Biosystematics of *Begonia squamulosa* Hook. f. and affiliated species in section *Tetraphila* A.DC.

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Biosystematics of *Begonia squamulosa* Hook.f. and affiliated species in section *Tetraphila* A.DC.

Proefschrift
ter verkrijging van de graad van doctor in de landbouw- en milieuwetenschappen, op gezag van de rector magnificus dr H.C. van der Plas, in het openbaar te verdedigen op vrijdag 3 april 1992 des namiddags te vier uur in de aula van de Landbouwuniversiteit te Wageningen.

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STELLINGEN

1

De bladachtige aanhangsels in de bloeiwijzen van de in dit proefschrift beschreven *Begonia*-soorten zijn niet homoloog met stipulae.

De Wilde, J.J.F.E. & J.C. Arends (1980). Misc. Pap. 19 (1980), Landbouwhogeschool Wageningen.
Dit proefschrift.

2

De opvatting van Irmscher dat er in *Begonia* zowel okselstandige als eindstandige bloeiwijzen voorkomen, is onjuist.

Irmscher, E. (1925: 558, fig. 257-1), in: Engler, A. & K. Prantl, Die natürlichen Pflanzenfamilien, Bd 21.

3

De septa in het ovarium van soorten binnen *Begonia* sectie *Tetraphila* zijn grotendeels 'placentair'.

Reitsma, J.M. (1983), Meded. Landbouwhogeschool Wageningen 83-9: 21–53.
Dit proefschrift.

4

De vaatbundels in de as van de meerhokkige ovaria van bijv. *Begonia dregei* en *B. socotrana* zijn geen ventrale carpelbundels, doch behoren tot het in dit proefschrift voor *Begonia* beschreven 'axial placental vascular system'.

Gauthier, R. (1950), Contr. Inst. Bot. Univ. Montréal no 66, 5–91.

5

Ofschoon (epitheem)hydathoden gewoonlijk gelegen zijn nabij bladnerf-uiteinden, is het niet juist om een nerf-uiteinde als een deel van een hydathode op te vatten.

Wilkinson, H. (1979) in: C.R. Metcalfe & L. Chalk, Anatomy of the Dicotyledons, Ed. 2.
Brouillet, L. et al. (1987). Can. J. Bot. 65: 34–52.

6

Het aantal hokken in een vruchtbeginsel mag niet zonder meer worden afgeleid uit het aantal stempels.

Barabé, D. (1981). Can. J. Bot. 59: 819–825.

7

Voor *Angraecum* (Orchidaceae) zijn tot op heden de chromosomale grondtallen x = 19, 21, 24 en 25 bekend. Deze grondtallen leveren een sterke aanwijzing dat dit genus geen monofyletische groep is.

Arends, J.C. & F.M. van der Laan (1986), Lindleyana 1: 33–41.

8

Het mag vandaag de dag van de auteur (van een deel) van een Flora-werk verwacht worden dat deze kennis heeft genomen van alle eerder verschenen taxonomische artikelen die betrekking hebben op de door hem behandelde taxa.

Davies, R.A. & K.M. Lloyd (1987). Kew Index for 1986: 29–30.
Maesen, L.J.G. van der (1986). *Cajanus* DC and *Atylosia* W. & A. (Leguminosae). Agric. Univ. Wageningen Pap. 85-4: pp 225.
Maxwell, R.H. (1991). Phaseoleae, in: Flora of Ceylon, deel 7: 348–356.

9

Het onderscheid tussen de BION-werkgemeenschappen 'Systematiek van mossen en vaatplanten' en 'Biologie van de soortvorming' is vooral pragmatisch.

10

Pleidooien van organisaties van natuurbeschermers, bosbouwers, oecologen en systematici voor het behoud van en inventariserend onderzoek aan tropisch regenwoud zijn geen preken voor eigen parochie.

Heijman, W.J.M. (1991). Depletable resources and the economy, Pudoc, Wageningen.

11

Intensivering van het biosystematisch onderzoek aan wilde tropische planten zal waardevolle argumenten leveren voor maatregelen tot behoud van de biodiversiteit van het plantendek op de aarde.

BION-projectvoorstel 440.024, werkgemeenschap Systematiek van mossen en vaatplanten; dit proefschrift.

12

Binnen de organisatie van CITES (the Convention on International Trade in Endangered Species of wild fauna and flora) is de haring in 1992 wisselgeld voor de olifant.

Amendments to appendix I and II of the convention

13

Hoewel de beiaard een specifiek Nederlands-Vlaamse uitvinding is, kan het worden uitgesloten dat dit muziekinstrument ooit de klomp, de molen of de tulp als symbool voor Nederland zal vervangen.

A. Lehr e.a. (1991). Beiaardkunst in de Lage Landen. Lannoo/Tirion.
B. Makken, NRC/Handelsblad, januari 1992.

14

De metafoor is een van de belangrijkste instrumenten van de muziekcriticus.

Stellingen behorende bij het proefschrift van J.C. Arends: Biosystematics of *Begonia squamulosa* Hook.f. and affiliated species in section *Tetraphila*.

Wageningen, 3 april 1992.

voor Dientje
Marlene en Arnoud
Hildo

Curriculum vitae

Johan Coenraad Arends werd op 15 juli 1940 geboren te 's-Gravenhage. Hij is gehuwd met Dientje Mollen. Er zijn twee kinderen: Marlene en Hildo.

Hij behaalde in 1959 het diploma HBS-b aan het Revius Lyceum te Doorn. Zijn opleiding vervolgde hij aan de Landbouwhogeschool te Wageningen, waar hij in januari 1969 afstudeerde in de studierichting Tuinbouwplantenteelt. Verschillende studiebeurzen stelden hem in de gelegenheid de studie te Wageningen te onderbreken. In de periode van juni 1966 tot september 1968 studeerde hij achtereenvolgens aan de Landbouwhogeschool te Kopenhagen en de University of Hawaii te Honolulu vanwaar hij als Master of Science in Horticulture naar Nederland terugkeerde. Sedert februari 1969 werkt hij bij de Landbouwhogeschool, eerst als wetenschappelijk assistent op het Laboratorium voor Tuinbouwplantenteelt en vanaf januari 1971 als wetenschappelijk medewerker op het Laboratorium voor Plantensystematiek en - geografie. Zijn huidige functie is universitair docent bij de vakgroep Plantentaxonomie.

Zijn onderzoek bij de vakgroep richt zich vooral op de karyosystematiek. Gewoonlijk met co-auteurs publiceerde hij o.a. over *Apocynaceae*, *Begonia*, *Cryptocoryne* en angraecoïde orchideeën.

Abstract

This study deals with the systematics of plants belonging to a part of *Begonia* section *Tetraphila* that occur in tropical Africa. Six taxa are recognized and accorded the rank of species. The names of three of these taxa, viz.: *B. elaeagnifolia* Hook.f., *B. longipetiolata* Gilg and *B. squamulosa* Hook.f., have been published validly by their authors. Engler (1921) considered *B. longipetiolata* to be conspecific with *B. squamulosa*, but as the result of the present study the former name is reinstated. The other three taxa: *B. karperi* J.C. Arends, *B. pelargoniiflora* J.J. de Wilde & J.C. Arends and *B. rwandensis* J.C. Arends, are new species described for the first time. All six species treated here are delimited from the other 24 species in the section *Tetraphila* by the combination of features mentioned in Chapter 1.

Many features have been studied in preserved field collections, while quite a few data have been obtained from observations of living plants of *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa*, both in the wild and in the greenhouse.

From the review of previous taxonomic treatments in Chapter 2 it appears that, in the past, vegetative features have been overemphasized in the recognition and the delimitation of the taxa dealt with here. In Chapters 4 to 8 the results of detailed morphological, anatomical and karyological studies are discussed and compared with data from previous investigations in *Begonia*.

Both *B. elaeagnifolia* and *B. squamulosa* comprise diploid as well as tetraploid populations. The 4x populations, which are interpreted to be interracial autopolyploids, are confined to the Crystal Mts in Gabon (Chapter 4).

As to vegetative structures (Chapter 5), stems and leaves usually show few specific differences. For example, both the stem and the leaf blade in *B. rwandensis* are thicker than those in the superficially very similar *B. karperi*. Both species have peltate leaves with an actinodromous venation, while the leaf venation in the other species is simple craspedodromous. The ratio of the length of the largest leaf blade and the length of the longest internode of a specimen is, in combination with reproductive features, often indicative for the identity of that particular specimen. The dimension and the shape of the leaf blades are hardly useful for the delimitation of the species recognized here.

The leaf margins are provided with tiny teeth which are both 'violoid' and 'tylate'. The apices of the teeth often include cells with suberized walls. Because of further suberization of tissue of both the teeth and adjacent parts of the blade, there may be regions of wound cork on the margin of older leaves. Complex hydathodes, which are associated with tracheids from vein terminations, are present on the upper surface of the leaf margin, including the teeth. The petioles of *B. longipetiolata* and *B. pelargoniiflora* are usually canaliculate, whereas those

of the remaining species are more or less terete. The indumentum of all the plants studied consists of short-stalked dentate scales, which according to their shape form an intergrading morphological series.

Several reproductive features are discussed in Chapter 6. As far as the number of flowers and the comparative length of the axes in the cymoid inflorescences are concerned, the species are usually distinct. The vascular anatomy of female flowers shows that the outer perianth segments are homologous with sepals and the inner ones with petals. The stamens have poricidal anthers. The 'front side' of the zygomorphic androecium in a lateral flower is always oriented towards the main inflorescence axis. The anther pores of the stamens on the front side of the androecium of *B. longipetiolata* have an adaxial orientation in relation to the main inflorescence axis, but in *B. squamulosa* their orientation is abaxial.

Although specific trends in both the number of stamens and the number of styles can be discerned, stamen number as well as style number are not constant specific characters. The anthers in *B. pelargoniiflora* and *B. rwandensis* are longer than those in the other species studied. Except for *B. longipetiolata*, whose style surface below the style arms and the stigmatic band is more or less papillose, that surface in the other species is smooth. In *B. squamulosa* the smooth style surface carries some dentate scales.

The ovaries investigated show both an axial and a parietal placentation in a single ovary. In *B. longipetiolata*, each septum with its two placental lobes is cross-shaped in transverse section, while, as far as could be studied, that in the other species is T- or arrow-shaped. The ovules in *B. squamulosa* have a pleurotropous position in the ovarial cavities, whereas those in the other species are epitropous. The number of styles does not always correspond with the number of septa and/or locules in the same gynoecium.

The placentae in the ovaries in *B. elaeagnifolia*, *B. longipetiolata* and *B. squamulosa* are supplied by two almost independent vascular systems. The finding of two systems, viz.: an axial and a parietal system, is in line with the observation of Charpentier et al. (1989) that the ontogeny of the ovary in *Begoniaceae* is determined by both a single axial meristem in the ovary base and several parietal meristems on the ovary wall. The present study supports Reitsma's (1983) hypothesis that in section *Tetraphila* the septa are more or less 'placental' (Chapter 7).

The investigation of pollen grains usually corroborates with Van den Berg's (1984) conclusions regarding the pollen morphology and pollen-type of the species studied here. However, this study indicates that there appears to be a transition between the **B. squamulosa pollen-type** and the **B. komoensis pollen-type**. Pollen grain size may be indicative for the ploidy level of a specimen of either *B. elaeagnifolia* or *B. squamulosa* (Chapter 8).

In Chapter 9, it is discussed why the taxa recognized here are accorded the rank of species. With the exception of *B. rwandensis*, the species are sympatric and appear to have more or less similar ecological requirements. Various observations and crossing experiments indicate that the sympatric taxa, which may be found growing close together in the same locality, are reproductively isolated.

Within their basic distribution several of the species have a localized topography that coincides with presumed African pleistocene rain forest refuges. It is inferred that gene flow among local populations is limited, while the possibility of gene flow among populations from geographically separated regions can be excluded. Finally, the phylogenetic relationships of the species are discussed.

The taxonomic treatment in Chapter 10 includes a key to the species. They are described, typified and illustrated. Full synonymy, references to taxonomic literature and all the available material are cited. Distribution maps show where the species have been collected.

Samenvatting

Dit werk behandelt de systematiek van planten die deel uitmaken van *Begonia* sectie *Tetraphila* en voorkomen in tropisch Afrika. Er worden zes taxa onderscheiden, elk met de rang van soort. De namen van drie van deze taxa, *B. elaeagnifolia* Hook.f., *B. longipetiolata* Gilg en *B. squamulosa* Hook.f., werden geldig gepubliceerd door hun auteurs. Engler (1921) plaatste *B. longipetiolata* in de synonymie van *B. squamulosa*, maar op grond van het onderhavige onderzoek wordt de eerste weer als afzonderlijke soort erkend. De andere drie taxa, *B. karperi* J.C. Arends, *B. pelargoniiflora* J.J. de Wilde & J.C. Arends en *B. rwandensis* J.C. Arends, zijn nieuwe soorten die hier voor het eerst worden beschreven. De zes hier behandelde soorten zijn afgegrensd van de overige 24 soorten in sectie *Tetraphila* door de combinatie van kenmerken genoemd in Hoofdstuk 1.

Veel kenmerken zijn bestudeerd aan geconserveerde planten. Bovendien is een aanzienlijke hoeveelheid gegevens verkregen uit onderzoek aan levende, wilde of gekweekte, planten.

Uit de bespreking van taxonomische publicaties in Hoofdstuk 2 blijkt dat het voorheen gemaakte onderscheid tussen de hier behandelde taxa vooral berustte op vegetatieve kenmerken. De resultaten van hier uitgevoerd morfologisch, anatomisch en karyologisch onderzoek worden behandeld in de Hoofdstukken 4 tot en met 8, en daar vergeleken met gegevens uit eerder onderzoek aan *Begonia*.

Binnen *B. elaeagnifolia* als ook binnen *B. squamulosa* komen zowel diploïde als tetraploïde populaties voor. De 4x populaties van beide soorten, die uitsluitend zijn gevonden in het 'Crystal' gebergte in Gabon, zijn vermoedelijk autopolyploïde afgeleiden van diploïde populaties welke daar in het verleden voorkwamen.

De vegetatieve plantedelen, die worden behandeld in Hoofdstuk 5, vertonen gewoonlijk weinig soortseigen kenmerken. Echter, zowel de stengel als de bladschijf van *B. rwandensis* zijn dikker dan die van de daarmee veel gelijkenis vertonende *B. karperi*. Beide soorten hebben handnervige en schildvormige bladeren, terwijl de bladeren van de overige soorten veernervig en niet schildvormig zijn. In combinatie met reproduktieve kenmerken levert de verhouding van de lengte van de grootste bladschijf en de lengte van het langste stengeldeel van een bepaalde plant dikwijls een aanwijzing op m.b.t. de identiteit van die plant. Op grond van hun bladmorfologie kunnen de hier behandelde soorten nauwelijks van elkaar worden onderscheiden.

De rand van de bladschijf is voorzien van 'violoïde' tandjes die tevens 'tylate' zijn. De wanden van cellen in de top van een tand zijn dikwijls verkurkt. De aanwezigheid van wondkurk op de bladrand is het gevolg van verdere verkur-

king van de tanden en aangrenzende delen van de rand. Epitheemhydathoden, die verbonden zijn met tracheïden van nerfeinden, zijn gelegen in het parenchym van de bladrand. De bladstelen in *B. longipetiolata* en *B. pelargoniiflora* zijn vrijwel altijd gevoord; die van de overige soorten zijn min of meer rolrond. Getande, kortgesteelde schubben komen gewoonlijk voor op de meeste plantedelen. Ze kunnen niet naar hun vorm worden ingedeeld.

De reproductieve delen worden behandeld in Hoofstuk 6. De soorten verschillen vooral in de opbouw van hun cymeuse bloeiwijzen die wordt bepaald door het aantal bloemen en de relatieve lengte van de assen. Op grond van het vaatbundelverloop in vrouwelijke bloemen wordt geconcludeerd dat de buitenste perianth-segmenten homoloog met kelkbladeren zijn en de binnenste met kroonbladeren. De helmknoppen openen met poriën. De 'voorzijde' van het tweezijdig symmetrische androecium in een bloem op een laterale as is altijd gericht naar de hoofdas van de bloeiwijze. In *B. longipetiolata* en *B. squamulosa* zijn de poriën van de meeldraden aan de voorzijde van het androecium in een laterale bloem gericht naar, resp. afgewend van de hoofdas van de bloeiwijze.

Hoewel er m.b.t. het aantal meeldraden en het aantal stijlen bepaalde soortskarakteristieke trends kunnen worden onderscheiden, zijn deze aantallen binnen de soorten niet constant. De helmknoppen van *B. pelargoniiflora* en *B. rwandensis* zijn langer dan die van de overige soorten. Het stijloppervlak beneden de stijlarmen is min of meer papilleus in *B. longipetiolata*; in de overige soorten is het glad. Op het gladde stijloppervlak van *B. squamulosa* komt een wisselend aantal schubben voor.

In de onderzochte vruchtbeginsels is de placentatie zowel hoekstandig als marginaal wandstandig. In dwarsdoorsnede is elk septum met de daarop geplaatste zaadlijsten òf kruisvormig (*B. longipetiolata*), òf T- tot pijlvormig (in de overige daarop onderzochte soorten). De positie van de zaadknoppen in de hokken is òf pleurotroop (*B. squamulosa*), òf epitroop (in de overige daarop onderzochte soorten). Het aantal stijlen komt niet altijd overeen met het aantal septa en/of hokken in dezelfde stamper.

De vruchtbeginsels hebben twee, van elkaar bijna onafhankelijke, vaatbundelsystemen. Het eerste systeem bevindt zich in de as en het tweede in de periferie van het vruchtbeginsel. Deze waarneming komt overeen met de conclusie van Charpentier et al. (1989) dat de ontogenie van het ovarium in *Begoniaceae* bepaald wordt door zowel een enkelvoudig meristeem in het centrale deel van de bodem van het ovarium als verscheidene hoger in het ovarium geplaatste parietale meristemen. Dit onderzoek ondersteunt de hypothese van Reitsma (1983) dat de septa in sectie *Tetraphila* min of meer 'placentair' zijn (Hoofstuk 7).

De conclusies van Van den Berg (1984) m.b.t. de pollenmorfologie en de door hem onderscheiden pollen-types worden hier gewoonlijk bevestigd. Het blijkt echter dat het **B. squamulosa pollen-type** niet duidelijk is af te grenzen van het **B. komoensis pollen-type**. De grootte van de pollenkorrels in een plant van zowel *B. elaeagnifolia* als *B. squamulosa* levert dikwijls een aanwijzing op aangaande het ploidieniveau van het onderzochte individu (Hoofdstuk 8).

In Hoofstuk 9 wordt besproken waarom aan alle hier onderscheiden taxa

de rang van soort wordt verleend. Met uitzondering van *B. rwandensis* zijn alle soorten sympatrisch. De sympatrische soorten komen voor in overeenkomstige habitats en ze zijn zelfs af en toe groeiende in elkaars nabijheid aangetroffen. In dergelijke omstandigheden werden nooit hybriden gevonden. Dit feit en de negatieve resultaten van kruisingsexperimenten tussen soorten wijzen er op dat deze reproduktief geisoleerd zijn. In het bijzonder *B. elaeagnifolia* en *B. squamulosa* komen voor in enkele deelarealen die samenvallen met veronderstelde wijkplaatsen van Afrikaans regenbos tijdens pleistocene ijstijden. Gene flow tussen in elkaars nabijheid gelegen locale populaties is vermoedelijk beperkt. Het kan worden uitgesloten dat er gene flow optreedt tussen populaties welke in verschillende deelarealen zijn gelegen. Het hoofstuk wordt afgesloten met een bespreking van de mogelijke fylogenetische betrekkingen tussen de soorten.

Het taxonomische deel in Hoofdstuk 10 bevat een determinatiesleutel tot de soorten. Deze worden beschreven, getypificeerd en geillustreerd. De volledige synonymie wordt gegeven en de verwijzingen naar de taxonomische literatuur vermeld. Al het beschikbare en bestudeerde materiaal wordt geciteerd. Verspreidingskaarten geven weer waar de soorten zijn verzameld.

Contents

1. Introduction

One of the major projects of the Department of Plant Taxonomy of the Agricultural University is an investigation of African species of *Begonia*. The present author has been responsible for its karyological aspects and a paper dealing with the cytotaxonomy of African *Begonia* is in preparation. For the section *Tetraphila*, it was found that the somatic chromosome numbers indicate two levels of ploidy. Counts of about 2n = 38 were found in the majority of its species, but as early as 1978 a number of about 2n = 76 was found in some plants from Gabon. These plants are now identified as *B. squamulosa* and *B. elaeagnifolia*. The finding of these apparently tetraploid numbers suggested that these species could be members of a polyploid complex. Moreover, a provisional analysis of herbarium material of these and other supposedly related species showed that they share many features and that there is considerable macromorphological variation, hampering their delimitation and recognition. This observation supported the idea that we were dealing with a polyploid complex incorporating an unknown number of sibling species. It was then decided that the author should attempt to clarify the taxonomic relationships of the species involved. Hence this study deals with a small group of species, previously referred to as the '*B. squamulosa* species aggregate', of *Begonia* section *Tetraphila* A.DC. The entire section as circumscribed in De Wilde & Arends (1979), comprises approximately 30 species and is confined to tropical Africa.

The species dealt with here are distinct from other species in the section by the combination of a creeping habit and usually unisexual inflorescences of which the female is predominantly single-flowered. The male flowers of these species are characterized by stamens with partially fused filaments arranged in a zygomorphic androecium. The gynoecium of the female flower consists of the inferior fusiform ovary crowned by two to five styles. These styles are fused at their base and each style has two spreading and slightly curved arms. Each style is provided with a horse shoe-shaped stigmatic band on the abaxial side. The upper ends of this stigmatic band are spirally twisted around the apical part of the style branches.

The species that have been described prior to this paper can be divided into two subgroups according to the number of flowers found in the male inflorescences.

The first subgroup has male inflorescences with many flowers (i.e. more than 5). It comprises the following validly published names:

B. squamulosa Hook.f., 1871, Gabon
B. longipetiolata Gilg, 1904, Cameroun
B. macrura Gilg, 1904, Cameroun

B. gracilipetiolata De Wild., 1908, Zaire
B. bipindensis Gilg ex Engl., 1921, Cameroun
B. crassipes Gilg ex Engl., 1921, Cameroun
B. gladiifolia Engl., 1921, Fernando Poo
B. nicolai-hallei Wilcz., 1969, Gabon

Of these, *B. squamulosa* Hook.f. is maintained by the present study, and *B. longipetiolata* Gilg, considered by Engler (1921) as a synonym of *B. squamulosa*, is reinstated. All other names of this subgroup are treated here as synonyms of *B. longipetiolata*. Besides these, the names *B. kribensis* Engl. (1921) and *B. ludwigsii* Gilg ex Wilcz. (1969) occur in the literature. These are nomima nuda attached to Camerounese collections which are now assigned to *B. longipetiolata*.

The second subgroup is characterized by male inflorescences with few flowers (usually 1 to 3, rarely 4 or 5). It comprises;

B. elaeagnifolia Hook.f., 1871, Gabon
B. schultzei Engl., 1921, Cameroun
B. wilczekiana N. Hallé, 1969, Gabon

Of these, the last two names are treated here as synonyms of *B. elaeagnifolia* Hook.f. A new species, *B. karperi* J.C. Arends, endemic to the Crystal and the Chaillu Mts in Gabon, is proposed and added to this group.

Two other new species are described. The first is *B. rwandensis* J.C. Arends, endemic to the border region of Zaire and Rwanda. With its male inflorescence having up to five flowers it shows an affinity with the second subgroup. The second, *B. pelargoniiflora* J.J. de Wilde & J.C. Arends, occurs on the island of Bioko (Fernando Póo) and in adjacent parts of Cameroun. Whereas many of its features are similar to those of the other species, it is unique because it may have bisexual inflorescences, while its female inflorescences have at least seven flowers. For these reasons it is kept apart from both subgroups. The taxonomic position of these two species will be discussed in Chapter 9.

The species treated in the present paper are distributed in tropical Africa in the region between 6 degrees latitude North and 6 degrees South and from 8 to 30 degrees longitude East. Plants have been collected in south-eastern Nigeria, Cameroun, Equatorial Guinea (including Fernando Póo), Gabon, western Congo, northern Angola (Cabinda), as well as in several disjunct localities in Zaire and finally in Rwanda.

The plants grow in humid tropical forests and prefer habitats near water courses and swamps. They are usually found on trees or decaying logs at various heights above the ground or river, but sometimes grow on rocks.

Within section *Tetraphila* the group defined above is also unique in demonstrating the occurrence of polyploidy, other species of this section being exclusively diploid (Arends, in prep.). The first tetraploid somatic chromosome numbers were observed in some cultivated plants introduced by Breteler and

De Wilde in August 1978 from the Crystal Mts in Gabon. Other plants from the same collection were found to be diploid. On the basis of the emended description of *B. squamulosa* Hook.f. of Hallé & Raynal (1966), these diploids were identified as belonging to this species. The diploid and tetraploid plants had many flowers in the male inflorescences, a characteristic of the first subgroup mentioned above, but the tetraploids differed from the diploids in having comparatively long internodes and thicker, more succulent tepals. We therefore postulated that *B. squamulosa* comprises diploid and tetraploid cytotypes. Consequently, when J.Reitsma (1983) studied the placentation in African *Begonia*, his results for *B. squamulosa* were presented separately for the diploid and tetraploid plants.

Apart from the two cytotypes of *B. squamulosa* there were also some other rather similar plants. They carried the few-flowered male inflorescences, as encountered in the second subgroup, and were provisionally identified as *B. schultzei* Engl. and/or *B. wilczekiana* N. Hallé. All these plants were found to be tetraploid. As they were characterized by long internodes it was assumed that tetraploidy is correlated with elongated internodes and consequently long creeping stems. On the other hand, there was another living introduction showing 1- to 2-flowered male inflorescences in combination with long internodes which was also found to be diploid. This particular plant was identified as *B. wilczekiana* as well, but in addition to its diploid chromosome number, it was distinct from the other plants in this subgroup by its peltate leaves with dentate scales on the upper surface.

Subsequently I found that pollen grains of the cultivated diploid plants were usually smaller than those of the tetraploid ones. When Van den Berg (1984) studied the pollen of African species of *Begonia*, he also attempted to find a correlation between pollen grain size and comparative internode length. Some specimens with long internodes (assumed to be tetraploids) were found to have small pollen grains, while other, similar, specimens had larger pollen grains. For specimens with short internodes similar conflicting results were obtained. Consequently, Van den Berg (op. cit.) concluded that there is no correlation between pollen grain size and ploidy level. While pollen grain size appeared to be of little diagnostic value for the taxonomy of most of the species mentioned above, the morphology of the pollen grains was found to be characteristic in the majority of these species. Their pollen grains were referred to by Van den Berg as the **Begonia squamulosa pollen- type**. Pollen grains which deviated from this pollen-type were found by Van den Berg for *B. nicolai-hallei* Wilcz. and for the two new species described here as *B. rwandensis* and *B. pelargoniiflora*. Further details are given in Chapter 8.

During the next expedition to Gabon (collectors De Wilde, Arends et al., 1983) the two presumed cytotypes of *B. squamulosa* and plants of *B. schultzei/wilczekiana* were re-collected in the Crystal Mts, occasionally even from the same locality. Samples of these plants were sent to WAG for cultivation and laboratory studies. Chromosome counts confirmed the presumed ploidy level of these plants. No triploids were found, and it was concluded that there may be crossing

barriers between these two sympatric cytotypes.

As an alternative to the hypothesis that the diploid and tetraploid plants represent cytotypes of one species, it was suggested that we might be dealing with sibling species, morphologically more or less similar, but reproductively isolated taxa.

In order to test the alternative hypotheses additional collections and field observations were necessary. To date there have been ten other expeditions in Gabon since 1983, and specimens of the taxa treated here were found during seven of these. Although localities with an apparently suitable habitat for the species were carefully searched, only a rather limited number of accessions could be acquired.

The analysis of several gatherings made in 1984 (collections Arends, De Wilde & Louis; Louis, Breteler & De Bruijn) led to the conclusion that the second of the above mentioned hypotheses is the more acceptable. In fact it was concluded that the two taxa of the first subgroup, as they occur in the Crystal Mts, viz. *B. squamulosa* 'tetraploid type' and *B. squamulosa* 'diploid type' represent *B. squamulosa* Hook.f. and *B. longipetiolata* Gilg respectively. Both species comprise diploid and tetraploid cytotypes. Similarly *B. elaeagnifolia* Hook.f., one of the two species of the second subgroup, comprises 2x and 4x cytotypes. These conclusions are based on the analysis of cultivated plants and demonstrate once again that the study of living plants is indispensable for clarifying the boundaries between species in *Begonia*. Not only are living plants a prerequisite for chromosome analysis, but they are also necessary for assessing the plasticity of the characters of the plants. In comparison, herbarium material proved to be invariably inadequate to demonstrate these characters, as was already pointed out by Hooker (1871, p. 569); '...they are, moreover, extremely difficult of analysis from dried specimens, and much allowance must be made for the following descriptions'.

The present study ends with the taxonomical treatment of the taxa involved. That part is preceded by a presentation and discussion of detailed studies of characters, that were supposed to be of value for the delimitation of the taxa, either singly or in combination. In this presentation the correct names of the taxa recognized are used. These are:

1. *B. squamulosa* Hook.f.
2. *B. longipetiolata* Gilg
3. *B. elaeagnifolia* Hook.f.
4. *B. karperi* spec.nov.
5. *B. rwandensis* spec.nov.
6. *B. pelargoniiflora* spec.nov.

2. Historical account of the species concerned

In this chapter the various species involved will be introduced chronologically. Some of their features as described in the original publications are considered only cursorily, as these will be discussed in detail in Chapters 5 and 6. The opinions and conclusions of taxonomists who dealt with various aspects of the species since their publication are reviewed.

All the species were first described from a single gathering, except for *B. wilczekiana* N. Hallé which was based on four collections. As most of these type specimens lack female flowers or fruits, it is not surprising that J.D. Hooker (1871, pp. 570 and 579) considered *B. elaeagnifolia* and *B. squamulosa*, both from Gabon, to be dioecious. He described the male inflorescence of *B. elaeagnifolia* as 2-flowered and that of *B. squamulosa* as 6 to 10-flowered.

When Gilg (1904, p. 92) described *B. longipetiolata* and *B. macrura*, he also noted the absence of female flowers in his type material. It should be noted that Gilg described the male inflorescences of both species as few-flowered with many bracts at the base and many bracteoles at the top. He erroneously placed both new species in the section *Scutobegonia*, which is characterized by bisexual inflorescences, flowers with two perianth segments and winged ovaries. According to Gilg's description the flowers of his new species had two 'sepals' each and this observation might be the cause for his error.

The type specimen of *B. gracilipetiolata* De Wild. has male and female inflorescences and an infructescence. De Wildeman (1908, p. 319) correctly placed his new species in the section *Fusibegonia* Warb. (= *Tetraphila* A.DC.), which is characterized by a fusiform ovary without wings. According to De Wildeman's description the male inflorescence of this species contains 2 to 5 flowers, whereas the female flowers are solitary.

In Engler's treatise of the African species of *Begonia* (1921) ten out of the twelve species names considered in the present paper are mentioned in the key to the species. They are included in the series Subaequilaterales Engl. of the section *Fusibegonia* Warb. The name of this series refers to the more or less symmetrical shape of the lamina of the leaves of the species concerned. Five of these species names had already been published by J.D. Hooker, Gilg and De Wildeman (see above). The remaining five comprise two validated manuscript names, i.e. *B. bipindensis* Gilg ex Engl. and *B. crassipes* Gilg ex Engl., and three new ones, i.e. *B. gladiifolia*, *B. kribensis* and *B. schultzei*, proposed by Engler himself. The validated names had been written by Gilg on the sheets before March 1905, soon after the plants had been received and mounted in the Berlin herbarium in 1904.

It should be noted that Engler (1921, p. 618) presented his new species in a differential key. According to this key the common characters of these species

are fusiform non-winged fruits, male and female flowers with four perianth segments, more or less fused stamens and three or two bifurcated styles with an uninterrupted stigmatic band. The delimitation of the new species is based exclusively on the shape and comparative dimensions of the leaves. Engler (op. cit.) refrained from any description of the inflorescences. An apparent omission from Engler's work is the absence of any reference to type material for his new species and there might be confusion as to which specimens Engler had seen. However, Mildbraed (1922, pp. 89, 97, 98 and 188) referred to Engler's new names when he cited the localities and the numbers of his gatherings. Moreover, the pertinent set of Mildbraed's collections in the Berlin Herbarium carries these new names in Engler's own handwriting. Consequently they are to be considered as the holotypes of Engler's species and there cannot be any doubt as regards the interpretation of the names of *B. gladiifolia*, *B. kribensis* and *B. schultzei*. Nevertheless, *B. kribensis*, as published in Engler's key, does not key out specifically, but in combination with two other species. No distinctive characters are mentioned. Therefore this species name has to be considered as a nomen nudem. It should be noted that Engler (op. cit. p. 620) placed *B. longipetiolata* Gilg in the synonomy of *B. squamulosa* Hook.f. without argument. It appears that Hallé & Raynal (1966) overlooked this point in stating that this synonomy was established by Keay in 1954.

In spite of Engler's opinion that *B. longipetiolata* is conspecific with *B. squamulosa*, Hutchinson & Dalziel (1927, p. 188) maintained it as a separate species in their treatment of *Begonia* in the first edition of the Flora of West Tropical Africa. They cited Kalbreyer nr 155 collected on Mt. Cameroun, of which there is a duplicate in Kew. In 1911 Gilg identified this specimen with doubt as *B. longipetiolata*. The key to the species in this first edition of FWTA is almost exclusively based on vegetative characters.

In the 2nd edition of the FWTA the collection of Kalbreyer was cited also by Keay (1954, p. 220). Apparently he accepted Engler's opinion concerning the status of *B. longipetiolata* as he re-identified Kalbreyer's collection as *B. squamulosa* in 1953. The key in this edition is based on vegetative as well as on some floral characters. According to Keay (op. cit.) *B. squamulosa* including *B. longipetiolata*, is characterized by four perianth segments, a non-winged fusiform fruit and densely clustered male flowers.

It is clear that when Keay studied some of the species treated here, their male inflorescences had been described quite imperfectly, whereas the female ones and fruits were still virtually unknown. This situation was alleviated by Hallé & Raynal (1966) when they presented a detailed description and illustration of a plant in cultivation referred to the coll. J. & A. Raynal nr 9707 and several herbarium collections which they considered to be *B. squamulosa*. However, as will be shown in Chapter 6 their description applies to *B. longipetiolata*. Also, without having seen the type of *B. bipindensis* Gilg ex Engl. they reduced this species into the synonymy of *B. squamulosa* Hook.f., citing among others Annet nr 223. In Hallé (1972) there is an illustration of a leaf of Annet's collection. In the caption it is identified by Hallé as *B. squamulosa* Hook. f. var. *bipindensis*

(Gilg ex Engl.) N. Hallé. The variety is based exclusively on leaf shape: 'Le *Begonia squamulosa* Hook.f. présente au Cameroun des formes variétales étroites qui ont d'abord été nommées *B. bipindensis* Gilg ex Engl.' (Hallé 1972, p. 365). Hallé did not give additional characters for his new variety and he only mentioned Engler's basionym, without direct reference to place and date of valid publication, rendering his combination invalid according to Art. 33.2 (ICBN). Moreover, the lamina ratio of the coll. Annet 223 is circa 7, but that of the type collection of *B. bipindensis*, Zenker 3098, varies from circa 2 to 4. On the basis of its leaf shape Annet 223 should have been assigned to *B. gladiifolia* Engl. as emended by Wilczek (1969b, p. 84). This species was described on the basis of a single collection, Mildbraed 6394, with a lamina ratio of circa 8. For a further discussion of leaf shape and its taxonomical significance see Chapter 5.

One of the more extensive treatises of African *Begonia* species was published in the flora of Zaire, Rwanda and Burundi (Wilczek, 1969a). According to Wilczek *B. schultzei*, *B. gladiifolia*, *B. elaeagnifolia*, *B. squamulosa* and *B. gracilipetiolata* occur in Zaire. Next to inflorescences much emphasis is given to leaf characters, both in the key to the species and in their delimitation. In another publication Wilczek (1969b, pp. 84 and 88) intended to validate *B. gladiifolia* Engl. and *B. schultzei* Engl. As pointed out above, I consider Engler's treatment in his key (Engler, 1921), in combination with the presence of qualified type specimens in the Berlin herbarium, to be sufficient for the valid publication of these two names. Their publication was effected before a Latin diagnosis and the indication of a nomenclatural type were required, in 1935 and 1958 respectively. Thus I consider Wilczek's validation to be superfluous.

According to Wilczek, (1969b, p. 84) the specimens assigned by him to *B. gladiifolia* are characterized by more or less narrow lamina ('lamina lanceolata vel anguste elliptica-lanceolata'). One of the collections he cited is Kalbreyer nr 155, which was earlier cited by Hutchinson & Dalziel (1927) as *B. longipetiolata* and by Keay (1954) as *B. squamulosa*. Kalbreyer 155 consists of two sheets, one in B, the other in K. Neither of these is annotated by Wilczek. According to an attached label, the duplicate in the Berlin herbarium was provisionally classified as *B. ludwigsii* Gilg (nomen nudem, see treatment of *B. longipetiolata* in Chapter 10) by Irmscher, who studied African begonias from 1961 to 1968 (De Wilde & Arends, 1980, p. 378).

As to *B. schultzei*, Wilczek (1969b, p. 89) cited the specimens Schultze in Mildbraed 6208 and 6229 from Cameroun together with the specimen Van Roeckhoudt nr 12 from Zaire. The two collections from Cameroun, present in the Berlin herbarium, are both indicated as type material of *B. schultzei* Engl., and they are cited by Mildbraed (1923, p. 98) in his reference to Engler's new species. However, it should be noted that only Schultze in Mildbraed 6229 carries a label written by Engler himself, stating '*Begonia schultzei* Engler'. The specimen Schultze in Mildbraed 6208 carrying five leaves and a fragmentary inflorescence, does not have annotations of Engler demonstrating that he used it in his description. Thus Schultze in Mildbraed 6229 is the holotype of the species. The coll.

Van Roeckhoudt 12 effectively shows a superficial resemblance to the type specimen of *B. schultzei*. Van Roeckhoudt nr 12 is assigned here to the new species *B. rwandensis*.

It appears from a sketch in the Brussels herbarium that the type specimen of *B. elaeagnifolia* Hook.f., Mann 1651 from Gabon, was seen by Wilczek in 1967. In 1969 he assigned three collections from Zaire to this species (Wilczek, 1969a, p. 21). One of them, Cabra nr 115, had been identified as *B. elaeagnifolia* by De Wildeman & Durand in 1900 (p. 25). The three collections resemble the type of *B. elaeagnifolia* in having fairly small, somewhat narrow leaves. In the present study they are identified as *B. longipetiolata* Gilg.

The description of *B. squamulosa* Hook.f. in Wilczek (1969a, p. 21) is almost similar to that given by Hallé & Raynal (1966). Of the Zaire collections cited by Wilczek for this species all but one (Christiaensen 1922) are assigned here to *B. longipetiolata* Gilg. Similarly the two collections including the type of *B. gracilipetiolata* De Wild. cited by Wilczek (op. cit., p. 22) for that species, are identified here as *B. longipetiolata*.

The type collection of *B. nicolai-hallei* Wilczek (1969b, p. 86) is provided with a field note by Hallé, in which the collector states that he considers his collection to be affiliated with *B. squamulosa* sensu Hallé & Raynal. However, Wilczek (op. cit.) described it as a new species in the alliance of *B. polygonoides* Hook.f. *B. nicolai-hallei* is transferred here to *B. longipetiolata*.

In Wilczek's paper (1969b, p. 91) *B. wilczekiana* was validly published by Hallé, who indicated its affinity to *B. squamulosa*. This view is fully supported, although in my concept it is placed in the synonomy of *B. elaeagnifolia* Hook.f.

In the Conspectus Flora Angolensis, Fernandes (1970, p. 293) discussed the identity of Gossweiler nr 7811 (Feb. 15, 1919), having studied duplicates in BM, COI, LISJC and LISU. The duplicate in BM has a label with an English translation of the field notes, the others have annotations in Portuguese. Fernandes noticed the similarity of the leaves with those of certain small-leaved plants of *B. squamulosa* Hook.f., but she identified the collection as *B. gracilipetiolata* De Wild., because of its fusiform immature fruits, while the fruit of *B. squamulosa* had previously been described by Hallé & Raynal (1966) as obpiriform. In the present study however, it has been found that the fruit of *B. squamulosa* as well as that of the other species studied usually is fusiform. In the same volume Fernandes (op. cit., p. 364) discussed the identity of another specimen collected by Gossweiler in 1919 as well. This specimen, present in K, consists of two small fragments and is labelled Gossweiler nr 9811 (not 7811) with, in English, almost identical field notes. Fernandes noted some errors in the translation and supposed that the collection number is erroneous. I am certain that Fernandes was right in her assumption. The K duplicate had been seen by Irmscher as well, who annotated it with 'material too scanty, 2 species?' and assigned it with doubt to *B. elaeagnifolia*. Because of the comparatively short internodes Fernandes concluded that Irmscher's identification might be in error and she speculated that the narrower leaves might be young not yet fully developed ones. She identified this additional duplicate as either *B. elaeagnifolia* or *B. gracilipetiolata* and

suggested that for a proper identification additional gatherings would be necessary. In this treatise Gossweiler's collection 7811 (including 9811) is identified as *B. longipetiolata*.

The preceding paragraphs indicate that, in the past, vegetative characters have been overemphasized in delimiting and recognizing the pertinent taxa.

3. Material & methods

Preserved plants

All collections consisted of dried material and three collections from before 1978 also contained spirit material. During the recent expeditions in Gabon dried as well as spirit collections were prepared. Dried material of *Begonia* is very brittle, so parts taken from a sheet needed to be moistened prior to removal. The material was then boiled in water for 3-5 minutes and studied in 70% ethanol. In order to further the flexibility of the material, the water contained three drops of Agepon photographic wetting agent per 100 ml and the ethanol 0.5 ml of glycerol per 100 ml. After analysis the material was dried again and remounted on the sheets.

In a few cases the labels of the specimens provided information about the geographical coordinates of the localities from which the plants had been collected. For the remainder of the collections these coordinates could usually be found by consulting one or more of the following sources: the gazetteers published by the U.S. Army Topographic Command, Washington D.C. (Official Standard Names Division); atlases of Barthlomew (1956), Haack (1925) and Scobel (1912); the phytogeographical study of Letouzey (1968) in combination with maps (scale 1:200.000) published by the Institute Géographique National-France (Paris) for Cameroun; similar maps and Raynal (1968) for Gabon and the gazetteer of the localities listed by Bamps (1982) for Zaire and Rwanda. In the citation of the specimens (Chapter 10) the coordinates are mentioned in the description of the localities.

Living plants

Plants of *B. squamulosa*, *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi* were studied in the living condition. All accessions listed in Table 4-1 are of known origin. Except for two accessions of *B. longipetiolata* from Cameroun, Leeuwenberg 9288 and W.J. de Wilde & De Wilde-Duyfjes 2020, all gatherings are from Gabon.

The plants that were received in Wageningen became part of the living plant collection of the Department of Horticulture, Agricultural University, Wageningen (T series). Since 1984 the introductions have been cultivated in the greenhouse of the Department of Plant Taxonomy of the Agricultural University (PT series).

The plants were grown on benches in pots with peat substrate or as 'epiphytes' on tree fern slabs. Parts of these cultivated plants have been preserved as voucher

material in the collection J. van Veldhuizen, WAG.

Plants of *B. longipetiolata* were usually individuals of a population from which other plants have been preserved in the field. Those of the other species were grown in most cases from top cuttings taken from side branches of plants before these were dried.

Chromosome studies

Somatic chromosomes in root tip cells were studied from permanent squash preparations. These were made according to the following method. Root tips were pre-treated in aerated 0.002 M 8-hydroxyquinoline for 3.5 hours at c. 20 °C; fixed and macerated in 1 N HCl at 60 °C for 2 min. Subsequently the material was transferred to 45% acetic acid for 30 min. and squashed. After removal of the cover slip in liquid nitrogen the slide was air dried on a hot plate. The slide was then hydrolysed for 5 min. in 1 N HCl at 60 °C; rinsed in running water for 30-45 min. and stained in Giemsa (1.5 ml Gurr's R66 stock solution in 100 ml phosphate buffer) for 3-6 min. When necessary, the cytoplasm was cleared by keeping the slides in oil of cloves for 1 hour prior to passing them through xylene before they were mounted with DPX (British Drug Houses) and cover slips.

Pollen staining

Pollen preparations were made using a modified acetolysis staining procedure according to Erdtman (1952). Anthers of dried flowers were moistened for 5 min. in water and transferred to a sieve (mesh gauge 80 μm). Anthers from spirit material were directly transferred to the sieve. Subsequently they were gently rubbed and washed through the sieve, using 10 ml. water. The filtrate was centrifuged and the residue rinsed for 5 minutes in glacial acetic acid; centrifuged again; acetolyzed in a mixture of 9 parts acetic anhydride and 1 part sulphuric acid (98%) for 9-10 min. at 100 °C; quickly cooled to room temperature and centrifuged after each of the following steps; rinsed once in glacial acetic acid; twice in water; and finally rinsed in a 1:1 mixture of water and glycerol. The tubes were kept upside down overnight after decanting the supernatant. The stained pollen was mounted on microscope slides according to the method introduced by Punt (1962) and described by Tj. Reitsma (1969, p. 200).

Histological studies

For microtome sectioning the tissue was fixed in the field in a formalin, acetic acid and ethanol mixture, that taken from cultivated plants in a mixture of 3 parts 96% ethanol and 1 part glacial acetic acid. The tissue-specimens were

embedded in Kulzer's Technovit after being passed through a graded series of water/ethanol. The 10 μm sections were stained with 0.2-0.5% Toluidine blue in 1 N HCl.

4. Somatic chromosome numbers

Table 4-1 shows that the 2n numbers of several accessions of *B. squamulosa*, *B. elaeagnifolia* and *B. longipetiolata* range from 71 to 76. These figures are approximately double the 36 to 39 which were found in other accessions of these species. The counts of 71 to 76 are considered here as tetraploid and those of 36 to 40 as diploid. In each of the three species it was found that the tetraploid plants are almost indistinguishable from the diploid ones (see below). In *B. karperi* the diploid numbers, 2n = 36 to 38, were found.

Except for one accession all these chromosome data are new. Legro & Doorenbos (1973) also reported 2n = 38 for PT00-650, culta coll. W.J. de Wilde 2020, from Ebolowa, Cameroun, but they identified it as *B. squamulosa*. Living material of the new species *B. pelargoniiflora* and *B. rwandensis* was not available for chromosome counting.

As to the terminology which is used here to designate the two ploidy levels, it has been pointed out that the term diploid may have a dual meaning (e.g. Löve & Löve, 1975 and Stace, 1989). The term diploid as '2x' is applied to the lowest diplophase number in a polyploid series. The chromosomal basic number 'x' represents the smallest monoploid number of such a series (Rieger, Michaelis & Green, 1968). In the present study it was found that the somatic chromosome numbers of the remaining species of the section *Tetraphila* range from 2n = 36 to 40. When the basic number of the section is assessed from the series 2n = 36 to 40 and 2n = 71 to 76 it follows that x = c. 18.

Raven (1975) presented evidence that the original basic number of the angiosperms is x = 7, but Grant (1982) showed that it is also possible that it is x = 8 or 9. On the basis of the conclusions of Raven and Grant it is evident that the high basic number of c. 18, as assessed here for the section *Tetraphila*, represents a derived and polyploid condition. So far a somatic chromosome number of 2n = 18 has not been found in a taxon of this section. According to De Wilde (pers. comm.) *Tetraphila* has a closer relationship to the African sections *Baccabegonia* and *Squamibegonia* than to any other section. The 2n numbers of *Baccabegonia* and *Squamibegonia* are similar to those on the diploid level of *Tetraphila* as they also range from 2n = 36 to 40. Comparatively low numbers of 2n = 22 have frequently been found in several sections of *Begonia* (see for example Legro & Doorenbos 1969 and 1971). However, these numbers have been recorded for sections with a taxonomic position that is remote from the section *Tetraphila*. The lowest chromosome number published to date, 2n = 16, was found by Legro & Doorenbos (1971) in *B. gigantea* Wall. of the Asiatic section *Monopteron*. During the present investigation I observed low numbers of 2n = 16 and 18 in two new species of the African section *Scutobegonia*. This section as well as the section *Monopteron* has less affinity to *Tetraphila* than the sections *Baccabe-*

Table 4.1. Somatic chromosome numbers in cultivated specimens of *Begonia* species

Entry nr. liv.coll.	Voucher Veldh.	Collection	Provenance	Ploidy level	2n
B. squamulosa					
T1210B	740	B & W 355	Gabon,Crystal Mts	4x	76
T1606	989	De Wilde (1983)-100	Gabon,Crystal Mts	4x	74
T1603	991	De Wilde (1983)-119	Gabon,Crystal Mts	4x	74,76
T1587	990	De Wilde (1983)-181	Gabon,Crystal Mts	4x	71,74
T1775	1218	Arends 371	Gabon,Chaillu Mts	2x	36,38
B. longipetiolata					
T1203	1219	B & W 356	Gabon,Crystal Mts	2x	36
T1210D	741	B & W s.n.,loc 355	Gabon,Crystal Mts	2x	36
T1207B	738	B & W s.n.,loc 335	Gabon,Crystal Mts	2x	36,38
T1207D	737	B & W s.n.,loc.335	Gabon,Crystal Mts	2x	36,38
T1616	988	De Wilde (1983)-s.n. loc. 931	Gabon,Cocobeach	2x	36
T1592	969	De Wilde (1983)-180	Gabon,Crystal Mts	2x	38
PT86-362		De Wilde, J.J. 8840	Gabon,Crystal Mts	2x	34
T1604	971	De Wilde (1983)-326	Gabon,Chaillu Mts	4x	72,73
T1608	972	De Wilde (1983)-483	Gabon,Chaillu Mts	4x	71,72
PT84-183	1217	Arends 483	Gabon,Chaillu Mts	2x	36
PT86-426	1254	De Wilde, J.J. 9270	Gabon,Doussa river	2x	38
T1060	458	Leeuwenberg 9288	Cameroun, Mt. Koupé	2x	36,38
PT00-650	1220	De Wilde, W.J. 2020	Cameroun,Ebolowa	2x	38
B. elaeagnifolia					
T1186	742	B & W 8	Gabon,Crystal Mts	4x	73,76
T1202	743	B & W 38	Gabon,Crystal Mts	4x	74
T1194	736	B & W s.n.	Gabon,Crystal Mts	4x	72,74
T1207E	756	B & W s.n.,loc.335	Gabon,Crystal Mts	4x	76
T1247	746	B & W s.n.	Gabon,Crystal Mts	4x	73,76
T1589	1049	De Wilde (1983)-s.n. loc. 100	Gabon,Crystal Mts	4x	76
T1593	970	idem	Gabon,Crystal Mts	4x	72,74
T1637	1048	De Wilde (1983)-179	Gabon,Crystal Mts	4x	72,76
PT85-516	1221	idem	Gabon,Crystal Mts	4x	72
T1640	996	De Wilde (1983)-s.n. loc. 180	Gabon,Crystal Mts	4x	76
T1686	1224	Louis, A.M. 1267	Gabon,Chaillu Mts	2x	38
PT84-184	1226	Arends 571	Gabon,Chaillu Mts	2x	38
PT84-186	1228	Arends 559	Gabon,Chaillu Mts	2x	36,37
PT86-286	1229	Breteler 8248	Gabon,Chaillu Mts	2x	37
PT88-25	1304	De Wilde, J.J. 9638	Gabon,Chaillu Mts	2x	38
PT88-27	idem		Gabon,Chaillu Mts	2x	38
PT84-192	1227	Arends 670	Gabon,Doudou Mts	2x	37
PT84-194	1225	Arends 681	Gabon,Doudou Mts	2x	39
PT85-47	1216	Reitsma 1958	Gabon,Doudou Mts	2x	37
PT86-424	1255	De Wilde, J.J. 9127	Gabon,Doudou Mts	2x	39
		De Wilde, J.J. 9810	Gabon,Rabi	2x	38
B. karperi					
T1207	744	B & W 335	Gabon,Crystal Mts	2x	38
T1596		De Wilde (1983)-158	Gabon,Crystal Mts	2x	37
T1597	1223	idem	Gabon,Crystal Mts	2x	36,38
T1620	1222	idem	Gabon,Crystal Mts	2x	36

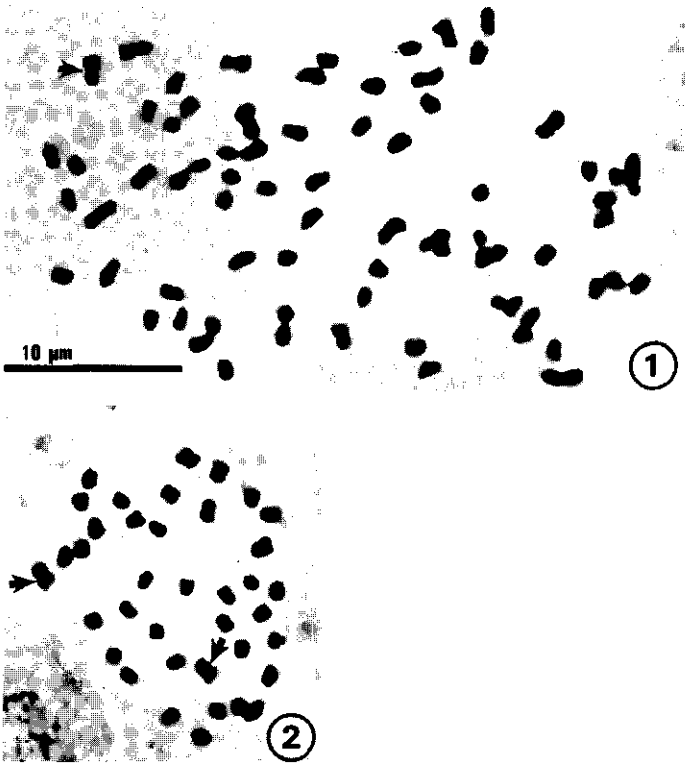
Abbreviations: Veldh. = van Veldhuizen collection (WAG);
B & W = Breteler & De Wilde (1978).
For details of provenances see Specimens examined.

gonia and *Squamibegonia* mentioned above. The numbers 2n = 16 and 18 are approximately half of the 36 to 40 found in *Tetraphila, Baccabegonia* and *Squamibegonia*. The occurrence of the numbers 2n = 16 and 18 in *Begonia* suggests that the basic number x = c.18 as assessed for *Tetraphila* might have originated from an original basic number of x = 9. This implies that the taxa with 2n = 36 to 40 could be considered as tetraploid and those with 2n = 71 to 76 as octoploid. The morphology of the somatic chromosomes at metaphase of the species with 2n = 36 to 39 as shown in this chapter (Figs. 4-2,-3, -4, -6 and -7) demonstrates that it is not possible to indicate differing sets of chromosome pairs within the karyotypes. As meiotic first metaphase configurations could not be studied, it can only be surmised that the tetraploid plants represent interracial autopolyploids (Grant 1981, p. 300). As mentioned above, taxa with 2n = c. 18 chromosomes have not been found in *Tetraphila* and there is no morphological or other evidence that may indicate which taxa might be considered as ancestral of the extant species of *Tetraphila*. It appears that diploids based on x = 9 do not exist any more. Therefore, the basic chromosome number of the section *Tetraphila*, although derived, is presented here as x_2 = c. 18 and not as x = c. 9. On the basis of this neo-basic number the plants investigated have to be designated as diploid and tetraploid respectively.

For 27 out of 42 records the table presents only a single chromosome number. These numbers are sometimes based on the analysis of a single metaphase plate, and, in general, the number of cells that has been analyzed varied from two to four, these low numbers due to the rarity of well-spread metaphase plates with distinct chromosomes in *Begonia*. Moreover, the interpretation of metaphase plates may be rather difficult, because two or more overlapping or touching small chromosomes can easily be misinterpreted as a single one. Meyer (1965, p. 573) who attempted to produce karyograms of tuberous *Begonia* species and hybrids, stated that 'out of 200 to 300 metaphase plates at most 3 to 5 permitted a more or less reliable analysis'.

From Table 4-1 it is evident that there is variation in chromosome number. With the exception of 2n = 34 in accession PT86-362 of *B. longipetiolata* the chromosome numbers on the diploid level range from 2n = 36 to 39 and those at the tetraploid level from 2n = 71 to 76. In several instances somewhat different numbers have been observed in a single root tip or in a slide containing two or three root tips from an individual specimen. A similar variation has been found between plants from a single population. This is demonstrated by the numbers presented for *B. karperi*, collected near Mela in the Crystal Mts of Gabon. Two accessions of *B. longipetiolata*, T1203 with 2n = 36 and PT 86-362 with 2n = 34, have been gathered from the same topodeme near Kinguélé in the Crystal Mts on different occasions. Another plant, T1592, collected not far away from the Kinguélé population showed 2n = 38 chromosomes.

The discovery of variable numbers of somatic chromosomes in *Begonia* is not new. Legro & Doorenbos (1969, 1971 and 1973) occasionally encountered some variation in the number and appearance of somatic chromosomes. They presented the results of their analysis of several species as 2n numbers with 1

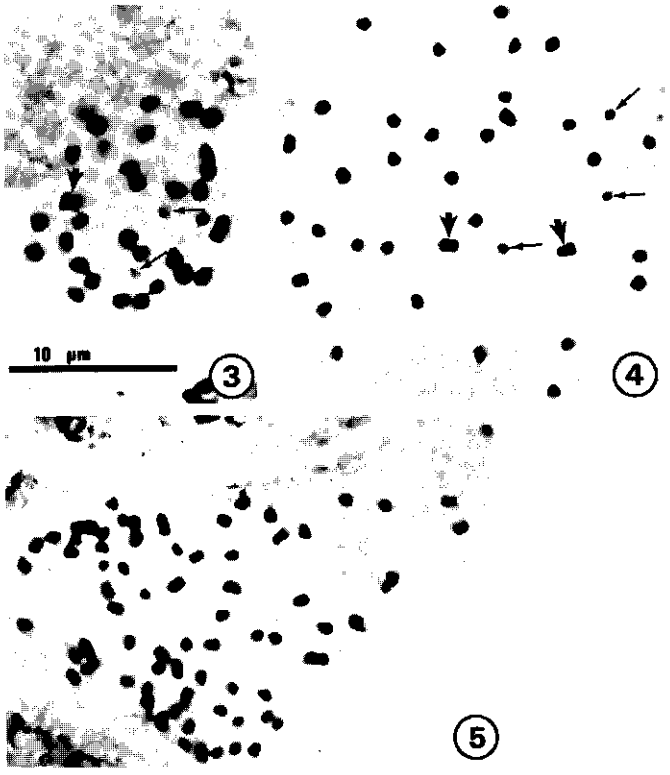


Figs. 4-1 and -2: Somatic metaphase plates in root tip cells of *B. squamulosa*; 4-1: 2n = 74 chromosomes in the tetraploid plant T1210B, culta Breteler & De Wilde (1978)-355, Crystal Mts, Gabon; 4-2: 2n = 38 chromosomes in the diploid plant T1775, culta Arends, De Wilde & Louis 371, Chaillu Mts, Gabon. Arrows indicate examples of chromosomes with distinct centromeres.

to 3 '+' symbols, indicating, as they stated, 'fragments or very small (or reduced) chromosomes'. In one case only they presented explicit evidence of the occurrence of different chromosome numbers within one plant (Legro & Doorenbos, 1969, p. 190). In that publication they reproduced a metaphase plate of *B. cathayana* Hemsl. with 2n = 20 chromosomes, but in the caption of the figure they stated that they usually observed 2n = 22 in that species. While Legro & Doorenbos indicated that there is sometimes minor variation in somatic chromosome number in *Begonia*, earlier reports state that the occurrence of extensive series of different chromosome numbers within an individual plant is a regular feature of the genus. Piton (1962, p. 177) found a series of 2n = 18 to 30 chromosomes in somatic (root) tissue of *B. natalensis* Hook. She proposed 2n = 24 as the diploid number of that species, because it was found the most frequently. Meyer (1965, pp. 564, 565 and 602) reported the occurrence of similar long series of somatic chromosome numbers in tuberous *Begonia* species and cultivars as well. She considered her observations as evidence of somatic instability or aneuso-

maty. Tuberous *Begonia* cultivars and species have also been investigated by Legro & Haegeman (1971), but they did not corroborate the conclusions of Meyer. Several years ago the present author counted the chromosomes of many plants of the cultivar group Compacta of the tuberous hybrid *Begonia* 'Bertinii' (unpublished). In accordance with Legro & Doorenbos (op. cit.), it was found that the somatic chromosome number in some cells may deviate by one or rarely two chromosomes from that seen in the majority of cells of a single specimen. I concluded that this variation in a single specimen is due to mitotic disturbances. The (tetraploid) numbers found in the different plants of the cultivar group form an aneuploid series of $2n = 51$ to 57 that is probably the result of non-disjunction during meiosis of the polyploid hybrid parent plants. Although I do not support Meyer's claim of extensive aneuploidy and aneusomaty in tuberous *Begonia*, it appears from the numbers presented here, and the evidence given in Legro & Doorenbos (op. cit.) and De Wilde & Arends (1979; 1980), that a minor variation in somatic chromosome number may occur within a species or even within an individual of *Begonia*. The variation in chromosome number found in *B. loranthoides* Hook.f., section *Tetraphila*, (De Wilde & Arends, 1979) and in *B. ampla* Hook.f. and *B. poculifera* Hook.f. of the section *Squamibegonia* (ibid. 1980) was attributed to either the presence or absence of accessory chromosomes interpreted as B chromosomes.

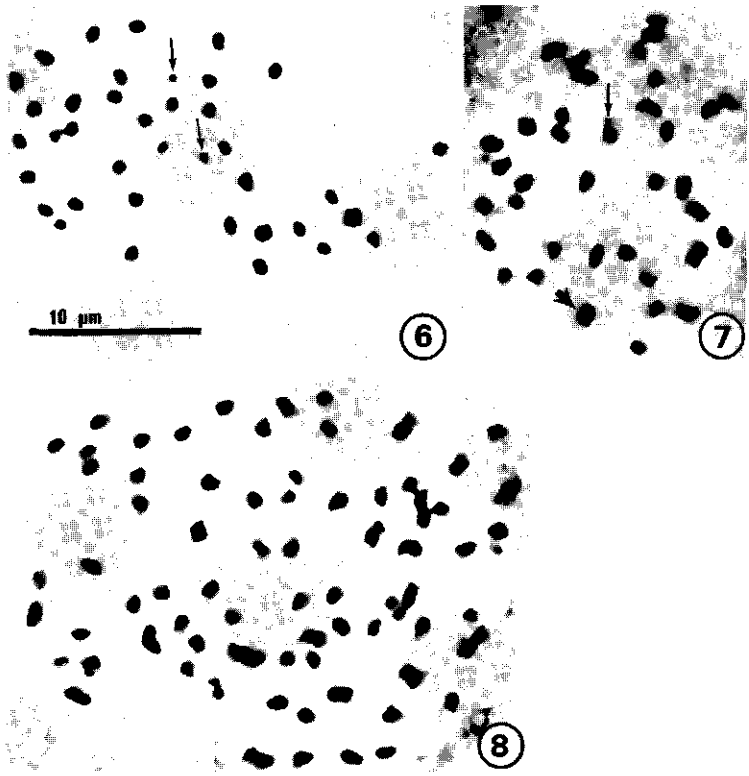
However, on the basis of a further investigation of new accessions of *Begonia*, including those of the species treated here, it now appears that, at least for the section *Tetraphila*, this interpretation was premature as the evidence is inconclusive. In Figs. 4-3,-4 and -6 one to three small structures are less intensely stained than the remainder of the chromosomes and could perhaps be interpreted as heterochromatic chromosomes. Whereas in these figures the presumed heterochromatic small chromosomes are separate from the other, darker-stained chromosomes, the configuration in Fig. 4-7 shows a similar structure very close to a larger chromosome and could thus be interpreted as a satellite. Therefore, it cannot be ruled out that the faintly stained structures shown in Figs. 4-3, -4 and -6 are satellites which have been detached from the chromosomes of which they are part. Fig. 4-2 shows that it is not always possible to distinguish between small autosomes and presumed B chromosomes, as all chromosomes are more or less similarly stained. Indicative of the presence of B chromosomes is their behaviour, which may differ from that of autosomes during cytokinesis in both mitotic and meiotic cells. In *Begonia* meiosis remains to be investigated. Sybenga (1972, p. 159) mentioned that in cultivated maize the accumulation of B chromosomes may yield high numbers (up to 30) of these accessories, but that in nature their number is rarely more than four. This suggests that a variation in chromosome number between $2n = 36$ and $2n = 38$ or 40 might be due to the occurrence of B chromosomes. Nevertheless, the evidence obtained so far is conflicting, and the cause of chromosome number variation in *Begonia* has still to be clarified. However, the extensive variation in somatic chromosome number found by previous workers may well be due to misinterpretations as *Begonia* chromosomes are rather difficult to handle.



Figs. 4-3 to -5: Somatic metaphase plates in root tip cells of *B. longipetiolata*; 4-3: 2n = 34 chromosomes in the diploid plant PT86-362, culta De Wilde, Arends & de Bruijn 8840, Crystal Mts, Gabon; 4-4: 2n = 38 chromosomes in the diploid plant T 1060, culta Leeuwenberg 9288, Mt. Koupé, Cameroun; 4-5: 2n = 71 chromosomes in the tetraploid plant T1608, culta De Wilde, Arends et al.(1983)-483, Chaillu Mts, Gabon. Thick arrows indicate examples of chromosomes with distinct centromeres, the thinner ones small chromosomes referred to in the text.

As concerns chromosome length, the metaphase plates presented in the illustrations show that the length of the chromosomes ranges from 0.5 to 2.5 µm. Some chromosomes, indicated by arrows, show a constriction that is probably the centromere. In most of the chromosomes the position of the centromere could not be seen. These chromosomes may be acrocentric, but it is also possible that the centromere region is not resolvable in them, as they are so small. Although some differences in overall chromosome size may be observed between the different metaphase plates, karyotype morphology cannot be an additional character for distinguishing the species treated here.

It was attempted to find a correlation between ploidy level and (macro)-morphological characters. Only two characters appear to distinguish the 2x and 4x cytotypes. Living and spirit material of the leaf petiole of tetraploid *B. squamu-*



Figs. 4-6 to -8: Somatic metaphase plates in root tip cells of *Begonia* species; 4-6: *B. karperi*, 2n = 38 chromosomes in plant T1207, culta Breteler & De Wilde (1978)-335, Crystal Mts, Gabon; 4-7 and -8: *B. elaeagnifolia*; 4-7: 2n = 37 chromosomes in the diploid plant PT 85-47, culta Reitsma 1958, Doudou Mts, Gabon; 4-8: 2n = 76 chromosomes in the tetraploid plant T1186, culta Breteler & De Wilde (1978)-8, Crystal Mts, Gabon. For the details indicated by the arrows see caption of Figs. 4-3 to -5.

losa is quite terete, whereas that of the diploid is slightly flattened above. The same petiole character is found in *B. elaeagnifolia* cytotypes. Living accessions of diploid *B. longipetiolata* have distinctly furrowed petioles with the exception of coll. Leeuwenberg 9288. The tetraploids, T1604 and T1608, have petioles that are hardly furrowed. Unfortunately, differences in petiole morphology are very difficult or even impossible to detect in dried specimens of *Begonia*. The petiole character is further discussed in Chapter 5, whereas the correlation between ploidy level and pollen size is discussed in Chapter 8. There it is demonstrated that pollen grains of 4x plants of *B. squamulosa* tend to be larger than those of 2x plants. A similar correlation occurs in *B. elaeagnifolia*. In *B. longipetiolata* there is an extensive variation in pollen size that cannot be correlated with ploidy level. Other characters, including stomata, did not provide useful differences.

Table 4-1 shows that the 2x and 4x plants of *B. elaeagnifolia* are geographically isolated from each other. So far the 4x plants of this species have been collected in the Crystal Mts, Gabon, whereas the 2x plants have been found elsewhere in that country. A similar phenomenon occurs in *B. squamulosa*. Because of the geographical basis of the karyological variation, it appears that in both species the plants from the Crystal Mts are members of a tetraploid cytological race (see Stuessy 1990, p. 190).

Two plants of *B. longipetiolata* with a tetraploid chromosome number have been collected only from a single topodeme in the central Chaillu Mts of Gabon. All other living accessions of this species, including a plant from the same region, proved to be diploid. An explanation for the occurrence of tetraploid races in both *B. elaeagnifolia* and *B. squamulosa* will be attempted in Chapter 9.

5. Aspects of vegetative morphology

5.1. General introduction

All the species in *Begonia* section *Tetraphila* have the alternate leaves arranged in two ranks. Several species which are not treated in this study, have upright stems and hold their leaves in a horizontal to ascending posture with the upper surface adaxial. In the species considered here the leaf arrangement and the orientation of the leaf surface is basically similar but not immediately obvious, as the petioles are attached to prostrate stems on the side away from the substrate and twisted in their proximal part. Owing to this twisting of the petioles the adaxial leaf surface is turned away from the stem, while the lower or abaxial surface actually faces the stem and the substrate.

Upper and lower surface of a living leaf can be told apart easily. In most of the plants studied the upper surface is glossy, green and glabrous, whereas the lower surface is dull, paler and provided with scales. The veins are more or less prominent on the lower surface so that the venation is more conspicuous on that surface than on the upper. The conspicuousness of the venation on the lower surface is often enhanced by a reddish colour of the veins and the adjacent parenchyma. In the dried condition,however, both surfaces are very similar in appearance and difficult to distinguish from each other. The only features which can be used to distinguish the surfaces of dried leaves are the indumentum and the prominent veins on the lower surface. The indumentum of scales remains on the leaf, but the veins become less prominent and distinct when the leaves are dried. Close observation of the base of a dried blade usually reveals that the vein which is continuous with the petiole was prominent before the leaf was dried, but sometimes it is necessary to boil the material to discern this. In two species scales are also present on the upper leaf surface, viz.: *B. karperi* and *B. pelargoniiflora*, but the scales on the upper surface are isolated and scattered, while on the lower surface they are much closer to each other and occur mainly near the veins and the margin.

