOCH, 1914

TYPE MATERIAL

GUATEMALA

PINNED

Livingston; 6.v, (*Barber & Schwartz*)— female (not associated with pupal exuviae) [HOLOTYPE] (NMNH, Type no. 15406) [The adult is lost. What only remains glued to a card a point is one hind leg and one wing] [The specimen bear several labels: White label with collector's name; Red label with type accession number; White label with black edges in MALLOCH'S hand "*Simulium aureopunctatum* Malloch"; White label "Holotype of *S. aureopunctatum* Malloch Examined: 1988 A.J.Shelley"; White label and handwritten in black ink "Synonym of *S. mexicanum* Bellardi Examined 1988 A.J.Shelley". Other labels here added: White label and printed in blue ink "*Simulium* …. Examined L.M.Hernández" and in L.M.HERNANDEZ'S hand "a*ureopunctatum* Malloch syn. of *S. tarsatum* Macquart… '10'; White label "Adult found missing during a visit to NMNH in June.2010 by L.M.Hernández"; White label "Digitally photographed Wing and hind leg L.M.Hernández 2010"].

***Simulium (Trichodagmia) virgatum* COQUILLET (complex)**

All material listed under *S. virgatum s.l.* and *S. paynei* in SHELLEY *et al.* (2002b, 2010) was re-examined within the context of the curren work. Some specimens identitifed as *S. virgatum s.l.* by the latter authors might represent specimens which I have here identified as *S. paynei*. The reader should consult the latter publications and the current work for an up- to-date on distribution of these two species.

TYPE MATERIAL

UNITED STATES OF AMERICA

New Mexico State

PINNED

Las Vegas, [Hot Springs]; 4.viii.[Without year.], (*H.S.Barber*)— male (genitalia on slide) [HOLOTYPE] (NMNH, Type no. 6183) [The holotype is in good condition. The specimen bear several labels: White round label with red edges "Holotype"; White label with locality information"; White label with collector's name; Red label "Type no. 6185 U.S.N.M."; White label with black lines around the edges and handwritten "*Simulium virgatum* Coq."; White label "Digitally photographed Thorax L.M.Hernández 2002". Other labels here added: White label "Material in slide collection male genitalia Holotype Exam: L.M.Hernández 2010"; White label "Digitally photographed Th. ant.+post., adomen lateral view Examined: L.M.Hernadez 2010"; White label "*Simulium virgatum* Coq. Holotype Examined L.M.Hernández 2010"].

SLIDES

Same date as pinned holotype— male (only genitalia) [HOLOTYPE] (NMNH, Type no. 6183) [The slide bear a Red label with black edges with species identification and author's name plus the locality information, date, collector's name and accession number handwritten in black ink. Other labels here added: White round label with red edges "Holotype"; Digitally photographed part(s) Parameres, gonostyle, gonocoxite, ventral plate, median sclerite Taken by L.M.Hernández (BMNH 2002)"; White label "Adult in pinned collection "Types Draw" Exam: L.M.Hernández 2010"; White label "*Simulium virgatum* Coq. Holotype Exam.: L.M.Hernández 2010"].

Synonym of *S. virgatum s.l.* as *S. rubicundulum* KNAB, 1915
TYPE MATERIAL

MEXICO
Veracruz State
PINNED
Córdoba, 17.xii.1907, (*Fred Knab*)— female (only head, thorax, wings and abdomen and one hind leg on slide) [HOLOTYPE] (NMNH, Type No. 19112) [The specimen is in good condition being glue to a card point by its right side. Its genitalia and one hind leg are on slide; three legs are missing] [The specimen bear several labels: White round lable with red edges "HOLOTYPE"; White label with locality information printed in black ink"; White label with the date handwritten in black ink; White label with collector's name printed in black ink; Red label "Type No. 19112"; White label and printed in black ink "Slide"; White label with black line around the edges and handwrittten in black ink "*Simulium rubicundulum* Knab"; White label "Digitally photographed parts(s): Thorax (scutal pattern) Taken by L.M.Hernández (BMNH 2002)". Other labels here added: White label "Material in slide collection genitalia, one hind leg Ex: L.M.Hernández 2010"; White label "Digitally photographed Thorax ant.+post., abdomen lateral view L.M.Hernández 2010"; White label "*Simulium rubicundulum* Knab syn of *S. virgatum* Coq. (complex) Examined: L.M.Hernández 2010"].

SLIDE
Córdoba, 17.xii.1907, (*Fredk Knab*)— female (only abdomen and one hind leg; remaider of adult pinned) [HOLOTYPE] (NMNH, accession number Type No. 19112] [The slide is in good condition] [The slide bear several labels: Red label with black lines around the edges and handwritten in blak ink with all relevant information as in the pinned adult. At the top of the right handside corner there is an acronym "AS" probably meaning ALAN STONE; White label "Digitally photographed part(s) genitalia, hind leg taken by L.M.Hernández (BMNH 2002). Other labels here added on the back of the slide: White label "*Simulium rubicundulum* Knab syn of *S. virgatum* Coq. s.l. Exam.: L.M.Hernández 2010"; White label "Adult in pinned collection L.M.Hernández 2010"].

OTHER MATERIAL

UNITED STATES OF AMERICA
Arizona State
SLIDES
Grand Canyon, Colorado River at National Canyon National Creek, 0.5 mi. above mouth; 18.vi.1991, (*J.S.Doughman*)— 2larvae (BMNH) [Identified as *S. virgatum* by P.H. ADLER].

SPIRIT
Grand Canyon, Colorado River at National Canyon National Creek, 0.5 mi. above mouth; 18.vi.1991, (*J.S.Doughman*)— numerous pupae and larvae (CUAC).

California State
PINNED
Andreas Canyon, Pal Springs; 11.iii.1955, (*W.R.Manson*)— 2females (not associated with pupal exuviae) (CNC) [Identified as *S. virgatum s.l.* Black Form L.M. HERNÁNDEZ 2008"]. Los Angeles Co.; vi.[Without year or collector's name.]— 1female (not associated with pupal exuviae) (CNC) [Identified as *S. virgatum s.l.* Black Form L.M.HERNÁNDEZ 2008"]. Kern Co., Pierre Ranch, N. Fork, Kaneah River; iii.v.1948, (*R.W.Coleman*)— 1female2males (not associated with pupal exuviae) (NMNH, male A2; B(B) number 4; B(B) 3) [Both males bear a handwritten label by A.STONE "*Simulium virgatum* Coq. A.Stone 40]. L.A., Santa Monica, California; 22.iv.1954, [Without collector's name.]— 1male (not associated with pupal exuviae) (NMNH). L.A., L. Elizabeth Can.; 26.iv.1950, [Without collector's name.]— 2males (not associated with pupal exuviae) (NMNH). Alameda Co., Sunol; 17.i.1939, (*T.G.Aitken*)— 2males (not associated with pupal exuviae) (NMNH) [One male bear a handwritten label by A. STONE "*Simulium virgatum* Coq. A.Stone 40"]. Arroyo Seco, Greenfield; 1.viii.1940, (*T.G.Aitken*)— 1female (NMNH) [All previous specimens identified as *S. virgatum* Coq. (complex) Black Form by L.M.HERNÁNDEZ 2010].

Sierra Laguna, La Laguna; 14.x.1914, (*Ross & Bohart*))— 1female (NMNH) [Identified as *S. virgatum* Coq. (complex) Brown Form by L.M.HERNÁNDEZ 2010]. Fresno Co., Dry Creek, 9 mi. NE Academy; 6.xi.1954, (*W.C.Bentick*) — 1female (reared) [Identified as *Simulium virgatum* Coq. (Complex) Black Form by L.M. HERNÁNDEZ 2010].

New Mexico State
PINNED
Catroy Co.; Gila Wilderness A. Woodland Park; 26.vii.1993, (*R. Durfee*)— 2males (reared) (NMNH) [All specimens identified as *S. virgatum* Coq. (complex) Black Form by L.M. HERNÁNDEZ 2010].

Texas State
SLIDES
Presidio Co., Big Bed Ranch St. Pk., Fresno Canyon, Fresno Creek; 29.iv.1996, (*D.E.Bowles*)— 1larva (BMNH) [Specimen identified as *S. virgatum* by P.H. ADLER].

SPIRIT
Bandera Co., Medina River, 1 mi. NW. Medina Rt. 16.; 8.v.1997, (*D.E.Bowles*)— 1female1male (not associated with pupal exuviae), pupal exuviae, larvae (CUAC) [Identified as *S. paynei* Vargas by P.H.ADLER 1997]. Presidio Co., Big Bed Ranch St. Pk., Fresno Canyon, Fresno Creek; 29.iv.1996, (*D.E.Bowles*)— several pupal exuviae and larvae (CUAC) [Specimens identified as *S. virgatum* by P.H. ADLER]. Williams Co.; 18.iv.1941, (*A.Stone*)— 1female (reared) (NMNH) [The specimen bear a White identification label in A. STONE'S hand as "*Simulium virgatum* Coql."].

Simulium (Trichodagmia) yepocapense DALMAT, 1949

TYPE MATERIAL

GUATEMALA
Chimaltenango Department
SLIDES
Yepocapa, R. Socoyá, Finca Niágara; 4.viii.1948, (*Jorge Aleman & Miguel Xinie*)— female (reared) [HOLOTYPE] (NMNH, no. 570-8) [The holotype has been dissected and it is mounted in seven slides containing the adult body parts and its pupal pelt; all slides are in good condition] [The slides bear several labels: White label with black border stating the locality information, date and collector's name; White label and handwritten in red ink "*Simulium yepocapens*e n.sp. H.T.Damat"; each slide have written in red ink the body parts it contains, and at the top of each label "ACC-Yepo-570-8". Other label here added: White label "Digitally photographed Holotype female L.M.Hernández 2009].

Synonymy of *S. yepocapense* as *Simulium ardeni* DALMAT, 1953

TYPE MATERIAL

GUATEMALA
SLIDES
San Pedro, Carchá, Alta Verapas, Rio Tzunuts; 16.xi.1944, (*G.F.Fairchild*)— male (reared, in seven slides containing the head, cibarium, legs, wings, pupal exuviae, gill filaments and genitalia) [HOLOTYPE] [The slides bear several labels: White label with black edges and handwritten in red ink by H.T.DALMAT "HOLOTYPE Male *Simulium (Dryarella) ardeni*, n.sp. H.T.Dalmat" and in black ink "acc. no. 5-24A"; one slide have in red ink "female"; White label with black ink in DALMAT'S hand with the locality information, date and collector's name. Other labels here added on the back of the slides: White label "*Simulium ardeni* Dalmat syn. of *S. yepocapense* Dalmat Ex: L.M.Hernández 2010"; White label "Digitally photographed wing, legs, genitalia and gill filaments L.M.Hernández 2010"]. Sn. Pedro Carcha; 16.xi.1944, (*Fairchild*)— 1pupal exuviae (only gill filaments) (INDRE) [The slides bear several labels: White label with red edge and in VARGAS'S hand "*S. ardeni* paratipo (=*yepocapense*)" and locality information; Blue label "PARATIPO"; White label "CAIMSimTp-00138"]. Sn. Pedro Carcha; 16.xi.1944, (*Fairchild*)— 1male (only genitalia) [PARATYPE] (INDRE) [The slide bear several labels:

White label with red edge and in VARGAS'S hand "*S. ardeni* paratipo (=*yepocapense*)" and locality information; Blue label "PARATIPO"; White label "CAIMSimTp-00137"].

OTHER MATERIAL

GUATEMALA

Chimaltenango Department

PINNED

Yepocapa, R. Socoyá, Finca Niágara; 28.viii.1948, (*Dalmat*)— 1female1male (not associated with pupal exuviae) (MLP, female no. 344-10, male no. 419-6). Yepocapa, Finca Niágara, R. Queleyá; 10.xii.1948, (*H.T.Dalmat*)— 1female (NMNH, accession no. 910-3) [Identified by H.T. DALMAT]. Yepocapa, R. Socoyá, Finca Santa Rosa; 1.xi.1948, (*H.T.Dalmat*)— 1male (not associated with pupal exuviae) (NMNH, acc. no. 1026-4).

SLIDES

Yepocapa, R. Socoyá, Finca Niágara; 28.viii.1948, (*Dalmat*)— 1female1male (not associated with pupal exuviae) (MLP, female no. 344-13, male no. 369.5).

MÉXICO

Guerrero State

SLIDES

Ayutla; xii.1942, (*A.Díaz Nájera*)— 5pupal exuviae (INDRE).

SPIRIT

Ayutla; xii.1942, (*A.Díaz Nájera*)— numerous pupal exuviae (INDRE).

3. PHYLOGENETIC ANALYSIS OF THE SUBGENUS *TRICHODAGMIA* ENDERLEIN BASED ON MORPHOLOGY

3.1. Summary

In this chapter, the phylogeny and classification of the subgenus *Trichodagmia* are described on the basis of a morphological cladistic analysis of male, female, pupae and larvae from 63 taxa, including two species belonging to the subgenus *Aspathia* and two species of the subgenus *Simulium s.str.* as outgroups. Analyses of the full data set with 67 characters were carried out using WinClada version 1.00.08 and NONA version 2.0 (for Windows), with multistate characters treated as unordered under equal weights. The strict consensus tree (SCT) for this data set was poorly resolved because of numerous polytomies within the TARSATUM species group [= *Hemicnetha*] and the CANADENSE species group [= *Hearlea*]. Nonetheless, the ALBELLUM species group [= *Obuchovia*] and the PICTIPES species group [= *Shewellomyia*] and some clades within the CANADENSE species group were supported with bootstrap and jackknife support values of more than 80%. In the most parsimonious cladograms, the position of *S. falculatum* was problematic as it was placed basal to *Trichodagmia*. The position of *Simulium jeteri*, albeit within the clade ORBITALE species group [= the *Trichodagmia* + *Thyrsopelma sensu* MIRANDA-ESQUIVEL & COSCARÓN, 2001] was also poorly resolved. This was certainly due to the numerous missing data in these two taxa. Therefore, they were removed from the data set together with other taxa in which three life stages (> 70% of the characters) were missing (*e.g.* *S. paracarolinae* and *S. tarsale*). A second analysis was then performed in WinClada on these 63 taxa and 67 characters. The parameters and outgroups for this data set were the same as for the full data set. In this analysis, the SCT was better resolved and all clades within the expanded concept of *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010) were recovered as monophyletic with support values of more than 50%. The clade ALBELLUM species group is monophyletic in a sister-group relationship with the other species groups in *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010). The ORBITALE clade was recovered as monophyletic by a combination of seven unique characters with 89% bootstrap support. In this clade, all species close to *S. guianense s.l.* were diagnosed by a combination of four characters, one of which (male ventral plate with a globular median process) defined this group. The position of *S. hirtipupa* is well resolved in this clade by the presence of spines in the frontoclypeus and thorax of the pupa. The TARSATUM species group and the CANADENSE species group were diagnosed by four and five characters, respectively. Within CANADENSE, only species with larvae having sclerotized plates in the posterior region of the abdomen were well resolved. Species in the TARSATUM species group were homoplastic. The PICTIPES species group is only diagnosed by homoplasies, but the combination of these characters is unique to this clade (polythetic taxon). In this study, the subgenus *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010) is monophyletic being diagnosed by seven synapomorphies. This study also supports some of the classification of SHELLEY *et al* (2010) in which they treated the subgeneric-names *Hearlea*, *Hemicnetha*, *Shewellomyia*, *Trichodagmia* + *Thyrsopelma* (*sensu* MIRANDA-ESQUIVEL & COSCARÓN, 2001) as species groups within the subgenus *Trichodagmia*. Moreover, this study also supports the proposal of *Obuchovia* as a junior synonym within the clade *Trichodagmia* to represent the ALBELLUM species group.

3.2. Introduction

The taxonomy and classification of the subgenus *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010; this work) is currently unstable because of the different opinions among Simuliidae workers. Moreover, few studies have addressed the phylogenetic relationships of *Trichodagmia* in the New World using cladistic analysis.

COSCARÓN (1987) first proposed a phylogeny for the subgeneric group names *Hemicnetha*, *Hearlea* and *Trichodagmia* (as *Thyrsopelma* and *Grenieriella*) and their relationships with other subgenera in the

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Neotropical Region based on morphological characters [for the taxonomic history see **Chapter 2**]. Although COSCARÓN's (1987) phylogenetic tree was poorly resolved because of polytomies, he proposed the monophyly of the clade including *Simulium s.str.*, *Hearlea*, *Hemicnetha*, *Grenieriella* and *Thyrsopelma* because of the presence of two synapomorphies: pupal abdomen without spine combs in the terminal tergites and terminal spines reduced or absent, and posterior circlet of larvae with more than 150 rows of hooks. In the same paper, COSCARÓN also discussed the sister-group relationship of *Hemicnetha* with *Trichodagmia* + *Thyrsopelma*, and their species groups and species recognized at this time. He also placed the group OVIEDOI in the clade *Psilopelmia* + *Ectemnaspis* because they shared a male gonostyle as long as the gonocoxite, subcylindrical and weakly curved in shape.

In the following years, COSCARÓN & COSCARÓN-ARIAS (1996) studied the distribution of Neotropical Simuliidae and its areas of endemism inspired by the biogeographic realms methodology of CABRERA & WILLINK (1973) and MÜLLER (1973). The latter was revisited by JUÑENT & COSCARÓN (2001) using cladistic methods as discussed in CRISCI *et al.* (1991) and WILEY (1988). In these papers the authors deemed the subgenus *Hearlea* to be restricted to the Mesoamerican mountains (except one species extending into North America) and stated that it is an ancient taxon, which diversified in this region and was unable to cross the Isthmus of Panama. For *Hemicnetha* the authors proposed a sister-group relationship with *Hearlea* and stated that *Hemicnetha* also show the greatest diversification in Mesoamerica (with a few Nearctic elements), but also reached South America, where it extends to the northern region of the continent, Brazil and north-western Argentina.

MIRANDA-ESQUIVEL & COSCARÓN (2001) carried out a cladistic analysis of the subgenera *Trichodagmia* and *Thyrsopelma*, in which they also dealt with *Hemicnetha* and *Hearlea*. The authors tested the monophyly of *Trichodagmia* + *Thyrsopelma* based on 34 morphological characters (five of the larva; five of the pupa; 16 of the female and seven of the male); and 13 terminal taxa of *Trichodagmia* (*sensu* CROSSKEY & HOWARD, 1997). MIRANDA-ESQUIVEL & COSCARÓN (2001) also employed taxa of the African subgenera *Anasolen* ENDERLEIN, *Freemanellum* CROSSKEY, *Xenosimulium* CROSSKEY and the Neotropical subgenera *Hearlea* (*S. capricorne*, *S. carolinae*, *S. larvispinosum*), *Hemicnetha* (*S. mexicanum* and *S. paynei*), and the OVIEDOI species group (*S. oviedoi*) as ingroups. The OVIEDOI group was included in their study because of its putative sister-group relationship to *Hemicnetha* and *Hearlea* (COSCARÓN, 1987). The same authors used species of *Paraustrosimulium* WYGODZINSKY & COSCARÓN, *Nevermannia* ENDERLEIN, *Pomeroyellum* RUBTZOV, and *Pternaspatha* ENDERLEIN as outgroups.

The work of MIRANDA-ESQUIVEL & COSCARÓN (2001) indicated *Trichodagmia* and *Thyrsopelma* to be monophyletic, thus they considered both names as valid subgenera and allotted seven and six valid species to each subgenus, respectively. They also discussed the sister relationship of *Trichodagmia* + *Thyrsopelma*, which was supported by the following synapomorphies: female with wide genital arms, male parameres with spines or reduced spines, and male gonostyle spindle-shaped. The monophyly of *Thyrsopelma* rested on the following characters: larval integument covered by lanceolate hairs, female with simple claw, and equal length/width ratio of the gonapophyses. The same authors also questioned the sister-group relationship of *Hemicnetha* first proposed in COSCARÓN (1987), because COSCARÓNS' hypothesis failed when Afrotropical subgenera were included in their analysis. They commented further that species of *Trichodagmia*/*Thyrsopelma* inhabit fast flowing creeks and rivers, and the same occurs in the African subgenera *Xenosimulium*, *Analosen* and *Freemanellum*, which could be due to convergence. Nonetheless, they regarded this biology also as synapomorphic because of the "extreme phylogenetic congruence" of *Trichodagmia*/*Thyrsopelma* with other Neotropical taxa.

The subgeneric name *Hemicnetha* was treated in a wider phylogenetic context by TAKAOKA & ADLER (1997), who also described the new subgenus *Daviesellum* from Thailand and Peninsular Malaysia, and commented on its phylogenetic relationship with that of the Palaearctic subgenus *Obuchovia* and the New World *Hemicnetha*, *Hearlea*, and *Shewellomyia*. They proposed that the *Daviesellum* pre-imaginal life stages share morphological characters with *Hemicnetha*, *Hearlea*, and *Shewellomyia* , which they believed were "undoubtedly convergent". These features included a densely woven, boot-shaped cocoon with a high neck; short compact gills with fairly stout filaments; an elongate, gradually expanded larval abdomen; an enormous numbers of hooklets in the posterior circlet and on the proleg; labral fans with short stems and stout primary rays; and hypostomium with smoothly curved anterolateral margins and dense row of thick bristles. TAKAOKA & ADLER (1997) also proposed that nearly all the latter characters are associated with simuliids that aggregate in clusters or mats in torrential water bodies. Furthermore, they argued that chromosomal similarities between *Daviesellum* and *Hemicnetha,* such as an expanded centromere region in chromosome I and a splayed end in IIIS, were judged to be convergent or plesiotypic.

Two recent studies have further contributed to our present knowledge on the phylogeny of *Trichodagmia* and allied taxa. The first is the revision of the subgenus *Hearlea* by COSCARÓN *et al.* (2004). These authors reviewed the taxonomy of this subgenus, and proposed a phylogeny for all species based on 33 morphological characters of adults and immature stages. They included the subgenus *Hemicnetha* (*S. rubrithorax*), one species of the OVIEDOI group (*S. oviedoi*), and *Simulium* (*Thyrsopelma*) *orbitale* as outgroups. They proposed that *Hearlea* is a monophyletic clade diagnosed by six synapomorphies found in the female and male genitalia, and the shape of the pupal gill. In the consensus trees obtained under implied weights *Hemicnetha*, the OVIEDOI species group and *S. orbitale* appeared together as the sister-group to *Hearlea.*

The second phylogenetic study was presented in the book, *Blackflies of North America*, by ADLER *et al.* (2004). In that review, the authors placed *Hemicnetha* in a monophyletic clade together with the ARGENTEOSTRIATUM species group, and the subgenera *Crosskeyellum* GRENIER & BAILLY-CHOUMARA, *Himalayum* LEWIS, the newly recognized *Aspathia* ENDERLEIN (*sensu* COSCARÓN *et al.*, 1999), and *Simulium s.str.*, on the basis of the synapomorphy "gonostyle markedly elongate, much longer than the gonocoxite". However, the resultant cladogram was poorly resolved because of numerous polytomies. ADLER *et al.* (2004) discussed that, although the taxa they assigned to this clade shared a large number of character states, none of them alone seemed to constitute convincing evidence of monophyly (see Fig. 9.2, page 159). They also argued that due to the "striking similarity of all life stages [it] was difficult not to think that they are derived from a common ancestor". Within *Hemicnetha* the monophyly of the clade comprising the CANADENSE (= *Hearlea*) and PICTIPES (= *Shewellomyia*) species groups was diagnosed by the male ventral plate being apically notched. Some members of *Obuchovia* [represented in their analysis as the AURICOMA species group] appeared as the sister-group of the MEXICANUM and PAYNEI species groups on the basis of the character "lateral arms of the genital fork without a ventrally directed spine". The presence of a spine [= internal process - this work] was apomorphic for the MEXICANUM and PAYNEI species groups. Thus, ADLER *et al.* (2004) subsumed the subgenera *Hearlea*, *Obuchovia* and *Shewellomyia* under *Hemicnetha* because the overall morphological similarities, and also advocated for further studies hinting at the possibility that additional subgenera would fall as synonyms.

Nonetheless, alpha-taxonomic studies carried out by COSCARÓN & COSCARÓN (2007) maintained the subgeneric names *Hearlea*, *Thyrsopelma* and *Trichodagmia* as valid, while CROSSKEY & HOWARD (2004) revalidated *Obuchovia*, and disagreement with regard to the taxonomic position of this taxon still exists (ADLER & CROSSKEY, 2008, 2009, 2010). More recently, SHELLEY *et al.* (2010) considered the subgeneric names *Hearlea*, *Hemicnetha* and *Thyrsopelma* to be junior synonyms of the subgenus *Trichodagmia* because of the overlapping of key morphological diagnostic characters among species placed in the latter taxa. To assess these nomenclatural problems and the controversy among the many authors with regard to the classification and phylogenetic relationships in the taxon *Trichodagmia*, the objectives of this chapter are to attempt to determine whether *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010; this work) is monophyletic, whether it should be maintained in its present circumscription, and to resolve the relationships among the species groups and species currently placed in the subgenus *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010; this work).

3.3. Material and Methods

3.3.1. Taxa examined

The collection of specimens, dissection techniques and anatomical terminology were detailed in **CHAPTER 2.** The specimens used in the analysis are housed in the institutions given in section "**2.3.7. Acronyms Used for Depositaries of Simuliidae**" and locality information, life stage and number of specimens examined is given in section "**2.1. APPENDIX 3. MATERIAL EXAMINED**". In broader terms, a similar phylogenetic approach to that of KITCHING *et al.* (1998), FOREY *et al.* (1992), HARBACH & KITCHING (1998), and REINERT *et al.* (2004, 2006, 2008, 2009) was used in this study. These authors employed four life stages (male, female, pupa and larva) in their cladistical analysis, which was also followed here. The list of taxa is given in TABLE 1.

3.3.2. Outgroup taxa

The outgroup comparison methodology of NIXON & CARPENTER (1993), KITCHING *et al.* (1998) and KITCHING (2002) was employed. Members of the subgenera *Aspathia* and *Simulium s.str.* have been hypothesized to be basal to the clade ARGENTEOSTRIATUM species group + *Crosskeyellum* + *Hemicnetha* + *Himalayum* by ADLER *et al.* (2004). Therefore, species in these two subgenera were used as the most suitable taxa for outgroup comparisons. *Simulium metallicum* BELLARDI (complex) and *S. jobbinsi* VARGAS, MARTÍNEZ PALACIOS & DÍAZ NÁJERA were used from the subgenus *Aspathia* and the North American *S. appalachiense* (TUBEROSUM species group), and the Palaearctic *S. posticatum* MEIGEN (complex) (VENUSTUM species group) were selected from the subgenus *Simulium s.str.* following ADLER *et al.* (2004). However, I am aware of the morphological variation shown in key diagnostic characters in the other species of the subgenera *Aspathia* and *Simulium s.str.*, especially the female cibarium, morphology of the female and male genitalia, and cocoon and gill configuration patterns. Both subgenera are in need of taxonomic revision using an integrated approach employing molecular and cytogenetic characters linked to morphological variation.

Two species, *S. oviedoi* and *S. rivasi*, are currently recognized in the TARSATUM species group (ADLER & CROSSKEY, 2010; SHELLEY *et al.*, 2010). However, these two species were not included in the analysis because their overall external morphological similarities to species in *Trichodagmia* is considered to be convergent. Moreover, the alpha-taxonomic revision of *S. oviedoi* and *S. rivasi* [see sections **2.6** in **Chapter 2**] revealed that these two species fall closer to the morphological ground plan of species in the subgenus *Psilopelmia* than in *Trichodagmia*, especially because of the subtrapezoidal shape of the male gonostyle and the triangular shape of the male ventral plate [see **Taxonomic Discussion** under relevant species in **Chapter 2**].

The above has resulted in four outgroup species and 63 ingroup ones (84% of the presently known taxa), totalling 67 taxa (see TABLE 1).

3.3.3. Coding protocol

In general, character data were derived from examination of more than 10 specimens of each life stage per species, and the scored taxa included at least the type species of each subgenus and/or the species bearing the species group name. I tried to avoid scoring data as missing by abstracting characters states from published species descriptions. It is well documented in the cladistic literature that characters coded as question marks or hyphens can lead to additional multiple most parsimonious cladograms (MPCs), and weakly supported groups (HARBACH & KITCHING, 1998; NIXON & CARPENTER, 1996). However, this could not be avoided completely and hence certain data points had to be coded "?" or "–" in TABLE 2. The use of presence/absence or character transformation methodology has been detailed by KITCHING *et al.* (1998) and SERENO (2007) and their rationale has been followed in this work. No polymorphic characters were detected in this analysis. In addition, no assumptions were made regarding the value of characters as a source of phylogenetic information, thus they were treated as unordered and unweighted. All characters were qualitative, and they were coded in a conventional way combining binary and multistate characters. I attempted to include as many characters as possible by using my own observations and digital images throughout the taxonomic range of *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010 and **Chapter 2** of this work) and other Simuliidae taxa. When certain terminal taxa were not available at the BMNH Simuliidae collection, an extensive survey in the literature was carried out, especially examination of original descriptions and key taxonomic monographs. Only four species belonging to the ALBELLUM species group [= the subgenus *Obuchovia*] were included in the analysis.

In total, 67 species and 67 characters were used in the analysis, of which 15 were based on the female morphology, 22 on the male, 15 on the pupal exuviae (including the cocoon), and 15 on the larva. The data matrix is given in TABLE 2.

3.3.4. Character choice and description

The papers of COSCARÓN *et al.* (2004), MIRANDA-ESQUIVEL & COSCARÓN (2001), ADLER *et al.* (2004), and the latest revision of COSCARÓN & COSCARÓN-ARIAS (2007) and SHELLEY *et al.* (2010), were reviewed in the search for morphological characters used in previous cladistic studies or in the delineation of different subgenera and species group. However, new characters are also proposed here based upon observations in the taxonomic chapter in this work (**Chapter 2**) and the Simuliidae Digital Imaging Archive held at the BMNH.

FEMALE

1. Cibarium, central trough, anterior margin: (0) straight; (1) concave; (2) with 1+1 prominences. The anterior margin of the cibarium in species of the ORBITALE and TARSATUM species groups in *Trichodagmia* is prominently concave (Figs. 5-7, 247-260, 264-282). However, certain species in the CANADENSE species group might have 1+1 central prominences at the base of cornuae (Figs. 229-246; see also COSCARÓN *et al.*, 2004, Fig 2A). The latter character is also common in species of the BICOLORATUM and PERFLAVUM species groups of the subgenus *Psilopelmia* (see SHELLEY *et al.*, 2010, Figs. 223-233). In certain species of *Aspathia* and *Simulium s.str.*, the margin is not concave centrally.

2. Cibarium, armature: (0) absent; (1) present. This is character 11 of MIRANDA-ESQUIVEL (2001) and character 3 in COSCARÓN *et al.* (1999). The presence or absence of teeth in the cibarium is of great importance in the epidemiology of the river blindness (SHELLEY, 2002) and is of great taxonomic value at the species level (*e.g.* Figs. 7, 229-282).

3. Cibarium, armature (if present) development: (0) armed with small tubercles; (1) armed with fine teeth; (2) armed with acute, well developed teeth. This is character 12 of MIRANDA-ESQUIVEL (2001). Most species of *Trichodagmia* do not have teeth on the cibarium (as in Figs. 5, 6), but in certain species such as *S. nigrimanum* and *S. wygodzinskyorum* the teeth are very prominent (*e.g.* Figs. 7, 254). In species of the TARSATUM species group such as *S. brachycladum*, *S. cristalinum*, *S. earlei* and *S. pulverulentum* small teeth are present on the pharyngeal membrane attached to the anterior margin of the cibarium (Figs. 264-282) [see also SHELLEY *et al.*, 2002, Figs. 27, 29; SHELLEY *et al.*, 2010, Figs. 244, 245]. However, this character could be overlooked because the membrane can be easily damaged during dissection. The presence of tubercles in the central trough of the cibarium is common in species of the ORBITALE groups (Figs. 247-260), for example *S. guianense s.l.* and *S. duodenicornium* (see also SHELLEY *et al.*, 2010, Figs. 237, 238). This character is best observed at higher magnifications.

4. Gonapophyses, development: (0) poorly developed, less than or nearly equal to width of eighth sternite at mid length; (1) well developed, longer than width of eighth sternite at mid length. The function of the gonapophyses during copulation is poorly understood, but it is believed that their development is a response to the size of the male gonostyle (ADLER *et al.*, 2004). They can be well developed and longer than the width of the eighth sternite in species of the TARSATUM species group (*e.g.* Figs. 8, 37-39, 562, 569), or small, less than width of the eighth sternite at mid length in species in the CANADENSE species group (*e.g.* Figs. 30, 31, 526-543).

5. Gonapophyses, general shape: (0) subquadrangular; (1) subtriangular. Subquadrangular gonapophyses are commonly found in some species of the CANADENSE species group (*e.g.* Figs. 30, 31, 526-543), while in the ALBELLUM and TARSATUM species groups they can be subtriangular in shape (*e.g* Figs. 37-39, 122, 566, 568). MIRANDA-ESQUIVEL (2001) gave this character three states (character 25), while

COSCARÓN *et al.* (1999) gave two states (character 6). The different shape of the gonapophyses can be a good diagnostic character in species of the ORBITALE and TARSATUM species groups (see Figs. 33, 34, 37-39, 526-581 for morphological variation; also SHELLEY *et al.*, 2010, Figs. 577, 580, 581).

6. Gonapophyses, apical region, shape: (0) rounded; (1) fine and pointed. A rounded apical region of gonapophyses can be founded in several species in the ORBITALE and PICTIPES species groups (*e.g.* Figs. 33-35, 544-552, 559-561; SHELLEY *et al.*, 2010, Figs. 582, 583). A fine apical region of the gonapophyses is a common feature in species placed in the TARSATUM species group (*e.g.* Figs. 37, 39, 562, 567, 569) [see also SHELLEY *et al.*, 2002b, Figs. 112, 114; SHELLEY *et al.*, 2010, Figs. 580-581].

7. Gonapophyses, sclerotization: (0) absent; (1) present. Most species of *Trichodagmia* and the genus *Simulium* have some sclerotization in the internal margin of the gonapophyses (*e.g.* Figs. 30-32). However, in certain species groups (the ORBITALE species group) the gonapophyses can be totally membranous (*e.g.* Figs. 34, 35, 122, 546-552).

8. Paraproct morphology, development of ventral extension of paraproct in relation to cercus: (0) poorly developed, nearly the same length of cercus; (1) well developed, nearly twice as long as the cercus. The degree of development of the ventral extension of the paraproct (as in Figs. 8, 14-29) is a good diagnostic character at the species group and species levels in the subgenus *Trichodagmia* (SHELLEY *et al.*, 2010), and is commonly used by simuliid workers in subgeneric delineation. However, certain species such as *S. lobatoi* (Fig. 25; SHELLEY *et al.*, 2010, Fig. 582) have short paraprocts, which are prominently covered by long hairs (see also Figs. 584-641).

9. Paraproct morphology, direction of the ventral extension in relation to ventral margin of cercus: (0) directed backwards along ventral margin of cercus; (1) pointing forward and away from ventral margin of cercus. The paraproct in species of *Aspathia* and *Simulium s.str.* curves slightly backwards along the ventral margin of cercus (COSCARÓN *et al.*, 1999, Fig 3A-V; SHELLEY *et al.*, 2010, Fig. 590). This character is also found in certain species such as *S. canadense* (Figs. 15, 586). However, it is commonly directed forward and away from the ventral extension of the cercus as in Figs. 21-29, 621-641.

10. Paraproct ventral extension, shape: (0) subrectangular; (1) subtriangular; (2) subquadrangular; (3) suboval. This is character 20 of MIRANDA-ESQUIVEL (2001). The shape of the paraproct is variable within species of *Simulium*, and it is of great taxonomic importance at the species group and species level (as in Figs. 14-29). In this study, subrectangular is defined by an elongated paraproct that does not form a strict square shape (*e.g. S. virgatum s.l.*, Figs. 29, 640). The subtriangular shape is characteristic of species in the ORBITALE species group with pointed apical region (*e.g.* Figs. 19, 20, 604, 605, 610). The suboval paraproct is not circular overall, as in *S. brachycladum* (Figs. 26, 621) or *S. paynei* (Figs. 24, 631).

11. Paraproct ventral extension, sclerotization: (0) fully sclerotized; (1) partially membranous. In species of the CANADENSE, TARSATUM and PICTIPES species groups, the paraproct can be sclerotized (*e.g.* Figs. 14-17, 22, 23, 28, 29). However, other species in the latter groups and in the ORBITALE group the paraproct can be membranous (as in Figs. 21, 24, 26) [see also Figs. 123, 127, 130, 134, 584-643 for detail of morphological variation].

12. Junction of paraproct ventral extension with cercus, membranous processes: (0) absent; (1) present. This character is common in species of the ORBITALE species group, where it is very important for species identification (Figs. 18-21, 603-617), and it is also present in certain species of the CANADENSE species group (Figs. 15, 584-602). However, the membrane can be damaged during specimen preparation and its presence or absence could have been overlooked in many species.

13. Paraproct ventral extension, membranous lobe(s) in apical or subapical region: (0) absent; (1) present. A character commonly found in species of the CANADENSE species group (Figs. 14, 15, 584-602), where one to three lobes can be seen (as in DALMAT, 1955).

14. Paraproct ventral extension, setation: (0) covered only by sparse long hairs and/or fine setae apically; (1) covered densely by hairs and microtrichiae, and sometimes with spiniform setae apically. This is character 20 in MIRANDA-ESQUIVEL (2001). Great variation is found in this feature across all the taxonomic range within *Trichodagmia*, where it can be highly setose (Figs. 24, 26) or have spiniform setae apically (Fig. 28). Very long hairs are found in *S. lobatoi*, which is unusual for taxa in the TARSATUM species group (Fig. 25, 630) [see also Figs. 584-641].

15. Genital fork morphology, internal process of lateral arms: (0) absent; (1) present. This is character 216, "ventrally directed internal spine", of ADLER *et al.* (2004), which these authors considered a synapomorphy for their MEXICANUM and PAYNEI species groups within *Hemicnetha*. Its absence, which is typical of the ALBELLUM species group, was considered plesiomorphic by ADLER *et al.* (2004) (Figs. 124, 128, 131, 135). It is commonly present in the ORBITALE, PICTIPES and TARSATUM species groups (*e.g.* Figs. 644-701; see also SHELLEY *et al.*, 2010, Figs. 739-751) and is a good character to separate closely related species, such as *S. tarsatum, S. tarsale* and *S. smarti.*

MALE

16. Gonostyle general morphology, width: (0) wide at base and narrow apically; (1) nearly same width throughout its length. The general morphology of the male gonostyle is of great importance in Simuliidae taxonomy. It is commonly employed to define species groups (as in SHELLEY *et al.*, 2010; see also Figs. 43-46, 128, 151, 154, 154, 162, 829-888).

17. Gonostyle, general morphology, shape: (0) relatively elongate; (1) spindle-shaped. The elongation of the gonostyle has been postulated by ADLER *et al.* (2010) as a synapomorphy for the subgenera *Aspathia*, *Simulium s.str.*, and taxa in *Hemicnetha* and *Freemanellum*. The spindle-shaped structure of the male gonostyle is typical in species of the ORBITALE species group (*e.g.* Figs. 44, 847-862), while an elongate gonostyle is found in species of the ALBELLUM species group (*e.g.* Figs. 148, 151).

18. Gonostyle, lateral margins: (0) weakly straight or sinuous; (1) prominently curved or sinuous. Flattened and prominently sinuous lateral margins are diagnostic for species in the TARSATUM species group (Figs. 46, 866-888), while weakly sinuous or straighter lateral margins are found in the CANADENSE and PICTIPES species group (Figs. 43, 45, 829-846, 863-865).

19. Gonostyle, internal surface: (0) with a flap-like process or carina; (1) without a flap-like carina. The presence of a flap-like carina is common in species belonging to the ALBELLUM, CANADENSE, PICTIPES species groups (Figs. 43, 45, 148, 151, 829-846, 863-865). It is also commonly found in species of the TUBEROSUM species group (ADLER *et al.*, 2004, Fig. 398), but is absent from species in the ORBITALE and TARSATUM species group (see Figs. 847-862, 866-888).

20. Gonostyle internal surface, teeth in carina (if carina is present): (0) absent; (1) present. The presence of teeth in the carina is common on species of the TUBEROSUM species group (ADLER *et al.*, 2004) and in the subgenus *Aspathia* (COSCARÓN *et al.*, 1999). Teeth are also found in certain species of the CANADENSE species group (as in Figs. 43, 829-846).

21 Gonostyle, spines on carina of gonostyle (if carina is present): (0) located only at the base of gonostyle; (1) extended to mid length of gonostyle or beyond. This is commonly found in species of the of the TUBEROSUM species group (ADLER *et al.*, 2004) and in the subgenus *Aspathia* (COSCARÓN *et al.*, 1999). It is also present in species of the CANADENSE and ALBELLUM species group (*e.g.* Figs. 43, 148, 151, 157).

22. Gonostyle apical region: (0) narrow; (1) rounded. In species of the CANADENSE, ORBITALE and PICTIPES group the apical region of the gonostyle is very narrow (Figs. 43-45, 829-865), whereas in the ALBELLUM and TARSATUM species groups it is often rounded (*e.g.* Figs. 46, 148, 151, 157, 866-888).

23. Gonostyle apical region, stout spine(s): (0) absent; (1) present. Stout spine(s) can be seen in species of the ORBITALE and TARSATUM species group (*e.g.* Figs. 44, 45, 869, 876), while they are reduced in the PICTIPES species group. In *S. nigrimanum*, specimens with two, three, or more than five apical spines have been found (SHELLEY *et al.*, 2000, Fig. 107).

24. Ventral plate, main body development: (0) poorly developed; (1) well developed. The main body of the ventral plate shows a wide range of variation within species of *Trichodagmia* (Figs. 47-60, 891-949) and in many species groups and/or subgenera of Simuliidae in general [see also examples in the illustrations of ADLER *et al.* (2004), COSCARÓN & COSCARÓN-ARIAS (2007), and SHELLEY *et al.*, (2010)]. Its development can be diagnostic in certain taxa within *Simulium s.str.* In most species of *Trichodagmia* the main body of the ventral plate is expanded centrally, where it might be covered by hairs (Figs. 47-60, 150, 153, 156, 159, 164). In contrast, in many species of the subgenera *Aspathia* and *Simulium s. str.*, the main body of the ventral plate is compressed at mid point forming a triangular or subrectangular shape (*e.g. S. metallicum s.l.*, SHELLEY *et al.*, 2002b).

25. Ventral plate, general shape: (0) subtriangular; (1) subquadrangular; (2) subrectangular; (3) suboval. The ventral plate general morphology is variable in species now placed in *Trichodagmia* (see ADLER *et al.* (2004, Figs. 399 d, e; SHELLEY *et al.*, 2002b, Figs. 228, 229). In the ALBELLUM species group it is always suboval in the species I have examined (Figs. 47-60, 150, 153, 156, 159, 164).

26. Ventral plate, anterior margin emargination: (0) absent; (1) present. In certain species of the CANADENSE and PICTIPES species groups, the anterior margin of the ventral plate can be prominently concave or notched (*e.g.* Figs. 47, 55, 893, 904, 924-926). The anterior margin can also be emarginate in some species of ORBITALE species group*,* for example *S. orbitale* and *S. perplexum* (*e.g.* Figs. 51, 54, 918, 919).

27. Ventral plate, median region process: (0) present; (1) absent. The presence of a process in the median region of the ventral plate is a common character in *Trichodagmia*, as well is many other taxa in Simuliidae [see Figs. 48, 51, 52, 59, 60 for examples of morphological variation].

28. Ventral plate, median region process (if present): (0) small; (1) prominent. The length of the process in species within *Trichodagmia* is variable. It is also of great taxonomic importance at the species level (*e.g.* Figs. 48, 51, 52, 927-930, 942-945).

29. Ventral plate, median process (if small), shape: (0) subtriangular; (1) rounded. The presence of a median process in the ventral plate is a common character shared by many species of the subgenus *Trichodagmia*, especially taxa in the CANADENSE (as in Fig. 48) and ORBITALE (as in Fig. 53) species groups [see also Figs. 47, 49-52, 891-949 for further detail of morphological variation].

30. Ventral plate, median process (if prominent) shape: (0) pointed; (1) globular; (2) snout-like. The globular shape of the median process is common in species of the ORBITALE species group (*e.g.* Figs. 51-52), while in the TARSATUM species group it can be snout-like in shape (*e.g.* Figs. 58-60) and is diagnostic at the species level. Great variation in this character is exhibited between species and species groups of *Trichodagmia* (Figs. 891-949).

31. Ventral plate, lateral shoulders: (0) poorly developed; (1) well to prominently developed. The development of lateral shoulders in the ventral plate is highly variable in species of *Trichodagmia* (*sensu*

SHELLEY *et al.*, 2010). They are prominent in species such as *S. hirtipupa* and *S. solarii* (Figs. 58, 911, 945), but poorly developed in other taxa, for example *S. tarsatum* (Figs. 56, 947), and species of the ALBELLUM group (*e.g.* Figs. 150, 153, 156).

32. Ventral plate, central carina: (0) absent; (1) present. This character is also highly variable within *Trichodagmia*, and it is commonly present within species of the CANADENSE (Figs. 47-50, 891-908) and TARSATUM (Figs. 56, 60, 927-949) species groups.

33. Ventral plate, posterior margin: (0) concave centrally; (1) nearly straight; (2) convex centrally. Variation in this character occurs throughout *Trichodagmia* (see Figs. 47-60, 150, 153, 156, 891-949). It is a diagnostic character for species in the ORBITALE species group (as in Figs. 53, 909-923) such as *S. wygodzinskyorum* and *S. huairayacu.*

34. Ventral plate, basal arms shape: (0) subparallel; (1) distinctly emarginate at mid length at which point they diverge posterolaterally. Although this character might be variable in species of *Trichodagmia* (Figs. 47-54, 891-949), it is diagnostic for species in the ALBELLUM species group (*e.g.* Figs. 150, 153, 156, 159.

35. Paramere, basal plates development: (0) well developed; (1) poorly developed. Parameres with well developed basal plates are common in species of the ALBELLUM, CANADENSE, PICTIPES and TARSATUM species groups (*e.g.* Figs. 61, 63-64, 149, 152, 155, 952-969, 984-1009), but they are poorly developed in taxa assigned to the ORBITALE species group (Figs. 62, 970-983).

36. Parameres, spines on central region of gonostyle: (0) well developed; (1) poorly developed. This is the character 32 of MIRANDA-ESQUIVEL & COSCARÓN (2001). Well developed spines in the central region of the paramere are common in species of the ALBELLUM, CANADENSE, PICTIPES and TARSATUM species groups (Figs. 61, 63-64), but they are poorly developed in taxa assigned to the ORBITALE species group (Fig. 62) [see also Figs. 952-1009 for morphological variation].

37. Median sclerite, width: (0) wide centrally; (1) thin centrally. The shape of the median sclerite is also a highly variable character in species of *Trichodagmia* (as in Figs. 891-949; see also SHELLEY *et al.*, 2010, Figs. 1049-1064). It is diagnostic for the ALBELLUM species group where most species have a very long and thin median sclerite (*e.g.* Figs. 149, 155), though in certain species of the TARSATUM species group it can also be very long as in *S. brachycladum* (Fig. 927), *S. hinmani* (Fig. 935) and *S. hieroglyphicum* (Fig. 934).

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38. Cocoon, general shape: (0) flattened dorsally; (1) not flattened dorsally. This character is diagnostic for certain species in the subgenus *Aspathia*, for example *S. metallicum s.l.* (PEPINELLI *et al.*, 2006, Fig. 29). This is character 28 in COSCARÓN *et al.* (2004).

39. Cocoon, lateral expansions: (0) present; (1) absent. This character is diagnostic for *S. metallicum s.l.* (PEPINELLI *et al.*, 2006, Fig. 29), but in the majority of species of *Trichodagmia*, the cocoon does not have lateral expansions (Figs. 65-69).

40. Cocoon, general shape: (0) slipper-shaped; (1) shoe-shaped; (2) boot-shaped. The general shape of the cocoon is commonly used in species descriptions within a sweet of characters in species identification (Figs. 65-69). In the work, a slipper-shaped cocoon is described as having the anteroventral not enclosed by silk so that the substrate forms the ventral margin of the cocoon opening (SMITH, 2002) (Fig. 65). In the shoe- and boot shaped cocoons, the anteroventral margin is enclosed by silk and raised (Figs. 66-69). A boot-shaped cocoon is further defined as having the anterior margin even more prominently elevated than in a shoe-shaped cocoon (Fig. 67). However, variation in this

character has been recorded in populations of the same species, especially in other subgenera of the genus *Simulium* (*e.g.* subgenus *Psaroniocompsa*, L.M. HERNÁNDEZ, unpublished data), although this variation has been poorly documented in the Neotropical Region.

41. Cocoon, anterior fenestrations: (0) absent; (1) present. EYMANN (1991) hypothesized that the presence of fenestrations is an adaptation for living in fast-flowing rivers, and its shape is a good diagnostic character (SMITH, 2002). These openings are purposely woven into the cocoon by the pharate pupa (STUART & HUNTER, 1998a,b) and their pattern is generally consistent for a particular species (SMITH, 2002). EYMANN (1991) also stated that anterior fenestrations in the cocoon aperture altered the water flow around the gill filaments, thus improving the oxygen intake. Anterior fenestrations in the cocoon in the subgenus *Trichodagmia* are only found in species of the TARSATUM species group (Figs. 69).

42. Frontoclypeus, tubercles on the integument: (0) with at least a few tubercles; (1) without tubercles. This is the character 25 of COSCARÓN *et al.* (2004). The most common state for the frontoclypeus in species of *Trichodagmia* is to have tubercles (Fig. 70), which can be pointed and/or rounded.

43. Frontoclypeus, black spiniform setae in the integument: (0) absent; (1) present. The presence of the black spiniform setae is found in species currently placed in the ORBITALE species group, *S. hirtipupa* (Fig. 71). However, other taxa can have irregular markings (Figs. 72), which are useful in species identification.

44. Frontoclypeus, irregular markings in the integument: (0) absent; (1) present. This character is only present in certain species of the TARSATUM species group (Fig. 72) and ALBELLUM species group (BMNH Simuliidae Digital Imaging Archive).

45. Thorax, tubercles on the integument: (0) present; (1) absent. The most common state for the pupal thorax in species of *Trichodagmia* is to have tubercles (Fig. 70), which can be pointed and/or rounded. However, their distribution and density can vary even between specimens of the same species, which has caused some taxonomic confusion in widely distributed species, for example *S. tarsatum* (recognized as *S. mexicanum* and *S. seriatum* by COSCARÓN & COSCARÓN-ARIAS, 2000). SHELLEY *et al.* (2006) analized the variation of this character in the AMAZONICUM species group of the subgenus *Psaroniocompsa* ENDERLEIN, and concluded that it cannot be used for species identification.

46. Thorax, black spiniform setae on the integument: (0) absent; (1) present. Black spiniform setae are only found in species of the ORBITALE species group, *S. hirtipupa.*

47. Thorax, irregular markings of the integument: (0) absent; (1) present. This character is only present in species of the TARSATUM species group (Figs. 74) and ALBELLUM species group (BMNH Simuliidae Digital Imagying Archive).

48. Pupal gill filaments, general morphology: (0) filaments very fine, sometimes twice as long as cocoon dorsal length; (1) filaments stouter, only about as long as cocoon dorsal length [see Figs. 65-68, 1011-1073 for morphological variation in this character].

49. Pupal gill filaments, girth: (0) all filaments of same girth; (1) with at least two filaments prominently expanded and of different girth. Pupal gill filaments that are prominently developed and expanded are found in species of the CANADENSE species group (*e.g.* Figs. 75-78, 1011-1015, 1017) and in *S. hieroglyphicum* of the TARSATUM species group (Figs. 84, 1058). In the majority of the *Trichodagmia* species, the girth is the same in all gill filaments (Figs. 79, 80-81, 83, 1011-1073).

50. Pupal gill filaments, apical region sclerotization: (0) without a sclerotized apex; (1) with at least two filaments with sclerotized apex. This is character 8 in MIRANDA-ESQUIVEL & COSCARÓN (2001). Most

species of *Trichodagmia* do not have gill filaments with sclerotized apices (*e.g.* Figs. 81-84, 165, 168, 174), but this is common within the species of the ORBITALE (Figs. 79, 80, 1030, 1031, 1042) and the CANADENSE species groups (Figs. 77, 78, 1016, 1023).

51. Pupal gill filaments, spicules on surface: (0) present; (1) absent. Most of the species of *Trichodagmia* have the surface of the gill filaments covered by spicules (SHELLEY *et al.*, 2010, Figs. 75, 76, 127-129; see also species descriptions in **Chapter 2** in this work), and they can be of relatively good taxonomic value to separate closely related species, such as *S. guianense s.l.* and *S. perplexum.* However, they are absent in many species taxa in the subgenus *Trichodagmia.*

52. Pupal gill filaments, pseudo-annulations: (0) absent; (1) with at least some filaments covered by pseudo-annulations. The presence of pseudo-annulations is most common in species of the CANADENSE species group (*e.g.* Figs. 75, 76, 1012, 1013). They are also found in *Paraustrosimulium anthracinum* BIGOT, a feature deemed by some authors to be convergent (WYGODZINSKY & COSCARÓN, 1962, 1973).

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53. Abdominal integument setation, hairs: (0) absent; (1) present. The larval abdominal integument in species of *Trichodagmia* is not covered by hairs, those few setae that can be seen are on the distal region on the anal sclerite.

54. Abdominal integument setation, ovoid setae: (0) absent; (1) present. This is the character 5 of MIRANDA-ESQUIVEL & COSCARÓN (2001). Ovoid setae [= lanceolate setae of other authors] are commonly found in species of the ORBITALE species group (Figs. 88, 89) [see also SHELLEY *et al.*, 2002].

55. Abdominal posterior region, sclerotized accessory plates: (0) absent; (1) present. Accessory plates occur in certain species of the CANADENSE species group (*e.g.* Figs. 87, 1081, 1084, 1283, 1289). COSCARÓN *et al.* (2004) suggested that their presence might be associated with the fixation of larva to the substrate in torrenticolous streams.

56. Abdominal posterior region, 1 + 1 papillae on segment VIII: (0) present; (1) absent. In certain species of the CAROLINAE species group 1+1 papillae occur (Figs. 87, 1287). The sclerotization of the papillae on segment VIII was also proposed by COSCARÓN *et al.* (2004) as being associated with fast flowing streams. However, in most of the species of *Trichodagmia*, ventral papillae are absent from the distal region of the abdomen (*e.g.* Figs. 88-90, 1085-1119).

57. Postgenal cleft, general shape: (0) dome-shaped; (1) triangular and pointed. The shape of the larval postgenal cleft is one of the best characters to identify species in the larval stage. It is prominently triangular in the majority of the species in *Trichodagmia* (as in Fig. 92), though sometimes it can be dome-shaped (Fig. 94) [see Figs. 1122-1173 for morphological variation in this character].

58. Postgenal cleft, apical tubular incision (0) absent; (1) present. An apical incision at the apex of the postgenal cleft is common in species of the CANADENSE species group (see Figs. 1122-1135) (COSCARÓN *et al.*, 2004), and in certain species of the TARSATUM species group (see Figs. 1154-1171).

59. Hypostomium, anterior margin shape: (0) convex; (1) nearly straight. This is character 30 of COSCARÓN *et al.*, 2010). The shape of the anterior margin was used by DÍAZ NÁJERA & VULCANO (1962b) in their pictorial key to separate species in the CANADENSE species group. It is a variable character that might not be useful for species identification (Figs. 93, 94, 1174-1226).

60. Hypostomial teeth, distribution: (0) teeth extending beyond margin of hypostomium; (1) teeth below anterior margin of hypostomium. The most common condition of the hypostomial teeth in species of *Trichodagmia* is to extend anteriorly beyond the anterior margin of the hypostomium (Figs. 93, 95). Nonetheless, in species within the ORBITALE species group, the teeth are arranged below the anterior margin of the hypostomium (Fig. 94) [see also Figs. 1174-1226 for morphological variation in this character].

61. Hypostomial teeth, arrangement on anterior margin: (0) evenly arranged along anterior margin; (1) centrally arranged and distinctly protruded forward. The most common pattern of the hypostomial teeth in species of *Trichodagmia* is to be evenly distributed along the anterior margin of the hypostomium (*e.g.* Figs. 93, 94, 1207, 1208). Nonetheless, in species within the TARSATUM species group the teeth might be concentrated in the central region of the hypostomium, from where they can prominently protrude forward (Figs. 95, 1215, 1218, 1219).

62. Hypostomium, median tooth development: (0) developed; (1) reduced. This is a good species diagnostic character. In most species of *Simulium* the median is well developed (*e.g.* Figs. 93, 95, 166, 169, 1206-1208, 1210, 1211, 1213). However, it can also be reduced in many species, as in taxa the ORBITALE group (Figs. 94, 1191-1196, 1198, 1199). Variation in this larval character has been poorly studied within Simuliidae species in the Neotropical Region.

63. Hypostomial sublateral setae, number: (0) four to six; (1) eight to eleven; (2) more than 13. Variation in this character is found in many taxa within the Simuliidae and might be of taxonomic value to separate closely related taxa (Figs. 93-95, 166, 169, 172, 1174-1226).