Each leaf is accompanied by two stipules which are attached to the node and free from the base of the petiole (see also Eames, 1961, p. 12). One stipule of each pair occupies a slightly more lateral position on the stem than the other, and this stipule always covers a single scaly bud. This implies that the buds which eventually may produce lateral branches or short flowering shoots (see page 55), are arranged in two ranks along the stem. The stipules are always formed before the leaves are produced. In *B. elaeagnifolia* and particularly in *B. karperi*, the extremity of the stem often is not yet provided with developed leaves, but expanded inflorescences may already be present at the nodes. Occasionally, leaves do not develop at all and consequently such nodes may remain

leafless. In *B. longipetiolata* one may find up to three of such nodes in succession.

5.2. Dimensions of leaf and stem

5.2.1. Leaf size

In several of the species considered in the present study, the size of the leaves varies considerably and may also be influenced by environmental conditions. For example, in the accession De Wilde, Arends & de Bruijn 9270 of *B. longipetiolata* the largest leaf-blade in the smallest plant is 8 cm long and 3 cm wide, that of the largest plant in the same collection measures 16 and 7 cm. Cultivated plants of the same collection produced blades of up to 24 x 11 cm.

The length of the petiole is variable and is not correlated with the size of the blade. The relative petiole-length (which is defined as the ratio of blade- and petiole-length) varies within a local population, but even in a single plant the relative petiole-length of a particular leaf may deviate considerably from that of another leaf. For example, the relative petiole-length for a leaf in Breteler & De Wilde 335 of *B. karperi* is 1.25, that of another leaf 0.55 and in the specimen Lambinon 78/279 of *B. squamulosa* two leaves have a ratio of 1.3 and 0.80 respectively. Similarly, two leaves in Satabié & Letouzey 343, which is assigned to *B. elaeagnifolia*, have a ratio of 1.10 and 0.50 respectively.

Growing conditions may have a considerable effect on the habit of the plant. This is demonstrated by a photograph (Fig. 5-1) showing three propagules of a plant of *B. elaeagnifolia* grown under different conditions. The two parts on the top of the sheet were grown on a tree-fern slab, whereas the large part on the bottom was grown in peat substrate under more shady conditions. The subdued light and the permanent supply of water and nutrients provided by the peat-substrate have a marked effect on the leaves as the blades are much larger and the petioles are approximately twice the length of the blades. The petioles and the blades in the specimens from the tree-fern slab are more or less equal in length. The plants at the top resemble the type specimen of *B. schultzei* and the bottom one looks like the type of *B. wilczekiana*, two taxa which are here considered to be conspecific with *B. elaeagnifolia*.

Recently, Sands (1990) described *B. malachosticta* in the Asian section *Petermannia*, which has petioles 2.5 to 6 cm long. According to Sands, his new species is very similar to *B. tawaensis* Merrill (also in section *Petermannia*). The petioles in that species were described by Merrill as having a length of up to 1 cm. However, Sands (op. cit., p. 62) found that the type specimen of *B. tawaensis* also has one leaf with a petiole of more than 4 cm long. Consequently, Sands concluded that petiole length may be of doubtful value in distinguishing between the two species. Considering all the evidence, I conclude that blade size and absolute or relative petiole length do not provide useful characters for distinguishing the taxa studied.

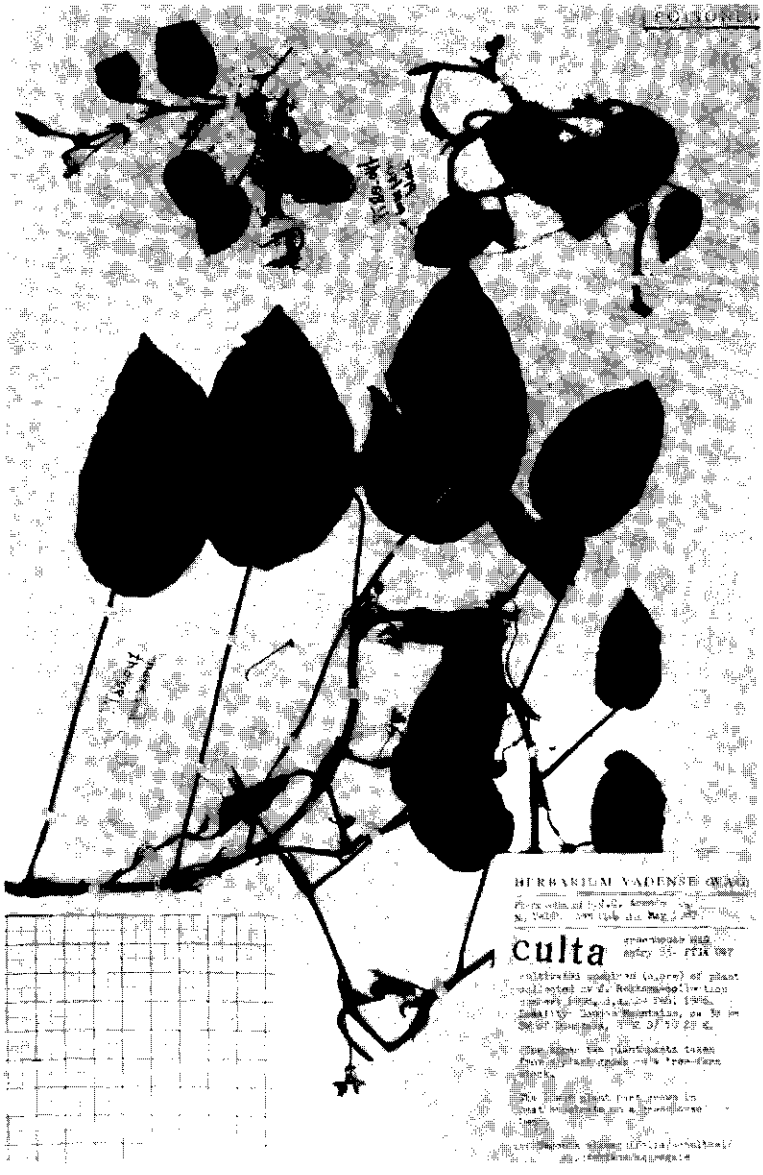


Fig. 5-1: *B. elaeagnifolia*, dried parts from the cultivated accession Reitsma 1958. The two parts at the top were taken from a plant cultivated on a tree-fern slab, the part at the bottom from a plant grown on peat substrate under more shady conditions.

5.2.2. Stem thickness

J.D. Hooker (1871) compared the thickness of the stem of *B. elaeagnifolia* and *B. squamulosa* with that of a quill of a sparrow and a goose respectively, and in the key to the species he used the thickness of the stem as a character to separate the species. The dried stem in Mann 1651, the type of *B. elaeagnifolia* is c. 1 mm and that in Mann 1654, the type of *B. squamulosa* c. 5 mm in diameter. Having studied all the collections which are now available, I conclude that the thickness of the stem is still a valid character to separate these two species, because in *B. elaeagnifolia* the dried stems have a diameter of 1 to 3 mm, whereas those in *B. squamulosa* are usually 5 to 8 mm thick.

The dried stems in *B. longipetiolata* are 2 to 5 mm thick, thus overlapping the size range of those of *B. elaeagnifolia* (1 to 3 mm in diam.). The size range of the stems in *B. longipetiolata* is continuous with that of *B. squamulosa*. Thus stem thickness is not always a useful character to separate the species.

Stem diameter may be used as an additional character to distinguish *B. karperi* and *B. rwandensis*. The dried stems in these species have a diameter of c. 1.5 – 2 mm and c. 2.5 – 5 mm, respectively. Because the thickness of living stems in about 15 collections of *B. elaeagnifolia*, *B. longipetiolata* and *B. squamulosa* has been recorded by the collectors before the plants were dried, a fairly accurate estimate of the diameter of the living stem in *B. rwandensis* can be made. Comparison of these records with the measurements of the dried plants reveals that stems in these *Begonia* species decrease approximately 20 to 40 (50)% in diameter when they are dried. This implies that the thinnest living stems in *B. rwandensis* probably were c. 3 – 3.5 mm and the thickest c. 6 – 7 mm in diameter. Living stems in cultivated vigorous plants of *B. karperi* were never thicker than 3 mm. Thus *B. rwandensis* invariably has thicker stems than *B. karperi*.

5.2.3. Stem length

The length of the stem is difficult to assess from dried specimens, because often only the extremity was collected. For example, among the specimens of *B. squamulosa*, Escherich 248 consists of the apex of the stem with a single expanded leaf, whereas personal field observations indicate that this species may have stems up to 1 m long. The stems in *B. longipetiolata* are much shorter, usually not exceeding 40 cm, although the stems of plants from Bélinga, Gabon also have a length up to 1 m. In *B. elaeagnifolia* and *B. karperi* the stems are often up to 2.5 m long. In cultivation, the stems of *B. longipetiolata* are always distinctly shorter than those of the other species mentioned.

5.2.4. Absolute and relative internode length

The length of the stem is correlated with the length of the internodes. In plants of *B. elaeagnifolia* and *B. karperi* the internodes are up to 7 cm long. The internodes in *B. longipetiolata* are frequently shorter than 1.5 cm and in *B. squamulosa* they usually measure 3.5 to 6 cm. Thus it appears that *B. longipetiolata* and *B. squamulosa* which resemble each other rather closely, could be distinguished on the basis of the length of their internodes. However, there are exceptions

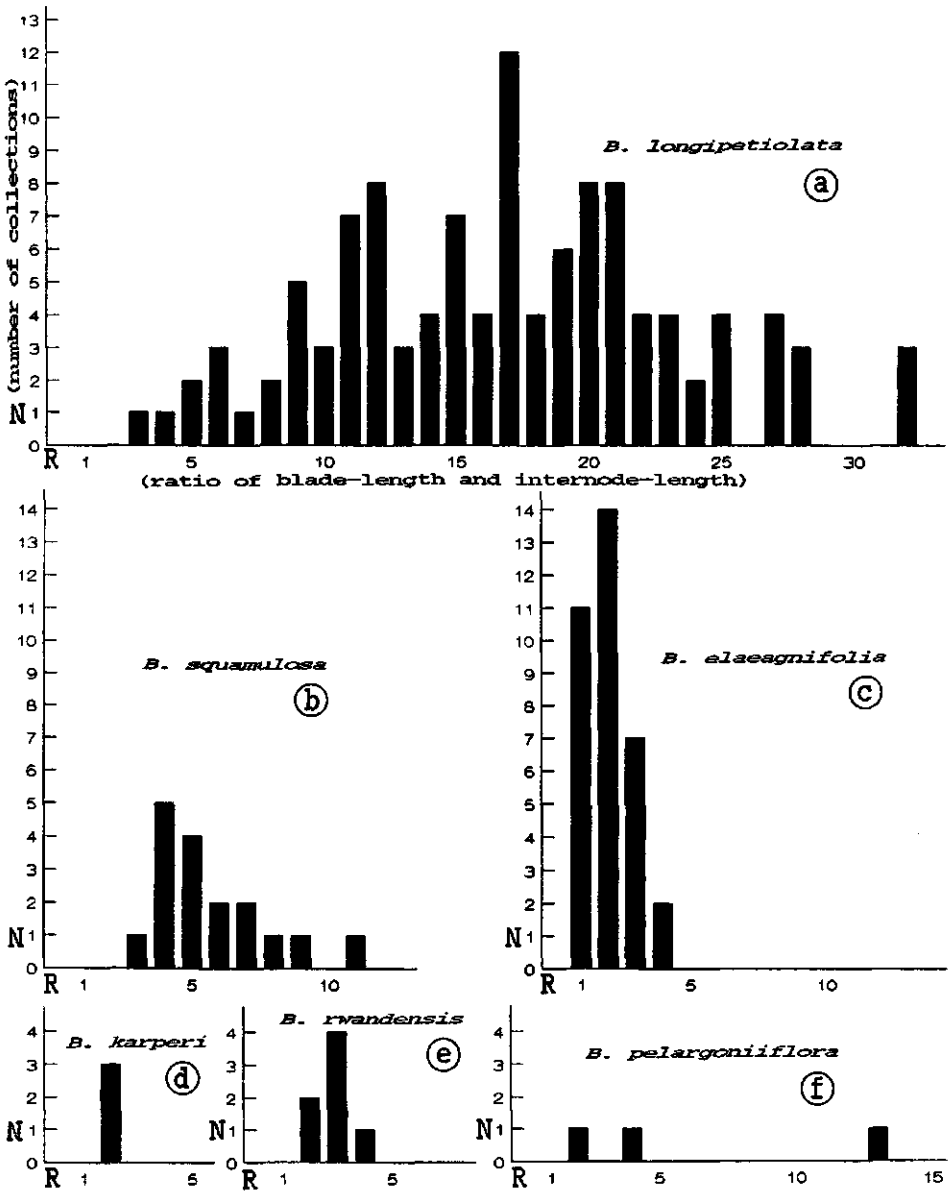


Fig. 5-2: Frequency distribution of the ratio of the blade- and internode-length in *Begonia* species. The value of the ratio for each gathering is calculated from the largest blade and longest internode.

and plants of these species can only be identified with certainty by other features, such as the petiole shape (see below) and the morphology of the male inflorescences.

It is evident that the general habit and appearance of a plant is determined by the size of its leaves and the overall length of its internodes. Blade size and internode length vary in a single plant. However, the relative internode length (RIL), which is defined as the ratio of the blade and the internode length, can be used as an additional character in the identification of the plants. For example, the RIL for a plant of *B. longipetiolata* with a blade of 14 cm long and an internode with a length of 1 cm is 14, whereas that for a plant of *B. elaeagnifolia* with a blade length of 12 cm and an internode length of 4 cm it is only 3. For most of the collections cited in Chapter 10 the value of the relative internode length was calculated by dividing the length of the largest blade with that of the longest internode in each collection. Fig. 5-2 presents the frequency distribution of the RIL for the species studied. Figs. 5-2c, 2d & 2e demonstrate that in *B. elaeagnifolia*, *B. karperi* and *B. rwandensis* the RIL is less than 5. The RIL values of *B. squamulosa* (Fig. 5-2b) are overlapping with those of *B. longipetiolata* (Fig. 5-2a), but in *B. squamulosa* they usually are less than 10 and in *B. longipetiolata* more than 10. Thus, in spite of the overlap there is a tendency in these very similar species to have a different and distinguishing relative internode length.

5.3. Leaf stalk and blade

5.3.1. Petiole morphology

As mentioned on page 19 the adaxial or upper side of the petiole in *B. longipetiolata* is usually more or less furrowed, thus giving the petiole a two ribbed appearance. The lamina margins are continuous with the petiole ribs. Transverse sections of a petiole of this species are presented in Figs. 5-3a & b.

When specimens are prepared for the herbarium, the petiole furrow, which is easily seen in fresh material, disappears. Although the petiole never regains its original shape, the groove can usually be seen by boiling a piece of the lamina with the top of the petiole from a large leaf. By this treatment a fragment of the type specimen of *B. longipetiolata*, Dinklage 1499 from Cameroun, proved to have a grooved petiole.

The grooved petiole was seen in all the plants collected in Gabon during the last decade. Most of these accessions have been investigated for their somatic chromosome number. Except for two accessions, viz.: De Wilde, Arends et al. (1983)-326 & 483 which are tetraploid, they proved to be diploid. These diploid plants have distinctly grooved petioles. A distinct furrow was also seen in the petiole of the diploid specimen W.J. de Wilde 2020 from Cameroun. Some cultivated plants of unknown, but probably Camerounese origin, which were found to be diploid by Legro & Doorenbos (1969) and cited by them as *B. squamulosa*, showed grooved petioles as well. However, in the two tetraploid accessions

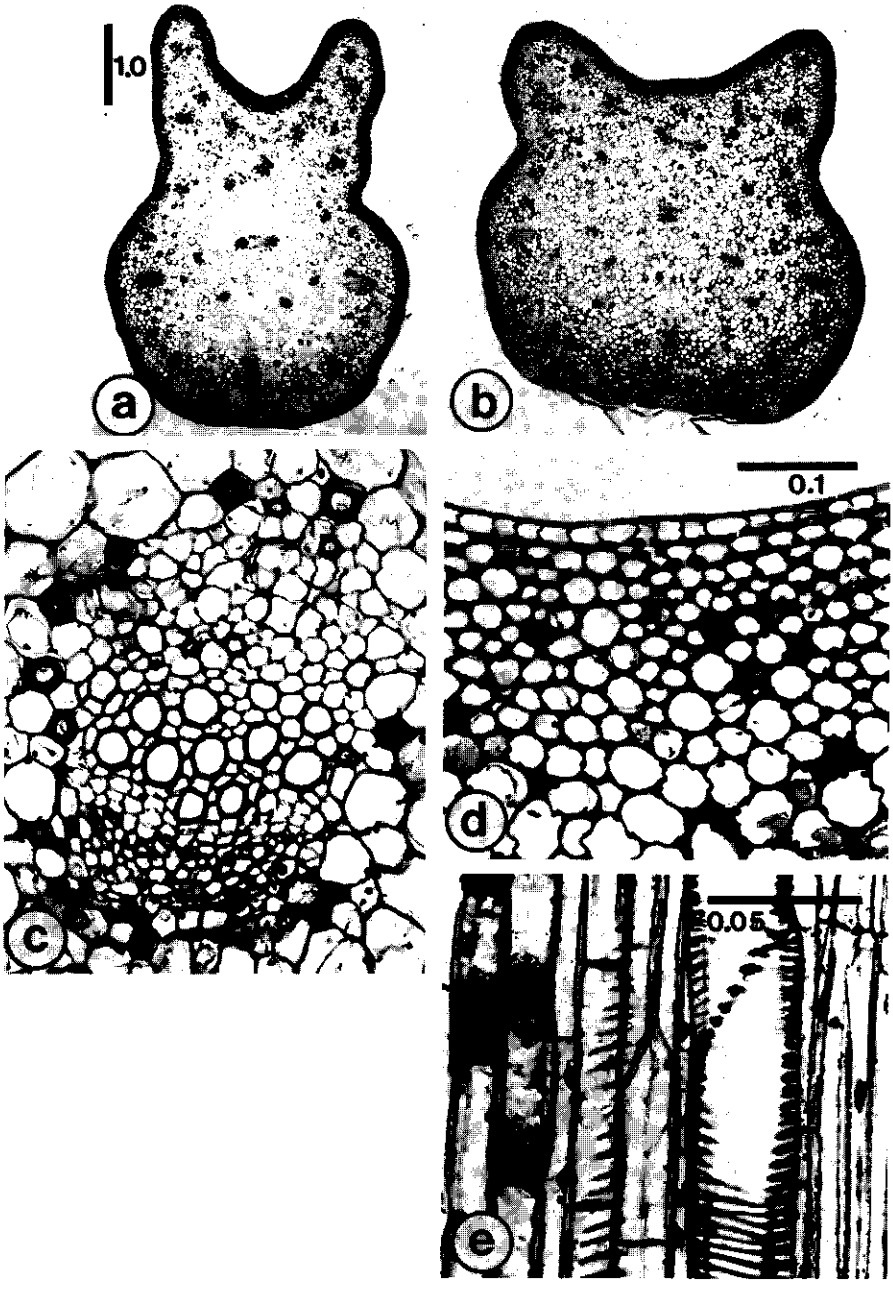


Fig. 5-3: *B. longipetiolata*, **a-d:** transverse and **e:** longitudinal sections of petiole. **a:** top **b:** base; **c** and **d:** details of section in b, **c:** medullary bundle; **d:** peripheral collenchyma layers; **e:** medullary bundle. Bars in mm, **a** & **b** at a similar magnification; **c** & **d** idem.
All from De Wilde, Arends & de Bruijn 8841, Crystal Mts, Gabon.

referred to above, the petioles are flat to scarcely grooved.

In *B. squamulosa* similar observations were made. All the plants from various localities in the Crystal Mts, Gabon, investigated cytologically proved to be tetraploid and they have terete petioles (Figs. 5-4a & b). Examination of the type of *B. squamulosa*, Mann 1654, also collected in the Crystal Mts, revealed that it would have had terete petioles in the living condition. All the living plants of *B. squamulosa* in the collection Arends, De Wilde & Louis 371 from the Chaillu Mts proved to be diploid and have weakly canaliculate petioles (Figs. 5-4c & d).

Similarly, all the plants of *B. elaeagnifolia* from the Crystal Mts in Gabon are tetraploid and have terete petioles, whereas plants from other regions in Gabon are invariably diploid and have very weakly flattened petioles.

The apparent correlation between ploidy level and petiole shape is not conclusive, because the accession Leeuwenberg 9288 of *B. longipetiolata* from Cameroun is diploid and has terete petioles. Similarly, distinctly terete petioles (Fig. 5-5) characterize the accessions of *B. karperi* from the Crystal Mts in Gabon, which are all diploid.

Petiole shape is a character of limited value, because in dried plants it is not possible to distinguish scarcely canaliculate petioles from terete ones. However, the distinct groove in the petiole of many *B. longipetiolata* specimens is used as a key character in distinguishing this species from *B. squamulosa*.

5.3.2. Petiole anatomy

The anatomical structure of the petioles of *B. squamulosa*, *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi* is similar. Most of the tissue consists of ground parenchyma surrounded by 5 to 10 peripheral layers of angular collenchyma immediately below the epidermis (Fig. 5-3d). Longitudinal sections reveal that the collenchyma cells are about three times longer than the isodiametric parenchyma cells. The ribs on the adaxial side of the canaliculate petioles of *B. longipetiolata* do not have any particular anatomical feature by which they can be distinguished from the remainder of the petiole, as the amount of supporting tissue in the ribs is similar to that in the lateral and abaxial parts of the petiole.

It was found that the number of vascular bundles varies with the diameter of the petiole. The free bundles are collateral and mainly arranged in a ring that is equidistant from the epidermis. Apart from this ring, there are always medullary bundles whose arrangement is much less obvious although an inner ring may sometimes be discerned (Figs. 5-4c & d). The bundles in the ring have their phloem oriented towards the periphery, but that of the central medullary bundles faces the abaxial side of the petiole. However, occasionally there are some wide medullary bundles which in fact are formed by two bundles whose xylem parenchyma is more or less fused (e.g. Figs. 5-3a, -4c & d). In such composite bundles each of the two phloem strands faces a lateral side of the petiole.

Composite bundles have not previously been reported in *Begonia*. Metcalfe & Chalk (1957, p. 682, fig. 154C) presented an illustration of a petiole section of *B. echinosepala* Regel in which all the bundles are free and arranged in a

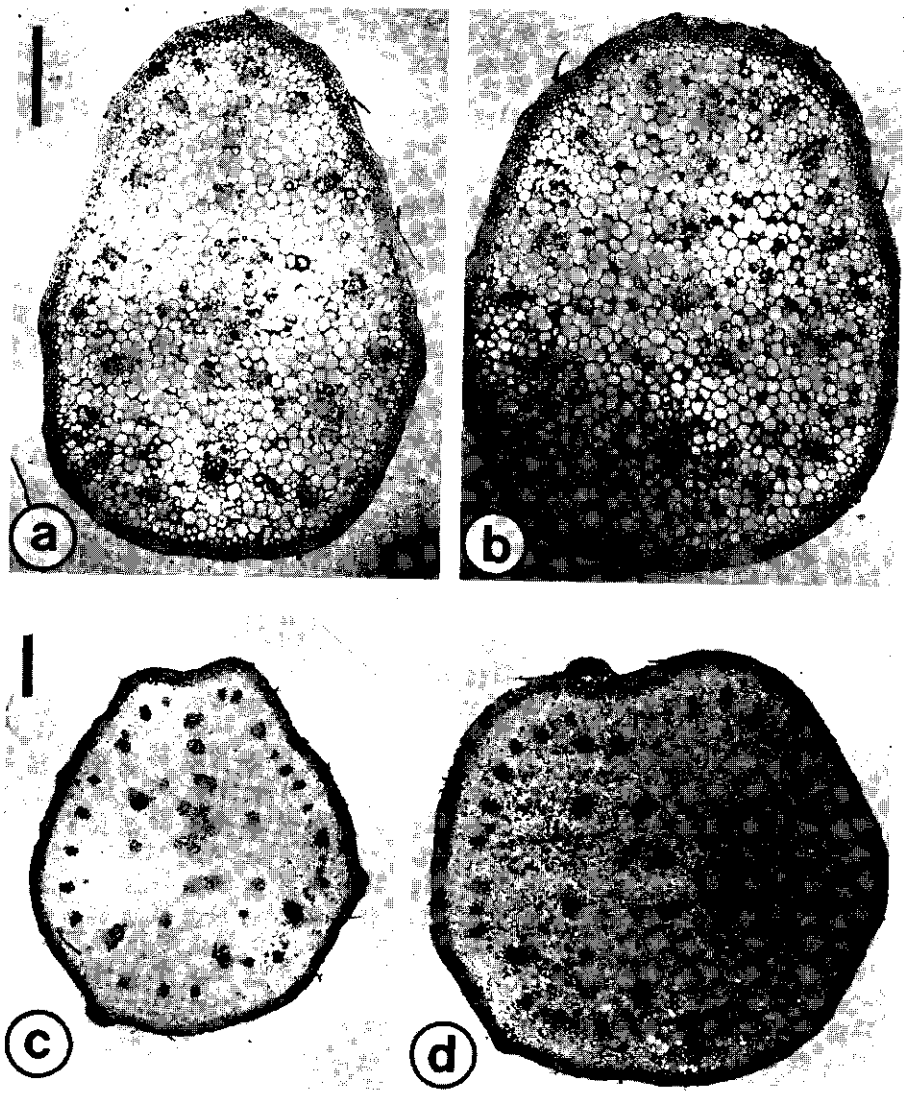


Fig. 5-4: *B. squamulosa*, **a** and **b**: transverse sections from the top (**a**) and the base (**b**) of a petiole of a tetraploid plant; **c** and **d**: idem, but prepared from a diploid plant. Bars represent 1 mm, **a** & **b** at a similar magnification; **c** & **d** idem. **a** & **b**: De Wilde, Arends & de Bruijn 8839, Crystal Mts, Gabon; **c** & **d**: culta Arends, De Wilde & Louis 371, Chaillu Mts, Gabon.

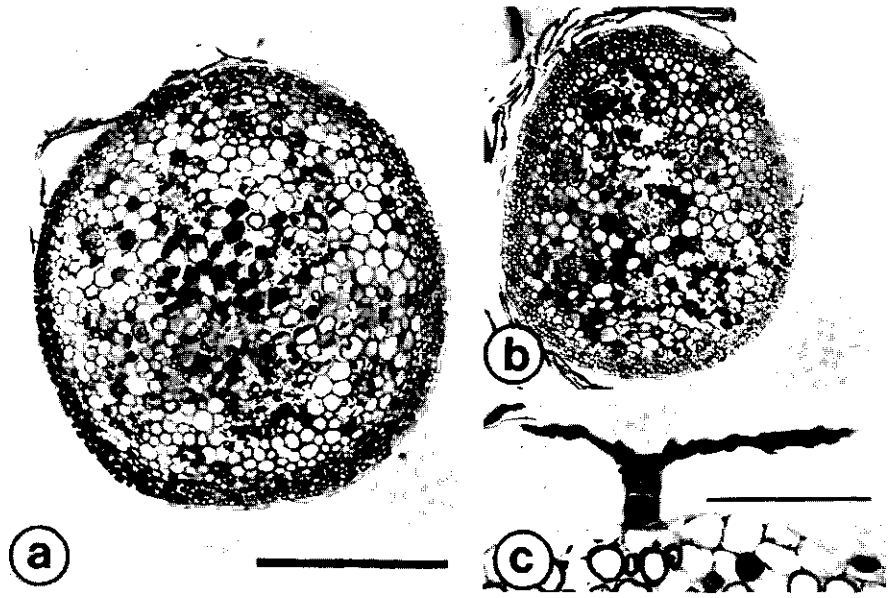


Fig. 5-5: *B. karperi*, transverse sections of petiole. **a:** base; **b:** top; **c:** trichome, detail of b.
Bar in **a** represents 1 mm, that in **c** 100 μm.
Culta Breteler & De Wilde (1978)-335.

single ring. Their illustration of a section of *B. manicata* Brongn. (loc. cit., fig. 154F) shows that in that species the majority of the bundles are also in a ring, whereas several other bundles have a medullary position. Thus the arrangement of the bundles in the petiole of the species studied here is more or less similar to that described in *B. manicata*.

The xylem of the vascular bundle consists of helically thickened tracheary elements and parenchyma (Fig. 5-3e). The vessel elements have simple perforations in their end walls, but scalariform perforations have also been seen. Fig. 5-3e demonstrates that the sclerenchyma fibres in the petiole are perivascular. These fibres were found to have a length of up to 3 mm.

5.3.3. Blade shape, texture and thickness

The blade of the species studied is usually only slightly asymmetric except at the base. Blades from most of the collections cited in Chapter 10 have been measured. As a rule the measurements were obtained from the largest and the smallest mature leaf of each gathering. A few gatherings have only a single leaf, while other gatherings have several leaves but most of them damaged and/or fragmentary. In such cases the leaf that could be measured was treated as the largest leaf. The leaf ratio, which represents the quotient of length and width of the blade, is variable and its range is considerable when a species is represented by many collections from different regions. For example, in *B. longipetiolata*

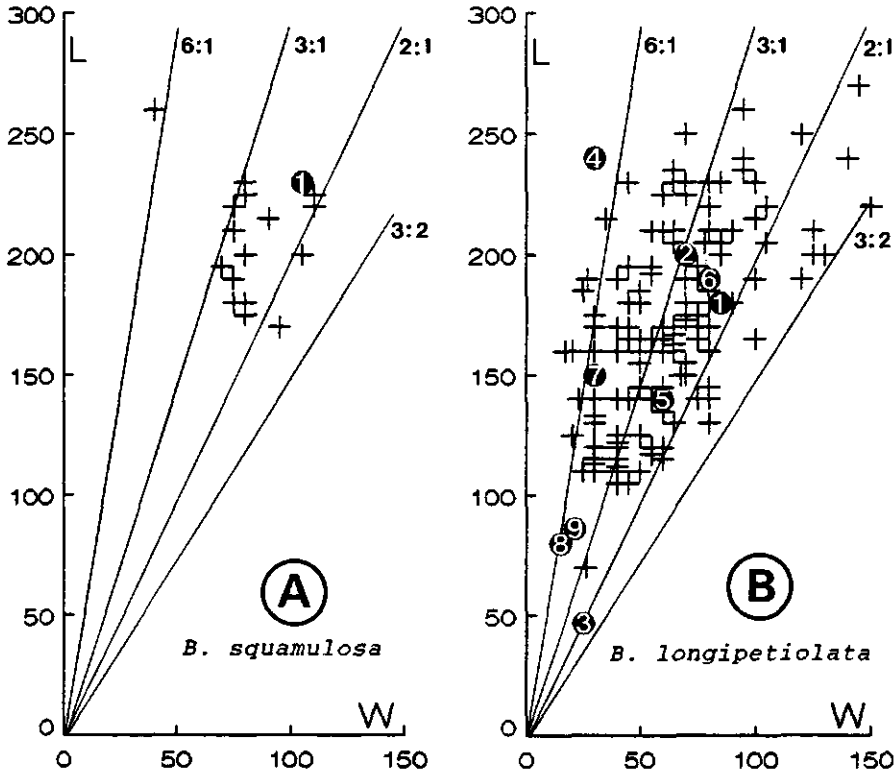


Fig. 5-6: Length (L) and width (W) in mm of the largest leaf blades in gatherings assigned to *B. squamulosa* (diagram **A**) and *B. longipetiolata* (diagram **B**). The numbered black dots represent type specimens.
In **A:** 1 = *B. squamulosa*; in **B:** 1 = *B. bipindensis*, 2 = *B. crassipes*, 3 = *B. gracilipetiolata*, 4 = *B. gladiifolia*, 5 = *B. kribensis*, 6 = *B. longipetiolata*, 7 = *B. ludwigsii*, 8 = *B. macrura*, 9 = *B. nicolai-hallei*. Further explanation in the text.

it varies from 1.5 to 9. Wilcoxon's test (Wijvekate 1972, p. 159) showed that the series of the ratios for the large leaves does not differ significantly from that of the small ones. Therefore, Figs. 5-6 to 5-8 present the blade dimensions of the large leaves only.

The diagrams are subdivided by lines, indicating standard leaf ratios (see e.g. Stearn 1973, p. 318). Thus, Fig. 5-6b shows that the leaves in *B. longipetiolata* with a ratio between 3:1 and 6:1 are lanceolate to narrowly elliptic while those with a ratio between 2:1 and 3:1 are simply ovate to elliptic.

The diagrams demonstrate that the most extensive variation in leaf size and shape occurs in *B. longipetiolata* (Fig. 5-6b). Plants having very narrow leaves, thus with a leaf ratio larger than 6:1, mainly belong to this species, but one plant with similar narrow leaves has been referred to *B. squamulosa*. Unfortuna-

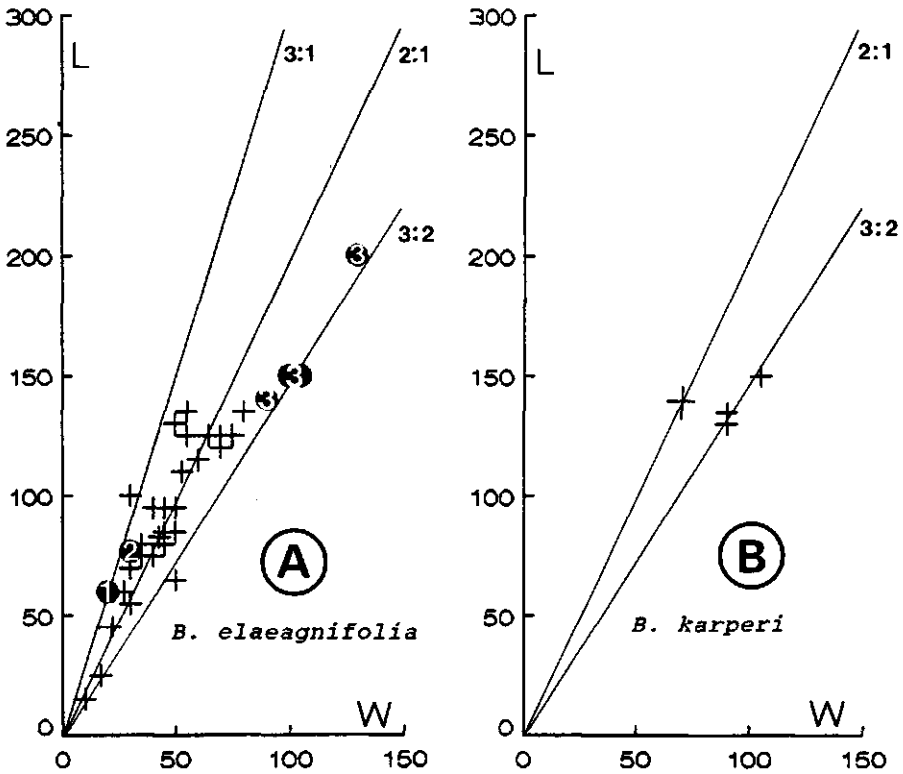


Fig. 5-7: Length (L) and width (W) in mm of the largest leaf blades in gatherings assigned to *B. elaeagnifolia* (diagram A) and *B. karperi* (diagram B). The numbered black dots in diagram A represent type specimens; 1 = *B. elaeagnifolia*, 2 = *B. schultzei*, 3 = *B. wilczekiana*. Further explanation in the text.

tely, this collection, Hallé & Villiers 5272, is sterile. However, the field notes recorded on the label state that the inflorescence had large bracts, globose buds and thick tepals. These features characterize *B. squamulosa*.

When the diagrams of the species are compared, it is obvious that any attempt to segregate the taxa by lamina shape inevitably leads to misinterpretations. For example, Engler (1921) who based his key exclusively on leaf morphology, was led to consider *B. longipetiolata* to be conspecific with *B. squamulosa*. Both the leaf ratio and the lamina size of the type of *B. longipetiolata* (**6** in Fig. 5-6b) are very similar to those of the type of *B. squamulosa* (**1** in Fig. 5-6a). Thus, on the basis of these leaf characters the two species cannot be distinguished. According to size and ratio, the leaves of *B. rwandensis* (Fig. 5-8a) are very similar to those of the type specimen of *B. schultzei* (**2** in Fig. 5-7a) which is here considered as conspecific with *B. elaeagnifolia*. In 1969 Wilczek identified Van

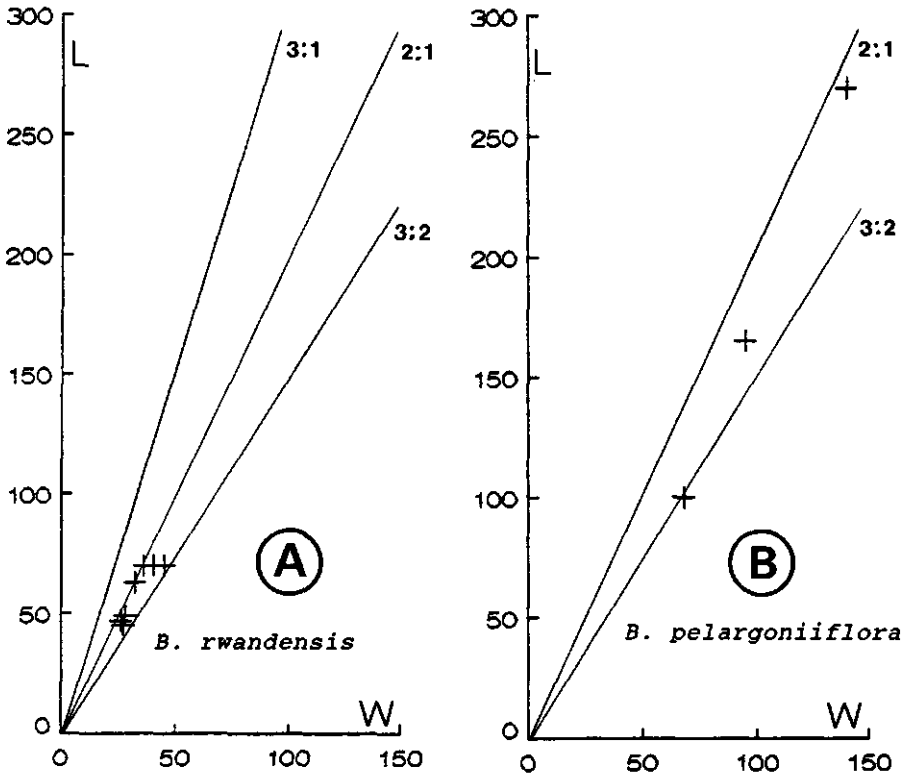


Fig. 5-8: Length (L) and width (W) in mm of the largest leaf blades in gatherings of *B. rwandensis* (diagram **A**) and *B. pelargoniiflora* (diagram **B**). Further explanation in the text.

Roeckhoudt 12, here assigned to *B. rwandensis*, as *B. schultzei*. The specimens now assigned to *B. pelargoniiflora* were identified by their collectors as *B. squamulosa*. No doubt they compared these collections with gatherings which are now identified as *B. longipetiolata*. Fig. 5-8b demonstrates that the leaves of *B. pelargoniiflora* are quite similar to those of *B. longipetiolata* with a leaf ratio between 3:2 and 2:1 (Fig. 5-6b). In the same way, several collections now assigned to *B. longipetiolata* were previously identified as *B. elaeagnifolia* because of their narrow leaves. In these scatter diagrams, the measurements obtained from type collections are indicated by numbers which are identified in the caption.

The diagrams show that the type specimens of the species differ from each other according to both blade size and leaf-ratio of their leaves. The dimensions of the blade in *B. longipetiolata* are shown in Fig. 5-6b and the diagram demonstrates that the gaps between the types of the taxa with many-flowered and lax inflorescences (see pp. 60, 66) which are here considered to be conspecific with *B. longipetiolata*, are more or less bridged by the other specimens. The type speci-

mens of *B. elaeagnifolia*, *B. schultzei* and *B. wilczekiana* are characterized by a few-flowered male inflorescence (see pp. 60, 66). Fig. 5-7a demonstrates that the leaf of the type specimens of *B. wilczekiana* is in general much larger than that of the types of the other species. However, *B. wilczekiana* cannot be distinguished by its large leaves, as recent collections show leaf sizes which completely bridge the gap between its leaf size and that of the other species.

As mentioned in Chapter 2, Wilczek (1969a & b) distinguished *B. gladiifolia* from other species by its narrow leaves. Hallé (1972) referred plants with narrow leaves which are here assigned to *B. longipetiolata*, to his (invalid) variety *B. squamulosa* var. *bipindensis*. Fig. 5-6b demonstrates that a segregation of plants into different taxa having either specific or infraspecific rank, can only be arbitrary.

The texture of the blade of several of the species included in this study has been described by previous authors as papery, fleshy or leathery (e.g. Hooker 1871, Wilczek 1979a & b). However, observation of plants in the field and in cultivation showed that they are invariably succulent.

The thickness of the blade cannot be assessed from dried plants, because boiled blades do not regain their original thickness. For example, Bridson (pers. comm.) informed me that the living leaves of *B. rwandensis* were approximately 2 mm thick when she collected this species. When boiled, blades of Bridson 380 and 474 and some other collections cited for that species have a thickness of c. 0.2 mm. Leaves in spirit or of living wild and cultivated plants of *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa* are up to 1 mm thick. Thus, in addition to some other features *B. rwandensis* is distinct by the thickness of its leaves.

5.4. The leaf margin

Except for the places where veins terminate, the margin is usually smooth. However, frequently that part of the margin between the terminations of two successive veins may be also more or less concave, so that the margin becomes sinuate. Where veins terminate in the margin there are projections which are always tiny in comparison with the size of the blade. Sometimes these projections are so small that they are overlooked. For example, De Wildeman (1908, p. 319) stated that the margin of *B. gracilipetiolata* is toothless, but the leaves of its type, Laurent 1702, definitely have minute projections.

The ultimate edge of the leaf is continuous with that of the projections so that a blade with a distinctly sinuate margin is also dentate. The margin of the type of *B. elaeagnifolia*, Mann 1651, is almost smooth and was described by J.D. Hooker (1871, p. 579) as 'obscurely few-toothed'. Similarly, in his key to the species, Engler (1921, 619) described *B. kribensis* (= *B. longipetiolata*) as 'entfernt gezähnelt' because the leaf margin in the type, Schultze in Mildbraed 6198, is almost smooth. However, Schlechter 12918 has a distinctly sinuate margin. It is the type of *B. macrura* Gilg (= *B. longipetiolata*). Gilg's (1904, p.92)

latin description was translated by Engler (loc. cit.) as 'entfernt gezähnt'. Engler used the measure of dentation of the leaf edge as a differential character to separate the species in his survey of African *Begonia*. The description of each species in his key is usually based on a single collection that often is also the type. In the present study it was found that the margin in a species may be smooth but also variably sinuate. Leaves with a more or less smooth margin may be interpreted as denticulate, while those with a more or less sinuate margin are designated as dentate. Obviously, this distinction is subjective, especially when intermediates occur. Thus, it is difficult to see how the shape of the margin can be used to distinguish the species treated in this paper now that more specimens have been examined.

In his emended description of *B. gladiifolia* (= *B. longipetiolata*) Wilczek (1969a & b) did not refer to teeth, but he described the margin of that species as provided with glands. In the type specimen, Mildbraed 6394, the leaf margin has minute rounded and brown projections. In the present study it was found that although the teeth of young expanding leaves may carry glandular cushions these could not be detected on dried plants (see below). Hence, it is not clear how Wilczek was led to describe the leaf margin in *B. gladiifolia* as glandular in the absence of fresh material.

Previous authors invariably designated the projections of the leaf margin in *Begonia* as teeth. According to Hickey & Wolfe (1975, p. 573) the tooth in the *Begoniales* is mainly cucurbitoid, but these authors stated that in the order there is also a trend towards the evolution of another type of tooth which they designated as begonioid. The cucurbitoid tooth type also occurs in the *Cucurbitales*, and this type is thought to be derived from the violoid tooth which is the more common type in this order. The violoid type obviously occurs also in *Violales*, but the basic type in that order is thought to be the theoid tooth which has been modified in the course of evolution. Modification of the theoid tooth not only resulted in the violoid but also the salicoid tooth. The tooth types mentioned above are illustrated on page 572 in Hickey & Wolfe (1975). These illustrations show that the violoid tooth is characterized by a single vein that coincides with the axis of symmetry of the tooth. The cucurbitoid tooth also has a vein coincident with the axis, but according to Hickey & Wolfe's illustration there is at least one other smaller vein present on each side of the main vein. The begonioid tooth is characterized by the presence of two veins, which according to the illustration are equal in size. Both veins have a distinctly excentric position within the tooth. Later, but without any reference to the material studied, Hickey (1979, p. 38) described the tooth in *Begoniaceae* and *Cucurbitaceae* as 'tylate', which he defined as 'with a translucent pad of densely packed cells (hydathodal or nectariferous tissue) into which the veins run and disappear'. Most likely, the term 'tylate' refers to a structure that has the shape of a knob (see Woods 1944, p. 248 and Stearn 1978, p. 535), but Hickey's (op. cit., fig. 4.5-121) drawing of a tylate tooth does not show a knob-like structure.

More recently, Brouillet, Bertrand et al. (1987) studied the leaves in *Hillebrandia sandwicensis* Oliv. and five *Begonia* species, each of a different section. They

interpreted the teeth of these species as 'begonioid'. However, they did not corroborate Hickey's statement that the teeth are 'tylate', because they found that the tips of the teeth consist of parenchyma cells instead of hydathodal or nectariferous tissue as described by Hickey (see above).

Brouillet, Bertrand et al. (op. cit.) also studied the anatomy of the hydathodes which are present on the adaxial surface of the leaf margin of the species they investigated. Their analysis showed that the hydathodes in these species differ from each other by several features and they suggested that the anatomy of hydathodes might prove useful in taxonomic and phylogenetic studies of the *Begoniaceae*.

According to Wilkinson (1979, p. 117), the term hydathode was introduced by Haberlandt. The term refers to structures which secrete water. Hydathodes *sensu* Haberlandt include both glandular trichomes and apertures in the plant surfaces, but Wilkinson restricted the term hydathode to the apertures. As in stomata, the apertures frequently have guard cells and in fact, hydathodes are believed to be phylogenetically derived from normal stomata (Denffer et al. 1976, p. 99). Consequently, the hydathodal aperture with its guard cells is often designated as a 'water stoma' or in French as a 'stomate aquifère' (e.g. Brouillet, Bertrand et al. op. cit.).

In early anatomical studies on *Begonia*, which are exclusively German, hydathodes were reported to occur occasionally on the upper surface of the leaf blade towards its edge (Fellerer 1892, p. 21 and Solereder 1899, p. 450). These authors designated the hydathodes as 'Wasserspalten' in order to distinguish them from 'echten Spaltöffnungen' or 'Luftspalten' (Ziegenspeck 1941, p. 49). However, in his study on the phylogeny of the hydathodes, Ziegenspeck (1949) designated the 'Wasserspalten' as 'stomatäre Hydathoden'. According to his table (op. cit., p. 305) such structures occur in seven out of nine *Begonia* species investigated at that time. Ziegenspeck did not specify the material that he investigated, but he referred in a somewhat inaccurate way to his previous papers on 'Spaltöffnungen' (Ziegenspeck 1938, 1941, 1948; Linsbauer & Ziegenspeck 1944). In these papers I could not find any information regarding the material studied by Ziegenspeck, except perhaps for *B. rex* Putzeys which is mentioned on p. 302 in Linsbauer & Ziegenspeck (1944). Neither in Ziegenspeck's papers nor in those of the other authors cited above there is any information regarding the anatomy of the 'Wasserspalten' or hydathodes.

Wilkinson (1979, p. 117) defined hydathodes in their simplest form as apertures in plant surfaces which occur predominantly on the toothed margin of leaves. According to the same author (loc. cit. & fig 10.7-b), hydathodes may also be of a more complex type. This type differs from the simple type by the presence of an epithem, which is a cushion of colourless, often loosely arranged, parenchyma cells situated below the aperture. The aperture and the epithem are separated from each other by a water cavity and the complex hydathodes are located near vein terminations. Wilkinson (loc. cit.) stated that tracheids from about one to three vein endings fan out at the base of the epithem.

The first illustration of a hydathode in *Begoniaceae* was presented by Maier

& Sattler (1977, p. 275, fig. 25). They observed the structures in longitudinal sections from the hairlike appendages on the upper leaf surface of *B. hispida* Schott var. *cucullifera* Irmsch. Their illustration shows a hydathode of the complex type *sensu* Wilkinson, because the structure consists of a water stoma with epithem that is associated with tracheids. Similar hydathodes were observed by Brouillet, Bertrand et al. (1987) in six taxa of *Begoniaceae*. However, it appears that these authors considered the principal tooth vein to be at least part of the hydathode as they wrote 'nervures élargies des hydathodes' (caption of their figs. 7 to 12) and even 'L'hydathode se présente comme une nervure elargie.' (p. 40). The hydathodes which have been studied here, are interpreted according to Wilkinson's (1979, p. 117) description of the complex type. Thus, in contrast with the opinion of Brouillet, Bertrand et al. (op. cit.) the wide extremity of the vein is considered to be not part of the hydathode.

In the present study, the morphology and anatomy of the teeth of cultivated specimens of *B. elaeagnifolia*, *B. longipetiolata* and *B. squamulosa* are described and compared with the findings of Brouillet, Bertrand et al. (op. cit.) Samples of the toothed part of the margin were taken from leaves in different phases of development. The morphology was studied from clearings which were prepared according to the method described by the authors mentioned above. Photographs of some of the clearings are presented in Fig. 5-9. The anatomy of the margin and teeth was studied from transverse leaf sections prepared as described in Chapter 3. For the sectioning, tissue with a tooth was oriented in such a way that the tooth was sectioned longitudinally. Photographs of some of the sections are presented in Figs. 5-10 to 5-12.

5.4.1. The structure of the teeth and hydathodes

5.4.1.1. Observations from tissue clearings

The tooth from an expanded young leaf of *B. elaeagnifolia* (Fig. 5-9a) strikingly resembles the 'tylate' tooth as illustrated by Hickey (1979, fig. 121). However, the darkly stained apex is neither hydathodal nor nectariferous tissue, but is composed of cells with suberized walls (see p. 44 and Figs. 5-12a & b). Moreover, the vein in the tooth does not run into and disappear in the apex, as Hickey described in the tylate tooth. Hydathodes are present on the adaxial surface of the lighter stained basal part of the tooth. They are associated with tracheids from veinlets which branch off from the vein in the tooth (arrow marked t).

The teeth of young leaves of *B. squamulosa* are presented in Figs. 5-9b & c. In still expanding leaves, the teeth are green *in vivo* and may carry up to three cushions which are distinctly paler than the remainder of the tooth. These cushions have a glossy surface which is attributed to the secretion of liquid, so that they are interpreted as glandular. Sections of other teeth from the same leaves demonstrate that the cells of the putative glands are associated with dark stained cells which in their turn are also associated with the palisade layer (see Fig. 5-11b). Glandular cushions have not been seen on the teeth of old leaves from the same or from other plants. Figs. 5-9b to d demonstrate that the teeth and the adjacent part of the margin become darker stained with age due to to the

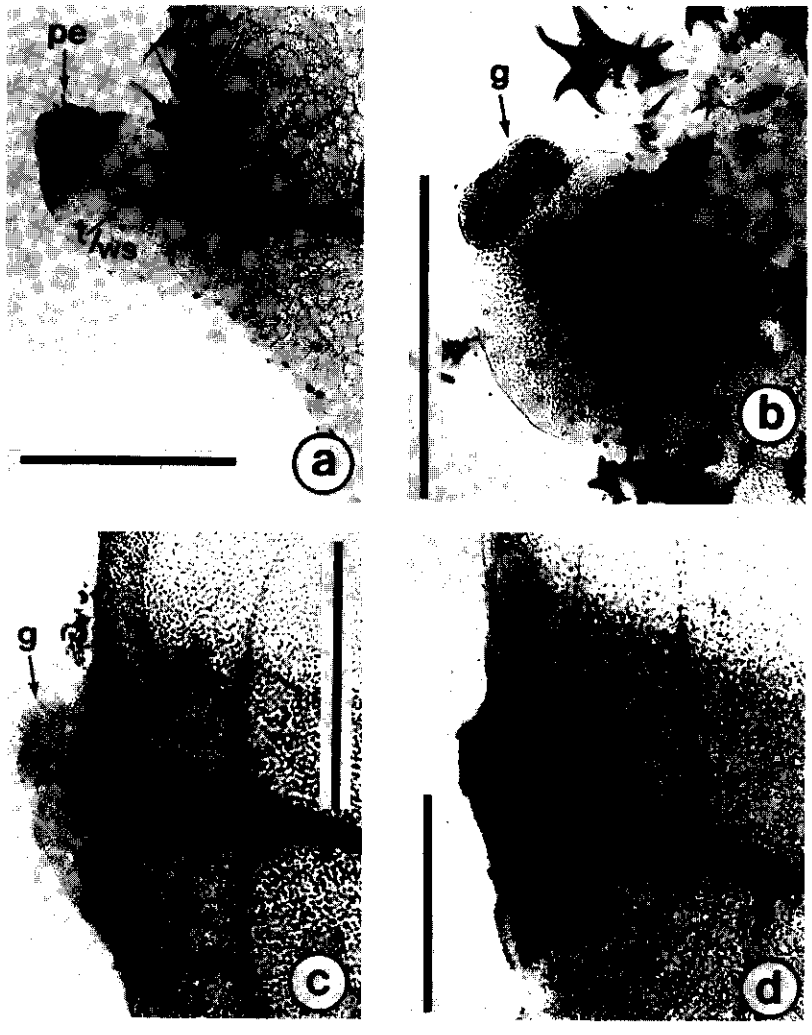


Fig. 5-9: Parts of the leaf margin in *Begonia* species, cleared and stained, where secondary veins terminate in the margin.
a: *B. elaeagnifolia*, young expanded leaf, tooth with vein, pe: periderm (compare with Figs. 5-12a & b). The arrow marked **t/ws** indicates the association of the tracheids from a veinlet with a hydathode on the adaxial side of the tooth. The water stoma of the hydathode is very inconspicuous; **b – d:** *B. squamulosa*, **b** and **c:** expanding and young expanded leaf respectively, the arrows indicate glands; **d:** older leaf. The dark tissue in the margin in figs. c and d is due to intense staining of suberized cells. Bars represent 500 μm.
a: culta De Wilde, Arends et al. 9810, **b – d:** culta Arends, De Wilde & Louis 371.

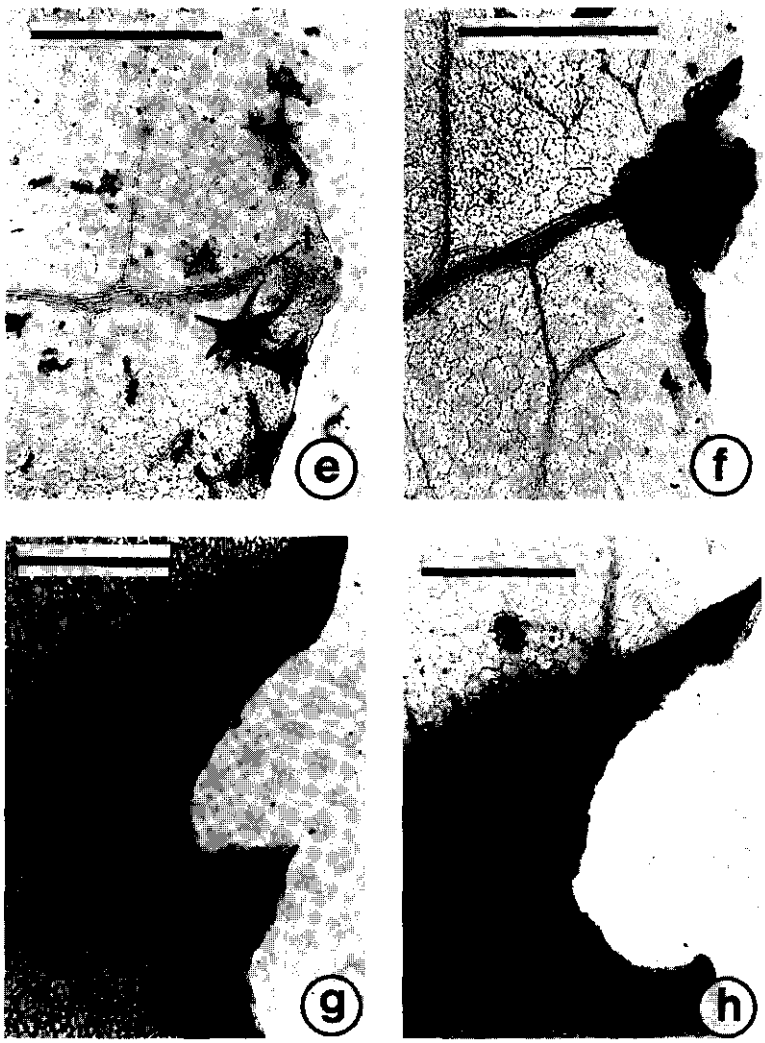


Fig. 5-9, continued; *B. longipetiolata*, **e:** expanding leaf, the arrow marked **t** indicates the termination of the (secondary) vein; **f** to **h:** expanded leaves of increasing age showing increasing suberization of the margin, in f and g the tooth is still present, whereas in h the margin is depressed. Bars represent 500 μm.
All prepared from culta De Wilde, Arends & de Bruijn 9270.

increasing amount of wound cork in these leaf parts.

The toothed part of the margin of leaves of increasing age of *B. longipetiolata* is presented in Figs. 5-9e to h. As in *B. squamulosa* (see above) the number of darkly stained suberized cells increases with age. The tooth is still present in Fig. 5-9f, but in Figs. 5-9g & h the teeth are partly, and completely lost respectively, so that the leaf margin in Fig. 5-9h shows a concave depression. The termina-

tion of the vein cannot be seen in the last photograph because of the wound cork formed by the darkly stained suberized cells.

The photographs in Fig. 5-9 demonstrate that the teeth have a single vein that coincides with the axis of symmetry. This implies that the teeth are neither of the cucurbitoid nor of the begonioid type as designated and illustrated by Hickey & Wolfe (1975, p. 572) for the *Begoniales*. In fact, all teeth are similar to the violoid type that is characterized by a single vein in the axis of symmetry (Hickey & Wolfe, loc. cit). Brouillet, Bertrand et al. (1987) designated the teeth which they observed as begonioid because they interpreted the principal vein as asymmetrical and excentric. However, for example their figure 8 of *B. augustinei* Hemsley shows that the principal vein in the teeth is not or hardly excentric and asymmetric. A large tooth has a principal vein plus a second thinner vein that joins the principal one in the tooth apex. The adjacent and smaller tooth in the same figure has only a single vein that is symmetrical and coincides with the tooth axis.

Thus, the evidence obtained in the present study does not support the view that the teeth are 'begonioid' in the sense of Hickey & Wolfe. The somewhat diagrammatic illustrations of Hickey & Wolfe (1975) show several distinct tooth types, e.g., the drawing of the cucurbitoid tooth (ibid. op. cit., p. 572) has a more or less pointed apex, while a photograph of the cleared margin of *Fevillea cordifolia* L. of the *Cucurbitaceae* (Hickey & Wolfe op. cit., fig 14F) clearly shows that the tooth apex is rounded and not distinct from the remainder of the tooth. Moreover, the photograph does not show a knob-like structure on the tooth. Thus, the tooth in *Fevillea cordifolia* is apparently not 'tylate' (*sensu* Hickey). So far, the occurrence in the *Begoniales* of the cucurbitoid tooth as claimed by Hickey & Wolfe is not corroborated by this study nor in the literature that I have traced. Further investigations are needed to establish whether the violoid tooth as seen in the present study is a common feature of the *Begoniales* or not.

None of the teeth shown in Fig. 5-9 has a distinctly acute or pointed apex, although the tooth of *B. elaeagnifolia* in Fig. 5-9a could be designated as almost acute. The teeth of the other species shown here are rounded and therefore it appears that on the basis of tooth shape these species could be distinguished from *B. elaeagnifolia*. However, teeth in other living accessions of *B. elaeagnifolia* were found to be comparatively short with an obtuse to rounded apex, so that they are intermediate in shape between the tooth of *B. elaeagnifolia* in Fig. 5-9a and the teeth of *B. squamulosa* and *B. longipetiolata* shown in Figs. 5-9b and 5-9e respectively. Thus, tooth shape is not a useful character to distinguish these species.

According to Hickey (1979, p. 28) a projection of the margin is a tooth when it has a pointed apex. Stearn (1973, p. 414) circumscribed the term toothed as 'with sharp teeth pointing outwards', whereas a margin with rounded projections is crenate (Hickey loc. cit.; Stearn op. cit., p. 409 & fig. 25-181). The projections seen in the present study are more or less obtuse to rounded. In the description of the species in Chapter 10, the projections are referred to as teeth in spite

of the fact that they do not have truly pointed apices. This is in accordance with Radford et al. (1974, p. 137) who stated that a dentate or denticulate margin has rounded or sharp teeth. The projections are small in relation to the size of the blade and widely separated on the leaf margin. Thus, the margin varies from remotely crenulate to remotely denticulate. However, when the margin is more or less sinuate, it appears to be crenate to dentate.

The projections of the leaf margin in several other *Begonia* species were interpreted in a similar way by Brouillet, Bertrand et al. (1987). For example, the margin at the vein termination may be smooth as in *B. coccinea* Hook. or carry a projection which, depending on the species, is more or less deltoid to triangular. These authors decribed the triangular and sharp projections of the margin in *B. augustinei* Hemsley as teeth, but they stated that the margin in *B. vellozoana* Brade is weakly dentate in spite of the fact that its very short projections have a smoothly rounded apex.

Glandular cushions as observed on the teeth of young leaves of *B. squamulosa* (Figs. 5-9b & c) are not always present or distinct on other teeth of the same leaf. The cushions are absent from the photographs of the teeth of *B. elaeagnifolia* and *B. longipetiolata* shown in Fig. 5-9, but they have been seen on the teeth of other living accessions of these species. Thus, glandular cushions are not an exclusive character of *B. squamulosa*. Whether their presence or absence is due to certain environmental conditions, e.g. high air humidity, remains to be investigated, but on old leaves they are always absent.

5.4.1.2. Observations from sections of the leaf margin and teeth

Hydathodes have been seen with the dissecting microscope, using transmitted light, on the adaxial surface of the living leaf. They appear as clear spots because of the colourless parenchyma cells of the epithem and they are particularly distinct when the surrounding cells contain anthocyanin. The hydathodes occur near the edge of the margin and the teeth, but they may also be present on other parts of the blade, e.g. a leaf of *B. longipetiolata* had a very few clear spots towards the midvein. However, this has not been verified by sections of that leaf part.

Fig. 5-10 presents transverse sections of the leaf margin between successive teeth of *B. elaeagnifolia* and it demonstrates that the margin is slightly curved downwards. Fig. 5-10a shows that both the upper and lower epidermis consist of a single cell layer. Immediately below each epidermis there is a hypodermis formed by two to three layers of parenchyma cells. Most likely, the hypodermis is not derived from the same initials as the epidermis since its anticlinal walls do not coincide with those of the epidermis. Between the upper hypodermis and the spongy parenchyma there is a single-celled palisade layer of parenchyma cells which are probably tanniniferous because they are densely stained. Fig. 5-10b presents the air stoma with chamber indicated by the triangle in the preceding photograph. A section of the other margin of the same leaf is shown in Fig. 5-10c. The palisade layer in that illustration is interrupted by a veinlet from which several tracheids supply the hydathode on the adaxial leaf surface (aster-

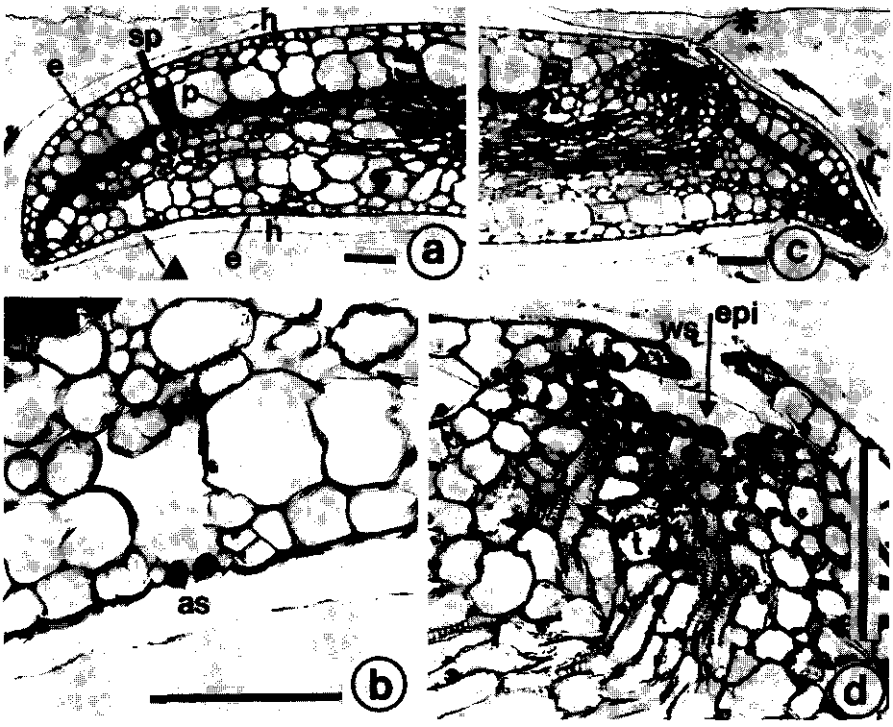


Fig. 5-10: *B. elaeagnifolia*. Transverse sections of the leaf margin between teeth. **a:** section showing the various tissues; from top to bottom: adaxial epidermis (e), hypodermis (h), palisade layer (p), spongy parenchyma (p), hypodermis (h) and abaxial epidermis (e). The triangle indicates the air stoma with chamber shown in **b** (as); **c:** the asterisk indicates a hydathode on the adaxial surface; **d:** detail of preceding photograph; ws = water stoma, epi = epithem, the arrows marked t indicate tracheids. Bars represent 100 µm.
All prepared from culta De Wilde, Arends et al. 9810.

isk). Although not shown here, the veinlet is produced by an intersecondary vein in the margin. The photograph in Fig. 5-10d demonstrates that the hydathode consists of a water stoma (ws) and, below the water cavity, an epithem (epi) that is associated with the terminal tracheids (t) of the veinlet. Thus, the structure of the hydathode complies with the complex type *sensu* Wilkinson (see page 36).

The histology of the tooth of *B. squamulosa* presented in Fig. 5-11a is basically similar to that of the leaf margin in *B. elaeagnifolia* in Fig. 5-10a. The hydathode on the right is associated with tracheids, whereas the one on the left apparently does not have such an association. However, in other sections which are not shown here, I have seen tracheids entering the epithem of that hydathode. The tooth apex of another young expanding leaf in Fig. 5-11b is provided with irregularly shaped parenchyma cells from a gland as observed on the cleared teeth of *B. squamulosa* in Figs. 5-9b and c. The densely stained cells in the tooth apex

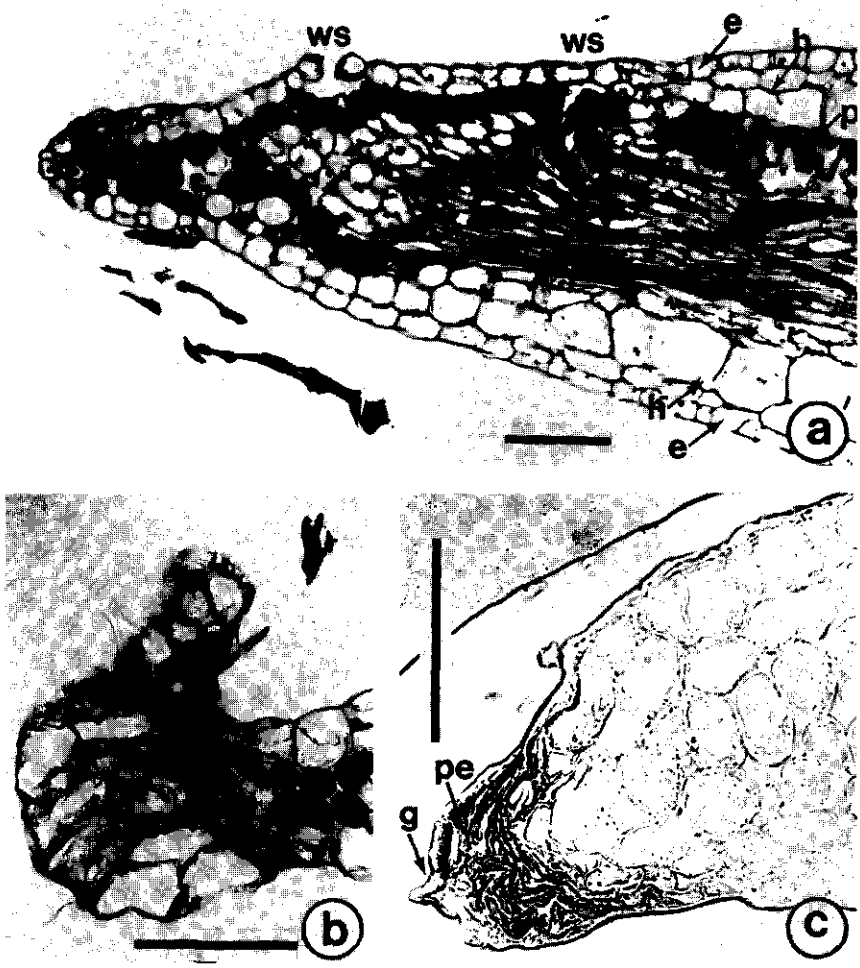


Fig. 5-11: *B. squamulosa*. Longitudinal sections of teeth. **a:** young expanded leaf, section showing two hydathodes (ws) on the adaxial surface and, from top to bottom, adaxial epidermis (e), hypodermis (h), palisade layer (p), vein, hypodermis (h) and abaxial epidermis (e); **b:** young expanding leaf, extremity of tooth showing thin-walled glandular tissue of epidermal origin; **c:** older expanded leaf, extremity of tooth stained with Sudan III showing remnants of glandular cells (g) and collapsed thick-walled periderm cells (pe) next to unstained parenchyma cells. Bars represent 100 µm.
All prepared from culta Arends, De Wilde & Louis 371.

in Fig. 5-11b are not only continuous with the palisade layer but also associated with the glandular parenchyma cells of the very apex. I postulate that these dark cells represent transfer cells which are involved in the transport of metabolic substances or water to the gland. However, with the light microscope it is not possible to detect whether the putative transfer cells have wall ingrowths which

usually characterize such cells (e.g. Cutter 1978, p. 195 and Juritza 1987, p. 90).