64. Hypostomium, postgenal bridge length in relation to hypostomium: (0) twice as long; (1) one and half times as long or less [see Figs. 93, 94, 166, 177, 1122-1171 for variation in this character].

65. Mandibles, development of mandibular comb teeth: (0) poorly developed; (1) prominently developed. Variation in the number of mandibular teeth has been poorly studied in Neotropical Simuliidae. It is a character of great taxonomic value at the species level where it is useful to separate closely related taxa (see Figs. 96, 97 for terminology and morphological variation). They can be very prominent in species of the TARSATUM species group (*S. virgatum s.l.*), but relatively smaller in the CANADENSE and ORBITALE species groups (see Figs. 1229-1282).

66. Rectal gill, number of small lobules per branch: (0) up to four; (1) more than 10. This is character 4 of MIRANDA-ESQUIVEL & COSCARÓN (2001). In most species of *Trichodagmia* there are three branches with numerous finger-like lobules (Fig. 98).

67. Anal sclerite, posterior arm: (0) reaching one third of the length of posterior circlet; (1) encircling posterior circlet. This character is only found in certain species within the CANADENSE species group (*e.g.* Figs. 87, 1286, 1289). It is a diagnostic character for taxa such as the genus *Gigantodax* ENDERLEIN and it is present in the Old World *Simulium* (*Gomphostilbia*) ENDERLEIN, *S.* (*Inseliellum*) RUBTZOV, *Austrosimulium* TONNOIR and *Crozetia* DAVIES. Its presence has been suggested to be a derived condition for taxa occurring in torrenticolous environments (COSCARÓN *et al.*, 2004; CRAIG & CURRIE, 1999).

3.3.5. Phylogenetic analysis

There is ongoing discussion among theoretical phylogeneticists with regard to the equal or differential weighting of characters in phylogenetic analysis (*e.g.* GOLOBOFF, 1993). An equal weighting regime implies that every character provides equally strong evidence of relationship and it is the only philosophically justifiable position within certain frameworks (KITCHING, 2002). However, some practising systematists would consider this unjustified (FARRIS, 1983; KITCHING, 2002). I do not consider that all characters deserve equal weight (and provide strong evidence of relationships) within *Trichodagmia*, but applying differential weighting (*e.g.* by using implied weights and varying the value of the concavity constant, *K*) to different data sets is time-consuming and computational demanding, and time constraints did not allow me to test these weighting strategies.

Therefore, to derive my phylogenetic hypotheses, an equal weighting regime was applied to the data set (KITCHING, 2002) using the program WinClada version 1.00.08 and NONA version 2.0 (for Windows) (NIXON, 1999). First, the full data set of 67 taxa and 67 characters was analyzed. This included those species with three unknown or poorly known life stages (>70% missing data). A second analysis was also carried out after removal of taxa with >70% of missing data. Therefore, *S. falculatum*, *S. jeteri*, *S. paracarolinae*, and *S. tarsale* were not included in this second analysis.

For both data sets, the standard tree search parameters as described by REINERT *et al.* (2009) within the heuristic search of WinClada were followed: Maximum trees to keep (hold) – 100,000; Number of replications (mult*n): 10,000; Starting trees per rep (hold/n) – 5 Search strategy – Multiple TBR (mult*), and the Search selected was "Unconstrained Search". Analyses stopped once the program found the most parsimonious cladograms (MPCs). A strict consensus tree (SCT) was used to find those groups common to all cladograms. The utility of this and other consensus methods in cladistics was reviewed in KITCHING *et al.* (1998). These authors stated that consensus methods should be considered an indirect method for resolving character conflict or incongruence in data sets. They reduce the number of fundamental cladograms to one tree showing their common components. Consequently, consensus analysis almost invariably produces trees that would not be supported as most parsimonious by the original data, and for the latter reason, some authors have argued against them [KITCHING *et al.* (1998) citing MIYAMOTO (1985) and CARPENTER (1988)]. Nevertheless, KITCHING *et al.* (1998) advocated that consensus trees are efficient for investigating data concordance amongst cladograms generated from different data sets and also for investigating "difficult" taxa that occur in different positions in the tree. Other authors have argued that because cladistic analyses often produce multiple MPCs, consensus trees should be considered as essential. This is because they provide the only reasonable summary of the information in a single tree. Clade support was assessed using parsimony jackknife procedures (detailed in FARRIS *et al.*, 1996) and bootstrap (KITCHING *et al.*, 1998) as implemented in WinClada (No of replication - 20,00; No of search resp (mult*N) - 10; Starting tree per hold – 1; Max tree - 100). Other methods to estimate clade support, such as Bremer support and relative Bremer support (BREMER, 1994; GOLOBOFF & FARRIS, 2001), were not applied due to the high computational demand and length of time that would be required to obtain these values. In both data set analyses, all multistate characters were treated as unordered (non-additive) and the cladograms were rooted on *Aspathia* and *Simulium s.str.*

KITCHING (2002) detailed an analysis of a data set from immature stages together with one derived from adults in accordance with the procedure of cladistic analysis of authors known as "total evidence". He (KITCHING, 2002) preferred this approach, in which all data, regardless of their source, are combined into a single analysis, because it maximizes congruence between all characters and thus provides the greatest possible explanatory power. However, he also warned about the problems that can arise when there is a high proportion of missing data in one or more subsets, and in terminal taxa. It is widely documented in the cladistic literature that high level of missing data caused by incomplete taxa may increase the number of most parsimonious cladograms recovered (NOVACEK, 1992), generate spurious cladograms through increased ambiguity (PLATNICK *et al.*, 1991), and can lead to lack of resolution (NIXON & CARPENTER, 1992). Cladistic analyses of separate and combined data sets between adults and immature stages have frequently been carried out in other Diptera, *e.g.* Culicidae (REINERT *et al.* 2004). With regard to Simuliidae, the same approach was carried out by MIRANDA-ESQUIVEL & COSCARÓN (2001), but these authors found that the adult and immature stage data gave more ambiguous results in their phylogeny than analysing all life stages in a single data matrix. The latter rationale has been followed in the current study.

In their study of the classification and phylogeny of the genus *Finlaya* (Culicidae, Aedini) REINERT *et al.* (2006) warned against the over-interpretation of the character mappings on strict consensus trees. These authors emphasized that SCT character mappings on branches immediately below and arising from polytomies, are not necessarily as parsimonious as they are on the MPCs from which the SCT was derived. In particular, they cautioned that parallel gains on branches arising from polytomies may be synapomorphies for groups of these clades on some (but not all) MPCs. The latter point was taken into account during the discussion of the results of the present study.

Illustrated cladograms were initially prepared in WinClada, exported as Windows metafile pictures (*.emf), then imported into PowerPoint 2003. Arrows and lines were produced using the Autoshapes function of PowerPoint and the bootstrap and jackknife values were mapped on the tree as text boxes. The final edited trees were saved as Windows enhanced metafiles and then imported directly into Microsoft Word 2003.

3.4. Results and Discussion

The analysis of the entire data set (67 taxa) using equal weights produced 10,000 MPCs. The strict consensus tree (SCT), shown in Fig. 1, collapsed 34 nodes (L=434, CI=0.17, RI=0.58). Groups with bootstrap and jackknife support values >50% are also indicated. The overall conclusion to be drawn from the SCT is that the data are very homoplastic, with certain clades quite poorly resolved, for example TARSATUM species group (old subgenus *Hemicnetha*) and CANADENSE species group (old subgenus *Hearlea*). Nonetheless, the subgenus *Trichodagmia* was recovered as monophyletic with bootstrap and jackknife values of 83% and 82%, respectively. The clade *Trichodagmia* is diagnosed by nine synapomorphies, including: male ventral plate well developed (character:state - 24:1); pupal gill filaments at least with two filaments prominently expanded and of different girth (48:1); abdominal posterior region of the larva without 1 + 1 papillae on segment VIII (56:1); and rectal gill with more than 10 small lobules per branch (66:1). In addition, certain other nodes were also recovered as monophyletic with >50% support values (Fig. 1): ALBELLUM species group (old subgenus *Obuchovia*), PICTIPES species group (old subgenus *Shewellomyia*) and ORBITALE species group (old subgenera *Thyrsopelma* + *Trichodagmia*, *sensu* MIRANDA-ESQUIVEL & COSCARÓN, 2001), together with some terminal groups within CANADENSE and TARSATUM species group. The clade ORBITALE was diagnosed by 14 synapomorphies, in particular a spindle-shaped male gonostyle spindle (17:1) and a poorly developed basal plate of the male paramere (35:1) and central spines of the male paramere (36:1).

The position of *S. falculatum* is problematic because it is placed in a basal trichotomy with all other species of *Trichodagmia* and is diagnosed by only a single, homoplastic character (6:1) [gonapophyses, apical region, shape: fine and pointed]. Other species with similar poor resolution were *S. jeteri* (58:0), *S. paracarolinae* (55:1; 61:1) and *S. tarsale* (1:0; 10:2; 16:0). These species all have more than 79% missing data, which was probably causing groups to collapse in the SCT.

The second analyses, where taxa with numerous missing data were not included, used a data set with 63 species and 67 characters. The analysis produced 13,107 MPCs and the SCT (L=325, CI=0.23, RI=0.76) collapsed only 21 nodes (Fig. 2). This SCT is better resolved, has less homoplasy as seen from the higher CI and RI values, and is the preferred topology in the current study. The subgenus *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010; this study) was recovered as monophyletic based on eight synapomorphies. Only seven characters from the previous analysis of the full data (Fig. 1) were also recovered in the second analysis, the exceptions being characters 32:1 and 40:1. However, a new synapomorphy was identified: female gonapophyses subtriangular (5:1). All species within the taxon names ALBELLUM, CANADENSE, ORBITALE, PICTIPES and TARSATUM (Figs. 2, 3) formed monophyletic groups, though species relationships within each of the clades was not fully resolved . The ALBELLUM species group, appears as the sister group of the rest of *Trichodagmia*, and it is defined by seven apomorphies of which two are uniquely placed: male gonostyle with a carina extending to mid length of gonostyle or beyond (21:1); and male ventral plate with basal arms distinctly emarginated at mid length at which point they diverge posterolaterally (34:1). The clade ORBITALE species group also appeared well supported, by seven apomorphies of which three are uniquely placed: male gonostyle spindle-shaped (17:1); basal plate of male paramere poorly developed (35:1); and central spines of the male paramere poorly developed (36:1). A subset of species in this clade and morphologically similar to *S. guianense s.l.* were diagnosed by four synapomorphies, of which one was uniquely placed: male ventral plate with a globular median process (30:1). The position of *S. hirtipupa* is well explained by the presence of black spiniform setae in the pupal frontoclypeus and thorax (characters 43:1; 46:1). High bootstrap and jackknife values support these findings (Fig. 2).

In contrast, the CANADENSE and TARSATUM species groups were only diagnosed by five and three apomorphies, respectively (Fig. 2). In CANADENSE, the character state 52:1 [pupal gill filaments with at least some filaments covered by pseudo-annulations] is uniquely placed in this group. A clade comprising all species with sclerotization on the posterior region of the larval abdomen (55:1) within *Hearlea* is recovered with 80% bootstrap and 87% jackknife support values. This clade agrees with the results of the study of COSCARÓN *et al.* (2004) and for which they created the CAROLINAE and JUAREZI species groups [these two species groups are not longer recognized – see ADLER & CROSSKEY, 2010]. COSCARÓN *et al.* (2004) recovered the JUAREZI species group by five apomorphies, with all the species arranged in a soft politomy, but this was not recovered in my analysis, and future studies are needed to address this problem, especially to describe the female, male and pupa of *S. paracarolinae*, the male, pupa and larva of *S. falculatum*, and the male of *S. temascalense*.

The TARSATUM species group is less well-supported, with only one uniquely placed character supporting this clade: male ventral plate commonly with a snout-like median process (30:2). A subclade comprising all species in the TARSATUM species group, except *S. lobatoi*, is supported by five characters, of which one is uniquely placed: apical region of the female gonapophyses fine and pointed (6:1). The species relationships in this clade are only diagnosed by homoplastic characters and the position of *S. lobatoi* is most problematic, and questionable (HERNÁNDEZ *et al.*, 2009; LUNA DIAS *et al.*, 2004). The female has short paraprocts and gonapophyses, and both structures are prominently covered by long, black hairs. This does not agree with the general variation found in species belonging in the TARSATUM species group. Nonetheless, the general morphology of the gonostyle and ventral plate, pupal gill configuration, and larval general morphology is within the range of variation found in species of this group.

The relationships of the PICTIPES species group, albeit monophyletic, were even less well supported because all the diagnostic characters are homoplastic. However, this could be an example of a polythetic taxon (REINERT *et al.*, 2009) in which the group is not diagnosed by unique characters, but rather a unique combination of characters. This clade is also well supported by high bootstrap and jackknife values (Fig. 2).

3.5. APPENDIX 1. FIGURES.

Fig. 1. Strict consensus tree for the full data set of 67 taxa, comprising 63 species of the subgenus *Trichodagmia* [which also includes four species of ALBELLUM species group], and the subgenera *Aspathia* (2 species) and *Simulium s.str.* (2 species) as outgroups. For comparisons of subgeneric names and current species groups see TABLE 1 [see also **Chapter 2,** section **2.9**, TABLE 1]. Bootstrap values are shown under/or near each node, while jackknife values are shown in square brackets. Unambiguously optimized characters are only shown. Uniquely placed characters are indicated by closed circles, homoplasies by open circles. *Bootstrap and jackknife values for the group *S. hinmani* and *S. yepocapense* that is recovered in the bootstrap and jackknife trees, but not clearly shown in the strict consensus tree.

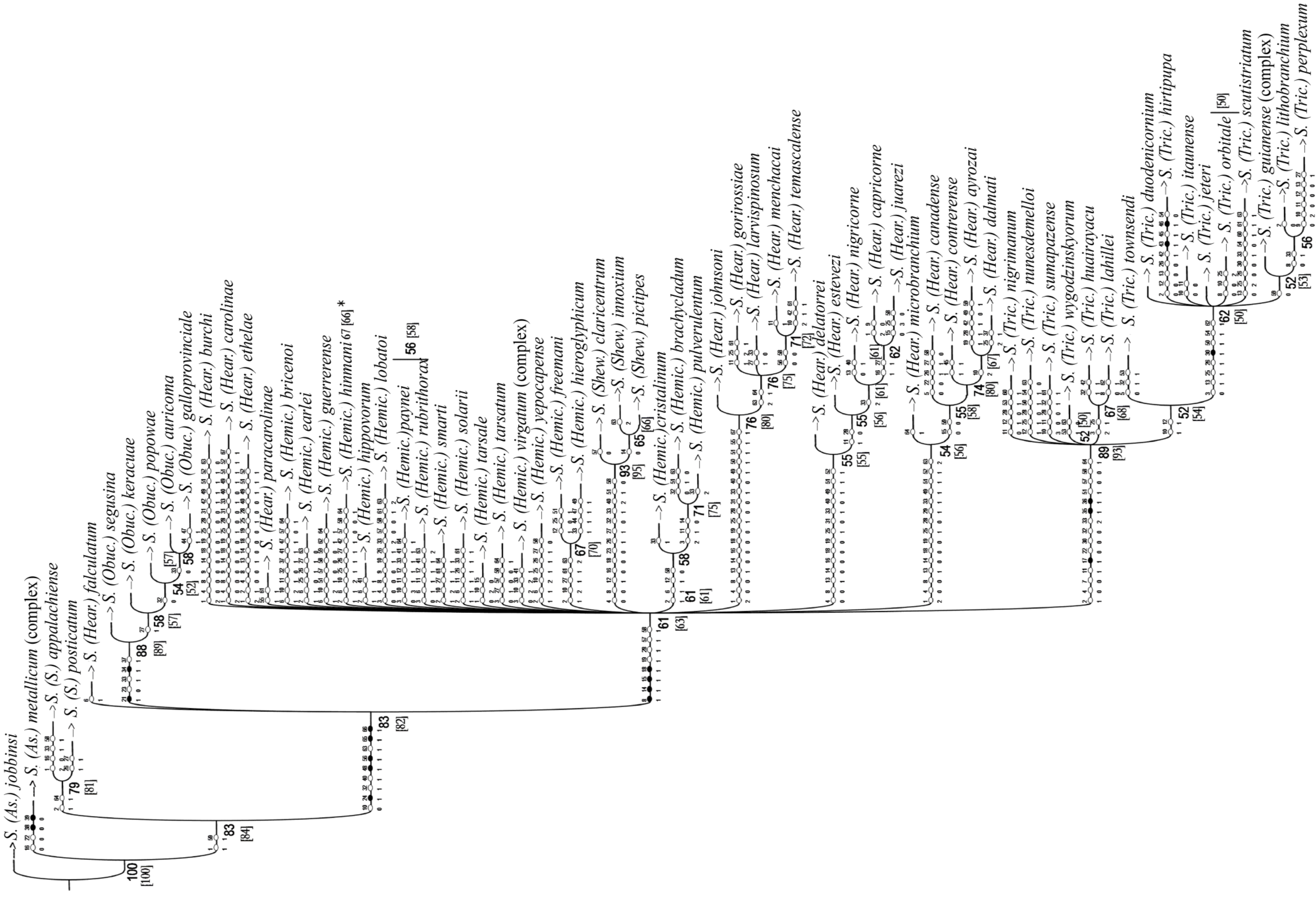


Fig. 2. Strict consensus tree for the reduced data set of 63 taxa containing 59 species of the subgenus *Trichodagmia* [which also include four species of *Obuchovia*], and the subgenera *Aspathia* (2 species) and *Simulium s.str.* (2 species) as outgroups. For comparisons of subgeneric names and current species groups see TABLE 1 [see also **Chapter 2,** section **2.9**, TABLE 1]. Bootstrap values are shown under or near each node, while jackknife values are shown in square brackets. Unambiguously optimized characters are only shown. Uniquely placed characters are indicated by closed circles, homoplasies by open circles. *Bootstrap and jackknife values for the group *S. hinmani* and *S. yepocapense* that is recovered in the bootstrap and jackknife trees, but not clearly shown in the strict consensus tree; ** as before for group *S. smarti*, *S. freemani*, *S. hieroglyphicum*.

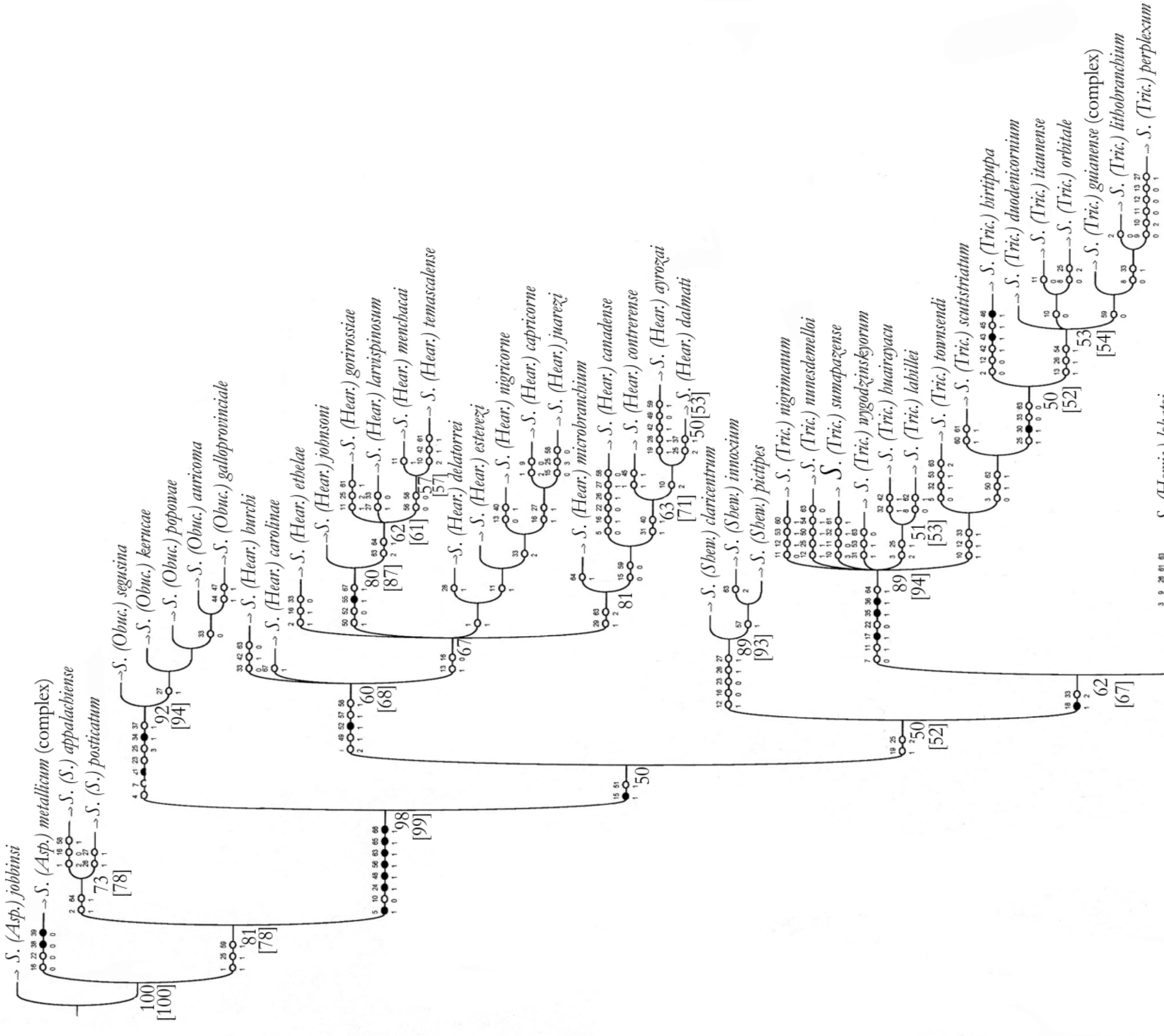
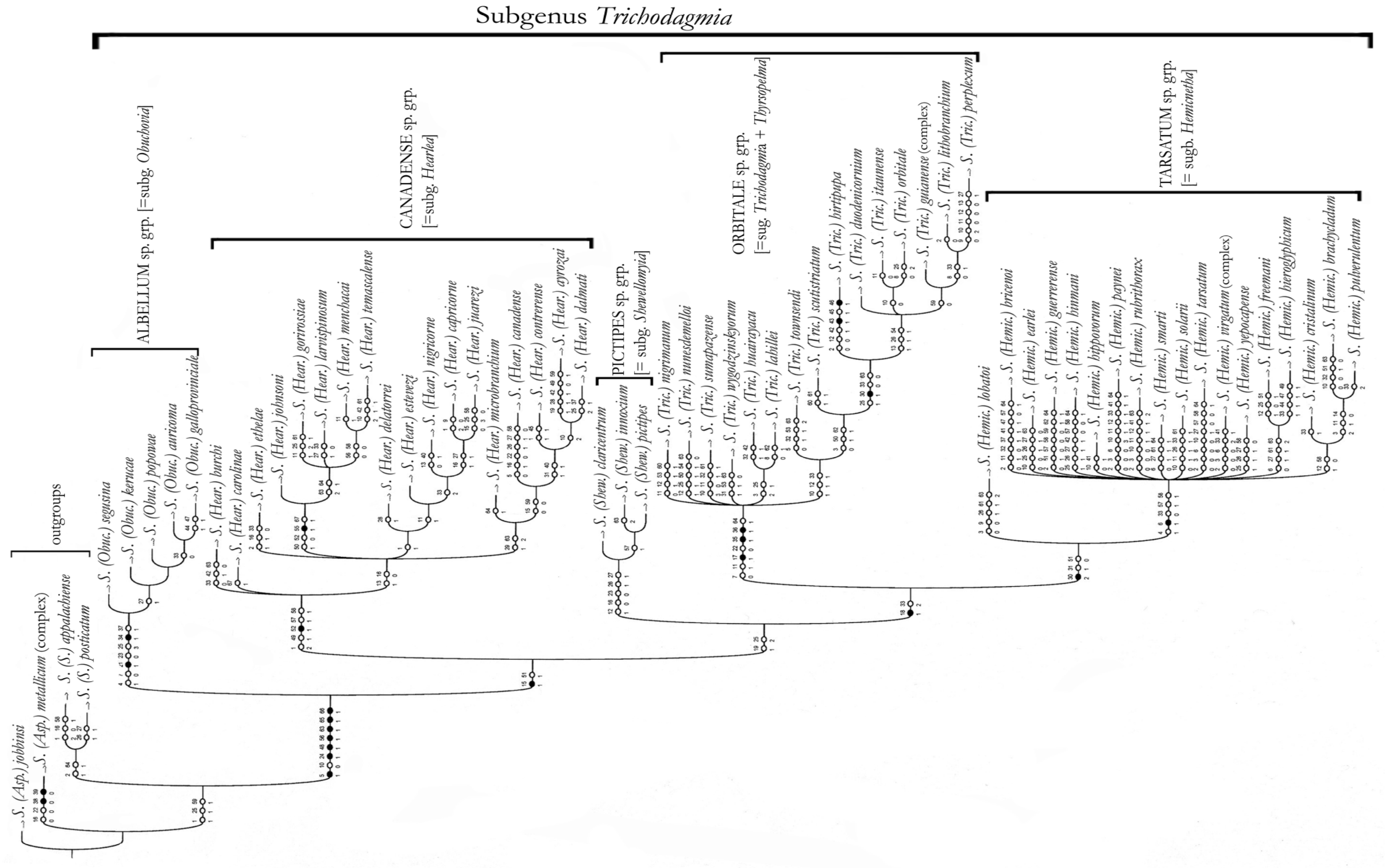


Fig. 3. Strict consensus tree showing the proposed classification of the subgenus *Trichodagmia* [see also **Chapter 2**, section **2.9**, TABLE 1].



3.6. APPENDIX 2. TABLES.

TABLE 1. List of taxa examined in detail for the phylogenetic analysis of species in the subgenus *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010 and this work). An asterisk (*) indicates a type species of a subgeneric-level taxon; two asterisks (**) a species bearing the name for the species group; and three asterisks (***) species names used in naming species groups but that are not longer recognized following ADLER *et al.* (2010) and SHELLEY *et al.* (2010). CA, Central America; SA, South America; NA, North America.

Genus	Subgenus [a]	Species groups	Species	Distribution
Outgroups				
Simulium	*Aspathia*		*S. metallicum* (complex)***	Neotropical
	Aspathia		*S. jobbinsi*	Neotropical
	Simulium s.str.	TUBEROSUM sp. grp.	*S. appalachiense*	Nearctic
	Simulium s.str.	VENUSTUM sp. grp.	*S. posticatum*	Palaearctic
Ingroups				
	(*Obuchovia*)	ALBELLUM sp. grp.	*S. auricoma*	Palaearctic
			S. galloprovinciale	Palaearctic
			S. keracuae	Palaearctic
			S. popowae	Palaearctic
			S. segusina	Palaearctic
	(*Hearlea*)	CANADENSE sp. grp.		
			S. ayrozai	Neotropical: CA
			S. burchi	Neotropical: CA
			*S. canadense**, **	Nearctic: NA; Neotropical: CA
			S. capricorne	Neotropical: CA
			S. carolinae	Neotropical: CA
			S. contrerense	Neotropical: CA
			S. dalmati	Neotropical: CA
			S. delatorrei	Neotropical: CA
			S. estevezi	Neotropical: CA
			S. ethelae	Neotropical: CA
			S. falculatum	Neotropical: CA
			S. gorirossiae	Neotropical: CA
			S. johnsoni	Neotropical: CA
			S. juarezi	Neotropical: CA
			S. larvispinosum	Neotropical: CA
			S. menchacai	Neotropical: CA
			S. microbranchium	Neotropical: CA
			S. nigricorne	Neotropical: CA
			S. paracarolinae	Neotropical: CA
			S. temascalense	Neotropical: CA
	(*Trichodagmia*, *Thyrsopelma*)	ORBITALE sp. grp.	*S. duodenicornium*	Neotropical: SA
			S. guianense	Neotropical: SA
			S. hirtipupa	Neotropical: SA

TABLE 1. Continued.