Sections of a tooth from a somewhat older leaf of *B. squamulosa* were stained with Sudan III reagent as a test for the presence of suberin in certain cell walls and the result of the procedure is illustrated in Fig. 5-11c. Except for the thick-walled and irregularly shaped cells of the tooth apex (arrow marked pe) no other tissue has red-stained layers in the cell wall. Therefore, the thick-walled cells are interpreted as corky cells which collectively form a secondary periderm. Moreover, the outermost part of the apex is formed by two or three layers of collapsed and inconspicuous cells (arrow marked g) which are the remnants of glandular cells as shown in the preceding photograph.

Sections were prepared from another tooth of the same leaf of *B. elaeagnifolia* from which a cleared and apparently 'tylate' tooth is presented in Fig. 5-9a. Some of the sections were stained with the usual toluidine blue and some others with Sudan III reagent. The toluidine-stained section in Fig. 5-12a demonstrates that the tooth consists of two parts. The top part is stained dark blue (arrow marked pe) whereas the parenchymatous basal part (arrow marked pa) which is continuous with the leaf margin is paler. The corresponding section in Fig. 5-12b which was stained with Sudan III demonstrates that the tooth apex consists of cells which have comparatively thick, suberized walls.

The sections presented in Figs. 5-12c to e were prepared from the tooth of an expanded leaf that was older than the leaf from which tooth sections are shown in the photographs a and b of the same plate. Figs. 5-12c and e demonstrate that the suberized apex which is present in a younger tooth (Figs. 5-12a and b) is gradually lost with the age of the leaf. Fig. 5-12c also shows three hydathodes which are apparently not associated with tracheids, but in other sections these elements have been seen to fan out from the vein in the tooth. An example of the association of tracheids with a hydathode is presented in Fig. 5-12d.

It was mentioned on page 41 that glandular cushions as observed on the tooth apex of young expanding leaves of *B. squamulosa* have also been seen on the teeth of other species. These cushions disappear with the age of the leaf, but Fig. 5-12e demonstrates that a tooth of an older leaf of *B. elaeagnifolia* carries a small cushion-like structure on its adaxial surface towards the tooth base (arrow marked g). Its position suggests that it is of epidermal origin. All cells of this small cushion are living as they have nuclei and it is postulated that they are glandular. A structure like that shown here has been seen only once in the course of these investigations.

Finally, sections were made from teeth of old leaves. An example of these sections in Fig. 5-12f demonstrates that both surfaces of the tooth are more or less covered with flat cells which have thick walls. The layers formed by such cells are brown in unstained sections and stain with Sudan III so that they are interpreted as wound cork.

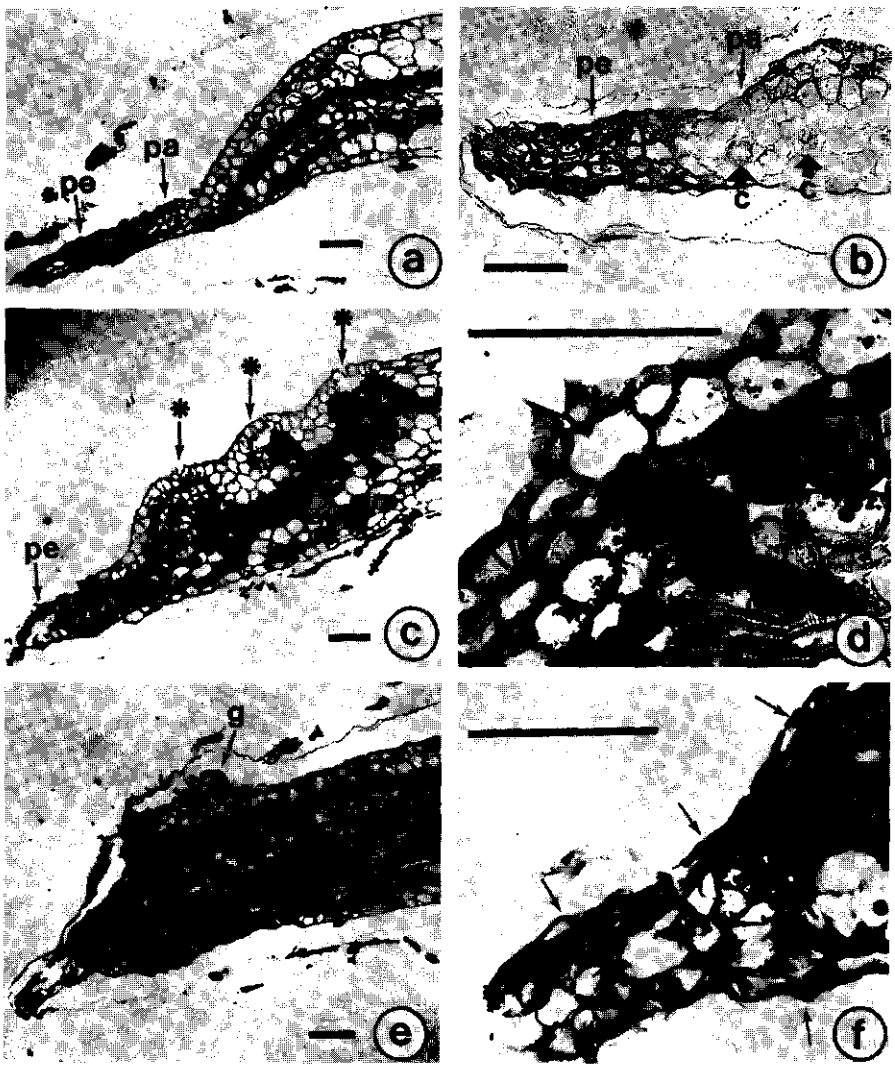


Fig. 5-12: *B. elaeagnifolia.* Longitudinal sections of teeth. **a:** young expanded leaf, the tooth with part of the lamina; the apex with dark stained suberized cells (pe), the base with lighter stained parenchyma (pa); **b:** idem, Sudan III staining, the periderm (pe) stained and the parenchyma (pa) with some crystal cells (c) unstained (compare a and b with Fig. 5-9a); **c:** older expanded leaf, very apex with damaged periderm (pe) and the adaxial surface with hydathodes (asterisks); **d:** another section showing a hydathode with small epithem associated with some tracheids; **e:** idem, but this section with glandular cells of epidermal origin (g); **f:** old leaf, extrimity of tooth with suberized cells (arrows). Bars represent 100 µm.
All prepared from culta De Wilde, Arends et al. 9810.

5.4.1.3. Discussion

The hydathodes studied here are very similar and neither their anatomy nor their position on the blade provide additional characters to separate the species. This conclusion is different from that of Brouillet, Bertrand et al. (1987) who found that various features of the hydathodes such as the size of the water stomata could be used to characterize the species they studied. Consequently, they stated that hydathodes might prove useful in taxonomic and phylogenetic studies of the *Begoniaceae*. These authors found (minor) differences in species which belong to *Hillebrandia* and different sections of *Begonia*. The species I investigated all have similar hydathodes which is not surprising since they belong to one section of the genus.

It is shown above that the morphology of the margin near the vein terminations changes with the age of the leaf. In young, still expanding leaves the margin has small but distinct projections which frequently carry one to several glandular cushions. Later, these cushions collapse and are lost, while simultaneously there is a formation of corky cells. Initially, such cells are formed at the apex but later there is also cork formation on the entire surface of the tooth and the adjacent margin. In still older leaves the teeth and the adjacent part of the margin are brown because of the presence of cork. In *B. longipetiolata* and *B. squamulosa* the teeth are often lost and the veins terminate in shallow depressions with wound cork.

The presence of glands on the teeth is in line with the description of the vegetative morphology of the subclass *Dilleniidae* by Hickey & Wolfe (1975, p. 563). According to these authors the presence of glandular teeth is one of the characters of the subclass which also includes the *Begoniales*. The tooth in both the *Cucurbitaceae* and *Begoniaceae* was designated by Hickey (1979, p. 38) as tylate, because he interpreted the apex of the tooth as a pad of nectariferous or hydathodal tissue. Hickey's interpretation is not supported by the observations in the present study. The apex of a tooth of an expanded leaf may be more or less suberized (p. 44). The glandular or nectariferous cells seen in this study form distinct cushions which are peripheral structures situated on the apex of a tooth of a young expanding leaf. The cushions have the shape of a knob which complies with the interpretation of the term 'tylate' in this study (p. 35). Therefore, I conclude that the teeth studied here are indeed tylate *sensu* Hickey.

This conclusion differs from that of Brouillet, Bertrand et al. (1987, p. 34) who stated that the teeth which they observed are not tylate. It appears that these authors also found it difficult to understand Hickey's description, because they thought that the densely packed cells of the pad *sensu* Hickey would correspond with the epithem of a complex hydathode. In conclusion, it appears that all the evidence so far obtained from detailed studies of the teeth in *Begoniaceae* leads to different interpretations regarding the type of the tooth (p. 40) as well as the glandular or nectariferous tissue of the 'tylate' tooth.

The presence of cork at the vein terminations in old leaves indicates that these *Begonia* species, which grow in the humid tropical forest, are adapted to survive in seasonally dry conditions. Moreover, most parts of the plant are usually also

covered by a more or less dense indumentum of scales (see below). The species are usually epiphytes and in particular *B. elaeagnifolia* and *B. squamulosa* grow on trees often at a considerable distance above the ground, but *B. longipetiolata* occurs on tree trunks and rocks usually within the reach of the collector. All species have in common that they occur in clearings or other open places in the forest such as river banks where the plants are regularly exposed to the sun. Obviously wound cork and indumentum are adaptive features which inhibit or reduce the evaporation by the plants under dry conditions.

5.5. Venation

5.5.1. Observations and comments

The venation was studied using leaves preserved in spirit and dried leaves. The latter were boiled and kept in 70% ethanol for several days after which they were sufficiently cleared so that most of the smallest veins could be distinguished with the microscope. Some of the leaves studied were cleared and stained according to the method described by Brouillet, Bertrand et al. (1987).

Figs. 5-13a and b present the venation in *B. elaeagnifolia* and *B. longipetiolata* respectively. The vertical vein that is sometimes termed the midrib or midvein is here designated as the primary vein following Hickey (1979). Consequently, the lateral veins which diverge from the primary vein are the secondary veins. Depending on the size of the blade the primary vein is more or less prominent abaxially, but the secondary veins are usually less conspicuous and in comparison with the primary vein only some of them are slightly prominent.

The illustrations demonstrate that in the species mentioned above the venation is pinnate. The secondary veins and their branches terminate in the margin so that it is concluded that the venation is of the simple craspedodromous type as described and illustrated by Hickey (1979, p. 30 and fig. 53). The illustrations also show that the terminal parts of the secondary veins are connected by intersecondary veins which are more or less parallel with the edge of the blade. Collectively, these intersecondary veins apparently form a vein which could be interpreted as an intramarginal one. However, a photograph of a cleared leaf of *Hibbertia ebracteata* Bur. ex Guillaum. (*Dilleniaceae*) demonstrates that the intramarginal vein in that species is independent and continuous, whereas its thickness is similar to that of the secondary veins (Hickey & Wolfe (1975, fig. 6). What appears to be an intramarginal vein in the leaves studied here is thinner than the secondaries and not truly continuous, as the junctions of a secondary vein and two successive marginal intersecondary veins do not quite coincide. The junctions on the same secondary vein may be so close to each other that in the drawings some of them apparently coincide. However, at a sufficient magnification it can be seen that they are in fact separate.

The venation in Figs. 13a and b is also slightly similar to the semicraspedodromous venation type as illustrated by Hickey (1979, fig. 54). According to Hickey that type is characterized by secondaries which branch just within the margin.

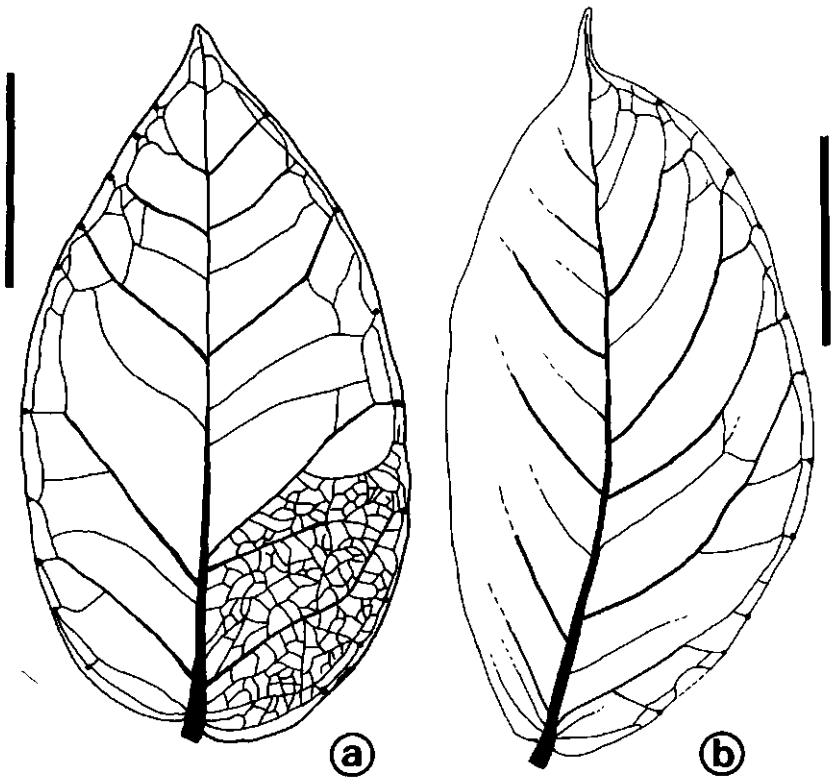


Fig. 5-13: Simple craspedodromous venation in the blade of *Begonia* species. **a:** *B. elaeagnifolia*, coll. De Wilde & Jongkind 9638; **b:** *B. longipetiolata*, culta, Wieringa s.n., Tchimbélé, Gabon. The bar in **a** represents 2 cm, that in **b** 5 cm.

Hickey's illustration demonstrates that one branch of each secondary vein forms a distinct marginal loop and joins the superadjacent secondary vein. The other branch is a short vein that diverges at the top of the loop and terminates in the margin. Such marginal loops with short veins which terminate in the margin definitely do not occur in the leaves of the species studied here. Thus, the venation discussed above is best described as simple craspedodromous. The venation in *B. pelargoniiflora* and *B. squamulosa* is similar to that shown here for *B. elaeagnifolia* and *B. longipetiolata*.

The peltate leaves of both *B. karperi* and *B. rwandensis* have an actinodromous and suprabasal venation which is shown in Figs. 5-14a & d. In both species, the blade is characterized by five primary veins which diverge from a single point. These primary veins comprise one medial ('vertical') and two pairs of lateral veins (compare with Hickey 1979, fig. 4.3-63). In the leaf of *B. karperi* two comparatively thin veins diverge from the same point towards the base (Fig. 5-14a), whereas in the leaf of *B. rwandensis* there are four thin veins which are more

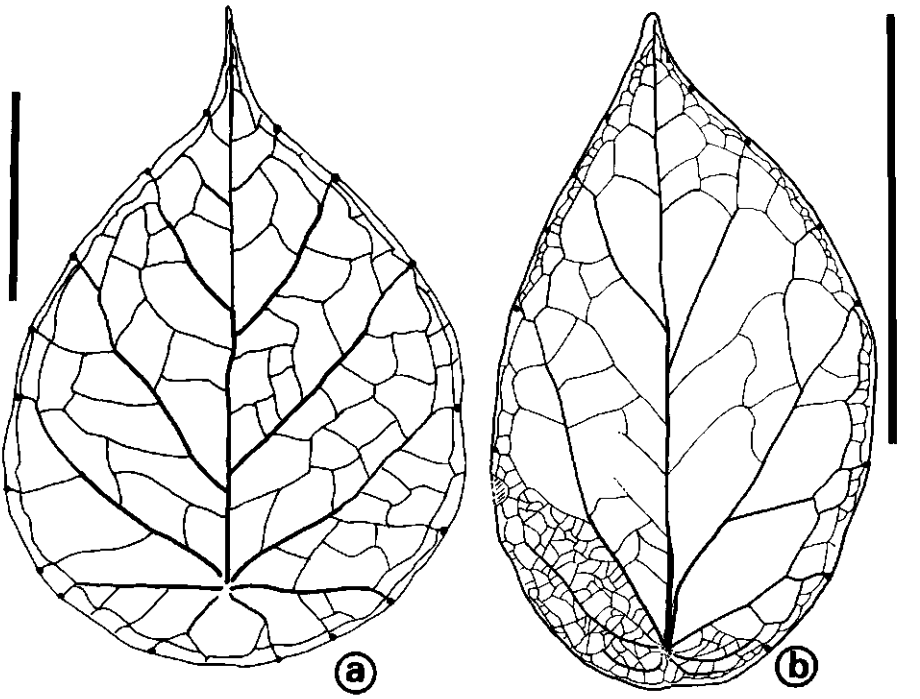


Fig. 5-14: Actinodromous venation in the blade of *Begonia* species. **a:** *B. karperi*, coll. Breteler & De Wilde (1978)-335; **b:** *B. rwandensis*, coll. Bouxin 1122. The bars represent 5 cm.

or less parallel with the leaf margin (Fig. 5-14b). These thin veins are interpreted as secondary veins produced by the lowest lateral primaries, although it is not possible to distinguish the point where they branch off. In the leaf margin of these species there are also veins which are more or less parallel with the edge. These veins are distinctly thinner than the primary and most of the secondary veins. These successive marginal veins are not strictly continuous so that collectively they do not form an intramarginal vein.

The secondary and the lateral primary veins as well as their branches in both the craspedodromous and the actinodromous venation type all terminate in the margin. As discussed above, the veins terminate more or less abruptly before reaching the edge of the blade. In older leaves, the margins by these terminations have corky teeth or depressions. In Figs. 5-13 and 5-14 the wide vein terminations and/or the teeth are indicated diagrammatically by dots. The illustrations show that the vein terminations are more or less evenly distributed.

The collection Satabié & Letouzey 343 which is here assigned to *B. elaeagnifolia* has several features by which it differs slightly from the other specimens cited for that species (see p. 171). Several leaves of this collection have been studied and an example of the venation is presented in Fig. 5-15. The leaf is unique

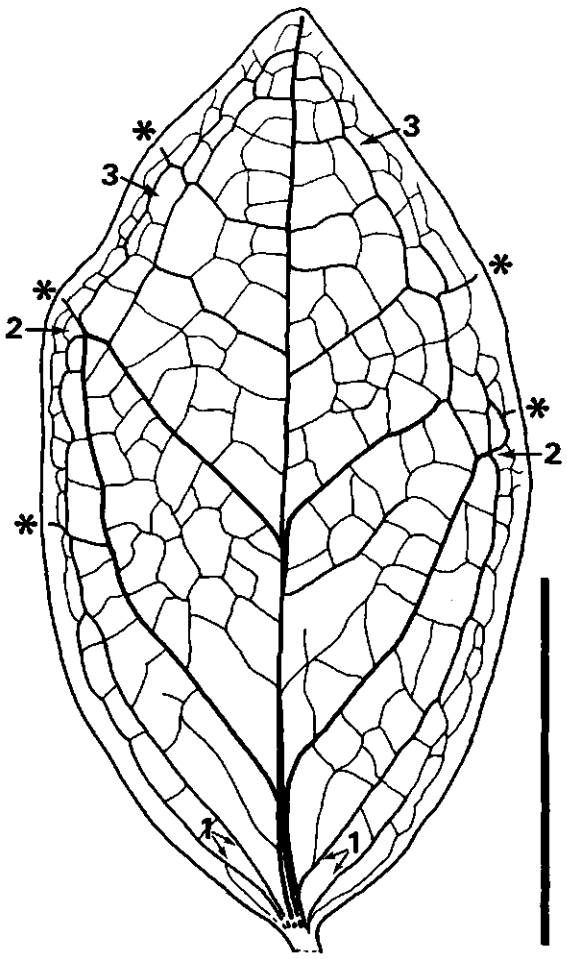


Fig. 5-15: Venation in the blade of the coll. Satabié & Letouzey 343 that is assigned to *B. elaeagnifolia*. Compare with Fig. 5-13a. Explanation in the text. The bar represents 5 mm.

by the apparent absence of teeth and the fact that the few secondary veins terminate in the margin of the upper half of the blade only (see asterisks). Moreover, apart from the vertical primary vein, there are on each side of this vein one or two comparatively thick veins which arise immediately from the petiole (arrows marked 1). They are more or less parallel with the margin and join the secondary veins approximately half-way along the length of the blade (arrows marked 2). The apical half of the blade is characterized by one or two thicker veins on each side of the primary vein (arrows marked 3). These veins are parallel with the margin and they join the midvein in the apex.

None of Hickey's (1979) illustrations of venation types matches the venation

observed in the collection Satabié & Letouzey 343. When Hickey's illustrations are compared with Fig. 5-15 it appears that the venation in this collection can be best described as brochidodromous. Nevertheless, the venation in Satabié & Letouzey 343 differs from the brochidodromous venation by its few secondaries which terminate in the margin. Hickey's illustration does not show any secondary vein that terminates in the margin. Hickey & Wolfe (1975, p. 563) stated that in the *Dilleniidae* there is a trend towards the development of an actinodromous venation which in its turn may yield a campylodromous venation. Their illustration of the latter type on page 544 demonstrates that on each side of the medial vein there are several veins which are continuous from the very base to the very apex. The veins marked 1 in Fig. 5-15 appear to be somewhat similar to these continuous veins in the campylodromous venation type, but they do not terminate in the apex, as they join the few secondary veins. According to the illustration of the campylodromous venation in Hickey & Wolfe (1975) and Hickey (1979), that type is characterized by the absence of secondary veins which terminate in the margin. Thus, the venation in Satabié & Letouzey 343 not only differs from that in the species discussed above but also from any type described and illustrated by Hickey.

5.5.2. Discussion

The observations discussed above show that apart from the peculiar venation in the collection Satabié & Letouzey 343 the venation is either simple craspedodromous ('pinnate') or actinodromous ('palmate').

In their phylogenetic studies of the leaf morphology Hickey & Wolfe (1975) stated that according to Takhtajan and Cronquist, the *Begoniales* are included in the subclass *Dilleniidae*. This subclass is among others characterized by basically simple leaves with a toothed margin, a pinnate venation and glands which are present on the teeth (Hickey & Wolfe op. cit., p. 563). These authors (op. cit., pp. 548 and 549) also pointed out that on the basis of all the evidence relating to leaf morphology, a pinnate venation represents a primitive character within the dicotyledons.

On the basis of venation type and shape of the blade, Hickey & Wolfe (op. cit., pp. 563 and 571) distinguished two taxonomically informal groups ('I' and 'II' respectively) within the *Dilleniidae*. Group 'I' is designated as the pinnate and group 'II' as the palmate *Dilleniidae*. The palmate group includes orders such as the *Begoniales*. Evidently, Hickey & Wolfe (op. cit., p. 573) were not aware that some *Begonia* species have a pinnate venation when they stated that the *Begoniales* has an actinodromous venation. In the *Begoniaceae* a pinnate venation is comparatively rare. For example, Irmscher (1925, p. 549) described the venation in the family as palmate ('handnervig') or occasionally pinnate ('fiedernervig'). It appears that in the *Begoniaceae* the palmate or actinodromous venation represents the primitive condition, because it occurs in the majority of its taxa including *Hillebrandia sandwicensis* (see e.g. Brouillet, Brouillet et al. 1975, p. 36 and fig. 6) which is commonly considered as the most primitive taxon in the family. Thus, the present evidence suggests that *B. karperi* and

B. rwandensis which have an actinodromous venation, are primitive taxa according to their venation.

As already mentioned above, the palmate *Dilleniidae* are characterized by an actinodromous venation. However, Hickey & Wolfe (op. cit. p. 571) stated that there are several evolutionary trends within that group of the subclass. One of these trends concerns the development of a pinnate venation by weakening of the lateral primaries in all orders but the *Begoniales*. The occurrence of a pinnate or simple craspedodromous venation in *B. elaeagnifolia*, *B. longipetiolata*, *B. pelargoniiflora* and *B. squamulosa* indicates that this trend also occurs in the *Begoniales*. The development of the pinnate venation in these species can be easily envisaged to be the result of a weakening of the lateral primaries in the actinodromous venation in *B. karperi* and *B. rwandensis* in combination with a shift of the point where the petiole is attached to the blade (compare Fig. 5-13 with Fig. 5-14). In fact, the presence of a craspedodromous venation in *B. elaeagnifolia* and on the other hand an actinodromous venation in *B. karperi* is strong evidence that the development of a pinnate from an actinodromous venation occurs in a group comprising only two species which are closely related. For a further discussion of the relation between *B. elaeagnifolia* and *B. karperi* see page 183. Thus, for the the species studied here, the pinnate (craspedodromous) character state of the venation is considered derived, while the palmate (actinodromous) character state represents the primitive condition.

As mentioned above the primitive condition of the venation in the dicotyledons is pinnate. This primitive condition occurs in the pinnate *Dilleniidae*, so that on the basis of its actinodromous venation the palmate *Dilleniidae* obviously is derived. Hence, the development of the pinnate condition from the actinodromous condition in the palmate group is a clear case of the reversal of an evolutionary trend.

5.6. Trichomes and indumentum

The trichomes which have been seen in the present study are either simple (papillae) or complex (dentate scales).

Papillae are present on the part of the style below the stigmatic surface in *B. longipetiolata*. These papillae are epidermal, short, single-celled and non-glandular Fig. 6-9d to f). Usually, the abaxial surface of the outer perianth segments is provided with dentate scales, but in a single collection, Satabié & Letouzey 343 here assigned to *B. elaeagnifolia*, short unbranched trichomes were seen on these segments in addition to the usual scales. Boiled material from Satabié & Letouzey 343 did not reveal whether these trichomes are uni- or multicellular, but most likely they are glandular because the contents of the apex are very dense in comparison with the remainder of the trichome.

The complex trichome which is designated as a dentate scale or simply 'scale', is multicellular, membranous, flat and more or less elliptic to circular in outline. Its margin is dentate and it is born by a short usually two-celled stalk (see Fig.

5-5c). The stalk usually has a more or less centric position on the scale. Moreover, when seen on the upper surface the scales are provided with a cobweb pattern of thick bands. The teeth of the margin are variable in shape and are broadly to narrowly triangular. Some examples of these trichomes are presented in Fig. 5-16.

The illustration shows that the number of teeth of a scale from a tepal is usually less than on the vegetative parts of the same plant, such as the blade. The lowest number of teeth has been counted in scales from the tepals in the collection Satabié & Letouzey 343 which is already referred to above. Nevertheless, it is not possible to classify the scales according to the number of teeth. The selection of scales presented in Fig. 5-16 demonstrates that they are completely intergrading according to their shape and it is concluded that the morphology of the scales of the plants studied does not provide a single character by which the plants could be distinguished. None of the trichomes illustrated by Theobald, Kruhalil & Rollins (1979) is similar to the scales observed here.

The scales are usually pale to dark brown, but very rarely they are almost colourless or silvery grey. Colourless scales have been seen on the tepals of the cultivated white-flowered specimen De Wilde, Arends et al. (1983)-326 of *B. longipetiolata*. Silvery grey scales are present on the upper surface of the blade of *B. karperi* and in the living condition they are conspicuous because their colour contrasts with that of the green leaf.

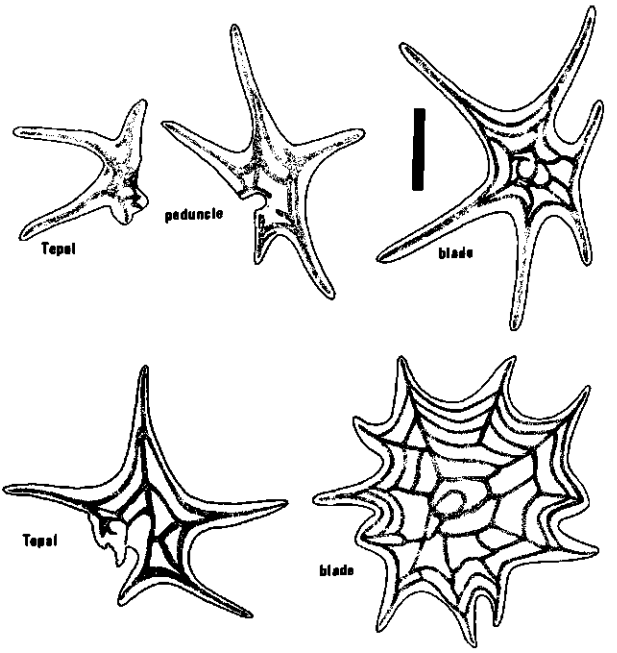


Fig. 5-16: *B. elaeagnifolia*: camera lucida drawings of trichomes on the surface of different plant parts in two gatherings. Upper row: coll. Satabié & Letouzey 343; lower row: coll. De Wilde, Arends et al. 9810. Bar represents 100 µm.

The density of the indumentum varies with the plant part on which it occurs. Very rarely a plant is almost completely glabrous. For example the type specimen of *B. nicolai-hallei*, a taxon that is here considered to be conspecific with *B. longipetiolata*, does not have any trichomes. A dense indumentum often may be found on the stem and the stipules; scattered trichomes, which usually do not touch each other, occur on the abaxial side of the large tepals. According to Hallé (1966) in his emended description of *B. squamulosa* (which in fact applies to *B. longipetiolata*) all plant parts are more or less pubescent. However, as a rule scales do not occur on the androecium, styles and the inner small tepals. There is one exception: in *B. squamulosa* the styles carry a few of these trichomes towards their base (see p. 211). Scales are usually found on the abaxial surface of the leaves, particularly on and near the veins and the margin. The adaxial leaf surface in all the species is invariably glabrous except in *B. karperi* and one of the collections of *B. pelargoniiflora*.

6. Aspects of reproductive morphology

6.1. Flowering habit

Preserved field collections of *Begonia* species are usually poorly provided with inflorescences. Many herbarium specimens carry labels with field notes describing inflorescences or flowers, but these fragile structures are often lost during drying and mounting procedures. Several collections described by other investigators no longer bear the inflorescences they saw, for example Dinklage 1499, the type of *B. longipetiolata*. Thus the analysis of the species in the present study was frequently hampered by the lack of sufficient reproductive material in the dried specimens.

Begonia flowers are either staminate ('male') or pistillate ('female'). All the species studied have unisexual inflorescences except *B. pelargoniiflora* which may have male and female flowers within the same inflorescence. Cultivated seedlings of *B. elaeagnifolia* may occasionally produce bisexual inflorescences, particularly in plants flowering for the first time.

Occasionally, two inflorescences may be inserted so close to each other that they appear to be situated at the same node. This is the case when a particular node produces a branch from the single lateral bud next to an inflorescence in the axil of its leaf. The initial internodes of the lateral branch often are extremely short. Consequently, an inflorescence that may be produced at its first node will be situated very close to the inflorescence on the main stem.

The type material of *B. nicolai-hallei* Wilcz., Hallé & Villiers 5381 (not 538 as cited erroneously in Wilczek 1969b), is accompanied by Hallé's field observation that some nodes of the plants carry both a male and a female inflorescence. The gathering is preserved on a single sheet and the material does not permit the removal of any part of the stem for a thorough analysis. Close examination of this gathering revealed that a male and a female inflorescence are usually one internode apart. Where two inflorescences are very close, they are interpreted as being inserted at two different nodes. One node is part of the stem, the other is part of a dwarf shoot that does not carry a leaf.

From observations of cultivated plants and, to a lesser extent, of plants in the field, I conclude that the species treated here are invariably monoecious. However, there are usually many more male inflorescences than female ones. In the recent gathering of *B. longipetiolata* De Wilde, Arends & de Bruijn 9270, the preserved as well as the living plants were selected from a population of at least 100 plants, among which only 6 female inflorescences were found. *B. karperi* is based on four collections, and only one of these had a single female inflorescence and one fruit. In *B. pelargoniiflora* two of the three gatherings carry female inflorescences or immature infructescences and in fact for this spe-

cies, the number of female elements is larger than that of the male ones. In *B. rwandensis* the few female elements available are mainly infructescences. In *B. squamulosa* less than one out of three gatherings contain female elements, and only half of these are flowers. Thus, for this species female flowers could be studied in less than one sixth of the gatherings cited in Chapter 10. For both *B. elaeagnifolia* and *B. longipetiolata* this ratio is also small, with female flowers present in one out of ten and one out of fifteen gatherings respectively.

In cultivated plants, male inflorescences also outnumber the female ones, and very often the latter are not present at all. A large cultivated specimen of *B. elaeagnifolia* produced more than 150 male inflorescences at one flowering but not a single female one. Hallé & Raynal (1966) stated that a plant grown from the collection J. & A. Raynal 9709 produced exclusively female flowers in cultivation. They attributed this to the amount of light available, but in the course of my study I found that some introductions regularly produce female flowers, whereas others, grown under similar conditions, hardly ever do so.

6.2. The architecture of the inflorescences

According to Irmscher (1925, p. 558) the inflorescences in *Begoniaceae* are either terminal or axillary, while the axillary ones are always determinate. The inflorescences of the plants studied here are axillary and it was found that all the axes of an inflorescence bear a terminal flower. Thus the inflorescences are indeed both axillary and determinate. Such an inflorescence that occasionally is designated as a cyme, is illustrated e.g. in Gifford & Forster (1989, fig. 19-63).

The branching of the cyme illustrated by Gifford & Forster (loc. cit.) follows a dichotomous pattern and their illustration shows that the inflorescence is a hierarchy of three-flowered units, for which Rickett (1955, p. 430) reserved the term dichasium. The dichasium in the sense of Rickett consists of a peduncle that is terminated by a flower and bears two opposite bracts, each of which subtends a lateral axis. These axes are also terminated by a flower and each may bear a pair of opposite bracts. A repetition of this mode of branching out of the axils of the bracts on the lateral axes results in a complex inflorescence like the cyme referred to above. Because of the dichotomous branching in the basic unit which is repeated in the complex inflorescence, such an inflorescence is often designated as a compound dichasium. In order to distinguish the compound dichasium from the (three-flowered) dichasium *sensu* Rickett, the latter inflorescence is sometimes referred to as a 'simple' dichasium (e.g. Heywood 1978, p. 21; Lawrence 1951, pp. 61, 63; Radford 1986, p. 420). Usually however, morphologists (e.g. Gifford & Forster, op. cit.; Troll 1964; Weberling 1981) do not distinguish between simple and compound dichasia. This is the view of Rickett (1944, p. 204) who considered the separation of inflorescences into simple and compound, which was introduced by Eichler (1875, pp. 38, 40), to be artificial.

The diagrammatic illustration of a dichasial cyme in Fig. 6-1 is referred to

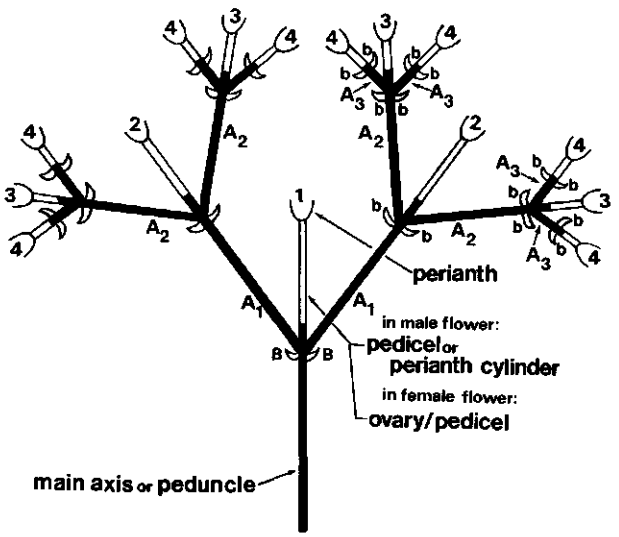


Fig. 6-1: Diagram of a regularly branched dichasial cyme. A_1 to A_3: lateral axes of the first to third order; **B**: bracts on the peduncle; **b**: superior bracts on the lateral axes; the numbers in the perianths indicate the sequence of anthesis. Further explanation in the text.

in the discussion of the inflorescences observed in the present study (see below). The illustration differs slightly from those of the cyme or the dichasium in Gifford & Forster (1989, fig. 19-63) and Weberling (1981, p. 224) respectively.

The axes of the inflorescence in Fig. 6-1 are indicated by solid black lines. Each axis is terminated by a flower whose pedicel (here perianth cylinder, see p. 59) or in the case of a female flower, the inferior ovary that is continuous with the pedicel, is indicated by a double line. In accordance with the illustration in Weberling (loc. cit.), all the axes, including the terminal lateral ones, bear a pair of leaf-like appendages which are here designated as bracts.

However, some authors in describing *Begonia* species, e.g. Sands (1990), distinguish between bracts and bracteoles. According to Radford (1986, pp. 418, 419) a bract is a modified leaf in the inflorescence, whereas a bracteole or prophyllum is a small bract that usually occurs on a pedicel.

In his discussion of the term bract, Rickett (1954, pp. 195, 196) stated 'It remains to be determined whether we are to limit the term to organs which subtend single flowers or branches of an inflorescence; whether we shall include also the bracteoles and other structures situated on the floral axes but not always subtending flowers or branches of the inflorescence' and 'Certainly it would be idle to attempt to formulate a definition of bract which excludes bracteole; the latter may or may not subtend flowers'. According to Rickett (op. cit., p. 196) the term bracteole was defined by Gray in 1864 to denote 'a bract seated on the pedicel or flower stalk'. He concluded that the concept of bracteole is

evidently vague and he said that 'perhaps it should remain so, having the sense merely of a small bract'. Nevertheless, Rickett (op. cit., p. 197) suggested defining the bracteoles rather strictly in the sense of the prophylls, the lateral organs on individual pedicels.

In the present study, observation of lax male inflorescences which are characterized by more or less elongated axes of the first and higher orders revealed that modified leaves or foliar structures never occur on pedicels ('perianth cylinder') or even on the exact point between the pedicel of a flower and the supporting axis. Thus, according to the definitions of Radford and Rickett cited above, the lateral foliar structures in the inflorescences are invariably designated as bracts.

It should be noted that according to Irmscher (1925, p. 562), the bracts in *Begonia* are 'pseudobracts', because he interpreted these structures to be homologous with stipules. However, in *Begonia*, the pair of stipules is always inserted on a node of the stem and these structures, hence Irmscher's 'pseudobracts', are free from the base of the peduncle which is situated in the very axis of the leaf on the same node. De Wilde & Arends (1980, p. 380) accepted the interpretation of Irmscher. However, they also interpreted the bracts on the axes of the first and higher orders as pseudobracts. In his illustration, Irmscher (1925, fig. 257-2b) shows two stipules on the stem near the base of the peduncle as well as several pairs of foliar structures at higher levels in the inflorescence. These foliar structures which are situated on the apices of the main axis (peduncle) and the axes of the first order are marked by Irmscher as 'Vorblätter' (= prophylls). It should be noted that Irmscher nowhere implies that his 'Vorblätter', which are here designated as bracts, are also pseudobracts, hence homologous with stipules. Each pair of these 'Vorblätter' subtends two branches of the next higher order: The interpretation of De Wilde & Arends (loc. cit.) that the bracts in species of section *Squamibegonia* are modified stipules, does not appear to apply to the species of section *Tetraphila* described here, because it is difficult to see how two stipules would subtend two branches arising from a single point. In *Begonia*, the two stipules on a node are always associated with a single bud on the same node. Evidently, this bud may produce a single branch only, not two. Thus, it appears that Irmscher's 'Vorblätter' are homologous with leaves rather than with stipules.

In the species studied, the first pair of bracts is situated at the top of the main axis or peduncle of the inflorescence. These bracts subtend the lateral axes of the first order and, in a more than three-flowered dichasium, the subsequent axes of the second and higher orders. Obviously, the bracts on all the lateral axes are always situated above the bracts on the peduncle. Therefore, the bracts on the lateral axes can be distinguished collectively from those on the peduncle by the designation 'superior bracts', a term introduced by Hallé & Raynal (1966).

It should be noted that Weberling (1981) interpreted the peduncle of the dichasium as subtended by a large foliar structure. The inflorescences studied here occur in the axils of leaves which are considered to belong to the vegetative part of the plant and not to the inflorescence. This interpretation is supported

by the illustrations of the other authors cited above. They do not indicate a large bract or 'Deckblatt' at the base of the peduncle.

6.3. Male inflorescences and flowers

6.3.1. Male inflorescences

The perianth and the androecium of each male flower is attached by a pedicel-like structure to the inflorescence axis which supports the flower. The connection of the pedicel-like structure to the axis is slightly articulate. In accordance with De Wilde & Arends (1980, p. 380), the pedicel-like structure is designated as the perianth-cylinder, because it is interpreted to be composed of the fused bases of the perianth segments. This interpretation is supported by the observation that the flowers when they drop eventually from the inflorescences, always include the pedicel-like structure that detaches from the supporting axis at the articulation.

6.3.1.1. *B. elaeagnifolia* and *B. karperi*

Cultivated plants of *B. elaeagnifolia* usually produce two- or three-flowered inflorescences, but vigorous plants often have inflorescences with four or, less frequently, five flowers. In nature, the specimens usually bear inflorescences with one or two flowers only. However, the field gathering De Wilde, Arends et al. (1983)-179 bears in addition to several three-flowered inflorescences a single four-flowered one. In the recent gathering De Wilde, Arends et al. 9810, I counted 52 male inflorescences which are mainly two- or three-flowered, while five of them have four or five flowers per inflorescence. Thus, on the basis of the specimens studied, I conclude that in *B. elaeagnifolia* the number of flowers per male inflorescence ranges preponderantly from one to three. Rarely, there are four or even five flowers in an inflorescence.

In 2- to 5-flowered inflorescences of *B. elaeagnifolia*, the lateral axes of the first and higher orders are not or scarcely developed ($\mathbf{A_1}$, $\mathbf{A_2}$ and $\mathbf{A_3}$ in Fig. 6-1). Consequently, the superior bracts (**b**) on these axes are inserted very close to the bifurcation of the peduncle. They are often inconspicuous and because of the reduction of the lateral axes, they are often more or less concealed by the comparatively large bracts (**B**) on the main axis. Within the species all bracts vary in size, and occasionally the bracts (**B**) may be very minute and the superior bracts (**b**) lacking. Absence or presence of the superior bracts in *B. elaeagnifolia* is not a constant feature in any particular population. Cultivated plants from various populations in Gabon are quite variable in this respect. When present, the bracts **B** in *B. elaeagnifolia* are opposite and separate. However, in the cultivated plant of the gathering Louis, Breteler & de Bruijn 1267, these bracts were found to be unilaterally fused and the apparently single bract below the bifurcation is more or less bidentate at the apex and has a slightly lateral position on the main axis.

In single-flowered inflorescences, the flower is either the flower that is born

on the main axis, or it is the flower that terminates one of the lateral axes $\mathbf{A_1}$. In the former case there are only two bracts below the flower, while in the latter case there are four bracts. These bracts comprise one pair of bracts **B** and a pair of superior bracts **b**. In two- or three-flowered inflorescences, the flower on the main axis is always present; the other flowers are either supported by one axis $\mathbf{A_1}$ or by both axes $\mathbf{A_1}$. When there are four or five flowers, the fourth and the fifth flowers appear to be supported by axes of the second and possibly the third order. The sequence of anthesis suggests that the development of the inflorescence becomes monochasial after anthesis of the flowers on the axes $\mathbf{A_1}$.

The male inflorescence of *B. karperi* is almost similar to that described for *B. elaeagnifolia*, but its bracts **B** on the peduncle are always unilaterally fused (see Plate 2-9, page 192). The cultivated plants of *B. karperi* very rarely produced inflorescences with three flowers. Usually the inflorescences were two-flowered. The inflorescences in the field gatherings contain one or two flowers.

6.3.1.2. *B. longipetiolata*

The flowers are usually arranged in lax inflorescences, and the axes are of various lengths. It was observed in cultivated plants that the peduncle, i.e. the part of the main axis below the bracts (**B**), may continue to elongate after anthesis of the terminal flower. Moreover, during the further development of the inflorescence the part of the main axis above the bracts up to the point of bifurcation of the two lateral axes ($\mathbf{A_1}$) usually continues to elongate as well (Plate 3-9, p. 196 and Fig. 6-2b). In young inflorescences of *B. longipetiolata* the bracts (**B**) are always unilaterally fused. During the further development, this apparently single bract usually splits into two more or less equal parts (Fig. 6-2d). However, sometimes it may remain entire as shown in Fig. 6-2a and in e.g. Thomas 4318. When the fused bracts (**B**) divide, these two parts are initially opposite, but it is characteristic for *B. longipetiolata* that in a later phase of development their position often changes, so that they no longer appear to be attached at the same level (Plate 3-8 and -9.

These complex inflorescences show a gradation between dichasial and monochasial branching of the axes at different levels. The axes of the first and the second order are usually branched in a more or less regular dichasial manner (Plate 3-9, – 10, p. 196 and Figs. 6-2a and -2b), and those of higher orders branch in a monochasial way to form cincinni (Plate 3-9, and Fig. 6-2b). However, there are exceptions. The plants in the collection De Wilde, Arends & de Bruijn 9270 were taken from a population that consisted of at least 100 individuals. Many of these were small plants with male inflorescences containing only 3 to 8 flowers. Such 'depauperate' inflorescences were not dried but preserved in spirit, as in drying some flowers are bound to get lost as well as their spatial arrangement. When I studied these inflorescences I found that there are various combinations of axes of the first to third order. The two axes $\mathbf{A_1}$ are always present. One of these $\mathbf{A_1}$ axes may have two axes $\mathbf{A_2}$, which in their turn both give rise to axes of the third order ($\mathbf{A_3}$). The other $\mathbf{A_1}$ axis is either terminated

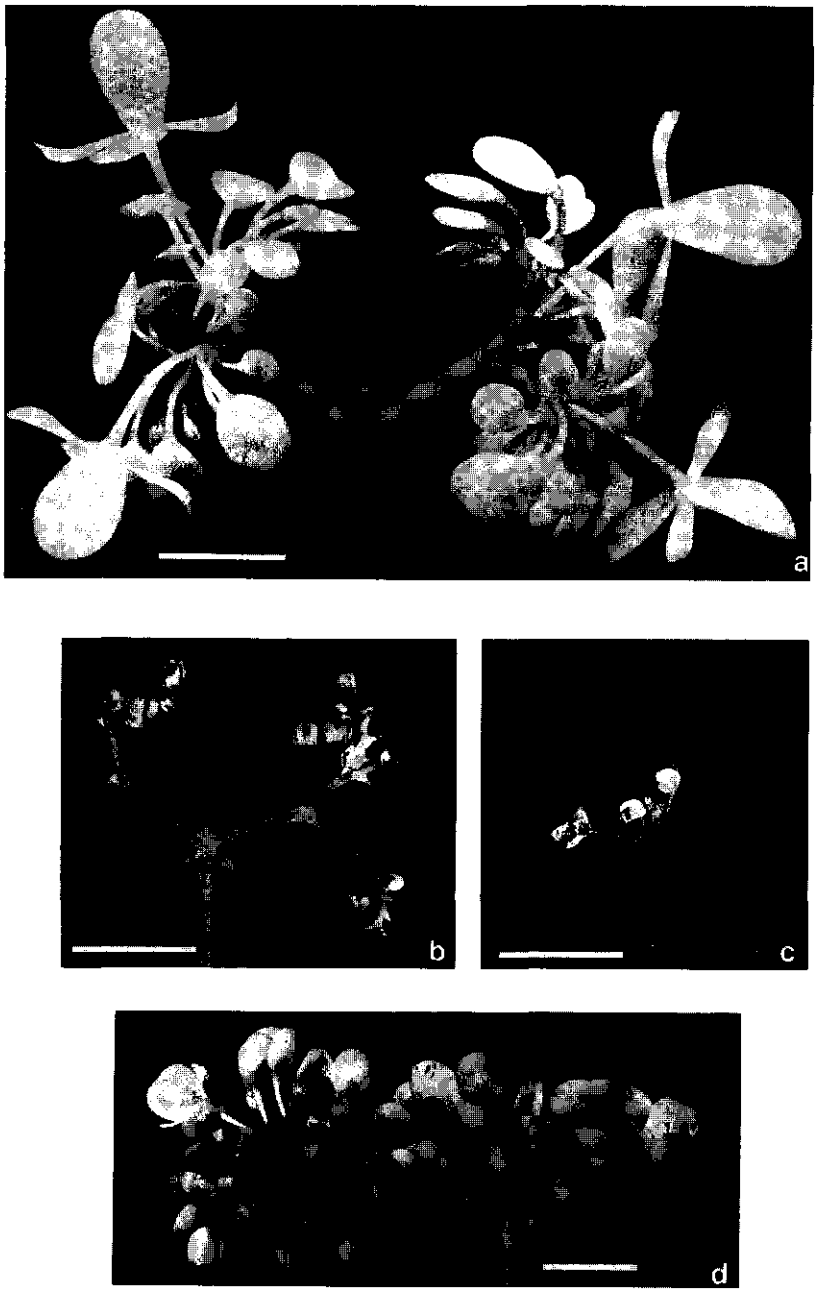


Fig. 6-2: *B. longipetiolata*, fresh and dried male inflorescences in cultivated (**a & d**) and wild specimens (**b & c**) respectively of the gathering De Wilde, Arends et al. (1983)-180; **a, b & c:** expanded inflorescences; in **d:** young inflorescences in various phases of development; to the right and in the middle: bracts on the main axis fused; to the left: bracts separated. Scales represent 1 cm.

by a flower, or has next to this flower a single axis A_2 with its flower. Thus the development of depauperate inflorescences may follow dichasial or monochasial patterns in various ways.

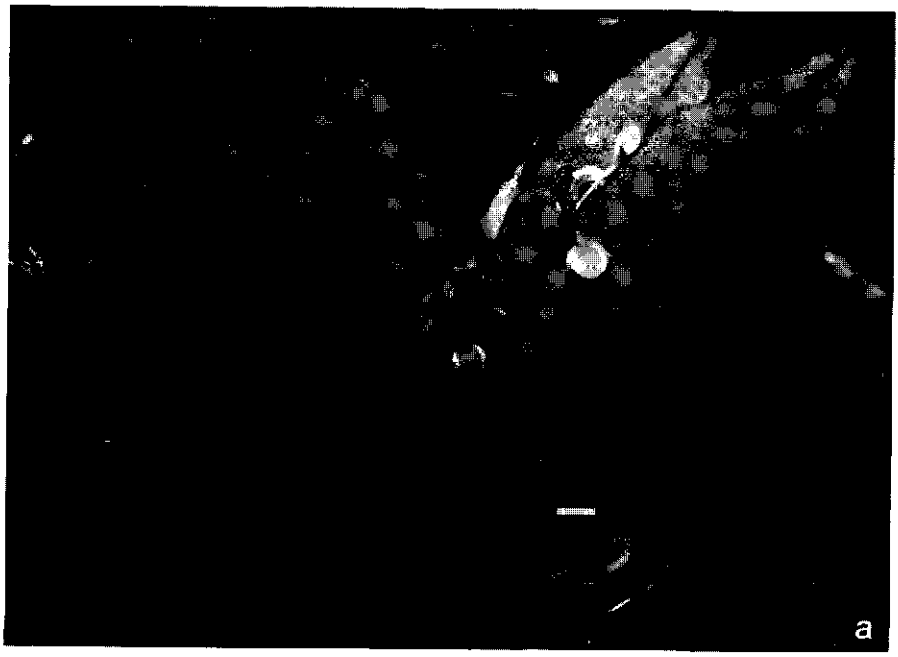
In *B. longipetiolata* the bracts on the main axis are sometimes persistent (Plate 3-10, p. 196), but usually they shrivel or disappear altogether (Plate 3-8 and -9). The superior bracts **b** on the axes A_1 and A_2 are usually present, whereas those of the axes of higher orders are either vestigial or absent.

The number of flowers per inflorescence is quite variable. As may be expected small plants generally have few flowers and comparatively large plants many. The variation in quantity of flowers between individual specimens of one topodeme is demonstrated by Figs. 6-2b and -2c. Fig. 6-2c shows a dried inflorescence with c. 5 flowers of an individual plant in the gathering De Wilde, Arends et al. (1983)-180 while the distal part of an inflorescence from another plant of the same gathering is depicted in Fig. 6-2b. In the field we counted up to 71 flowers per inflorescence in this gathering. In cultivation, plants from this gathering produce inflorescences with numerous flowers (Fig. 6-2a), but if the plants are neglected the number of flowers is considerably lower.

A plant of *B. longipetiolata*, De Wilde, Arends & de Bruijn 9270, was photographed in the field (Fig. 6-3a). Fig. 6-3b shows another individual from this collection when it flowered in the greenhouse three weeks after its introduction. Its inflorescence is 2-flowered and resembles the 2-flowered inflorescences of *B. elaeagnifolia* (see above). Such reduced or 'depauperate' inflorescences of *B. longipetiolata* may be distinguished from those of *B. elaeagnifolia* by their comparatively long lateral axes which usually are more than 1 mm long and by the absence of superior bracts. The inflorescence in Fig. 6-3b has one lateral axis of about 2 mm. Those of *B. elaeagnifolia* are scarcely elongated. The plant shown in Fig. 6-3b eventually produced inflorescences with about 25 flowers.

In conclusion, it appears that the male inflorescences of *B. longipetiolata* are initially many-flowered dichasia. When they continue to develop, the branching of the inflorescences becomes monochasial and the flowers on the axes of the higher orders are arranged in cincinni.

As mentioned already (page 55) the type material of *B. longipetiolata* no longer bears inflorescences. Nevertheless, I am convinced that the plant from which it was prepared, from Kribi, Cameroun, carried male inflorescences like those described above. This conclusion is based on comparison of the descriptions and type material of both *B. longipetiolata* and *B. macrura* which were described simultaneously by Gilg (1904, p. 92). Gilg stated that the base of the peduncle in *B. longipetiolata* was provided with many bracts and its apex with many bracteoles. According to Gilg the peduncle of *B. macrura* similarly carries 'bracts' and 'bracteoles'. Examination of the type of *B. macrura*, Schlechter 12918, revealed that the node that carries the inflorescence also has scales near the base of the peduncle. I interpret these scales to be several crowded pairs of stipules on a dwarf shoot in which the internodes are extremely short. Gilg's descriptions of *B. macrura* and *B. longipetiolata* show that the types of these species are very similar. According to Gilg's note (op. cit., p. 93), the former species only differs



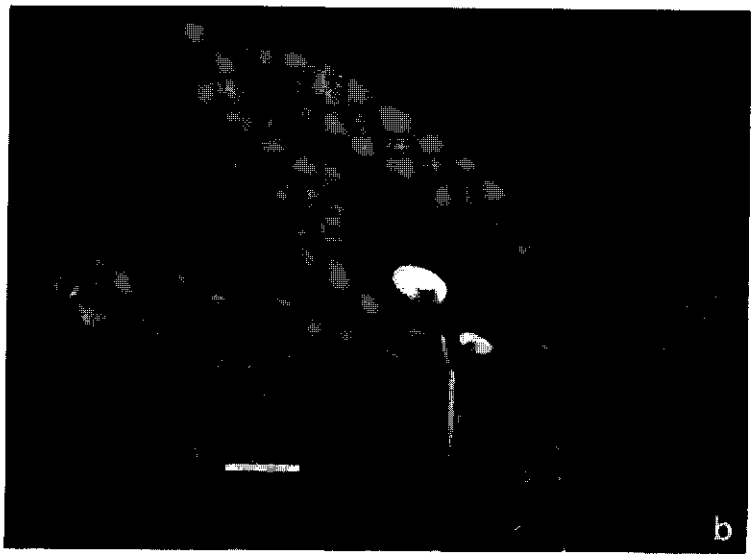


Fig. 6-3: *B. longipetiolata*, De Wilde, Arends & de Bruijn 9270, Doussa river, Gabon. **a:** plant on the trunk of *Baillonella toxisperma* Pierre with many-flowered male inflorescences; **b:** cultivated plant from the same gathering three weeks after its introduction showing a depauperate male inflorescence. Scales represent 1 cm.

from the latter by the dimension of all its parts which are distinctly smaller. The inflorescence of *B. macrura* which is depauperate and lax, carries few bracts and some flat buds (see page 67). More recent collections from the vicinity of the type locality of *B. longipetiolata* invariably have lax inflorescences which are more or less similar to that of *B. macrura*. Thus all the evidence indicates that the type of *B. longipetiolata* had the lax inflorescence(s) as described above. Moreover, it also has leaves with a distinctly canaliculate petiole that is characteristic for the species (see page 26).

6.3.1.3. *B. squamulosa*

In *B. squamulosa*, the structure of the male inflorescence is similar to that in *B. longipetiolata*. This is not immediately obvious as all the axes are very much reduced in length, forming a dense cluster at the top of the peduncle (Plate 6-3, p. 211 and Figs. 6-4c and -4d). As in *B. longipetiolata* the bracts of the main axis are initially laterally fused (Fig. 6-4a). The superior bracts on the reduced axes of the first and higher orders are often more or less concealed by the flowers and the buds, but sometimes they are quite long and protrude between the buds (Plate 6-3). After the flowers are shed, the peduncle with the shrivelled bracts remains for some time (Fig. 6-4b). In wild plants the number of buds and flowers appears to range from c. 5 – 10, but because of the tight flower arrangement small, young buds are easily overlooked. In cultivation the number of flowers per inflorescence may be low, e.g. 6, but a cultivated specimen of Arends, de Wilde & Louis 371 produced up to 65 flowers in a single inflorescence.

The type of *B. squamulosa* from the Crystal Mts in Gabon, is characterized by the dense male inflorescence which has numerous persistent bracts (see above) and, in addition, globose buds, thick outer perianth segments and terete petioles (see pp. 66 and 28).

6.3.1.4. *B. rwandensis*

Most of the dried specimens available have only one to four flowers, but for some specimens it is evident that some flowers have been lost, as their axes and bracts are still present. In other specimens the comparatively low number of flowers per inflorescence is interpreted as the result of developmental reduction. The hypothesis for this reduction is supported by observations on flower numbers in the other species discussed above. As living material of *B. rwandensis* was not available, it can only be surmised that the number of flowers might increase in cultivation. So far, the highest number of flowers counted in a single, young, inflorescence is five (Bouxin 1122, LG). This suggests that the male flowers of *B. rwandensis* are borne in an essentially more than 3-flowered cymose inflorescence. Plate 6-4 (p. 208) shows the inflorescence of Van Roeckhoudt 12. This inflorescence is asymmetric due to the unequal development of the first lateral axes. The lateral axis on the left has a single-flowered secondary axis. The axis on the right lacks this feature. Except for the distinct pairs of bracts, the inflorescence resembles some of the depauperate male inflorescences observed in *B. longipetiolata*.

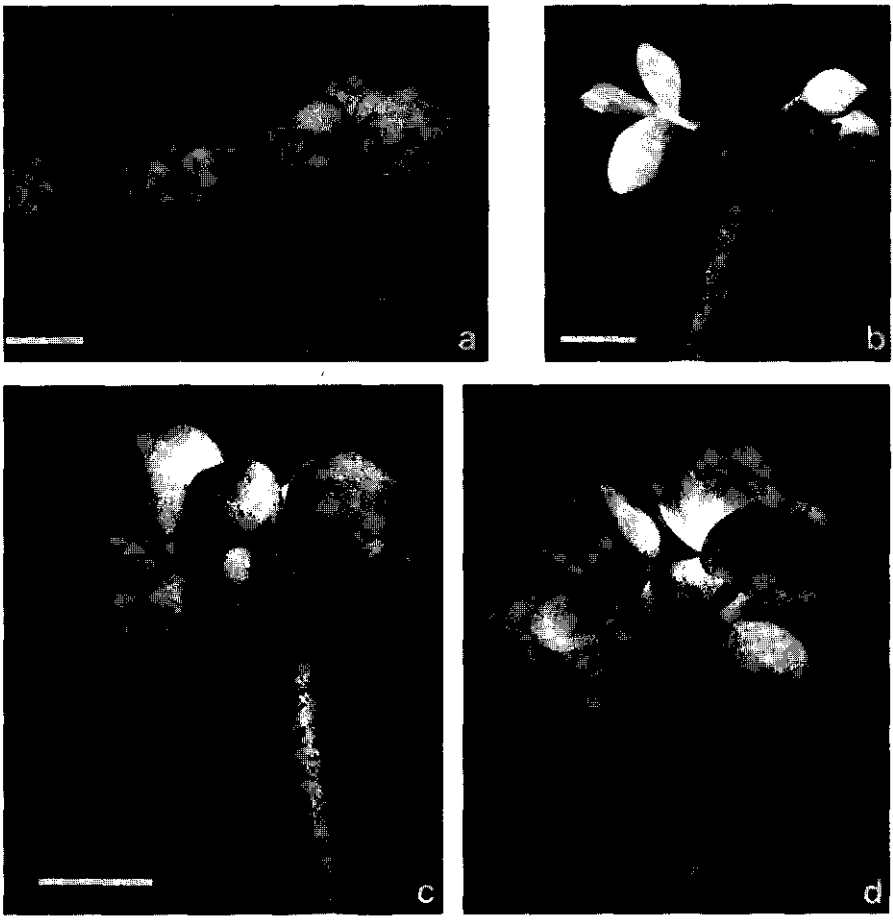


Fig. 6-4: *B. squamulosa*, male inflorescences of cultivated plants. **a:** young inflorescences in various phases of development; to the left: bracts on the main axis fused, in the middle and to the right: bracts divided; **b:** distal part of peduncle at the end of flowering; **c & d:** distal part of an inflorescence; **c:** side of inflorescence showing partly split bracts on the main axis; **4d:** other side of the same inflorescence; note that the front of the androecium is oriented towards the inflorescence axis. Scales represent 1 cm.
a & b: plant T1775, culta Arends, de Wilde & Louis 371, Waka, Gabon; **c & d:** plant T1603, culta De Wilde, Arends et al. (1983)-100, Crystal Mts, Gabon.

In *B. rwandensis* the bracts in fully developed lax inflorescences are invariably opposite. In young inflorescences the bracts are never joined and it seems unlikely that they have ever been fused in an earlier developmental phase of the inflorescence. Wilczek (1969a, p. 16 and 1969b, p. 89) interpreted the male inflorescence of Van Roeckhoudt 12 as up to eight-flowered. However, he assigned this specimen to *B. schultzei* (= *B. elaeagnifolia*), a taxon whose type material is characterized by a two-flowered inflorescence, and, unfortunately, he emended the description of *B. schultzei* accordingly.

6.3.1.5. *B. pelargoniiflora*

This species bears three kinds of similar inflorescences, male, female and bisexual. The single bisexual inflorescence that has been seen only on the dried specimen Letouzey 14448 is unfortunately of poor quality. I postulate that some inflorescences may initially produce male flowers followed by female ones. Additional, preferably living, gatherings are required to substantiate this supposition as it is exceptional within the section *Tetraphila*.

The inflorescences of *B. pelargoniiflora* are interpreted as regularly branched cymes with reduced lateral axes except for the two axes of the first order. The flowers are apparently closely arranged on these axes in the absence of axes of the second or higher orders. Next to a pair of bracts on the distal part of the peduncle, several superior ones were found also, supporting the hypothesis that the inflorescence is a many-flowered dichasium (Plate 4-1 and -8, p. 204).

6.3.1.6. The origin of the few-flowered inflorescences

In the course of the study De Wilde and I have discussed whether the up to 5-flowered inflorescences should be considered to represent the derived or the primitive state in relation to the more than 5-flowered ones. The prevalence of the more than 5-flowered inflorescence type in section *Tetraphila* and in species of the sister groups has led to the conclusion that the up to 5-flowered inflorescence is the derived condition.

We have also discussed the question whether it is valid to apply the terminology 'simple dichasia' and 'compound dichasia' to the inflorescence types seen in this study. It is occasionally reported in the morphological literature that compound dichasia have developed from simple ones. However, according to Rickett (1944, p. 217), the compound dichasium is not necessarily later in evolutionary history than the simple one. In order to avoid any confusion in respect to our conclusion I have preferred to refrain from using this terminology and I designate the inflorescences as either few- or many-flowered.

6.3.2. Male flowers

As was mentioned in the discussion on the male inflorescences (page 59), the male flower consists of the perianth with the perianth cylinder, which poses as a flower stalk, and the androecium.

6.3.2.1. Perianth segments

The perianth consists of two whorls each formed by two similar segments. The segments or tepals of the outer whorl are large in relation to those of the inner whorl. In bud, the outer whorl completely envelops the inner whorl. At anthesis, the perianth assumes the shape of a cross, because the inner segments alternate with the outer ones. For a further discussion of the nature of the perianth see pp. 81 and 142.

The shape of the perianth is one of the few characters that are useful in distinguishing *B. squamulosa* and *B. longipetiolata*. The segments, particularly the outer ones, of *B. squamulosa* are opaque, thick and succulent (see Fig. 6-4; Plate

6-3 & -4, p. 211), whereas those of *B. longipetiolata* are thin and sometimes slightly transparent (see Fig. 6-2a and Plate 3-8 & -11, p. 196). The flower buds of these two species are also different. In *B. squamulosa* the buds are globular (Fig. 6-4 and Plate 6-3), whereas in *B. longipetiolata* they are flattened (Figs. 6-2a and 6-3). Observations of living plants in the field and in cultivation revealed that the perianths in *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi* are quite similar in shape and texture of their segments. It was also found that the outer segments, in particular, change in shape as the flowers age. The flower buds of *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi* are rather flat, and in profile the outline of the outer segments is more or less circular. After anthesis the outer segments elongate progressively and eventually they become elliptic or even (elliptic)-obovate. In *B. squamulosa*, the outer segments do not change very much after the buds open. *B. pelargoniiflora* is quite distinct from the species mentioned above by its comparatively large and subcordate outer segments.

6.3.2.2. Androecium

6.3.2.2.1. Stamen arrangement

The male flowers of the species treated here have numerous stamens, usually more than 10, which are arranged in a zygomorphic fascicle. Each stamen consists of a terete filament and a well-differentiated basifixed anther. The proximal ends of the collective stamens are connate and together they form a terete solid structure ('trunk'), from which the free distal parts of the filaments variably branch off at different levels. The free parts of the filaments vary in length; they can either be very short, almost absent, or as long as the pertinent anther. The stamens with the short free filaments form the proximal part and those with the long free filaments the other, distal part of the androecium. This arrangement determines the zygomorphic condition of the flower. The proximal part of the androecium is considered here the 'front' of the androecium. Consequently, the androecia depicted in Plates 1 to 6 in Chapter 10, are shown in front, reverse and lateral view.

The front of the androecium always faces the upper large tepal. Moreover, the flower terminating the main inflorescence axis excepted, all the other flowers of the inflorescence are arranged in such a way that their upper large tepals as well as the front of their androecia are in an adaxial position in regard to the main axis of the inflorescence (see Fig. 6-4d). This has been found for all species of which living and/or spirit material was available. In dried material the original arrangement of the flowers within an inflorescence is difficult to assess, but I assume that in the living condition the flower arrangement of *B. pelargoniiflora* and *B. rwandensis* is similar to that of the other species treated here.

6.3.2.2.2. Anther structure

The anthers of the species involved have two equal thecae. The lateral side of each theca is provided with a longitudinal groove that merges into an apical

pore. As both pores of the anther are oriented in a frontal, non-lateral, position on the stamen, the distal parts of the grooves are diverted towards them from their lateral position. The side with the pores is called the 'front' and consequently the opposite side is the 'rear' of the anther. This terminology is applied instead of the terms introrse and extrorse, or adaxial and abaxial dehiscence, which are not sufficiently precise for the *Begonia* species involved, because of the combination of a zygomorphic androecium and a variable anther-pore orientation within the fascicles. Anther-pore orientation will be considered in more detail below.

Previously the anther-dehiscence of *B. squamulosa* has been described by Hallé & Raynal (1966, p. 115) as 'à sutures sublatérales, qui se fendent seulement à la partie supérieure en deux pores'. A similar description in Latin, 'rimis longitudinalibus sed foramine apicali tantum apertis instructae', is given for *B. wilczekiana* (Hallé in Wilczek 1969b, p. 92) and for *B. gladiifolia* (Wilczek 1969b, p. 85). However, Wilczek's French description (1969a, p. 19) of *B. gladiifolia* only states 'déhiscentes par 2 pores apicaux'. In the same publication a similar phrase is used for the anthers of *B. gracilipetiolata*, *B. elaeagnifolia* and *B. squamulosa* (Wilczek 1969a, pp. 20-22). It should be noted that for *B. squamulosa*, Wilczek (op. cit.) does not refer to the sublateral sutures mentioned by Hallé & Raynal (1966) in their emended description of that species. Wilczek apparently failed to notice the apical pores in the material that he used for his emended description of *B. schultzei* (1969b, p. 88 and 1969a, p. 16), as he stated 'rimis longitudinalibus lateralibusque instructae' and 'à déhiscence longitudinale' respectively. His emended description is based on Schultze in Mildbraed 6208 and 6229, and on Van Roeckhoudt 12, that is identified in the present study as a new species, *B. rwandensis*. All three of these collections, in fact, have anthers with apical pores.

The terms 'sutures' and 'rimis' as used by Hallé and Wilczek suggest that these authors thought that the anthers are provided with longitudinal clefts not merely grooves. Wilczek's French translation of the Latin phrase in his emended description of *B. schultzei* (see above) would appear to emphasize this interpretation. In the course of observations of cultivated and dried plants during the past decade, I have never seen anthers that dehisced longitudinally; the pollen grains were invariably released through the apical pores.

The apical pores are not conspicuous in the anthers of dried specimens; the anthers are always shrunken diametrically and when moistened and boiled they do not regain their original shape. Moreover, the pores are more or less hidden by a cap that is formed by the apical parts of the rear and lateral walls of the anther. In order to ascertain that the feature interpreted here as a longitudinal groove is not a cleft of which the rims separate from each other only in the distal part, transverse sections of the stamens of *B. squamulosa*, *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi* were made. The stamens were taken from open flowers with anthers in their final phase of development because changes in stamen structure may occur during the ontogeny of the androecium (e.g. Keijzer, 1983).