Genus	Subgenus	Species groups	Species	Distribution
			S. huairayacu	Neotropical: SA
			S. itaunense	Neotropical: SA
			S. jeteri	Neotropical: SA
			S. lahillei	Neotropical: SA
			S. lithobranchium	Neotropical: SA
			S. nigrimanum	Neotropical: SA
			S. nunesdemelloi	Neotropical: SA
			S. orbitale	Neotropical: SA
			S. perplexum	Neotropical: SA
			S. scutistriatum	Neotropical: SA
			S. sumapazense	Neotropical: SA
			S. townsendi	Neotropical: SA
			S. wygodzinskyorum	Neotropical: SA
	(*Shewellomyia*)	PICTIPES sp. grp.	*S. claricentrum*	Nearctic: NA
			S. innoxium	Nearctic: NA
			*S. pictipes**	Nearctic: NA
	(*Hemicnetha*)	TARSATUM sp. grp.	*S. brachycladum*	Neotropical: SA
			S. bricenoi	Neotropical: NA, SA
			S. cristalinum	Neotropical: SA
			S. earlei	Neotropical: SA
			S. freemani	Neotropical: NA, SA
			S. guerrerense	Neotropical: SA
			S. hieroglyphicum	Neotropical: SA
			S. hinmani	Neotropical: SA
			S. lobatoi	Neotropical: SA
			*S. paynei**	Neotropical: NA, CA, SA
			S. pulverulentum	Neotropical: SA
			S. rubrithorax	Neotropical: SA
			S. smarti	Neotropical: SA
			S. solarii	Nearctic: NA
			S. tarsale	Neotropical: SA
			*S. tarsatum***	Neotropical: SA, CA
			S. virgatum s.l.	Nearctic: NA
			S. yepocapense	Neotropical: CA

[a] Old subgeneric names (in parentheses) are those employed by previous authors for the placement of species that are currently recognized as species groups in the subgenus *Trichodagmia* in this work [see also ADLER & CROSSKEY (2010), COSCARÓN & COSCARÓN-ARIAS (2007) and SHELLEY *et al.* (2010)].

TABLE 2. Data matrix for 67 taxa and 67 characters used in the phylogenetic analysis of the subgenus *Trichodagmia*. See text for explanation of codes and subgenera.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
S. (Aspa.) jobbinsi	0	0	—	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1
S. (Aspa.) metallicum s.l.	0	0	—	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
S. (S. s.str.) appalachiense	2	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
S. (S. s.str.) posticatum	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1
S. (Obuc.) auricoma	1	0	—	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1
S. (Obuc.) galloprovinciale	1	0	—	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1
S. (Obuc.) keracuae	1	0	—	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1
S. (Obuc.) popowae	?	0	—	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1
S. (Obuc) segusina	1	0	—	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1
S. (Hear.) ayrozai	2	0	—	0	1	0	1	0	1	2	0	0	1	0	0	0	0	0	1	1	0	1
S. (Hear.) burchi	2	0	—	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
S. (Hear.) canadense	2	0	—	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0
S. (Hear.) capricorne	2	0	—	0	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	1	0	1
S. (Hear.) carolinae	2	0	—	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
S. (Hear.) contrerense	1	0	—	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1
S. (Hear.) dalmati	2	0	—	0	1	0	1	0	1	2	0	0	1	0	0	0	0	0	0	1	0	1
S. (Hear.) delatorrei	1	0	—	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1
S. (Hear.) estevezi	1	0	—	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	1	0	1
S. (Hear.) ethelae	2	1	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1
S. (Hear.) falculatum	1	0	—	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?
S. (Hear.) gorirossiae	2	0	—	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	1	0	1
S. (Hear.) johnsoni	2	0	—	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1
S. (Hear.) juarezi	1	0	—	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1
S. (Hear.) larvispinosum	2	0	—	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1
S. (Hear.) menchacai	2	0	—	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	1	0	1
S. (Hear.) microbranchium	2	0	—	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1
S. (Hear.) nigricorne	1	0	—	?	?	?	?	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1
S. (Hear.) paracarolinae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. (Hear.) temascalense	2	0	?	0	1	0	1	0	1	2	0	0	1	0	1	?	?	?	?	?	?	?
S. (Tric.) duodenicornium	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	—	—	0
S. (Tric.) guianense s.l.	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	—	—	0
S. (Tric.) hirtipupa	1	0	—	0	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	—	—	0
S. (Tric) huairayacu	1	1	2	0	1	0	0	1	1	0	1	0	0	1	1	1	1	1	1	—	—	0
S. (Tric.) itaunense	1	1	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	—	—	0

TABLE 2. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
S. (Tric.) jeteri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	—	—	0
S. (Tric.) lahillei	1	1	2	0	1	0	0	0	1	0	1	0	0	1	1	1	1	1	1	—	—	0
S. (Tric.) lithobranchium	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	—	—	0
S. (Tric.) nigrimanum	1	1	1	0	1	0	0	1	1	0	0	1	0	1	1	1	1	1	1	—	—	0
S. (Tric.) nunesdemelloi	1	1	1	0	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	—	—	0
S. (Tric.) orbitale	1	1	0	0	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	—	—	0
S. (Tric.) perplexum	1	1	0	0	1	0	0	0	0	2	0	0	0	1	1	1	1	1	1	—	—	0
S. (Tric.) scutistriatum	1	1	0	0	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	—	—	0
S. (Tric.) sumapazense	1	1	1	0	1	0	0	1	1	3	0	0	0	1	1	1	1	1	1	—	—	0
S. (Tric.) townsendi	1	1	1	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	—	—	0
S. (Tric.) wygodzinskyorum	1	1	1	0	1	0	0	1	1	0	1	0	0	1	1	1	1	1	1	—	—	0
S. (Shew.) claricentum	1	0	—	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	1	—	—	1
S. (Shew.) innoxium	1	0	—	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	1	—	—	1
S. (Shew.) pictipes	1	0	—	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	1	—	—	1
S. (Hemic.) brachycladum	1	1	2	1	1	1	1	1	1	0	1	1	0	0	1	1	0	1	1	—	—	1
S. (Hemic.) bricenoi	1	0	1	1	1	1	1	1	1	2	1	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) cristalinum	1	1	1	1	1	1	1	1	1	2	0	1	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) earlei	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) freemani	1	1	1	1	1	0	1	1	1	2	0	1	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) guerrerense	1	0	—	1	1	1	1	1	1	2	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) hieroglyphicum	1	1	1	1	1	0	1	1	1	2	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) hinmani	1	1	1	1	1	1	1	1	1	2	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) hippovorum	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) lobatoi	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) paynei	1	0	0	1	1	0	1	1	1	3	1	1	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) pulverulentum	1	1	2	1	1	1	1	1	1	2	1	1	0	0	1	1	0	1	1	—	—	1
S. (Hemic.) rubrithorax	1	0	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) smarti	1	1	1	1	1	0	1	1	1	2	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) solarii	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) tarsale	0	0	?	1	1	0	1	1	1	2	0	0	0	1	0	1	0	1	1	—	—	1
S. (Hemic.) tarsatum	1	0	0	1	1	0	1	1	1	0	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) virgatum s.l.	1	0	0	1	1	0	1	1	1	2	0	0	0	1	1	1	0	1	1	—	—	1
S. (Hemic.) yepocapense	1	1	1	1	1	1	1	1	1	2	0	0	0	1	1	1	0	1	1	—	—	1

TABLE 2. Continued.

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
S. (Aspa.) jobbinsi	0	0	0	0	0	0	0	—	0	0	0	0	0	0	1	1	1	0	0	0	0	0
S. (Aspa.) metallicum s.l.	1	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. (S. s.str.) appalachiense	1	0	1	0	0	0	1	—	0	0	1	0	0	0	0	1	1	0	0	0	0	0
S. (S. s.str.) posticatum	1	0	1	1	1	—	—	—	0	0	0	0	0	0	0	1	1	0	0	0	0	0
S. (Obuc.) auricoma	0	1	3	0	1	—	—	—	?	0	0	1	0	0	1	1	1	1	0	0	0	0
S. (Obuc.) galloprovinciale	0	1	3	0	1	—	—	—	?	0	0	1	0	0	1	1	1	2	0	0	0	1
S. (Obuc.) keracuae	0	1	3	0	1	—	—	—	?	1	1	1	0	0	1	1	1	2	0	0	0	0
S. (Obuc.) popowae	0	1	3	0	1	—	—	—	?	0	1	1	0	0	1	1	1	?	0	0	0	0
S. (Obuc) segusina	0	1	3	0	0	0	0	—	?	1	1	1	0	0	1	1	1	1	0	0	0	0
S. (Hear.) ayrozai	1	1	1	0	0	1	—	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0
S. (Hear.) burchi	1	1	1	0	0	0	0	—	0	1	0	0	0	0	0	1	1	1	0	1	0	0
S. (Hear.) canadense	1	1	1	1	1	—	—	—	0	1	1	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) capricorne	1	1	1	0	1	—	—	—	?	1	2	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) carolinae	1	1	1	0	0	0	0	—	0	1	1	0	0	0	0	1	1	0	0	?	0	0
S. (Hear.) contrerense	1	1	1	0	0	0	1	—	1	1	1	0	0	0	0	1	1	1	0	0	0	0
S. (Hear.) dalmati	1	1	2	0	0	0	1	—	1	1	1	0	0	0	1	1	1	1	0	0	0	0
S. (Hear.) delatorrei	1	1	1	0	0	1	0	—	0	1	1	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) estevezi	1	1	1	0	0	0	0	—	0	1	1	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) ethelae	1	1	1	0	0	0	?	—	—	1	0	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) falculatum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. (Hear.) gorirossiae	1	1	2	0	0	0	0	—	0	1	1	0	0	0	?	1	1	0	0	0	0	0
S. (Hear.) johnsoni	1	1	1	0	0	0	0	—	0	1	1	0	0	0	?	1	1	0	0	0	0	0
S. (Hear) juarezi	1	1	3	0	1	—	—	—	0	1	2	0	0	0	?	1	1	0	0	0	0	0
S. (Hear.) larvispinosum	1	1	1	0	1	0	—	—	?	1	0	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) menchacai	1	1	1	0	0	0	0	—	?	1	1	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) microbranchium	1	1	1	0	0	0	1	—	0	1	1	0	0	0	0	1	1	0	0	0	0	0
S. (Hear.) nigricorne	1	1	1	0	0	0	0	—	0	1	2	0	0	0	?	1	1	1	0	0	0	0
S. (Hear.) paracarolinae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?
S. (Hear.) temascalense	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	1	0	0
S. (Tric.) duodenicornium	1	1	1	1	0	1	—	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) guianense s.l.	1	1	1	1	0	1	—	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) hirtipupa	1	1	1	0	0	1	—	1	1	0	0	0	1	1	0	1	1	1	0	1	1	0
S. (Tric) huairayacu	1	1	1	0	0	1	—	0	?	1	2	0	1	1	0	1	1	1	0	1	0	0
S. (Tric.) itaunense	1	1	1	1	0	1	—	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0

TABLE 2. Continued.

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
S. (Tric.) jeteri	1	1	?	?	?	?	—	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0
S. (Tric.) lahillei	1	1	1	0	0	1	—	0	0	0	2	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) lithobranchium	1	1	1	1	0	1	—	1	1	0	1	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) nigrimanum	1	1	2	0	0	0	—	—	0	0	2	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) nunesdemelloi	1	1	1	0	0	0	—	—	0	0	2	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) orbitale	1	1	2	1	0	1	—	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) perplexum	1	1	1	1	1	—	—	—	1	0	1	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) scutistriatum	1	1	2	0	0	1	0	0	1	0	1	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) sumapazense	1	1	2	0	0	0	—	—	—	1	2	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) townsendi	1	1	2	0	0	1	—	0	—	1	1	0	1	1	0	1	1	1	0	0	0	0
S. (Tric.) wygodzinskyorum	1	1	2	0	0	1	—	0	1	0	2	0	1	1	0	1	1	1	0	0	0	0
S. (Shew.) claricentum	0	1	2	1	1	—	—	—	—	0	1	0	0	0	0	1	1	2	0	0	0	0
S. (Shew.) innoxium	0	1	2	1	1	—	—	—	—	0	1	0	0	0	0	1	1	2	0	0	0	0
S. (Shew.) pictipes	0	1	2	1	1	—	—	—	—	0	1	0	0	0	0	1	1	2	0	0	0	0
S. (Hemic.) brachycladum	1	1	2	0	0	1	—	2	1	0	0	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) bricenoi	1	1	2	0	0	1	—	2	1	0	0	0	0	0	1	1	1	1	1	0	0	0
S. (Hemic.) cristalinum	1	1	2	0	0	1	—	2	1	1	1	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) earlei	1	1	0	1	1	—	—	—	—	1	0	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) freemani	1	1	0	0	1	—	—	—	—	1	0	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) guerrerense	1	1	2	0	0	—	—	—	1	1	0	0	0	0	?	1	1	1	0	0	0	0
S. (Hemic.) hieroglyphicum	1	1	2	0	1	—	—	—	—	1	1	0	0	0	0	1	1	1	0	0	0	1
S. (Hemic.) hinmani	1	1	1	1	1	—	—	—	—	1	0	0	0	0	0	1	1	1	0	1	0	0
S. (Hemic.) hippovorum	1	1	2	0	0	1	—	2	1	1	0	0	0	0	0	1	1	1	1	0	0	0
S. (Hemic.) lobatoi	1	1	2	1	0	1	—	2	1	1	2	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) paynei	1	1	2	0	0	1	—	2	1	1	1	0	0	0	0	1	1	1	1	0	0	0
S. (Hemic.) pulverulentum	1	1	2	0	0	1	—	—	1	1	2	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) rubrithorax	1	1	2	0	0	1	—	2	1	1	0	0	0	0	0	1	1	1	1	0	0	0
S. (Hemic.) smarti	1	1	2	0	1	—	—	—	—	1	0	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) solarii	1	1	2	1	0	1	—	2	1	1	1	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) tarsale	1	1	2	0	0	1	—	2	1	1	0	0	0	0	0	1	1	1	0	?	?	?
S. (Hemic.) tarsatum	1	1	2	0	1	—	—	?	—	1	0	0	0	0	0	1	1	1	0	0	0	0
S. (Hemic.) virgatum s.l.	1	1	2	0	0	1	—	2	1	1	2	0	0	0	0	1	1	1	1	0	0	0
S. (Hemic.) yepocapense	1	1	1	1	1	—	—	—	—	1	0	0	0	0	0	1	1	1	0	0	0	0

TABLE 2. Continued.

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
S. (Aspa.) jobbinsi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
S. (Aspa.) metallicum s.l.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. (S. s.str.) appalachiense	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
S. (S. s.str.) posticatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
S. (Obuc.) auricoma	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0
S. (Obuc.) galloprovinciale	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0
S. (Obuc.) keracuae	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0
S. (Obuc.) popowae	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0
S. (Obuc.) segusina	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0
S. (Hear.) ayrozai	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	2	0	1	1	0
S. (Hear.) burchi	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0
S. (Hear.) canadense	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	2	0	1	1	0
S. (Hear.) capricorne	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0
S. (Hear.) carolinae	?	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	1
S. (Hear.) contrerense	1	0	0	1	1	0	1	1	0	0	0	1	1	?	0	0	0	0	2	?	1	1	0
S. (Hear.) dalmati	0	0	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	2	0	1	1	0
S. (Hear.) delatorrei	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0
S. (Hear.) estevezi	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0
S. (Hear.) ethelae	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0
S. (Hear.) falculatum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. (Hear.) gorirossiae	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	1	0	2	1	1	1	1
S. (Hear.) johnsoni	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	1	0	1	1	1
S. (Hear.) juarezi	0	0	0	1	1	0	1	1	0	0	0	1	1	0	1	0	0	0	1	?	1	1	0
S. (Hear.) larvispinosum	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	2	1	1	1	1
S. (Hear.) menchacai	0	0	0	1	1	1	1	0	0	0	1	0	1	0	?	0	0	0	2	?	1	1	1
S. (Hear.) microbranchium	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	2	1	1	1	0
S. (Hear.) nigricorne	0	0	0	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. (Hear.) paracarolinae	?	?	?	?	?	?	?	?	?	0	1	1	1	1	1	0	1	0	1	0	1	1	0
S. (Hear.) temascalense	0	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0	1	0	2	1	1	1	1
S. (Tric.) duodenicornium	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	1	1	1	0
S. (Tric.) guianense s.l.	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	1	0	1	1	1	0
S. (Tric.) hirtipupa	1	1	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	1	1	1	0
S. (Tric) huairayacu	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0
S. (Tric.) itaunense	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	1	1	1	0

TABLE 2. Continued.

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
S. (Tric.) jeteri	0	0	0	1	0	1	1	0	?	?	0	1	0	0	1	0	0	1	0	1	?	1	0
S. (Tric.) lahillei	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1	1	1	1	0
S. (Tric.) lithobranchium	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0
S. (Tric.) nigrimanum	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1	1	0
S. (Tric.) nunesdemelloi	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	0	0	1	1	1	0
S. (Tric.) orbitale	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	1	1	1	0
S. (Tric.) perplexum	0	0	0	1	0	1	1	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
S. (Tric.) scutistriatum	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	0
S. (Tric.) sumapazense	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	1	1	0
S. (Tric.) townsendi	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	2	1	1	1	0
S. (Tric.) wygodzinskyorum	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0
S. (Shew.) claricentum	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0
S. (Shew.) innoxium	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	2	0	1	1	0
S. (Shew.) pictipes	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	1	1	0
S. (Hemic.) brachycladum	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0
S. (Hemic.) bricenoi	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	0
S. (Hemic.) cristalinum	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	0
S. (Hemic.) earlei	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0
S. (Hemic.) freemani	0	0	0	1	0	0	1	0	0	0	0	1	1	1	1	0	1	0	2	0	1	1	0
S. (Hemic.) guerrerense	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0
S. (Hemic.) hieroglyphicum	0	0	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	2	0	1	1	0
S. (Hemic.) hinmani	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0
S. (Hemic.) hippovorum	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0
S. (Hemic.) lobatoi	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	2	0	1	1	0
S. (Hemic.) paynei	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0
S. (Hemic.) pulverulentum	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	0
S. (Hemic.) rubrithorax	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	2	0	1	1	0
S. (Hemic.) smarti	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	0
S. (Hemic.) solarii	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	1	1	0
S. (Hemic.) tarsale	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
S. (Hemic.) tarsatum	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1	0
S. (Hemic.) virgatum s.l.	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1	1	0
S. (Hemic.) yepocapense	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1	1	0

4. THE UTILITY OF DNA BARCODING FOR SPECIES IDENTIFICATION WITHIN THE SUBGENUS *TRICHODAGMIA* ENDERLEIN AND RELATED TAXA

4.1. Summary

In this chapter, the utility of *COI* as a DNA barcoding region for the identification of species in the subgenus *Trichodagmia* and related taxa is investigated. In total, 24 morphospecies within the current expanded taxonomic concept of *Trichodagmia* were analyzed. In addition, three species of the subgenus *Aspathia* and 10 species of the subgenus *Simulium s.str.* were also included in the analysis because of their putative phylogenetic relationship with *Trichodagmia*. In the Neighbour Joining analysis tree (NJ) derived from the DNA barcodes most of the specimens grouped together according to species or species groups as recognized by the morphotaxonomic study (see **Chapter 2** and **Chapter 3**). The interspecific genetic divergence averaged 11.2% (range 2.8-19.5%), whereas intraspecific genetic divergence within morphologically distinct species averaged 0.5% (range 0-1.2%). In species complexes, maximum values of genetic divergence (3.2-3.7%) indicate the presence of cryptic diversity. The existence of well defined groups within *S. piperi*, *S. duodenicornium*, *S. canadense* and *S. rostratum* highlighted the possible presence of a species complex or cryptic species within these taxa. Also, the suspected presence of a sibling species in *S. tarsatum* and *S. paynei* is supported. DNA barcodes also showed that specimens from species that were taxonomically difficult to delimit such as *S. hippovorum*, *S. rubrithorax*, *S. paynei,* and other related taxa (*S. solarii*), grouped together respectively in the NJ analysis, confirming the correctness of their species status. The use of midi and mini barcodes from specimens held in collections proved to be time consuming and problematic with regards to PCR success. However, in cases when a readable sequence was obtained, they provided good resolution for species identification. Larvae preserved in 'weak' Carnoy's solution (9:1 ethanol:acetic acid) provided full DNA barcodes. Adding legs directly to the PCR mix from recently collected and preserved adults was a cheap and fast methodology to obtain full barcodes. Specimens more than 10 years old did not yield good PCR products. In summary, it is concluded that DNA barcoding in combination with a sound morphotaxonomic framework is an effective approach for the identification and delineation of species and the discovery of hidden diversity in the subgenus *Trichodagmia.*

4.2. Introduction

Rapid and reliable identification of species is paramount in all aspects of biological research but especially so in systematics, ecology, evolutionary biology, conservation biology, biodiversity and biomonitoring. RIVERA & CURRIE (2009) stress that correct species identification not only allows access to critical literature for a specific taxon, but also permits the implementation of adequate control measures for species of medical or agricultural importance. These authors also argue that mis-identifications could lead to inadequate control measures with devastating economical implications. In addition, the constant threat of biodiversity loss caused by anthropogenic change, and the ever-increasing loss of taxonomic expertise (knowns as the taxonomic impediment) (HOAGLAND, 1995; HOUSE OF LORDS, 2002; WHEELER *et al.*, 2004), have spurred the scientific community on to find faster ways for species delineation and identification (CYWINSKA *et al.*, 2006; GODFRAY, 2002; MONAGHAN *et al.*, 2005). However, species identification relies heavily upon morphology-based procedures, which are

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To be submitted to *Memórias do Instituto Oswaldo Cruz* as: Hernández[1], L. M., L. Crainey[2], A. Hall[1], J. MacKenzie-Dodds[1], A. J. Shelley[1], X. Zhou[3], R. J. Post[1], & P. N. D. Hebert[3]. The utility of DNA barcoding for species identification within the blackfly subgenus *Trichodagmia* Enderlein (Diptera, Simuliidae) and related taxa.

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The proposal of HEBERT *et al.* (2003a,b) to use a small portion of the mitochondrial gene cytochrome *c* oxidase unit I (*COI*) as a standardised universal DNA marker (DNA barcode) for species time consuming and not always satisfactory at the species level (CYWINSKA *et al.*, 2006; PACKER *et al.*, 2009).identification has invigorated taxonomy in the last seven years, and it is now widely implemented by taxonomists worldwide. In early tests HEBERT *et al.* (2003a,b) demonstrated that DNA barcodes reliably identified nearly 96.4% of the seven phyla they tested. When applied to the eight insect orders of Hexapoda, the methodology identified 100% of taxa to the correct order. Within the order Lepidoptera, a hugely biodiverse group, the success rate was 100% using a sample of 200 species from five different families. In a further study, HEBERT *et al.* (2004) applied DNA barcoding to a common New World butterfly species, *Astraptes fulgerator* WALCH (Hesperidae). They reared numerous caterpillars from the Guanacaste Conservation Area in Costa Rica, and barcoded all caterpillars and their respective emerged adults, and also specimens of the adult butterfly held in museums. After correlating the DNA barcode with caterpillar coloration patterns and their different food plants, the authors discovered that *Astraptes fulgerator* was a complex of ten cryptic species, which appeared as different clusters in a Neighbour-Joining analysis tree. The freshly collected specimens clustered nicely with those specimens held in museum collections. As a consequence, HEBERT *et al.* (2003a,b) and HEBERT *et al.* (2004) (also detailed in STOCKLE & HEBERT, 2008) advocated that integrating DNA barcoding into traditional taxonomic tools would be a valuable approach for disclosing hidden biodiversity at a much faster rate, and more reliably than traditional methods alone. This is because phenotypic plasticity and morphological variation more easily lead to mis-identifications. They further argued that using identification keys is time consuming, and more and more people lack the taxonomic expertise to use them correctly.

There are many studies that have discussed why mitochondrial genes are good universal markers for taxonomy and systematics. For example, mitochondrial genes might be better makers than nuclear genes because of their abundance (1000's copies per cell), lack of introns, limited exposure to recombination and haploid mode of inheritance (HEBERT *et al.*, 2003a,b; RUIZ, 2010; SACCONE *et al.*, 1999; SIMON *et al.*, 1994, 2006). Similar to the other 12 protein-coding genes in the animal mitochondria, mithocondrial *COI* third codon positions shows a high incidence of base substitutions, leading to a rate of molecular evolution that is about three times greater than that of the ribosomal genes 12S or 16S (KNOWLTON & WEIGHT, 1998). Therefore, the evolution of the *COI* can be fast enough to allow for the delineation of closely related or sibling species, and even phylogeographic groups within a single species (ABASCAL *et al.*, 2006; COX & HEBERT, 2001; HEBERT *et al.*, 2003a,b; HUNTER *et al.*, 2008; ILMONEN *et al.* 2009; PRAMUAL *et al.*, 2005; SHUFRAN *et al.*, 2010). However, *COI* appears to have a greater range of phylogenetic signals than other mitochondrial genes such as cytochrome *b* (DIJKSTRA *et al.*, 2003; SIMMONS & WELLER, 2001), because changes in the *COI* amino-acid sequence occur more slowly. Thus, by examining amino acid substitutions it may be possible to assign any unidentified organism to a higher taxonomic group (*e.g.* phylum or order) (HEBERT *et al.*, 2003a,b), before examining nucleotide substitutions to determine its species identity. Another advantage of the *COI* gene is that universal primers for this gene are robust, enabling the recovery of its 5' end from most, if not all, animal phyla (FOLMER *et al.*, 1994; HEBERT *et al.*, 2003a; ZHANG & HEWITT, 1997).

Since the advocacy of HEBERT *et al.* (2003a,b) for DNA barcoding in taxonomy, the approach has been both praised and dismissed for its simplicity. LANE (2009) described how many people assume that the DNA barcode misses taxonomic subtleties that can only be revealed through either traditional systematics and/or more extensive sequencing. Other potential problems that have been described include: the need for specimens (either from the field or from collections) that have been reliably identified by morphotaxonomists (thus *a priori* taxonomic resolution is paramount); the inability of *COI* barcoding to recognize hybrids because of maternal inheritance (MORITZ & CICERO, 2005; KRESS & ERICKSON, 2008); the presence of introgression, heteroplasmy and pseudogenes (HLAING *et al.*, 2009) is very common in natural populations of species (which can mislead the results in phylogenetic analysis, especially non-monophyly); and DNA barcoding is "just" a diagnostic tool not a Tree of Life (A. RADULOVICCI, University of Quebec, pers. comm.). A further argument is that *COI*, as a typical mtDNA marker, is particularly prone to selective sweeps and its populations dynamics may be driven by intracellular symbionts.

In addition, the use of museum specimens for selected species is sometimes the only material available to gather DNA data for molecular analysis as a result of habitat destruction (SCHANDER & HALANYCH, 2003). This presents another problem for DNA barcoding campaigns as it may be unknown how the specimens were collected originally, or what were the environmental conditions in which they were kept before being accessioned into the collection. It is well documented that collecting and preservation techniques can have a direct effect on the quality of the DNA yield from museum specimens (QUICKE *et al.*, 1999; KNÖLKE *et al.*, 2005). In groups such as blackflies, the presence of parasites in the gut and pigments in the adults' head are known to inhibit the PCR reaction (KOCH *et al.*, 1998). Also, it is common practice for simuliid larvae to be collected in Carnoys' fixative (a mixture of 3:1 parts of absolute alcohol and glacial acetic acid) for cytological analysis. However, the acetic acid is often suspected to degrade DNA rendering specimens unsuitable for molecular studies (KOCH *et al.*, 1998; RIVERA & CURRIE, 2009). It is not always appreaciated that specimens from a museum have not not always been correctly identified. Consequently, if a DNA sequence is obtained from a specimen which has been incorrectly identified and then submitted to a databases such as GenBank, this would only contribute to the perpetuation of poor taxonomy (LINTON *et al.*, 2002; RUIZ, 2010). Nonetheless, certain approaches such as the use of a shorter amplicon of the DNA *COI* region (*c.* 100 bp to *c.* 180 bp) (minibarcode) are being tested (HAJIBABEI *et al.*, 2007; MEUSNIER *et al.*, 2008) to overcome these museum issues. In addition, DNA protocols standardized by KRÜGER (2000) and CONFLITTI *et al.*, 2010) have shown that genetic data can be recovered from larvae preserved in Carnoy's solution, if analyzed up to two to three months or longer after collection.

In essence, DNA barcoding has being postulated as a viable tool to enhance taxonomic research by discovering new taxa and verifying morpho-taxonomic hypotheses, as well as a tool for rapid identification. However, because of the above problems, DNA barcoding has been the subject of a vigorous debate in the scientific community between those embracing it (*e. g.* KRESS & ERICKSON, 2008; MILLER, 2007; SCHINDEL & MILLER, 2005), and those opposing it (EBACH & HOLDREGE, 2005; HICKERSON *et al.*, 2006; ALLET & WILLMOTT, 2003; MEYER & PAULAY, 2005; MORITZ & CICERO, 2005; DESALLE *et al.*, 2005; VOGLER & MONAGHAN, 2007; WHEELER; 2005; WILL *et al.*, 2005). However, LANE (2009) [citing DONALD HICKEY, an evolutionary molecular biologist] concluded that whatever the argument "the fact is that these short sequences yield surprisingly accurate information about the composition of the entire genome". In addition, HAJIBABAEI *et al.* (2007a) and HEBERT & GREGORY (2005) argued that the proposal of HEBERT *et al.* (2003a,b) was never intended to replace morphotaxonomy, but to complement it. DNA barcoding has been labelled "The renaissance of taxonomy" by MILLER (2007) and SCHINDEL & MILLER (2005), while other authors questioned if this taxonomic impetus is truly a renaissance or a "Tower of Babel" (MALLET & WILLMOTT, 2003). Systematists such as WHEELER (2005) have called it "the return to the failed paradigms of phenetics and single character typology" and "an excursion into futility", and LIPSCOMB *et al.* (2003) believed that barcoding would "reduce taxonomy to a mere technical service". Furthermore, poor success in certain taxa such as Cnidaria (HEBERT *et al.*, 2003b) and plants (GOLDING *et al.*, 2009) has only fuelled the debate.

Nonetheless, in spite of some of the arguments over its limitations, empirical evidence is increasingly showing that DNA barcoding can be very useful for species identification in many biodiversity-rich groups of organisms (PACKER *et al.*, 2009), such as butterflies (BURNS *et al.*, 2007, 2008, 2009, 2010; HAJIBABAEI *et al.*, 2006; HEBERT *et al.*, 2003a; JANZEN *et al.* 2005), mosquitoes (CYWINSKA *et al.*, 2006; KUMAR *et al.*, 2007; RUIZ, 2010), tachinids (SMITH *et al.*, 2006; 2007; 2008), beetles (MONAGHAN *et al.*, 2005), birds (HEBERT *et al.*, 2004; KERR *et al.*, 2007), fishes (IVANOVA *et al.*, 2007; WARD *et al.*, 2005; ZEMLAK *et al.*, 2009), amphibians (SMITH *et al.*, 2007) and mammals (BORISENKO *et al.*, 2007; CLARE *et al.*, 2007) [for further information on international barcoding campaigns see http://ibol.org as detailed by RATSNASINGHAM & HEBERT (2007)]. Its application has also proven successful in rapid biodiversity assessment studies and biomonitoring (HAJIBABEI *et al.*, 2007b; SMITH *et al.*, 2005), in the forensic sciences (DAWNEY *et al.*, 2007), in the investigarion of the illegal trade of endangered species (ALLEN, 2009), in studies on feeding ecology (BOURLAT *et al.*, 2008; EMERY *et al.*, 2009), and conservation initiatives (HAJIBABAEI *et al.*, 2007b; SMITH *et al.*, 2005). But perhaps most importantly, DNA barcoding has proved a versatile tool in the study of taxonomically difficult blackfly taxa, where identification is hampered due to cryptic species or phenotypic plasticity (RIVERA & CURRIE, 2009) or in facilitating the association between different developmental life stages (AHRENS *et al.*, 2007; RIVERA & CURRIE, 2009). It also has the advantage that it may provide the association of museum specimens, whose DNA is degraded, with more recently collected specimens of the same species (HAJIBABAEI *et al.*, 2006; MEUSNIER *et al.*, 2008).

With regard to the Simuliidae, the first studies employing the *COI* DNA barcoding relevant to the Nearctic Region were those of RIVERA CASTILLO (2008) and RIVERA & CURRIE (2009). They examined 10 genera and 65 species of Simuliidae in North Americ, and found genetic divergences between species of 2.83-15.33% and intraspecific genetic divergences of 0-3.84% for morphologically distinct species. They revealed that DNA barcodes correctly identified nearly 100% of the morphologically distinct species, and within species complexes (only 13% of the sampled taxa) maximum values of divergence were much higher, which indicated the presence of cryptic diversity. In Europe, DNA barcodes contributed to the confirmation of the species status of *S. galeratum* EDWARDS (DAY *et al.*, 2008) and the presence of *S. petricolum* (RIVOSECCHI) (DAY *et al.*, 2010) in Britain, and the delineation of the *Simulium vernum* group in Finland and Sweden (ILMONEN *et al.*, 2009). In a similar molecular marker framework approach but using part of the cytochrome oxidase subunit II (*COII*), HELLGREN *et al.* (2008) carried out a study to decipher the associations between bird hosts, blood parasites and the simuliid vectors using female blood meals in Sweden.

There is paucity of DNA barcoding data for Simuliidae in the Neotropical Region. However, preliminary information have been obtained by PEPINELLI *et al.* (2009) for 63 nominal species of the genera *Gigantodax* (11 species), *Lutzsimulium* (three species), *Pedrowygomyia* (one species) and *Simulium* (48 species). PEPINELLI *et al.* (2009) have barcoded 11 anthropophilic *Simulium* species of which three taxa are known vectors of *O. volvulus* (*S. guianense s.l.*, *S. metallicum s.l.* and *S. oyapockense*). Similarly, L.M. HERNÁNDEZ [unpublished data, see projects in http://www.boldsystems.org] has barcoded 70 nominal species of the genera *Cnesia* (three species), *Gigantodax* (11 species), *Paraustrosimulium* (one species) and *Simulium* (53 species). Of the genus *Simulium* 14 species are anthropophilic of which five are known or suspected to be vectors of *O. volvulus* (*S. ganalesense*, *S. gonzalezi*, *S. guianense s.l.*, *S. metallicum s.l.*, *S. oyapockense* and *S. quadrivittatum*). More recently, HAMADA *et al.* (2010) described the new species *S. lithobranchium* from Brazil, based upon morphological differences of the male genitalia, the presence of dorsal tubercles in the larvae, and a high intraspecific genetic divergence (>4%) in the barcoding sequences they analyzed.

Chapter 2 of this work dealt with the classical taxonomy of the subgenus *Trichodagmia*, and outlined the haematophagous behaviour of several *Trichodagmia* species along with their medical importance as vectors of human onchocerciasis (*e.g. S. guianense s.l.*) or as putative etiological agents of *Pemphigus Foliaceus* in Brazil. The presence of aquatic (egg, larva and pupa) and aerial (adult) life stages, in combination with their structural homogeneity, makes the taxonomy of *Trichodagmia* (and of Simuliidae in general) a difficult task. A further complication is the presence of known sibling species complexes in *S. guianense s.l.* and *S. virgatum s.l.*, which would require the examination of the larval salivary gland polytene chromosomes for identification. Therefore, blackflies provide good candidates for species identification facilitated by DNA barcoding (RIVERA AND CURRIE, 2009) in the same way that this is being carried in other vector groups such as mosquitoes (*e.g.* CYWINSKA *et al.*, 2006; KUMAR *et al.*, 2007; RUIZ, 2010).

The objectives of this chapter are threefold : 1- To test the robustness of DNA barcoding for the identification of species of the subgenus *Trichodagmia* (and related taxa) using specimens already identified by morphological traits; 2- To test the use of DNA barcoding to reveal hidden diversity in the subgenus *Trichodagmia* and related taxa; 3-To provide preliminary results on the use of midi- and mini-barcodes for the identification of *Trichodagmia* species held in the BMNH Simuliidae collection.

4.3. Material and Methods

4.3.1. Collection of specimens

In general, standardised collection protocols of the BMNH were used as detailed in HERNÁNDEZ (2007). Larvae, pupae and preferably link-reared adults were collected in various countries throughout South America. Specimens from North America were identified, and loaned or donated to the BMNH by P.H. ADLER (CUAC) (TABLE 1), and DNA barcoding sequences of some other non-South American taxa related to the subgenus *Trichodagmia* (such as the subgenera *Aspathia* and *Simulium s.str.*) were downloaded from GenBank [http://www.ncbi.nlm.nih.gov/genbank]. Sequences from *Simulium posticatum* were provided by J. DAY (Centre for Ecology and Hydrology, Wallingford, UK) (TABLE 1), while sequences of the recently described *S. lithobranchium* (HAMADA *et al.*, 2010) and related taxa (*S. duodenicornium*, *S. guianense s.l.*, *S. orbitale* and *S. scutistriatum*) were provided by M. PEPINELLI, Brazil (see also **APPENDIX 3**)

Recently collected material (2005-2010) preserved in alcohol was maintained at low temperature (5°C) until taken to the laboratory for molecular analysis, while pinned material (female man-biting or link-reared adults) was kept at room temperature in insect drawers without naphthalene.

4.3.2. DNA barcoding

Fresh material

Larvae of species to be used for molecular analyses had their digestive track removed to reduce contamination following RIVERA & CURRIE (2009). Larval specimens were either cut in half or a long strap of the posterior abdominal wall was removed, while the head and thorax were retained as vouchers following the protocols of the CANADIAN CENTRE FOR DNA BARCODING (CCDB - http://www.dnabarcoding.ca). When pupae were selected for analysis, part of the thorax, gill and cocoon was retained as a voucher; and only the pupal abdomen and part of the thorax were used for the DNA extraction. In the case of adults preserved in alcohol or pinned, three legs were removed from the specimen for DNA extraction, and the remainder of the body retained as a voucher. In the case of pinned material, a yellow label stating "Legs removed for DNA barcoding" was attached to the pin as recommended by GOLDING *et al.* (2009). Forceps used for dissection were flame-sterilised between specimens to avoid transfer of DNA (RIVERA & CURRIE 2009).

All body parts were deposited into 96 well plates and DNA extraction, PCR and sequencing was carried out at the high throughput facility at the Institute of Biodiversity (BIO), University of Guelph, Canada. A digital image of each specimen was taken at the Digital Imaging Suite at BIO employing a Leica compound microscope equipped with a Z-stepper and attached to a digital camera. The detailed specimen records, sequence information (including trace files), and digital images were uploaded to the Barcoding of Life Database (BOLD - http://www.boldsystems.org). The information for specimens and digital images can be found in the published project files in BOLD: 'New World Blackflies Hernández_2008' and 'Blackflies of the New World_Hernández 2009'.

The DNA extraction, PCR amplification and sequencing of the specimens followed the CCBD protocols (IVANOVA, DEWAARD & HEBERT - www.dnabarcoding.ca). In general, extractions were performed using a 96 multichannel Biomek NX robotic liquid handler (Keckman Coulter Inc.) with a Thermo Cytomat hotel. Polymerase chain reaction primers were those developed by FOLMER *et al.* (1994), which are considered standard to amplify *c.* 658-bp long target region of the *COI* gene (HEBERT *et al.*, 2003a,b): LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO 2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3'). Samples that did not yield DNA, were reamplified using a different cocktail of primers (FOLMER *et al.*, 1994) to amplify a shorter fragment (between 200-400 bp) of the *COI* DNA barcoding region (midi-barcode): LepF (5'-ATT CAA CCA ATC ATA AAG ATA TTG G-3'); and LepR (5'-TAA ACT TCT GGA TGT CCA AAA AAT CA-3').

Both forward and reverse strands were sequenced using BigDye Terminator (version 3.1) or ABI PRISM 3730 capillary sequencer (Applied Biosystematics). All DNA extractions, PCR amplification conditions and sequencing protocols are available at www.dnabarcoding.ca/CCDB_sequencing.pdf.

Museum collections

In order to avoid some of the problems outlined in the introduction of this chapter with regard to using specimens housed in museum collections for molecular analysis, a working rationale was established to barcode specimens of *Trichodagmia* deposited at the BMNH Simuliidae collection. Specimens were only used when it was clear that they had been collected in accordance with protocols for blackflies implemented by R.W. CROSSKEY and A.J. SHELLEY at the BMNH (HERNÁNDEZ, 2007). In addition, specimens of *Trichodagmia* were only used when identification labels showed that they had been identified either by P.H. ADLER, S. COSCARÓN, R.W. CROSSKEY, A.J. SHELLEY, or L.M. HERNÁNDEZ. The methods below were all performed at the Molecular Biology Facility (MBF) of The Natural History Museum, London.

Eighty-eight specimens from 12 species, and of various ages from 1-30 years (either pinned or preserved in 80-96% alcohol), were selected for DNA extraction (TABLE 2). In addition, specimens of *S. ornatum* of the subgenus *Simulium s.str.* preserved in 'weak' Carnoy's solution (9:1 ethanol:acetic acid) identified by R.J. POST (BMNH) were DNA barcoded one year after they were collected (TABLE 2).

Two destructive and two non-destructive DNA extraction methodologies were employed as follows:

Non-destructive method 1: Two to three legs were detached from pinned specimens and added directly into the PCR tubes which contained 7.35ul of water plus 2.5ul of PCR buffer (HH4). The remaining ingredients for the PCR mix was subsequently added once the legs were already inside the tubes. PCR was carried out directly on the detached legs without an actual DNA extraction being carried out.

Non-destructive method 2: Pinned specimens were softened in a humidity chamber overnight. Abdomens were subsequently removed and placed immediately in ATL buffer (Qiagen DNeasy blood and tissue kit) for several hours. After incubation, the abdomens were washed in water, then in alcohol, and placed in a small plastic vial containing glycerine attached to the pinned adult, as retaining voucher specimens is essential for DNA barcoding projects (HUNTER *et al.*, 2008). DNA was extracted from the ATKL buffer lysate using a Qiagen DNeasy kit following manufacturer's instructions.

Destructive method 1: Adults or immature stages preserved in spirit were first placed into 1xTE solution and stored at 4°C until they sank. The TE solution was then replaced with 100µl of lysis buffer including proteinase K (0.1% SDS, 0.004% EDTA, 0.015% NaCl, 0.005% TrisHCL and 0.1µg per µl of proteinase K), and the samples homogenised with with Kontes pellet pestle motor with plastic disposable pestles (Anachem Ltd.). After 2.5 hours incubation at 56°C, 20ul of Lysate was added to 200µl of 5% Chelex solution, which was placed in a shaking incubator at 56°c 200rpm for 1 hour. Samples were centrifuged at 13krpm for 1 min, before the supernatant was used as template for the PCR reactions.

Destructive method 2: Only immature stages preserved in more than 80% alcohol were used. Part of the larvae and pupal abdomen were cut in half. The abdomen or thorax to be extracted were placed in 1xTE and incubated at 4ºC until the body part sunk in the Eppendorf tube (normally after two hours). The TE was then removed and 200µl of ATL buffer was added to the Eppendorf tube. Each sample was ground using an electric pestle and incubated at 56ºC overnight. The tube containing the sample was then transferred to -20ºC until completely frozen, and the samples were then thawed at room temperature. This process maximized the breakdown of cells through the formation of ice crystals. DNA was then extracted using either a Qiagen DNeasy blood and tissue kit, or Qiagen QiaAmp mini kit following the manufacturer's recommendation. When legs or abdomens were used from pinned specimens, yellow labels were added to the pin stating that this structure had been removed for barcoding (GOLDING *et al.*, 2010).

PCR amplification was first attempted for the full DNA barcode region using the primers HCO and LCO (FOLMER *et al.,* 1994) following the PCR conditions of HEBERT *et al.* (2003a,b). Specimens that did not provide a full barcode, were then amplified using the midi-barcode primers MLepF1/LepR1, and LepF1/MLepR1 as in the CCDB protocols (see above). Samples that yielded a full or a midi-barcode were not further tested. However, specimens of selected species which had not yielded amplicons were then used for PCR amplification employing the mini-barcode primers (Uni-MinibarR1: 5'-GAA AAT CAT AAT GAA GGC ATG AGC-3'; Uni-MinibarF1: 5'-TCC ACT AAT

CAC AAR GAT ATT GGT AC-3') and PCR conditions detailed by HAJIBABEI *et al.* (2007) and MEUSNIER *et al.* (2008).

PCR products were visualized on 1% Agarose gels, and samples that showed a well defined band were sent for sequencing at the NHM, MBF. Successful PCR products were cleaned using Millipore multiscreen PCR 96 filter plates according to manufacturer's instructions and sequenced bi-directionally using BigDye terminator reaction mix v3.1, in a 3730xlDNA analyser (Applied Biosystems).

4.4. Sequence analysis

Paired nucleotide sequences (amplified with the LCO1490 and HCO2198 primers) were used to produce a single consensus sequence from each of the full length barcode amplicons. To achieve this, individual forward and reverse sequences were oriented, edited and aligned using the Sequencer (v.4.5; Genes Codes Corporation, Ann Harbour, MI), GenDoc (v. 2.6.02) and ClustalX sequence analysis programs. These edited consensus sequences were then aligned together with *COI* sequences of a set of taxonomically relevant species downloaded from GenBank (Table 1; **APPENDIX 3**). The resultant trimmed alignment required no manual adjustments and spanned 606 nucleotide positions.

Following conceptual translation using the mitochondrial genetic code in the emboss transeq tool (available from the EMBL web site – www.ebi.ac.uk/Tools/emboss/transeq) and BLASTp homology comparison with sequences from the NCBI non-redundant protein database, all of the consensus sequences were seen to code for the uninterrupted open reading frame from the *COI* protein sequence. The sequences generated from the midi-barcode analysis (*c.* 220 to 450 bp) were aligned and edited in the same way. Where possible, a synthetic full-length barcode was created from a contig made with the 5' prime and 3' prime sequences amplified with the two midi-barcode amplicons for selected species. These sequences are identified in the alignment and Figure 1 with the prefix "ConSC".

These alignments were used in a variety of analyses, which were carried out using the PHYLIP v.3.67 software package suite (FELSENSTEINS, 2007; available at www.evolution.genetics.washington). Distance matrixes were generated using the Dnadist program implementing the Kimura 2-parameter model option (K2P). Neighbour Joining (NJ) trees were inferred from these matrices using the Neighbor program. Trees generated in this way were visualised with TreeView 1.6.6. (Win32) (PAGE, 2001) and/or FigView (RAMBAUT, 2007). The trees were exported as "GIF.files" to be edited in Photoshop (v.7.0.1). The robustness of the trees generated by these methods was tested using 1000 pseudoreplicates, generated in Seqboot, and compiled using the Consense program. Consensus trees are not shown in this chapter, but informative bootstrap-supported nodes (identified from the consensus trees) are indicated where appropriate on the representative distance trees that are shown. Only more than 80% support values were shown on the tree following ELIAS (2007) and PALOWSKI & LECROQ (2010). The full data set was also analyzed in MEGA5 (TAMURA *et al.*, 2007, available at http://www.megasoftware.net) as recommended by CYWINSKA *et al.* (2006) and HEBERT *et al.* (2003a,b).

Pairwise distances (K2P) for species complexes and suspected species complexes were calculated separately as recommended by RIVERA & CURRIE (2009). They proposed this approach because it helps to evaluate the level of genetic divergence within each species complex, thereby testing cytological evidence that implies a degree of cryptic diversity.

The identification capability of the midi- and mini-barcodes was first assessed using the BLAST search engine at NCBI (http//www.ncbi.nlm.nih.gove/genbank), which is now connected to the *COI* library database in BOLD. Sequences were selected for further analysis when they agree with the species identification based on the morphology. All such sequences were reduced to 416 bp long to make the data comparable. A NJ analysis was carried out using the K2P to represent their clustering pattern. Mini-barcodes were analyzed in a similar way, but they were not mapped in the NJ tree.

4.5. Results and Discussion

4.5.1. Full length barcodes

A total of 25 species belonging to the subgenus *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010), and three species of the subgenera *Aspathia* and nine species in *Simulium s.str.* were included in the analysis. The studied taxa are represented by a varying number of individuals, often including representatives of different populations through their distribution range (TABLE 1). In total, 350 full sequences of the Cytochrome Oxidase I barcoding region were used in the analyses.

The DNA barcoding *COI* sequences showed a T+A bias in nucleotide content (mean = 37.6 % and 27.9 %) relative to the C+G content (mean = 18.0% and 16.5%), which is typical for the family Simuliidae (RIVERA & CURRIE, 2009) and other arthropods (CREASE, 1999; HEBERT *et al.*, 2003a, 2003b). All sequences lacked indels or stop codons supporting their origin from the mitochondrial genome.

In most cases, individuals of the same species grouped together even when samples were geographically distant. However, three specimens did not show this pattern (Fig. 1). A single specimen of *S. guianense s.l.* grouped with *S. lithobranchium*. This is not surprising as *S. guianense s.l.* is morphologically and genetically very similar to *S. lithobranchium* (SHELLEY *et al.*, 2002a; HAMADA *et al.*, 2010). A single species of *S. tuberosum s.l.* clustered with *S. rostratum* with a 90% bootstrap value. These species are also morphologically similar and were nested together in the NJ tree of RIVERA & CURRIE (2009). These results could be a consequence of misidentification, genetic introgression between closely related species, or incomplete lineage sorting. However, a single specimen of *S. virgatum s.l.* nested within specimens of *S. guianense s.l.* and these species are only distantly related in separate species groups. A possible explanation is that this is a result of DNA contamination, or perhaps a labelling error in the database. However, the original data were checked in combination with the quality of this sequence and neither of these issues were found. In general, members of the same subgenus or species group tended to be grouped together, *e.g.* subgenus *Aspathia*, *Simulium* and the ORBITALE and PICTIPES species groups, although this did not hold true in the CANADENSE and TARSATUM species groups (Fig. 1). Nonetheless, certain groups of morphospecies identified in **Chapter 3** related to *S. virgatum s.l.* appear as a single group in the NJ tree (*S. hippovorum*, *S. paynei*, *S. rubrithorax*, and *S. virgatum s.l.*).

Levels of sequence divergence were variable across the taxa examined. Thus, while conspecific individuals collected from a single site often exhibited zero or small divergence values, other specimens sometimes exhibited higher values (within *S. huairayacu* for example) (Table 1). The intraspecific divergence averaged 0.5% (range 0-1.2%) (Table 1), while interspecific genetic divergence averaged 11.2% (range 2.8-19.5%) (Table 3).

Genetic divergence values were higher between species from different previosyly assigned subgenera [now recognized as species groups in this work; also see **Chapter 2** and **Chapter 3**]. The most divergent pairs were *S. itaunense* [ORBITALE species group] and *S. innoxium* [PICTIPES species group] (18.4%), and *S. pictipes* [PICTIPES species group] (18.9%) and *S. earlei* [TARSATUM species group] (19.5%). As expected, smaller values were found among species within the same species group, *e.g. S. orbitale* and *S. lithobranchium* (3.0%) and *S. hirtipupa* and *S. itaunense* (2.8%) [ORBITALE species group] (TABLE 3).

Although sibling species were not identified in the present study, it would be expected that a high level of genetic divergence within a particular complex would be indicative of cryptic diversity. This would be shown in the NJ tree by relatively deep divergent groups within species complexes. Known species complexes (*S. guianense s.l.*, *S. virgatum s.l.*, *S. arcticum s.l.*, *S. tuberosum s.l.*) (ADLER *et al.*, 2004; RIVERA & CURRIE, 2009; CHARALAMBOUS *et al.*, 1996) or suspected complexes (*S. murmanum*, *S. paynei*) (ADLER *et al.*, 2004) were each subdivided into different subgroups in the barcode NJ tree (Fig. 1), suggesting that more than one species might be represented. Interestingly, five other species (*S. piperi*, *S. canadense*, *S. tarsatum*, *S. duodenicornium* and *S. rostratum*) also formed subclusters with well supported bootstrap values in the NJ tree (Fig. 1). Therefore, they were analyzed in combination with known or putative species complexes (see Table 4). High levels of genetic divergence were found among members of some known sibling species complexes, *S. tuberosum s.l.* (3.7%), *S. virgatum s.l.* (3.3%) and *S. venustum s.l.* (2.6%), but other confirmed species complexes showed smaller values (*S. metallicum s.l.* – 1.2% and *S. ornatum s.l.* – 1.0%) probably because of the relatively small number of specimens examined. In addition, these specimens were also collected at the same locality, making it possible that only one sibling species was barcoded from the complex.

Putative species complexes such as *S. murmanum* (RIVERA & CURRIE, 2009) and *S. paynei* (ADLER *et al.*, 2004), showed high values of genetic divergence (3.5% and 3.0%) indicating that they might consist of sibling species. *Simulium paynei* showed three subgroups with more than 80% support values: group I - Belize, group II – USA, and group III - Costa Rica, while *S. murmanum* split in two subgroups in the USA (Fig. 1).

In those morphospecies with well supported subgroups in the NJ (see above), high levels of intraspecific divergence was only obtained from *S. tarsatum* (3.2%) and *S. rostratum* (3.0%). In the remaining three species (*S. piperi*, *S. canadense*, and *S. duodenicornium*) the level of divergence ranged between 0.9% to 1.3%. RIVERA & CURRIE (2009) also found a high level of genetic divergence within *S. rostratum*, and they could find no obvious geographical pattern. Similarly, the species *S. piperi* and *S. duodenicornium* showed well supported splits (above 80%) [labelled I and II in the NJ] (Fig. 1), but their level of genetic divergence was relatively low. In spite of the low level of divergence between specimens of *S. canadense* (1.3%), two subclusters were identified with 89% and 94% bootstrap support values. ADLER & CROSSKEY (2010) have postulated the probable existence of species complexes in *S. piperi* and *S canadense* based on their extended distribution (Canada, Mexico and USA), morphological variation in the gill pattern and female thoracic coloration (of *S. piperi*), and preliminary cytological data information (in *S. canadense*), although the presence of cytologically recognized sibling species remains to be confirmed.

With regard to *S. tarsatum*, the level of genetic divergence is much higher than in the other species (3.2%). The specimens form two well defined subgroups (here designated as groups I and II) in Costa Rica, which are morphologically identical. The pattern of intraspecific variation in species with a wide distribution, and its significance for DNA-based identification has not been well evaluated, although RIVERA & CURRIE (2009) found positive correlations in at least some species, and it seems that this could be true of *S. tarsatum*. HERNÁNDEZ & SHELLEY (2005) and SHELLEY *et al.* (2002b) detailed the complicated taxonomy, biology and distribution of *S. tarsatum*, and postulated that *S. tarsatum* might be a species complex because it is widely distributed in South America and extends into Central America and the Caribbean. In the majority of localities *S. tarsatum* is zoophilic, but there are records of this species biting human in Colombia, Ecuador and Venezuela (SHELLEY *et al.*, 1989), which is sometimes an indication of the existence of a species complex in Simuliidae (SHELLEY *et al.*, 2000). The DNA barcoding data obtained here seem to support this possibility.

Interspecific pairwise K2P genetic divergence between species complexes ranged from 3.8% to 17.4%. Of these, species complexes within the same subgenus or species groups showed smaller values of divergence (*e.g.* ORBITALE species group: *S. guianense s.l.*, *S. duodenicornium* – 3.8%), while species from different subgenera had higher values (*e.g.* ORBITALE species group – *S. guianense s.l.*, and subgenus *Aspathia*, *S. piperi* – 17.4%) (Table 5).

4.5.2. Midi- and mini-barcodes

The process by which a shorter DNA barcoding sequence could be obtained from selected taxa of the subgenus *Trichodagmia* proved to be troublesome and time consuming. Although there is a paucity of the DNA barcoding data obtained from museum specimens in this study (Table 2), a number of conclusions can be drawn from the tests carried out with regard to specimen's preservation, age and extraction techniques.

In general, numerous specimens produced no detectable DNA from the second PCR amplification at BIO. Positive second PCRs at the MBF also gave no results in the sequencing stage for many samples, and in other cases, multiple bands (contamination) were obtained. (Table 2). A total of 52 midi-barcode sequences was obtained either at BIO or MBF out of approximately 80 specimens tested. BLAST searches retrieved only 31 sequences correctly identified (59% identification success).

Twenty sequences were identified to a different species or even a different subgenus, and chimera sequences were also identified in two cases. The species for which midi-barcodes provided a correct identification were as follows: *S. duodenicornium* (1 specimen), *S. freemani* (3 specimens), *S. guianense s.l.* (10 specimens), *S. hirtipupa* (4 specimens), *S. itaunense* (1 specimen), *S. nigrimanum* (9 specimens), *S. orbitale* (1 specimen), *S. rubrithorax* (1 specimen), and *S. scutistriatum* (1 specimen). When the midi-barcodes were analyzed together with full barcode sequences, most of the midi-barcodes specimens clustered in the NJ tree with other members of the same species or species groups (shown in Fig. 2) with more than 80% bootstrap support.

Similarly, obtaining mini-barcodes also proved problematic. Eighteen specimens were tested for mini-barcodes with ages of one, two, three, five, eight and 73 years old, and preserved either pinned or in alcohol. Of these, only five specimens gave readable sequences (27% success), and problems with DNA contamination and multiple bands were encountered (Table 2). This may be due to DNA contamination of non-specific amplification. However, BLAST searches of these five readable sequences provided a correct species identification: *S. hirtipupa* (three specimens, eight years old) and *S. duodenicornium* (two specimens, five years old).

With regard to the different methodologies employed, adding legs from recently collected (1-2 yrs old), link-reared specimens directly to the Eppendorf tube containing the PCR mix was a fast and cheap method to obtain molecular data. Ten specimens tested all produced good PCR products and readable sequences. Problems encountered with static electricity within Eppendorf tubes proved to be troublesome making the handling of the legs difficult [legs did not stay in the tube where they were placed jumping outwards and sticking to the tip of the forceps]. Nonetheless, DNA barcoding campaigns in blackflies or other insect groups might benefit from this approach in terms of cost, speed, and reliability. In Simuliidae, it also has added values that *COI* data can be linked to reliably identified specimens, as link-reared material usually provides the best range of diagnostic characters for both pupae and adults. Once the *COI* sequence database is developed, it will be possible to even identify larvae to the correct species.