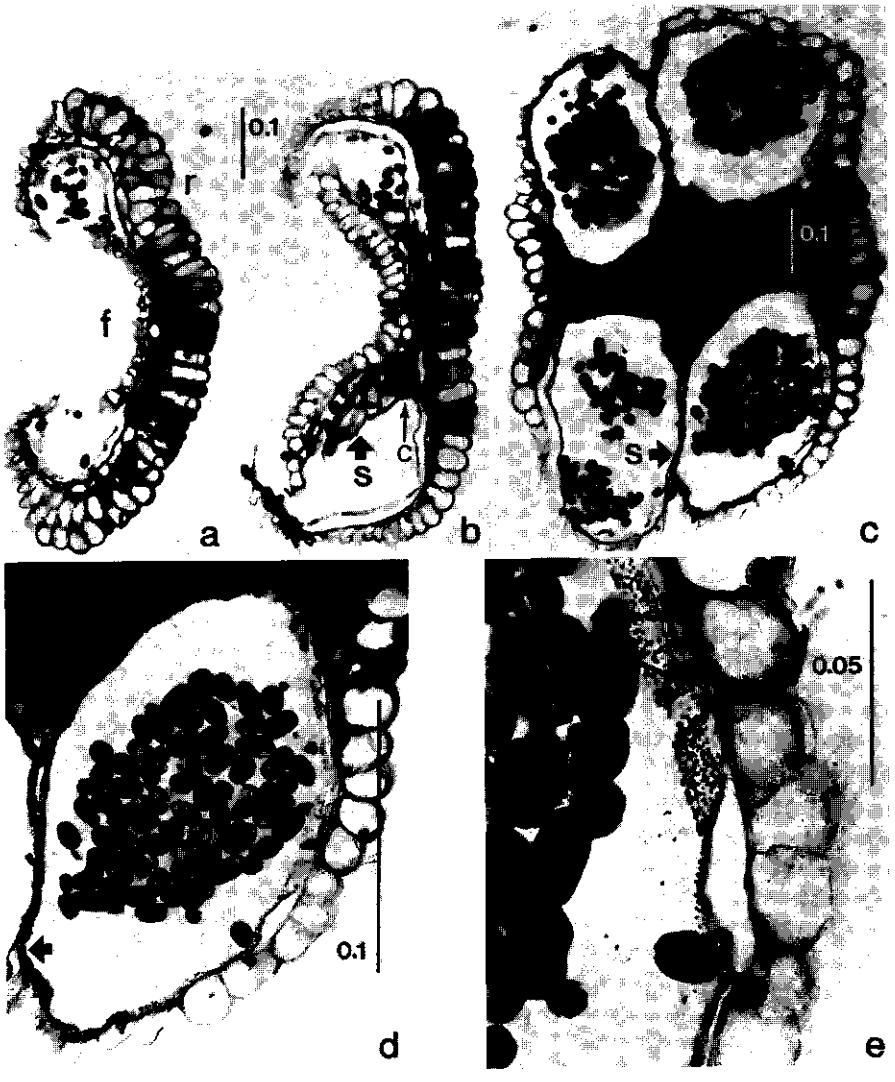


Fig. 6-5: Transverse sections of an anther of *B. longipetiolata*. **a** & **b:** sections through the apex; in **a** the two pores united, in **b** the two pores separated by a 2- or 3-celled layer of connective tissue (c), at s an incomplete parenchymatous separation layer between the two united microsporangia; in **a:** f= front wall, r= rear wall; **c:** section half-way along the anther length, at s degenerated parenchymatous layer, the arrow s indicates the connection between the separation layer and the wall at the groove; **d:** detail of 5c, one microsporangium with more or less ellipsoid pollen grains; **e:** detail of 5d, anther wall. Scales in mm.
Culta De Wilde, Arends & de Bruijn 9270.

The stamen anatomy of *B. longipetiolata* is presented in Fig. 6-5. The anther contains two pairs of microsporangia for most of its length (Fig. 6-5c). The two microsporangia of each pair are separated by a layer of degenerated parenchymatic cells. Except in the apical part of the anther, this separation layer is always connected to the lateral wall of the anther lobe (Fig. 6-5d). The wall of the anther, in particular at the front and rear (Fig. 6-5c), consists of a single layer of thin-walled cells of irregular size. The mature wall of the anther does not show the differentiation into exothecium, endothecium, middle layers and secretory tapetum as described for *Begoniaceae* by Davis (1966, p. 56) and for *B. dichroa* Sprague by Maheswari Devi, Naidu et al. (1982, p. 299). However, according to Bhandari (1984, p. 57), *Begoniaceae* is among those angiosperms whose anthers have a single-layered external covering of the sporangial wall, which may remain intact.

In *B. longipetiolata* and the other species considered here, the wall of the anther mainly consists of the epidermal layer and, locally, of remnants of the other layers (Fig. 6-5e). In the apical part of the anther the separation layer between the two adjacent microsporangia gradually disappears, rendering each lobe of the anther unilocular. The cells of the rear wall are radially slightly more elongated than those found below the apical part of the anther. The photographs in Figs. 6-5a and -5b show that in the apical part of the anther, the connective tissue decreases in number of cell layers, and the front wall of the anther gradually recedes towards the inside of the rear wall. Moreover, the front wall laterally recedes as well, and the apex of the anther is entirely open. Thus it has been established that the anthers are provided with grooves and not with sutures, and that the pollen grains of these species are released through two pores that distally become united.

The section *Tetraphila* has species with longidehiscent anthers as well, e.g. *B. subalpestris* A.DC., a species endemic to Saõ Tomé. Photographs of a cross section of its anther are shown in Figs. 6-6b to -6d. When studied with a dissecting microscope the anther distinctly shows lateral clefts which are open in water so that the pollen grains are visible. It was observed, however, that these clefts were gradually closing during the preparation of the anther in the graded ethanol series before it was embedded in the sectioning medium. The dehisced part of the anther wall is shown in Figs. 6-6b and -6c. The anthers of *B. subalpestris* are characterized by a stomium (Fig. 6-6c). The anther wall consists of a layer of radially elongated epidermal cells and a non-differentiated endothecium (Fig. 6-3d). Moreover, the exothecium also contains cells with wall thickenings. Fig. 6-3d shows that the thickenings are U-shaped and situated on the inner radial and tangential walls of the cells. The connective of the anther is laterally extended and contains towards the vascular bundle parenchymatic cells which are stained dark and most likely contain tannins (Fig. 6-6b). This photograph also shows that the thecae of the anther are unilocular; probably they have become unilocular by degeneration of the separation layer during the development of the stamen.

In conclusion it appears that within the section *Tetraphila* there are at least

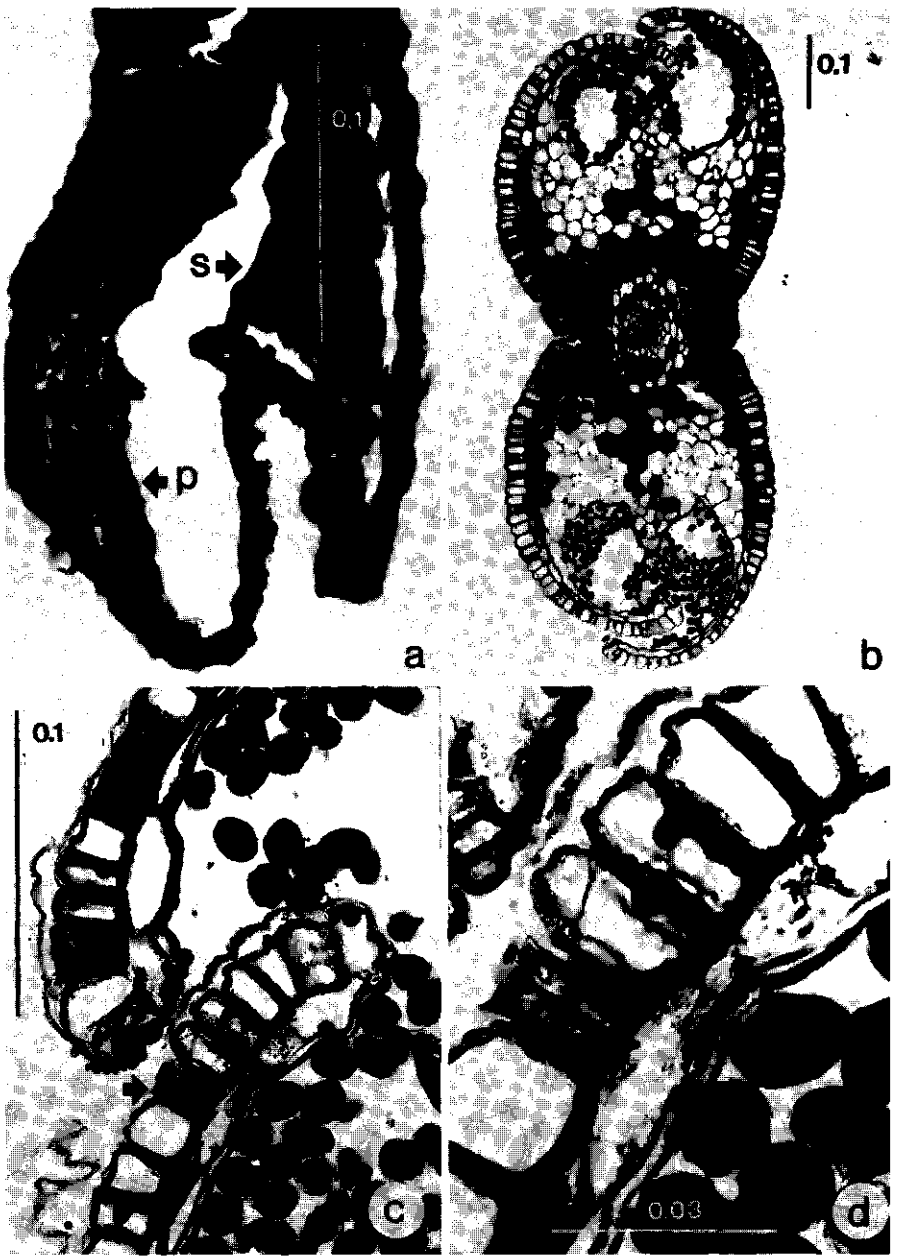


Fig. 6-6: Transverse sections of anthers of *Begonia* species. **a:** *B. pelargoniiflora*, c. 1 mm below the apex of an anther from a dried specimen, the arrow s indicates the separation layer, the arrow p the mass of collapsed and deformed pollen grains (see Chapter 8); **b** to **d:** *B. subalpestris*, c. 0.5 mm below the apex of an anther from spirit material; **b:** the pairs of microsporangia united; **c:** stomium of dehisced anther, arrow indicates an example of cells with thickened wall; **d:** detail of 6c. Scales in mm.

a: Letouzey 14448, Mt. Nlonako, Cameroun (herbarium); **b** to **d:** Groenendijk 137, São Tomé (spirit).

two types of anther dehiscence. One is poricidal and is found in the species treated in the present study. These poricidal anthers are characterized by a permanent separation layer below the apex of the two sporangia. The other anther type dehisces by longitudinal clefts and the sporangia of a pair are united at maturity. The vascular bundle in the connective is amphicribal in both anther types.

Although the anther of *B. pelargoniiflora* was at first considered to be poricidal, this interpretation was not certain until sections were made from a boiled anther of a dried, open flower. Although all cells of the anther are collapsed, Fig. 6-6a shows that the parenchymatous separation layer extends from the connective to the groove and is connected to the lateral anther wall. Because of the poor quality of the study material, the sections of the apical part of the anther are very difficult to interpret. Nevertheless, it appears that the apex is similar to that of the anthers of the other species affiliated with *B. squamulosa* and is indeed poricidal.

Eames (1961, p. 112) stated that anther structure is usually constant within a genus and often throughout a family, so that the finding of two modes of anther-dehiscence within a single section of a genus is interesting. Irmscher, in Engler & Prantl (1925, p. 563) stated that anthers with apical pores occur rarely in *Begonia* and that those with clefts represent the usual situation. Irmscher's (1925, p. 572) drawing of the anther of the monotypic genus *Hillebrandia* shows that it is longidehiscent. It is generally accepted that within *Begoniaceae* this genus is comparatively primitive. The anthers of *B. salaziensis* (Gaud.) Warb., of the African section *Mezierea*, dehisce with longitudinal clefts, and this species is considered to have many primitive character states (De Wilde & Arends, 1989). On the basis of the present evidence therefore it can be postulated that poricidal anther dehiscence represents an advanced character state in African *Begonia*.

6.3.2.2.3. Anther pore orientation

As discussed above (page 68), the apical pores of the anthers are situated on one side of the anther, which is called here the 'front'. It was found that in *B. longipetiolata* and *B. karperi* the front of every anther is oriented in a similar fashion towards the proximal part of the androecium (see Plates 2-10 (p. 192); 3-12, -14 (p. 196), and Hallé & Raynal, 1966). This implies that the pores of the stamens at the front side of the androecium in these species are oriented adaxially in relation to the main axis of the inflorescence. In *B. squamulosa* most of the anther pores have an adaxial orientation also, but the peripheral stamens have their pores oriented towards the 'centre' of the androecium, so that the stamens at the proximal part or front side of the androecium have an abaxial pore orientation in relation to the inflorescence axis. The pore orientation of the stamens at the front side of the androecium of the species involved is summarized in Table 6-1. The pore orientation of the proximal stamens in *B. squamulosa* and B. *longipetiolata* is an additional character in distinguishing these two species. It is not always easy to assess the stamen orientation from dried specimens: large buds provide the best material. In *B. pelargoniiflora* and *B. rwandensis*

Table 6-1. Anther pore orientation in *Begonia* species

		Anther pore orientation of stamens of front side of androecium		
		adaxial	abaxial	variable
B. longipetiolata		+	−	−
B. squamulosa		−	+	−
B. karperi		+	−	−
B. elaeagnifolia	(Crystal Mts)	+	+	+
idem	(Chaillu Mts)	−	+	+
idem	(Doudou Mts)	−	+	+

all stamens have a similar, presumably adaxial, orientation (see Plates 4-4 and 5-8). Table 6-1 shows that *B. elaeagnifolia* is quite variable in this respect.

6.3.2.2.4. Number of stamens and anther length

The information presented in Fig. 6-7 and Table 6-2 demonstrates that the species studied do not have a fixed number of stamens in each male flower. The diagrams in Fig. 6-7 present the frequencies of occurrence of the 'average' number of stamens observed in field gatherings. Only part of the specimens cited in Chapter 10, could be analyzed for their stamens as quite a few of them are sterile or only have fragments of inflorescences. Plants of *B. elaeagnifolia* and *B. karperi* usually have very few inflorescences each carrying not more than one or two flowers. An exact count of stamens always damages or even destroys the androecium, as the anthers have to be separated from each other. Therefore, I have been reluctant to dissect more than one flower from an inflorescence. This also explains why the 'average' number of stamens in the table is always identical to the number actually observed when only a single flower in a specimen has been analyzed. In many dried specimens it was impossible to count the stamens as they remained brittle, tightly packed and inseparable, even after extended boiling and soaking.

In the early phase of the investigation, I supposed that the 2x and 4x plants of *B. squamulosa* from the Crystal Mts in Gabon, now identified as *B. longipetiolata* and *B. squamulosa* respectively, were characterized by different numbers of stamens (Table 6-2). For example, in *B. longipetiolata* three collections, nrs 21, 22 and 23, showed 13, 12, and 25 stamens respectively, whereas in *B. squamulosa*, collection nr. 2, 32 and 35 stamens were found. This was supported by similar counts in both species of the collection De Wilde, Arends et al. (1983), also from the Crystal Mts.

However, when I counted the stamens in collections from Cameroun, I found that plants identified as *B. longipetiolata* had numbers approximately similar to those in the Gabonese collections of *B. squamulosa*. Moreover, it was found that the number of stamens in a single gathering often varied between different inflorescences. In *B. longipetiolata*, nr. 32 from Ekouk, Cameroun, the number varies from 25 to 58, and the nrs 28 and 39, both from Ekekam/Nkol Djobe,

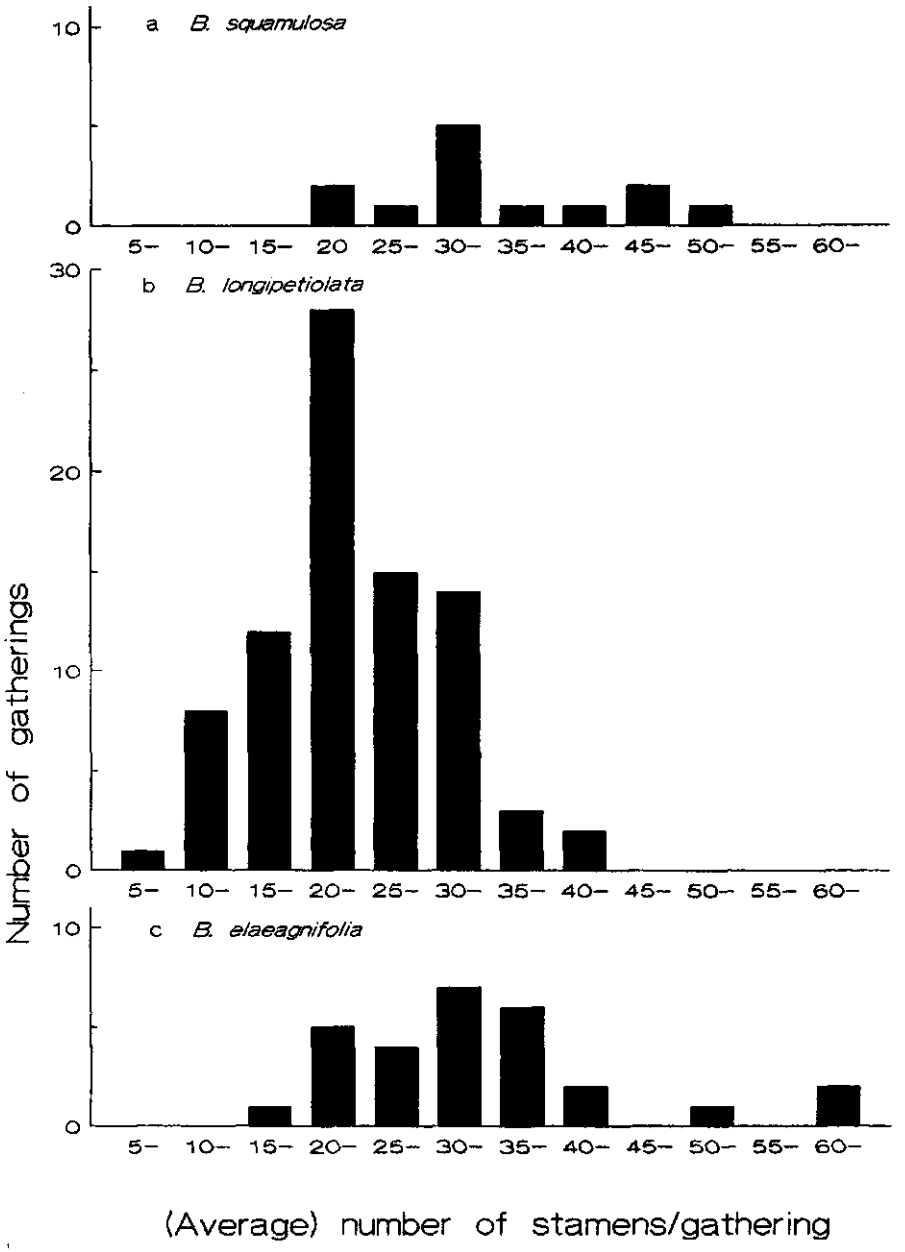


Fig. 6-7: Distribution of stamen numbers in field collections of *Begonia* species.
a: (top): *B. squamulosa*; **b:** *B. longipetiolata*; **c:** *B. elaeagnifolia*.

Table 6-2. Number of stamens and anther length in *Begonia* species.
Figures separated by / are numbers in different inflorescences.
Figures between ( ) are counts by the collector or a previous worker.

		(average) number	anther length (mm)
B. squamulosa			
1. Arends 371	52, 45	49	2.0
-idem, culta	54-67/52-60		
2 .B & W (1978)-355	35, 32	33	2.2
-idem, culta	42, 42/51-91		
3. Christiaensen 1904	20	20	1.8
4. De Wilde 8839	27, 28, 28	28	1.8
5. De Wilde et al. (1983)-100	51	51	2.5
-idem, culta	41-60		
6. De Wilde et al. (1983)-119	46	46	2.0
-idem, culta	48, 59		
7. De Wilde et al. (1983)-181	30, 38, 41, 57	42	2.0
-idem, culta	57, 67		
8. De Wilde et al. (1983)-220	24	24	2.0
9. De Wilde et al. (1983)-288	34	34	2.0
10. Escherich 248	34	34	2,0
11. Lambinon 78-279	28, 31, 32	31	2.0
12. Le Testu 5454	31	31	1.8
13. Mann 1654	35	35 1.7	
B. longipetiolata			
14. Annet 424 31 31 1.3			
15. Barabé 86-99	24	24	1.8
16. Bates 300	36, 38/33, 40/42, 44	40	1.7
17. Bates 594	13	13	1.5
18. Bequaert 6474	17	17	1.4
19. Bos 4070	13	13	
20. Bos 6194	29	29	1.5
21. B & W (1978)-204	13	13	1.8
22. B & W (1978)-323	12	12	1.8
23. B & W (1978)-356	–		
-idem, culta	25	25	
24. B & W (1978)-600	23/22/23/23	23	1.2
25. Breyne 2751	20	20	1.2
26. Cabra 115	33	33	1.6
27. Cambr. Congo Exp. 1959-295	16	16	1.5
28. Dang 655	30	30	1.0
29. Dang 675	40	40	1.0
30. De Wilde, J.J. 7463	22, 23/26	24	1.8
31. De Wilde, J.J. 7538	31, 35/ 27, 29	31	1.6
32. De Wilde, J.J. 7724	25/25/27/28/37/37/ 46/49/55, 58	39	1.6
33. De Wilde, J.J. 8841	21/23, 24, 25	23	1.8
-idem, culta	17-26		
34. De Wilde, J.J. 9270	21/23/25/26	23	1.5
-idem, culta	20-23/33-40/23-37		
35. De Wilde et al. (1983)-156	16	16	

Table 6-2. (continued)

		(average) number	anther length (mm)
36. De Wilde et al. (1983)-180	9, 11/10/13/13/ 12, 12/9, 9	11	1.2
-idem, culta	7-11		
37. De Wilde et al. (1983)-216	7, 9	8	
38. De Wilde et al. (1983)-326	–		
-idem, culta	22		1.5
39. De Wilde et al. (1983)-483	10, 12, 14	12	1.5
-idem, culta	7-17		
40. De Wilde, W.J. 2020	30	30	1.5
-idem, culta	25-40		
41. Elias & S. in Louis 2334	21, 25, 26, 27	25	1.8
42. Elias & S. in Louis 2360	14, 19/22/20/20, 21	19	1.5
43. Evrard 4740	30	30	
44. Goossens 1579	22	22	1.5
45. Hallé 3246	31, 34	32	1.8
46. Hallé 3363	23	23	1.5
47. Hallé 3372	(32), 28	30	1.5
48. Hallé 4011	26	26	1.7
49. Hallé & Villiers 4558	20	20	
50. Hallé & Villiers 5381	(15), 13	14	1.3
51. Jackson in Keay, FHI 46309	27	27	1.5
52. Keay in FHI 37551	24	24	1.3
53. Keay in FHI 37714	25	25	1.2
54. Laurent 1695	28	28	1.8
55. Lebrun 5164	26	26	1.0
56. Lebrun 5595	15	15	1.5
57. Le Testu 5265	30	30	2.2
58. Le Testu 5275	36	36	1.7
59. Le Testu 5409	30, 36	33	1.4
60. Le Testu 5429	21,22	22	1.2
61. Leeuwenberg 9294	20/22	21	1.8
62. Léonard 1605	21	21	1.5
63. Léonard 1664	22	22	1.6
64. Léonard 3916	16	16	1.3
65. Letouzey 4121	35	35	1.5
66. Letouzey 8201	34	34	1.5
67. Letouzey 9005	18, 20, 24	21	1.0
68. Letouzey 9993	22	22	1.2
69. Letouzey 10982	20	20	1.1
70. Letouzey 12704	33	33	1.8
71. Letouzey 12808	31	31	1.4
72. Letouzey 14146	22	22	
73. Letouzey 14450	22	22	1.2
74. Letouzey 14665	19	19	1.2
75. Letouzey 15136	24	24	1.5
76. Ludwigs 600	33/35	34	1.2
77. Mildbraed 5636	22, 25	23	1.9
78. Mildbraed 5925	20	20	1.5
79. Mildbraed 6394	26	26	1.0
80. Onochie in FHI 34803	16	16	1.5
81. Raynal, J. & A. 10349	28	28	1.7

Table 6-2. (continued)

		(average) number	anther length (mm)
82. Reitsma 3246	25, 27	26	1.7
83. Satabié 295	21	21	1.2
84. Schlechter 12918	18	18	1.0
85. Schultze in Mildbraed 6183	24	24	1.0
86. Schultze in Mildbraed 6189	19	19	1.2
87. Thomas 3176	16	16	
88. Thomas 4318	18/19	19	1.5
89. Thomas 5573	21	21	1.5
90. Troupin 2455	11	11	1.0
91. Van Meer 1168	23	23	1.2
92. Villiers 781	23	23	1.4
93. Villiers 1481	25	25	1.0
94. Zenker 3098	24	24	1.2
95. Zenker 3152	23, 28, 30	27	1.5
96. Zenker s.n. (1918)	26	26	1.5
B. elaeagnifolia			
97. Arends 559	61	61	1.5
-idem, culta	61, 52/55/69, 60		
98. Arends 571	–		
-idem, culta	36	36	
99. Arends 670	23	23	1.3
100. Arends 681	35/36	36	1.0
-idem, culta 32/34	33		
101. B & W (1978) -8	36/39	36	1.5
-idem, culta	22/36/38/40/45		
102. B & W (1978) -38	31	31	1.3
103. B & W (1978) -276	21		21
104. B & W (1978) -381	33/28	31	1.5
105. Breteler 8248	60	60	1.2
-idem, culta	36, 30/ 41/46/42, 36	36	
106. De Wilde, J.J. 9127	19	19	
-idem, culta	24, 26/25, 23		
107. De Wilde, J.J. 9638	35, 36, 35/40, 38	36	1.2
-idem, culta	30, 26/45, 45/40, 35		
108. De Wilde et al. (1983)-31	34	34	1.8
109. De Wilde et al. (1983)-35	24	24	1.9
110. De Wilde et al. (1983)-43	29	29	1.5
111. De Wilde et al. (1983)-179	38, 30	34	1.3
-idem, culta	32, 28/36, 23/52, 40		
112. De Wilde et al. (1983)-262	42	42	1.6
113. Hallé & Villiers 4531	31	31	
114. Hallé & Villiers 4560	35/(50)	42	1.2
115. Hallé & Villiers 5374	(54)	(54)	
116. Letouzey 12765	24	24	1.3
117. Louis, A.M. 1267	38	38	1.5
118. Mann 1651	(c. 25)	(25)	1.2
119. Reitsma 1958	30	30	1.2
-idem, culta	31, 29, 30/26/29/32/38		
120. Sanford 5860	28	28	1.3

Table 6-2. (continued)

		(average) number	anther length (mm)
121. Satabié & Letouzey 343	16/24	20	1.0
122. Schultze in Mildbraed 6229	c. 25	25	
B. karperi			
123. B & W (1978)-335	–		
-idem, culta	40, 38/45, 39/57, 41		
124. De Wilde et al. (1983)-158	47	47	1.5
125. Hallé & Villiers 4885	45	45	1.5
B. rwandensis			
126. Auquier 3360	22	22	3.0
127. Bouxin 257	20, 24/22	22	2.8
128. Bridson 380	c.18	18	
129. Van Roeckhoudt 12	18, 20, 22	20	

Cameroun, have 30 and 40 stamens respectively. In *B. longipetiolata* from Bélinga, Gabon, average numbers of 19 to 32 were found, whereas in *B. elaeagnifolia* from the Crystal Mts, Gabon, the number of stamens ranged from 21 to 54. Thus different individuals in a single topodeme or in a population, probably comprising several topodemes, may differ in number of stamens. Hallé counted 50 stamens in nr. 114, but I found 35 in another flower of the same specimen. Obviously, stamen number is not always uniform. On the other hand, the numbers found in *B. karperi* indicate that it may be constant in that species.

If plants from a wild population are taken into cultivation, the number of stamens may increase. This phenomenon is clearly illustrated in *B. squamulosa* nrs 2 and 7, and in *B. longipetiolata* nr. 34. However, nr. 105 of *B. elaeagnifolia* illustrates that the opposite, a decrease in number of stamens in cultivated compared with wild plants, may also occur.

The number of stamens may vary in different flowers in a single inflorescence. In cultivated *B. elaeagnifolia* the terminal flower usually has more stamens than the lateral ones. In *B. squamulosa* and *B. longipetiolata* some inflorescences were found with a fairly constant number of stamens, but here some lateral flowers often have a higher number than in the terminal flower on the main axis.

The data in Fig. 6-7 show a considerable overlap in the numbers of stamens of *B. squamulosa*, *B. longipetiolata* and *B. elaeagnifolia*. The frequencies in *B. longipetiolata* (Fig. 6-7b) suggest that the number of stamens in this species have a normal distribution culminating in a stamen number of 20 to 25. Very few collections of *B. squamulosa* were available but the counts (Fig. 6-7a) suggest a tentative peak at 30 to 35. As shown in the diagram (Fig. 6-7c) most of the collections of *B. elaeagnifolia* have a stamen number ranging from 20 to 40. The number of stamens found in the two field collections of *B. karperi* is approximately 46 and this is almost equal to that found in several collections of *B.*

elaeagnifolia. The number of stamens found in *B. rwandensis* ranges from 18 to 22 and that in *B. pelargoniiflora* from 16 to 28 (see species description, Chapter 10). It is clear that the number of stamens is not a useful character for species delimitation, although certain tendencies in specific stamen numbers can be discerned.

The length of the anther is variable as is evident from the measurements shown in the last column of Table 6-2. *B. rwandensis* and *B. pelargoniiflora* have anthers which are distinctly longer than those of the other species, c. 3.0 mm and 4 mm long respectively. The anthers of *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi* cannot be distinguished on the basis of their length or size. The very similar species *B. squamulosa* and *B. longipetiolata* differ only slightly in anther length.

6.4. Female inflorescences and flowers

6.4.1. Female inflorescences

The few female elements available on dried specimens were found to be rather difficult to analyse. Thus the interpretation of the female inflorescences of *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa*, is mainly based on observations of cultivated plants. Nevertheless, the observations on the structure of the female inflorescences, which are discussed in the following paragraphs, are in line with what can be detected in some of the field collections.

Usually, the female inflorescences in cultivated plants of the species mentioned above are single-flowered. *B. karperi* very rarely produced more than one flower, but some plants of the other species regularly had two or even three flowers in an inflorescence. This applies to e.g. *B. squamulosa* from the Chaillu Mts, Gabon (coll. Arends, De Wilde & Louis 371). In contrast, plants of *B. squamulosa* from the Crystal Mts, Gabon, always produced single-flowered inflorescences.

In *B. longipetiolata*, De Wilde, Arends et al.(1983)-s.n. (voucher Van Veldhuizen 988), from Cocobeach, Gabon, 2-flowered inflorescences were occasionally observed. The accessions De Wilde, Arends et al.(1983)-326 and -483, from the Chaillu Mts, Gabon, regularly had 2- but also 3-flowered inflorescences. Also in *B. longipetiolata*, the cultivated specimen of the gathering De Wilde, Arends et al. 10037 from the Crystal Mts, Gabon, usually had 2- or 3-flowered inflorescences, but very recently this introduction produced a single inflorescence with four flowers. Cultivated plants of *B. elaeagnifolia* often produced 2-flowered inflorescences but never 3-flowered ones. Optimal growth conditions apparently promote the development of more flowers per inflorescence, because the 2- or 3-flowered inflorescences are usually produced on exuberant plants cultivated in peat substrate. However, the plant of *B. elaeagnifolia* (culta De Wilde, Arends et al. (1983)-179) that was cultivated on a tree-fern slab and consequently remained comparatively small, also produced 2-flowered female infloresescences.

At the time of its introduction, the living plant of *B. elaeagnifolia* in the gathering De Wilde & Jongkind 9638, from the Chaillu Mts, Gabon, had several young female inflorescences, and these continued their development in cultivation. Anthesis occurred within two to three weeks, and the majority of the inflorescences were 2-flowered. One of these 2-flowered female inflorescences is shown in Fig. 6-8b. Afterwards, the plant produced a branch carrying four single-flowered inflorescences on subsequent nodes.

The inflorescence of a cultivated specimen of *B. squamulosa* shown in Fig. 6-8a is 2-flowered, but, initially, it carried a third bud that did not continue its development and eventually aborted.

Except for Hallé & Villiers 5381, the type of *B. nicolai-hallei*, plants with 2-flowered inflorescences have not been found among the field collections. However, infructescences with two fruits were found in *B. elaeagnifolia* (De Wilde, Arends et al.(1983)-262), in *B. longipetiolata* (De Wilde 7724 and Laurent 1702) and in *B. squamulosa* (Lambinon 78-279). The infructescence of Lambinon 78-279 has next to two well-developed fruits even a third one that is smaller and apparently abortive.

In *B. squamulosa*, bracts are usually present at the main axis (Fig. 6-8a and Plate 6-10, -16 and -17, p. 211), but those of the lateral axes are much smaller, vestigial or even absent. Sometimes, a single-flowered female inflorescence represents the terminal flower on a lateral axis, because a single small bract, or less frequently, a pair of these bracts may be inserted above the comparatively large bract(s) on the main axis. In the other species bracts are often absent (Fig. 6-8b). However, a three-flowered inflorescence of *B. longipetiolata*, culta De Wilde, Arends et al.(1983)-483, had, in addition to inconspicuous bracts on the main axis, two vestigial bracts on one of the lateral axes, while on the other

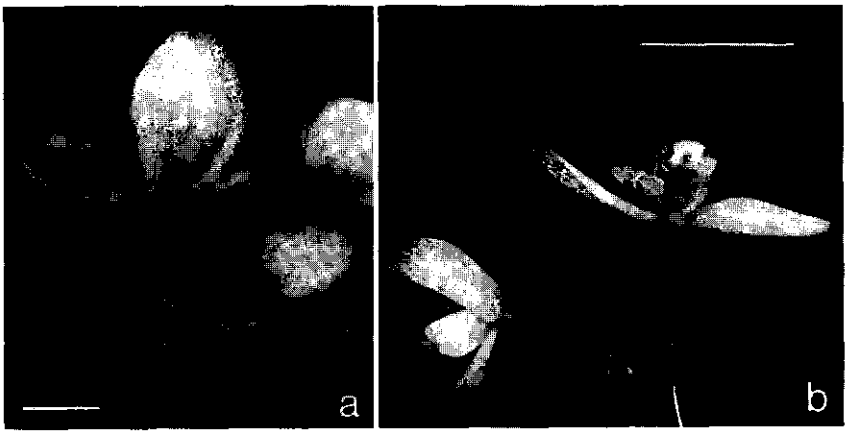


Fig. 6-8: Two-flowered female inflorescences in *Begonia* species. **a:** *B. squamulosa*, culta Arends, De Wilde & Louis 371; **b:** *B. elaeagnifolia*, culta De Wilde & Jongkind 9638, two weeks after its introduction. Scales represent 1 cm.

axis such structures were absent.

The fully developed female inflorescence of *B. rwandensis* shown in Plate 5-4 (page 208) is the only one available to date. The flower in this inflorescence from Bridson 380 is interpreted as the terminal flower on a lateral axis, because in Bouxin 164 I found some young 3-flowered inflorescences with one lateral axis that is more developed than the other lateral axis (Plate 5-2, -3). This observation suggests that the female inflorescence of *B. rwandensis* may be a three-flowered dichasium that becomes modified to form a monochasium. In this species all the axes are provided with bracts.

These observations suggest that the single- or 2-flowered female inflorescences in the species mentioned above may have evolved through reduction of an originally 3-flowered dichasium that, in its turn, was derived from a more than 3-flowered inflorescence. This postulate is further supported by observations on species of the section *Tetraphila* which are not treated here (De Wilde, pers. comm.).

All the axes, including the main one, in the female inflorescences in all the species mentioned above are usually quite short, and actually, they are frequently so much reduced in length that they seem to be absent. Consequently, especially in single-flowered inflorescences, the female flower appears to be inserted directly on the node that bears the inflorescence. In such a situation, only the presence of up to four, often vestigial, bracts near the pedicel and/or the base of the ovary indicates that the apparently sessile flower is part of a very much reduced inflorescence.

In the female inflorescence of *B. pelargoniiflora* however, the flowers are situated well away from the stem, because the main inflorescence axis is comparatively long. Within the section *Tetraphila* the presence of an elongated main axis is interpreted as a primitive character state. The female inflorescence is many-flowered, as it contains at least 7 flowers. Within the section a many-flowered inflorescence most likely also represents a primitive character state. According to Van den Berg (1984), *B. pelargoniiflora* is characterized by a pollen-type that is more primitive than the pollen-types in the other species studied. Thus, the above mentioned character states suggest that *B. pelargoniiflora* is the most primitive taxon of the species dealt with here.

6.4.2. Female flowers

6.4.2.1. The perianth

The perianth of the female flower is similar to that of the male flower. However, when female and male flowers occur simultaneously on the same plant, the perianth segments of the female flower are usually larger than those of the male flower. The perianth segments of *Begonia* have been designated in various ways (see e.g. Barabé, 1980). Except for their size, the segments are quite similar and consequently, they can be designated simply as tepals. However, according to their vascular anatomy, the outer segments are homologous with sepals and the inner ones with petals (see p. 142).

6.4.2.2. Style and stigma

The two-armed style and the horse shoe-shaped stigma are characteristic for the species treated in this study. Initially, I suspected the degree of coiling of the stigmatic band around the style arms to be of diagnostic value. For example, in cultivated plants of *B. squamulosa* the band is often coiled twice, whereas *B. longipetiolata* frequently shows only a single coil. Cultivated plants of *B. elaeagnifolia* from the Crystal Mts, Gabon, usually have one complete coil as well. However, when living specimens of *B. elaeagnifolia* collected from the Chaillu Mts, Gabon, (Arends, De Wilde & Louis 571) produced their first female flowers, each end of the stigmatic band showed two coils. Although it was found that the stigmatic band in the plants from the Chaillu Mts has the tendency to twist a little further as compared to that in the plants from the Crystal Mts, the number of coils in *B. elaeagnifolia* was found to be variable. In cultivated plants which may produce comparatively large flowers, the styles tend to increase in length and such styles are often provided with stigmatic tissue that twists twice around the distal part of the style arms. Similarly, in *B. longipetiolata* it was found that the stigmatic band may coil once to almost twice, even within a single field collection (Plate 3-21 and -22, page 196). In comparatively small cultivated specimens of *B. squamulosa* the female flowers are usually small, and in such small flowers there usually is only a single coil.

The stigmatic surface of the species studied consists entirely of bottle-shaped capitate glandular cells (Fig. 6-9a). The stigmatic surfaces seen in the present study can be assigned to group b as distinguished by Baranov (1977, p.285).

Except for the stigmatic surface the remainder of the style is smooth in *B. squamulosa*, *B. elaeagnifolia* and *B. karperi* (Figs. 6-9b & c). However, in *B. longipetiolata* it is more or less papillose. This is demonstrated in Figs. 6-9d to f for three gatherings from widely separated localities in its geographical range. There is no indication that these papillose cells are secretory.

In cultivated plants of *B. squamulosa*, the styles below the arms are usually provided with a few, 1 to 6, dentate scales. These have been found in the few female flowers available in field collections as well (Plate 6-11, page 211).

6.4.2.3. Number of styles

The number of styles seen in the species studied ranges from 2 to 5 and is without conclusive diagnostic value.

In herbarium material of *B. longipetiolata* 4 styles are usually present. However, in Bos 6194 individual flowers with 2, 3 and 4 styles respectively were found. In Hallé & Villiers 5831, all female flowers have 3 styles and Laurent 1702 probably has 3 styles also.

Cultivated plants of *B. longipetiolata* usually produce flowers with 4 styles. Two different gatherings from the same site near Mouyanama in the Chaillu Mts, Gabon, showed that the number of styles may vary within a single topodeme. The gathering De Wilde, Arends et al. (1983)-326 produced flowers with 4 styles, while the other gathering, De Wilde, Arends et al. (1983)-483, usually had flowers with 2 or 3, but rarely 4 styles. Sometimes, the latter gathering pro-

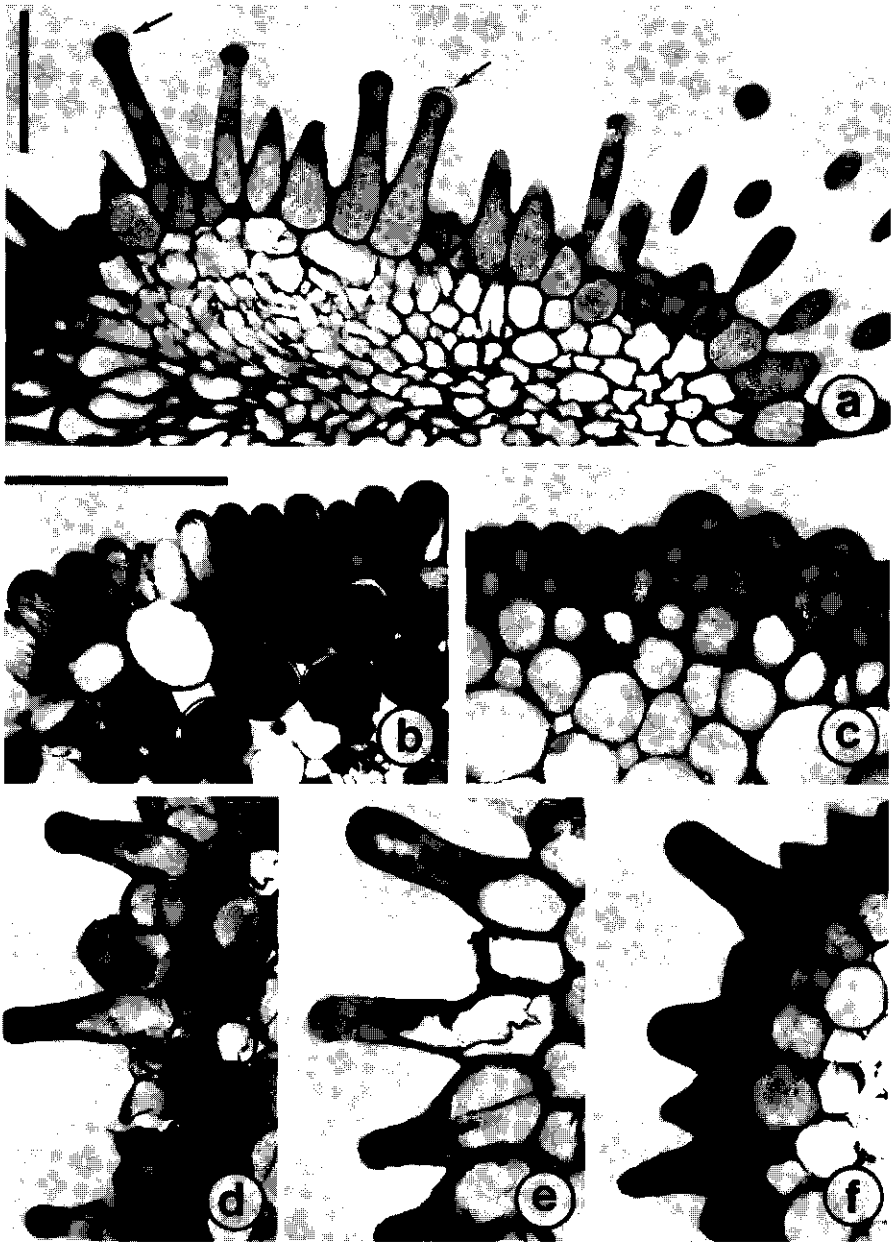


Fig. 6-9: Segments of styles in *Begonia* species (TS). **a:** *B. elaeagnifolia*, apex of one style arm with secretory stigmatic cells, the arrows indicate the fluid on the top of some of these cells; **b** to **f:** surface of styles below the style arms; **b:** *B. elaeagnifolia*; **c:** *B. squamulosa*; **d, e & f:** *B. longipetiolata*. Scales represent 100 µm, **b** to **f** at a similar magnification.
a: culta De Wilde, Arends et al.(1983)-179; **b:** De Wilde & Jongkind 9638, Chaillu Mts, Gabon; **c:** culta Arends, de Wilde & Louis 371; **d:** De Wilde 7724, Ekouk, Cameroun; **e:** Elias & Sterck in Louis 2334, Bélinga, Gabon; **f:** De Wilde, Arends & de Bruijn 9270, Doussa river, Gabon.

duced a 2-flowered inflorescence. In that case the terminal flower had 3 and the lateral one 2 styles. Recently, it produced a 3-flowered inflorescence with the terminal flower having 3, and the lateral flowers 2 and 4 styles respectively. Plant T1616 of *B. longipetiolata*, coll. De Wilde, Arends et al (1983)-s.n., voucher Van Veldhuizen 988, was collected in North-Western Gabon. In cultivation it often had 4 styles, but during one flowering it produced three inflorescences. Two of these inflorescences were single-flowered, the flowers containing 3 and 4 styles respectively. The third inflorescence that was 2-flowered, had 5 styles in its terminal flower, while the lateral flower had 4 styles. It should be noted that plants with less than 4 styles do not belong to a particular population, but have been collected in different localities in the species range. Similarly, *B. squamulosa* usually has flowers with four styles, but flowers with five styles may be regularly produced by exuberant specimens. Rarely a flower had three styles.

Cultivated plants of *B. elaeagnifolia* from the Crystal Mts in Gabon have produced flowers with either 2 or 3 styles but never 4. The female inflorescence in this species is often 2-flowered and it was found that in a 2-flowered inflorescence the terminal flower may have 3 styles, while the lateral one has only 2. Therefore, early in my study I thought that *B. elaeagnifolia* could be distinguished from both *B. longipetiolata* and *B. squamulosa* by the number of styles, as these species usually have 4 styles.

The first living accession of *B. elaeagnifolia* from the Chaillu Mts in Gabon showed 2 styles. This plant of Louis, Breteler & de Bruijn 1267 was collected near Waka in 1983. In 1984 the species was found again in the Chaillu Mts, between Mouila and Yeno. In the field, the plants from that locality (Arends, De Wilde & Louis 559 and 571) did not have female flowers, but in cultivation they produced female flowers with 4 styles. Except for the smooth style surface, such flowers cannot be distinguished from those of *B. longipetiolata*. More recent accessions from the same locality between Mouila and Yeno (Breteler, Lemmens & Djabi 8248 and De Wilde & Jongkind 9638) usually produced 4 styles also, although some flowers had 3 styles. At one flowering, the latest introduction (De Wilde & Jongkind 9638) carried four single-flowered inflorescences simultaneously. Two flowers had 4, and the other two 3 and 5 styles respectively. All the gatherings of *B. elaeagnifolia* from the Doudou Mts in Gabon, produced female flowers with 2 or 3 styles.

Of *B. karperi*, Breteler & De Wilde (1978)-335 usually showed 3, and occasionally 4 styles. However, another gathering from the same topodeme near Mela in the Crystal Mts, Gabon (De Wilde, Arends et al.(1983)-158), regularly produced 2, sometimes 3, but never 4 styles.

All these examples demonstrate that style number is not a constant specific character, although the number in both *B. longipetiolata* and *B. squamulosa* in general is 4. In *B. elaeagnifolia*, plants from the Crystal and the Doudou Mts have 2 or 3 styles, while those from the Chaillu Mts usually have 3 or 4. In *B. karperi* the style number ranges from 2 to 4. The finding that in *Begonia*, the number of styles may vary within a species or even within a single individual

is not new. Barabé (1981, p. 820) showed that in *B. handelii* Irmsch., the style number usually is 4, but in some flowers he observed 5 styles.

6.4.2.4. The ovary and its placentation

6.4.2.4.1. Introduction

In the species studied, the fusiform ovary is usually more or less curved and tapers gradually into the pedicel. The exact point of transition between the solid pedicel and the multilocular base of the ovary can be determined by making a series of transverse sections of this part of the flower. The first sections with cavities indicate the point of transition between the pedicel and the ovary (see also page 101).

In two- or three-flowered female inflorescences the ovary and the pedicel of the terminal flower are usually similar to those of a lateral flower except in *B. longipetiolata*, where ovary and pedicel of the terminal flower are usually longer than those of a lateral flower (Plate 3-19, page 196).

The morphology and placentation of the ovary have always been considered to be important characters in taxonomical studies of *Begoniaceae*. For example, Warburg (1894, pp. 136-139) used various features of the ovary in the delimitation of the sections he recognized in *Begonia*. More recently, Reitsma (1983) and De Wilde & Arends (1989) proposed models for the evolution of placentation types. These models are in line with the interpretation of Gauthier (1959) that, in *Begoniaceae*, the parietal condition is the primitive character state and the axile condition is derived.

6.4.2.4.2. The nature of the ovary in *Begoniaceae*; literature review

In the past, several morphologists, viz.: Saunders (1925), Bugnon (1926) and Gauthier (1950, 1959) dealt with the nature of the ovary in the *Begoniaceae*. These authors based their conclusions, which are contradictory, on the interpretation of the vascular anatomy of the female flower. In the present study the vascularisation of the female flower of *B. elaeagnifolia*, *B. longipetiolata* and *B. squamulosa* is discussed in Chapter 7.

Saunders (1925, p. 183) investigated the flower of *B. corallina* Carrière of section *Gaerdtia*. She concluded that no axial tissue can envelop the ovary and that her observations adduced definite proof that the ovary wall in *Begonia* is exclusively foliar. According to her interpretation the wall is formed by concrescence of different foliar whorls. On the other hand, Bugnon (1926) who studied the flower of *B. x duchartrei* Haage & Schmidt, a hybrid taxon within the section *Huszia*, concluded that the ovary wall is exclusively axial. According to Bugnon, the ovary in *Begonia* is a cup-shaped floral receptacle with the carpels inserted on its rim and extending downwards into the receptacular cavity.

Gauthier (1950) studied the flowers of five *Begonia* species, including the African species *B. dregei* Otto & Dietr. and *B. socotrana* Hook. f. (both of the section *Augustia*) and reported that the vascularisation of the ovary shows a foliar pattern. He concluded that the perianth is adnate to the ovary which implies that

the ovary is entirely formed by appendicular organs. Gauthier's interpretation was based on the fact that the longitudinal vascular traces in the ovary wall ramify at the very top of the ovary where the perianth segments are inserted. The longitudinal traces continue into the styles, but their branches leave the ovary and dissipate into the perianth segments. Consequently, the longitudinal traces in the ovary wall are considered to be compound vascular bundles formed by both carpel and perianth bundles which are intimately fused. Thus, according to Gauthier the ovary wall in *Begonia* is foliar.

Soon after Gauthier's (1950) publication, Bugnon & Bugnon (1953) attempted to show that the arguments of Gauthier were based on ill-founded hypotheses and they reiterated the view that the ovary wall in *Begonia* is axial. The contradictory interpretations of Bugnon and Gauthier were discussed by Douglas (1957, p. 14) in her review of the literature dealing with the inferior ovary. She concluded that Gauthier's detailed study showed that the interpretation of classical morphology can be retained and stated that the *Begonia* ovary is appendicular and is composed of carpels which are congenitally united with the floral tube. Douglas (op. cit., p. 16) rejected the interpretation of Bugnon.

A few years later, Gauthier (1959) published his account of the vascular anatomy of the female flower of *Hillebrandia sandwicensis* Oliv., which belongs to a monotypic genus in *Begoniaceae* and, among other features, differs from *Begonia* by its semi-inferior ovary. His observations corroborated his previous conclusion that the ovary in *Begoniaceae* is appendicular. The recent studies of Lecocq (1977), Barabé (1981), Barabé & Chrétien (1983) and Barabé, Brouillet & Bertrand (1985) also support Gauthier's interpretation of the inferior *Begonia* ovary.

Gauthier's (1950) drawings of transverse sections of the ovary demonstrate that the placentation in the *Begonia* species he investigated is axile, because the placentae are situated along the central axis in the multilocular compound ovary. However, it should be noted that Gauthier (op. cit., p. 21) stated that in *B. dregei* 'The carpels are incompletely united at the center of the flower; this structural condition is due to the fact that the margin of each carpel is fused with that of the adjacent carpel more intimately than with the other margin of the same carpel. An exaggeration of this opening would bring about a one-celled ovary with parietal placentation, as in the section *Mezierea* of the genus *Begonia*'. Douglas (op. cit., p. 15) who summarized the conclusions of Gauthier in her review, wrote 'The unilocular condition and the parietal placentation in the upper part of the ovary in some forms is made possible by the union in pairs of ventrals belonging to adjacent carpels'.

The lower part of the ovary in *Hillebrandia* is multilocular, but the upper part is unilocular. While the placentation in the multilocular lower part is axile, it is distinctly parietal in the unilocular upper part, because the placentae in that part are situated on intruding partitions of the compound ovary (see the illustrations in Gauthier 1959). Thus, the ovary of *Hillebrandia* is characterized by both an axile and a parietal placentation. Logically, Gauthier compared the placentation in *Hillebrandia* with that in *Begonia* and in respect of the latter

genus he explicitly stated 'Au niveau où les loges communiquent entre elles, les carpelles des *Begonia* sont unis latéralement, mais les deux marges de chaque carpelle ne sont pas soudeés. Il suffirait d'agrandir vers le bas et de prolonger vers le haut cette ouverture, et l'on obtiendrait la condition qui prévaut dans l'*Hillebrandia*' (see Gauthier 1959, p. 77). It is evident that Gauthier had the strong feeling that the placentation in *Begonia* and *Hillebrandia* is basically similar.

Gauthier (op. cit., p. 83) stated that the placentation in *Hillebrandia* is fundamentally parietal and he postulated that the axile placentation in the lower part of the ovary is in fact '*pseudo-axile*'. This terminology is a translation into French of the term '*falsely axile*' which was introduced by Parkin (1955, p. 54) who stated 'placentae parietally situated may grow inwards and more or less cohere at the centre, thus making the ovary again as it were plurilocular'. Parkin's statement is in accordance with the idea of Puri (1952, p. 608) who explained the multilocular condition in an actually parietal placentation 'by assuming the septum as being formed by inward extension of the two placentae themselves and not by the carpellary margins'. Puri (op. cit., p. 609) also stated that he 'was inclined to believe that a multilocular condition of this type, brought about by fusion of the placentae and not of the carpellary margins, is more common than has been realized hitherto'.

It appears that Gauthier's interpretation of the axile placentation in *Begoniaceae*, which is based on the ideas of Puri, was generally accepted. For example, Melchior et al. (1964, p. 339) stated that the ovary in *Begonia* is multilocular ('fächerig') as a result of strong fusion of the placentae. Lanjouw et al. (1968, p. 181) and Stoffers et al. (1982, p. 165) described the ovary in *Begonia* as multilocular and *pseudo*-multilocular respectively, because of inward growth of the placentae. However, Hutchinson (1969, p. 226 and 1973, p. 301) only stated that the placentation is axile.

Reitsma (1983) studied the placentation in 53 African species of *Begonia*. He classified these species into two main groups according to their placentation type. Reitsma's first main group comprises species with both pseudo-axile and parietal placentation in a single ovary, a condition which is similar to that in *Hillebrandia* (Reitsma op. cit., pp 31, 48). He postulated that the septa in the lower and multilocular part of the ovary consist of both carpellary and, towards the axis of the ovary, of placental tissue (Reitsma op. cit., pp 31, 40).

Reitsma's second main group comprises species with a 'real axile' placentation (op. cit., pp 49, 50). This *real* axile condition – as opposed to the *pseudo* axile condition in the other group – is, according to Reitsma, explained by the fact that the margins of the same carpel are fused, while the sides of each carpel are fused with those of the adjacent carpels up to the centre of the ovary. As a consequence, Reitsma interpreted the septa and the placenta-bearing centre of the ovary to consist entirely of carpellary tissue (Reitsma op. cit., pp 30, 49, 50 and figs. 2f-2h).

It is obvious that Reitsma's separation of the two species groups depends on the interpretation of carpel fusion. In the first group the margins of different,

adjacent carpels are fused, whereas in the second group the fused margins belong to a single carpel that is folded in a conduplicate or involute manner. Reitsma's species group with 'real axile' placentation includes *B. dregei* and *B. socotrana* which were also studied by Gauthier (1950). It now appears that Reitsma overlooked the statements of Gauthier (op. cit.) and Douglas (1957) which are cited above (page 86). The statements of these authors deal with both the fusion of the margins and the union of the ventral vascular bundles of adjacent carpels which, according to them, account for a unilocular and parietal condition in the top of the ovary with an otherwise axile (or, *sensu* Reitsma 'real axile') placentation. Moreover, Reitsma did not, apparently, consider the possibility that the multilocular condition in his 'real axile' placentation species could also be caused by inward growth and fusion of parietal placentae. Other authors, such as Melchior (1962), Lanjouw (1964) and Stoffers (1982), considered fusion of the placentae to account for the axile placentation in *Begonia*.

The conclusions of all the authors cited above are based on the study of mature flowers. These conclusions are occasionally controversial because the authors interpreted similar features of the flower in different ways. Very recently, new light has been shed on the problem of the ovary in *Begoniaceae* by Charpentier, Brouillet & Barabé (1989a and 1989b) who studied the ontogeny of the female flower of two *Begonia* species and *Hillebrandia sandwicensis*. The first paper of Charpentier et al. (1989a) deals with the flower of *B. horticola* Irmsch. in section *Tetraphila*. The mature flower very much resembles that of the species treated in the present study. The fusiform ovary of that species is four-locular with an axile (or pseudo-axile *sensu* Reitsma) placentation in its lower part, whereas it is unilocular with a parietal placentation in its upper part.

Charpentier et al. found that the multilocular condition and the axile placentation in the lower part of the ovary is due to the development of tissue initiated by a meristem of the floral apex that has an axial position in the base of the young ovary. Simultaneously with the development of this axial tissue, there is also tissue development at a higher level of the young ovary. The tissue at the higher level is initiated by four similar meristems which are situated on the wall of the ovarial cavity. Each one of these parietal meristems produces a longitudinal ridge. During the subsequent development of the flower, these four ridges remain free from each other, but each individual ridge forms a double placenta that carries ovules at anthesis. These placentae-bearing ridges in the unilocular upper part of the mature ovary were designated by Charpentier et al. (1989b, p. 3632) as 'parietal septa', whereas they designated the partitions in the multilocular lower part of the ovary as 'axile septa'. Thus simultaneous growth, initiated by different meristems which are either axial or parietal, accounts for a placentation which is axile in the lower part and parietal in the upper part of the mature ovary of *B. horticola*.

Charpentier et al. distinguished an axile and a parietal zone in the ovary which are initiated very early in the ontogeny of the flower of this species. These zones can already be discerned in the young ovary, but cannot be delimited precisely from each other as there is a transition zone between them (Charpentier et al.

1989a, fig. 24). The authors found it difficult to determine whether the cells of the transition zone originate from the floral apex or from the ovary wall (Charpentier et al. 1989b, p. 3632).

The ovary of the mature flower of *B. dregei* is apparently three-locular over its entire length and is characterized by an axile (or 'real axile' *sensu* Reitsma, 1983) placentation.

Charpentier et al. (1989b) found that the ontogeny of the flower of *B. dregei* is basically similar to that of *B. horticola* described above. As in *B. horticola*, the placentation in *B. dregei* is also determined by an apical or axial meristem situated in the base of the young ovary and, at a higher level, several (in *B. dregei* three) parietal meristems on the wall of the ovarial cavity. In fact, during a certain phase of their ontogeny the ovaries of *B. dregei* and *B. horticola* are very similar. The young ovary in both species consists of both an axile zone and a parietal zone which are separated from each other by a transition zone (compare fig. 14 in Charpentier 1989b with fig. 24 in Charpentier 1989a). The subsequent development of the ovary of *B. dregei* is determined by the elongation of the axile zone which becomes much more developed than that of the parietal zone. Moreover, in contrast with *B. horticola*, the longitudinal ridges on the wall of the parietal zone of *B. dregei* do not form placentae or ovules (Charpentier 1989b, p. 3632). Thus, the preponderant growth of the axile zone in combination with the absence of placenta and ovule formation in the parietal zone accounts for the fact that the mature ovary of *B. dregei* shows an axile placentation for almost its entire length. It is now clear that Gauthier (1950) was correct in his interpretation that the very apex of the ovary of *B. dregei* is unilocular (see above, page 86).

The ontogeny of the semi-inferior ovary of *Hillebrandia* is basically similar to that of *Begonia* (Charpentier et al. 1989b, p. 3634). In *Hillebrandia*, the part of the mature ovary above the insertion of the perianth segments is formed by growth initiated at a meristematic rim which is situated just above the perianth primordia in the young flower. Charpentier et al. (1989b, p. 3634) found that in *B. dregei* a similar rim is present, but here it does not develop. The mature ovary in *Hillebrandia* differs by its 'open' apex from that in *Begonia*, because the apex in the *Begonia* species they investigated is 'closed'. However, Charpentier et al. found that during a certain phase of its development the young ovary of *Begonia* is also open.

Depending on the comparative growth rate of the axile and the parietal zones in the young ovary, the mature ovary in *Begoniaceae* is axile either over its entire length or in its basal part only. The axile condition is determined by the axial meristem in the floral apex, whose growth is already initiated in a very early phase of the development of the flower. Thus the axile condition is definitely not due to postgenital fusion of parietal placentae or intrusions from the ovary wall and the axile placentation in *Begoniaceae* is because of its origin, not 'pseudo-axile' as postulated by Gauthier (1959), but 'truly' axile.

The strict classification of African *Begonia* species into two groups according to placentation type proposed by Reitsma (1983) is refuted by Charpentier et

al. (1989b, p. 3636). The models of the evolution of placentation types in *Begonia* presented by Reitsma (1983, p. 50) and De Wilde & Arends (1989, p. 38) are based on the postulates of Gauthier (1959) that the placentation in *Hillebrandia* is fundamentally parietal and that the parietal condition is primitive in comparison with the axile condition. Reitsma accepted Gauthier's interpretation and consequently he considered species with ovaries which are distinctly unilocular in the upper part, as primitive according to their placentation. It should be noted that Puri (1952, p. 631) was apparently sceptical about Gauthier's interpretation because he stated 'Gauthier, on the other hand, wants us to believe that the union is more intimate and (phylogenetically) earlier between the two adjacent carpels than between the two margins of the same carpel'.

Charpentier et al. (1989b, pp 3636-3638) dealt with the question whether the semi-inferior ovary of *Hillebrandia* represents the primitive character state of the ovary in *Begoniaceae*. They concluded that on the basis of evidence from some other families, the semi-inferior position of the ovary in *Hillebrandia* might be considered as a derived character state (Charpentier et al., op. cit p. 3637). However, according to the same authors (op. cit. p. 3638) other evidence indicates that on the basis of its mixed placentation the genus might be considered as a primitive taxon. Thus, on the basis of the position and the placentation of the ovary it is not possible to conclude whether *Hillebrandia* is a derived or a primitive taxon. Moreover, Charpentier et al. (1989a, p. 571; 1989b, p. 3625) concluded that on the basis of the present evidence it is not possible to decide which of the two placentation types is the primitive one in *Begoniaceae*.

As already mentioned above, Gauthier (1959) stated that the placentation in *Hillebrandia* is fundamentally parietal and primitive. The placentation in the African sections *Mezierea*, *Squamibegonia* and *Tetraphila* is very similar to that in *Hillebrandia*. Thus, Reitsma (1983) assumed that these sections could be considered as primitive taxa in the genus *Begonia*. The trends in the evolution of the placentation in African *Begonia* as proposed by Reitsma (1983, p. 50) are based on the postulate that the parietal condition is primitive, whereas the axile condition is derived. However, Charpentier et al. (1989b) concluded that it is not possible to decide which placentation type is primitive. Thus it appears that the acceptance by De Wilde & Arends (1989) of Reitsma's (1983) proposals regarding evolutionary trends in *Begonia* may have been premature.

As already mentioned above, the axile placentation in the base of the ovary in *Begonia* and *Hillebrandia* is due to growth which is initiated by the axial meristem of the floral apex. Therefore, the basal part of the ovary could be considered as acarpellate and the upper part as carpellate (Charpentier et al. 1989a, p. 571). These authors referred to Sattler (1974) who cited examples where placentae and ovules are formed by the floral apex. According to Sattler (op. cit. p. 25) acarpellate gynoecia are characterized by placentae and ovules which are formed on the floral apex and not on gynoecial primordia. He stated that, in the cases where the placentae are formed by the floral apex, the concept of carpel no longer applies since a carpel is defined as a unitary appendage that bears placentae and/or ovules.

According to Charpentier et al. (1989b, p. 3638) the development of the female flower in *Begoniaceae* hardly corresponds with the ontogenetic models used in the interpretation of the appendicular or axial nature of the ovary wall. The wall is not appendicular because the development of the flower does not clearly indicate that the wall is the result of exclusive growth of the adnate base of the perianth-segments. On the other hand, it is not receptacular either, because it is impossible to be certain that there is only intercalary growth below the insertion of the perianth segments. They therefore suggested that the ovary wall might be regarded as a structure intermediate between the axial and appendicular organs (op. cit., p. 3625 & p. 3638). Their interpretation is in line with the summary of Sattler (op. cit., p. 25) who stated 'Traditionally, the wall of inferior ovaries is interpreted as the congenital fusion product of carpels and other phyllomes or receptacle. There is, of course no developmental evidence for this interpretation: the wall of inferior ovaries is formed by an intercalary growing region (zonal growth) in a ring-zone at the base of the floral appendages. Thus, the floral appendages, including the gynoecial appendages, are carried up on the wall of the inferior ovary during their development. The gynoecial primordia develop only into styles and/or stigmas, i.e. they are sterile. The placenta(e) and/or ovule(s) arise in the ovarial portion which is an intercalation formed by zonal growth'.

Charpentier et al. (op. cit., p. 3637) concluded that the inferior ovary in *Begoniaceae* probably is an intermediate structure between appendicular and axial organs that did not originate from postgenital fusion of conduplicate carpels. Furthermore, they stated that it is difficult to interpret the evolution of the inferior ovary in the *Begoniaceae* in terms of the classical theory of the flower, since its constituent parts would not be exact homologues of carpels.

It should be noted that, with the exception of Bugnon (1926), all other authors who dealt with the vascular anatomy of the female flower in *Begoniaceae*, based their interpretations on the assumption that its ovary is formed by leaf-like structures only. In the present study several phenomena were discovered which may be interpreted as an indication that the base of the ovary is not leaf-like. It appears that the vascularisation of the female flowers I have studied corresponds with the development of the ovary demonstrated by Charpentier et al. in other species (see Chapter 7).

6.4.2.4.3. Placentation, ovule position and number of locules

In 1983, Reitsma studied the placentation of several plants belonging to the species treated here. At that time the plants were identified as *B. schultzei*, *B. wilczekiana* and the 'diploid and tetraploid forms' of *B. squamulosa* (Reitsma 1983, pp. 27, 35 and 37). In the present study, these plants are identified as *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa* respectively.

Like in *Hillebrandia*, the placentation of all these *Begonia* species is axile in the multilocular lower part and parietal in the unilocular upper part of the ovary. When the ovaries are opened longitudinally and studied under the dissecting microscope, it can be seen that the placentae are lamellae which are situated

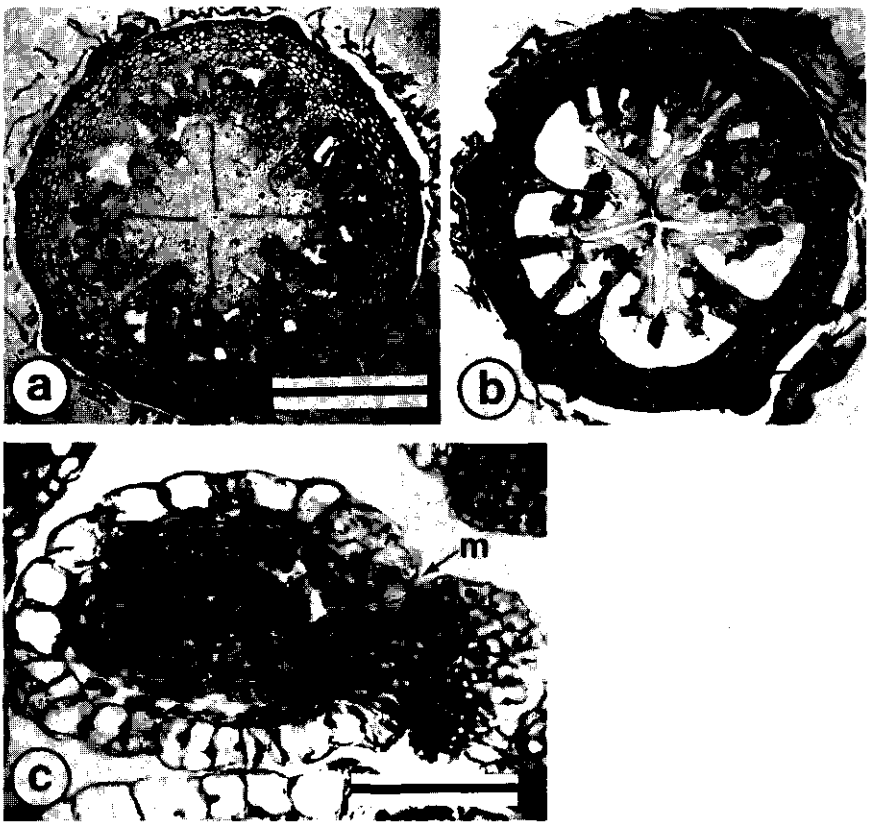


Fig. 6-10: *B. squamulosa*, transverse sections of different ovaries approximately half-way along their length; note that the ovules are predominantly shown in longitudinal section, because of their pleurotropous position in the locules. **a:** diploid plant; axile condition showing four axile septa; **b:** tetraploid plant; parietal condition showing five parietal septa; **c:** longitudinal section of an ovule in the diploid plant, m = micropyle. Scale in a represents 2 mm, that in c 100 μm; a and b at a similar magnification. **a & c:** culta Arends, de Wilde & Louis 371; **b:** De Wilde, Arends et al.(1983)-119.

along the 'axile' or, depending on the level in the ovary, 'parietal' septa (page 88). In *B. elaeagnifolia*, *B. karperi* and *B. squamulosa* the placentae are attached to the septa in the centre of the ovary (Figs. 6-10, 6-11c & d; 6-12). In transverse sections of a two-locular ovary, as found e.g. in *B. elaeagnifolia*, each septum with its two placentae is more or or less T-shaped, but in three- to five-locular ovaries it has the shape of an arrow-head ('fer de lance', Gauthier 1959, p. 75). This is shown in Figs. 6-10, 6-11c & d and 6-12. However, in *B. longipetiolata* each septum carries two opposite placentae approximately half-way between the axis and the wall of the ovary, so that in transverse section each septum with the placentae has the shape of a cross (Figs. 6-11a & b). This placentation

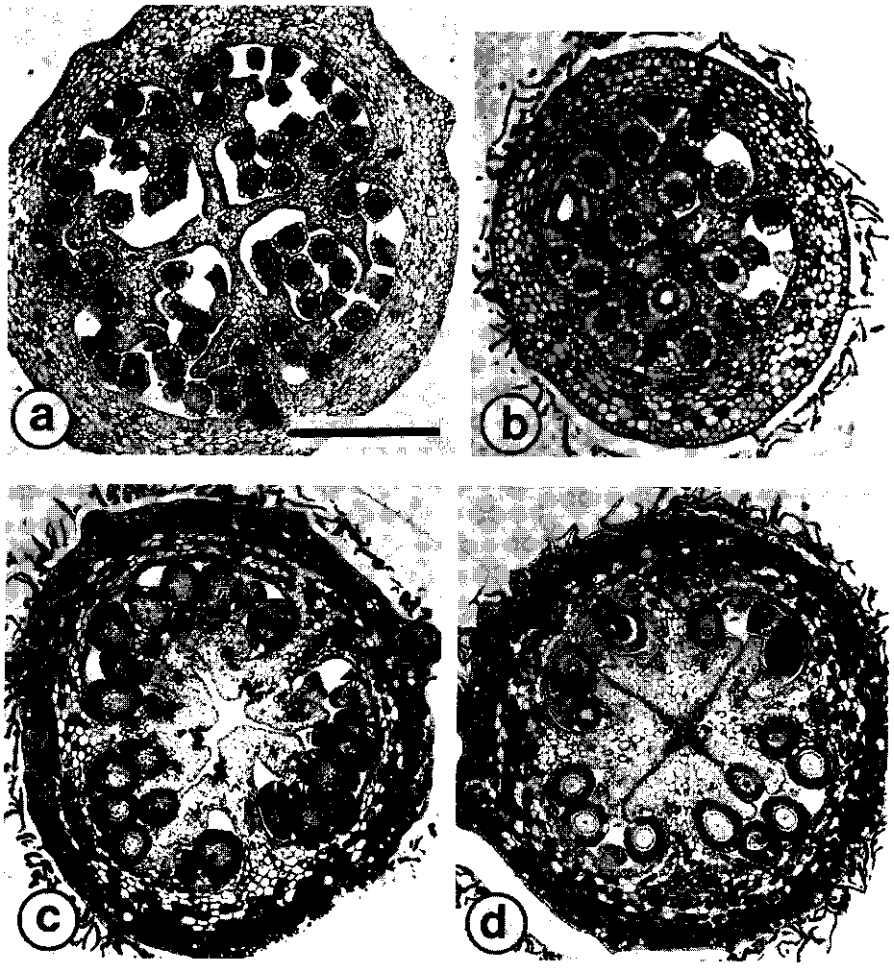


Fig. 6-11: transverse sections of ovaries approximately half-way along their length in *Begonia* species; note that the ovules are predominantly in cross section because of their epitropous position in the locules. **a** & **b:** *B. longipetiolata*, in **a:** axile condition, in **b:** parietal condition; **c** & **d:** *B. elaeagnifolia*, parietal condition in the ovary of different flowers produced during one flowering; in **c:** three parietal septa and in **d:** four parietal septa. Scale in a represents 1 mm, all figs. at a similar magnification. **a:** De wilde, Arends & de Bruijn 9270; **b:** Elias & Sterck in Louis 2334; **c** & **d:** culta Arends, de Wilde & Louis 571.

type was described as septal by Reitsma (1983, pp. 29, 35).

In order to avoid confusion it should be noted that at the time of Reitsma's investigation some plants were identified as '**diploid** *B. squamulosa*' and other plants as '**tetraploid** *B. squamulosa*'. Now, that the taxonomy of these very similar plants has been clarified, it is established that the 'diploid *B. squamulosa* plants' in fact belong to *B. longipetiolata*, which is reinstated here, whereas the

'tetraploid *B. squamulosa* plants' belong to the true *B. squamulosa*. In the present study, it was found that both *B. longipetiolata* and *B. squamulosa* comprise 2x and 4x plants (Chapter 4). The placentation in both 2x and 4x individuals of each of these species is found to be similar. This is shown in Figs. 6-10a & b for *B. squamulosa*.

The present study corroborates the statement in the literature that the ovule in *Begonia* is anatropous (e.g. Boesewinkel & De Lange 1983; Heywood 1978, p. 114; Lecocq 1977, p. 528). Fig. 6-10c presents an ovule in a transverse section of an ovary of *B. squamulosa*. The ovule is shown in longitudinal section, indicating that the ovule with its bent funicle has a perpendicular orientation in relation to the longitudinal axis of the ovary, because the ovules have a more or less pleurotropous position in the locules (Figs. 6-10a & b; 6-12 and Plate 6-14, page 211). However, in *B. elaeagnifolia*, *B. karperi* and *B. longipetiolata* the ovules are usually epitropous, so that transverse ovary sections of these species show most of the ovules in transverse section as well (Fig. 6-11). Thus, *B. squamulosa* can be distinguished from *B. longipetiolata* on the basis of both the attachment of the placental lamellae to the septa and the position of the ovules in the locules.

The number of styles in a flower usually equals that of the septa and/or locules. For example, a transverse section of a flower with three styles produced by *B. elaeagnifolia* (culta Arends, De Wilde & Louis 571) shows three septa (Fig. 6-11e), whereas a section from another flower having four styles, that was produced by the same plant, shows four septa (Fig. 6-11d). However, exceptions have been found. The flower of *B. squamulosa* depicted in Plate 6-10 (page 211) shows four styles. When sections were prepared from its ovary it showed a five-locular condition (Fig. 6-10b). The flower of *B. karperi* depicted in Plate 2-5 (page 192) has three styles, but its ovary was found to be four-locular (Plate 2-22 to 24). Similarly, a section from another flower with three styles from the same individual of *B. karperi* showed a four-locular condition.

An interesting phenomenon was observed in sections prepared from a flower of *B. squamulosa* with four styles (culta Arends, De Wilde & Louis 371). The lower part of the ovary was found to be four-locular, but towards the apex of the ovary, in the zone where the placentation is parietal, the sections show five septa, each with a double placenta (Fig. 6-12). The increase of the number of septa is due to a lateral division of one of the four septa (Figs 6-12e to f). This observation indicates that in a syncarpous ovary, a carpel may be incompletely developed. Eames (1961, p. 231) stated that where carpel fusion is incomplete distally, the styles and stigmas are free, but that the number of styles and stigmas does not necessarily indicate the number of carpels involved in the fusion.

6.5. Fruits and seeds

The fruits available in dried field collections are all closed. As far as they have been described, these fruits were always interpreted as non-dehiscent (Wilczek

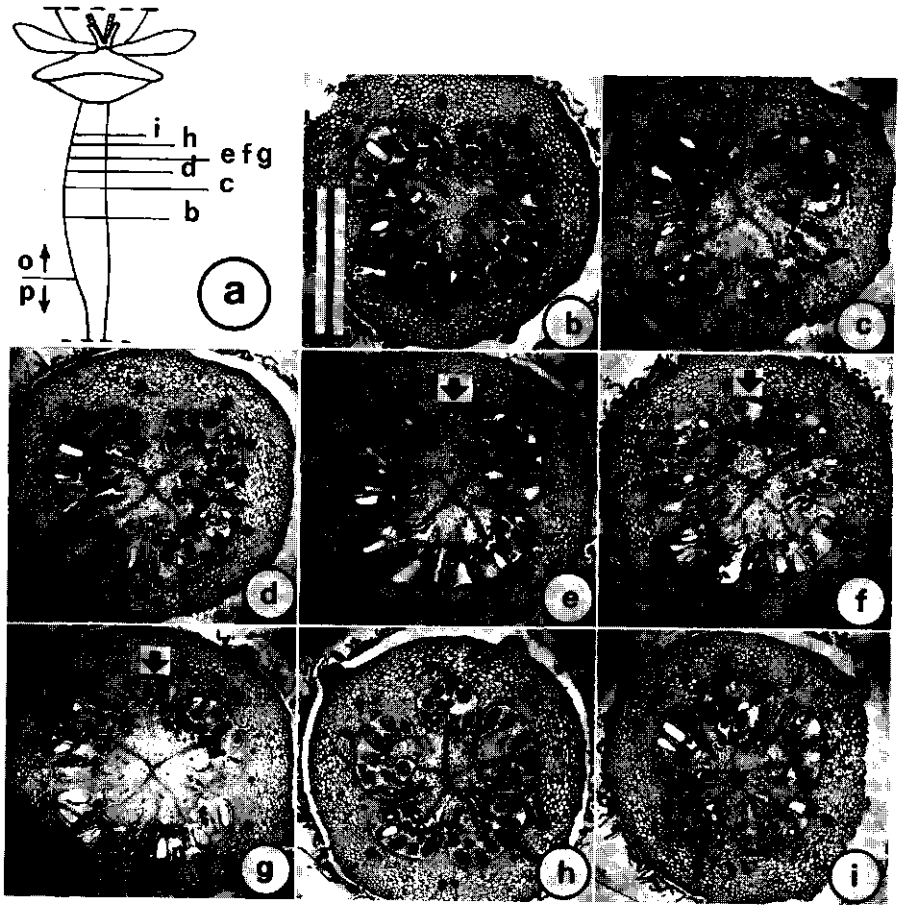


Fig. 6-12: *B. squamulosa*. Serial transverse sections demonstrating four and five locules in a single ovary. **a:** diagram of flower, p = pedicel, o = ovary; the letters b to i indicate the levels of the sections shown in the photographs in b to i; **b:** four locules and axile placentation; **c:** transition between the axile and the parietal condition; **d:** parietal condition with four parietal septa; **e, f & g:** appearance of the fifth locule (thick arrow); **h:** five parietal septa **i:** fusion and disappearance of the placental lobes (slender arrow). Scale in a represents 2 mm, all figs at a similar magnification. Culta Arends, De Wilde & Louis 371.

1969a & b). However, it was observed in the course of the present study that the fruits of cultivated plants may open with one to four longitudinal clefts in their walls. Before the fruits dehisce, they do not show regions of a specific weakness where ruptures will occur.

The fruits studied were produced after artificial pollination and it was found that the development of a fruit takes about two months before its dehiscence. As far as could be seen in the open fruits, the clefts are situated near the septa.

Moreover, the septa themselves with their seed-bearing placentae become detached from the wall. The septa and their placentae more or less adhere to each other, and collectively they form a seed-carrying column that is very weak in texture. A very small portion of each septum remains attached to the wall as a shallow longitudinal ridge. Almost simultaneously with the dehiscence of the fruit, the column disintegrates and some of its fragments with the seeds may be spilt before the remainder of the fruit eventually drops from the plant. In *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa* the base and the apex of the fruit both remain intact when the fruit opens (see Plate 6-17, p. 211). When the first cleft appears, the further dehiscence of the fruit proceeds in a rather irregular manner. There may appear additional transverse slits and the entire disintegrating structure usually drops from the plant within less than 12 hours.

In the field, three dehisced fruits have been found on three different occasions. In *B. elaeagnifolia* a fruit with one cleft was found (Breteler & De Wilde (1978)-8) and another fruit had three clefts (De Wilde, Arends et al. 9777). The gathering De Wilde, Arends et al.(1983)-119 of *B. squamulosa* has one dehisced fruit with four clefts (see Plate 6-17). These dehisced fruits were preserved in spirit, and not in herbarium, but even when kept in liquid they tend to fall apart.

The fruits of *B. rwandensis* in the gathering Bridson 380 are mature, as they contain fully developed seeds. However, they do not show any cleft or slit. So far, all species of the section *Tetraphila* of which good material was available, are characterized by dehiscent fruits, their mode of dehiscence varying among the species (De Wilde, pers. comm.). Whether and how the fruits in *B. rwandensis* open remains to be discovered. This also applies to *B. pelargoniiflora*, of which the dried specimens have young fruits only.

Hallé & Raynal (1966) described the fruit of *B. squamulosa* as oblong or obpyriform, but now that more material has been studied I suggest that the obpyriform fruit which they saw (in Hallé 2193, = *B. longipetiolata*), is aberrant in shape. All the fruits observed in the present study were fusiform in shape. In the caption of their illustration, Hallé & Raynal (op. cit., pl. 1-8) described the obpyriform fruit of Hallé 2193 as mature, whereas according to their description (op. cit., pl. 1-7) the oblong fruit in Raynal 9709 (not 9790 as stated) is immature. Neither the drawing of the obpyriform fruit nor that of the oblong fruit shows any opening. Consequently, Wilczek (1969b, p. 21) interpreted the fruit of *B. squamulosa* as non-dehiscent and described it accordingly. It can be surmised that Hallé & Raynal would have found the fruit to be dehiscent, if they had pollinated a female flower of their cultivated plant and followed the complete development of its ovary after fertilization.

With the exception of *B. pelargoniiflora* of which there were no seeds available, the micromorphology of the seeds of the species treated in this study, was investigated by De Lange & Bouman (in preparation). The seeds which I supplied to them were taken from wild as well as from cultivated plants.

De Lange & Bouman found that the seeds of *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa* are very similar. The length/width ratio of the

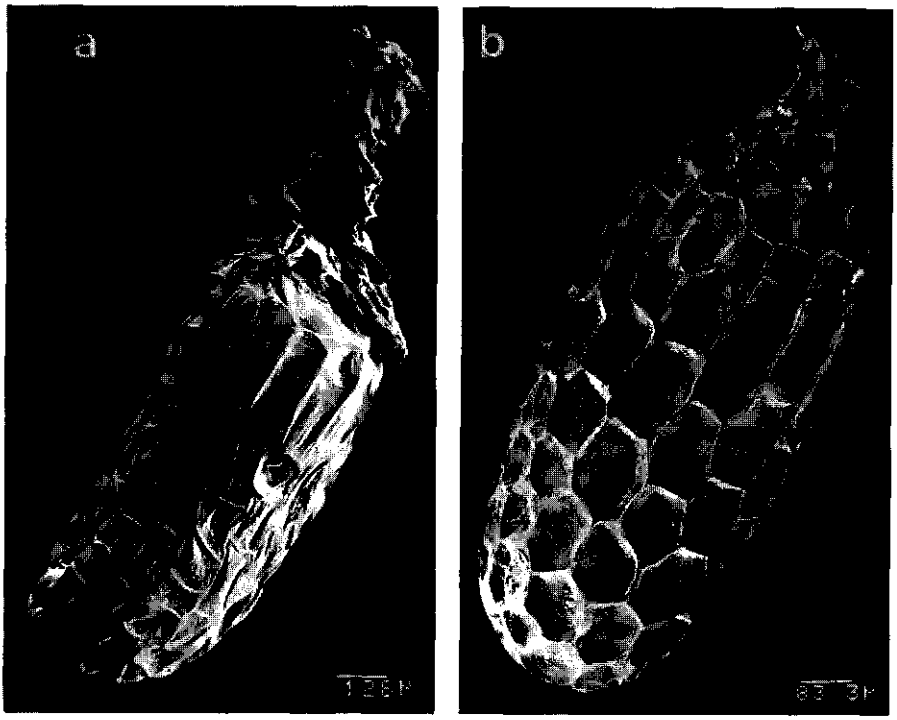


Fig. 6-13: SEM photomicrographs of *Begonia* seeds. **a:** *B. elaeagnifolia*, testa cells predominantly hour glass-shaped (Breteler, Lemmens & Nzabi 8248); **b:** *B. rwandensis*, testa cells polygonal (Bridson 380).
Courtesy A. de Lange and F. Bouman, Hugo de Vries Laboratory, Amsterdam.

seeds ranges from 2.1. to 2.6, but that of the seed of *B. squamulosa* is c. 1.8. The length varies from c. 835 to 1100 µm. In these species, most of the cells of the testa have the shape of an hour-glass (Fig. 6-13a). This shape is caused by a weak depression of the longitudinal anticlinal walls. Moreover, the outer periclinal walls are stretched as a drumhead between the anticlinal walls. The former walls tend to break up because they are thin and brittle.

It should be noted that De Lange & Bouman also studied the seeds of the gathering Hallé & Villiers 5381, the type of *B. nicolai-hallei* Wilcz. The morphology of the seed of that taxon, which is here considered as conspecific with *B. longipetiolata*, matches with that of the other species mentioned above.

According to De Lange & Bouman, the seed of *B. rwandensis* with a length/width ratio of 2.2, has an average length of 875 µm. This dimension falls within the range of the seed-length of the species mentioned above. Thus, *B. rwandensis* cannot be distinguished from the other species by the general shape and the size of its seed.

However, the seed of *B. rwandensis* is distinct from that of the other species by the polygonal shape of the cells of its testa (Fig. 6-13b). In addition, the inner periclinal wall of these cells differs in particular from that of other species of *Begonia* section *Tetraphila* investigated by De Lange & Bouman, because it is reticulately pitted. In mature seeds, the outer periclinal wall has collapsed and consequently, it tightly covers the inner wall. In this situation the reticulate pitted character of the inner wall is readily visible.

It is concluded here that the species considered in the present study, have seeds which can be distinguished into two distinct types which are shown in Fig. 6-13. The first type represents the seeds of *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa*, while the second type represents the seed of *B. rwandensis*. The seed of *B. pelargoniiflora* has not yet become available for study.

7. The vascularisation of the pistillate flower*

7.1. Introduction

7.1.1. General

This chapter deals with the vascular anatomy of a female flower of three species, viz.: *B. longipetiolata*, *B. squamulosa* and *B. elaeagnifolia*. The analysis and interpretation of the vascularisation is based on the investigation of transverse sections of complete flowers. The sections were prepared from flowers with a more or less straight ovary following the method described in Chapter 3.

There were several reasons for this detailed study:

(i) The nature of the perianth needed further investigation.

(ii) According to Reitsma (1983) each septum in the ovary in several African sections of *Begonia*, including section *Tetraphila*, consists of both carpellar and placental tissue. I decided to investigate this interpretation further.

(iii) The recent studies of the ontogeny of the pistillate flower in *Begoniaceae* which were carried out by Charpentier et al. (1989a & b) showed that it is not appendicular, whereas investigations of the vascular anatomy suggest that it is indeed appendicular. It was thought that it would prove worthwhile to look for further evidence which might elucidate this issue.

These points will now be discussed in further detail:

(i) Often, the perianth parts in *Begonia* are designated as tepals because they are very similar. According to the vascular anatomy of the segments, those supplied by several vascular bundles may be designated as sepals, while segments which are supplied by a single bundle may be designated as petals.

(ii) Reitsma's opinion about the nature of the septa in the ovary of *Begonia* section *Tetraphila* was inferred from the way the mature fruits dehisce. According to De Wilde (pers. comm.) most of the species in this section have fruits which open with more or less regular valves. Apart from the valves, the dehisced fruit consists of the fruiting stalk which carries a seed-bearing column (e.g. De Wilde & Arends, 1979, p. 361, photo 1). This column is formed by the placental lobes and the inner portions of the septa. The outer portions of the septa remain

*) in cooperation with Astrid Musampa Nseya

attached to the wall of the dehisced fruit. According to Reitsma's interpretation, the portion of each septum that is part of the column is placental, while the portion of the septum that remains on the wall is carpellar. Reitsma's interpretation of the composite nature of the septa is illustrated in his diagram of a transverse section of the mature ovary of *B. cavallyensis* A. Chev. (Reitsma op. cit., fig. 2d).

Reitsma (op. cit., p. 40) also included a photograph of another section of the same ovary of *B. cavallyensis* that, according to his interpretation, shows in one of its two septa a 'kind of constriction'. He considered this constriction to be the transition zone between carpellar and placental tissue. However, the photographs of the sections in the present study show that these tissues are not distinguishable from each other. Therefore, I examined the slides prepared by Reitsma and I found that the 'constriction' only occurs in a few successive sections of the ovary of *B. cavallyensis*. Moreover, there are no constrictions in any of the other ovaries studied by Reitsma. Similarly, Charpentier et al. (1989b, p. 3632) did not find evidence for the occurrence of a constriction. I interpret the transition-zone shown on page 40 of Reitsma's paper to be necrotic, possibly suberized tissue. The absence of a marker for the postulated boundary between carpellary and placental tissue is in line with Mauseth (1988, p. 403) who stated that 'frequently, the placenta is indistinguishable anatomically and cytologically from nonplacental tissue'.

(iii) Charpentier et al. (1989a & b) not only showed that the pistillate flower in *Begoniaceae* is not appendicular, but according to their interpretation it is not truly receptacular either. The development of the flower is due to growth initiated by both the axial meristem of the floral apex and several similar parietal meristems. Their ontogenetic studies indicated that the ovary wall might be interpreted as a structure intermediate between axial and appendicular organs, whereas the base of the ovary with its axile placentation could be interpreted as acarpellate. Thus, the components of the inferior ovary in *Begonia* would not be exact homologues of carpels.

The analysis of the vascularisation in the present study was finished before Charpentier et al. published their accounts on the ontogeny of the female flower in *Begoniaceae*. In fact, several phenomena were encountered which I found very difficult to understand on the basis of the hypothesis that the ovary is entirely carpellate. Their studies provided the necessary stimilus for a re-interpretation of my observations and a more complete understanding of their significance.

7.1.2. Descriptive terms in the text and markers in the illustrations

For each of the flowers studied, a selection of diagrammatic drawings of transverse sections are mounted in plates (Figs. 7-2, 7-7, 7-11). They are diagrammatic because **a)** ovules are omitted from the ovarial cavity; **b)** locules and stylar canals with transmitting tissue are indicated by hatched surfaces; **c)** the orientation of the phloem and xylem strands in the vascular bundles is not indicated.

The vertical scale in each plate indicates the four zones which are distinguished in the flower. The markers **ped**, **ova**, **P** and **sty** indicate the pedicel, ovary, perianth and stylar zones respectively. The boundary between the pedicel and the ovary is determined by the level of the first sections which show locules. The ovary extends up to the level where the sections show tissue of the perianth that is continuous with tissue of the ovary. The perianth zone extends to the level where its segments are free from the fused carpels which, at that level, form the connate proximal parts of the styles. The vertical scales are also provided with letters which indicate the level of the corresponding drawings, while numbers correspond with photographs mounted in other plates. Usually, the markers in the diagrams and photographs are abbreviations of morphological or anatomical terms. For example, a lateral trace is marked **L** and a locule **loc**.

The drawings and photographs of the transverse sections do not give sufficient information about the origin of the bundles which they show. This is demonstrated e.g. by Fig. 7-11-e, where there are two bundles in the ovary wall marked $\mathbf{l}_1$ and $\mathbf{d}_1$ respectively. In Fig. 7-11-g which depicts a section from a higher level, there are bundles $\mathbf{l}_1$ and $\mathbf{d}_1$ as well, but these bundles are not the same bundles as shown in Fig. 7-11-e. This is demonstrated by Fig. 7-12A, the diagram of the longitudinal vascular pattern in the ovary wall. Another example is Fig. 7-7-d which shows two bundles with the marking $\mathbf{p}_1$ in the septum opposite trace $\mathbf{L}_1$. The diagram of the placental vascular pattern of this flower in Fig. 7-9 demonstrates that the bundle $\mathbf{p}_1$ is sectioned twice because of its arching course in the septum. These examples show that for a full understanding of the entire vascular system, illustrations should depict the pattern in both transverse sections and in longitudinal diagrams.

In preparing this thesis, it is impossible to present a comprehensible illustration of the complex 3-dimensional pattern of the vascularisation of the wall and septa of the ovary. To overcome this difficulty, the ovary is laid open and the wall spread out, so that the vascularisation of the wall is presented in a single plane. Similarly, every septum of an ovary is spread out in a single plane. The vascularisation of each of these septa is combined in a single diagrammatic illustration. In these illustrations, the axial and/or placentae-bearing parts of the septa are arranged towards the axis of the diagram. Moreover, the diagrammatic pattern of the vascularisation also includes the lateral trace that is situated in the wall near the transition zone between the wall and the septum opposite to the trace.

In literature, a vascular bundle of a carpel or an ovary is variously referred to by more or less synonymous terms. These terms are 'vascular cord' (Saunders 1925, Gauthier 1950), 'trace' (Hall 1949), 'strand' or synonymously 'trace' (Cutter 1971b) and 'vein' (Bierhorst 1971). According to Bierhorst, the veins in a carpel may be distinguished into major and minor veins. The major veins comprise the dorsal vein, the lateral and/or the ventral veins of a carpel. In the present study, the term **vein** is reserved for any major vein of the carpels which constitute the compound ovary.

However, the vascular bundles in the compound ovary which correspond with

Bierhorst's 'major veins' are designated as **traces**. Thus, e.g., a dorsal **trace** in the ovary corresponds with the dorsal **vein** of a single carpel, whereas a 'fused ventral **trace**' in the ovary corresponds with a pair of ventral **veins**, each one belonging to different and adjacent carpels. The **traces** are often direct continuations of particular vascular bundles in the transition zone between the pedicel and the ovary. Moreover, they run parallel with the floral axis and extend up to the perianth-zone or may enter the styles. According to their ultimate position in the ovary, the **traces** are referred to as dorsal, lateral and ventral traces. In the illustrations, they are marked **D**, **L** and **v** respectively.

In contrast with the vascular bundles in the *ovary* which are designated as **traces**, other vascular bundles in the ovary are designated simply as **bundles**. The latter are not formed in the transition zone between the pedicel and the ovary, but they are produced by the traces at various levels in the ovary. They are marked according to their origin. For example, a trace marked $\mathbf{D_1}$ produces a bundle $\mathbf{d_1}$, while a trace $\mathbf{L_1}$ produces a bundle $\mathbf{l_1}$, etc. Any trace (e.g. one marked **L**) may ramify several times at different levels in the ovary. Consequently, there may be different bundles which are all marked similarly. Often, a lateral trace (**L**) may produce a bundle marked **l**, while the adjacent, viz. dorsal, trace (**D**) produces a bundle that is obviously marked **d**. The two bundles **l** and **d** may fuse and the resulting single bundle is marked by a symbol such as a triangle or an asterisk.

Bundles in the ovary often remain more or less parallel with the traces from which they originate. Consequently, in longitudinal diagrams, such bundles and the traces are indicated by vertical lines. Other bundles however, may be more or less horizontal when they turn off abruptly from a trace. A bundle that peters out is indicated by a line that is terminated by a cross.

All the vascular bundles in the *pedicel* are also designated simply as 'bundles'. Except in those cases where it would not be clear from the context that the term bundle refers to a vascular bundle in the pedicel, such a vascular bundle may be explicitly referred to as 'pedicel bundle' or 'strand'. Similarly, the vascular bundles of the perianth segments may be referred to as 'perianth bundles'.

The flowers studied here have both an **axial** placental vascular system and a **parietal** placental vascular system. The **axial** system consists of traces marked **PC** and **PCD**, which is short for 'complex placental' and 'divided complex placental' respectively. In drawings of transverse sections, these traces are indicated by open bundles. The traces **PCD** produce bundles which supply the placentae. Consequently, these bundles are designated as placental bundles and in the drawings they are coloured black. The **parietal** system consists of the united marginal veins of the carpels and placental bundles which are produced by these veins. The united marginal veins form traces which are marked **vf** and/or **L**, whereas the placental bundles (or simply 'placentals') are coloured black, marked **p** or otherwise.

The illustrations included in the descriptive part of this chapter complement each other. Cross-references in the illustrations or in the captions help to clarify the vascular pattern and to demonstrate the phenomena which have been

encountered in the present study. In summary, the principal markers in the illustrations are:

In photographs and/or drawings of transverse sections

hatched surface	ovarial and stylar cavities
D	dorsal or median trace
L	lateral trace
v	ventral trace
vf	fused ventral trace
v'	bundle in the wall produced by a ventral trace
d	bundle produced by a trace **D**
l	bundle produced by a trace **L**
p or black bundle	placental bundle
open bundles in the centre of a section or bundles marked	
PC or	complex placental trace
PCD	divided complex placental traces

In longitudinal diagrams, the same markers are used. Placental lobes are indicated by shaded bands. The traces and bundles are indicated by lines. Occasionally, two vascular bundles have to be depicted in such a way that they seem to be connected, whereas they are actually free from each other. Such situations are indicated by a semi-circular or semi-elliptic portion in one of the lines.

7.2. Observations and comments

7.2.1. Some common morphological features

Figs. 7-2 (*B. longipetiolata*), 7-7 (*B. squamulosa*) and 7-11 (*B. elaeagnifolia*) show that the ovary of these species is multilocular in its lower part and unilocular in its upper part. The placentation in the lower and multilocular part is axile, whereas it is parietal in the upper and unilocular part. In the very base of the ovary, the placentae are entire (Figs. 7-2-b & – c; 7-7-b and 7-11-d & -e), but successive sections show that within a short distance, they gradually become bifid, so that each locule in the multilocular condition contains two placental lobes. According to the classical theory of the ovary which postulates that the ovary is entirely made up of carpels, the two lobes in a single locule belong to the same carpel. In the unilocular condition, the two placental lobes of a single carpel are no longer attached to each other (Figs. 7-2-e & -f; 7-7-g & – h; 7-11-h & -i), so that each intrusion or 'parietal septum' (see Charpentier et. al., 1989b, p. 3632) carries two opposite placental lobes. These lobes belong to different and adjacent carpels. Towards the perianth and the styles, the placental lobes and the locules gradually disappear, whereas a single composite

stylar canal becomes visible (e.g. Figs. 7-2-g &-h; 7-7-i). In the very top of the ovary and the perianth-zone, the composite stylar canal gradually divides, so that the base of each style is provided with a single canal with transmitting tissue (e.g. Figs. 7-2-k to -n; 7-7-m to -o).

Prior to the present investigation, the vascular anatomy of the female flowers of several taxa of *Begoniaceae* have been described and three of them exhibit a placentation that is similar to that of the species treated here. These taxa are: *Begonia horticola* Irmsch. of section *Tetraphila* (see Charpentier, Brouillet & Barabé 1989a), *B. masoniana* Irmsch. of section *Coelocentrum* (see Barabé, Brouillet & Bertrand 1985) and *Hillebrandia sandwicensis* Oliv. (see Gauthier 1959). Therefore, the interpretation of the present observations is based on a comparative study of the vascular pattern of the female flowers of all the species mentioned above.

7.2.2. The vascularisation

7.2.2.1. *B. longipetiolata*

The sections studied were prepared from the flower from a single-flowered inflorescence of the cultivated specimen De Wilde, Arends & de Bruijn 9270. The flower had four styles.

The proximal part of the pedicel was curved and slightly twisted so that the sections of that part show vascular tissue that was sectioned obliquely. Such sections are difficult to analyse, but it was possible to discern that the vascular bundles which are arranged in a ring divide tangentially, whereas there is also anastomosis. The bundles form a network and it is not possible to detect precisely how the bundles shown in Figs. 7-1-1 and 7-2-a have originated. The stele in the latter figure comprises approximately 20 bundles which can only be discerned at high magnification.

The process of simultaneous ramification and fusion continues up to a higher level (Figs. 7-1-3 & -4). Between the levels 5 and 6, the vascular bundles become arranged in two concentric rings (Figs. 7-1-5 & -6). The vascular bundles in the outer ring of Fig. 7-1-6 continue without further ramification and can be interpreted because of their position in the base of the ovary of which sections are shown in Figs. 7-2-b & -c. The vascular bundles in the wall opposite the locules are interpreted as the dorsal or median carpel traces and indicated by $\mathbf{D_1}$ to $\mathbf{D_4}$. The other vascular bundles in the wall, those which are situated opposite the septa, are interpreted as lateral traces and indicated by $\mathbf{L_1}$ to $\mathbf{L_4}$. Each trace **L** is considered to be compound, because it is postulated that each trace includes two lateral veins of adjacent carpels. It should be noted that the traces $\mathbf{D_4}$ and $\mathbf{L_4}$ in Fig. 7-1-6 are the result of a tangential division of the pedicel bundle marked **4** in Fig. 7-1-5.

The inner ring in Fig. 7-1-6 consists of numerous vascular bundles. However, within a very short zone (see the scale in Fig. 7-2), four pairs of vascular bundles move out towards the periphery. In Figs. 7-1-7 & -8 two of these pairs are indicated by arrows and these illustrations show that each pair is situated opposite a lateral trace (for a detail see Fig. 7-1-9). Because of their ultimate position

in the base of the ovary, each pair is interpreted to comprise the marginal or ventral veins of two adjacent carpels. Initially, the ventral veins in each pair are free from each other (see Figs. 7-1-9 and 7-1-11), but at higher levels they are more or less intimately fused and together they form a fused ventral trace marked **vf** (see the photograph in Fig. 7-1-14 and the drawings in Figs. 7-2-b to -j).

While the ventral vascular bundles move out towards the periphery, there is another important phenomenon in this zone of the flower. Except for the four outwardly shifting pairs of ventrals, the remaining vascular tissue in the centre of the flower forms a network by simultaneous ramifications and anastomoses (Figs. 7-1-12 & -13). The photograph in Fig. 7-1-14 shows that, at a slightly higher level, several bundles assemble in the very axis of the flower where they form a compound vascular bundle. The assembled bundles of the compound bundle show both anastomosis and separation in this short zone of the flower. Observation of some sections revealed that possibly four double, thus eight single bundles are involved in the formation of the compound bundle. The other bundles around the compound strand move out from the centre and dissipate into the axial portions of the septa, from where they gradually supply the placental lobes and the ovules (see Fig. 7-2-c).

Thus, the vascular tissue in the centre of the Figs. 7-1-7 & – 8 consists of four pairs of ventral vascular bundles and numerous placental bundles which have been produced by the ventrals. This interpretation is supported by observations from *B. masoniana* (Barabé et al. 1985, p. 405). These authors found that immediately after the origin of the ventral vascular bundles, these bundles give off placental bundles. This implies that the vascular tissue within the ring of the four fused ventral traces (**vf**) shown in Figs. 7-1-12 to -14, exclusively consists of placental bundles. Consequently, the compound bundle in the centre of Fig. 7-1-14 is formed by placental bundles only. A similar compound placental bundle also occurs in *B. masoniana* (Barabé et al. 1985, plate 1F) and *B. horticola* (Charpentier et al. 1989a, **PC** in fig. 4E).

In conclusion, the section of the ovary base of *B. longipetiolata* (Fig. 7-2-c) shows four kinds of vascular traces. These are: 1) the dorsal traces ($\mathbf{D_1}$ to $\mathbf{D_4}$) in the wall opposite the locules; 2) the lateral traces ($\mathbf{L_1}$ to $\mathbf{L_4}$) also in the wall, but opposite the septa; 3) the fused ventral traces (**vf**) in the transition-zones between the septa and the wall and 4) the single complex placental trace in the very centre.

The vascular bundles are collateral, with the xylem of the traces in the wall oriented towards the axis of the ovary. This observation is in line with that of the authors cited above. The orientation of the xylem of the fused ventral traces is also adaxial. This finding however, does not corroborate the interpretation of e.g. Barabé et al. (1985, plate 1, figs. E, F, G) who indicated in their illustrations that the fused ventral traces are reversed in relation to the other traces.

The interpretation of the vascular bundles in the ovary of *B. longipetiolata* which are here designated as traces, is in line with the interpretation of the vascular anatomy of the ovaries of *Begoniaceae* studied by the authors cited above. However, there are some minor differences between the species. These are now discussed briefly.

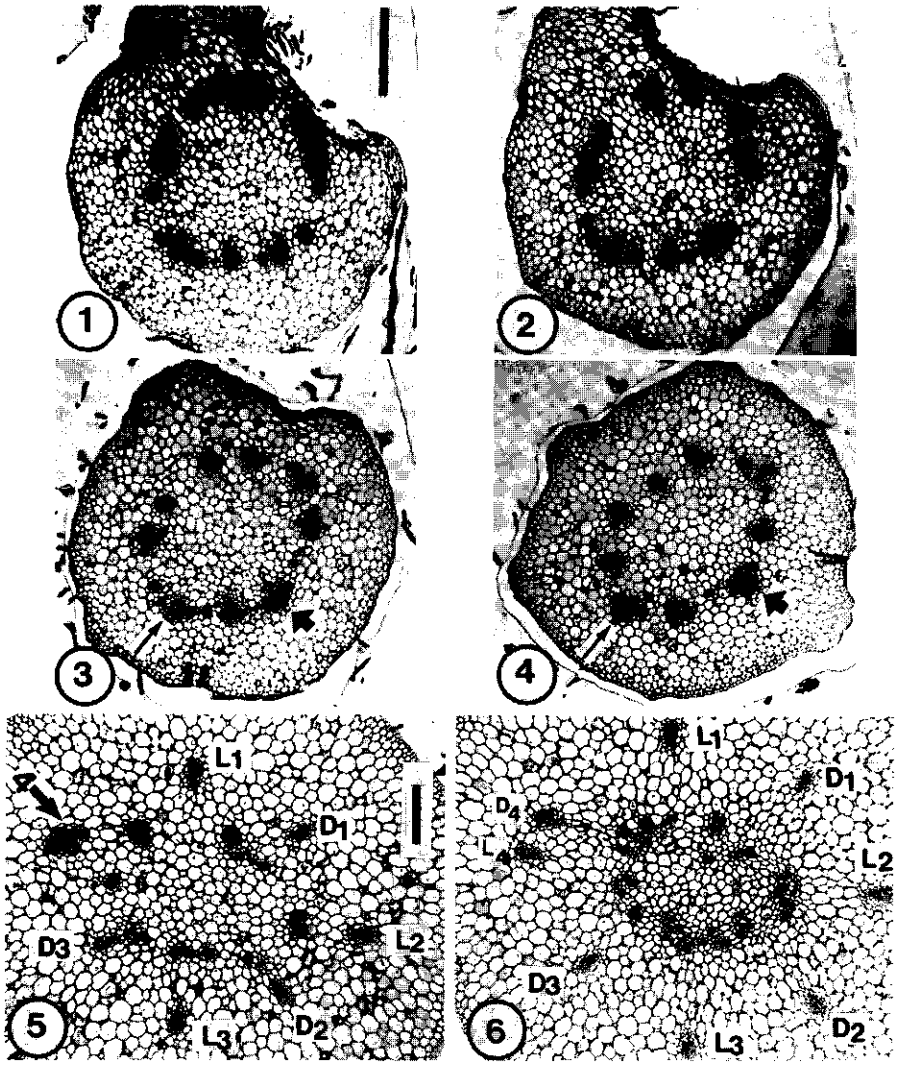


Fig. 7-1: *B. longipetiolata*, photographs of consecutive transverse sections of the pistillate flower of which sections are shown diagrammatically in Fig. 7-2. The level of each section is indicated by a number corresponding with that in the scale in Fig. 7-2. For markers and abbreviations see page 103 and compare with Figs. 7-3 and 7-4.
1 to **6**: pedicel zone, in **1** to **4**: vascular bundles showing tangential divisions as well as anastomosis. The small arrows in **3** and **4** indicate anastomosis, the large arrows ramification. In **5**: all the strands which, in the base of the ovary, become the dorsal traces (D) and the lateral traces (L) leave the stele simultaneously, the arrow indicates the strand marked 4 that begins to yield two strands which, at a higher level, become the dorsal trace D_4 and the lateral trace L_4; D_4 and L_4 are separately visible in **6**; The outer ring in **6** consists of four dorsal (D) and four lateral (L) traces which have already given off ventral and placental bundles towards the centre.
1 – 4 and 5 – 6 same scale respectively; bar in 1 represents 500 μm; bar in 5: 250 μm.

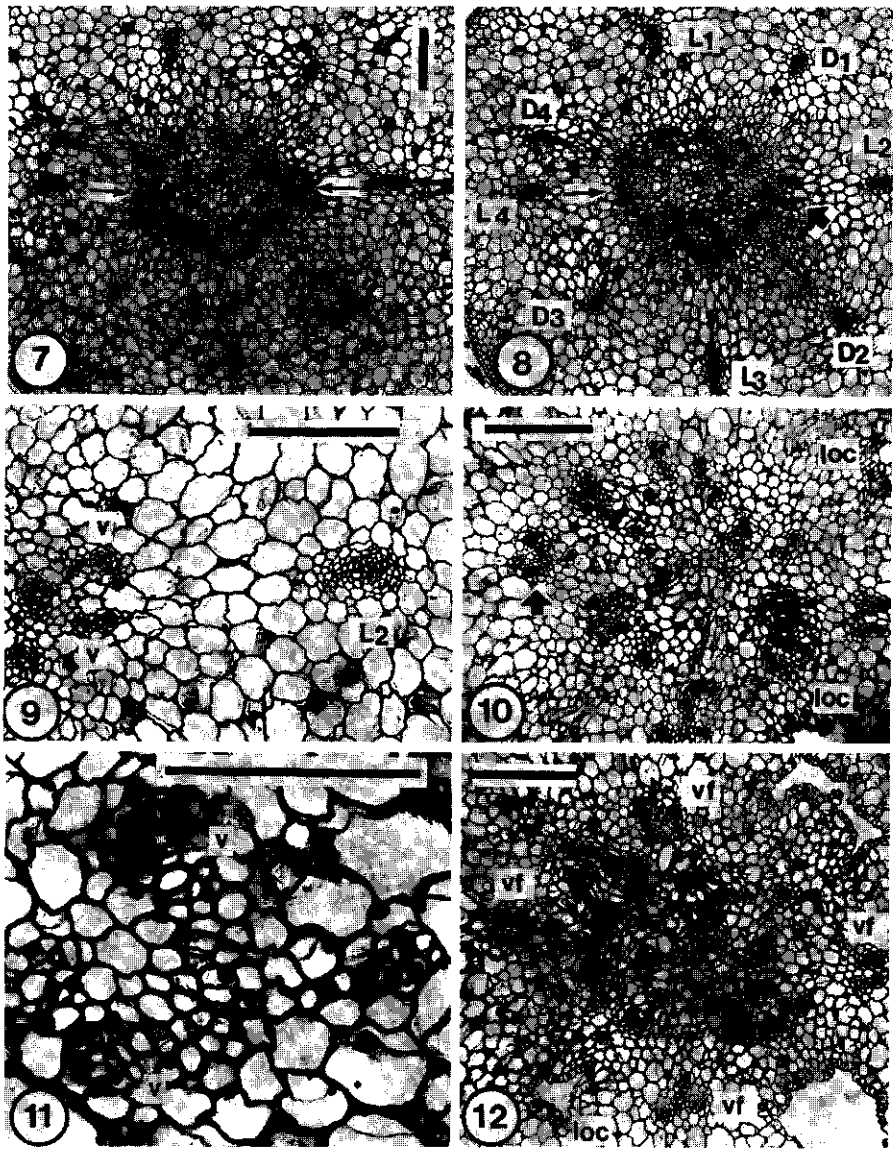


Fig. 7-1, **7** to **12:** transition between pedicel and ovary. **7** and **8:** two pairs of ventral vascular bundles (arrows) diverging from the centre towards the periphery of the pedicel, the thick arrow in 8 indicates the detail shown in **9:** two free ventrals (v) of adjacent carpels opposite the lateral L_2; **10:** base of the ovary zone, two locules (loc) are visible, in the centre of ovary a network of vascular tissue, the arrow indicates the detail shown in **11:** two free ventrals (v) opposite the lateral L_4 which is not shown; **12:** three locules show their lumen, four pairs of more or less fused ventrals (vf) and vascular network in the centre.
7 – 8 same scale, 9 – 12 variable. Bars represent 250 μm except that in 11 (= 100 μm).

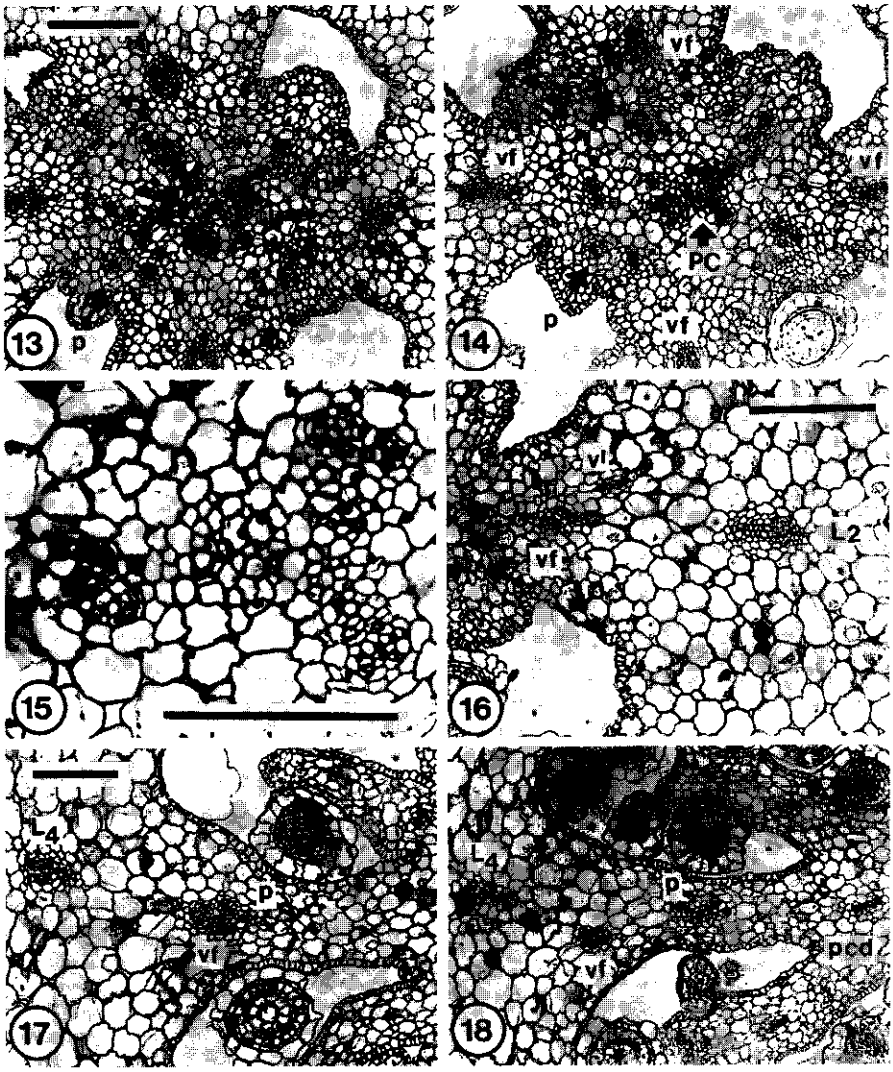


Fig. 7-1, **13** to **18:** base of ovary; **13:** four locules alternating with four fused ventrals and continuing network in the centre, the small free bundles are placentals which higher in the ovary enter the placental lobes, one of them is indicated by the arrow (p); **14:** idem, but the complex placental trace (PC) has been formed in the axis of the ovary; **15:** detail c. 100 μm above 14 showing the complex placental; **16:** ramification of the pair of fused ventrals (vf) opposite the lateral L_2. This trace vf has produced a bundle v' that passes into the wall between the traces L_2 and D_1 (compare with Fig. 7-2, diagram b and Fig. 7-3, L_2 at level 16); **17** and **18:** ramification of the fused ventral (vf) opposite the lateral L_4, producing the placental (p) that enters the septum on its way to the placentae (compare with Fig. 7-2, diagram c and Fig. 7-4, L_4 at levels 17 and 18).
13 & 14 and 17 & 18 at the same scale respectively, bar in 15 represents 100 μm, other bars 250 μm.

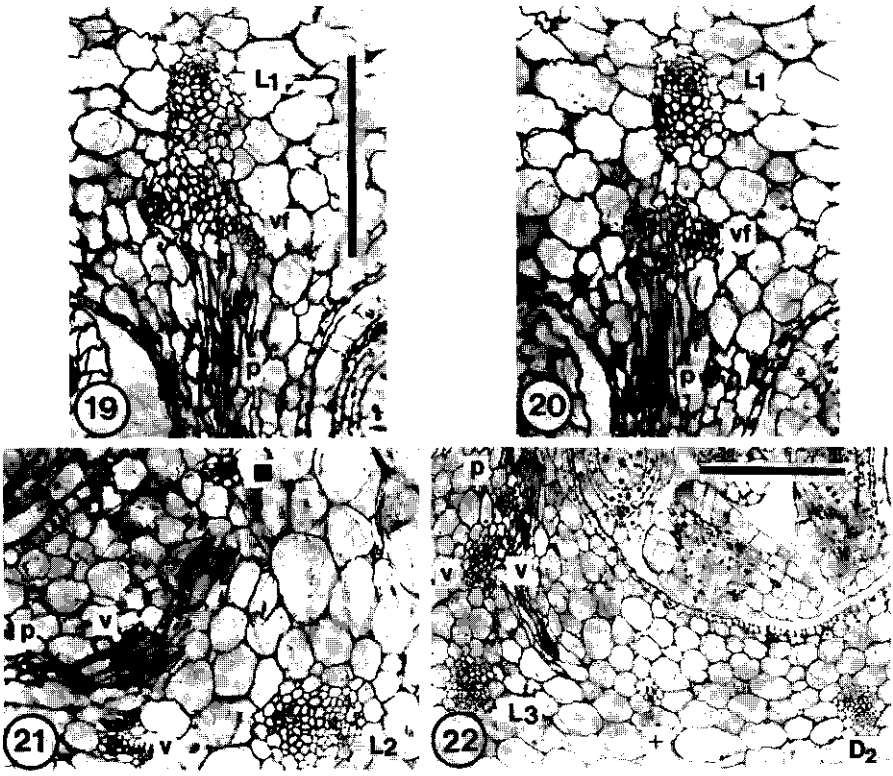


Fig. 7-1, **19** and **20:** production of parietal placentals by the pair of fused ventrals opposite the trace L_1 (compare with Figs. 7-3 and 7-4, L_1 at levels 19 and 20); **21** and **22:** connections of placental (p) and ventral vascular bundles (v) with bundles in the ovary wall (see Fig. 7-3 at the levels 21 and 22 for the marking and origin of the latter bundles.
19 to 21 at the same scale, bars represent 250 μm.

In *Hillebrandia sandwicensis* (Gauthier 1959, fig. 5), *B. masoniana* (Barabé et al. 1985, plate 1-F) and *B. horticola* (Charpentier et al. 1989a, fig. 4E), the dorsal and lateral traces have a similar position in the ovary as described for *B. longipetiolata*. However, in *B. masoniana*, each trace opposite a septum comprises the united **external** lateral veins of adjacent carpels. This is due to the fact that in the carpel of *B. masoniana* there are two kinds of lateral veins (viz.: internal and external), whereas in the carpels of the other species mentioned above there is only one kind.

The fused ventral traces in *H. sandwicensis* are situated in the septa (**vv** in fig. 5 in Gauthier 1959), but in *B. masoniana* (**vf** in plate 1-6 in Barabé et al. 1985) and *B. longipetiolata* (**vf** in Fig. 7-2) they are situated in the transition-zones between the septa and the wall. As to the ventral bundles or traces in *B. horticola*, Charpentier et al. (1989a, fig. 4F) presented a drawing of a section

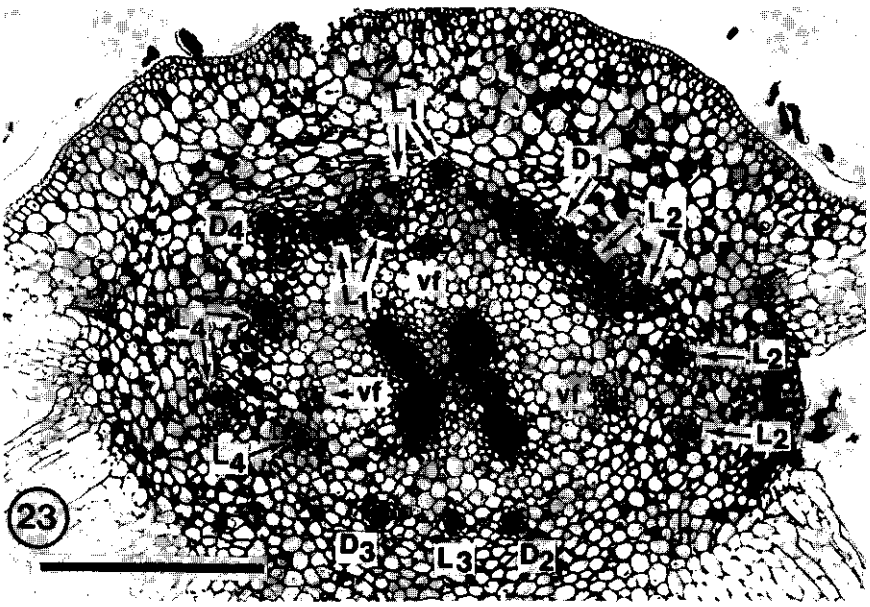


Fig. 7-1, **23:** section of the perianth zone slightly above the section shown in Fig. 7-2-diagram k. The photograph shows anastomosis between bundles produced by the traces L_4, D_4, L_1, D_1 and L_2.
Bar represents 500 μm.

which shows four bundles (marked **v**) in the centre of the ovary. They interpreted these bundles as ventrals and according to the statement on page 566 and the drawing in their paper, these bundles peter out in the placental lobes. The interpretation of these particular bundles as ventrals is different from that of the present study.

The diagrams in the Figs. 7-3 and 7-4 demonstrate that all the traces mentioned above continue in a vertical manner, because the traces **D**, **L** and **vf** are parallel with the axis of the ovary. The trace **PC** and its ramifications **PCD** coincide more or less with the axis. The diagrams also show that at various levels in the ovary, the traces produce bundles which do not proceed into the perianth-zone (see top part of Fig. 7-3).

The dorsal traces **D** remain single up to the perianth-zone (see Fig. 7-2-j). It has been mentioned on page 104 that the lateral traces **L** are interpreted as compound because it is postulated that each lateral trace **L** is formed by fusion of two lateral veins of adjacent carpels. This postulate is in line with the conclusion of Gauthier (1959, p. 73 & fig. 3), that in *H. sandwicensis*, each vascular bundle opposite a septum which he marked **lps**, represents two united lateral veins of adjacent carpels.

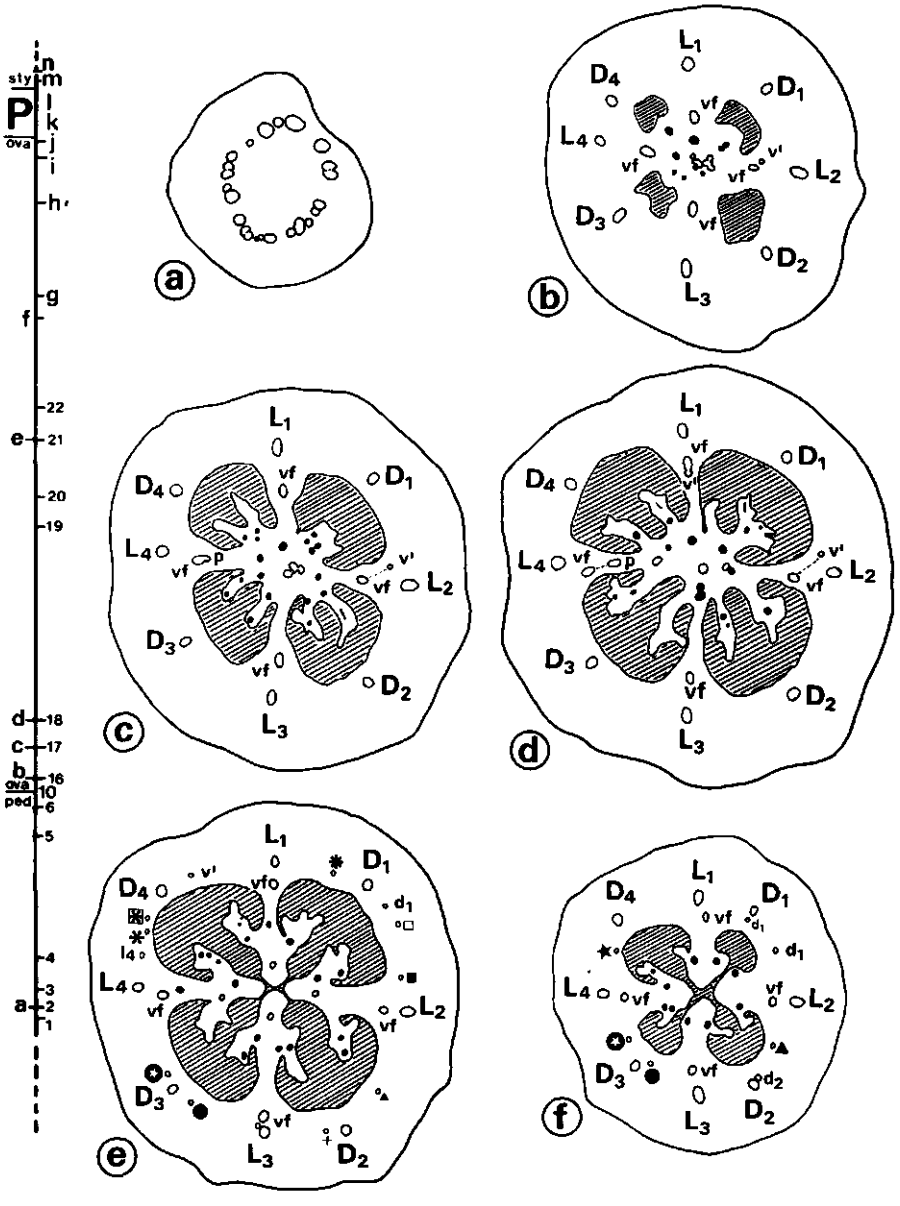


Fig. 7-2: *B. longipetiolata*, diagrammatic drawings of consecutive transverse sections of the pistillate flower of which Fig. 7-1 presents photographs of sections. The letters along the scale indicate the level of the sections, the numbers that of the sections presented in Fig. 7-1. For the abbreviations and markers see page 103 and compare with Figs. 7-3 and 7-4.
In **a** the pedicel; in **b**, **c** and **d** the four-locular condition with axile placentation, from **e** and up the uni-locular condition with parietal placentation. The black bundles in the centre are placentals; the open bundles represent the complex placental trace and divided complex placental traces (PC and PCD respectively in Fig. 7-4).

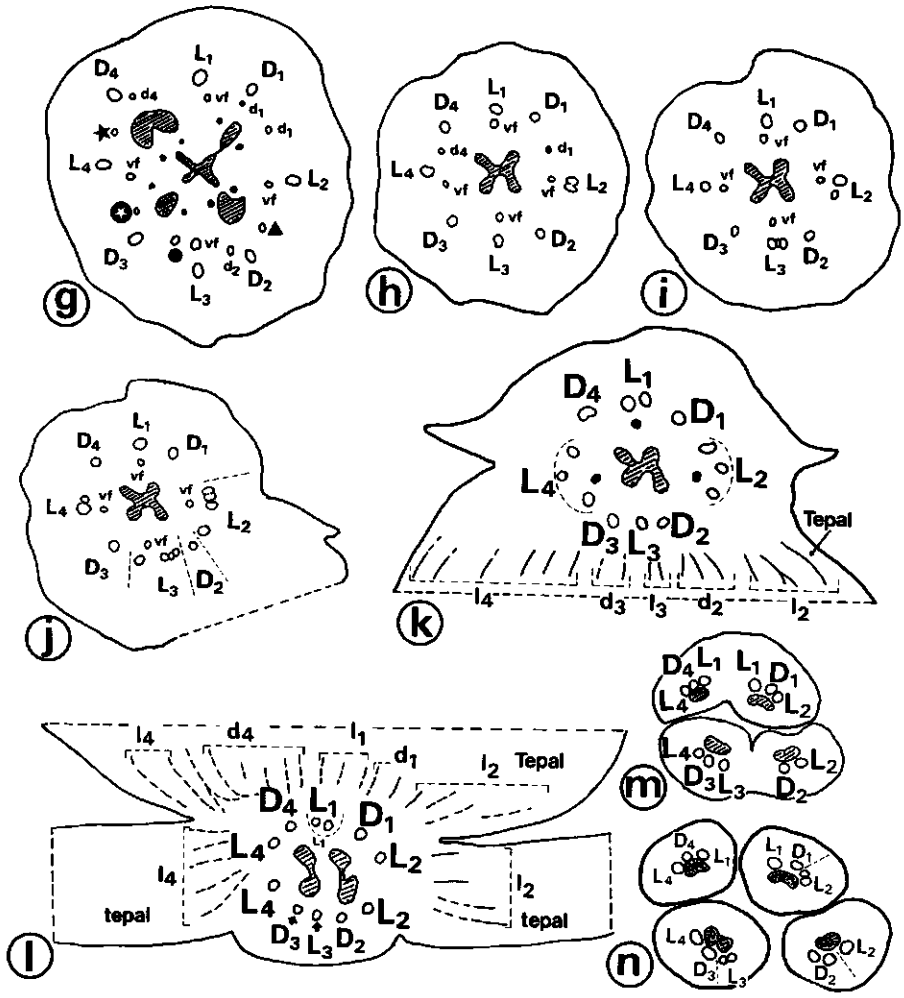


Fig. 7-2, **g** to **i**: upper part of ovary; **j** to **l**: perianth zone; **m** & **n**: bases of the four styles. In **g** four small locules without placentae and in the centre the stylar canal; **h** & **i**: begin of the ramification of the dorsal and lateral traces; **j**: transition between the ovary and the perianth zone where the four pairs of fused ventrals (vf) are still present, but at the higher level **k** trace L_3 has already fused with the trace vf belonging to the same pair of adjacent carpels; the remaining traces vf are here indicated in black; **k** and **l**: diagrams showing the vascular supply of the perianth segments; **m**: idem of the styles, which are still connate in pairs; **n**: idem, but the styles completely free from each other.

In *B. horticola*, Charpentier et al. (1989a, p. 560) found that the two lateral veins of adjacent carpels may be intimately fused and thus continue as a single compound bundle. However, other lateral veins of adjacent carpels in that species are not fused and these veins continue separately. The fused lateral veins in *B. horticola* were indicated by the marker **lf**, and the single veins simply by **l** (see Charpentier op. cit., figs. 4D – 4H). The photographs in Figs. 7-1-16 to -22 show that there is no clear cytological evidence that in *B. longipetiolata*, each trace **L** indeed represents two fused lateral veins. This implies that the postulated fusion is very intimate. The lateral traces begin to divide in the top of the ovary, just below the perianth-zone (see $\mathbf{L_2}$, $\mathbf{L_3}$ and $\mathbf{L_4}$ in Figs. 7-2-h, -i & -j respectively).

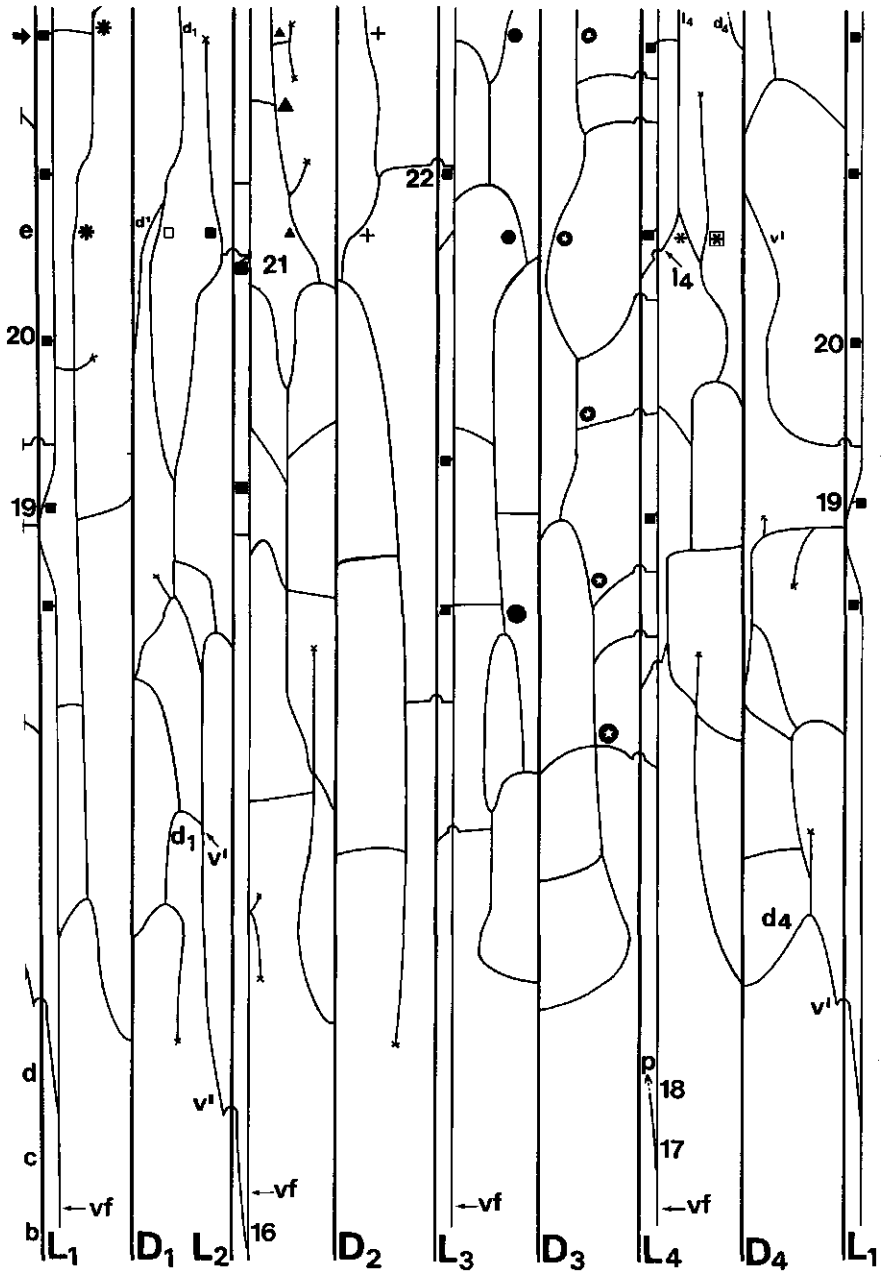
The fused ventral traces (**vf**) which are situated in the transition-zones between the septa and the wall, run parallel with the lateral traces (**L**). Fig. 7-3 shows that the traces **vf** and **L** remain free from each other for the entire length of the ovary, but at a single point in the ovary a trace **vf** is very close to the trace $\mathbf{L_1}$ (at level 19) and there might be a weak anastomosis between these two traces (see Fig. 7-1-19). Very rarely, a short horizontal bundle forms a connection between a ventral and the nearest lateral trace (see Fig. 7-3, trace $\mathbf{L_2}$ below level 19 and above e).

In *Hillebrandia sandwicensis*, the ventral and lateral traces also remain free from each other (Gauthier 1959). However, Barabé et al. (1985, plate 1-H) found that in the very base of the ovary of *B. masoniana*, each trace **vf** fuses with the nearest trace **le**. The resulting compound trace (thus **le + vf**) continues as a single trace in the ovary wall and because of its position, the authors (op. cit., p. 408) conveniently marked the new compound trace **le**.

In *B. longipetiolata*, a trace **vf** occasionally shows that it consists of two veins which are closely aligned. In some transverse sections, a ventral trace **vf** appears as a double bundle. This phenomenon occurs in particular at the points where the traces **vf** produce bundles which either pass into the septa (Fig. 7-1-21) or into the wall (Fig. 7-1-22). I consider such phenomena as evidence that each trace **vf** is indeed formed by two ventral veins of adjacent carpels. The traces **vf** become very thin in the perianth-zone (Figs. 7-1-23 and 7-2-k) and each trace **vf** fuses with one or two bundles which have been produced by the nearest lateral trace **L**. Because of the anastomosis in the perianth-zone which is shown in Fig. 7-1-23, I have not been able to ascertain whether the ventral traces are involved in the vascular supply to the styles.

The diagram of the apparently intricate vascular pattern in the wall (Fig. 7-3) demonstrates that the bundles which are produced by the traces **D**, **L** and **vf** form two kinds of connections between the traces.

The first kind concerns the connection between ventral and dorsal traces. For example, Fig. 7-3, at the level marked 16, shows that the trace **vf** near trace $\mathbf{L_2}$ produces a bundle that proceeds into the wall. This bundle, marked **v'**, remains free from the lateral trace, and at a higher level in the ovary it anastomoses with a bundle $\mathbf{d_1}$ that has been produced by the dorsal trace $\mathbf{D_1}$. Similarly, in the lower part of the ovary, a bundle v' is produced by the trace **vf** near the


e
20
19
d
c
b
22
21
16
18
17
vf
d1
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L1

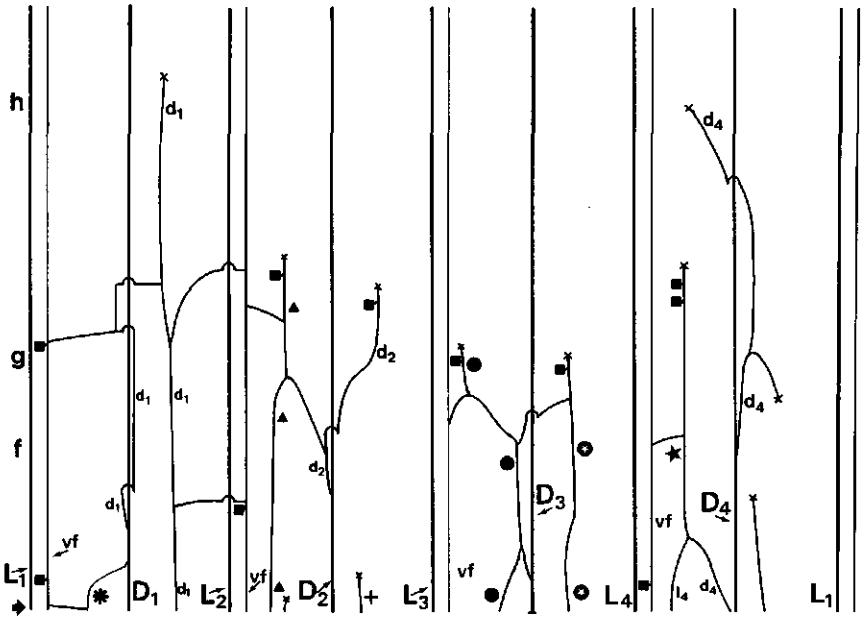

Fig. 7-3, continued (Top)

lateral trace L_1 (see Fig. 7-3, right hand side). This bundle v' fuses with a bundle d_4 produced by the dorsal trace D_4. The diagram shows that a similar phenomenon occurs rather frequently.