The specimen's age also affected the DNA yields. No specimens of more than 10 years old gave good PCR products, which agrees with the findings of HEBERT *et al.* (2003a, 2003b). It seems that more sensitive techniques such us Phenol-Chloroform extraction methods might have to be used for these specimens, but these methods are known to be even more time consuming, labour intensive and are hazardous (KRAMVIS *et al.*, 1996). Thus, the use of old museum specimens might not be the right approach, if a rapid identification *COI* barcoding library needs to be developed.

Non-destructive DNA extraction techniques, such as adding abdomens into a lyses buffer showed promising results. All nine specimens collected within the last eight years and processed in this way yielded a full length barcode sequence (TABLE 2). After treatment abdomens were very clean and transparent, and therefore did not require the usual maceration and clearance stage before dissection to examine the structure of their genitalia. In general, destructive DNA extraction techniques for specimens preserved in alcohol 80-100% gave the best results in 8 to 10 year old specimens with regard to DNA yield and sequence quality (TABLE 2). However, both larval specimens preserved in 'weak' Carnoy's (9:1) also provided full barcodes. Thus, the latter preservation condition might be ideal for obtaining DNA and cytogenetic data from the same specimen.

4.6. APPENDIX 1. FIGURES.

Fig. 1. Bootstrapped Neighbour Joining (NJ) tree constructed using the Kimura 2-parameter (K2P) genetic distances of the DNA barcoding region profile (606bp) for 25 species of the subgenus *Trichodagmia* (as proposed in **Chapter 2** and **Chapter 3**), three species for the subgenus *Aspathia*, and nine species for the subgenus *Simulium s.str*. Six species complexes and two suspected species complexes were included in the analysis. Bootstraps values higher than 80% are shown in the tree below each node. Red arrows highlight those specimens that did not group with the corresponding species cluster.

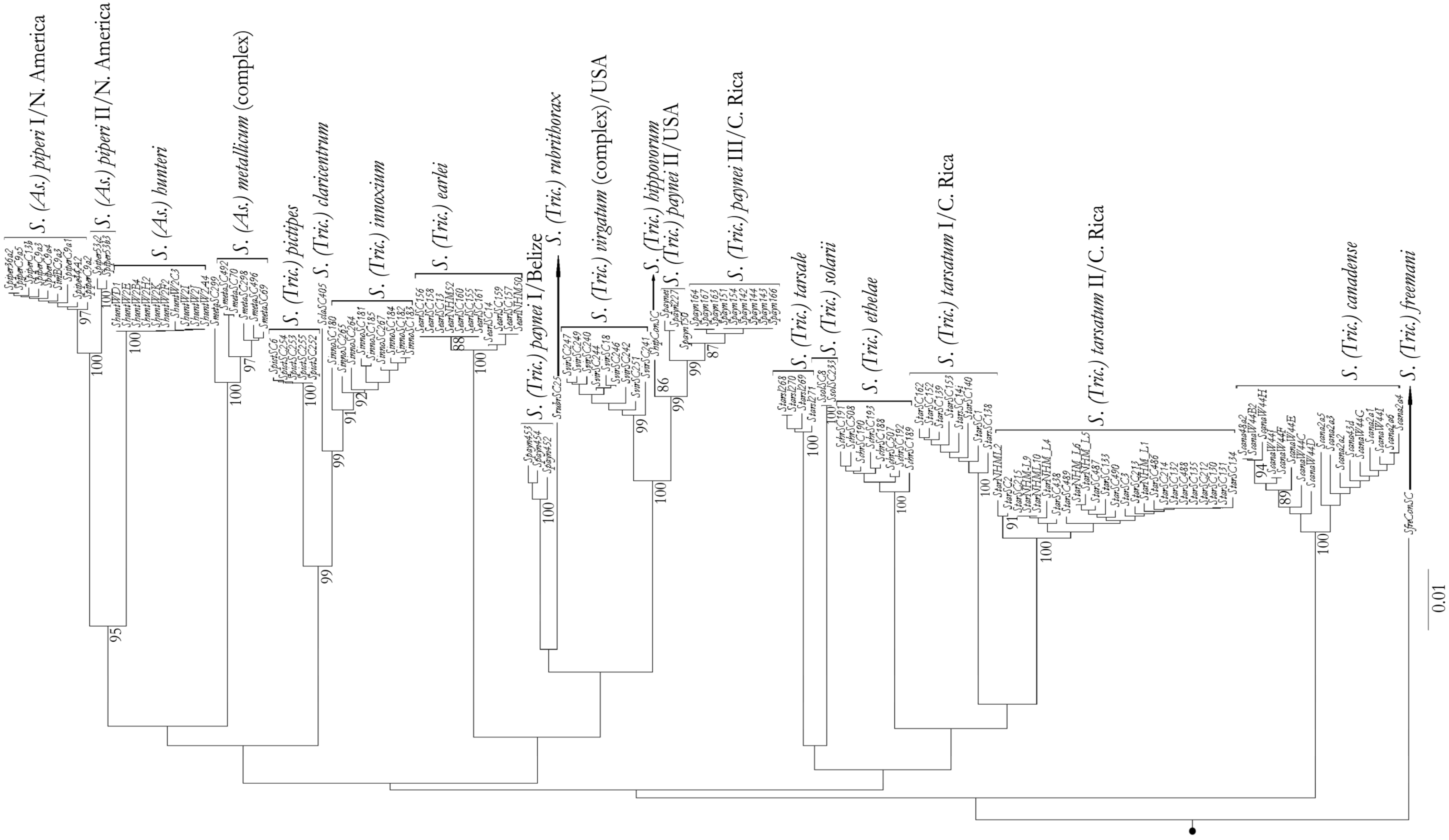


Fig. 1. Continued.

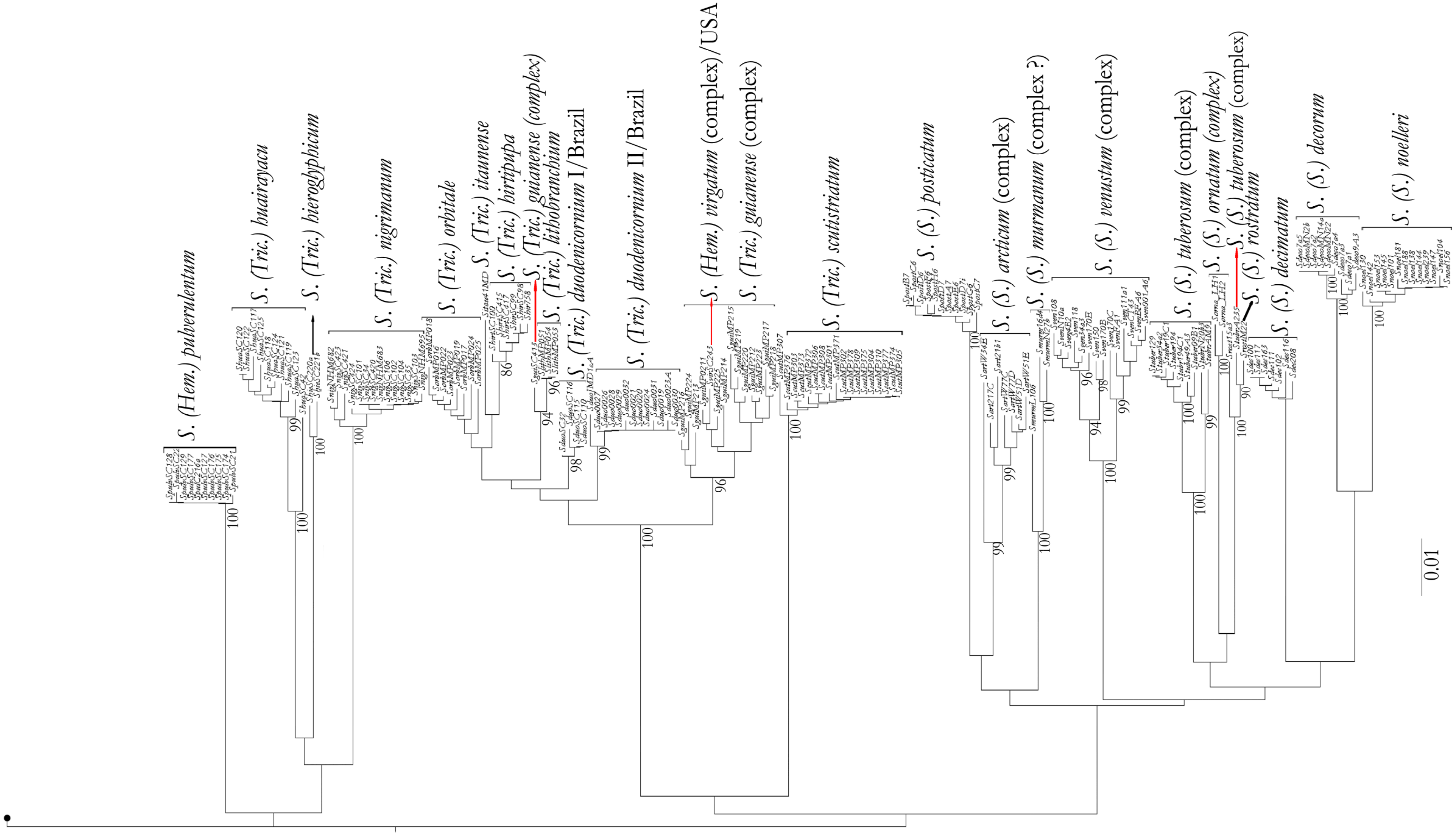


Fig. 2. Bootstrapped Neighbour Joining (NJ) tree constructed using the Kimura 2-parameter (K2P) genetic distances showing the clustering pattern of the COI DNA midi-barcode region (*c.* 220 to 416 bp) for 30 specimens belonging to the subgenus *Trichodagmia* (highlighted in red). Bootstraps values higher than 80% are shown in the tree below each node.

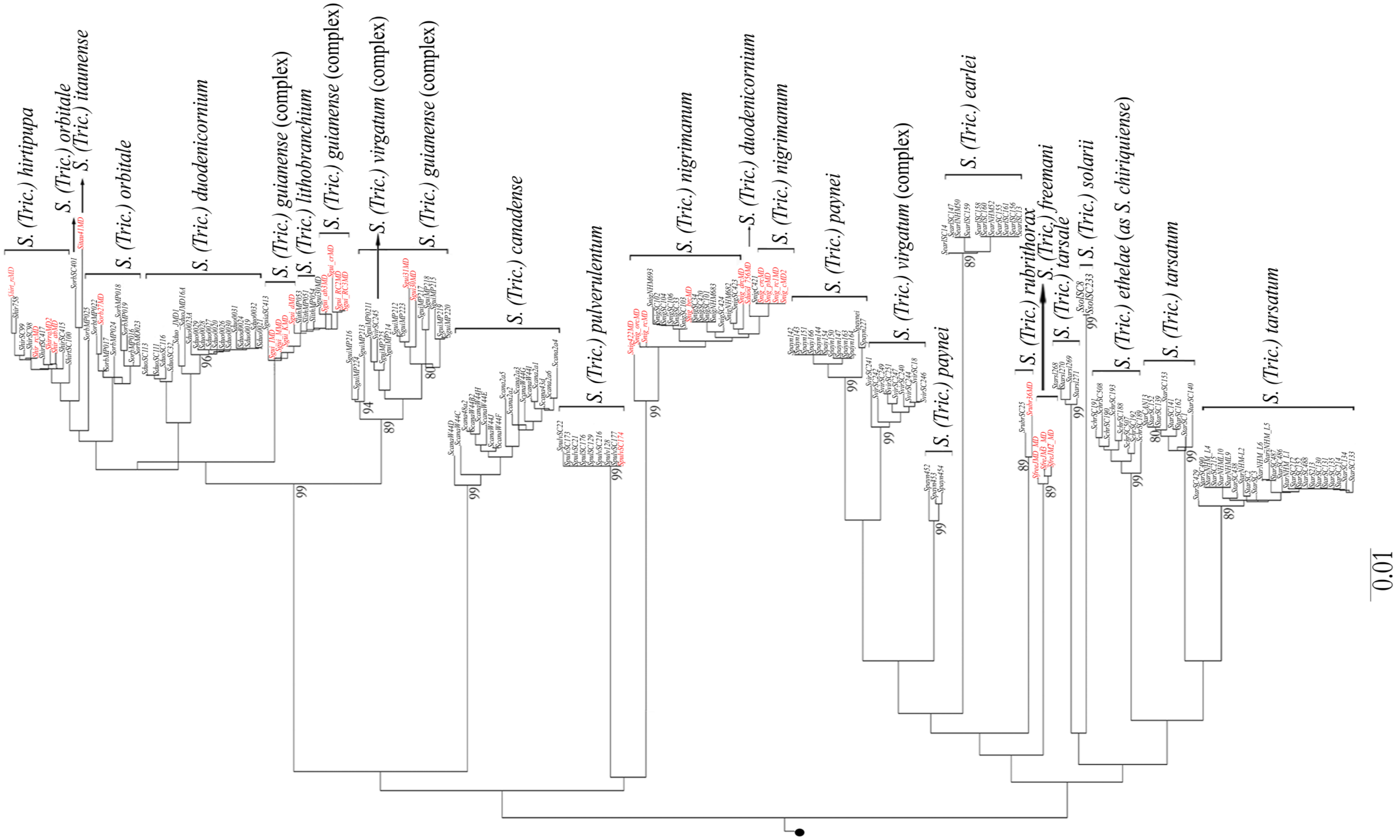
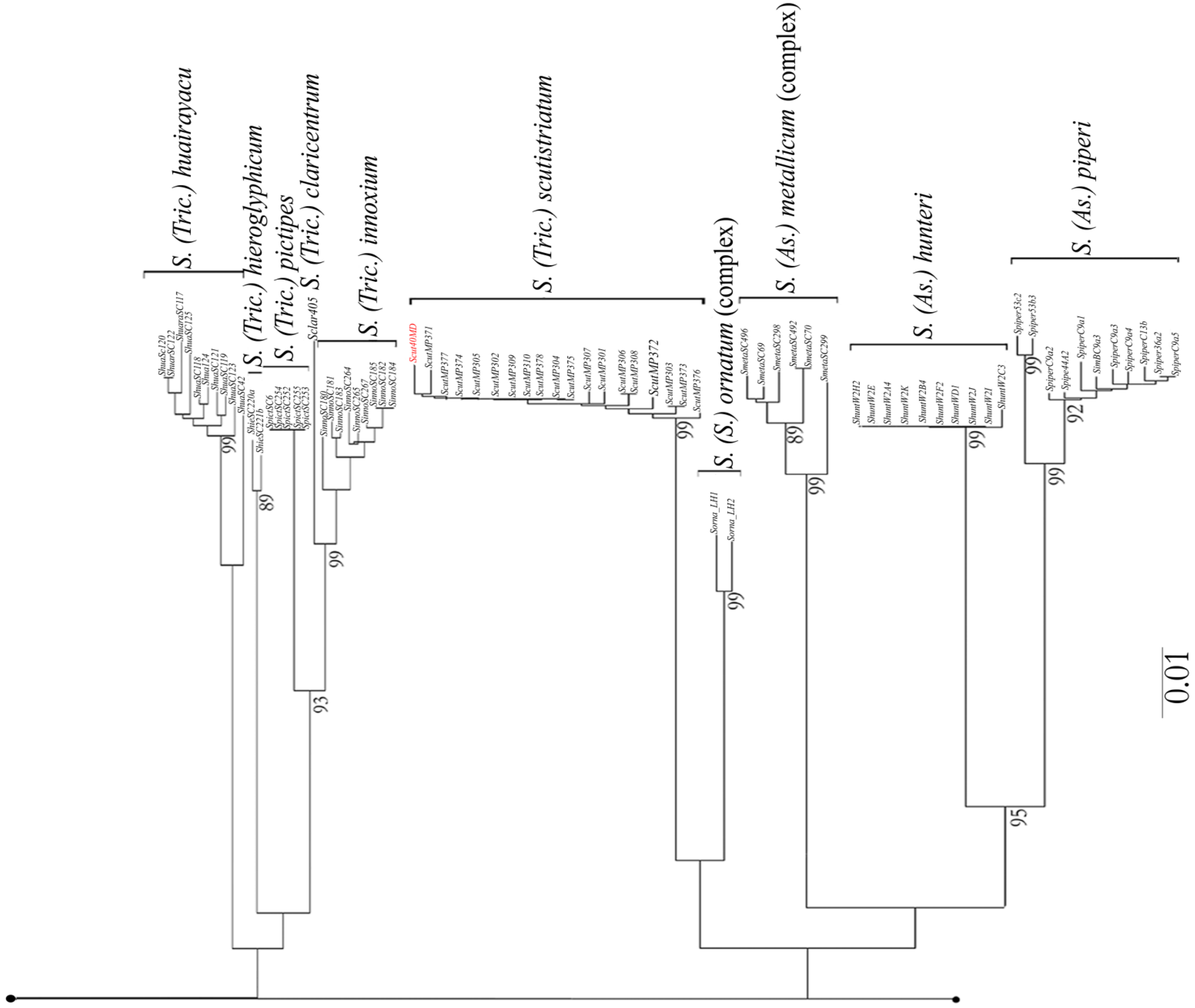


Fig. 2. Continued.



4.7. APPENDIX 2. TABLES.

Table 1. List of *Trichodagmia* species and related taxa and number of specimens (*n*) used in the full barcode data set. Mean (%) intraspecific values of genetic divergence (K2P) are shown, with missing entries indicating that only a single specimen was analyzed. Species complexes (*) or taxa suspected to be complexes (see Table 4) are marked with asterisks (**).

Species	Collection country	*n*	mean (%)
Simulium (Aspathia) hunteri	USA	20[GB]	0.03
*Simulium (Aspathia) metallicum s.l.**	COSTA RICA	6	See Table 4
*Simulium (Aspathia) piperi***	USA	11[GB]	See Table 4
*Simulium (Simulium) arcticum s.l.**	USA	7[GB]	See Table 4
Simulium (Simulium) decimatum	USA	7[GB]	0.36
Simulium (Simulium) decorum	USA	9[GB]	0.46
Simulium (Simulium) noelleri	USA	13[GB]	0.19
Simulium (Simulium) posticatum	UK	11[JD]	0.27
*Simulium (Simulium) ornatum s.l.**	UK	2	See Table 4
*Simulium (Simulium) murmanum***	USA	3[GB]	See Table 4
*Simulium (Simulium) rostratum***	USA	2[GB]	See Table 4
*Simulium (Simulium) tuberosum s.l.**	USA	10[GB]	See Table 4
*Simulium (Simulium) venustum s.l.**	USA	14[GB]	See Table 4
CANADENSE sp. gp.			
Simulium (Trichodagmia) canadense	USA	17[GB]	See Table 4
Simulium (Trichodagmia) ethelae (*S. chiriquiense*)	COSTA RICA	8	0.59
TARSATUM sp. gp.			
Simulium (Trichodagmia) earlei	COSTA RICA	11	0.24
Simulium (Trichodagmia) freemani	USA	1	—
Simulium (Trichodagmia) hieroglyphicum	PANAMA	2	1.17
Simulium (Trichodagmia) hippovorum	USA	1	—
*Simulium (Trichodagmia) paynei***	BELIZE, COSTA RICA, USA	15	See Table 4
Simulium (Trichodagmia) pulverulentum	COSTA RICA	10	0.05
Simulium (Trichodagmia) rubrithorax	BRAZIL	1	—
Simulium (Trichodagmia) solarii	USA	2	0
Simulium (Trichodagmia) tarsale	DOMINICA	4	0.36
*Simulium (Trichodagmia) tarsatum***	COSTA RICA, BELIZE, MEXICO	33	See Table 4
*Simulium (Trichodagmia) virgatum s.l.**	USA	10	See Table 4
PICTIPES sp. grp.			
Simulium (Trichodagmia) claricentrum	USA	1	—
Simulium (Trichodagmia) innoxium	USA	9	0.71
Simulium (Trichodagmia) pictipes	USA	5	0
ORBITALE sp. grp.			
*Simulium (Trichodagmia) duodenicornium***	BRAZIL	17[MP]	See Table 4
*Simulium (Trichodagmia) guianense s.l.** [MP]	BRAZIL	14[MP]	See Table 4
Simulium (Trichodagmia) hirtipupa	BRAZIL	6	0.44
Simulium (Trichodagmia) huairayacu	ARGENTINA	10	1.28
Simulium (Trichodagmia) itaunense	BRAZIL	1	—
Simulium (Trichodagmia) lithobranchium[MP]	BRAZIL	3[MP]	0
Simulium (Trichodagmia) nigrimanum	BRAZIL	11	0.45
Simulium (Trichodagmia) orbitale[MP]	BRAZIL	8[MP]	0.86
Simulium (Trichodagmia) scutistriatum[MP]	BRAZIL	18[MP]	0.24

[GB] *COI* sequences downloaded from GenBank; [JD] *COI* sequences provided by John Day, UK; [MP] *COI* sequences provided by Mateus Pepinelli, Brazil, and published in Hamada *et al.* (2010) [for *S. guianense s.l.* 13 sequences were provided].

TABLE 2. List of *Trichodagmia* species, extraction methods and PCR success for full, midi and minibarcodes from specimens of Simuliidae held in the BMNH collection. F= female; M= male; P=pupa; L=larva; n/a= not tested; m/cont= multiple bands and/or contamination.

EXCTRACTION METHOD SPECIES	DATE	AGE	PRESERVATION (*n*)	LIFE STAGE	FULL/ MIDI BARCODES POSITIVE PCRs	READABLE SEQ. (*n*)	MINIBARCODES POSITIVE PCRS	GOOD SEQ. (*n*)
NON-DESTRUCTIVE			**PINNED**					
1-Legs into PCR Mix								
S. tarsatum	2009	1 yr	10	F/M	8	8	n/a	n/a
S. guianense s.l.	1990s'	>10 yrs	43	F/M	0	0	n/a	n/a
S. perplexum	1937	>73 yrs	2	F	0	0	2	m/cont
DESTRUCTIVE /NON-DESTRUCTIVE			**PINNED**					
2- Abdomens								
S. nigrimanum	2002	8 yrs	9	F	9	9	2	m/cont
S. nigrimanum	1995	16 yrs	1	F	1	1	1	m/cont
DESTRUCTIVE			**ETHANOL**					
3-Part of body								
S. guianense s.l.	2001	10 yrs	5	P	4	4	5	m/cont
S. guianense s.l.	1984	26 yrs	3	P	1	0	3	m/cont
S. duodenicornium	2005	5 yrs	2	P	6	4	2	1
S. hirtipupa	2002	8 yrs	4	P	4	3	3	2
S. earlei	2009	1 yr	2	P	2	2	n/a	n/a
S. hippovorum	1998	12 yrs	1	L/P	1	1	n/a	n/a
S. virgatum s.l.	1999	11 yrs	1	L	1	1	n/a	n/a
S. freemani	1998	13 yrs	2	L	2	2	n/a	n/a
S. solarii	1995	15 yrs	1	L	1	0	n/a	n/a
4- Diluted Carnoy's			**CARNOY'S**					
S. ornatum s.l.	2009	1 yr	2	L	2	2	n/a	n/a
TOTAL			88		42	37 (88.9%)	18	5 (25%)

TABLE 3. Interspecific (between groups) pairwise K2P genetic divergence of unique DNA barcodes (*c.* 606), representing 19 species of the subgenus *Trichodagmia*, one species of the subgenus *Aspathia* and four species of the subgenus *Simulium s.str.* Highest pairwise distance (most divergent taxa) and lowest pairwise distance (most closely related taxa) are highlighted in blue and yellow, respectively.

	hip	*rub*	*free*	*hier*	*inno*	*picti*	*clari*	*hunt*	*sola*	*tars*	*ethe*	*earl*	*pulv*	*litho*	*orbi*	*ita*	*hirt*	*scut*	*deci*	*dec*	*noel*	*posti*	*huai*
S. hippovorum																							
S. rubrithorax	0.106																						
S. freemani	0.117	0.093																					
S. hieroglyphicum	0.131	0.116	0.096																				
S. innoxium	0.131	0.125	0.115	0.126																			
S. pictipes	0.142	0.107	0.116	0.124	0.060																		
S. claricentrum	0.132	0.138	0.122	0.119	0.035	0.078																	
S. hunteri	0.137	0.155	0.127	0.139	0.139	0.143	0.147																
S. solarii	0.158	0.135	0.122	0.139	0.152	0.147	0.162	0.160															
S. tarsale	0.126	0.111	0.106	0.117	0.132	0.127	0.140	0.146	0.115														
S. chiriquiense	0.137	0.121	0.112	0.130	0.111	0.103	0.119	0.136	0.116	0.111													
S. earlei	0.126	0.137	0.130	0.148	0.140	0.153	0.147	0.162	0.141	0.146	0.137												
S. pulverulentum	0.125	0.123	0.109	0.126	0.129	0.139	0.141	0.147	0.113	0.127	0.109	0.120											
S. lithobranchium	0.166	0.143	0.127	0.155	0.159	0.151	0.153	0.154	0.146	0.153	0.133	0.162	0.128										
S. orbitale	0.163	0.152	0.130	0.151	0.174	0.166	0.169	0.161	0.143	0.145	0.141	0.167	0.131	0.030									
S. itaunense	0.189	0.185	0.162	0.169	0.184	0.174	0.189	0.195	0.166	0.182	0.145	0.194	0.150	0.050	0.032								
S. hirtipupa	0.150	0.142	0.119	0.138	0.147	0.145	0.149	0.150	0.132	0.139	0.123	0.146	0.114	0.046	0.036	0.029							
S. scutistriatum	0.161	0.142	0.130	0.127	0.151	0.151	0.156	0.147	0.126	0.145	0.136	0.162	0.125	0.145	0.143	0.163	0.127						
S. decimatum	0.132	0.140	0.136	0.150	0.130	0.130	0.137	0.144	0.156	0.132	0.132	0.170	0.140	0.154	0.149	0.162	0.142	0.169					
S. decorum	0.165	0.158	0.152	0.162	0.151	0.158	0.149	0.163	0.173	0.157	0.144	0.177	0.143	0.171	0.172	0.180	0.169	0.165	0.117				
S. noelleri	0.169	0.156	0.144	0.172	0.152	0.155	0.166	0.181	0.179	0.157	0.142	0.167	0.144	0.172	0.169	0.177	0.161	0.158	0.113	0.072			
S. posticatum	0.174	0.148	0.147	0.163	0.140	0.143	0.159	0.152	0.167	0.152	0.149	0.178	0.156	0.164	0.160	0.184	0.152	0.148	0.131	0.129	0.130		
S. huairayacu	0.135	0.122	0.122	0.120	0.132	0.132	0.135	0.147	0.164	0.127	0.131	0.154	0.125	0.147	0.161	0.182	0.146	0.147	0.146	0.153	0.163	0.133	
S. nigrimanum	0.153	0.149	0.130	0.122	0.136	0.143	0.139	0.148	0.143	0.157	0.144	0.166	0.119	0.147	0.154	0.168	0.136	0.138	0.158	0.170	0.186	0.173	0.134

TABLE. 4. Levels of genetic divergence in known and suspected species complexes and number of individuals per taxon (full barcode data set).