The second kind, viz. the connection between the dorsal and lateral traces, occurs only very rarely. An example is shown in the first part of Fig. 7-3. Here, the first ramification of the dorsal trace D_4 yields an unmarked bundle towards trace L_4. This bundle joins another unmarked bundle that is also produced by D_4. After the fusion, the resulting bundle soon bifurcates. One branch continues in a vertical manner and peters out, whereas the other branch anastomoses with an (unmarked) bundle produced by trace L_4. A similar phenomenon also occurs between the traces D_4 and L_4 slightly above the level marked 20.

The occurrence of bundles which form connections between the traces as discussed above, has not been shown or described precisely in the previous studies cited above. Barabé (1985, p. 405) only stated that, in *B. masoniana*, ventral

Fig. 7-3: *B. longipetiolata*, the ovary laid open with the longitudinal pattern of the vascular system in the wall. For the markers and abbreviations see page 103, the short lines with black squares attached to the traces vf represent placental bundles which pass through the septa towards the placentae. The letters in the left margin along the trace L_1 refer to the diagrams in Fig. 7-2; the numbers 16 to 22 in the figure to the photographs in Fig. 7-1.

bundles may be fused for a short distance with lateral and dorsal bundles.

Fig. 7-4 demonstrates that the fused ventral traces **vf** produce bundles which pass through the septa and enter the placentae. Obviously, these bundles are placentals which accords with Cutter (1971, pp. 238 & 239) who stated that usually the ventral strands supply the placentae and the ovules. In Fig. 7-3, the connections between the placental bundles and the traces **vf** are indicated by black squares.

Each placental bundle is single for the largest part of its course in a septum, but towards the placentae the bundle usually begins to ramify. The branches from a placental bundle may join the bundles which are already present in the septum between the placental lobes of adjacent carpels, or they leave the septum and supply the placentae. The placental bundles and the ventral traces collectively constitute the **parietal placental system**. The system is parietal because the placental bundles originate in the periphery of the ovary.

It should be noted that,in general, the parietal placental bundles occur towards the top of the ovary. There is only a single parietal placental bundle in the base of the ovary (Fig. 7-4, L_4, level 17). This bundle proceeds in the septum in a vertical and upward manner before it supplies the placentae on the septum opposite to the lateral trace. The remainder of all the parietal placental bundles run in a more or less horizontal or even in a downward fashion (see Figs. 7-4 and 7-1-19 & -20).

It has been described on page 113 how the ventral traces are frequently linked with the dorsal traces by connecting bundles. Sometimes, a connecting bundle between a dorsal and a ventral trace appears to be continuous with a placental bundle. An example of this phenomenon is shown in Fig. 7-1-22, where a placental (**p**) is attached to a single ventral trace (**v**). The point where **p** and **v** are connected is linked by a thin, more or less horizontal bundle to the thin vertical bundle in the wall marked +. The bundle +, in its turn, is linked to the dorsal trace D_2 (see Fig. 7-3, between D_2 and L_3, just below level 22). This implies that the vascularisation of the placentae on the septum opposite the trace L 3 is linked with the dorsal trace D_2. It should be noted that this linkage system does not involve the lateral trace L_3, because the horizontal bundle that connects the ventral with the vertical bundle +, passes along the lateral trace L_3 (Fig. 7-1-22 and Fig. 7-3, level 22). A similar linkage system is shown in Fig. 7-1-21. The diagrams in both the Figs. 7-3 and 7-4 show that such linkage is in fact a common phenomenon.

As to the vascular supply of the placentae, Fig. 7-4 shows that a variable number of placental bundles are produced by the the branches **PCD** of the trace **PC** which are situated in the axis of the ovary. Consequently, this vascular system comprising the traces **PC**, **PCD** and placental bundles, is designated as the **axial placental system**. Thus, in addition to the vascular supply from the periphery, the placentae are also supplied from the axis of the ovary.

The axial placental system terminates slightly above the level where the ovary is unilocular (see Fig. 7-2, diagram e). Fig. 7-4 shows that except for the trace **PCD** situated in the septum opposite the trace L_1, all the other branches peter

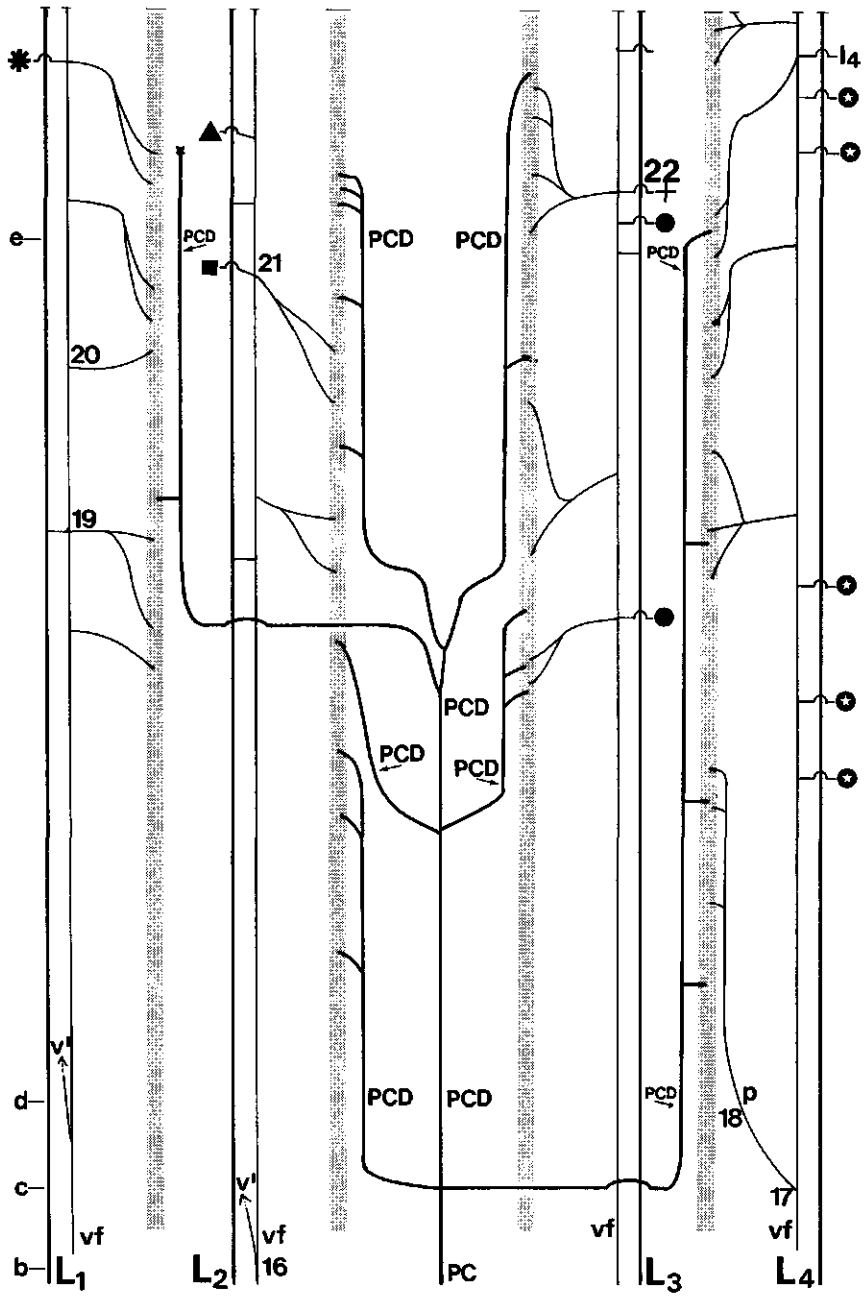

Fig. 7-4: *B. longipetiolata*, diagram demonstrating the longitudinal pattern of the placental vascular system. The system formed by the traces PC and PCD represents the axial placental system. The unmarked bundles in the upper part of the diagram are parietal placentals produced by the fused ventral traces (vf). The placentals and the traces vf constitute the parietal placental system. The parietal placental bundles pass through the septa and supply the placentae. The latter are indicated by shaded bands; each band represents two placental ridges belonging to adjacent carpels. The letters in the left margin along the trace L_1 refer to the diagrams in Fig. 7-2; the numbers in the figure to the photographs in Fig. 7-1. For markers and abbreviations see page 103.

out in a placental lobe. The traces **PCD** do not anastomose with any of the other traces in the ovary. Moreover, the axial system is almost independent from the parietal placental system; the two systems only cohere in the inner portions of the septae and/or the placentae where their ultimate branches, viz. the placental bundles, anastomose.

The lateral traces begin to divide slightly below the perianth-zone, while the dorsal traces remain single (Figs. 7-2- h, -i & -j). In the perianth-zone, all the traces **L** and **D** give off bundles which dissipate into the perianth segments (Figs. 7- 2-k & -l). These illustrations show that five traces in the ovary wall are involved in the vascular supply of each of the outer segments (**Tepals**). The bundles near the sides of both outer segments are produced by the traces $\mathbf{L_2}$ and $\mathbf{L_4}$, whereas each of these lateral traces also supplies a single inner segment (**tepal**). It is not always possible to detect precisely the origin of the bundles which supply the perianth, because there is a more or less intense anastomosis between the traces just before the bundles turn off into the segments (Fig. 7-1-23).

Each style receives a dorsal trace which represents the midvein of a carpel (Figs. 7-2-m & -n). The styles with the traces $\mathbf{D_3}$, $\mathbf{D_4}$ and $\mathbf{D_1}$ are also supplied with two lateral traces, whereas the style with the trace $\mathbf{D_2}$ has only one lateral trace. The pattern of the traces in the styles indicates that the carpels in this zone of the flower are no longer fused, because each carpel is characterized by its own veins. Moreover, the pattern also supports the hypothesis that each lateral trace in the wall of the ovary includes two intimately fused lateral veins of adjacent carpels. For example, the lateral trace $\mathbf{L_4}$ which is single in the wall (see Figs. 7-2-g to -i) ramifies in such a way that, in addition to the vascular supply of the perianth segments, it yields two single vertical traces $\mathbf{L_4}$. One of these single traces $\mathbf{L_4}$ supplies the style with the trace $\mathbf{D_3}$, whereas the other trace supplies the adjacent style with $\mathbf{D_4}$. The style with the trace $\mathbf{D_2}$ does not receive a trace $\mathbf{L_3}$, while the adjacent style with $\mathbf{D_3}$ receives a trace $\mathbf{L_3}$ (Figs. 7-2-m & -n).

7.2.2.2. *B. squamulosa*

The sections studied were prepared from the lateral flower in a 2-flowered inflorescence of a cultivated specimen of the gathering Arends, De Wilde & Louis 371. The flower had four styles.

Fig. 7-5 presents a diagram that summarizes how the traces in the ovary base (B) originate from the vascular bundles in the pedicel (A). Details of the various phenomena which occur in the transition-zone between the pedicel and the ovary base are shown in photographs (Figs. 7-6-1 to -12).

The interpretation of the vascular bundles in the base of the ovary is in line with the interpretation of those in the base of the ovary of *B. longipetiolata* (see above). In the ovary base of *B. squamulosa* (Figs. 7-5-B and 7-6-12), there are eight vascular bundles in the wall. Four of these bundles are interpreted as the fused lateral veins of adjacent carpels (marked $\mathbf{L_1}$ to $\mathbf{L_4}$), because each is situated in the wall opposite a septum. The other vascular bundles in the wall are situated opposite the locules, but only three of these are dorsal traces (marked

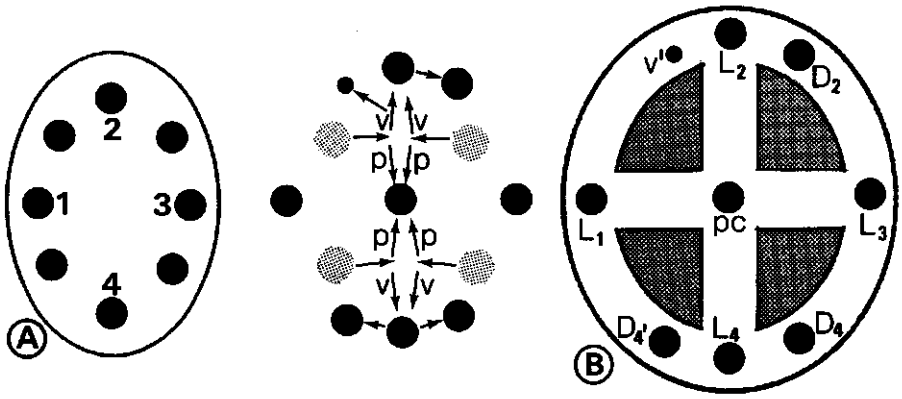

Fig. 7-5: *B. squamulosa*, diagram of the vascular pattern in transverse sections of A) the pedicel (compare with Fig. 7-6-photog. 1) and B) the base of the ovary (compare with Fig. 7-6-photog. 12 and Fig. 7-7-diagram a). The diagram between A and B summarizes how the various traces in B originate from the strands in A. Compare the middle diagram with Figs. 7-6-1 to -12. For markers and abbreviations see page 103.

D), because they continue in the ovary wall and each of them supplies a style (Fig. 7-7-n). The bundle v′ between the traces L_1 and L_2 is also situated opposite a locule, but it is not a dorsal trace (see below, page 123). The vascular bundle in the axis is interpreted as a complex placental trace (**PC**). When the vascular pattern in the ovary base of *B. squamulosa* (Figs. 7-5-B and 7-6- 12) is compared with that of *B. longipetiolata* (Figs. 7-2-b & – c), it is obvious that in *B. squamulosa* ventral traces are apparently absent.

The stele in the pedicel comprises eight vascular bundles which are arranged in a ring (Figs. 7-5-A and 7-6-1). Four of them are marked (**1** to **4**) and they continue into the ovary in a vertical manner without a shift in their position, so that the lateral traces L_1 to L_4 in the ovary are direct continuations of the pedicel bundles **1** to **4**. The four unmarked pedicel bundles between the bundles **1** to **4** gradually move towards the axis of the pedicel (Figs. 7-6-2 to -6). During their deplacement, each of the unmarked bundles divides frequently, while some of the ramifications fuse again. Each group of bundles originating from an unmarked pedicel bundle gradually segregates into two subgroups. The first subgroup moves towards the axis, while the other subgroup moves towards the periphery of the ovary (see e.g. Fig. 7-6-5).

The bundles of the inner groups (marked **p**) assemble in the axis and collectively they yield a compound trace (Figs. 7-6-6 to -12). This trace is a complex placental trace **PC**, because it ramifies into traces **PCD** which, in their turn, give off placental bundles. The latter supply the placentae and the ovules. A similar axial placental system also occurs in *B. longipetiolata* and *B. masoniana* (see page 105). It has been shown that, in these species, the trace **PC**, which is the base of the axial placental system, results from fusion of placental bundles which

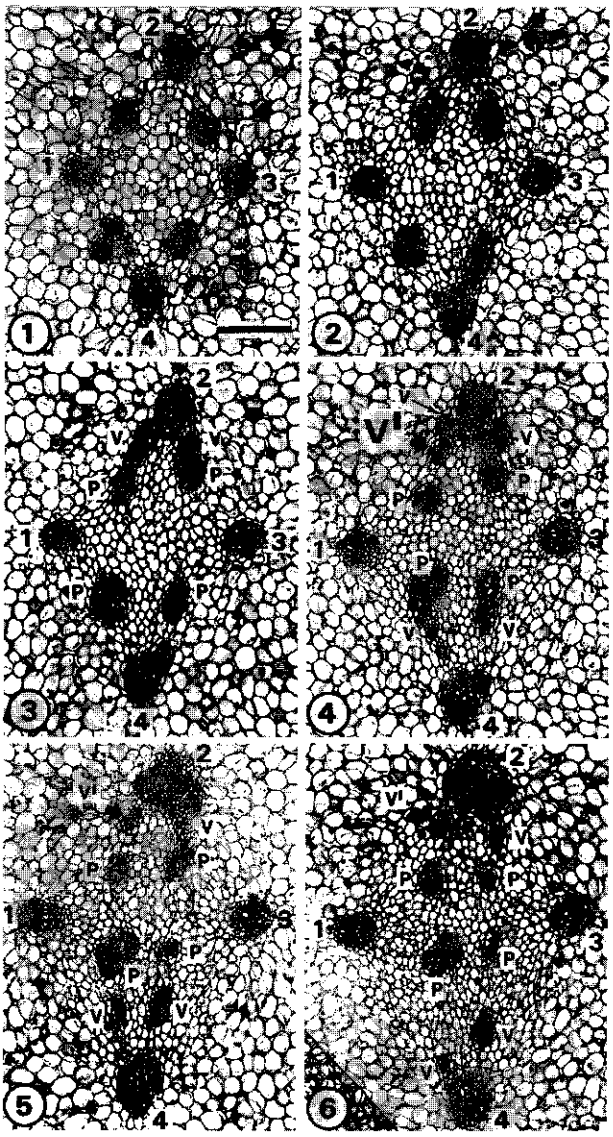

Fig. 7-6: *B. squamulosa*, photographs of consecutive transverse sections of the flower of which transverse sections are shown diagrammatically in Fig. 7-7; the level of each section is indicated by a number corresponding with that in the scale in Fig. 7-7. For markers and abbreviations see page 103.

1 to **6**: pedicel zone; **1** and **2**: eight vascular bundles comprising four strands marked 1 to 4 and four unmarked strands **3** to **6**: the four unmarked strands move towards the centre and subsequently towards the strands or pedicel bundles 2 and 4, while they segregate into ventrals (v) and placentals (p); **4**: the bundle v between the pedicel bundles 1 and 2 fuses with the bundle 2 (small arrow) and simultaneously gives off the bundle v′ (thick arrow) that passes along the pedicel bundle 2 into the wall between the laterals L_1 and L_2 (compare with Fig. 7-6-photog. 12, Fig. 7-7-diagram a and Fig. 7-8, L_1 and L_2 levels a to e).

1 – 6 same scale, bar in 1 represents 250 µm.

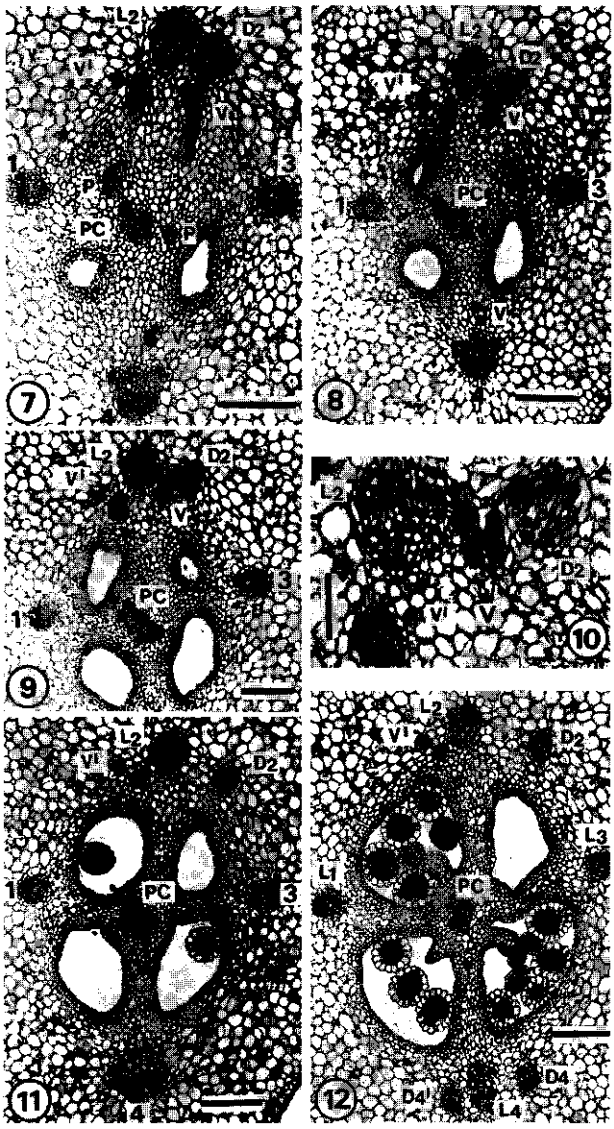

Fig. 7-6, **7** to **12**: base of ovary; **7** and **8**: two and three locules respectively and gradual formation of the complex placental trace (PC) in the centre; in **7** the pedicel bundle 2 begins to ramify into the dorsal trace D_2 and the lateral trace L_2, which are separated in **8**; **9:** four locules and the trace PC completed, in the top of the photograph a bundle v that begins to anastomose with the lateral L_2; simultaneously v gives off a small bundle that fuses with the dorsal D_2 (see detail in **10**); **11**: four locules, two of them with an ovule, the pedicel bundle 4 begins to ramify and in **12** it has produced two dorsal traces (D_4' and D_4 respectively) and one lateral trace (L_4). The latter trace is a direct continuation of the strand or pedicel bundle 4 in the pedicel and the very base of the ovary. Photograph 12 also shows placental lobes in three of the four locules, each lobe is still entire and is formed by the margins of a single carpel.
Bar in 10 represents 100 μm, in the other figures 250 μm.

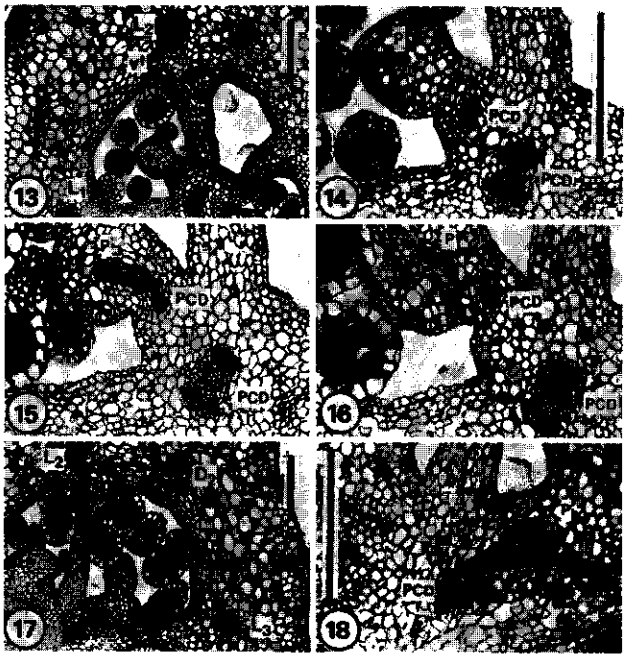

Fig. 7-6, **13** to **18**: Examples of the vascular supply of the placentae by divided complex placental traces (PCD) in the axis of the ovary; **13**: very base of the ovary (see the scale in Fig. 7-7 and compare with the diagram in Fig. 7-9 (traces PCD at the level 13 – 16); **14**: detail of 13 showing the two traces PCD and a placental bundle (p) in the placenta in the locule between the laterals L_1 and L_2; **15**: the same, but slightly above 14, the placenta is supplied by a horizontal branch from one of the traces PCD; **16**: above 15, the placental bundle p and the trace PCD are no longer connected, and both continue vertically (compare with Fig.7-9, lobes L_1/L_2, levels 13 – 16); **17**: section of the ovary below level c in Fig. 7-9, showing the vascular supply of the placenta in the locule between the lateral traces L_2 and L_3 (compare with Fig. 7-9, lobes L_2/L_3, level 17 – 18); **18**: detail of 17.
14 – 16 same scale, bars represent 250 μm.

are produced in the transition of the pedicel and the ovary. Similarly, the bundles which form the trace **PC** in *B. squamulosa*, are interpreted as placentals.

The bundles of the outer groups (marked **v**) continue to shift outwards, and gradually they fuse with the pedicel bundles **2** and **4** (Figs. 7-6-3 to -8) which continue in the ovary as the lateral traces $\mathbf{L_2}$ and $\mathbf{L_4}$. The bundles which fuse with the pedicellar bundles are interpreted as ventrals, because they produce the placental bundles which yield the trace **PC** (Figs. 7- 6-3 to -11). A fusion of ventral bundles with lateral bundles in the base of the ovary was also observed by Barabé et al. (1985, p. 406) in *B. masoniana*.

The fusion of ventral bundles with the pedicel bundles **2** and **4** indicates that the resulting traces $\mathbf{L_2}$ and $\mathbf{L_4}$ are 'complex' compound vascular bundles, because each comprises two lateral vascular bundles of adjacent carpels which are presumably intimately fused, as well as an indeterminate number of ventral bundles.

The pedicel bundles **1** and **3** do not receive any bundle from the centre of the flower. This implies that the traces $\mathbf{L_1}$ and $\mathbf{L_3}$ which are continuations of the pedicel bundles **1** and **3**, are 'simple' compound bundles, as each of them only includes two lateral veins of adjacent carpels.

The dorsal traces $\mathbf{D_4'}$ and $\mathbf{D_4}$ result from two independent tangential divisions of the pedicel bundle **4** which both occur at the same level (see Figs. 7-5-B and 7-6-12). Similarly, a tangential division of the pedicel bundle **2** yields the dorsal trace **D** 2 (see Figs. 7-6-6 to -12). The origin of the dorsal traces appears to be rather odd, since they are produced by a bundle that continues as a lateral trace in the ovary. A similar phenomenon has never been reported for *Begoniaceae* or in any other document on the vascular anatomy of the ovary that I have seen. Barabé et al. (1985, p. 405) stated that in *B. masoniana*, the dorsal bundles are always the first ones which leave the stele. Similarly, Charpentier et al. (1989a, p. 560) stated that in *B. horticola*, the dorsal bundles are a direct continuation of certain vascular bundles in the stele. It should be noted that in the flower studied here, the formation of the dorsal traces does not leave an opening or 'gap' in the stele.

Figs. 7-5-B and 7-6-12 show that except for the traces **D** and **L** there is also a bundle **v'** in the wall. This bundle is a branch of a ventral bundle that fuses with the pedicel bundle **2** (Figs. 7-6-3 & -4). Similar bundles **v'** occur in the ovary wall of *B. longipetiolata*, where they are ramifications from the ventral traces (see above and Fig. 7-3). The traces and the bundle **v'** are shown diagrammatically as vertical lines in Fig. 7-8. All the traces in the base of the ovary (Figs. 7-6-12 and 7-7-a) are still present in the very apex of the ovary (Fig. 7-7-j) and the lower part of the perianth-zone (Figs. 7-7-k & -l). However, bundle **v'** does not continue so far; it peters out above level e in Fig. 7-8 (see also Figs. 7-7-e & -f).

The traces $\mathbf{D_2}$, $\mathbf{D_4}$ and $\mathbf{D_4'}$ remain single in the ovary wall and they also continue as single vertical traces in the part of the gynoecium above the perianth-zone (Fig. 7-7-n). This illustration and Fig. 7-7-o show that each one of the traces $\mathbf{D_2}$, $\mathbf{D_4}$ and $\mathbf{D_4'}$ supplies a single style. Figs. 7-7-n & -o show that the style which stands over the locule between $\mathbf{L_1}$ and $\mathbf{L_2}$ is supplied by a trace marked $\mathbf{D_2''}$ (compare with Figs. 7-7-g to -i). Trace $\mathbf{D_2''}$ is a side branch of the lateral trace $\mathbf{L_2}$ that is produced at level h. At level d in Fig. 7-8, the trace $\mathbf{L_2}$ already produced the dorsal trace $\mathbf{D_2'}$, but this dorsal trace peters out above level i. This implies that the diagrams g, h, and i in Fig. 7-7 show two dorsal traces ($\mathbf{D_2'}$ and $\mathbf{D_2''}$) between the lateral traces $\mathbf{L_1}$ and $\mathbf{L_2}$. Although trace $\mathbf{D_2'}$ does not supply the style that stands over the locule between $\mathbf{L_1}$ and $\mathbf{L_2}$, it is interpreted as a true dorsal trace. The evidence for this interpretation is based on two facts: **i)** The other dorsal traces $\mathbf{D_2}$, $\mathbf{D_4}$ and $\mathbf{D_4'}$ originate by a tangential division of the pedicel bundles **2** and **4** which continue without any interruption or shift in their position as lateral traces. Similarly, $\mathbf{D_2'}$ is produced by a tangential division of the lateral trace $\mathbf{L_2}$ that is a direct continuation of the pedicel bundle **2**. **ii)** Like the other dorsal traces, $\mathbf{D_2'}$ is linked with placentae by bundles which are not attached to lateral traces (page 131).

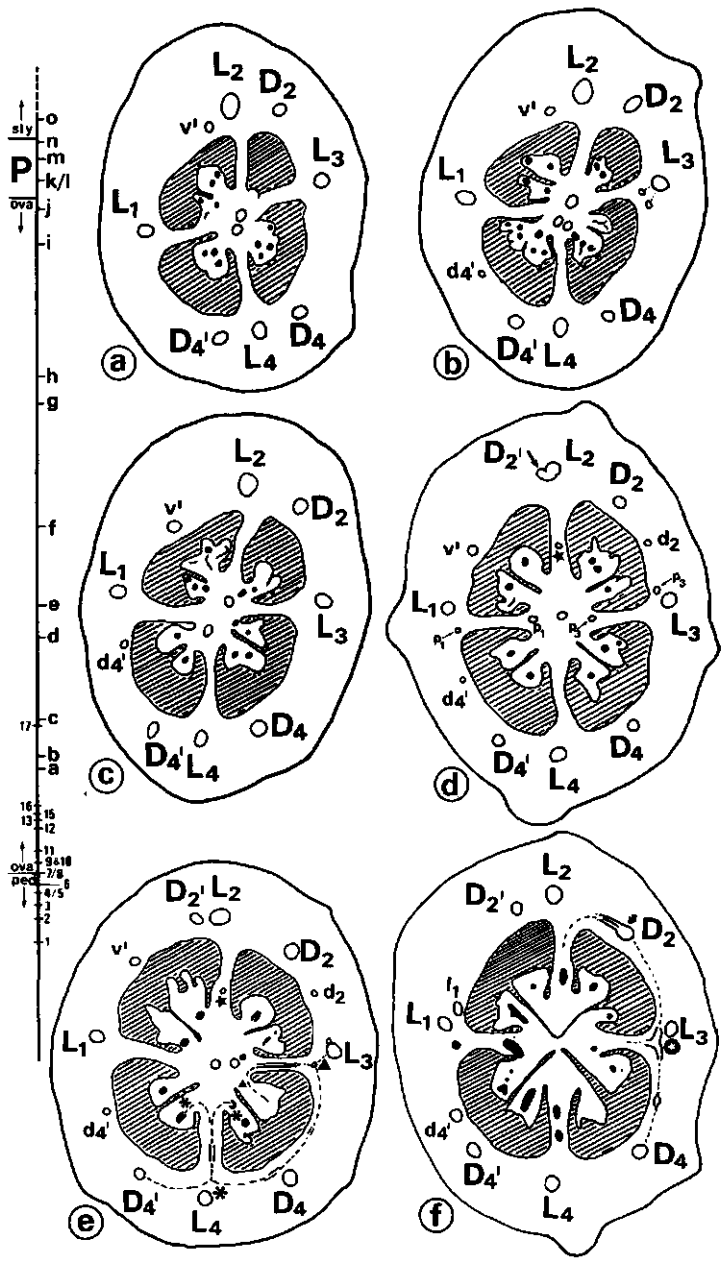

Fig. 7-7, *B. squamulosa*, diagrammatic drawings of consecutive transverse sections of the pistillate flower of which Fig. 7-6 presents photographs of sections. The letters along the scale indicate the level of the sections, the numbers that of the sections presented in Fig. 7-6. For abbreviations and markers see page 103 and compare with Figs. 7-2 and 7-9.

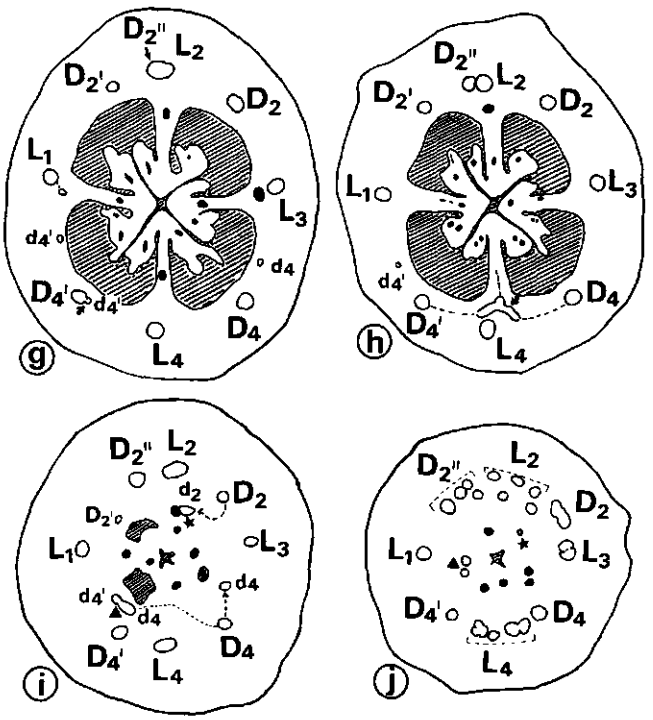

Fig. 7-7, **g** & **h**: unilocular situation with parietal placentation; trace L_2 begins to produce the trace marked D_2'' that supplies the style standing over the locule between L_1 and L_2 (compare with Fig. 7-8, L_2 & D_2'', levels h to i, and Fig. 7-7-diagram o); in **h**: the dotted lines indicate the connections of the traces D_4 and D_4' with a placental bundle that passes through the septum opposite to the trace L_4 (compare with Fig. 7-8, level h); **i** & **j**: top of ovary; in **i**: in the centre the stylar canal and three small locules without placentae; the triangle indicates the anastomosis of the bundles d_4' and d_4 (see Fig. 7-8, between D_4' and L_1, level i); **j**: all traces except L_1 have started to ramify; note that bundle D_2' has petered out (compare with Fig. 7-8, L_1 and D_2', between levels i and j);

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a to **f**: 4-locular situation with axile placentation; in **a** to **e**: the black bundles in the centre are placentals and the open bundles divided complex placental traces (PCD in Fig. 7-9).
a: base of ovary, the placentae in locules still entire (for sections below this level see Figs. 7-6-1 to -12); **b**: the placentae in three of the four locules bifid **c**: all locules with bifid placentae; **d**: the parietal placental bundle (p_1) that is produced by the trace L_1 is sectioned twice because it follows an arching course in the septum; similarly, the placental bundle p_3 produced by L_3 is sectioned twice (see Fig. 7-9, L_1 and L_3, level d); trace L_2 begins to ramify and produces the bundle marked D_2' that peters out below the perianth (compare with Fig. 7-8, D_2', levels d to i); **e**: dotted lines indicate the connections of placental bundles passing through the septae opposite to the traces L_3 and L_4 (compare with Fig. 7-8, traces L_3 to D_4', level e and Fig. 7-9, level e); **f**: idem for the placental bundles passing through the septa opposite to the traces L_2 and L_3 (compare with Fig. 7-8, L_2 to D_4, level f). For the origin and marking of the various traces and bundles see Figs. 7-8 and 7-9.

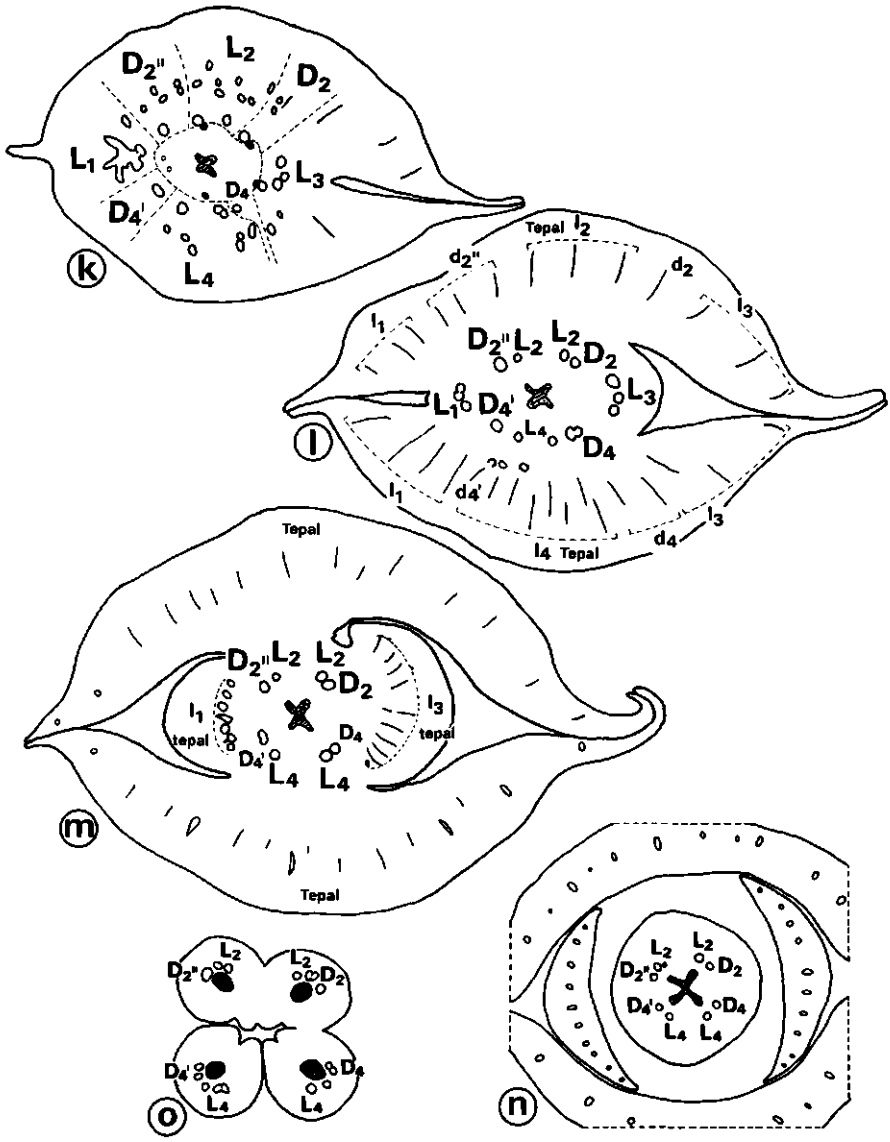


Fig. 7-7, **k** to **m**: perianth zone; in **k**: transition between top of ovary and perianth; **l**: the vascular supply of the large perianth segments (Tepals); **m**: idem of the small perianth segments (tepals); **n** & **o**: stylar zone; in **n**: the four perianth segments are free from each other and no longer attached to the four styles which are fused with their bases; **o**: the vascular supply of the four styles which are almost free from each other,

The presence of the two dorsal traces D_2' and D_2'' opposite the locule between L_1 and L_2 (Figs. 7-7-h & -i) suggests that two incompletely developed carpels are involved in the formation of the ovary wall. The presence of incompletely developed carpels is also apparent in transverse sections of the ovary of a flower with four styles which may show a five-locular condition. The presence of four styles would suggest that the gynoecium is formed by four carpels, while the sections indicate that the flower is in fact five-carpellate (see Chapter 6, p. 94).

As in *B. longipetiolata*, the flower of *B. squamulosa* studied here is characterized by two more or less independent vascular systems which supply the placentae. Fig. 7-9 shows that the placentae in the lower part of the ovary are supplied by bundles from the axis of the ovary, while at a higher level in the ovary they are supplied by bundles produced by the lateral traces which are situated in the wall.

The origin of the trace **PC** and its branches **PCD**, which represents the axial placental system, is discussed on page 119. The photograph in Fig. 7-6-12 shows that ovules have developed in the very base of the ovary. Although not shown in the drawings of the sections in the Figs. 7-7-a & -b, the placentae in these sections bear ovules as well. However, these drawings do show that the placentae are vascularized. The shaded bands in Fig. 7- 9 represent the placentae which have thin vascular bundles in their parenchyma. The illustration indicates that these thin vascular bundles are vertical continuations of several more or less horizontal ramifications of the traces **PCD**. Except for the locule between L_1 and L_2, these horizontal ramifications occur above the levels a and b in Fig. 7-9. Because there is already vascular tissue in the placentae below the levels a and b, it is evident that the vascular bundles in the placentae run in both a downward and an upward fashion as soon as they are produced by the horizontal ramifications of the traces **PCD** into the placentae. Details of the vascular supply of the placentae by the axial placental system in this zone of the ovary are presented in Figs. 7-6-13 to -18.

The next paragraphs deal with bundles which enter the septa and supply the placentae from the traces in the ovary wall. Collectively, these traces and bundles constitute the parietal placental system. The pattern of these bundles is shown diagrammatically in the Figs. 7-8 and 7-9.

Fig. 7-9 shows that the trace L_1 and the opposite trace L_3 produce the bundles marked p_1 and p_3. These bundles follow an arching course in the septa before they anastomose with the vascular tissue in the placentae. Bundle p_1 supplies a single lobe in the locule between the traces L_1 and L_2, whereas p_3 supplies both opposite lobes on the septum that is opposite to trace L_3. The traces L_2 and L_4 produce bundles (p_2 and p_4) which proceed in a more or less horizontal manner in the septa. Each of these bundles supplies the two opposite lobes on the pertaining septum. The bundles p_1 to p_4 are situated somewhat below the level where the placentation becomes parietal (see Fig. 7-7-h).

Each of the bundles p_1 to p_4 links the placentae on a septum with the lateral trace that is opposite to the septum. However, above the zone where the bundles p_1 to p_4 are situated, there are other bundles which constitute connections be-

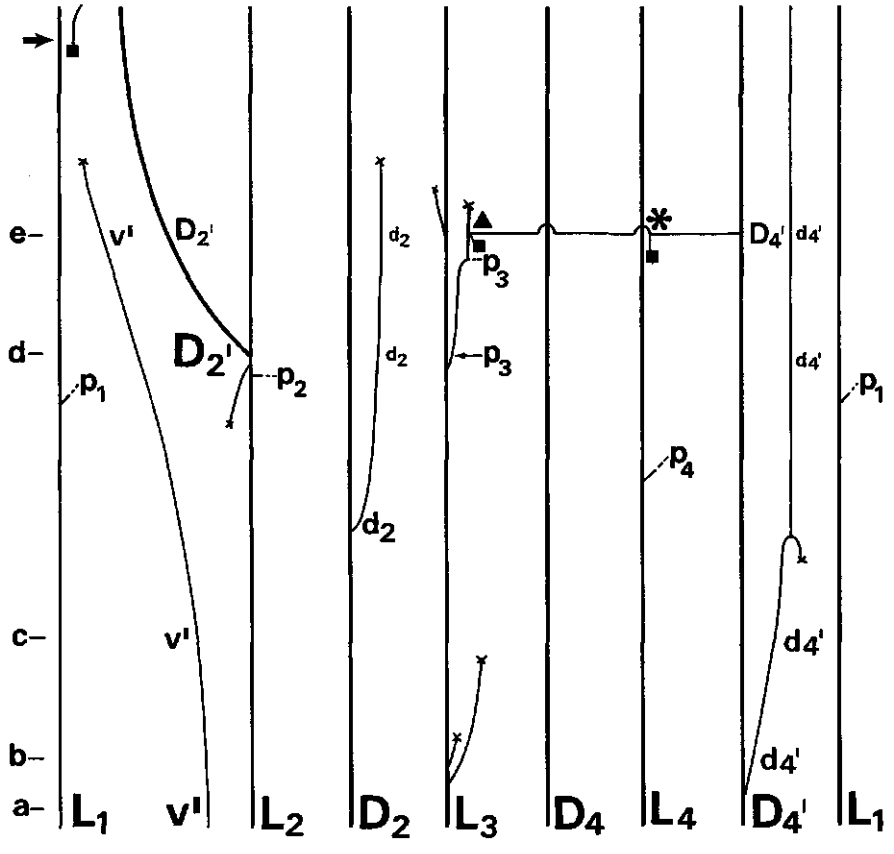
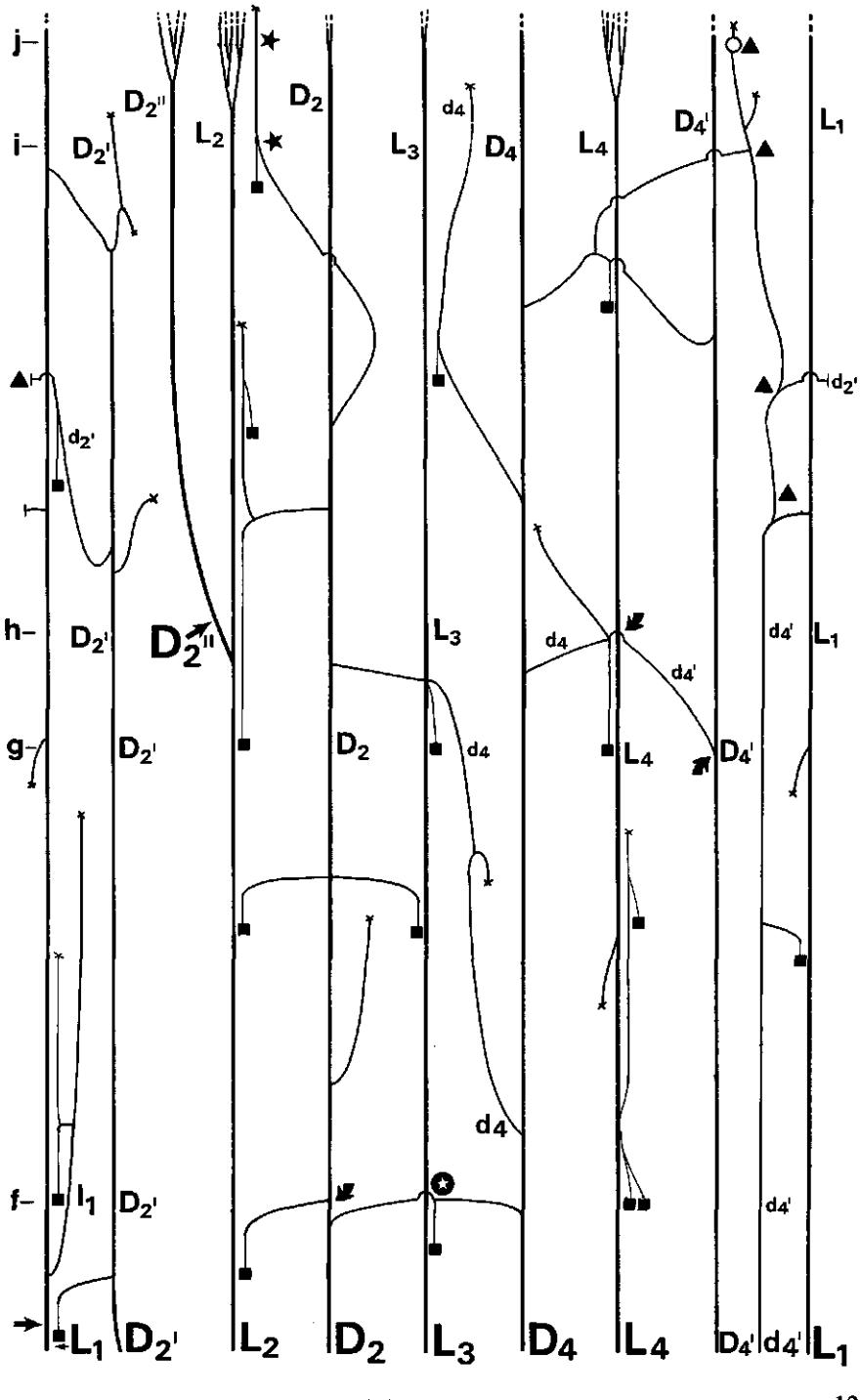


Fig. 7-8, *B. squamulosa*, the ovary laid open with the longitudinal pattern of the vascular system in the wall. For markers and abbreviations see page 108, the lines with black squares represent bundles passing through the septa towards the placentae. The letters in the left margin along trace L_1 refer to the diagrams in Fig. 7-7. Top of diagram continued overleaf.

Fig. 7-8, continued (Top).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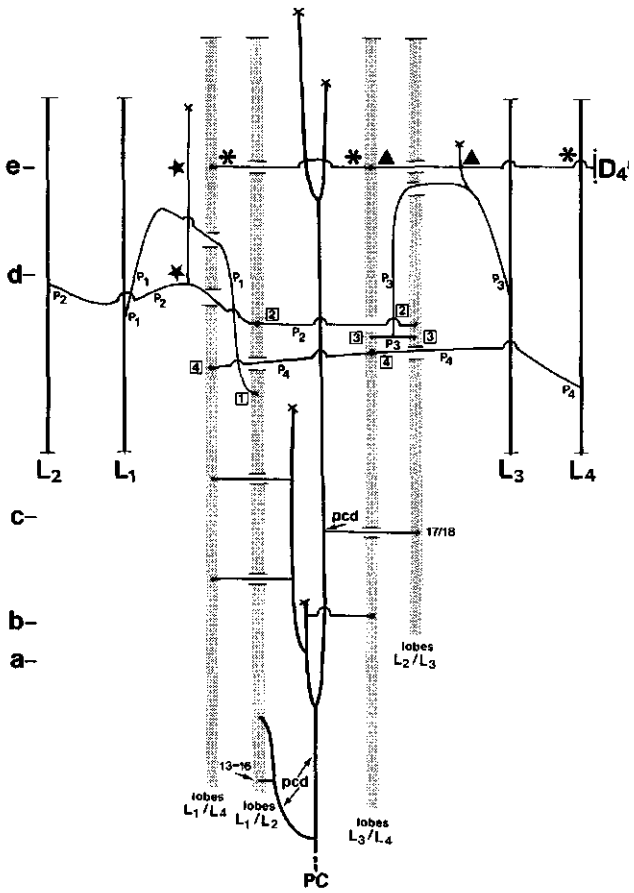


Fig. 7-9, *B. squamulosa*, diagram demonstrating the longitudinal pattern of the placental vascular system. The traces marked PC and PCD in the axis of the flower represent the axial placental system. The bundles marked p between the levels c and d are parietal placentals produced by the traces L. The placentals p_1 to p_4 and the traces L_1 to L_4 form the parietal placental system. The parietal placental bundles pass through the septa and supply the placentae. The latter are indicated by shaded bands; each band represents an entire or, at a higher vertical level, a bifid placental ridge, which is formed by the margins of a single carpel. The letters in the left margin along trace L_2 refer to the diagrams in Fig. 7-7; the numbers in the illustration to the photographs in Fig. 7-6. For markers and abbreviations see page 103.

tween the placentae and dorsal traces. These connections are shown especially in the top part of Fig. 7-8. Similar connections have also been observed in the ovary of *B. longipetiolata*. An example of these connections which may be quite complex, is shown in the section illustrated in Fig. 7-7-e.

In this section, partially dotted lines indicate that the dorsal trace D_4' is linked by a horizontal bundle to the placental lobes of adjacent carpels on the septum

opposite L_4. Along its course in the ovary wall, the horizontal bundle remains free from both the traces L_4 and D_4 and it proceeds towards the trace L_3. The bundle remains free from L_3 when it passes through the septum into the placentae. Near trace L_3, the horizontal bundle forms a joint with the vertical branch of the bundle p_3 before the branch peters out (see also the triangle at level e in Figs. 7-8 and 7-9). Thus the horizontal bundle links the dorsal trace D_4' with the placentae situated on the septa which are opposite to the lateral traces L_4 and L_3. Similarly, another horizontal bundle links the placentae on the septum opposite to L_3 and the dorsal traces D_2 and D_4 (Fig. 7- 7-f). This horizontal bundle between D_2 and D_4 is also shown diagrammatically in the top part of Fig. 7-8, level f.

It has been mentioned on page 123 that the trace D_2' is interpreted as a true dorsal, because apart from its origin, it is linked with placental tissue. The top of Fig. 7-8 (left side) shows that above level h, the trace D_2' produces a bundle d_2' that passes along trace L_1 and is connected with a placental bundle in the septum opposite to L_1. The bundle d_2' forms a joint with a vertical bundle marked by triangles (Fig. 7-8, right side). The bundle marked by the triangles, in its turn, forms a joint with an unmarked bundle (level i) that is a continuation of a transverse curved bundle between the traces D_4 and D_4'. Near trace L_4, the transverse bundle is connected with a placental bundle in the septum opposite to L_4. Thus the dorsal trace D_2' is linked with the placentae on the septa opposite to L_1 and L_4 by means of several bundles following devious courses.

Diagrams 7-7-n & -o show that each style receives a single dorsal trace that represents the mid-vein of a carpel. It was postulated on page 13 that each lateral trace represents at least two intimately fused veins of adjacent carpels. This postulate is supported by the observation that each one of the traces L_2 and L_4 supplies two adjacent styles (Fig. 7-7-n). However, this diagram shows that the lateral traces L_1 and L_3 do not contribute to the vascularisation of any of the styles. It should be noted that L_2 and L_4 are 'complex' bundles, while L_1 and L_3 are 'simple', because L_2 and L_4 include bundles which are interpreted as ventrals. The latter fuse with the pedicel bundles **2** and **4** which are the precursors of the traces L_2 and L_4. A fusion of ventral bundles with the pedicel bundles **1** and **3** does not occur (page 123).

Each of the outer perianth segments is supplied by five traces (**Tepals** in Fig. 7-7-l). This illustration shows that the sides of both segments receive bundles which are produced by the lateral traces L_1 and L_3 (see **Tepals** in Fig. 7-7-l). Diagram 7- 7-m shows that each one of the traces L_1 and L_3 also supplies a single inner perianth segment (**tepal**).

7.2.2.3. *B. elaeagnifolia*

The sections studied were prepared from a single-flowered inflorescence of a cultivated specimen of the gathering Breteler & De Wilde (1978)-8. The flower had two styles. Another ovary of the same specimen, but referred to as *B. schultzei* Engl., was investigated by Reitsma (1983, fig. 7B). His drawing of a section shows three parietal septa.

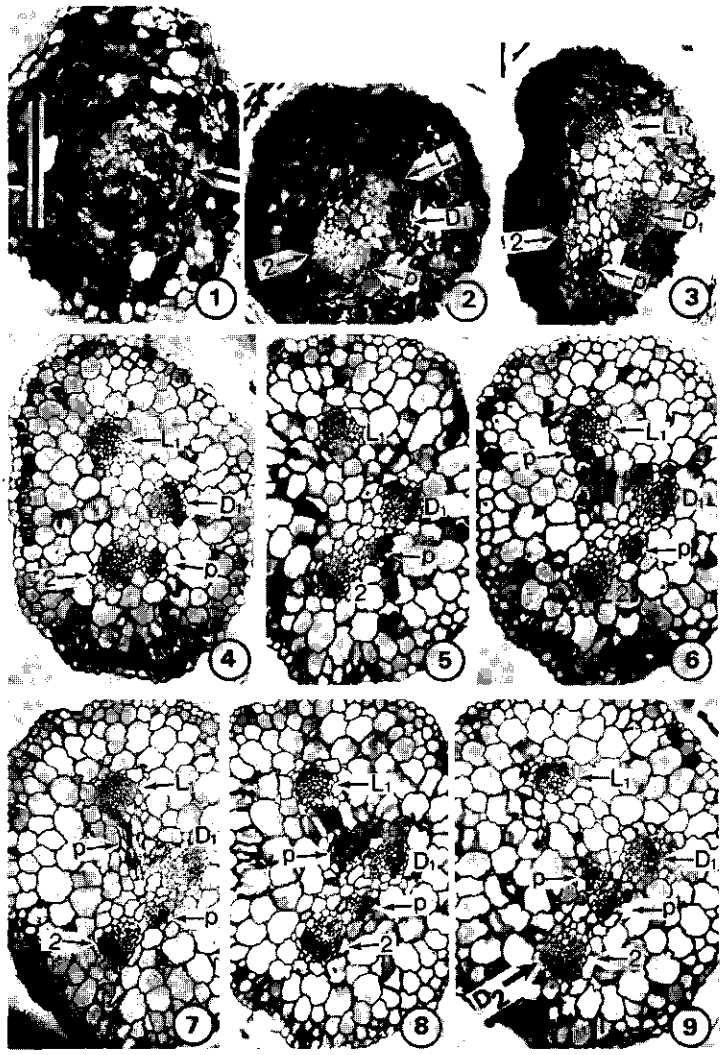


Fig. 7-10: *B. elaeagnifolia*, photographs of consecutive transverse sections of the pistillate flower of which sections are shown diagrammatically in Fig. 7-11. The level of each section is indicated by a number corresponding with that in the scale in Fig. 7-11. For markers and abbreviations see page 103 and compare with Fig. 7-12.
1: base of the pedicel with two strands separated by a single layer of parenchyma cells (arrow); **2:** four closely aligned strands **3:** the four strands separated, note that one strand in photograph 1 has produced two strands which, in the base of the ovary, become the lateral (L_1) and dorsal (D_1) traces, while the pedicel bundle or strand 2 has produced a placental (p); **4** and **5:** idem; **6:** the strand marked L_1 produces the second placental (p); **7:** the placental bundle (p) free from L_1, note the minute bundle that connects the placental with the dorsal trace D 1; **8:** the two placentals still separate, but in 9 and 10 (overleaf) they are closely aligned forming the complex placental trace PC; **9:** the thick arrow indicates the begin of the formation of the dorsal trace D 2 by the pedicel bundle or strand 2. Compare 1 with Fig. 7-10-diagram a and 9 with Fig. 7-10-diagram b.
All figures at a similar scale, bar in 1 represents 250 µm.

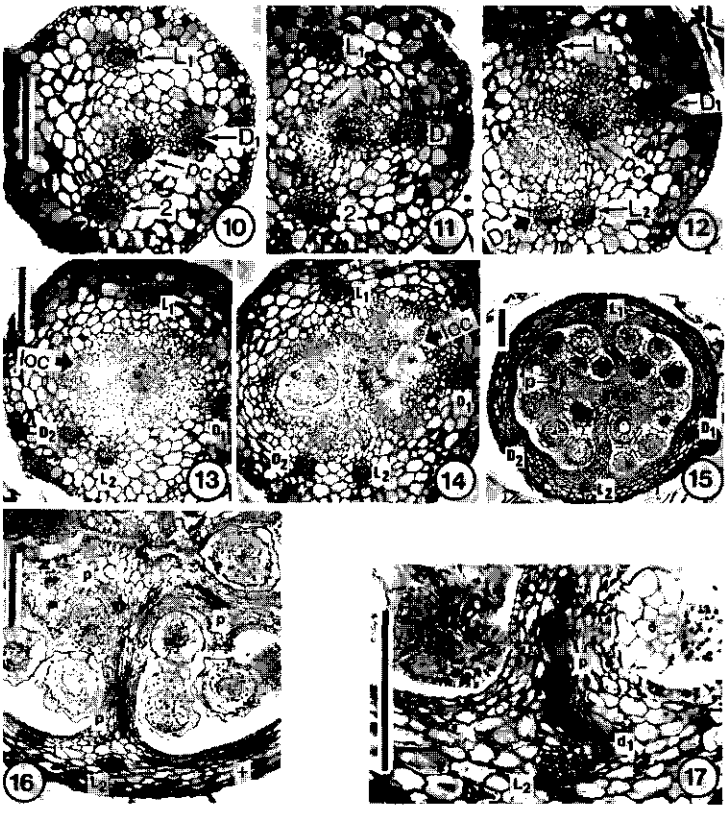


Fig. 7-10, **10** to **14**: transition between pedicel and base of ovary; in **10:** formation of the complex placental trace (PC) in the centre of the pedicel by anastomosis of the two placentals; **11:** the arrows indicate small parenchyma cells which cover the ovarial cavities; **12:** the pedicel bundle or strand 2 has produced two strands which, at a higher level, become the lateral trace L_2 and the dorsal trace D_2 (thick arrow); **13 & 14**: base of ovary showing one and two locules respectively, the dorsal and lateral traces in the ovary are in place (compare 14 with Fig. 7-11- diagram c); **15:** bundle (p) in one of the placentae produced by a divided complex placental trace PCD at a slightly higher level (compare with Fig. 7-12B, level 15); **16:** parietal placental bundle (p) produced by the trace L_2. The placental passes through the septum in a more or less horizontal manner and supplies the two opposite lobes belonging to adjacent carpels (compare with Fig. 7-11B, L_2, level 16); **17:** connection between the placental (p), trace L_2 and the bundle d_1 (compare with Fig. 7-11-diagram i and with Fig. 7-12A & B, L_2, level 17); the bundle d_1 is produced by the trace D_1 (see Fig.7-12A, D_1 between the levels h and i). For the markers and the origin of the bundles and traces see Fig. 7-12.
10 – 12 and 13 & 14 respectively same scale, bars represent 250 µm.

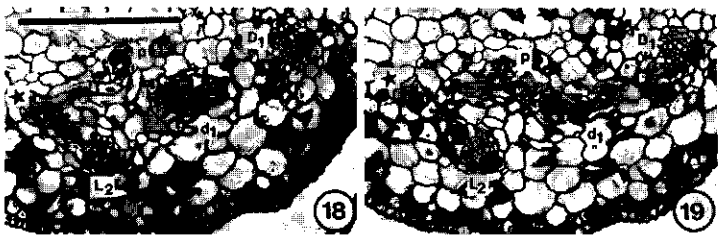


Fig. 7-10, **18** & **19**: top of ovary without locules; successive sections demonstrating the connection between the vascular bundles shown in Fig. 7-11-diagram k; for the marking and the origin of the bundles see top of Fig. 7-12 A & B, L_2, level 18/19 above level k.
18 & 19 same scale, bar in 18 represents 250 µm.

The interpretation of the vascular bundles in the base of the ovary shown in Figs. 7-11-c & -d is in line with that of *B. squamulosa*. The vascular bundles opposite to the locules are the dorsal traces $\mathbf{D_1}$ and $\mathbf{D_2}$, whereas those that are opposite to the septa are the lateral traces $\mathbf{L_1}$ and $\mathbf{L_2}$. The dorsal traces originate from the pedicel bundles **1** and **2** by tangential division, while the lateral traces are direct continuations of these pedicel bundles. The origin of the traces is indicated diagrammatically by arrows in Figs. 7-11-b and -c. A similar origin of the dorsal traces from the pedicel bundles has been observed in *B. squamulosa* (see above). In particular, the origin of the dorsal trace $\mathbf{D_2}$ as a side branch from the pedicel bundle **2** that continues as the lateral trace $\mathbf{L_2}$ is clearly demonstrated in the photographs depicted in Figs. 7-10-1 to -14.

In the very base of the pedicel (Figs. 7-10-1 and 7-11-a), the vascular tissue forms a solid column that is situated in the axis. The tissue in the column consists of two strands, **1** and **2**, which are separated from each other by a very thin and inconspicuous layer of parenchyma. When the two strands begin to separate further, both strands ramify simultaneously (Fig. 7-10- 2). The first strand that represents the pedicel bundle **1**, yields two vascular bundles which, in the base of the ovary, become the traces $\mathbf{L_1}$ and $\mathbf{D_1}$. The other strand, marked **2**, gives off a bundle marked **p** in Figs. 7-10-3 and -4 before it yields the trace $\mathbf{D_2}$ and continues as the lateral trace $\mathbf{L_2}$. Initially, the bundle **p** remains situated between bundle **2** and trace **D** 1 (Figs 7-10-4 to -9), and Fig. 7-10-9 shows that it joins another bundle **p** which is produced by **L** 1 (Figs. 7-10-6 to -8). The two bundles **p** associate into the trace **PC** that rapidly shifts into the axis of the ovary (Fig. 7-10-10). Trace **PC** is the base of the axial placental system shown diagrammatically in Fig. 7-12B. Observation of various sections revealed that the trace **PC** consists of three to five individual vascular bundles which anastomose and divide repeatedly. Thus in the base of the ovary (Figs. 7-10-13 to -15 and 7-11-d) there are five traces, viz.: $\mathbf{D_1}$, $\mathbf{D_2}$, $\mathbf{L_1}$, $\mathbf{L_2}$ and **PC**.

Diagram 7-12B shows that the axial placental system consisting of the trace **PC**, its branches **PCD** and several horizontal ramifications, supplies the placental lobes in the base of the ovary. The axial system terminates below level f, so that the section in Fig. 7-11-e still shows three open bundles which represent the branches **PCD** in its centre.

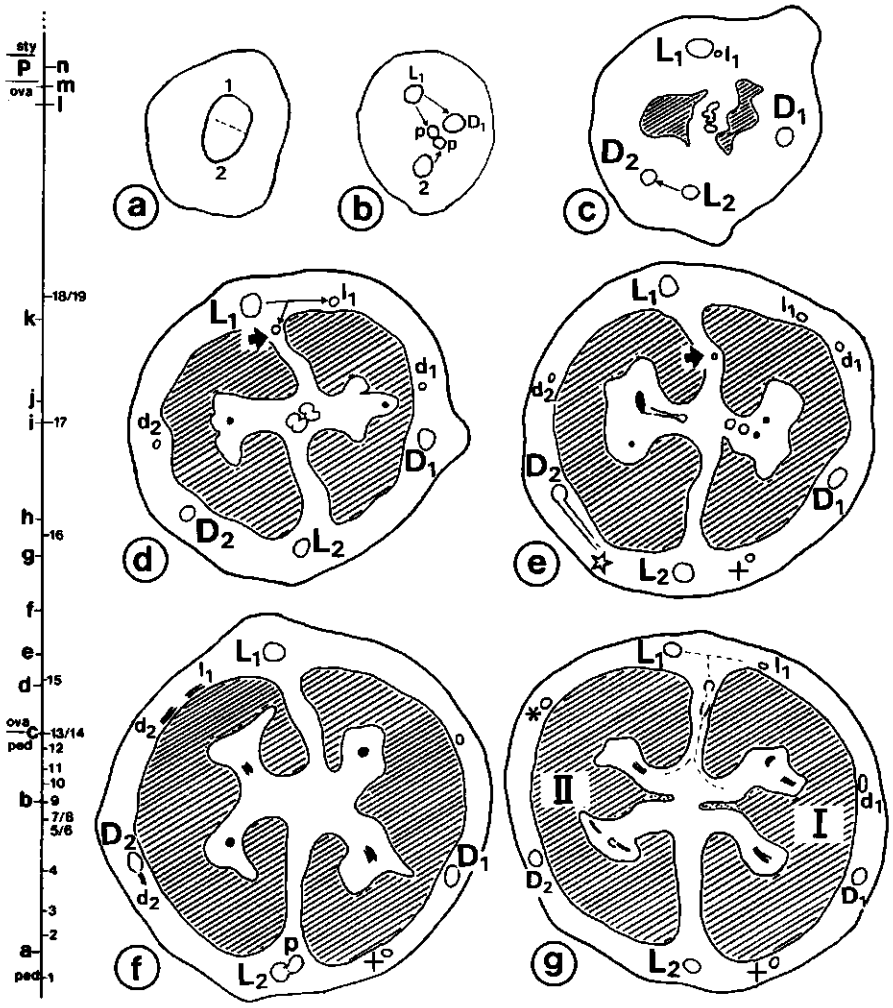


Fig. 7-11: *B. elaeagnifolia*, diagrammatic drawings of transverse sections of the pistillate flower of which Fig. 7-10 presents photographs of sections. The letters along the scale indicate the level of the sections, the numbers that of the sections in Fig. 7-10. In the centre of the diagrams, the unmarked black bundles are placentals, the open bundles in **c** to **e** are complex and/or divided complex placental traces (PC and PCD respectively, see Fig. 7-12B, below level f).
a and **b:** pedicel zone; **c** to **g:** ovary zone with a two-locular situation and axile placentation. **a:** two vascular strands separated by a single layer of parenchyma (see Fig. 7-10-photog. 1); **b:** pedicel bundle or strand 1 in diagram a has ramified into three strands which, at a higher level, become the lateral trace L_1, the dorsal trace D_1 and a placental bundle (p); between the levels a and b, the pedicel bundle or strand 2 has produced a placental bundle (p); **c:** base of ovary with two locules, in the centre the complex placental trace, the dorsal trace D_2 and the lateral trace L_2 have been produced by the pedicel bundle or strand 2 shown in diagram b (see Figs. 7-10-9 to -14, and Fig. 7- 12A between levels b and c), trace L_2 is a direct continuation of the pedicel bundle 2; **d** & **e:** two-locules; in each locule an entire placenta that is formed by the margins of a single carpel, the arrow indicates a parietal placental bundle produced by trace L_1 that does not enter the placentae (compare with Fig. 7-12A & B, L_1, levels d and e); **f** and **g:** the placentae in each locule bifid, in **f:** the bundle marked p near L_2 is a parietal placental bundle that supplies the placental lobes belonging to adjacent carpels (see Fig. 7-12, L 2, level f); in **g:** the locules marked I and II are opposite the dorsal traces D_1 and D_2 respectively. For the markers and the origin of the traces and bundles see Fig. 7-12.

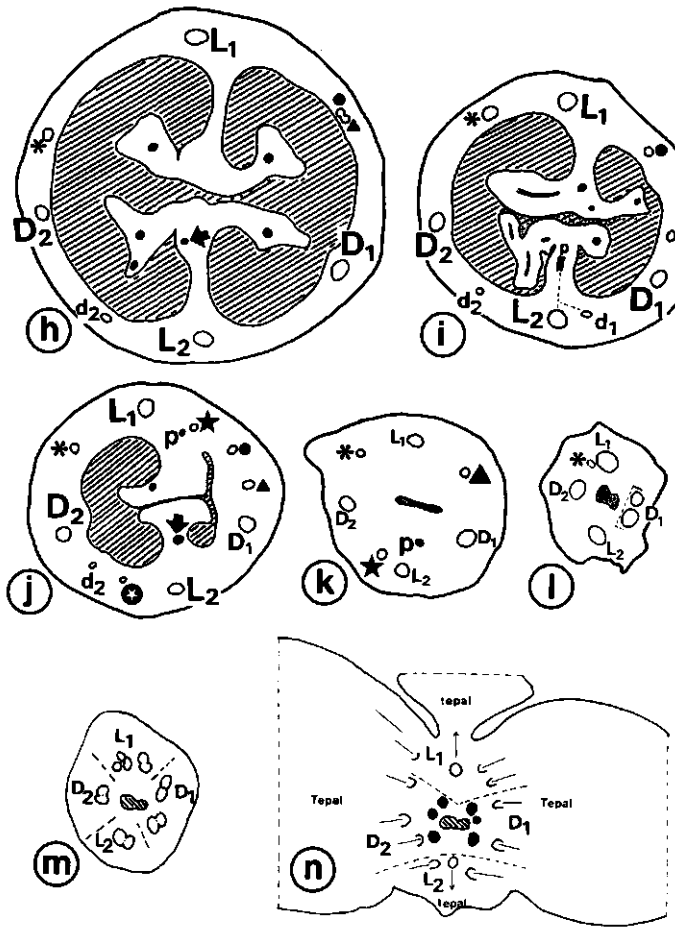


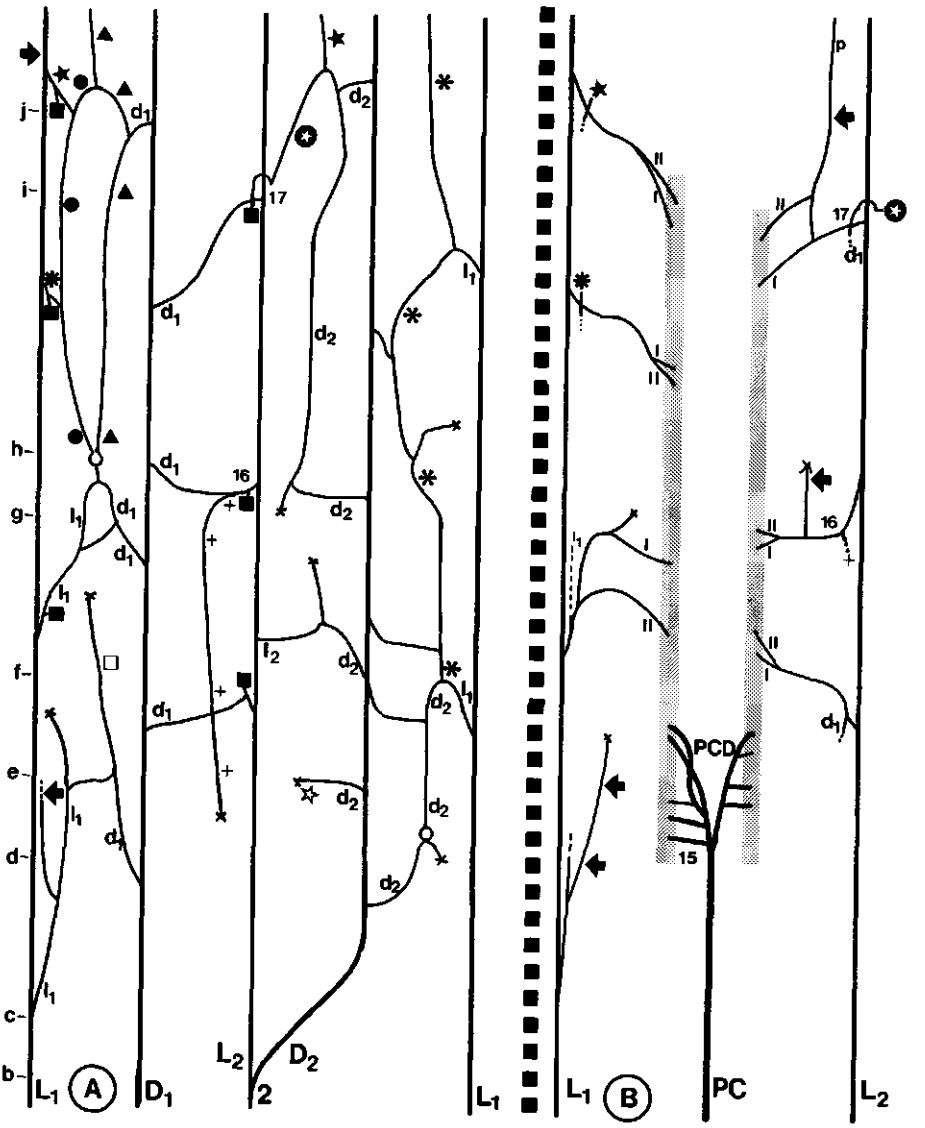
Fig. 7-11, **h** to **j**: uni-locular situation with parietal placentation, the placentae attached to a septum belong to adjacent carpels; in **h**: the arrow indicates a placental bundle that peters out in the septum (see Fig. 7-12B, level h); **i**: the dotted line indicates the connection between a placental, trace L_2 and the bundle d_1; **j**: the arrow indicates a placental bundle that recedes from the placentae and at a higher level fuses with trace L_2 (see Fig. 7-12B, L_2, level k); **k** to **m**: very top of ovary with in l and m ramification of the traces; **n**: perianth zone, diagram showing the origin of the bundles which supply the perianth segments and the two styles; the black bundles which are derived from the dorsal traces, enter the styles. One style receives bundles produced by D_1 and the other style bundles produced by D_2. For the markers and origin of the traces and bundles see Fig. 7- 12.

Diagram 7-12B also shows that above the axial placental system, the placentae are supplied by bundles from the ovary wall. These parietal placental bundles are produced by the traces $\mathbf{L_1}$ and $\mathbf{L_2}$. Initially, each bundle that proceeds into a septum is single, but the diagram shows that the bundles usually bifurcate into two branches, each of which enters a lobe of adjacent carpels. A photograph of a more or less horizontal parietal placental bundle **p** that bifurcates and supplies opposite lobes is reproduced in Fig. 7-10-16. It should be noted that in the very base of the ovary, trace $\mathbf{L_1}$ produces an ascending bundel $\mathbf{l_1}$ that proceeds in the wall towards trace $\mathbf{D_1}$. Where the bundle is opposite to the septum, it branches and gives off a single bundle that passes into the septum in an upward fashion. The bundle in the septum does not reach a placenta, but peters out so that is is interpreted as a 'vestigial' placental bundle (see Figs. 7-12A & B).

The same diagrams demonstrate that the parietal placental bundles are connected to bundles in the wall which follow a rather irregular course before they are attached to the dorsal traces. This implies that the dorsal traces in this zone of the ovary are linked with the placentae. A similar linkage has been observed in the ovaries of both *B. longipetiolata* and *B. squamulosa*. However, there is also another connection. As already discussed above, the diagram in Fig. 7-12 illustrates that the bundles in the wall are attached to the parietal placental bundles which in their turn are attached to the lateral traces. Because of these connections, the traces **L** are linked by both the placental bundles and the bundles in the wall to the dorsal traces **D**. An example of a part of this complex linkage system is shown in the diagram in Fig. 7-11-i as well as in the photograph of Fig. 7-10-17. In the illustration, trace $\mathbf{L_1}$ has produced the parietal placental bundle **p** that passes though the septum into the placentae. The bundle **p**, in its turn, is attached to the ascending bundle $\mathbf{d_1}$ that has been transversely sectioned. The bundle $\mathbf{d_1}$ is produced by trace $\mathbf{D_1}$. The pattern of the linkage between all these veins is shown diagrammatically in Figs. 7-12A & B (see $\mathbf{L_2}$, just below level i at number 17).

A similar linkage that involves connections between the traces $\mathbf{L_2}$ and $\mathbf{D_2}$, a placental bundle **p** and two bundles in the wall, also occurs in the top part of the ovary where there are no longer placental lobes (Fig. 7-11-k). The connections between all these veins are also shown in the photographs in Figs. 7-10-18 & 19.

The Figs. 7-11-l & m show that there are no bundles in the very apex of the ovary. However, these illustrations show that all the traces ramify just below the perianth-zone. Finally, the diagram in Fig. 7-11-n demonstrates that each of the styles is supplied by bundles produced by a single dorsal trace or midvein of a carpel. Each of the outer perianth segments is supplied by the two lateral traces and a single dorsal trace. Note that the bundles in the sides of both segments originate from the lateral traces. A similar phenomenon has been observed in the outer segments of the other species investigated. Each of the inner perianth segments is supplied by a single lateral trace.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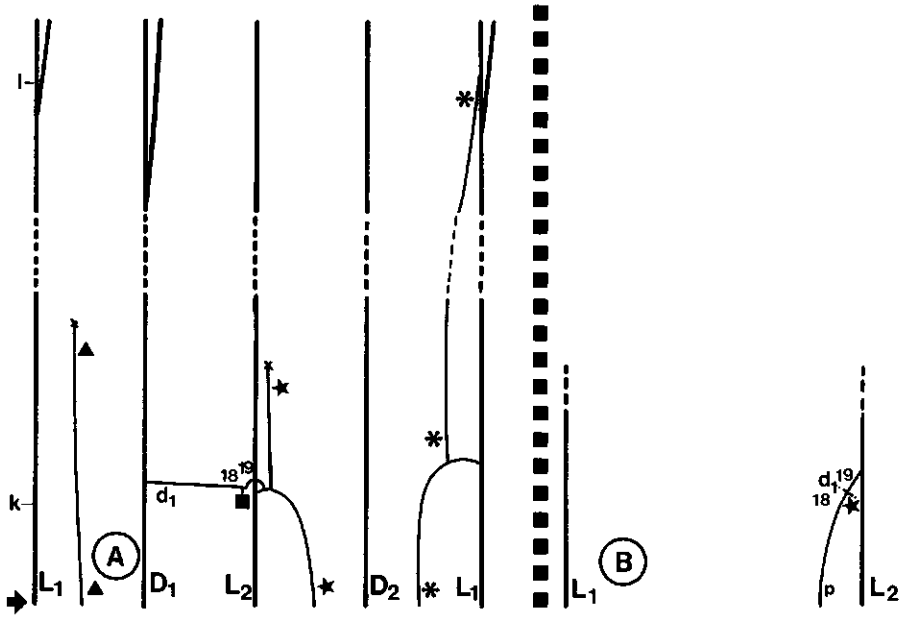


Fig. 7-12, continued (Top).

Fig. 7-12: *B. elaeagnifolia*, longitudinal pattern of the vascularisation of the ovary. At the left side of the blocked band the vascular system in the wall which is laid open (**A**), at the right that of the placental system (**B**). The letters along trace L_1 in the left margin refer to the diagrams shown in Fig. 7-11, the numbers in the figure to the photographs in Fig. 7-10. In **A**: the short lines with black squares represent placental bundles which pass through the septa and supply the placental lobes In **B:** The traces marked PC and PCD in the axis of the flower represent the axial placental system. The unmarked lines attached to the traces L represent parietal placental bundles which supply the lobes of adjacent carpels indicated by shaded bands. A branch marked I supplies a lobe opposite to trace D_1, a branch II a lobe opposite D_2. These placental bundles and the traces L_1 and L_2 constitute the parietal placental system. For markers and abbreviations see page 103.

7.3. Discussion and conclusions

7.3.1. The interpretation of the traces in the ovary

In the present study it has been found that the vascularisation of the ovary of *B. longipetiolata* differs from that of the other two species by the presence of fused ventral traces **vf**. In *B. squamulosa* and *B. elaeagnifolia* ventral traces are apparently absent. However, the vascularisation of the flowers studied can be supposed to be basically similar, as the species belong to the same section. This supposition also is supported by the observations of Charpentier et al. (1989b) who demonstrated that the ontogeny of the flowers in different taxa of *Begoniaceae* is basically similar.

The interpretation of the traces in the wall, viz.: the dorsal and lateral traces, complies with that of previous authors who investigated the flower in *Begoniaceae*. With the exception of Bugnon (1926), the interpretation of all other authors is in line with the classical concept of the carpel that has a single dorsal or median vein and one or, sometimes, several veins on each side of the dorsal vein (Bierhorst 1971, p. 519; Cutter 1971b, p. 238).

According to Cutter (loc. cit.), the ventral carpel veins or 'strands' *sensu* Cutter, usually supply the placentae and the ovules. As to the position of the ventral traces in the ovary of different *Begonia* species, Gauthier (1950) invariably interpreted the bundles in the axis of the ovary to be the ventral traces. The placentation in the species studied by Gauthier is axile for the entire length of the ovary. In contrast with the interpretation of Gauthier, Barabé et al. (1985) found that the vascular bundles in the axis of the ovary of *B. masoniana* are fused placental bundles which collectively unite into a complex placental trace **PC**, while each ventral trace is situated in the transition zone between the ovary wall and a septum. The placentation in *B. masoniana* is similar to that of the species studied here, because it is axile in the lower part and parietal in the upper part of the ovary.

It has been shown above that in *B. longipetiolata*, the placentae are supplied by two different and independent vascular systems, viz.: the axial and the parietal placental systems (see Fig. 7-4). The axial system consists of the trace **PC** and its branches **PCD** which supply the placental lobes from the axis of the ovary. Although the branches **PCD** with their ramifications supply the placentae, the branches do not represent ventral traces, which according to Cutter (see above) usually supply placentae, because each of the true ventrals is situated in the transition-zone between the ovary wall and a septum (see the traces **vf** in Figs. 7-2-b to -e). The traces **vf** in *B. longipetiolata* produce numerous placental bundles which supply the placentae from the periphery of the ovary (Fig. 7-4).

The presence of both an axial placental system and a parietal placental system in *B. longipetiolata* provides the key to the understanding of the vascular supply of the placentae in the ovaries of both *B. squamulosa* and *B. elaeagnifolia*. In these species there is also an axial placental system (Figs. 7-9 & 7-12B), but as already mentioned above, fused ventral traces are apparently absent. However, Fig. 7-9 demonstrates that in *B. squamulosa*, each trace marked **L** produces

a single bundle from the periphery of the ovary that passes through a septum and supplies the placentae. Similarly, Fig. 7-12B shows that in *B. elaeagnifolia*, each of the traces marked **L** produces three bundles which supply the placentae from the periphery of the ovary. In these syncarpous ovaries there happens to be only a single trace on each side of the dorsal trace. Because of their position in the wall, each of these traces is designated as a lateral trace **L**. Thus, the pattern of the traces in the wall indicates that each carpel has three veins, viz.: a single dorsal and two laterals. In the absence of other veins, each lateral trace **L** is assumed to represent the fused outermost veins of two adjacent carpels. As such, the traces **L** function as fused ventrals, and actually they could have been marked **vf**, because they produce parietal placental bundles.

In conclusion, it is clear that the ovaries of the three species studied are characterized by two independent placental vascular systems. The presence of an axial system and a parietal system in a single ovary at anthesis corresponds with the presence of two kinds of meristems in the young ovary in *Begoniaceae*. Charpentier et al. (1989a & b) demonstrated that a single axial meristem and, depending on the species, a variable number of parietal meristems determine the ontogeny of the ovary. These authors observed several vascular bundles in the axis of the ovary of *B. horticola* which peter out in the placentae. They interpreted these bundles to be 'placentals', but it is most likely that these bundles actually are branches **PCD** of the axial placental system. In the present study, these branches were found to peter out in a similar way.

It has been shown above that the dorsal traces in the ovaries of *B. squamulosa* and *B. elaeagnifolia* are side branches of pedicel bundles which continue as lateral traces. Figs. 7-1-5 & – 6 indicate that a similar phenomenon also occurs in *B. longipetiolata*. The origin of the dorsal traces as observed here, is very difficult to understand when it is assumed that the ovaries studied are entirely carpellate, hence foliar. Moreover, the formation of the dorsal traces is not accompanied by the formation of a 'gap' in the stele. According to Eames & MacDaniels (1925, p. 117), there is always a gap in the stele of a stem when the stele produces a vascular trace that supplies a leaf. In my opinion, the odd origin of the dorsal bundles and the absence of gaps indicate that the transition between the pedicel and the ovary or even the base of the ovary is not foliar but axial. This interpretation is supported by Charpentier et al. (1989b) who proposed the hypothesis that the ovary wall in *Begonia* is an intermediate structure between axial and appendicular organs.

7.3.2. The nature of the septa

Reitsma (1983) inferred from the way mature fruits dehisce, that each septum in species of e.g. *Begonia* section *Tetraphila* consists of both carpellar and placental tissue. Charpentier et al. (1989a, p. 570) did not support Reitsma's postulate.

There can be no doubt that the placentae in the species studied here, are situated on the margin or are part of the margin of the carpels which constitute the compound ovary. It has been discussed above that the traces **vf** or **L** represent the fused outermost veins of adjacent carpels. Theoretically, the outermost veins

are situated near or in the margins of a carpel. This implies that the position of the fused outermost veins of adjacent carpels would indicate where the carpel margins in the compound ovary have fused. Thus, from the position of the traces **vf** or **L** in transverse sections of an ovary, it can be inferred what regions in these sections correspond with the fused margins of adjacent carpels. Consequently, the portions of the septa situated on the adaxial sides of the traces **vf** or **L** in e.g. Figs. 7-2-d, 7-7-b and 7-11-e may be interpreted to be placental tissue. According to this interpretation, Reitsma's postulate can be supported.

7.3.3. The vascular supply of the perianth and the designation of the perianth parts

The outer perianth segments of the flowers studied are supplied by several traces from the ovary wall. In *B. longipetiolata* and *B. squamulosa* there are five traces and in *B. elaeagnifolia* three traces which yield the bundles that spread into these segments. Each of the inner segments is invariably supplied by a single lateral trace from the ovary wall.

According to anatomical literature, in dicotyledons a sepal usually has as many traces as a foliage leaf, while a petal receives one, sometimes three or more traces (Esau 1965, p. 544; Fahn 1967, p. 367). Barabé (1981, p. 822) found that in *B. handelii* Irmsch. of section *Sphenanthera*, the large segments receive eight bundles, while the small segments receive only one. Consequently, he described the large and small segments as sepals and petals respectively. Later, Barabé & Chrétien (1983, p. 315) investigated the female flower of *B. roxburghii* A. DC. also of section *Sphenanthera*, whose perianth parts are all of a similar size. They found that the parts of the inner whorl which are homologous with the petals in *B. handelii*, are supplied by two or three traces. Because of the similarity of all the perianth parts, they concluded that in *B. roxburghii* the parts of the outer whorl should be designated as petaloid sepals and those of the inner whorl as petals. According to Barabé et al. (1985, p. 410) the perianth parts of the female flower in *B. masoniana* Irmsch. of section *Coelocentrum* are arranged in a very flat spiral. The two or three large perianth parts in this species are sepals, because they are each supplied by eight bundles, while the single small part, which receives a single bundle, is a petal. Except for its subulate styles, the flower of *B. horticola* Irmsch. of *Begonia* section *Tetraphila*, very much resembles the flowers investigated here. The illustrations 4I and 4J in Charpentier et al. (1989a, p. 562) show that each of the outer segments is supplied by five traces, while each inner segment is supplied by a single trace. The authors (p. 560) designated the outer segments as petaloid sepals and the inner ones as petals.

Considering all the anatomical evidence presented above, I conclude that in the species analysed in this chapter, the outer segments represent sepals and the inner ones petals. Nevertheless, for practical purposes I have refrained from using these terms in the descriptions of the species considered in this study. Although the perianth parts in *Begonia* may differ in size, they are usually similar in colour and texture. The outer segments or sepals resemble the petals instead

of the foliage leaves, so that they may be designated as *petaloid* sepals. However, when the parts of the perianth are so similar, it is also valid to designate them simply as tepals (Weberling 1981, p. 16). In taxonomic studies in *Begonia*, this term is applied in e.g. De Wilde (1984), De Wilde & Arends (1979; 1980), Hallé (1972), Kéraudrin-Aymonin (1983), Sands (1977; 1990) and Wilczek (1969a & b).

Throughout this study, the four perianth segments are distinguished into a pair of outer segments and a pair of inner ones. This is in line with the terminology used by De Wilde in his inclusive study of *Begonia* section *Tetraphila*. However, in the illustrations of the vascular supply of the perianth (Figs. 7-2-k & -l; 7-7-l &-m and 7-11-n), the outer pair is indicated by 'Tepals' and the inner pair by 'tepals'.

7.3.4. The styles

Each style of the flowers investigated here is always supplied by a single dorsal trace. As to the supply by other traces, a single style may also receive bundles from two different lateral traces (*B. longipetiolata*) or from a single lateral trace (*B. squamulosa*). The styles in *B. elaeagnifolia* do not receive bundles from any lateral trace in addition to the supply by the dorsal traces. A similar supply of the styles was observed in the flower of *B. horticola* (see Fig. 4K in Charpentier et al., 1989a). Thus, from the observations in the present study and in Charpentier et al. (op. cit.) it appears that in *Begonia* section *Tetraphila*, the styles are always supplied by dorsal traces, whereas the supply by lateral traces is variable. The drawings in studies which were published before that of Charpentier in 1989, indicated that in *Begoniaceae*, a style is invariably supplied by all the major veins, viz.: dorsal, lateral and ventral veins of the pertinent carpel (e.g. Gauthier, 1950).

The pattern of the vascularisation of the styles of the flowers studied here demonstrates that each style is part of a single carpel, so that it is concluded that the styles are carinal. This conclusion corroborates those of Gauthier (1950) and Hall (1949) who refuted the interpretation of Saunders (1925) that in *Begonia*, a style would receive half of its vascular supply from each of two adjacent carpels, a situation that is denoted as commissural.

7.3.5. The nature of the ovary wall

Saunders (1925) was the first author who interpreted the pistillate flower in *Begonia* to be appendicular. Her conclusion, which is based on scanty evidence, was rejected by Bugnon (1926). This author interpreted the wall to be axial, whereas Gauthier (1950) supported Saunders's conclusion. For example, Gauthier (pp. 21, 22) stated that in *B. dregei* Otto & Dietr., the pistillate flower is the result of adnation of the calyx and the gynoecium. A longitudinal section of such an epigynous flower in which the hypanthium or floral tube is fused with the lower part of the gynoecium, is shown diagrammatically in Gifford & Forster (1989, fig. 19-32D). In their illustration, the hypanthium is shaded, while the ovary is white, so that the diagram suggests that both parts of the ovary *sensu lato*

can be distinguished. However, the photographs in this study as well as those in previous ones, e.g. Barabé et al. (1985), show that the tissue of the ovary is indistinguishable from that of the putative hypanthium. Therefore, on the basis of the assumption that the *Begonia* flower is appendicular, it must be postulated that the ovary and the hypanthium are merged completely.

Apparently, Gauthier (loc. cit.) also based his conclusion on this postulate. He supposed implicitly that both the ovary and hypanthium have their own vascular bundles. He designated the bundles in the ovary as 'cords' and those of the hypanthium as perianth bundles. This is evident from the way he indicated the vascular bundles in the ovary wall ('d.s'). Gauthier supposed such a dorsal vascular bundle to be compound, viz.: comprising a single dorsal ovary bundle or 'cord' and at least one bundle of the perianth or 'sepal strand', because the compound bundle supplies a style, while in the perianth-zone it yields bundles which dissipate into a sepal. Similarly, Gauthier (op. cit.) marked other vascular bundles in the ovary wall 'o.l.s', since he interpreted these bundles to consist of two outer carpellary veins belonging to adjacent carpels, and a certain number of sepal bundles. Other authors, e.g. Charpentier et al. (1989a, fig. 4), adopted the method of Gauthier and they marked the dorsal vascular bundles in the ovary wall of *B. horticola* 'dse', since they found that each of these bundles supplies both a style and a sepal.

On the basis of the assumption that the traces in the ovary are compound bundles, it is evident from the drawings of the supply of the perianth segments that in this study the traces **D** could be indicated by the formula 'd/se', because each of these traces always supplies a style and a sepal. The lateral traces **L** do not always supply the styles, but invariably they are involved in the supply of the perianth segments (see above).

In *B. elaeagnifolia*, each of the traces **L** comprises two outermost veins of adjacent carpels, because it produces parietal placental bundles (Fig. 7-12). Moreover, in the perianth-zone, each trace **L** supplies both sepals as well as a single petal (Fig. 7-11-n) Therefore, each trace **L** could be indicated by the formula 'l.l/se.se/pe'. It is concluded that in the perianth-zone of the flower, the fused carpel veins are no longer united with the bundles of the hypanthium. This indicates that in that zone of the flower, the perianth has become free from the ovary.

In *B. squamulosa*, the vascular pattern is more complex than that in *B. elaeagnifolia*. In the former species, each of the traces $\mathbf{L_2}$ and $\mathbf{L_4}$ supplies two adjacent styles and perianth segments, while $\mathbf{L_1}$ and $\mathbf{L_3}$ only supply the perianth segments (Figs. 7-7-l to -o). Thus, $\mathbf{L_1}$ and $\mathbf{L_3}$ show a behaviour that is similar to that observed for the lateral traces in *B. elaeagnifolia*.

Each of the traces $\mathbf{L_1}$ and $\mathbf{L_3}$ supplies two sepals and a single petal. Thus, e.g. $\mathbf{L_1}$ could be indicated by the formula 'se.se/pe'. However, Fig. 7-9 shows that at level d, $\mathbf{L_1}$ produces a single parietal placental bundle, so that it is evident that below that level the trace also includes two carpel veins of the carpels $\mathbf{L_1/L_2}$ and $\mathbf{L_1/L_4}$ respectively. Above level d, $\mathbf{L_1}$ does not produce any placental bundle. This phenomenon and the fact that the trace does not supply a style would sug-

gest that above level d, L_1 no longer includes fused veins of adjacent carpels. Consequently, it can be postulated that above level e, the ovary is no longer fused with the hypanthium. A similar postulate can be deduced from similar phenomena regarding the opposite trace L_3.

The postulate that above level d, the ovary is less intimately fused with the hypanthium is supported by the observation that in the part of the ovary above level e, the dorsal traces are linked by bundles with the placentae. The lateral traces L_1 and L_3 which exclusively supply the perianth segments, are not involved in this linkage system (Fig. 7-8).

As to the lateral traces L_2 and L_4, each of of these traces could be indicated by the formula '1.1/se', because each trace supplies two adjacent styles and one sepal (Figs. 7-7-l & -m). Thus, in contrast with the postulate deduced for L_1 and L_3, viz.: the ovary is less intimately fused with the hypanthium, the supply of the styles by the traces L_2 and L_4 indicates that these two parts are indeed merged completely. However, in the part of the ovary above level e, the traces L_2 and L_4 are, like L_1 and L_3, not involved in the linkage system of the dorsal traces with the placentae. This observation would suggest that above level e, the ovary and the hypanthium are less intimately fused. Thus, it is clear that all the evidence from a detailed study of the path of the traces L_2 and L_4 leads to conflicting conclusions. Some evidence suggests that the ovary and the hypanthium are completely merged, while other evidence indicates that these parts are less intimately fused.

In *B. longipetiolata*, each of the traces L is involved in the supply of the styles. Each trace represents a compound bundle, so that e.g. L_1 could be indicated by '1.1/se' and L_2 by '1.1/se.se/pe' (Fig. 7-2-l). The supply of the styles by the lateral traces suggests that the ovary *sensu stricto* and the hypanthium are fused for the entire length of the ovary *sensu lato*, because the perianth bundles leave the traces in the perianth-zone.

In conclusion, it appears from this brief study of the vascular anatomy of three *Begonia* flowers that the evidence for the postulate that the ovary *s.l.* is formed by fusion of the ovary *s.s* and a floral tube or hypanthium is not conclusive. According to Mauseth (1988, p. 393), the clearest evidence for the fusion of the ovary *s.s.* with the hypanthium or floral tube is the presence of vascular bundles of the perianth in the tissues surrounding the ovary. Such a distinctive arrangement of bundles has not been observed in the present or in any previous anatomical study of the flower in *Begoniaceae*. The perianth bundles are only free from the ovary bundles in the perianth- zone. The observation of anastomosis between the traces when they have entered the perianth-zone (Fig. 7-1-23), would indicate that the perianth segments are only present at the top of the ovary. Moreover, the photographs of longitudinal sections of young flowers in the studies of Charpentier et al. (1989a & b) do not show any differentiation of tissue indicating an appendicular condition prior to anthesis. The vascular anatomy of the flower of *B. squamulosa* provides very weak evidence that the *Begonia* flower could be interpreted to be appendicular towards the top of the ovary.

Thus, the absence of a differentiation between tissue of the ovary and that of the putative hypanthium as well as the absence of vascular bundles in any tissue that may surround the ovary, indicates that there is no evidence at all that the wall of the 'ovary' is formed by concrescence of tissue of the ovary *s.s.* and tissue of a floral tube or hypanthium. This conclusion is in line with that of Charpentier et al. (1989b) who, on the basis of ontogenetic studies, concluded that the flower is not appendicular. These authors pointed to the fact that previous anatomical studies invariably lead to the conclusion that the flower is appendicular, whereas their ontogenetic studies do not support that conclusion. It seems to me that previous workers may have attributed too much significance to the supply of the perianth segments that only occurs in the very short perianth-zone. In a truly appendicular situation, vascular bundles of the floral tube which are free from those of the ovary *s.s.* should be present in the ovary *s.l.* at a level far below the apex of the ovary or the perianth-zone. From the conclusion that the ovary is not appendicular, it does not follow automatically that it would be axial. The pattern of the vascularisation definitely shows that the ovary is made up of carpels, hence of foliar structures. However, the origin of the ovary traces from the pedicel bundles indicates that the base of the ovary is axial. Thus, the observations in the present study support the hypothesis of Charpentier et al. (1989b) that the ovary wall is a structure intermediate between axial and appendicular organs.

7.3.6. The significance of the present investigations

The ovaries of the flowers investigated are multilocular with an axile placentation in the lower part and unilocular with a parietal placentation towards the apex. Charpentier et al. (1989a & b) made the important observation that the ontogeny of the ovary in *Begoniaceae* is determined by two kinds of meristems. In the base of the young ovary there is always a single axial meristem that determines the multilocular and axile condition in the lower part, and several parietal meristems on the wall which determine the unilocular and parietal condition in the upper part of the ovary at anthesis. They also found that, depending on the comparative growth rate of the two kinds of meristems, at anthesis, an ovary may have both an axile and a parietal placentation or only an axial placentation.

In species like those studied here, which have an ovary that is both multi- and unilocular, both kinds of meristems contribute equally to the development of the ovary, while in species whose ovary is apparently entirely multilocular, the development is determined by preponderant growth of the axial meristem. It has been shown above that the species investigated are characterized by both an axial and a parietal placental vascular system. As to the species investigated by Gauthier in 1950 which have an entirely axile placentation, the author interpreted the bundles in the axis of the flower to be ventral traces or 'cords'. However, the present investigation strongly indicates that the axial bundles in the species studied by Gauthier actually represent an axial placental system. This implies that in these species, a parietal placental system has not developed. Recently, many *Begonia* species of the African section *Scutobegonia* have been

investigated in our laboratory for their floral anatomy. These species have ovaries with an entirely axile placentation. Gauthier (op. cit.) concluded that the axial bundles he saw are ventrals, because, according to him, the bundles occur in pairs. He interpreted each pair to comprise the ventral veins of two adjacent carpels. However, according to Musampa (pers. comm.), the axial bundles in the ovaries in species of *Scutobegonia* do not occur in pairs, such as described by Gauthier. Therefore, I suggest that the axial bundles in multilocular ovaries such as those in *Scutobegonia*, which occasionally assemble in a single trace, actually are a trace **PC** and its branches **PCD**.

Regarding the species having an ovary with both a multilocular and an uniłocular condition, I suggest that the axial and the parietal placental vascular systems may not be equally important for the vascular supply of the placentae. An indication for this preposition is the finding that, in *B. longipetiolata*, there are numerous parietal placental bundles, whereas in *B. elaeagnifolia* there are only three, and in *B. squamulosa* even a single one of such bundles for each one of the traces which represent the fused outermost veins of adjacent carpels.

My somewhat anthropocentric view of this feature supposes that the vascular supply by the axial placental system may be so preponderant that an additional supply to the placentae from the periphery of the ovary is just not necessary. Recently, Quené and the present author (unpublished) did a preliminary investigation of the vascular anatomy of a female flower of *B. meyeri-johannis* Engl. of the African section *Mezierea*. The ovary of that species is similar to that of the species studied here and e.g. that of *B. masoniana* (Barabé et al., 1985) in having a mixed placentation. We found that the placentae of *B. meyeri-johannis* are almost exclusively supplied from the axis of the ovary. Only towards the apex of the ovary we observed a single horizontal bundle that passes from the periphery into the axis of the ovary. Further investigations of other flowers and other species of *Begonia* are required to find out to what extent my interpretation may be correct.

8. Pollen morphology

8.1. Introduction

Van den Berg (1984) analyzed the pollen grains of collections that were considered to belong to the *B. squamulosa* species aggregate. His conclusions were based on observations of 25 dried collections and a similar amount of cultivated specimens. Van den Berg's circumscription of his **B. squamulosa pollen-type** shows that there is an occasional variation in pollen shape, because he described it as characterized among others by 'often concave sides'. However, the pollen grains of some gatherings, having the macromorphological characters of the *B. squamulosa* species aggregate (page 1), were assigned by Van den Berg to other pollen-types. Therefore, he suggested that these gatherings might represent new species. In order to find out whether the differences in pollen morphology as seen by Van den Berg have taxonomical significance, several collections studied by him were reinvestigated and many others included in a further investigation of which the results are presented here.

Moreover, after the completion of Van den Berg's investigations in 1984, additional plants now identified as *B. squamulosa* and *B. elaeagnifolia* were collected in Gabon. These plants proved to be diploid, whereas those that had been analyzed by Van den Berg are tetraploid. It is well known that pollen grains of tetraploid plants are often larger than those of diploid plants. This implies that within the same species, a comparison of grain size of gatherings whose chromosome numbers are not known, may yield an indication for the occurrence of infraspecific polyploidy. So I attempted to compare the grain size of these recent diploid collections with that of the previous tetraploid ones.

8.2. The influence of preparation methods on pollen grain size

The slides with the pollen grains studied were prepared according to the procedure described in Chapter 3. In order to avoid differences in grain size which might be caused by differences in the treatments, the procedure that includes acetolysis of the grains, was strictly maintained for all samples. Prior to the investigations of Van den Berg and the present ones, I studied the grains of some cultivated *Begonia* plants. These grains were not acetolyzed, but stained in a 0.05% solution of safranine in water. The stained grains were dried before they were mounted in the usual glycerine jelly on the slides. It was found that both the level of the temperature and the length of the drying period have a significant influence on grain size. I attribute this phenomenon to an 'elasticity' of the *Begonia* pollen grain wall that has been described by Erdtman (1952, p. 69) as 'very thin'.

No doubt also because of the thin wall whose exine is usually less than 0.5 μm thick (Van den Berg 1984, p. 19), the grains of *Begonia* are quite vulnerable. Especially herbarium material proved to contain deformed and collapsed grains. Some samples contained deformed grains only, others only a few good ones. This is indicated in Table 8-1 (last column) with either 'poor' or with the number of grains measured. For an example of collapsed grains see Fig. 6-6a that shows a transverse section of a boiled anther from a dried specimen. Such deformed grains are irreparably damaged and cannot be made to regain their original shape. Grains in material from cultivated plants which were dried under laboratory conditions with temperatures between 50 and 100 °C are not or hardly damaged. Therefore, I suppose that the frequent occurrence of damaged pollen grains in herbarium specimens prepared from wild plants is due to high and/or uneven temperatures when plants are dried plants under field conditions.

8.3. Variation in size of pollen grains

The gatherings studied for their pollen grains are listed in Table 8-1. This table also presents the averages of the length of the polar axis (**P**), the equatorial diameter (E) and the P/E ratios calculated for these pollen samples. The figures are based on measurements of 10 grains from each sample. These grains were selected at random out of those in perfect equatorial view, and with one colpus situated exactly between the sides (see Figs. 8-4 to 8-19).

The diagrams in Figs. 8-20 to 8-22 demonstrate that pollen grain size may vary considerably within a species. An example of the difference in size that occurs within a single sample is shown by Figs. 8-14 and 8-15.

Pollen grain size of different plants from one locality may be rather similar. This is concluded from a comparison of the P and E values of several gatherings of *B. longipetiolata* (Table 8- 1). For this species, five specimens out of the gathering De Wilde nr 7724 (Ekouk, Cameroun) have been investigated for their pollen. For these specimens the P values range from 23.20 to 25.30 and the E values from 11.10 to 12.10 μm. When the variance of these figures is taken into account, it is clear that the five specimens of this gathering cannot be distinguished on the basis of the dimensions of their pollen grains.

A similar conclusion can be drawn for the gatherings Breteler & De Wilde (1978)-600, Elias & Sterck in Louis 2334, 2360 and Hallé 2992, 3246, 3372, all from Bélinga, Gabon. Their P values range from 29.40 to 31.30; the E values from 12.20 to 12.90 μm. A third example is based on the analysis of pollen grains from the gatherings De Wilde 7463 and Raynal 9709, both from Akoakas, Cameroun. Their P values range from 26.60 to 29.60; the E values from 11.80 to 12.40 μm. This example also shows that the P values of two specimens of the same gathering may be different, while the E values are equal (see Table 8-1, coll. De Wilde 7463).

The mean length of the polar axis of the grains in the specimens of the gather-

Table 8-1. Dimensions of pollen grains in µm of *Begonia* species.
P = length of polar axis; E = equatorial diameter. The mean dimensions are calculated from measurements of 10 grains, except when indicated therwise.

	Entry	Slide	P		E		P/E	
			mean	var.	mean	var.		
B. squamulosa								
Arends et al. 371		613	28.80	1.23	12.30	0.67	2.34	
idem, culta	T1775	505	29.30	0.82	11.10	0.57	2.64	
Breteler & De Wilde (1978)-355		77	34.50	0.85	12.60	0.52	2.74	
Christiaensen 1904		564	30.40	0.84	13.40	0.52	2.27	
De Wilde. J.J. et al. 8839		610	31.60	1.07	12.90	0.32	2.45	
De Wilde. J.J. et al.(1983)-100		612	30.90	1.20	12.50	0.53	2.47	
idem, culta	T1606	465	35.10	0.99	13.60	0.70	2.58	
De Wilde. J.J. et al.(1983)-119		509	31.70	0.48	12.10	0.57	2.64	
idem, culta	T1603	510	35.70	1.16	15.40	0.84	2.32	
De Wilde. J.J. et al.(1983)-181		611	30.40	1.17	14.70	0.67	2.07	
idem, culta	T1587	435	34.30	1.42	14.70	0.82	2.33	
De Wilde. J.J. et al.(1983)-288		563						poor
Escherich 248		562	33.30	1.89	12.30	0.67	2.71	
Hallé & Villiers 4410		604	31.60	0.97	13.90	0.74	2.27	
Lambinon 78-279		646	27.00		12.00		2.25	n = 5
Le Testu 5454		535	26.90	1.20	13.50	0.53	1.99	
Mann 1654		504	32.50	1.27	12.30	0.48	2.64	
B. longipetiolata								
Annet 223		82	29.70	1.06	11.90	0.57	2.49	
Annet 424		605	25.60	0.70	11.70	0.48	2.18	
Barabé 86-99		548	26.50	0.71	11.00	0.67	2.41	culta
Bates 300		636	24.40	0.70	10.60	0.52	2.30	
Bates 594		552	26.90	1.20	11.20	0.42	2.40	
Bequaert 6474		86	31.20	0.92	10.80	0.42	2.88	
Bos 4070		555	25.30	1.34	11.70	0.67	2.16	
Bos 6194		584	24.60	0.70	12.00	0.67	2.05	
Breteler & De Wilde (1978)-196		66	28.10	1.10	11.00	0.82	2.55	
Breteler & De Wilde (1978)-204		73	30.10	0.74	12.00	0.00	2.51	
Breteler & De Wilde (1978)-297		550	30.00	0.82	11.30	0.48	2.65	
Breteler & De Wilde (1978)-323		71	27.90	0.99	10.20	0.42	2.73	
Breteler & De Wilde (1978)-356 culta	T1203	58	28.90	1.10	12.30	0.82	2.35	
Breteler & De Wilde (1978)-600		76	31.30	1.06	12.50	0.53	2.50	
Breyne 2751		568	26.10	1.10	11.70	0.67	2.23	
Cabra 115		540	28.20	1.03	10.50	0.85	2.69	
Cambridge Congo Exp.(1959)-295		635	29.80	1.32	10.70	0.48	2.78	poor
De Wilde, J.J. 7463		589	26.60	1.26	11.80	0.42	2.25	
De Wilde, J.J. 7463		588	28.70	1.15	11.80	0.42	2.43	
De Wilde, J.J. 7538		587	26.40	0.97	11.70	0.48	2.26	
De Wilde, J.J. 7538		586	26.20	1.99	11.40	0.52	2.29	
De Wilde, J.J. 7724		560	25.30	1.42	12.00	0.67	2.11	
De Wilde, J.J. 7724		559	24.10	0.99	11.10	0.32	2.17	
De Wilde, J.J. 7724		558	23.20	1.43	11.10	0.74	2.09	
De Wilde, J.J. 7724		557	25.10	0.88	11.90	0.74	2.11	
De Wilde, J.J. 7724		556	24.90	0.57	12.10	0.57	2.06	
De Wilde, J.J. et al. 8841		532	27.20	1.23	10.80	0.63	2.52	
De Wilde, J.J. et al. 9270		553	25.80	1.81	10.10	0.57	2.55	

Table 8-1. (continued)

	Entry	Slide	P		E		P/E	
			mean	var.	mean	var.		
idem, culta	PT86-462	629	25.80	1.23	10.00	0.47	2.58	
De Wilde, J.J. et al.(1983)-180		531	24.00	1.56	10.00	0.70	2.40	
idem, culta	T1592	412	29.60	1.26	12.10	0.74	2.44	
De Wilde, J.J. et al.(1983)-326 culta	T1604	508	30.80	0.79	13.60	0.52	2.26	
De Wilde, J.J. et al.(1983)-483		501	27.20	1.23	12.00	0.67	2.27	
idem, culta	T1608	511	30.50	1.08	12.30	0.48	2.48	
De Wilde, W.J. & B. 2020		545	26.10	0.74	11.50	0.53	2.27	
Elias & Sterck in Louis 2334		651	29.80	1.13	12.60	0.84	2.36	
Elias & Sterck in Louis 2360		650	30.30	1.25	12.90	0.79	2.35	
Goossens 1579		84	28.20	1.32	11.50	0.53	2.45	
Hallé 2194		544	26.10	0.88	12.70	0.48	2.06	
Hallé 2992		571	30.80	0.92	12.90	0.74	2.39	poor
Hallé 3246		537	29.60	0.97	12.20	0.63	2.43	
Hallé 3363		538						poor
Hallé 3372		643	29.40	0.70	12.30	0.67	2.39	
Hallé 4011		70	29.50	1.17	11.30	0.67	2.61	
Hallé & Villiers 4558		543	27.70	1.42	13.00	0.47	2.13	
Hallé & Villiers 5381		645	26.40	0.97	12.30	1.25	2.15	
Jackson in Keay (FHI 46309)		526	25.60	1.43	11.70	0.48	2.18	culta
Jacques-Felix 9173		580	24.00	0.82	11.60	0.97	2.07	
Keay (FHI 37551)		529	23.90	0.74	11.10	0.87	2.15	
Keay (FHI 37714)		573	24.90	0.74	11.30	0.48	2.20	
Koufani 149		530	24.90	1.10	12.00	1.05	2.07	
Laurent 1695		541	30.40	1.43	12.90	0.74	2.36	
Lebrun 5164								poor
Le Testu 5265		525	25.20	0.63	11.80	0.63	2.13	
Le Testu 5275		536	25.00	0.82	11.20	0.79	2.23	
Le Testu 5429		534	29.10	1.10	13.10	0.74	2.22	
Leeuwenberg 9288		79	27.20	0.63	11.10	0.32	2.45	
idem, culta	T1060	640	29.20	1.13	10.70	0.82	2.73	
Leeuwenberg 9294		83	28.10	0.57	10.10	0.57	2.78	
Léonard 1605		583	25.50	1.27	11.90	1.10	2.14	
Léonard 3916		585						poor
Letouzey 4121		569	28.80	1.40	11.00	0.67	2.62	
Letouzey 8201		547	26.70	0.95	11.80	0.42	2.26	
Letouzey 9005		644	27.10	0.74	12.10	0.74	2.24	
Letouzey 10982		609	25.80	0.79	10.80	0.63	2.38	
Letouzey 10982		549	24.10	0.88	11.20	0.63	2.15	
Letouzey 12808		85	28.50	1.17	10.70	0.48	2.66	
Letouzey 14146		577	25.30	0.67	10.80	0.92	2.34	
Letouzey 14450		574						poor
Letouzey 14665		624	25.60	0.70	10.50	0.53	2.44	poor
Letouzey 15136		576	27.70	0.67	11.00	0.67	2.52	
Mildbraed 5636		606	30.30	0.48	11.90	0.87	2.54	
Mildbraed 5925		75	31.40	1.26	11.90	0.74	2.64	
Mildbraed 6394		614	22.62	0.74	10.25	0.46	2.21	n=8
Onochie (FHI 34803)		528	23.70	1.42	11.60	1.07	2.04	
Raynal, J. & A. 9709		570	29.60	1.43	12.40	0.97	2.39	
Raynal, J. & A. 10349		581	25.80	1.14	12.20	0.42	2.11	

Table 8-1. (continued)

	Entry	Slide	P		E		P/E	
			mean	var.	mean	var.		
Reitsma 3246		642	25.50	0.97	12.10	0.57	2.09	
Satabié 295		546	26.00	0.82	11.50	0.53	2.26	
Schlechter 12918		639	25.00		11.00		2.30	n = 3
Schultze in Mildbraed 6183		554	25.50	1.18	11.60	0.70	2.20	
Schultze in Mildbraed 6189		578	26.00		10.00		2.60	n = 4
Thomas 4318		506	27.60	0.84	10.60	0.70	2.60	
Troupin 2455		551	29.30	0.67	13.20	0.79	2.22	
Van Meer 1168		533	25.20	1.23	11.20	0.63	2.25	
Villiers 781		575	27.60	1.17	12.00	0.00	2.30	
Villiers 1481		542	24.50	1.08	10.50	0.71	2.33	poor
Zenker 3152		80	29.30	1.06	11.40	0.52	2.57	poor
B. elaeagnifolia								
Arends et al.		559	593	28.30	1.34	11.90	1.20	2.38
idem, culta	PT84-187	632	29.00	0.82	12.40	0.52	2.34	
Arends et al. 571								
idem, culta	PT84-184	631	28.90	0.99	11.40	0.52	2.54	
Arends et al. 670		590	28.60	0.84	12.10	0.32	2.36	
Arends et al. 681		591	27.40	1.17	12.10	0.57	2.26	
idem, culta	PT84-194	628	28.20	1.13	11.80	0.63	2.38	
Breteler & De Wilde (1978)-8		597	31.80	0.79	11.30	0.48	2.81	poor
idem, culta	T1186	110	36.10	0.73	12.90	0.57	2.80	
Breteler & De Wilde (1978)-38		63	35.90	1.29	12.50	0.53	2.87	
idem, culta	T1202	24	37.20	1.25	13.00	0.67	2.86	
Breteler & De Wilde (1978)-276		62	34.60	1.43	12.40	0.84	2.79	
Breteler & De Wilde (1978)-381		594	35.90	1.37	11.70	0.67	3.07	
Breteler et al. 8248		627	28.60	1.17	11.60	0.52	2.47	
idem, culta	PT86-286	638	27.70	1.42	11.70	0.48	2.36	
De Wilde et al. (1983)-31		598	28.00	0.67	12.50	0.71	2.24	poor
De Wilde et al. (1983)-35		599	30.40	0.96	12.00	0.47	2.53	
De Wilde et al. (1983)-43		600						poor
De Wilde et al. (1983)-179		601	32.20	1.55	12.40	0.52	2.59	
idem, culta	T1640	466	34.20	0.79	14.20	0.42	2.40	
idem, culta	T1637	411	36.60	2.07	14.40	0.70	2.54	
Hallé & Villiers 4452		64	35.50	1.18	13.20	0.63	2.69	
Hallé & Villiers 4560		61	29.20	0.92	10.50	0.71	2.78	
Letouzey 12765		59	29.63	1.19	11.87	0.64	2.50	poor
Louis, A.M. et al. 1267		607	28.70	1.25	10.90	0.32	2.63	poor
Mann 1651		592	31.90	0.74	12.20	0.42	2.61	
Reitsma 1958		626	29.00	0.67	12.10	0.32	2.40	
idem, culta	PT85-47	630	26.80	1.13	12.60	0.70	2.13	
Sanford 5860		625	32.40	1.17	11.10	0.57	2.92	
Satabié & Letouzey 343		647	28.80	1.40	12.50	0.70	2.30	
Schultze in Mildbraed 6208		69	30.20	0.79	11.60	0.52	2.60	
B. karperi								
Breteler & De Wilde (1978)-335		608	31.20	0.79	11.90	0.57	2.62	poor
idem, culta	T1207	15	33.70	1.06	10.90	0.32	3.09	
De Wilde. J.J. et al. (1983)-158		602	27.20	0.63	11.40	0.52	2.38	
idem, culta	T1596	437	31.90	1.37	13.10	1.20	2.43	

Table 8-1. (continued)

	Entry	Slide	P		E		P/E	
			mean	var.	mean	var.		
Hallé & Villiers 4885		603	29.50	1.08	12.40	0.52	2.37	poor
B. rwandensis								
Bouxin 257		637	25.50	0.97	13.90	0.74	1.83	
Bridson 380		561	25.10	0.99	11.70	0.48	2.15	
Van Roeckhoudt 12		395	25.40	1.17	13.50	0.53	1.88	
B. pelargoniiflora								
Letouzey 14448								poor
Sanford 4442		648	20.80	0.42	12.00	1.05	1.73	
Sanford 4440								poor

ing from Ekouk ranges from 23.20 to 25.50 µm, whereas that in the gatherings from Bélinga ranges from 29.40 to 31.30 µm (see above). Thus, there is a gap of approximately 4 µm between the P values calculated for the gatherings from these two localities. According to Van den Berg (1984, p. 23) a gap of that order is taxonomically not interesting. Table 8-1 shows that there is a gap of approximately 9 µm between the largest polar axis and the smallest one in the specimens investigated, because the mean length of the polar axis in Bequaert 6474 is 31.20 µm, while that in Mildbraed 6394 is 22.26 µm. However, I conclude from a comparison of these two gatherings that on a macromorphological basis, they cannot be interpreted to represent different taxa. This interpretation is supported by the fact that the gap between the values of 31.20 µm and 22.26 µm is completely bridged by the values found for the other specimens of *B. longipetiolata* which were investigated for their pollen grains (Fig. 8-21).

In the course of the present study it was noticed that the size of pollen grains of cultivated plants often differs from that of plants collected in the wild. Table 8-2 presents the average dimensions of the polar axis (Pw) and the equatorial diameter (Ew) for some field collections. From these collections plants have been cultivated and their pollen was studied as well. The dimensions of the pollen grains of these cultivated plants are presented as Pc and Ec. The discrepancies between the average measurements of the wild and cultivated material are presented in the table as comparative change (Cc) expressed as a percentage. For example, for the field coll. Arends et al. 371 of *B. squamulosa*, the average length of the polar axis (Pw) is 28.80 µm. That of the cultivated specimen (Pc) is 29.30 µm. This means that the grains of the cultivated specimen are on the average 0.5 µm longer than those of the field collection, an increase of 0.5 : 0.288 = 1.7%. The comparative change of the equatorial diameter is calculated similarly. The comparative change of the polar axis ranges from -7.6 to 21.7% (Table 8-2), the length of the axis of cultivated specimens being in general longer than that of plants collected in the field. A decrease in length was found in only two cases.

Table 8-2. Size of the pollen grains in µm in *Begonia* species collected in the wild and of cultivated plants from the same accessions. Pw = length of the polar axis of wild material; Pc = idem of cultivated plants; Ew = equatorial diameter of wild material; Ec = idem of cultivated plants; Cc = comparative change from the value calculated for the grains of wild material in per cent. Further explanation see text.

	Pw	Pc	Cc (%)	Ew	Ec	Cc (%)
B. squamulosa						
Arends et al. 371	28.80	29.30	+ 1.7	12.30	11.10	− 9.7
De Wilde et al.(1983)-100	30.90	35.10	+13.6	12.50	13.60	+ 8.8
De Wilde et al.(1983-119	31.70	35.70	+12.6	12.10	15.40	+27.3
De Wilde et al.(1983)-181	3O.40	34.30	+12.8	14.70	14.70	0
B. longipetiolata						
De Wilde et al. 9270	25.80	25.80	0	10.10	10.00	0
De Wilde et al.(1983)-180	24.00	29.60	+21.7	10.00	12.00	+19.8
De Wilde et al.(1983)-483	27.20	30.50	+12.1	12.00	12.30	+ 2.5
Leeuwenberg 9288	27.20	29.20	+ 7.4	11.10	10.70	− 3.6
B. elaeagnifolia						
Arends et al. 559	28.30	29.00	+ 2.5	11.90	12.40	+ 4.2
Breteler et al. 8248	28.60	27.70	− 3.2	11.60	11.70	+ 0.9
Arends et al. 681	27.40	28.20	+ 2.9	12.10	11.80	− 2.5
Reitsma 1958	29.00	26.80	− 7.6	12.10	12.60	+ 4.1
Breteler & De Wilde (1978)-8	31.80	36.10	+16.7	11.30	12.90	+14.2
Breteler & De Wilde (1978)-38	35.90	37.20	+ 7.2	12.50	13.00	+ 4.0
De Wilde et al.(1983)-179	32.20	34.20	+ 6.2	12.40	14.20	+14.5
De Wilde et al.(1983)-179*	32.20	36.60	+13.7	12.40	14.40	+14.5
B. karperi						
Breteler & de Wilde (1978)-335	31.20	33.70	+ 8.0	11.90	10.90	− 8.4
De Wilde et al.(1983)-158	27.20	31.90	+17.2	11.40	13.10	+14.9

* = second cultivated specimen

The table shows that similar conclusions can be drawn for the equatorial diameter.

It may be assumed that growing conditions in the natural habitat differ in some way from those in the greenhouse. Consequently, I postulate that differences between growing conditions in the forest and those in the greenhouse affect the size of cells or in particular, that of pollen grains. This postulate is supported by Löve & Löve (1975, p. 98) who wrote 'Cell size can also vary because of genetical differences between demes at the same level of polyploidy, and it is affected by some environmental factors, so comparison ought to be made only between material grown under similar conditions'. Thus, differences in pollen grain size should be interpreted with caution.

Further, it is obvious that deviations in the polar length as well as in equatorial diameter have an influence on the P/E ratios calculated for a single accession.

For example, that of the field coll. Arends et al. 371 of *B. squamulosa* is 2.34, whereas that of the cultivated specimen is 2.64 (Table 8-1).

8.4. Pollen-types in African *Begonia*

With the exception of the specimens Van Roeckhoudt 12, Sanford 4442 and Hallé & Villiers 5381, Van den Berg (1984) assigned the grains of all the collections studied by him to his **B. squamulosa pollen-type**. Van den Berg (op. cit.) referred the specimens he investigated to various taxa, viz.: *B. bipindensis*, *B. crassipes*, *B. gladiifolia*, *B. gracilipetiolata*, *B. schultzei*, *B. squamulosa* and *B. wilczekiana*. Apart from type specimens of *B. crassipes* (coll. Zenker 3152), *B. schultzei* (coll. Schultze in Mildbraed 6208) and *B. wilczekiana* (coll. Hallé & Villiers 4560), the collections cited by Van den Berg had been identified provisionally by De Wilde. However, *B. gracilipetiolata*, also mentioned by Van den Berg as having the **B. squamulosa pollen-type** is not linked to a particular specimen. This name most likely pertains to the coll. Hallé & Villiers 4452. Van den Berg cited it as *B. schultzei*, but I found that this specimen had been inserted in a herbarium cover marked with *B. gracilipetiolata*. The coll. Letouzey 12808, which in the present study is identified as *B. longipetiolata*, was cited by Van den Berg as *B. polygonoides*. Nevertheless, he assigned the pollen of this collection to the **B. squamulosa pollen-type**.

The **B. squamulosa pollen-type** of Van den Berg (1984, p.32) is characterized by pollen grains that are perprolate in equatorial view (i.e. the P/E ratio is larger than 2.0), often with concave sides and pointed poles. Furthermore, its grains are 3-zono-colporate, hence with three compound apertures. The ectocolpi running from pole to pole, are bordered by distinct margines with a sculpture that differs from that of the remainder of the wall, the mesocolpium. That part of the wall, is characterized by a striate ornamentation formed by more or less parallel muri. This is shown in the present study in Fig. 8-1 by a SEM-photograph of a pollen grain of *B. longipetiolata*.

In addition, there are three more or less elliptic endoapertures, each with rather heavy costae situated at the equator. They are clearly visible in several LM-photographs reproduced here in Figs. 8-5, 8-9 and 8-12. Similar details are shown in the photographs of grains of the **B. squamulosa pollen- type** given by Van den Berg in his treatise of African *Begonia* pollen. In that study his Figs. 15 & 16 (p. 45) show a grain of, according to the caption, *B. squamulosa* (coll. Letouzey 12765). This collection however, is here identified as *B. elaeagnifolia*. Another (SEM) photograph in Van den Berg (op. cit., p. 50, Plate 10.3) shows a grain of *B. wilczekiana* (coll. Breteler & De Wilde (1978)-335, not as erroneously mentioned 385). This specimen is here assigned to the new species *B. karperi*, a close relative of *B. elaeagnifolia*. At the time Van den Berg prepared his manuscript, a clear concept of the taxonomy of the species mentioned by him in the context of the **B. squamulosa pollen-type** was not yet available. Plants having the floral characters as given on page 1 were then considered to belong

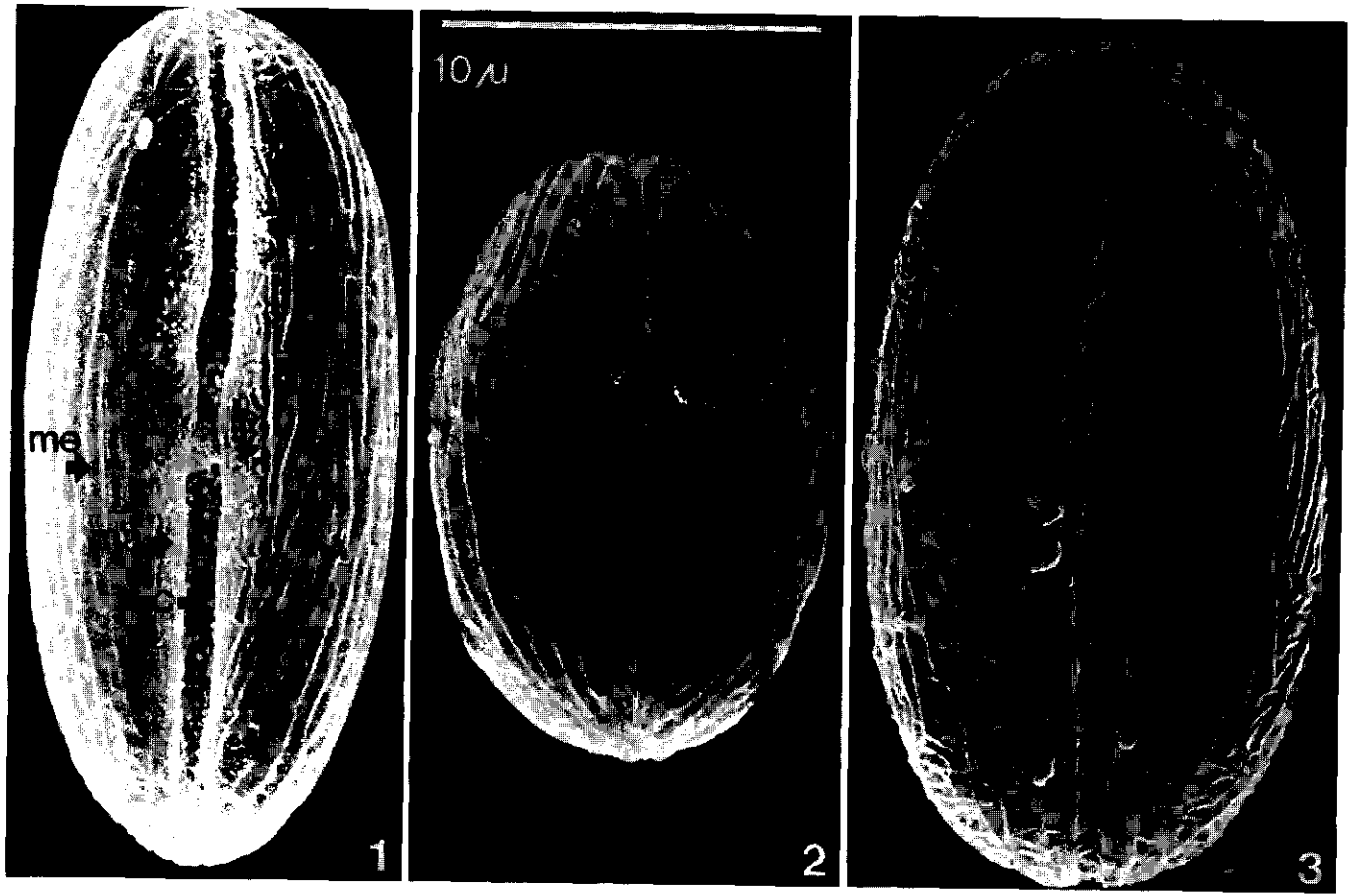
to the '*B. squamulosa* species aggregate'. In the concept proposed in this study, the wording *B. squamulosa* species group is restricted to *B. squamulosa* and *B. longipetiolata*. The photographs of Van den Berg referred to above, show the grains of *B. elaeagnifolia* and of *B. karperi*. Thus, further investigation demonstrates that Van den Berg did not show a photograph of a pollen grain of a specimen, now assigned to either *B. squamulosa* or *B. longipetiolata*.

The photographs in Van den Berg (op. cit., pp. 45 and 50) demonstrate that his **B. squamulosa pollen-type** is indeed characterized by having often concave sides. However, the SEM-photograph of a grain of *B. longipetiolata* (coll. Leeuwenberg 9288) made by Van den Berg and included in the present study (Fig. 8-1) shows that it is ellipsoid in equatorial view. Another collection, Onochie in FHI 34803, cited by Van den Berg as *B. squamulosa*, is here assigned to *B. longipetiolata*. Van den Berg's preparation nr 78 of that gathering contains among many collapsed grains a few good ones, and these are more or less ellipsoid. In a new preparation of this material (Table 8-1) I found collapsed grains, but the presence of ellipsoid grains was confirmed. Similarly Van den Berg's preparation nr 151 of Halle' & Villiers 5381, the type of *B. nicolai-hallei*, contains many collapsed grains next to ellipsoid ones. This was also confirmed by a new preparation of this collection (Table 8-1 and Fig. 8-7). On the basis of their form and comparatively small dimensions, the pollen grains of Hallé & Villiers 5381 were assigned by Van den Berg (op. cit., p. 30) to the **B. komoensis pollen-type**. In the present study similar features have frequently been seen in pollen preparations of collections identified as *B. longipetiolata*. It is therefore concluded that the occurrence of ellipsoid pollen grains is common in this species. A grain of *B. longipetiolata* shown in Fig. 8-9 has slightly concave sides, but Figs. 8-7 and -8 show grains with more or less convex sides. Thus both pollen grain forms occur in this species.

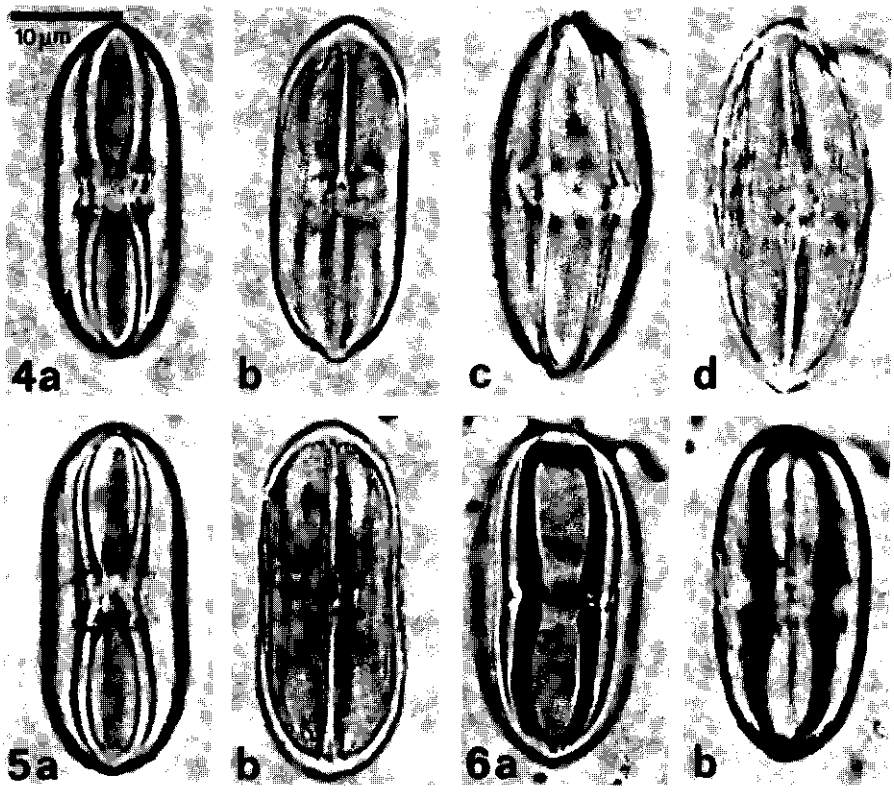
Photographs of pollen grains of *B. squamulosa* (Figs. 8-4a & b, and 8-5) demonstrate that the sides of the grains of this species are usually straight to slightly concave. This was found for most of the accessions investigated, but, as in *B. longipetiolata* ellipsoid grains do occur in *B. squamulosa* (Figs. 8-4c & d, and 8-6).

The pollen grains of *B. elaeagnifolia* and *B. karperi* generally have straight to slightly concave sides, but a few slightly ellipsoid grains have been found as well. The photographs presented here (Figs. 8-10 to 8-17) are more or less similar to those of Van den Berg (op. cit., Plate 5, p. 45 and Plate 10, p. 50). The pollen grains of these two species fit Van den Berg's circumscription of the **B. squamulosa pollen-type** (op. cit., p. 32).

From the present observations it is concluded that the pollen shape of the species mentioned above is rather more variable than the circumscription and, in particular, the schematic representation of the **B. squamulosa pollen-type** in Van den Berg (1984, p. 66, pollen-type nr 8) suggests. Grains which comply with the **B. squamulosa pollen-type** are mainly found in *B. elaeagnifolia* and *B. karperi*. Moreover, the key to the pollen types in Van den Berg (op. cit., p. 26) may occasionally lead to erroneous identifications of the grains studied.



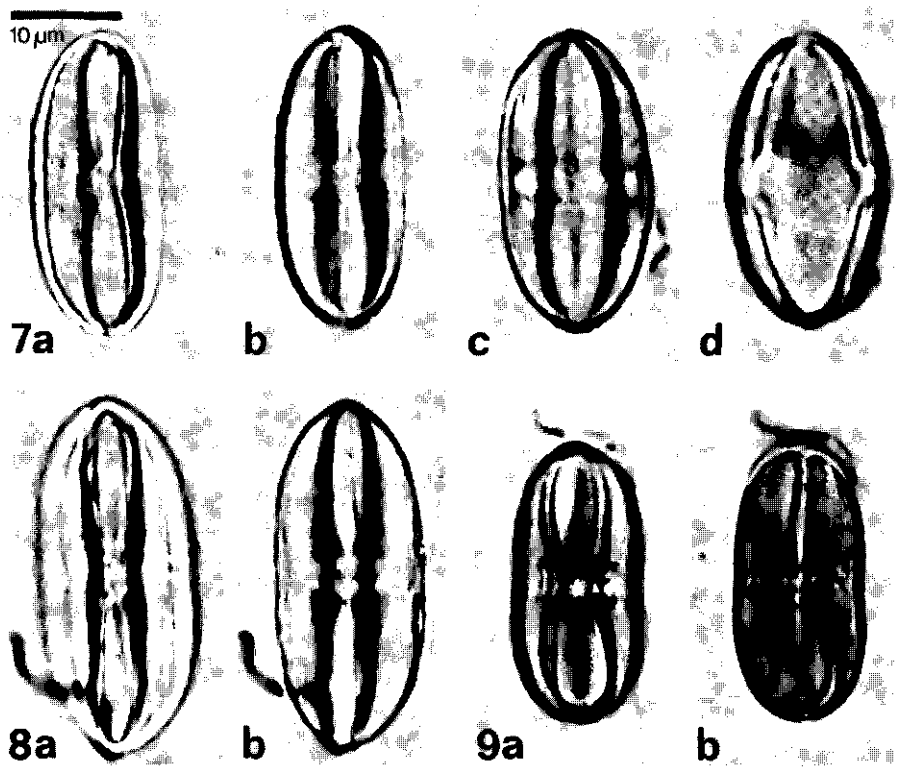
Figs. 8-1 to -3. SEM photographs of pollen grains of *Begonia* species. **1:** *B. longipetiolata* (coll. Leeuwenberg 9288), the arrows indicate the colpus (c), margo (ma) and mesocolpium (me); **2:** *B. pelargoniiflora* (coll. Sanford 4442); **3:** *B. rwandensis* (coll. Van Roeckhoudt 12). Courtesy R.G. van den Berg.



Figs. 8-4 to -6: LM photographs of pollen grains (equatorial view) in three collections of *B. squamulosa*, in the a/b or c/d photographs the same grain focused differently; **4:** coll. Arends, De Wilde & Louis 371 (diploid); **4a & b:** grain with slightly concave sides; **4c & d:** another grain from the same preparation with convex sides; **5a & b:** coll. De Wilde, Arends & de Bruijn 8839, (tetraploid), grain with concave sides; **6a & b:** coll. De Wilde, Arends et al.(1983)-181, (tetraploid), grain with convex sides.