Species complex status	Source of information	*n*	% of divergence (max)
Confirmed species complexes			
S. (Aspathia) metallicum s.l.	Conn *et al.* (1988; 1989)	6	1.24
S. (Trichodagmia) virgatum s.l.	Adler *et al.* (2004); Rivera & Currie (2009)	10	3.38
S. (Simulium) arcticum s.l.	Adler *et al.* (2004); Rivera & Currie (2009)	7	2.61
S. (Simulium) ornatum s.l.	Post (1980); Adler & Crosskey (2010)	2	1.00
S. (Simulium) tuberosum s.l.	Adler *et al.* (2004); Rivera & Currie (2009)	10	3.79
S. Simulium) venustum s.l.	Adler *et al.* (2004); Rivera & Currie (2009)	14	2.69
S. (Trichodagmia) guianense s.l.	Charalambous *et al.* (1996); Shelley *et al.* (2010)	15	2.05
		15	
Suspected species complexes			
S. (Trichodagmia) paynei	Adler *et al.* (2004)	15	3.07
S. (Simulium) murmanum	Rivera & Currie (2009)	3	3.57
With well supported splits in the NJ (> 80% bootstrap values)			
S. (Aspathia) piperi	Adler *et al.* (2004). This work [see subgroups in Fig. 1]	11	0.91
S. (Trichodagmia) canadense	Adler *et al.* (2004). This work [see subgroups in Fig. 1]	17	1.37
S. (Trichodagmia) tarsatum	Shelley *et al.* (2002a). This work [see Fig. 1]	33	3.28
S. (Trichodagmia) duodenicornium	This work [see Fig. 1]	17	0.94
S. (*Simulium) rostratum*	Rivera & Currie (2009). This work [see Fig. 1]	2	3.07

TABLE 5. Interspecific (between groups) pairwise K2P genetic divergence of unique DNA barcodes (*c.* 606bp), for known or suspected species complexes of six species of the subgenus *Trichodagmia*, two species of the subgenus *Aspathia* and six species of the subgenus *Simulium s.str.* Highest pairwise distance (most divergent taxa) and lowest pairwise distance (most closely related taxa) are highlighted in blue and yellow, respectively. Suspected species complexes documented in the literature are marked with an asterisk (*). The probable existence of a species complex is marked with two asterisks (**).

	virga	*payn*	*pipe*	*metal*	*tars*	*cana*	*duod*	*guia*	*tube*	*ros*	*orna*	*venu*	*arct*
S. virgatum s.l.													
S. paynei *, **	0.060												
S. piperi **	0.168	0.160											
S. metallicum s.l.	0.145	0.157	0.144										
S. tarsatum **	0.115	0.116	0.143	0.138									
S. canadense **	0.127	0.139	0.144	0.155	0.103								
S. duodenicornium	0.134	0.148	0.170	0.161	0.130	0.129							
S. guianense s.l.	0.137	0.155	0.174	0.158	0.130	0.137	0.0386						
S. tuberosum s.l.	0.137	0.133	0.154	0.138	0.129	0.138	0.1456	0.150					
S. rostratum *, **	0.129	0.123	0.145	0.120	0.118	0.128	0.152	0.155	0.097				
S. ornatum s.l.	0.155	0.141	0.132	0.1398	0.128	0.149	0.157	0.164	0.104	0.101			
S. venustum s.l.	0.150	0.145	0.152	0.159	0.141	0.153	0.147	0.154	0.124	0.118	0.11		
S. arcticum s.l.	0.168	0.171	0.142	0.158	0.135	0.141	0.136	0.1431	0.124	0.121	0.119	0.118	
S. murmanum *, **	0.161	0.159	0.160	0.1517	0.136	0.1403	0.142	0.146	0.130	0.123	0.111	0.117	0.1013

4.8. APPENDIX 3. ACCESSION NUMBERS OF THE COI DNA BARCODING REGION SEQUENCES USED IN THIS PAPER.

1. The sequences of species of *Trichodagmia* and related taxa not stated below can be found at BOLD - www.boldsystem.org. They are held under the project titles "**New World Blackflies Hernández_2008**" and "**Blackflies of the New World_Hernández 2009**"; and the forthcoming project "**New World Trichodagmia_Hernández 2010**".

2. The sequences of *S. posticatum* are only currently available at request to John Day (Centre for Ecology and Hydrology, Wallingford, UK).

Simulium (Simulium) posticatum
Spos UHey05 COI M13F D07_JDPLATE07-D7; Spos_Lhan01_COI_M13F_C06_JDPLATE07-C6
Spos_Lhan02_COI_M13F_D06_JDPLATE07-D6; Spos_Lhan03_COI_M13F_E06_JDPLATE07-E6
Spos_Lhan05_COI_M13F_F06_JDPLATE07-F6; Spos_Lhan06_COI_M13F_G06_JDPLATE07-G6
Spos_UHey01_COI_M13F_H06_JDPLATE07-H6; Spos_UHey02_COI_M13F_A07_JDPLATE07-A7;
Spos_UHey03_COI_M13F_B07_JDPLATE07-B7; Spos_UHey04_COI_M13F_C07_JDPLATE07-C7;
Spos_UHey05_COI_M13F_D07_JDPLATE07-D7;

2. The following sequences were downloaded from GenBank and originate from the paper of RIVERA & CURRIE (2009).

Simulium (Aspathia) hunteri
ACBBsimW2K; ACBBsimW2J; ACBBsimW2I;ACBBsimW2H2; ACBBsimW2G1; ACBBsimW2F2; ACBBsimW2E1; ACBBsimW2D1. ACBBsimW2C3; ACBBsimW2B4; ACBBsimW2A4

Simulium (Aspathia) piperi
ACBSimBC53c2; ACBSimBC53b3; ACBSimBC36a2; ACBSimBC36a1; ACBSimBC13b; ACBSimBC9a5; ACBSimBC9a4; ACBSimBC9a3; ACBSimBC9a2; ACBSimBC9a1; ACBSimW44A2

Simulium (Trichodagmia) canadense
ACBBsimBC2a6;ACBBsimBC2a5;ACBBsimBC2a4; ACBBsimBC2a3; ACBBsimBC2a2; ACBBsimBC2a1; ACBSimBC48a2; ACBSimBC43d; ACBSimW44J; ACBSimW44I; ACBSimW44H; ACBSimW44G; ACBSimW44F; ACBSimW44E; ACBSimW44D; ACBSimW44C; ACBSimW44B2

***Simulium (Simulium) arcticum* (complex)**
ACBSimW217C; ACBSimW34E; ACBSimW51D; ACBSimW51E; ACBSimBC21b1; ACBSimW77C; ACBSimW77D

Simulium (Simulium) decimatum
ACBSim100; ACBSim102; ACBSim117; ACBSim111; ACBSim163; ACBSim116; ACBSim208

Simulium (Simulium) decorum:
ACBSimAL107a5; ACBSimAL107a4; ACBSimAL107a3; ACBSimAL107a2;ACBSimAL107a1; ACBSimW109A3; ACBSimMN22; ACBSimMN14a; ACBSimMN2b

***Simulium (Simulium) murmanum* (suspected complex)**
ACBSimMN16d4; ACBSimMN27b; ACBSimAL106

Simulium (Simulium) noelleri
ACBSim188; ACBSim156; ACBSim138; ACBSim153; ACBSim145; ACBSim104; ACBSim101; ACBSim181; ACBSim239; ACBSim130; ACBSim147; ACBSim142; ACBSim144; ACBSim181; ACBSim239; ACBSim130; ACBSim147; ACBSim142; ACBSim144

Simulium (Simulium) noelleri
ACBSim188; ACBSim156; ACBSim138; ACBSim153; ACBSim145; ACBSim104; ACBSim101; ACBSim181; ACBSim239; ACBSim130; ACBSim147; ACBSim142; ACBSim144; ACBSim181; ACBSim239; ACBSim130; ACBSim147; ACBSim142; ACBSim144

Simulium (Simulium) rostratum
ACBSim235; ACBSimAM22; ACBSimNO15a3.

***Simulium (Simu.) tuberosum* (complex)**
ACBBsimW249A3; ACBSim129; ACBSimW194C1; ACBSimMN20b3; ACBSimMN34a2; ACBSimAM9; ACBSimW19C1; ACBSimW109B1; ACBSim194

***Simulium (Simulium) venustum* (complex)**
ACBSimBFA1; ACBSimBFA6; ACBSimCT43; ACBSim118; ACBSim150; ACBSim108.

3. The following sequences were provided by MATEUS PEPINELLI; Universidad de São Paulo; Brazil. They originate from the paper of HAMADA *et al.* (2010)

Simulium (Trichodagmia) duodenicornium
BNBMP01909|BNB200019; BNBMP02009|BNB200020; BNBMP02109|BNB200021;
BNBMP02209|BNB200022; BNBMP02309|BNB200023; BNBMP02409|BNB200024
BNBMP02609|BNB200026; BNBMP02709|BNB200027; BNBMP02809|BNB200028
BNBMP02909|BNB200029; BNBMP03009|BNB200030; BNBMP03109|BNB200031
BNBMP03209|BNB200032

***Simulium (Trichodagmia) guianense* (complex)**
MPBNB21107|UFSCAR MP00211; MPBNB21207|UFSCAR MP00212; MPBNB21407|UFSCAR MP00214;
MPBNB21507|UFSCAR MP00215; MPBNB21607|UFSCAR MP00216; MPBNB21707|UFSCAR MP00217
MPBNB21807|UFSCAR MP00218; MPBNB21907|UFSCAR MP00219; MPBNB22007|UFSCAR MP00220;
MPBNB22307|UFSCAR MP00223; MPBNB22407|UFSCAR MP00224; MPBNB22507|UFSCAR MP00225

Simulium (Trichodagmia) lithobranchium
BNBMP05109|BNB200051; BNBMP05309|BNB200053; BNBMP05409|BNB200054

Simulium (Trichodagmia) orbitale
MPBNB01607|UFSCAR MP00016; MPBNB01707|UFSCAR MP00017; MPBNB01807|UFSCAR MP00018;
MPBNB01907|UFSCAR MP00019; MPBNB02207|UFSCAR MP00022; MPBNB02307|UFSCAR MP00023
MPBNB02407|UFSCAR MP00024; MPBNB02507|UFSCAR MP00025

Simulium (Trichodagmia) scutistriatum
BNBMP30109|BNB200301; BNBMP30209|BNB200302; BNBMP30309|BNB200303;
BNBMP30409|BNB200304; BNBMP30509|BNB200305; BNBMP30609|BNB200306
BNBMP30709|BNB200307; BNBMP30809|BNB200308; BNBMP30909|BNB200309
BNBMP31009|BNB200310; BNBMP37109|BNB200371; BNBMP37209|BNB200372
BNBMP37309|BNB200373; BNBMP37409|BNB200374; BNBMP37509|BNB200375
BNBMP37609|BNB200376; BNBMP37709|BNB200377; BNBMP37809|BNB200378

5. GENERAL DISCUSSION

In this work, the systematics of the subgenus *Trichodagmia* has been reassessed employing an integrated taxonomic approach (WILL *et al.*, 2005) based upon revisionary morphological taxonomy, phylogenetic (cladistics) analysis of morphological characters, and DNA barcoding. The subgenus *Trichodagmia* includes one of the primary vectors of onchocerciasis in Brazil (*S. guianense s.l.)* and other highly anthropophilic species of medical or veterinary importance such as *S. nigrimanum*, *S. orbitale* and *S. townsendi*. Many other species are morphologically very similar to these taxa (*e.g. S. duodenicornium*, *S. lithobranchium*, and *S. rubrithorax*), making their identification a difficult task. Therefore, an integrated approach is essential for the correct delineation of species boundaries and species identification, and thus also for our understanding of simuliid species distribution.

Needless to say, a correct identification of a given simuliid taxon will immediately facilitate access to other important taxon-related information such as current classification, distribution, biology and its medical importance. The latter is of paramount importance for the ongoing river blindness eradication campaigns in South America (*e.g.* RODRÍGUEZ-PÉREZ, 2004, 2006). Correct species identification is also essential for current assessments of freshwater macroinvertebrates as water quality indicators in Central America (SPRINGER & ERMEÑO CHICAS, 2010).

5.1. Taxonomic contribution

Different hypothesis have been postulated on the correct classification of Simuliidae in the Neotropical region (COSCARÓN & COSCARÓN-ARIAS, 2007; SHELLEY *et al.*, 2010) (**Chapter 1**). Although these are congruent at a certain level, researchers seem unable to agree which taxonomic ranking should be given to certain taxa such as *Cerqueirellum*, *Coscaroniellum*, *Inaequalium*, *Psaroniocompsa*, *Hemicnetha*, and *Trichodagmia*. In this work, the history of the classification and taxonomy of the subgenus *Trichodagmia* has been detailed to provide a context for the most up-to-date views of simuliid systematists in South America (*e.g.* COSCARÓN & COSCARÓN-ARIAS, 2007; SHELLEY *et al.*, 2010) and in North America (*e.g.* ADLER *et al.*, 2004) (**Chapter 2**).

Firstly, some taxonomic changes are proposed in this work based upon the examination of numerous specimens, including newly collected ones, and type material for most of the species. Three new junior synonymies are proposed (*Simulium chiriquiense* FIELD = *S. ethelae* DALMAT **n. syn.**; *S. biuxinisa* COSCARÓN & IBÁÑEZ-BERNAL = *S. paynei* VARGAS **n. syn.**; and *S. keenani* FIELD = *S. earlei* VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA **n. syn.**). A neotype is designated for *S. lahillei* (PATERSON & SHANNON) and a lectotype for *S. pulverulentum* KNAB. In addition, *Simulium falculatum* ENDERLEIN is transferred from the TARSATUM species group to the CANADENSE species group based on the morphology of the female genitalia. *Simulium oviedoi* and *S. rivasi* are now placed in the subgenus *Psilopelmia*, BICOLORATUM species group, based on the structure of the female cibarium and the male genitalia.

Moreover, the subgenus *Obuchovia* is here considered a **new junior synonym** of *Trichodagmia*, and now all *Obuchovia* constituent species are placed in the ALBELLUM species group thus including a Palaearctic element within the subgenus *Trichodagmia*. MIRANDA-ESQUIVEL & COSCARÓN (2001) postulated a Gondwanan origin for the subgenus *Trichodagmia* and other related taxa, and the proposed synonymy is concordant with this hypothesis.

Type material has been illustrated for the first time by using modern Digital Imaging Analysis systems, especially in the poorly known CANADENSE species group (most of the species) and certain species within the ORBITALE, PICTIPES and the TARSATUM species groups. Furthermore, keys to separate all species groups and individual species based on the adults, pupae and larvae are also provided, with details on the distribution, biology and medical importance for each species. This should facilitate the identification of those taxa of medical importance by non-taxonomists and epidemiologists.

The most relevant literature scattered across a plethora of multi-language papers is also unravelled, and clarification of the tangle of names of types, their condition, type localities and type depositaries is given. These issues are essential for the understanding of the ecology not only of species in the subgenus *Trichodagmia* but also of the whole family Simuliidae, which is still poorly understood in

South America (HAMADA & McCREADIE, 1999). With regards to species complexes in the subgenus *Trichodagmia*, this work also provides the necessary basic information and identification tools to undertake further integrated taxonomic studies in species complexes of medical importance such as *S. guianense s.l.*, especially in Venezuela and Brazil (where it is a vector of onchocerciasis). Another complex that still requires further work is that of *S. virgatum s.l.* (mainly in the USA) in relation to the closely related taxa *S. hippovorum*, *S. solarii* and *S. paynei*. MUHAMMAD (1988) showed through cytological analysis of larvae collected mainly from southwestern USA and Guatemala that *S. virgatum* is a sibling species complex of four cytotypes (denominated A-D). However, PETERSON & KONDRATIEFF (1995), in their review of the black flies of Colorado State in the USA, recommended a review of the taxonomy of this species complex because collections made in the same and other localities collected by MUHAMMAD in Texas suggested to these authors that he may have misidentified some of his specimens and was dealing with morphologically different species and not just *S. virgatum s.str.*

5.2. Phylogenetic analysis

Taxonomy and systematics are the bedrock of all biological sciences (GRANT, 2009) and the estimation of a group's phylogenetic history can identify historical events that led to contemporary patterns of biodiversity, can provide a more objective classification based on an explicit evolutionary hypothesis, and can help understand the origins and evolution of particular traits such as anthropophily (ADLER *et al.*, 2010). However, phylogenetic studies will be facilitated by an initial sound taxonomic understanding of the species involved, in terms of taxon sampling and interpretation of results.

In order to establish the phylogenetic relationships in *Trichodagmia* species, and to translate this in a classification reflecting their evolution, a cladistic analysis was carried out using morphological characters of the females, males, pupae and larvae of 67 species. Analyses of the full data set with 67 characters were carried out using WinClada with multistate characters treated as unordered under equal weights (**Chapter 3**, Figs. 1, 2). The analysis of separate data sets derived from immature and adult stages in insects with complete metamorphosis is common in cladistics, but a "total evidence approach" was adopted because it maximizes congruence between all characters and thus provides the greatest possible explanatory power (KITCHING, 2002). In Diptera, phylogenetic estimations using total evidence have been commonly carried out at the family level (for example by REINERT *et al.*, 2004, on Culicidae, and ADLER *et al.*, 2010, on Simuliidae), at the subgeneric level (in Simuliidae by MIRANDA-ESQUIVEL & COSCARÓN, 2001, on *Trichodagmia* and *Thyrsopelma*), but also to infer deeper phylogenies within the order Diptera (*e.g.* YATES & WEIGMAN, 1999), and hence this rationale was followed in the current work.

It was demonstrated that the subgenus *Trichodagmia* is monophyletic and is defined by a combination of seven unique characters (**Chapter 3**, Figs. 1, 2). Species placed in the ALBELLUM species group (old subgenus *Obuchovia*) are monophyletic in a sister-group relationship with the other species groups in *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010). This relationship confirmed the proposal of ADLER *et al.* (2010) with regard to the overall similarity of species of ALBELLUM with that of the TARSATUM species group (old subgenus *Hemicnetha*) and *Trichodagmia*, which led them to consider the subgenus *Obuchovia* as a synonym of *Hemicnetha*. Moreover, the clade ORBITALE species group (old subgenera *Trichodagmia* + *Thyrsopelma*) was recovered as monophyletic by a combination of seven synapomorphies with 89% bootstrap support (**Chapter 3**, Fig. 2). In this clade, species related to *S. guianense s.l.* were diagnosed by a combination of four characters, one of which (male ventral plate with a globular median process) was unique to this group. The position of *S. hirtipupa* is well resolved in the latter clade by the presence of black spiniform setae on the frontoclypeus and thorax of the pupa. MIRANDA-ESQUIVEL & COSCARÓN (2001) obtained similar results, but these authors gave both *Trichodagmia* and *Thyrsopelma* generic rank. This view is not followed in the current work, nor by other taxonomists (*e.g.* ADLER & CROSSKEY, 2010; SHELLEY *et al.*, 2010).

The CANADENSE (old subgenus *Hearlea*) and TARSATUM clades were diagnosed by five and three apomorphies, respectively (**Chapter 3**, Fig. 2). Within CANADENSE only species with larvae having sclerotized plates in the posterior region of the abdomen were well resolved, which is in agreement with the results of COSCARÓN *et al.* (2004). Species within the TARSATUM clade were defined by homoplasious characters only.

Similarly, taxa in the PICTIPES species group (old subgenus *Shewellomyia*) were only diagnosed by homoplasies, but the combination of these characters was unique for this clade. The latter might be an example of a polythetic taxon (REINERT *et al.*, 2009) in which the group is not diagnosed by unique characters, but rather a unique combination of characters (**Chapter 3**, Fig. 2). The latter highlights that more work is still needed in order to resolve these issues, most probably by employing mitochondrial and nuclear molecular markers and cytogenetics linked to the variation in morphological characters. This might confirm the comparative flexibility of the homoplasies, or falsify the present hypothesis about the phylogenetic structure of the group concerned.

5.3. Implication of the phylogenetic analysis on the classification of the subgenus *Trichodagmia*

The long history of many changes in the classification of subgenus *Trichodagmia* outlined in **Chapter 2** and **Chapter 3** show that there is no general agreement amongst authors with regards to the taxonomy of *Trichodagmia*. This study updates this issue through new studies and provided a detailed morphotaxonomic framework of all species presently included in the subgenus *Trichodagmia*. However, a question that remains is: What constitutes *Trichodagmia*? As shown in this study, the subgenus *Trichodagmia* is monophyletic being delineated by eight apomorphies and a bootstrap value of 98% and jackknife value of 99%, respectively (**Chapter 3**, Fig. 2). Moreover, the taxon names of previous authors [see section **5.2** of this chapter**,** and also section **2.9 APPENDIX 3**, TABLE 1 in **Chapter 2**] such as *Hearlea* (*sensu* COSCARÓN *et al*., 2004), *Obuchovia* (CROSSKEY & HOWARD, 2004), *Shewellomyia*, *Trichodagmia* + *Thyrsopelma* [the ORBITALE species group of MIRANDA-ESQUIVEL & COSCARÓN, 2001], and *Hemicnetha* were recovered as monophyletic, also with relatively good support values (Fig. 2). *Obuchovia* and *Trichodagmia* + *Thyrsopelma* are diagnosed by two and three unique characters, respectively, with bootstrap and jackknife values of >85%. *Hearlea* and *Hemicnetha* were only supported by a single unique character, while *Shewellomyia* was solely diagnosed by homoplasies, though still with high support values for this group. In general, the phylogenetic relationships between the species in each subgenus were relatively less resolved, although a clade within *Hearlea* (*S. johnsoni*, *S. gorirossiae, S. larvispinosum, S. menchacai* and *S. temascalense*) and another within *Trichodagmia* comprising species closely related to *S. guianense s.l.* (*S. duodenicornium*, *S. itaunense*, *S. lithobranchium*, *S. orbitale*, and *S. perplexum*) were delimited by unique characters. The general distribution of homoplastic characters with regard to species relationships within *Hemicnetha* is not unexpected, given the close morphological similarities between all taxa in this clade. Further work is needed to resolve this issue, perhaps using a combination of nuclear and mitochondrial molecular markers and chromosomal banding patterns.

It is difficult to decide which level of taxonomic ranking should be given to the clades defined in phylogenetic studies, including this study. A rather conservative approach to the classification of the subgenus *Trichodagmia* has been adopted in this thesis. The recognition of a smaller number of genera and subgenera in the family Simuliidae has been postulated by numerous authors*,* for example ADLER *et al.* (2004), ADLER & CROSSKEY (2008, 2009, 2010) and SHELLEY *et al.* (2010). These authors have advocated for such rationale until molecular and cytogenetic characters can be linked to morphological variation. Moreover, in Neotropical Simuliidae knowledge of the morphological variation in larval characters is still in the alpha-taxonomic stage. Larval features still remain unknown or poorly described and/or illustrated for many taxa. These conservative views were first postulated by the early works of R.W. CROSSKEY (as detailed in CROSSKEY, 1988, 1990), who argued that the erection of too many genera (or subgenera), diagnosed on variable morphological characters, will offer little biological information and will most likely prove unstable. Furthermore, it would also unbalance the classification system of the family Simuliidae in comparison to other Diptera families. However, RUBTZOV (1974) postulated that splitting the family so that there were hundred species within a single genus created practical problems, especially with regards to the species identification. For this reason he (RUBTZOV, 1974) proposed the erection of genera which each contained 10 to 20 species. Wether groupings of this size are a practical convenience or not, this is not argument to having a large number of genera, because these "convenient size groupings" could be considered as subgenera or species groups.

Because of the arguments mentioned above, it is proposed in this work that the subgeneric names *Hearlea*, *Hemicnetha*, *Obuchovia*, *Trichodagmia* + *Thyrsopelma* and *Shewellomyia* should be recognized as informal species groups within the subgenus *Trichodagmia* (**Chapter 3**, Fig. 3). With the inclusion of the subgenus *Obuchovia* as a junior synonym of *Trichodagmia*, the subgenus *Trichodagmia* now consist of five species groups: the ALBELLUM species group [= old subgenus *Obuchovia*]; CANADENSE species group [= old subgenus *Hearlea*]; PICTIPES species group [= old subgenus *Shewellomyia*]; ORBITALE species group [= the old subgeneric names *Trichodagmia* + *Thyrsopelma* of MIRANDA-ESQUIVEL & COSCARÓN (2001) and COSCARÓN & COSCARÓN-ARIAS (2007)]; and the TARSATUM species group [= old subgenus *Hemicnetha*] [see also **Chapter 2**, section **2.4.3 "Checklist of *Trichodagmia* species"**].

The phylogenetic estimation was not in general at variance with taxonomic decisions which had been based upon the classical morphotaxonomic study (**Chapter 2**). The main value of the phylogenetic study was that it gave objective taxonomic credence to the subjective classification based upon the classical morphotaxonomy. However, the results in **Chapter 3** (see Figs. 2, 3) should stimulate further research that may bring about modification and improvement of the classification (as discussed by ZAVORTINK, 1979). The phylogeny was generally not taxonomically helpful at the species level, for example in determining species boundaries or characters for species identification.

5.4. Molecular markers - DNA barcoding

The relative morphological homogeneity of blackflies does not lead to a straightforward taxonomy for most subgenera of the genus *Simulium*. There is a requirement for the application of potentially more sensitive methods such as molecular markers for both species identification and phylogenetic inference (especially because of the medical importance of Simuliidae). In recent years, technological advances have enabled the use of DNA sequences to estimate the evolution of the Simuliidae at the genus and subgenus levels, albeit with poor success (MOULTON, 2000, 2003). However, molecular markers have proved useful as an aid for identification of the vector species of *O. volvulus*, and in the separation of other closely related taxa (ADLER *et al.*, 2010; AGATSUMA *et al.*, 1993; BROCKHOUSE *et al.*, 1993; POST & FLOOK, 1992; PRUESS *et al.*, 1992; RODRÍGUEZ-PÉREZ, *et al.*, 2004, 2006; SAWYER, 1991; SCARPASSA & HAMADA, 2003; TOÉ *et al.*, 1997).

At present, the DNA barcoding region of the mitochondrial *COI* gene is the front-runner as a molecular marker for species identification of animals in general, and possibly for the discovery of cryptic diversity (HEBERT *et al.*, 2003a,b). It has also been shown that DNA barcoding can be a versatile tool in species identification in many groups of organisms, when it is integrated in morphological frameworks (*e.g.* HEBERT *et al.*, 2003a; JANZEN *et al.* 2005; SMITH *et al.*, 2006, 2007, 2008). The detailed morphotaxonomic revision of the subgenus *Trichodagmia* in the current work (**Chapter 2**) paved the way to test the robustness of DNA barcoding for species identification and for revealing hidden diversity in a group of morphologically difficult species.

CYWINSKA (2006) claimed that in order to be effective a DNA-based identification needs to satisfy three conditions: 1- it must be possible to recover the target DNA from all species; 2- the sequence information must be easily analyzed, and 3- the information content of the target sequence must be sufficient to enable species-level identification. The three conditions were met for *Trichodagmia* using *COI* barcodes, especially from specimens that had been recently collected and were preserved in alcohol or pinned.

DNA barcoding campaigns also require a sufficient level of taxonomic expertise in the target group, as reliable *a priori* identifications need to be associated with each specimen. They also require sufficient manpower, because this is critical for the taxon sampling, sequencing and input of the specimens' data (including digital images) into a taxonomic database such as BOLD. These conditions are critical and the loss of taxonomic expertise in certain groups (and the lack of funding for taxonomy) can endanger the success of barcoding campaigns. Moreover, barcoding campaigns frequently advocate prospecting specimens held in museums in order to obtain DNA data. This requires that: 1- the specimens have been correctly identified (and this is not always the case – even in Museums); 2- personnel are available and are capable of sampling the collection; and 3- the museum/institution agrees. With regards to the subgenus *Trichodagmia*, these conditions were fully met.

Nearly all well-established morphospecies in the subgenus *Trichodagmia* formed defined groups in the Neighbour Joining (NJ) tree based on DNA barcodes (**Chapter 4**, Fig. 1). Genetic divergence between morphospecies averaged 11.2% (range 2.8-19.5%), whereas intraspecific genetic divergence within morphologically distinct species averaged 0.5% (range 0-1.28%) (**Chapter 4**, TABLE 1).

In species complexes, maximum values of genetic divergence (3.28-3.79%) indicated the presence of cryptic diversity (**Chapter 4**, TABLE 4), and these values agree with those observed by RIVERA & CURRIE (2009) for Nearctic Simuliidae, and those observed by CYWINSKA (2006) for Nearctic mosquitoes. The existence of well defined groups in the NJ tree within *S. paynei* is concordant with its putative status as a sibling species complex, and similarly well defined groups within the morphospecies *S. piperi*, *S. duodenicornium*, *S. canadense*, *S. rostratum* and *S. tarsatum* highlighted the possible existance of species complexes (especially *S. tarsatum* with high levels of within species diversity.

It was possible to recover and align the *COI* DNA barcode fragment in the majority of the species of the subgenus *Trichodagmia.* Adding legs directly to the PCR mix from relatively freshly collected and link-reared specimens was a cheap and fast methodology for obtaining full barcodes. However, specimens collected more than 10 years ago did not yield reliable and readable sequences. Efforts to obtain a shorter barcode sequence (midi- and mini-barcodes) proved to be problematic in terms of the quality of the sequence and also time-consuming, especially the optimization of the DNA extraction and PCR methods. However, in cases where a readable sequence was obtained, they provided a good resolution in species identification (**Chapter 4**, Fig. 2), as was also found by HAJIBABEI *et al.* (2007) and MEUSNIER *et al.* (2008). Nonetheless, this approach should not be seen as an easy option for sampling taxa for which no fresh or recently collected material is at hand.

RIVERA & CURRIE (2009) have explored some of the limitations of the DNA barcoding of blackflies, especially the difficulty of obtaining DNA from larvae fixed in Carnoy's solution. They recommended dividing the larvae in three parts soon after collection, with the abdomen preserved in Carnoy's for cytological analysis, the thorax in alcohol for molecular analysis, and the head retained as a voucher in alcohol for morphological studies. This would be rational, but this process is tedious and time consuming. However, recent studies have shown that DNA can be recovered from specimens in Carnoy's if they have been collected within three months or longer (*e.g.* CONFLITTI *et al.*, 2010; KRÜGER, 2010), and this study also showed (**Chapter 4,** Table 2) that preservation in a 'weak' Carnoy's solution (9:1) yielded full DNA barcode sequences, potentially simplifying the process of molecular and cytological screening of the same individual simuliid larva.

Regardless of the current arguments against the use of *COI* barcoding gene in phylogenetic studies (**Chapter 4**), it can be expected that the *COI* gene carries some phylogenetic signal. In this study, the DNA barcode NJ tree profile of the subgenus *Trichodagmia*, and the related subgenera *Aspathia* and *Simulium s.str.*, exhibited some degree of concordance with that of RIVERA & CURRIE (2009), and the morpho-phylogenetic concept proposed in this work for certain species groups (**Chapter 3**) and ADLER *et al.* (2004). When the full barcode dataset was analyzed employing the maximum likelyhood algorithm [tree not shown], species of the subgenus *Aspathia* and *Simulium s.str.*, and the PICTIPES and ORBITALE species groups formed monophyletic groups. In addition, species related to the complex *S. virgatum s.l.* in the TARSATUM species group were also recovered in a single cluster (*S. hippovorum*, *S. paynei* and *S. rubrithorax*). However, a combination of other mitochondrial markers (*e.g. ND4*, *COII*) with nuclear region markers such as ITS, and DNA data from species of the ALBELLUM species group, might enable the reconstruction of the deeper phylogenetic relationships of the subgenus *Trichodagmia* within the tribe Simuliini.

Of the 340 valid South American simuliid species recognized by SHELLEY *et al.* (2010) and this work (**Chapter 1**, section **1.5**), only 118 species belonging to the genera *Cnesia*, *Gigantodax*, *Lutzsimulium*, *Paraustrosimulium*, *Pedrowygomyia* and *Simulium* have been barcoded to date (including this study). No barcode data exist for species of the genus *Tlalocomyia*, and only a handful of species (1-3 taxa) have been barcoded in the subgenera *Aspathia*, *Pternaspatha* and *Psilopelmia.* This work also adds barcoding data from three species occurring in North America (*S. claricentrum*, *S. innoxium*, and *S. pictipes*). Even though some of the main river blindness vectors in Latin America (*e.g. S. guianense s.l.*, *S. metallicum s.l.*, *S. oyapockense*) or highly anthropophilic species such as *S. nigrimanum*, *S. quadrivittatum* and *S. ganalesense* (PEPINELLI *et al.*, 2009; L.M. HERNÁNDEZ, unpublished data) have been barcoded, there is still much work to be done in this area. For example, no data is available for other vectors species such as *S. ochraceum s.l.*, and *S. exiguum s.l.*, nor for populations of these species in different foci of the disease.

With regards to the species complexes, little is known about the DNA barcoding profile of each of the main vector complexes in combination with their chromosomal banding pattern across their distribution range, thus highlighting the continuing need for research using an integrated taxonomic approach on the family Simuliidae in the Neotropical Region.

In summary, the *COI* barcoding gene correctly distinguished nearly 100% of the morphologically distinct species in the subgenus *Trichodagmia*, demonstrating its versatility as a DNA identification system in this subgenus. It has also been shown in this work that *COI* barcoding might be a versatile tool in revealing high levels of genetic diversity in known species complexes (*S. guianense s.l.*, *S. virgatum s.l.*), supporting the existence of putative complexes (*S. paynei*), and indicating the presence of new complexes (*S. tarsatum*). For other taxa, with low level of genetic diversity, the *COI* barcoding profile showed several well-supported divergences in the NJ tree, highlighting the possibility of the existence of cryptic species (*e.g. S. canadense*, *S. duodenicornium*). I envisage that DNA barcoding might be a powerful identification tool and a versatile aid in establishing species boundaries when coupled with morphotaxonomy.

This study has also demonstrated that the employment of an integrated taxonomic approach is the way forward to study the systematics of the subgenus *Trichodagmia* and other taxa of Simuliidae in the Neotropical Region. The phylogenetic analysis helped to give confidence in the classification herein proposed based on morphotaxonomy, but provided little assistance to problems of species delineation. In contrast, the DNA barcoding was extremely successful in providing characters for species identification (of all life stages) and added valuable information to species delineation issues, by indicating cryptic diversity within morphospecies (both in support of cytotaxonomy and in the absence of cytotaxonomic studies). However, the DNA barcoding data was less useful for classification, because it only reflected a few "groups" obtained in the phylogenetic analysis. Thus, the combination of the three approaches yielded the best result.

Nonetheless, much work is still required to assess the evolutionary relationships of the subgenus *Trichodagmia* and its constituent species, especially in those groups that have been relatively neglected such as the CANADENSE species group. Further collecting is still required to obtain new material for poorly known species such as *S. falculatum*, *S. jeteri*, *S. nigricorne*, *S. paracarolinae*, *S. perplexum*, *S. temascalense*, and *S. tarsale*, which will augment the currently available data-set to address some of the issues still pending in *Trichodagmia*.

5.5. Future work

The current integrated taxonomic approach for the delineation of species in the subgenus *Trichodagmia* has confirmed the valid taxonomic status of related species delimited upon morphological traits and has also revealed or highlighted the presence of species complexes in selected taxa. This taxonomic approach has thus provided the basis for other researchers to probe deeper into the phylogeny and/or phylogeography of this subgenus, perhaps employing other molecular makers and cytogenetics to better understand the evolution of specific traits (morphological or otherwise).

The taxonomic and phylogenetic issues addressed in this work can also be applied to other subgenera of the genus *Simulium*, in the Neotropical Region or elsewhere. For example, there are still pending classification problems in the subgenus *Psilopelmia* with regards to that of *Ectemnaspis*, and *Psaroniocompsa* with regards to *Inaequalium*. The latter taxa include some of the most highly anthropophilic species in the region, the AMAZONICUM species group (SHELLEY *et al.*, 2010). The same is also applicable to the subgenus *Pternaspatha*.

Certain genera in South America have been relatively well studied, for example *Cnesia*, *Cnesiamima*, *Gigantodax* (COSCARÓN & COSCARÓN-ARIAS, 2007). However, recent work in Patagonia carried out by the author of this thesis has shown that even these genera are in need of revision, especially to unravel their position with regards to *Paraustrosimulium*. Discrepancies between authors concerning the status of *Lutzsimulium, Araucnephia* and *Araucniphiodes* (GIL-AZEVEDO, 2010; SHELLEY *et al.*, 2010) also highlight the need to carry out taxonomic research, even at the generic level. In addition, further collecting is still needed especially in unexplored areas of northern Patagonia, the Amazon basin, the Andean mountain range, the Guiana Shield, Central America and the Caribbean. These areas are in need of biodiversity surveys and revisionary studies, which will probably reveal new morphospecies. Steps have been taken in this direction by initiating new collaboration projects in Costa Rica and Mexico. These surveys will undoubtedly produce larval specimens of many species for which this life stage is unknown. There is also a need for current morphological descriptions of larvae employing colored digital images to detail the larval morphological variation of the hypostomial and mandibular teeth with an aim at correct species identification.

Blackflies are sometimes described as keystone species in the biotic environment because of their unique ability to recycle dissolved organic matter. However, it is because of the medical and veterinary importance of Simuliidae and their use as indicators of freshwater contamination in combination with their problematic taxonomy that blackflies are one of the five target groups within two international barcoding initiatives, "*HealthBOL*" and "*Freshwater Biosurveillance*" [www.boldsystems.org; www.ibold.org]. The main objective of these initiatives is to provide DNA barcodes for most of the valid species of Simuliidae, with special emphasis on the pest and vector species.

6. SUMMARY

Systematics of the blackfly subgenus *Trichodagmia* ENDERLEIN (Diptera: Simuliidae: S*imulium*) in the New World

The systematics of the New World subgenus *Trichodagmia* has been reassessed by employing an integrated taxonomic approach based upon revisionary taxonomy, phylogenetic (cladistics) analysis, and DNA barcoding. This subgenus included several species of great medical importance, which are all morphologically very similar. The history of the taxonomy and classification of the subgenus *Trichodagmia* has been put into context with other subgenera within New World Simuliidae, while descriptions and keys to the identification of species in this subgenus are also given.

The subgenus *Obuchovia* is here considered a **new junior synonym** of *Trichodagmia*, and all its constituents' species are now placed in the ALBELLUM species group to represent a Palaearctic element within this subgenus. Three new junior synonymies are here proposed: *Simulium chiriquiense* FIELD is a synonym of *S. ethelae* DALMAT **n. syn.**; *S. biuxinisa* COSCARÓN & IBÁÑEZ-BERNAL is a synonym of *S. paynei* VARGAS **n. syn.**; and *S. keenani* FIELD is a synonym of *S. earlei* VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA **n. syn.** A neotype is designated for *S. lahillei* (PATERSON & SHANNON) and a lectotype for *S. pulverulentum* KNAB.1 *Simulium falculatum* ENDERLEIN is transferred from the TARSATUM species group of to the CANADENSE species group based on the morphology of the female genitalia. Two species, *S. rivasi* RAMÍREZ PÉREZ and *S. oviedoi* RAMÍREZ PÉREZ, are transferred from the TARSATUM species group to the subgenus *Psilopelmia* based on the morphology of the male gonostyle and the ventral plate. Keys to separate all species groups and species based on the adults, pupae and larvae are also provided.

The phylogeny and classification of the subgenus *Trichodagmia* is delineated using a cladistic analysis of 63 taxa based on males, females, pupae and larvae, including two species belonging to the subgenus *Aspathia* and two species of the subgenus *Simulium s.str.* that served as outgroups. Analysis of the original full data set [67 taxa and 67 characters] with multistate characters treated as unordered under equal weights led to poorly resolved trees, with many polytomies within TARSATUM [= old subgenus *Hemicnetha*] and CANADENSE [= old subgenus *Hearlea*]. Nonetheless, the ALBELLUM [= old subgenus *Obuchovia*] and PICTIPES [= old subgenus *Shewellomyia*] species groups, and some clades within the CANADENSE species group were well supported. In the most parsimonious cladograms, the position of *S. falculatum* was problematic as it was placed basal to *Trichodagmia*. The position of *S. jeteri*, albeit within the ORBITALE [= old subgenera *Trichodagmia* + *Thyrsopelma* of MIRANDA-ESQUIVEL & COSCARÓN, 2001] clade, was also poorly resolved. This was certainly due to the numerous missing data in these two taxa. Therefore, they were removed from the data set together with other taxa in which three life stages (> 70% of characters) were missing (*e.g. S. paracarolinae* and *S. tarsale*). A second analysis was then performed with 63 taxa and 67 characters. In this analysis, the Strict Consensus Tree was better resolved and certain clades within the expanded concept of *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010) were recovered as monophyletic with high support values. The ALBELLUM species group is monophyletic in a sister-group relationship with the other species groups in *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010). The ORBITALE species group clade was recovered as monophyletic by a unique combination of seven characters with 89% bootstrap support. In this clade, all species close to *S. guianense s.l.* were better diagnosed by a combination of four characters, one of which (male ventral plate with a globular median process) was unique to this group. The position of *S. hirtipupa* is better resolved in the latter clade by the presence of black spiniform setae in the frontoclypeus and thorax of the pupa.

In contrast, the TARSATUM and CANADENSE species groups were diagnosed by only four and five characters, respectively. Within the CANADENSE species group only species with larvae having sclerotized plates in the posterior region of the abdomen were well resolved. Species in the TARSATUM group were homoplastic. The PICTIPES group is only diagnosed by homoplasies, but the combination of these characters is unique to this clade (polythetic taxon). In general, this study supports some of the taxonomic changes proposed in SHELLEY *et al.* (2010), in which the subgeneric-names *Hearlea*, *Hemicnetha*, *Shewellomyia*, *Trichodagmia* + *Thyrsopelma* (*sensu* MIRANDA-ESQUIVEL & COSCARÓN,

2001) are treated as species groups within the subgenus *Trichodagmia*. Moreover, this study also supports the proposal of *Obuchovia* as a junior synonym within the clade *Trichodagmia* to represent the ALBELLUM species group.

The utility of the *COI* DNA barcoding methodology for identification of species in the subgenus *Trichodagmia* and related taxa has been tested. In total, 24 morphospecies within the current expanded morphological concept of *Trichodagmia* were analyzed. In addition, three species of the subgenus *Aspathia* and 10 species of the subgenus *Simulium s.str.* were also included in the analysis because of their putative phylogenetic relationship with *Trichodagmia*. Within the barcoding neighbour-joining tree, most of the specimens were grouped together according to morpho-taxon (species groups and species). Mean genetic distance amongst groups (morphospecies) averaged 11.2% (ranged 2.8-19.5%), whereas intraspecific genetic divergence within morphologically distinct species averaged 0.5% (range 0-1.3%). In known species complexes, maximum values of genetic divergence (3.28-3.79%) indicate the probable presence of cryptic diversity. DNA barcoding achieved nearly 100% success in identifying all specimens of the subgenus *Trichodagmia* and related taxa.

The existence of well defined groups within *S. piperi*, *S. duodenicornium*, *S. canadense* and *S. rostratum* highlighted the possible presence of species complexes in these taxa. In addition, the suspected presence of a sibling species in *S. paynei* and *S. tarsatum* among populations of Belize, Costa Rica, and the USA is confirmed. The use of shorter barcodes (midi and minibarcodes) from specimens held in collections was problematic with regards to the DNA quality and PCR success. However, in the cases that a readable sequence was obtained, they were sufficient for reliable species identification. With regards to the different extraction and preservation techniques tested, larvae preserved in diluted Carnoy's (10% acetic acid) provided full DNA barcodes. Furthermore, legs added directly to the PCR mix from freshly collected individuals provided full length barcodes sequences. However, specimens of more than 10 years old did not yield good PCR products. In short, I conclude that DNA barcoding in combination with a morphological benchwork platform is an effective approach for identification and delineation of species in the subgenus *Trichodagmia*, and the discovery of hidden diversity in this taxon.

SAMENVATTING

Systematiek van het zwarte vlieg subgenus *Trichodagmia* ENDERLEIN (Diptera: Simuliidae: *Simulium*) in de Nieuwe Wereld

De systematiek van het Nieuwe Wereld subgenus *Trichodagmia* is herzien door de toepassing van een integrale taxonomische aanpak gebaseerd op taxonomische revisies, fylogenetische (cladistische) analyse, en DNA barcoding. Dit subgenus bevat verschillende soorten van groot medisch belang, die allen morfologisch sterk op elkaar lijken. De geschiedenis van de taxonomie en classificatie van het subgenus *Trichodagmia* is in de context gezet van andere subgenera binnen Simuliidae uit de Nieuwe Wereld, terwijl ook beschrijvingen en identificatiesleutels tot de soorten in dit subgenus worden gegeven.

Het subgenus *Obuchovia* wordt hier beschouwd als een **nieuw jonger synoniem** van *Trichodagmia* en al haar soorten worden nu geplaatst in de ALBELLUM soortengroep en vertegenwoordigen zo het Palearctisch element binnen dit subgenus. Drie nieuwe jongere synoniemen worden hier voorgesteld: *Simulium chiriquiense* FIELD is een synoniem van *S. ethelae* DALMAT **n. syn.**; *S. biuxinisa* COSCARÓN & IBÁÑEZ-BERNAL is een synoniem van *S. paynei* VARGAS **n. syn.**; en *S. keenani* FIELD is een synoniem van *S. earlei* VARGAS, MARTÍNEZ PALÁCIOS & DÍAZ NÁJERA **n. syn.** Voor *S. lahillei* (PATERSON & SHANNON) is een neotype aangewezen en voor *S. pulverulentum* KNAB een lectotype. *Simulium falculatum* ENDERLEIN is overgeplaatst van de TARSATUM soortengroep naar de CANADENSE soortengroep op basis van de morfologie van de mannelijke gonostyle en de ventrale plaat. Sleutels om alle soortengroepen en soorten te herkennen op basis van volwassen, pop of larvaal stadium zijn opgenomen.

De fylogenie en classificatie van het subgenus *Trichodagmia* wordt onderbouwd door middel van een cladistische analyse van 63 taxa gebaseerd op mannelijke en vrouwelijke exemplaren, poppen en larven, waaronder ook twee soorten behorend tot subgenus *Aspathia* en twee soorten van het subgenus *Simulium s.str.* die dienen als outgroups. Analyse van the originele totale dataset [67 taxa en 67 kenmerken], waarbij multistate kenmerken als ongeordend werden behandeld en met gelijk gewicht, leidde tot slecht opgeloste bomen, met vele polytomiëen binnen TARSATUM [=voormalige subgenus *Hemicnetha*] en CANADENSE [=voormalige subgenus *Hearlea*]. Desalniettemin werden ALBELLUM [=voormalige subgenus *Obuchovia*] en PICTIPES [=voormalige subgenus *Shewellomyia*] en sommige clades binnen de CANADENSE soortengroep goed ondersteund. In het meest parsimone cladogram was de positie van *S. falculatum* problematisch, omdat het basaal t.o.v. *Trichodagmia* werd geplaatst. De positie van *S. jeteri*, hoewel binnen de ORBITALE [=voormalige subgenera *Trichodagmia* + *Thyrsopelma* van MIRANDA-ESQUIVEL & COSCARÓN, 2001] clade, was ook slecht opgelost. Dit was zeker ten gevolge van de vele ontbrekende gegevens in deze twee taxa. Daarom werden deze uit de dataset verwijderd, tezamen met andere taxa waarbij drie levensstadia (> 70% van de kenmerken) ontbraken (*e.g. S. paracarolinae* en *S. tarsale*). Een tweede analyse met 63 taxa en 67 kenmerken werd toe uitgevoerd. Hierin was de Strict Consensus Tree beter opgelost en enkele clades binnen de ruime opvatting van *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010) werden aangemerkt als monofyletisch met hoge support waarden. De ALBELLUM soortengroep is monofyletisch in een zuster-groep relatie met de andere soortengroepen in *Trichodagmia* (*sensu* SHELLEY *et al.*, 2010). De ORBITALE soortengroep clade werd aangemerkt als monofyletisch middels een unieke combinatie van zeven kenmerken met 89% bootstrap support. In deze clade werden alle aan *S. guianense s.l.* verwante soorten beter gekarakteriseerd via een combinatie van vier kenmerken, waarvan er één (mannelijke ventrale plaat met bolvormige centrale uitstulping) uniek was voor deze groep. De positie van *S. hirtipupa* in deze clade wordt bepaald door de aanwezigheid van zwarte stekelige borstels op de frontoclypeus en thorax van de pop.

Daarentegen werden de TARSATUM en CANADENSE soortengroepen ondersteund door respectievelijk slechts vier en vijf kenmerken. Binnen *Hearlea* waren slechts de soorten met larven met gesclerotizeerde platen in de posterieure regio van het abdomen goed opgelost. Soorten in de TARSATUM groep waren homoplastisch. De PICTIPES groep wordt slechts gekarakteriseerd door homoplasiëen, maar de combinatie van deze kenmerken is uniek voor deze clade (polytetisch taxon). In zijn algemeenheid ondersteund deze studie enkele van de taxonomische wijzigingen voorgesteld in SHELLEY *et al.* (2010), waarin de subgenerische namen *Hearlea*, *Hemicnetha*, *Shewellomyia*, *Trichodagmia* + *Thyrsopelma* (*sensu* MIRANDA-ESQUIVEL & COSCARÓN, 2001) worden behandeld als soortengroepen binnen het subgenus *Trichodagmia.* Bovendien ondersteund deze studie ook het voorstel om *Obuchovia* als jonger synoniem binnen de *Trichodagmia* clade te behandelen waarbij het de ALBELLUM soortengroep vertegenwoordigd.

De bruikbaarheid van de *COI* DNA barcode methode voor de identificatie van soorten in het subgenus *Trichodagmia* en verwante taxa werd getoetst. In totaal werden 24 morfo-soorten binnen het huidige verruimde morfologische concept van *Trichodagmia* geanalyseerd. Daarboven werden ook drie soorten van het subgenus *Aspathia* en 10 soorten van het subgenus *Simulium s.str.* opgenomen in de analyse, vanwege hun gesuggereerde fylogenetische relatie met *Trichodagmia.* Binnen de barcode neighbour-joining boom werden de meeste exemplaren volgens hun morfo-taxon (soortengroepen en soorten) gegroepeerd. De gemiddelde genetische afstand tussen groepen (morfo-soorten) was 11.2% (variërend tussen 2.8-19.5%), terwijl de intraspecifieke divergentie binnen morfologisch aparte soorten gemiddeld 0.5% bedroeg (variërend tussen 0-1.3%). Binnen bekende soortcomplexen geven de maximale waarden van genetische divergentie (3.28-3.79%) de mogelijke aanwezigheid van cryptische diversiteit aan. DNA barcoding boekte bijna 100% succes bij het identificeren van alle exemplaren van het subgenus *Trichodagmia* en verwante taxa.

Het bestaan van goed gedefinieerde groepen binnen *S. piperi*, *S. duodenicornium*, *S. canadense* en *S. rostratum* onderstreepte de mogelijke aanwezigheid van soortcomplexen binnen deze taxa. Bovendien is de vermoedelijke aanwezigheid van een sibling soort in populaties van Belize, Costa Rica en de VS van *S. paynei* en *S. tarsatum* bevestigd. Het gebruik van kortere barcodes (midi- en mini-barcodes) bij exemplaren uit collecties was problematisch ten aanzien van de DNA kwaliteit en het PCR succes. Echter, in het geval dat een leesbare sequentie werd verkregen, waren deze voldoende voor een betrouwbare soort-identificatie. Uit tests met verschillende extractie en conservering methodes bleek dat larven bewaard in verdunde Carnoy's oplossing (10% azijnzuur) volledige DNA barcodes opleverde. Bovendien bleek dat het direct aan het PCR mengsel toevoegen van poten van vers verzamelde exemplaren een snelle methode was om volledige barcodes te verkrijgen, alhoewel exemplaren van meer dan 10 jaar oud geen goed PCR product opleverden. Om kort te gaan, concludeer ik dat DNA barcoding in combinatie met een sterke morfologische basis als uitgangspunt een effectieve benadering is voor de identificatie en afgrenzing van soorten in het subgenus *Trichodagmia*, alsook voor het ontdekken van verborgen diversiteit in dit taxon.

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9. CURRICULUM VITAE

I was born in the city of Güira de Melena, La Havana, Cuba on 29th December 1964. I studied Biology at the University of Havana where I graduated as a Bachelor of Science with a degree in Biological Sciences in July 1987. In September of the same year, I took a position as a Research Entomologist at the Institute of Ecology and Systematics (IES), Cuban Academy of Sciences. During this time at the IES, I worked for approximately eight years on the systematics and taxonomy of insects of agricultural importance, especially on the Order Heteroptera (True Bugs) and Isoptera (Termites), mainly of Cuba, but also in the Caribbean Region. In March 1995, I won an International Darwin Initiative Fellowship from the United Kingdom Government, to carry out specialization work in the Heteropteran Family Miridae (Plant Bugs) under the supervision of Dr. Gary Stonedahl based at the International Institute of Entomoloy (IIE) within the Entomology Department, The Natural History Museum, London (NHM). I continued working at the IES and NHM on several projects in collaboration with specialists at these institutions between 1997 and 2000. In December 2000, I was appointed a 3-years Research Assistant position in the Simuliidae and Onchocerciasis Research Programme, Biomedical and Veterinary Division at the NHM under the supervision of Dr. Anthony (Tony) J. Shelley. Under Tony Shelley's supervision. I gained a vast field work experience and broaden my taxonomic expertise and skills working on the systematics and taxonomy of the medically important family Simuliidae.

After Dr. Shelleys' retirement in September 2003, I was appointed a tenure position as a Research Entomologist on 1st January 2004 at the NHM, where I am presently carrying out research on the morphotaxonomy and systematics of Blackflies (Diptera, Simuliidae). Since my appointment, I have worked and published extensively in the taxonomy of blackflies, especially in the Neotropical Region, where I have developed a sound international collaboration [see section **8. REFERENCES** under HERNÁNDEZ, L. M. and/or SHELLEY, A. J.]. Areas on which I recently developed a research collaboration are Argentina (northern Patagonia, Nahuel Huapi National Park), Costa Rica (country wide) and, more recently, Mexico. I am also working on a revision of the Simuliidae in Thailand, especially on those taxa collected at Doi Inthanon National Park, Chiang Mai Province.

I have co-authored two books on the *Host Plants of Moth and Butterflies Caterpillars of the Oriental and Nearctic Regions* with the late Dr. Gaden S. Robinson, and I am the second author on a third book, *The Blackflies (Diptera: Simuliidae) of Brazil* published in March 2010. Furthermore, I have also published another book on *The Plant Bugs, or Miridae (Hemiptera: Heroptera) of Cuba* in collaboration Dr. Thomas J. Henry, U.S.D.A, Smithsonian Institution. In addition, I have also produced 34 peer-reviewed scientific papers and monographs, as well as nearly 14 documents in abstract books at International Meetings, Reports, Newsletters and/or via the world wide web, for example shttp//:www.nhm.ac.uk/research-curation/research/projects/cockayne and http://www.blackflies.info.

9. 1. PUBLICATION LIST (SIMULIIDAE) [L. M. HERNÁNDEZ]

Books

SHELLEY, A. J., **L. M. HERNÁNDEZ**, M. MAIA-HERZOG, A. P. A. LUNA DIAS & P. R. GARRITANO (2010): *The Blackflies of Brazil (Diptera, Simuliidae). In*: J. ADIS, J. ARIAS, S. GOLOVATCH, K. M. MANTZEV, G. RUEDA-DELGADO & E. DOMÍNGUEZ (Eds.), Aquatic Biodiversity in Latin America (ABLA Series), Vol. 6., Pensoft, Sofia-Moscosw, 814 pp.

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MONTES DE OCA, F. & **L. M. HERNÁNDEZ,** (2010, IN PRESS): Guia para la identificación de insectos acuáticos del Lago Nahuel Huapi, Patagonia, Argentina. Capitulo 8.3: Simuliidae. – Parques Nacional Nahuel Huapi, Patagonia, Argentina, 13 pp.

HERNÁNDEZ, L. M., F. MONTES DE OCA, M. PENN, J. MASAFERRO, A. GARRE & S. BROOKS (2009): "Jejenes" (Diptera: Simuliidae) of Nahuel Huapi National Park, Patagonia, Argentina: Preliminary Results. – Revista de Entomología de Argentina **68**: 193-200.

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9. 2. Other Publications

Books

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Fontenla, J. L. & **L. M. Hernández** (1993): Relaciones de coexistencia en comunidades de hormigas en un agroecosistema de caña de azúcar. – Poeyana **438**: 1-15.

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Abstracts

Lotta, I., N. Matta, L. Moncada, M. C. Carrasquilla, G. Spinelli & **L. M. Hernández** (2010): Blood-feeding insects from high altitude region of Colombia. – The 76th Annual meeting of the

American Mosquito Control Association. 28thMarch-1st April, 2010, Lexington, Kentucky, USA, pp: 24.

Hernández, L. M. (2009): Systematics of Neotropical Simuliidae (Diptera, Simuliidae): British Simuliid – Group Bulletin, supplement **31**: 13.

Brooks, S. J., **L. M. Hernández**, J. Massaferro, G. Spinelli (2008): La Iniciativa Darwin para la creación de capacidad taxonómica para el studio de los insectos acuáticos en el norte de Patagonia, Argentina. – VII Congreso Argentino de Entomología, 21 al 24 de Octubre de 2008, Argentina, Huerta Grande, Córdoba, Libro de Resúmenes, pp: 30.

Penn, M., J. Masaferro, F. Montes De Oca, A. Garré, **L. M. Hernández** & S. Brooks (2008): A preliminary vegetation analysis, mapping and classification of the Nahuel Huapi Nationla Park, Argentina. – VII Congreso Argentino de Entomología., 21 al 24 de Octubre de 2008, Huerta Grande, Córdoba, Libro de Resúmenes, pp: 43.

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Hernández, L. M., A. J. Shelley, A. P. A. Luna Dias & M. Maia-Herzog (2006): An overview of the subgenus *Inaequalium* in the Neotropical Region. – British Simuliidae Group Bulletin **27**: S6-S7.

Hernández, L. M., A. J. Shelley & M. Penn (2002): Human onchocerciasis in Central America, can it be dispersed to Belize?. – Acta Tropica **83**: S49-50.

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Back cover (from top to bottom):
Waterfall at Blancaneaux Lodge, Mountain Pine Ridge, Belize; Waterfall La Paz, Costa Rica; Sixaola River, Costa Rica (Photographs Luis M. Hernández)

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