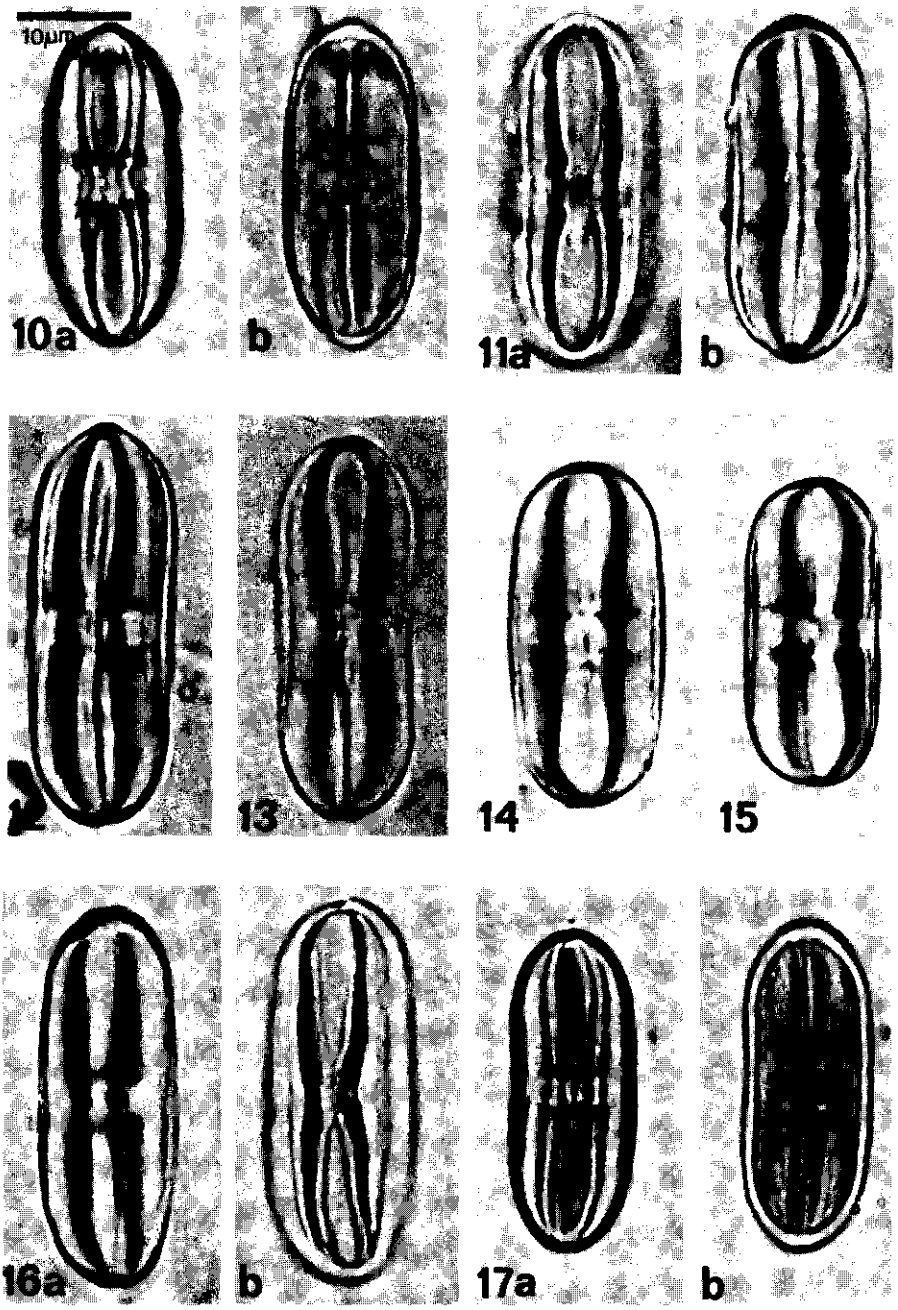
8.5. Delimitation of pollen-types

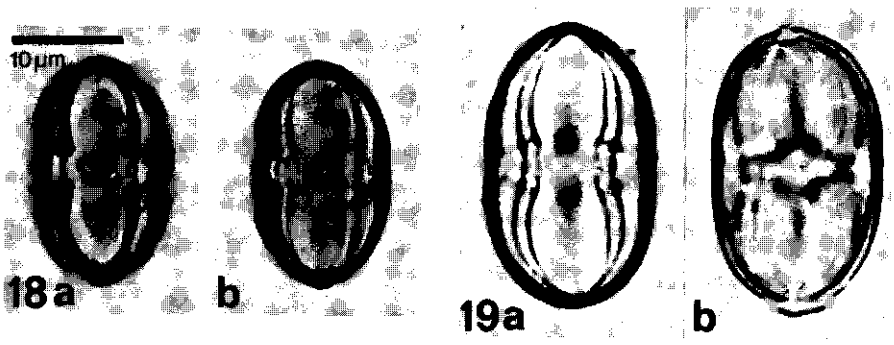
Notwithstanding variation in form and dimension, the pollen grains of *B. squamulosa*, *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi* have several morphological characteristics in common; viz. margines, a similar mesocolpium ornamentation and non-emarginate poles. The largest pollen grains found in *B. squamulosa* (see Fig. 8-20) are in size quite similar to those assigned by Van den Berg (op cit, p.31) to the **B. cavallyensis pollen-type**, particularly when they are ellipsoid. However, the grains of that pollen-type have emarginate poles due to anastomosing colpi. Pollen grains of *B. squamulosa* do not have this character.



Figs. 8-7 to -9: LM photographs of pollen grains (equatorial view) in three collections of *B. longipetiolata*, in the a/b or c/d photographs the same grain focused differently; **7:** coll. Hallé & Villiers 5381 (holotype of *B. nicolai-hallei*), **7a & b:** a grain with slightly convex sides; **7c & d:** another grain from the same preparation with convex sides; **8a & b:** coll. Mildbraed 5636, grain with straight sides; **9a & b:** coll. Reitsma 3246, grain with concave sides.

Figs. 8-10 to -17: LM photographs of pollen grains (equatorial view) in *Begonia* species, in the a/b photographs the same grain focused differently; **10** to **15:** *B. elaeagnifolia*; **10a & b:** coll. Breteler, Lemmens & Nzabi 8248 (diploid), grain with straight sides; **11a & b:** coll. Reitsma 1958 (diploid), grain with concave sides; **12:** coll. De Wilde, Arends et al.(1983)-179 (tetraploid), grain with concave sides; **13:** coll. Sanford 5860, grain with concave sides; **14** and **15:** coll. Satabie & Letouzey 343, two grains with straight to slightly concave sides from the same slide; **16** and **17:** *B. karperi*; **16a & b:** coll. Breteler & De Wilde (1978)-335, grain with straight sides; **17a & b:** coll. De Wilde, Arends et al.(1983)-158, grain with slightly concave sides.


10µm
10a
b
11a
b
12
13
14
15
16a
b
17a
b



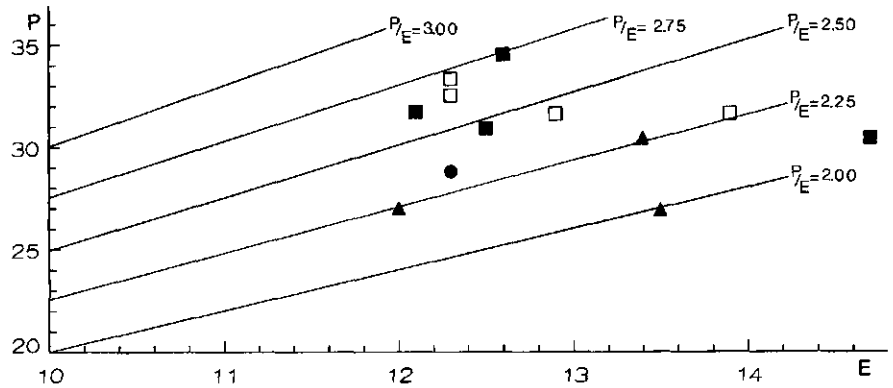
Figs. 8-18 and -19: LM photographs of pollen grains (equatorial view) of *Begonia* species, in the a/b photographs the same grain focused differently; **18a & b:** *B. pelargoniiflora*, coll. Sanford 4442; **19a & b:** *B. rwandensis*, coll. Bouxin 257.

For the same reasons the comparatively large grains of *B. elaeagnifolia* and *B. karperi* are different from the **B. cavallyensis pollen-type**. Moreover, the grains of these two species are never ellipsoid. The comparatively small and frequently ellipsoid pollen grains found in *B. longipetiolata* (see Fig. 8-21), would almost fit in with the description given by Van den Berg (op. cit., p. 30) for the **B. komoensis pollen-type**. This similarity will be considered below, where the P/E ratio is discussed.

The pollen grains of the two new species *B. pelargoniiflora* and *B. rwandensis* were already studied by Van den Berg (1984) and he excluded them from the **B. squamulosa pollen-type**. Van den Berg assigned the grains of *B. pelargoniiflora* to the **B. eminii pollen-type** and those of *B. rwandensis* to the **B. komoensis pollen-type**. SEM-photographs of the grains of these two species are presented in Figs. 8-2 and 8-3.

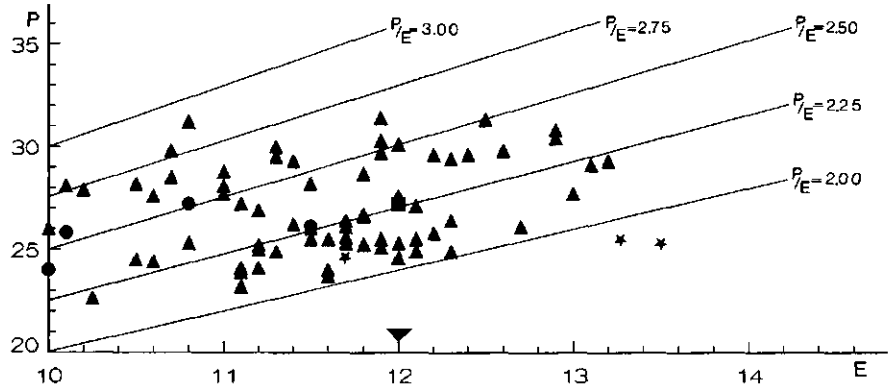
Figs. 8-2 and 8-18 and the diagram in Fig. 8-21 show that grains of *B. pelargoniiflora* are much smaller than those of the other species considered in this study. Moreover, the pollen grains of this species are distinctly prolate (Table 8-1 and Fig. 8-21), almost syncolpate (see Van den Berg op. cit., p. 41, figs. 4 and 5) and do not have margines (Fig. 8-2).

The more or less syncolpate pollen grains of *B. rwandensis* have an ornamentation that is different from that of any other species treated in the present study. Next to some parallel muri, the sculpture shows more or less transverse ridges, whereas a differentiation between margines and mesocolpium is absent (Fig. 8-3). Unfortunately, such details can hardly be seen in the light microscope. Figs. 8-21 and 8-22 show that the pollen of this species is usually prolate to slightly perprolate. All these characters indicate that, at least on the basis of pollen morphology, the gatherings (including Van Roeckhoudt nr 12) here assigned to the new species *B. rwandensis*, are different from those identified as *B. elaeagnifolia*. Wilczek (1969b) identified Van Roeckhoudt nr 12 as *B. schultzei*, a taxon that is here considered to be conspecific with *B. elaeagnifolia*.



B. squamulosa ● diploid ■ tetraploid □ putative tetraploid ▲ ploidy unknown

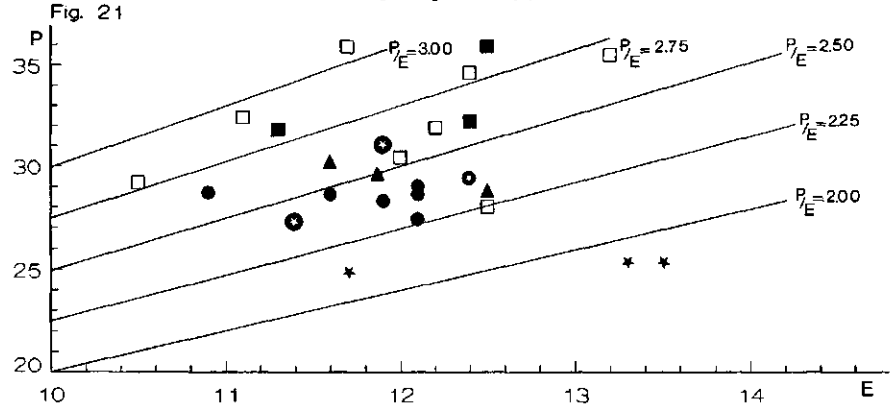
Fig. 20



B. longipetiolata ● diploid ■ tetraploid ▲ ploidy unknown

B. rwandensis ★ *B. pelargoniiflora* ▼

Fig. 21



B. elaeagnifolia ● diploid ■ tetraploid □ putative tetraploid ▲ ploidy unknown

B. karperi ⊙ diploid ⊙ putative diploid *B. rwandensis* ★

Fig. 22

Figs. 8-20 to -22: pollen grain dimensions (in μm) in *Begonia* species; vertical axis: length of polar axis (P), horizontal axis: equatorial diameter (E). **20:** *B. squamulosa*; **21:** *B. longipetiolata*, *B. pelargoniiflora* and *B. rwandensis*; **22:** *B. elaeagnifolia*, *B. karperi* and *B. rwandensis*.

On the basis of its pollen morphology Van den Berg (op. cit.) concluded that Van Roeckhoudt nr 12 might represent a new species. His conclusion is corroborated on other grounds also. Van den Berg (pers.comm.) included the pollen grains of Van Roeckhoudt nr 12 in the **B. komoensis pollen-type**, because of their shape and dimensions. However, the ornamentation of the pollen grains of *B. rwandensis* differs so much from that of the grains of the taxa included in the **B. komoensis pollen-type**, that I consider it to be hardly possible to combine the grains of *B. rwandensis* with those of other taxa in that pollen-type. Thus, it appears that the grains of *B. rwandensis* do not fit in any of the pollen-types distinguished by Van den Berg.

When the pattern of the symbols representing the dimensions of the pollen grains is considered (Figs. 8-20 to -22), it is clear that *B. pelargoniiflora* and, to a lesser degree, *B. rwandensis* have pollen grains which are distinct by size from those of the other species treated in this study. Thus, in conclusion it appears that these species have grains which are distinct by their size and/or ornamentation of the wall.

The diagrams demonstrate a considerable overlap in pollen grain size of *B. squamulosa*, *B. longipetiolata*, *B. elaeagnifolia* and *B. karperi*. In fact, the grains of these species cannot be distinguished from one another. Nevertheless, some tendencies regarding pollen grain size can be discerned. The grains of *B. squamulosa* are in general larger than those of *B. longipetiolata* and to a lesser degree also larger than those of *B. elaeagnifolia* and *B. karperi*. The grains of many accessions of *B. longipetiolata* are among the smallest observed in the present study.

8.6. P/E ratio of the **B. squamulosa pollen-type** and the **B. komoensis pollen-type**

With respect to P/E ratio it is evident that the pollen grains of *B. elaeagnifolia* and *B. karperi* are perprolate as their P/E values are always above 2.25 (Fig. 8-22). The pollen grains of *B. squamulosa* are generally perprolate also, but the grains of two collections were found to be almost prolate (Fig. 8-20). Most samples of *B. longipetiolata* show perprolate pollen grains, but quite a few with P/E values between 2.00 to 2.25 should be considered as almost prolate (Fig. 8-21). These almost prolate grains never show emarginate poles. On page 162 it has already been mentioned that in LM these pollen grains resemble those of species assigned by Van den Berg (1984, p. 30) to the **B. komoensis pollen-type**. One of the characteristics of that pollen type is that it is 'sometimes syncolpate', but the pollen grains of *B. kisuluana* Büttn. included in that pollen-type, are not or hardly syncolpate (see EM-photograph in Van den Berg op. cit., p. 49, fig. 4). When Van den Berg's photograph of the *B. kisuluana* pollen grain is compared with that of *B. longipetiolata* which is reproduced in the present study (Fig. 8-1), the resemblance of the pollen grains of these two species is quite obvious. The occurrence of so many prolate to slightly perprolate grains in collections of *B. longipetiolata* combined with other similarities to the pollen grains

of *B. kisuluana* suggests that there is a transition between the **B. squamulosa pollen-type** and the **B. komoensis pollen-types**.

8.7. Evolutionary levels

In his discussion of the pollen-types distinguished in African *Begonia*, Van den Berg (op. cit., p. 67) stated that the section *Tetraphila* appears to be heterogeneous in its pollen morphology. He considered the **B. squamulosa pollen-type** and the **B. komoensis pollen-type** as advanced in comparison with the **B. eminii pollen-type**, which represents the most primitive condition of pollen within the section *Tetraphila*. The comparatively large and perprolate grains with straight to concave sides observed in *B. elaeagnifolia*, *B. karperi* and usually also in *B. squamulosa* should be considered as the most advanced within the phylogenetic pollen series distinguished by Van den Berg within the section *Tetraphila*. According to that view, the smaller more or less ellipsoid grains with a P/E ratio between 2.00 and 2.25 observed in many collections of *B. longipetiolata* are comparatively primitive. Similarly, the pollen of *B. rwandensis*, that is assigned to the **B. komoensis pollen-type**, is comparatively primitive as well, whereas that of *B. pelargoniiflora*, assigned to the **B. eminii pollen-type**, appears to be the most primitive. Hence there appears to be a series of evolutionary levels, according to pollen type, for the species studied here.

8.8. Pollen grain size and ploidy levels

The occurrence of different levels of ploidy within a species is often expressed by different dimensions of pollen grains. In Chapter 4 it is reported that collections of both *B. elaeagnifolia* and *B. squamulosa* from the Crystal Mts in Gabon are tetraploid. Other collections of these species from the same region could not be investigated for their chromosome number, as living plants were not available. It is assumed that these are tetraploid as well. All plants of *B. elaeagnifolia* gathered in the Chaillu Mts, the Doudou Mts and elsewhere in Gabon are diploid. Of *B. squamulosa*, the gathering Arends, De Wilde & Louis 371 from the Chaillu Mts is diploid also (Table 4-1).

In Figs. 8-20 to 8-22 the squares represent the dimensions of the grains of (putative) tetraploid collections and the circles those of diploid collections. When the positions of the squares and circles in these diagrams are compared, it is obvious that these symbols form more or less separated groups. The position of the squares indicates that the grains of the tetraploid plants are in general larger than those of diploid collections. It appears that P/E values above 2.50 are indicative for tetraploidy and those lower than 2.50 for diploidy. There are a few exceptions, however. One pollen sample of a putative tetraploid collection of *B. elaeagnifolia* has a P/E of 2.24 and thus it occupies a deviating position in Fig. 8-22. This value is found for the grains of the coll. De Wilde, Arends

et al.(1983)-31, which are in general collapsed. In contrast, the pollen samples of two putative tetraploid collections of *B. squamulosa* with comparatively low P/E values of 2.07 and 2.27 respectively do not show particularly deformed grains. These grains have the largest equatorial diameter found in all pollen samples studied, however (Fig. 8-20).

Taking all the evidence in consideration, it is apparent that, in *B. elaeagnifolia* as well as in *B. squamulosa*, the pollen grains of diploid collections can be distinguished from those of tetraploid ones. This implies that in some instances the ploidy level of plants for which chromosome counts are not available, may be cautiously predicted. In Fig. 8-22 there are three triangles representing the pollen grain dimensions of *B. elaeagnifolia* collections from Cameroun. The position of two of these symbols with an equatorial diameter between 11.50 and 12.00 µm does not provide a firm basis to decide whether these collections (Letouzey 12765 and Schultze in Mildbraed 6208) are diploid or tetraploid. The position of the third triangle at an equatorial diameter of 12.50 µm and representing the grain dimensions of the coll. Satabié & Letouzey 343 suggests that this collection is diploid.

Similarly, the position of the triangles in Fig. 8-20 for *B. squamulosa* suggests that the collections with P/E values of 2.25 and 2.00 are diploid. However, here the position of squares representing pollen samples of tetraploids with P/E values of 2.50 and lower, indicates that the evidence for diploidy for the collections with unknown chromosome numbers is not conclusive.

The diagram presenting the dimensions of the pollen grains found in *B. longipetiolata* (Fig. 8-21) shows that many collections have grains that are larger than those of the tetraploid collection of De Wilde, Arends et al.(1983)-483. The position of the square (at E = 12.0 and P = 27.2) indicates that the pollen grains of this sample are slightly larger than those of collections with a known diploid chromosome number (circles). It is clear that in this instance it is not possible to make an assessment as to whether the other collections with unknown chromosome number are tetraploid or diploid. *B. longipetiolata* has the widest distribution of the species considered here. Also according to the view expressed by Löve & Löve in 1975 (see page 155) it is questionable whether it is valid to compare the pollen grain size of plants from e.g. the northwestern Cameroun with that of plants from eastern Zaire. For a reliable assessment of the occurrence of polyploidy in *B. longipetiolata* by means of pollen grain size, additional chromosome counts of plants from different geographical areas are required.

8.9. Conclusions

The present study supports the conclusion of Van den Berg (1984) that the pollen grains of the new species *B. pelargoniiflora* and *B. rwandensis* are distinctly different from those of the other species considered here, because of their size and/or ornamentation.

The grains of *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa*

are similar and their dimensions overlap, so that these species are not distinguishable by their grains. According to Van den Berg, the **B. squamulosa pollen-type** is among others characterized by sides which are often concave. However, in this study it is found that in many specimens, the sides of the grains are convex. Such ellipsoid pollen grains have been observed especially in *B. longipetiolata*. These observations indicate that there is a transition between the **B. squamulosa pollen-type** and the **B. komoensis pollen-type** as distinguished by Van den Berg.

The occurrence of diploid and tetraploid plants in *B. elaeagnifolia* and *B. squamulosa* cannot be assessed with certainty from the dimensions of their pollen grains. The dimensions of the grains in *B. longipetiolata* do not provide an indication at all as to the ploidy level of plants whose chromosome number is unknown.

Variation in grain size may be attributed to different levels of ploidy, but it appears that some conditions in the environment in which the plants investigated have grown, may also affect grain size. Further, variation may be caused by different treatments in the preparation of the pollen samples.

9. Discussion: the rank and the delimitation of the taxa; various biological aspects of the species recognized

9.1. The species concept

All the taxa recognized in the present study are accorded the rank of species. This term denotes the basic taxonomic units classified within a taxonomic system and used in phylogenetic studies. The species is a concept whose definition depends on the plant group studied and on the methods employed by the practising taxonomist studying a particular group. Radford (1986, p. 208) listed six types or concepts of the species. In the present study, the units recognized are interpreted according to two of the concepts listed by Radford: the taxonomic or typological species concept and the biological species concept.

The typological concept emphasizes morphological differences as the criterion in the recognition of the species (Grant 1957, p. 42). According to Grant (p. 45), the typological species definition leads to the conclusion that the species is a subjective entity. As to the biological species concept, Grant (op. cit., p. 50) stated that the biological species, or biospecies, possesses **i)** its own distinctive morphological character states which are separated from those of other species by a prominent gap in the variation pattern, **ii)** its own particular ecological requirements which reduce the competition with other sympatric taxa and **iii)** a combination of reproductive isolating mechanisms which prevent or greatly inhibit gene exchange with other species. However, in his more recent definition, Grant (1981, p. 45) only referred to the third of the characteristics mentioned in 1957. He then defined the biospecies as a fundamental unit of organization of biparental organisms. It is the reproductively isolated system of breeding populations. Similarly, Radford (1986, p. 208), Stace (1989, p. 145) and Stuessy (1990, p. 172) referred to the third characteristic mentioned above, as they defined the biological species as a group of interbreeding populations which are genetically or reproductively isolated from other such groups. According to Stuessy (op. cit., p. 173), Mayr suggested in 1982 a modification of the definition of the biological species by stressing ecological aspects along with reproductive isolation. However, Stuessy (loc. cit.) remarked that the ecological criterion seems to cause more problems than it solves and consequently he recommended against its use. Thus, it appears that, at present, most authors agree that a biospecies can be delimited by studying and elucidating its reproductive isolating mechanisms or barriers to hybridization.

Stuessy (1990, p. 172) pointed out that a practising plant taxonomist rarely has sufficient data regarding the breeding system and reproductive isolating mechanisms of the plants being studied. Nevertheless, according to him (1972, p. 9; 1990, pp 172 & 181) plant taxonomists generally assume that qualitative and quantitative morphological discontinuities used for species delimitation do

indeed reflect genetic differences that in some fashion are responsible for maintaining the integrity of each specific unit.

In the present study, *B. pelargoniiflora* and *B. rwandensis* are true typological species, because the recognition of these taxa is based exclusively on morphological characters observed in dried specimens. The remaining taxa, viz.: *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa*, are also morphologically distinct. However, for these taxa there are some data which indicate that they are reproductively isolated, so that, according to more recent definitions (e.g. Grant 1981, p. 45), they may be considered to be biospecies.

9.2. Reproduction

The plants studied are sexual organisms, because their female flowers only produce fruits and seeds after pollination. Until very recently it was unknown how pollen grains are transferred from the male flowers to the female flowers. In the absence of field observations of visiting insects which would act as a vector, I initially supposed that the female flowers would be pollinated by means of air currents, but in the course of the study I did not see any evidence for this supposition. However, it is now assumed that an insect like the bee *Nomia mengonis* Ckll. (Hymenoptera, Apoidea) acts as a vector, since very recently, on January 24, 1991 at 1 p.m., De Wilde (pers. com.) observed that four individuals of that species frequently visited the flowers of one of the *B. longipetiolata* plants preserved in the gathering De Wilde, Sosef & Van Nek 10195 from the Crystal Mts, Gabon.

In crossing experiments, success or failure in the formation of fruits with well-developed and/or viable seeds depends on the combination of the parent plants chosen in a cross (see below). Pollination of female flowers with pollen from male flowers of the same plant always results in the formation of fruits and seeds. Thus, the development of the ovary is apparently preceded by geitonogamy, i.e.: fertilization between neighbouring flowers on the same plant.

Success or failure of a cross-pollination was inferred from the amount of good seed in a mature dehiscing fruit. In some combinations however, the ovary did not develop into a fruit and sooner or later the complete flower dropped from the inflorescence. Seeds are considered to be good when they are solid and their shape is botuliform. Good seeds usually sink in water, while empty ones float. Whether good seeds are also viable can only be inferred from germination experiments. Some apparently good seeds germinate, whereas others do not. The resulting seedlings may not always continue to develop into flowering plants; some may be chlorotic and die soon. Owing to limited facilities, only a very small number of seed batches have been sown and, if the seeds germinated, grown into mature plants. Thus, the evidence on which the following conclusions are based, is scanty.

9.3. The biological species concept *sensu* Grant (1957) applied to the plants studied.

The three characteristics of the biological species as defined by Grant (1957) are now discussed for the taxa distinguished here.

9.3.1. Morphological characteristics

Comparison of the species descriptions and especially the key to the species in Chapter 10 shows that the taxa are rather similar. Usually, a set of characters has to be studied before a plant can be identified. This applies in particular to dried plants, whereas living plants are easier to identify. Occasionally, plants of *B. longipetiolata* and *B. squamulosa* may be phenotypically very similar, and dried plants of these species may be almost indistinguishable, especially when the specimens are fragmentary. Therefore, I included them in the '*B. squamulosa* species group', which is in line with Grant (1957, p. 57) who recommended to identify the plants of such species as to species group rather than as to species. Occasionally, plants of *B. longipetiolata* with comparatively long internodes and depauperate male inflorescences are difficult to distinguish from those of *B. elaeagnifolia*. Therefore, I am not fully certain about the correctness of my identification of some of the specimens of these two species.

As to *B. elaeagnifolia*, I suspect that the gathering Satabié & Letouzey 343, that I have assigned to that species, might represent a new species. The gathering was made at the Ngovayang Mts, Cameroun, the northernmost of the localities were plants of *B. elaeagnifolia* have been found.

The stem of Satabié & Letouzey 343 is among the thinnest and its leaves are the smallest observed in *B. elaeagnifolia*. Moreover, it was found that the venation of the leaf blade differs from that seen in any of the specimens of the other species treated here (see p. 49). I observed four styles in the female flowers of this gathering, while its outer perianth segments are, in addition to the usual scales, provided with short unbranched and probably glandular trichomes.

The number of styles ranges from 2 to 4 in *B. elaeagnifolia*, being 2 or 3 in specimens from the Crystal and Doudou Mts in Gabon. Therefore, I initially thought that Satabié & Letouzey 343 could be distinguished as a separate taxon because of its number of styles. However, when plants from the Chaillu Mts, Gabon, became available, it was found that the specimens from that region, which definitely belong to *B. elaeagnifolia*, always produce 3 or 4 styles. Therefore, I have refrained from describing Satabié & Letouzey 343 as a new species. Stem thickness and leaf blade size are not always reliable characters, while the presence of the simple trichomes on the perianth segments and, in particular, the pattern of the venation in the blade cannot be ascertained easily by ordinary means. In order to elucidate its status, at least a second, preferably spirit and/or living, gathering should be made. Anatomical, karyological and further morphological studies might reveal particular features warranting the possible specific status of this peculiar *Begonia* population in the Ngovayang Mts.

Superficially, *B. rwandensis* very much resembles *B. karperi* and even *B.*

elaeagnifolia. However, the micromorphology of the seed of *B. rwandensis* differs so much from that of the other species whose seeds could be studied (De Lange & Bouman, in prep.), that I have no doubt that the taxon represents a distinct species. Moreover, the unique ornamentation of the pollen grain wall of *B. rwandensis* (Van den Berg 1984) supports this interpretation.

B. pelargoniiflora is quite distinct by its female inflorescence that has a comparatively long peduncle and carries more than seven flowers. Vegetatively, this species is hardly distinguishable from plants of *B. longipetiolata*. Sometimes, plants of *B. pelargoniiflora* have scales on the upper leaf surface, whereas that surface in *B. longipetiolata* is invariably glabrous. Thus, in spite of the occasional presence of scales on the upper leaf surface of *B. pelargoniiflora*, sterile specimens of that species will almost certainly be confused with *B. longipetiolata*.

B. karperi differs from all other species considered here by the combination of peltate leaves and scales on the upper leaf surface. The separation of *B. karperi* from *B. elaeagnifolia* is discussed below.

9.3.2. Ecological characteristics

Data from Barret (1983), Bouxin (1973), Evrard (1968), Letouzey (1968) and Pécrot & Léonard (1960) show that in the region where the species occur, the yearly amount of rainfall ranges from ca 1.600 mm to ca 3.400 mm, but near Douala and Victoria, Cameroun, it is as high as 4.000 mm. This rainfall is not evenly distributed throughout the year; in the dry season, with a length of approximately 2 or 3 months, it may be as little or even less than 50 mm per month. According to Whyte (1983, p. 74), the distribution of many species in the Guinean-Congolian region is poorly correlated with rainfall, while the relative importance of rainfall and relative humidity is imperfectly understood. Because of the usual presence of marshes and streams in the localities where the species studied occur, I assume that the relative humidity in these localities remains high throughout the year. According to Cutler (1978, p. 84), the relative humidity inside the canopy of the rain forest normally approaches 100 per cent. Epiphytic orchids, which usually are also present in the sites where the *Begonia* plants were collected, have aerial roots with velamen which absorbs and retains atmospheric moisture during periods when there is little rainfall. The *Begonia* species may be adapted to survive in such seasonally dry conditions by their indumentum and leaf margins which may be corky near the vein terminations (page 46).

The mean monthly temperature ranges, in general, from 21 °C to 27 °C. However, the prevailing annual temperature in the area in Zaire and adjacent Rwanda where *B. rwandensis* has been found (see Map 1, page 188), is as low as 16 °C. This figure was estimated by Bouxin (1974, p. 139), because there are no weather-stations in that area. Thus I conclude that so far as temperature is concerned, *B. rwandensis* differs from the other species studied in its ecological requirements.

Except for *B. rwandensis*, the species recognized are sympatric (see the maps in Chapter 10). Different species may be found in the same habitat, as the following examples demonstrate. In Gabon, plants of *B. elaeagnifolia* (coll. De Wilde

et al. (1983)-179) have been collected together with plants of *B. longipetiolata* (coll. De Wilde et al. (1983)-180) and *B. squamulosa* (coll. De Wilde et al. (1983)-181). Similarly, in Kivu, eastern Zaire, *B. longipetiolata* (coll. Van der Veken 9724) and *B. squamulosa* (coll. Lambinon 87-279) grow in the same habitat, as both gatherings were made along the Luhoho river in that area. Most of the plants cited for *B. karperi* have been collected near Mela, Gabon. Very close to the trees on which these plants grew, a small population of *B. longipetiolata* (coll. De Wilde et al. (1983)-158) was found on some stumps of fallen trees. Plants of *B. pelargoniiflora* and *B. longipetiolata* grow together in the same site on Mt. Nlonako, Cameroun. This is evident from the records on the labels and the sequence in numbers of two gatherings of Letouzey. The former species is represented by Letouzey 14448, the latter by Letouzey 14450.

From the evidence discussed above, I conclude that with the exception of *B. rwandensis*, the species studied have very similar ecological requirements. The plants always grow in very wet and humid environments, such as near marshes and streams. Throughout the regions visited, the environmental conditions in these habitats appear to be very similar. However, my field observations indicate that the taxa occupy specific niches. *B. elaeagnifolia*, *B. karperi* and *B. squamulosa* are epiphytes which usually grow high above the ground, so that they can only be collected from trunks and branches of trees which are fallen or have been cut. Of these three species, *B. elaeagnifolia* appears to have the largest ecological amplitude, because plants of that species have also been found on trunks and stumps near the ground. *B. longipetiolata* always occurs on trees and rocks up to 3 m above the ground. This indicates that this species and *B. squamulosa*, which may resemble each other superficially, have their own specific niches which probably differ in their microclimate. The record on the label of the gathering Letouzey 14448 of *B. pelargoniiflora* states that the species grows in the understorey of the submontane forest. As to *B. rwandensis* the labels with the specimens only state that the plants are epiphytes.

9.3.3. Reproductive isolating characteristics

It is mentioned in the preceding paragraph that *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa* were sometimes found growing close together. In the field, the living plants of these four species could each be identified with certainty. When different species were found together, I looked for plants whose features might suggest that they could be hybrids, but I never found any. Because the flowers of the species involved are extremely similar, it may be assumed that an insect like the bee that visits *B. longipetiolata* (see above), would also visit the other species and consequently act as an agent of interspecific cross-pollination. From the absence of hybrid plants in the natural habitat, I inferred that the phenotypically distinct taxa are apparently reproductively isolated and hence represent good species.

In order to test the hypothesis that barriers to hybridization exist, I attempted to cross cultivated plants of different species. The number of combinations that can be envisaged, was necessarily very limited, because of the fact that the culti-

vated plants produced very few female flowers. Moreover, plants of older accessions usually had died before additional living plants from other areas or regions were introduced.

The evidence obtained so far, indicates that *B. elaeagnifolia* cannot be hybridized with either *B. longipetiolata* or *B. squamulosa*. In most crosses of *B. elaeagnifolia* with *B. longipetiolata*, or in the reciprocal crosses, the female flowers usually dropped from the plants within one or two weeks, but sometimes an ovary developed into a fruit that opened only one month after pollination. The seeds in such fruits were usually empty, whereas apparently good seeds did not germinate or yielded very few weak seedlings which showed poor growth. I assume that such seedlings would not survive in the natural habitat. Similar observations have been made in crosses between *B. elaeagnifolia* and *B. squamulosa*.

The plants of *B. longipetiolata* and *B. squamulosa* which were crossed originated from the Crystal Mts in Gabon. In any combination, the female flowers always dropped from the plants within a few days. As mentioned in Chapter 4, *B. longipetiolata* from that region is diploid, while *B. squamulosa* from the same region is tetraploid. However, all the living individuals belonging to a single collection of *B. squamulosa* from the Chaillu Mts (Arends et al. 371) proved to be diploid. Cross-pollination of these diploid *B. squamulosa* plants with diploid *B. longipetiolata* plants did not result in the formation of fruits. In these crosses, the female flowers also aborted within a few days. Consequently, I infer from these experiments that, irrespective of the ploidy level of the plants, there exists a strong barrier to hybridization between *B. longipetiolata* and *B. squamulosa*.

Cross-pollinations of plants of *B. elaeagnifolia* from the Crystal Mts in Gabon, which are exclusively tetraploid, with plants of *B. karperi*, which are diploid, usually failed to produce fruits with apparently good seeds. However, in a single combination of *B. karperi* (2x, culta coll. Breteler & De Wilde 335) with *B. elaeagnifolia* (4x, culta coll. Breteler & De Wilde 8) a fruit was produced that contained approximately ten seeds. Five of these seeds germinated, from which only two seedlings developed. Initially, these plantlets showed a rather poor growth and only a single one could be grown into a flowering plant. As expected, this plant proved to be triploid and it did not produce fruits after self-pollination. Most interesting, the hybrid plant was similar in all its features to the male parent plant of *B. elaeagnifolia*. For example, the leaves in the hybrid were not peltate. Later, *B. elaeagnifolia* was also found in the Chaillu Mts, Gabon. The plants of these accessions proved to be diploids (Chapter 4). Cross-pollination of these diploid plants with the (diploid) *B. karperi* resulted in the formation of several fruits which contained a number of viable seeds. The seeds from one fruit were sown and some of these seeds germinated. Three of the resulting seedlings, which proved to be diploid, were almost indistinguishable from the male parent *B. karperi*, with leaves which were slightly peltate and the upper leaf surface provided with scales. Thus, the hybridization experiments between *B. elaeagnifolia* and *B. karperi* indicate that, in the Crystal Mts, these

species are reproductively isolated. Gene exchange between the (diploid) plants of *B. karperi* from the Crystal Mts and the diploid plants of *B. elaeagnifolia* from the Chaillu Mts is evidently prevented by their geographical separation.

The finding of both reproductive and spatial isolation between *B. karperi* and *B. elaeagnifolia* indicates that it is justifiable to rank these taxa as species. Recently, in 1989, Louis & Nzabi (coll. nr 2952) collected a plant in the Chaillu Mts, Gabon, that is very similar to the plants of *B. elaeagnifolia* from that region. It differs from them by its peltate leaves and the presence of scales of the upper surfaces of the leaves. Because of these features I assigned the gathering Louis & Nzabi 2952 to *B. karperi*. As no living plants of *B. karperi* from the Chaillu Mts are available for chromosome counting, the ploidy level of this species in that region remains unknown.

Diploid plants of *B. elaeagnifolia* can be easily crossed artificially with tetraploid plants of that species. Infraspecific cross-pollination always resulted in the formation of dehiscing fruits with ample good seeds. Similar observations were made after cross-pollination of diploid and tetraploid plants of *B. squamulosa*. The seeds from these infraspecific crosses were found to germinate in a regular fashion and, subsequently, yield vigorous plants which are triploid and sterile.

As already mentioned on page 120, the tetraploid plants of *B. elaeagnifolia* occur in the Crystal Mts, whereas the diploid plants of that species have been found outside that region (see Map 1, page 188). A similar disjunct distribution of diploid and tetraploid plants occurs in *B. squamulosa* (Map 3, page 206). This topic is further discussed on page 180.

9.4. The modern distribution of the taxa and pleistocene forest refuges

The disjunct distribution of *B. elaeagnifolia* corresponds with three of the forest refuges distinguished by Maley (1987) in west tropical Africa below the Sanaga river in Cameroun. The distribution of *B. squamulosa* is also disjunct and the areas of that species correspond with Maley's refuges in Gabon/Equatorial Guinea and Kivu in Zaire.

Refuges or core areas (Hamilton 1988, pp 15 & 20) are places of relative climatic stability which continued to carry forest during arid and colder periods in the past. These periods occurred during several successive major world glaciations, of which the last one reached its maximum around 18.000 BP and ended abruptly at 12.500 – 12.000 BP. The map of the localities of the refuges published by Hamilton (1988, fig. 2.1) and that of Kingdon (see Hamilton, op. cit., fig. 2.3) were inferred from the modern distribution of, mainly passerine, birds and guenons (primates) respectively. Maley based his map on similar evidence, but also on palaeobotanical data and temperature fluctuations of the sea surface along the Atlantic coast of tropical Africa. The maps of these authors differ slightly from each other.

Regarding the very disjunct distribution of *B. squamulosa* which occurs in Gabon and Kivu, Zaire, I postulate that before the glaciations, the species also

occurred in the zone between the two regions where it became extinct by the temperature and precipitation depressions prevailing during the glaciations. From the modern distribution of *B. elaeagnifolia* it cannot immediately be inferred that, in the past, the species also had a much wider distribution. However, because the ecological requirements of *B. elaeagnifolia* are similar to those of *B. squamulosa* and *B. longipetiolata* (see above) and both *B. squamulosa* and *B. longipetiolata* occur disjunctly in western and eastern Africa, it can be postulated that *B. elaeagnifolia*, or a parental taxon, could have been present in the region eastwards of its present distribution.

It is noteworthy that several gatherings of *B. elaeagnifolia* have been made in the area 2-3°S/10-11°E (Map 1, page 188). This area that includes the Doudou Mts in Gabon, coincides with a part of Kingdon's southwestern refuge, but it does not coincide with any refuge shown by Hamilton or Maley. According to Maley, the area included savanna during the last glacial period. Maley's nearest refuge is situated in the Chaillu Mts (1-2°S/ca 11°E). The occurrence of *B. elaeagnifolia* in the Doudou Mts can be explained in two different ways. Either the presence of the species in that region is the result of westward migration out of the Chaillu Mts, or the region itself represents a refuge that still has to be revealed by palaeobotanical evidence.

As to *B. longipetiolata*, Map 2 (page 198) shows that this species has the widest distribution of the species studied. Plants of the species have been collected in all the areas where *B. elaeagnifolia* and *B. squamulosa* occur, but *B. longipetiolata* also occurs in the area that coincides with Maley's forest refuge situated in western Cameroun/southeast Nigeria. Moreover, the species is distributed in several areas which, depending on the interpretation of the authors mentioned above, coincide with refuges. For example, the area 4° 30′-5° 30′N/12-13°E coincides with Hamilton's 'Angola minor core area' (see fig. 2.1 in Hamilton 1988) and the area 0-1°S/ca 18E with Kingdon's 'southern Zaire basin refuge' (see fig. 2.3 in Hamilton, op. cit.). Finally, *B. longipetiolata* has been collected in the area 0° 30′N/ca 13°E that includes the Bélinga Mts in Gabon. None of the authors mentioned above suggests that this area represents a refuge, but I am inclined to think that it is, because the Babiel ridge at Bélinga is at least as high as the Crystal and Chaillu Mts. Therefore, the forest in Bélinga, like those in other mountainous regions, might have escaped extinction during the glaciations. I further assume that the presence of a population in Bélinga would not be due to migration out of other comparatively near regions, because the plants of the Bélinga population are subtly different from those of other populations.

The localities investigated for the various species concerned are usually closed plant communities. In such localities, I found that a species is often represented by a single individual only. A similar observation was made by Reitsma when he made his gathering 3246 of *B. longipetiolata* in the Doudou Mts in Gabon. Reitsma (pers. comm.) informed me that he vainly searched the vicinity of the specimen for additional plants. Along the Mbei river near Kinguélé in the Crystal Mts, I found three solitary specimens of the same species (De Wilde, Arends et al. 8840, 8841, 8848) which grew at least 50 m apart. Sometimes however,

there may be up to five individuals within a radius of less than 1.5 m. Thus, in closed plant communities, the subpopulations are very restricted in size and the number of individuals is quite low. This conclusion is in line with Grant (1981, p. 16) who stated that in such communities, the chances of the establishment of seedling progeny are small due to competition.

In contrast with the situation just described, a subpopulation may occasionally contain numerous and gregarious individuals. An outstanding example of such a population is represented by the gathering De Wilde, Arends & de Bruijn 9270, that was made near Mayumba in southwest Gabon. This population, occupying a surface of approximately 8 x 12 m, contained at least 100 individuals. These plants grew on small trees situated in the dell of a tiny affluent of the Doussa river, where, most evidently not long ago, a large tree had been removed from the forest. De Wilde (pers. comm.) informed me that the specimens in his collection 7463 from Akoakas in Cameroun, were taken from a fairly large population in a site that was definitely disturbed by man. Similarly, also in *Begonia*, the many specimens of the terrestrial *B. zenkeriana* L.B. Smith & Wassh., section *Scutobegonia*, were collected by Bos (nrs 3425, 4615, 4869, 7183) at various restricted forest sites near Kribi, Cameroun. According to Bos (pers. comm.) these sites represent places where during the first decade of this century, German foresters exploited the forest. Recently, De Wilde & Sosef (pers.comm.) visited the type locality in the Crystal Mts, Gabon, of *B. aggelopterа* N. Hallé, a rare species in section *Scutobegonia*. In undisturbed forest, they found a very few solitary plants, but along an approximately 20 years old track near the locality they observed numerous plants growing gregariously. All these observations indicate that in a closed plant community which is opened up by partial habitat destruction, the number of individuals in a population may increase.

9.5. Dispersal and gene flow

My observations in the field indicate that in very few cases, the dispersal of the species studied may be attributed to transfer of propagules such as stem pieces or even complete plants. In the Chaillu Mts in Gabon, at the site where the gathering Arends, De Wilde & Louis 571 was made, I observed a broken tree branch with a small plant of *B. elaeagnifolia* lying on a rock in the streambed of the river. This branch had fallen from a tree crown above the river. Evidently, such a plant would be moved by the river when the water rises after rainfall. However, establishment of a new population from such a founder individual would require some additional events: **i)** the plant itself should become established at the site where the branch is deposited, **ii)** the plant should continue to flower and eventually produce seeds, and **iii)** most importantly, the seeds should be transferred to tree stations well away from the water's surface. Apparently, *B. elaeagniolia* does not survive in situations where the plants will be submerged occasionally, because I never observed plants growing in situations

where they may be in direct contact with open water. The same conclusion applies to the other taxa studied.

The creeping stems of the species studied are always firmly attached to the substrate by the roots. Therefore, I have no doubt that the dispersal of these sessile organisms is mainly due to the transfer of fruits and/or seeds. Unfortunately, there are no records or observations available indicating how these diaspores are transported, but in the course of this study De Wilde and I frequently speculated about the dispersal of the plants.

In most of the species of section *Tetraphila*, the open fruits show brightly coloured placentae and valves, and therefore, may be attractive to frugivorous vertebrates. Although the species studied here have dull yellowish brown placentae, it cannot be excluded that these parts are also eaten.

At fruit maturity, the small seeds of the *Begonia* plants studied are embedded in the soft placental tissue of the fruit and it is probable that vertebrates consume the placentae without removing the seeds. If it is assumed that birds forage on the dehisced fruits, it seems likely that these birds are residents and not migrants, because throughout the seasons, the environmental conditions in the tropical forest are more or less stable. Moreover, migratory birds, which are rarely in one locality for a long time, usually are unaware of food locations (Stiles 1989, p. 105). Like resident birds in temperate zones, such birds in the tropical forest have restricted territories. Consequently, when the seeds are voided, they will be deposited not very far from the site where the placentae and the seeds were consumed.

Apart from resident birds, frugivorous bats and primates may be dispersal agents of the seeds. According to Stiles (op. cit., p. 108), flying vertebrates can move seeds for long distances, but the majority of seeds are not carried far. He cited two examples indicating that bats move seeds over distances not exceeding 200 to 300 m. Various examples of frugivorous monkeys cited by Stiles (loc. cit.) indicate that these animals consume and subsequently disseminate seeds within their home ranges. Both bats and monkeys in the tropical forest have restricted territories.

Recently, De Lange & Bouman (1992) supposed that the funicular aril of the seeds in section *Tetraphila* might act as an elaiosome and they postulated that the seeds could be transported by ants. According to Keeler (1989, p. 232), little is known of ant dispersal in tropical Africa, but she cited an example of ant-dispersed seeds that were carried only 75 cm. She stated that, although in some systems ants carry seeds further, myrmecochory is not very effective for long-range dispersal.

As already discussed, the mature dehiscing fruits soon disintegrate and the detached parts either remain on the same substrate to which the fruit carrying plant is attached, or they drop to a much lower level. When it is assumed that the seeds germinate in the substrate onto which they have fallen, this would be a case of geocarpy, a term denoting that the diaspores are buried near the mother plant (Van der Pijl 1982, p. 94). According to that author (p. 95), geocarpy also occurs in *B. hypogaea* H.J. Winkler. However, assuming that birds

or ants could remove the fruits parts and/or the seeds from low stations to higher ones, this would explain why the plants always occur well above the ground in trees or occasionally on rocks.

As the range of the presumed vectors does not exceed 300 m, it is clear that seed dispersal occurs only over limited distances. In case the animals deposit seeds outside their territories or beyond the limits of the local *Begonia* population, the environmental conditions in the new site should favour the establishment of new plants. Evidently, this is not always the case, because the plants studied only occur near or along streams or marshes. Some undefined and as yet undetected factors may determine the establishment and hence the distribution of the species. In this respect, it is interesting that along the recently constructed road Mouila-Yeno, which can be considered to be a transect of the Chaillu Mts in Gabon, *B. elaeagnifolia* only occurs at a distance of 13 km beyond Mouila. As the various collections of that species along the transect have been made at sites above 400 m, it would appear that *B. elaeagnigolia* is adapted to altitudes of 400 m and higher. However, such a conclusion is not supported by the fact that the species also occurs at a low elevation of only 10 m near the Atlantic coast in Gabon by the Rabi-Kounga oil fields.

Thus, it appears that gene flow among the local populations through the dispersal of seed is limited. Gene flow is also determined by the flight distance of pollinating insects. Data on the flight distance of the solitary bee *Nomia mengoensis* that visits plants of *B. longipetiolata*, are lacking (page 170). Grant (1981, table 2.1) presented a table from which it appears that gene flow through pollen dispersal by North-American bees mainly occurs over distances of less than 100 m. If it is assumed that the flight distance of *Nomia mengoensis* is similar to that of the North-American bees, it is clear that gene flow by pollen dispersal among plants of adjacent subpopulations which are more than 100 m apart, will be small.

From the discussion above, it appears that the possibility of gene flow among populations from different regions, e.g. the Chaillu Mts and Crystal Mts, or Chaillu Mts and Doudou Mts, can be excluded. These regions are geographically separated from each other by regions without suitable habitats for the species studied. Nevertheless, various experimental crosses between plants belonging to the same species, but from widely separated localities, indicate that the included populations of a single species are potentially interbreeding. The result of an experimental cross within *B. longipetiolata* is particularly interesting in this respect.

From this species, the living plant of the accession Leeuwenberg 9288 from Mt. Koupé, Cameroun, was crossed with that of the accession Breteler & De Wilde 356 from Kinguélé, Gabon. The collecting sites, at elevations of 800 m and 70 m respectively, are ca 450 km apart, so that it can be ruled out that there is direct gene flow among the plants from these localities. Nevertheless, the fruit produced contained approximately 200 seeds, which after sowing, germinated. From the seedlings, 50 flowering plants were grown. According to the size of the plants, the progeny of the cross was fairly heterogeneous. Some plants

remained quite small and somewhat resembled e.g. the type of *B. macrura*, a taxon that is considered to be conspecific with *B. longipetiolata*. Other plants were as large as the cultivated specimen of Breteler & De Wilde 356.

According to Grant (1981, p. 25), subpopulations living in different parts of an area are often exposed to different environmental conditions and hence to different natural selection pressures. Selection then acts in combination with the breeding structure of the species. Under conditions of random mating on a wide scale in a large population, the effects of selection for adaptation to any given local environment tend to be swamped by the continual influx of genes from other localities.

As concluded above, gene flow by dispersal of seeds and pollen in the plants studied appears to be low. Moreover, it appears that in solitary plants there would be self-pollination, whereas in subpopulations with few plants, breeding would only occur within these subpopulations. This suggests that a large population in a given area is subdivided into small panmictic units, in which selection operates on genetic variations without interferences from gene flow from other such areas. In such a situation, selection favours the formation of a series of local races adapted to their respective environments. The effect of the selection in a certain site or area may be reflected by some particular morphological traits of the plants in such a site. I consider the two populations of *B. longipetiolata* occurring in Bélinga, Gabon and the Korup National Park in Cameroun, as good examples of such a morphological differentiation. The plants in Bélinga are characterized by comparatively long internodes and stems, while those of the plants in Korup are comparatively short. In the plants from Korup, the two bracts at the top of the peduncle of the male inflorescence remain fused and the leaf blades are comparatively large. In the plants from Bélinga however, the bracts become separated and the blades are comparatively small. In fact, I could predict the origin of some collections which arrived for identification after I had studied most of the specimens of the species cited in Chapter 10. Although, occasionally, plants from different localities may be distinguishable, it would be futile to recognize this fact by giving them a formal taxonomic status.

9.6. The occurrence of the tetraploid chromosomal races within *B. elaeagnifolia* and *B. squamulosa* in the Crystal Mts, Gabon

The evidence discussed in Chapters 4 and 8 indicates that tetraploid plants of both *B. elaeagnifolia* and *B. squamulosa* are confined to the Crystal Mts in Gabon. In each of the species, the tetraploid plants are usually almost indistinguishable from the diploid ones.

As to the question why tetraploid plants only occur in the Crystal Mts, it appears to be significant that this mountainous region is, in comparison with other such regions, a rather rugged terrain, so that, theoretically, a large continuous population may become divided into smaller subpopulations, each of these situated in a particular locality. Therefore, the subpopulations of the species

considered can be interpreted as local races, whose formation is due to both different selection pressures and limited or even inhibited gene flow among the subpopulations situated in the different localities.

There can be no doubt that the tetraploid plants have arisen in the past from diploid progenitors. It is most likely that in a geographical situation as found in the Crystal Mts, these progenitors represented local races which were diploid. I postulate that before the origin of the tetraploid plants, chromosomal evolution resulted in the formation of chromosome sets which were at least different genically. Of course it cannot be ruled out that evolution also produced structurally different chromosome sets. However, I could not observe meiotic chromosome pairing in modern plants, so that, unfortunately, there is no evidence that evolution of structurally different genomes might have occurred in the extinct diploid local races.

The postulate that the tetraploid plants evolved from diploid progenitors supposes that several successive events have occured during evolution. Supposedly, plants belonging to different local races, which differed genically, hybridized and yielded a F 1 progeny that was at least partially sterile and/or had a more or less irregular meiosis. It is well known that irregular meiosis may lead to the production of unreduced gametes, so that, when the F 1 plants breed, union of such gametes yields a subsequent hybrid progeny that is tetraploid and most likely quite fertile.

Because diploid plants of both *B. elaeagnifolia* and *B. squamulosa* are apparently absent from the Crystal Mts, it may be concluded that the tetraploid hybrid progeny gradually expanded at the expense of the diploid parental races, now extinct. This conclusion is in line with Löve (1954) who stated that in some cases it is very probable that a diploid species has been split up into isolated races, which became extinct except for a polyploid formed by chance from some of these races. Thus, the postulate regarding the origin of the tetraploid races of both species considered here, implies that these tetraploids are not derived from the present diploids as e.g. found in the Chaillu Mts. Löve (op. cit.) listed numerous examples of pairs of corresponding taxa with more or less disjunct distributions. In Löve's examples, each taxon of a pair is characterized by its own level of ploidy. Because of the inferred origin of the polyploid taxon, viz.: the polyploid is derived from extinct interracial diploids, Löve denoted the polyploid as a substitution taxon or false vicariad. He advocated considering each one in a pair of corresponding taxa as different species and indeed, such taxa have often been described as distinct species, in spite of the fact that they only differ in chromosome number. It is evident that such morphologically indistinguishable taxa, which Stuessy (1990, p. 173) considered to be cytotypes of the same species, are reproductively isolated, as a hybrid of the taxa will be sterile. I concur with Stuessy that such reproductive isolation should not be regarded as an absolute criterion for species recognition and I have not suggested that the diploid and tetraploid races in *B. elaeagnifolia* and *B. squamulosa* should be accorded specific or even subspecific rank. In the dried condition, specimens of the different chromosomal races are quite indistinguishable by macromor-

phological characters, although with standardized preparation methods, pollen grain size may be a useful character for inferring the ploidy level of the specimens.

9.7. Species relationships

Modern taxonomy endeavours to classify the taxa recognized in a given group of organisms in such a way that the classification reflects the phylogenetic relations of the taxa. Phylogenetic classifications usually employ the philosophy and the methodology of cladistics that attempts to present the most parsimonious cladogram. Such a cladogram is generated from a data matrix that includes the character states of a certain number of characters in each of the taxa or evolutionary units under consideration. The methodology of cladistics requires that the taxa studied belong to a single monophyletic group. Further, in each of the evolutionary units, both the primitive or plesiomorphous and the advanced or apomorphous character states should be deduced for as many as possible characters throughout the group. All the character states of a certain character must be homologous. There can be no doubt that the section *Tetraphila*, which includes the species studied, represents a monophyletic group, since it is characterized by a combination of several features which is unique or very rarely encountered in other groups within *Begoniaceae*.

The plants studied here, hence the species recognized, have a similar habitus, because of their creeping prostrate stems and more or less similar entire leaves. Moreover, they are characterized by female flowers with two-armed styles, each provided with a spirally twisted horse-shoe shaped stigma, and male flowers having a zygomorphic androecium with poricidal anthers. The combination of these features in each of the taxa places them distinctly apart from the other taxa in the section *Tetraphila*. Of the character states, the zygomorphic androecium and the poricidal anthers are most likely advanced. The presence of these advanced character states might lead to the conclusion that, in their turn, the taxa would belong to a monophyletic group within the section. However, in discussing the evidence for this supposition with De Wilde, we hesitated to accept this, because we could not exclude the possibility that the similar character states could have evolved as the result of evolutionary parallelisms. I have abstained from doing a cladistic analysis, as it would be more appropriate to include all the taxa of the section *Tetraphila* in such an analysis.

Nevertheless, on the basis of the present knowledge, it appears that *B. pelargoniiflora* as well as *B. rwandensis* would occupy separate positions in a cladogram which are quite apart from those of the other taxa considered here. Moreover, their position would most likely indicate that they are the more primitive ones of the taxa studied. This is now discussed.

In *B. pelargoniiflora*, the pollen grains belonging to Van den Berg's **B. eminii pollen-type**, as well as the more than 7-flowered female inflorescence appear to represent primitive character states.

In *B. rwandensis*, the pollen grains belong to the **B. komoensis pollen-type** that, in comparison with the **B. squamulosa pollen-type** found in the four remaining species, is also more primitive. The actinodromous venation of its peltate leaf blade represents a primitive character state. As to the micromorphology of its seed, it remains to be ascertained whether the unique features of the testa would support the supposition that the species is a primitive taxon. The leaf blade of the species is considerably thicker than that in the other species studied. Thus, a further comparative anatomical study of the leaf blade of *B. rwandensis* and that of other species in section *Tetraphila* would be most interesting.

As to the remaining species, viz.: *B. elaeagnifolia*, *B. karperi*, *B. longipetiolata* and *B. squamulosa*, these are distinguishable into two groups, each comprising a pair of rather similar species.

The first group, including *B. longipetiolata* and *B. squamulosa*, is characterized by male inflorescences with more than five flowers. In the second group, including *B. elaeagnifolia* and *B. karperi*, these inflorescences are up to 5-flowered. Most likely, the more than 5-flowered condition represents the primitive character state from which the up to 5-flowered condition evolved by reduction. Consequently, on the basis of the reduced number of flowers in the male inflorescences, the second pair of species is considered to be advanced in relation to the first pair. From the fact that the species in the first pair are phenotypically rather similar to those of the second pair, I infer that both species pairs are related and very probably had a common ancestor.

I find it very difficult to make a sensible statement as to what character states in *B. longipetiolata* and *B. squamulosa* would indicate which of these often very similar species might be the more advanced. For example, Reitsma's (1983) proposals regarding evolutionary tendencies in the placentation in African *Begonia* might be useful in solving this problem. In his illustration, Reitsma (fig. 11) proposed that T- or arrow-shaped septal/placental tissue in transverse sections of an ovary would represent the most primitive character state, whereas cross-shaped septal/placental tissue would represent a more advanced character state. The latter situation occurs in *B. longipetiolata* and the former in *B. elaeagnifolia*, *B. karperi* and *B. squamulosa*. Thus, according to Reitsma's proposals regarding placental evolution, *B. longipetiolata* would be more advanced than the other species mentioned above. However, the present data on pollen morphology in *B. longipetiolata* do not support this supposition, because the pollen grains in that species are frequently similar to those assigned by Van den Berg (1984) to his **B. komoensis pollen-type**, which is considered to be more primitive than the **B. squamulosa pollen-type** that characterizes *B. elaeagnifolia*, *B. karperi* and *B. squamulosa*. Thus, proposals regarding evolutionary trends in both placentation and pollen types lead to opposite conclusions regarding the evolutionary relationship between *B. longipetiolata* and *B. squamulosa*. I suggest that these phenotypically very similar taxa, which are also sympatric and reproductively isolated, are probably sibling species which evolved from a common ancestor.

Similarly, *B. elaeagnifolia* and *B. karperi* most likely have a common origin. Because of its actinodromous venation, the latter species is the more primitive

one. In the Crystal Mts, the diploid *B. karperi* is reproductively isolated from the tetraploid race of *B. elaeagnifolia*, because their hybrid is sterile. The production of fertile and vigorous progeny in the cross of the diploid *B. karperi* from the Crystal Mts with the diploid race of *B. elaeagnifolia* from the Chaillu Mts suggests that the latter species might have evolved from an ancestor that had an actinodromous venation and hence was quite similar to *B. karperi*.

In conclusion, I predict that in a cladogram of the evolutionary units of the section *Tetraphila*, both *B. pelargoniiflora* and *B. rwandensis* will occupy different and separate positions which indicate that, in relation to the two species pairs cited above, they are more primitive taxa. The two pairs of sister species will be sister groups of each other, while in the pair of *B. elaeagnifolia* and *B. karperi*, the latter will be the most primitive.

The postulate that *B. karperi*, *B. pelargoniiflora* and *B. rwandensis* are comparatively primitive taxa, in addition to the fact that these taxa have narrow distributions, implies that their present populations may be relicts of populations which, in the past, occupied larger surfaces on the African continent. As to *B. karperi* and *B. pelargoniiflora*, this supposition is supported by the fact that specimens of each of these species have been collected from two disjunct subpopulations, which are approximately 200 to 300 km apart. *B. rwandensis* is strictly endemic in Kivu, Zaire and adjacent Rwanda. So far, the ornamentation of its pollen wall as well as the structure of the testa of its seed are unique features in *Begonia*. These features as well as its narrow distribution endorse my interpretation that the taxon is a good and natural species, in spite of the fact that it superficially resembles *B. elaeagnifolia* and *B. karperi*.

10. Taxonomy

The key and the descriptions are based on field collections, except when stated otherwise. Cultivated material may deviate beyond the limits given here.

Key to the species

1. Leaves peltate
   2. Fresh leaf blade c. 2 mm thick, upper surface without scales, stipules (broadly) triangular, peduncle of expanded male inflorescence 45–75 mm long, bracts on the apex of the peduncle boat-shaped, opposite, axes of the first order elongated, up to c. 5 mm long, anther c. 3 mm long . . . . . **5. B. rwandensis**
   2. Fresh leaf blade c. 1 mm thick, upper surface with scales, stipules narrowly triangular, peduncle of expanded male inflorescence 10–15 mm long, bracts on the apex of the peduncle more or less flat, unilaterally fused, clasping the peduncle, axes of the first order absent or very short, up to c. 1 mm long, anther c. 1.5 mm long . . . . . **2. B. karperi**
1. Leaves not peltate
   3. Outer perianth segments subcordate, at least 20 x 15 mm, anthers c. 4 mm long, female inflorescence more than 7-flowered, peduncle more than 20 mm long . . . . . **4. B. pelargoniiflora**
   3. Outer perianth segments rounded at the base, not subcordate, up to 17 x 10 mm, anthers less than 3 mm long, female inflorescence 1-, rarely up to 3-flowered, peduncle up to 8 mm long
      4. Male inflorescences more than 5-flowered (but depauperate inflorescences may contain less flowers), ratio of blade- and internode-length predominantly more than 5, styles papillose or provided with scales . . . . . *B. squamulosa* species group
         5. Expanded male inflorescences lax, bracts on the main axis frequently not opposite, main axis often extending above the bracts, bracts on the axes of the first and higher orders few, vestigial or absent, fresh flower buds flattened, outer perianth-segments thin, when fresh 0.3–0.6 mm, styles more or less papillose, fresh petiole usually canaliculate, ratio of blade- and internode-length usually more than 10 . . . . . **3. B. longipetiolata**
         5. Expanded male inflorescences a dense cluster, bracts on the main axis opposite, main axis not extending above the bracts, bracts on the axes of the first and higher order many, fresh flower buds globose, outer perianth-segments thick, when fresh 0.7–1.4 mm, styles

with some scales, not papillose, fresh petiole terete, rarely somewhat flattened, scarcely canaliculate, ratio of blade- and internode-length usually less than 10 . . . . . **6. B. squamulosa**

4. Male inflorescences up to 3-(very rarely 4- or 5-) flowered, ratio of blade- and internode-length less than 5, styles without trichomes . . . . . **1. B. elaeagnifolia**

1. **B. elaeagnifolia** Hook. f. **Plate 1 (p. 187), Map 1 (p. 188)**
Figs. 4-7, 4-8, 5-1, 5-2c, 5-7A, 5-10, 5-12, 5-13a, 5-15, 5-16, 6-7c, 6-8b, 6-9a & b, 6-11c & d, 6-13a, 7-10 to 7-12, 8-10 to 8-15.

B. elaeagnifolia J. D. Hooker in Oliver, Fl. Trop. Afr., 2: 579, 1871; Engler in Engl. & Drude, Veg. Erde, 9 (3.2): 619 (in clavi), 1921; Smith, Wasshausen et al., Begoniaceae, Smithsonian Contr. Bot., 60: 382, Fig. 14.15, 1986.
Type: Gabon, Crystal Mts, *Mann 1651* (holotype K)

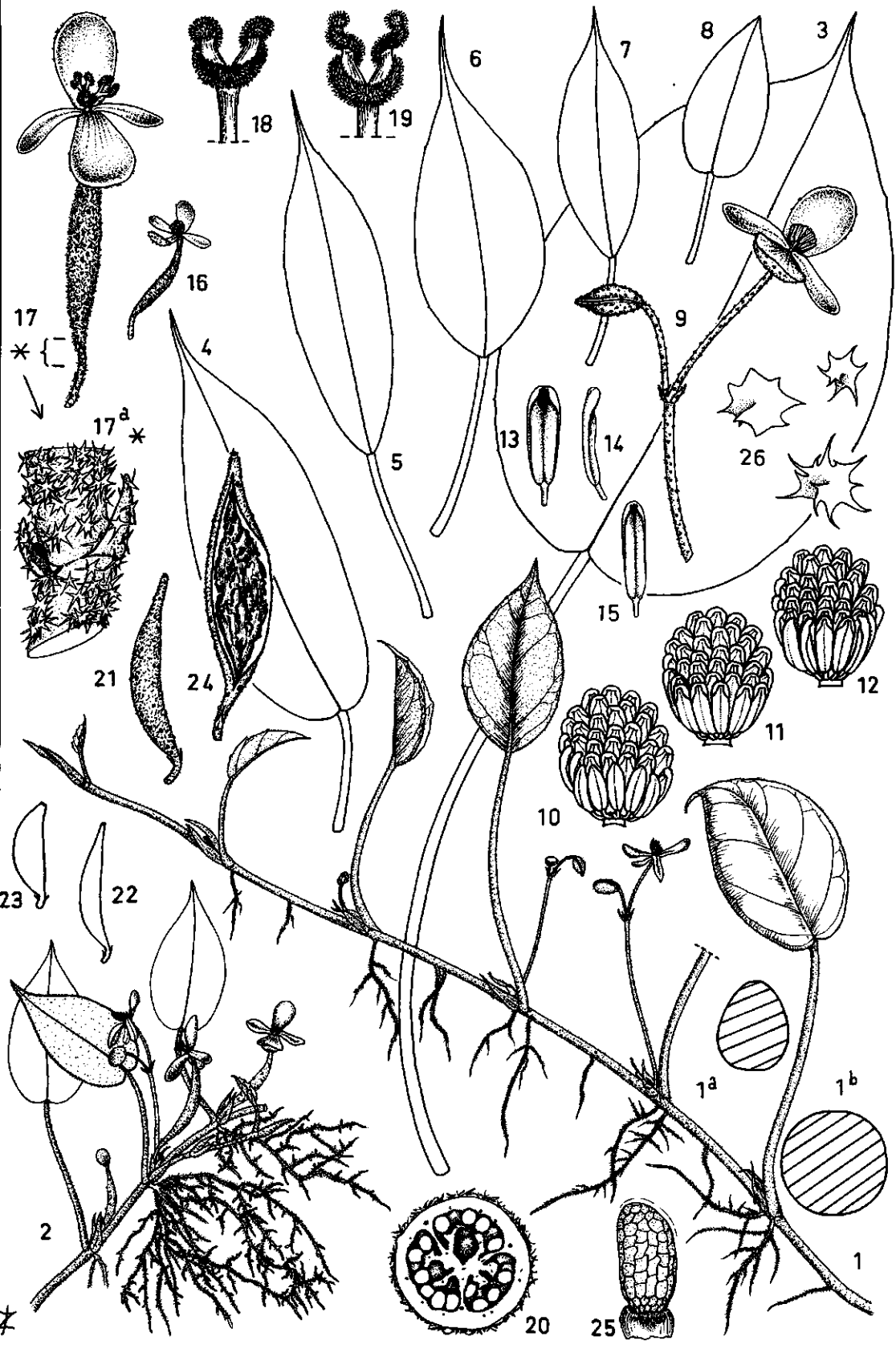
heterotypic synonyms:

B. schultzei Engler in Engl. & Drude, op. cit.: 619 (in clavi), 1921; Mildbraed, Wiss. Ergebn. Zweit. Deutsch. Zentr.-Afr.-Exp., 1910-1911, 2: 98, 1922; Smith, Wasshausen et al., op. cit.: 295, Fig. 3.7, 1986. **synon. nov.**
Type: Cameroun, between Ebolowa and Campo, falls in the Kom river, *Schultze in Mildbraed 6229* (holotype B, isotype HBG)

B. wilczekiana N. Hallé in Wilczek, Bull. Jard. Bot. Nat. Belg., 39: 91, 1969; Smith, Wasshausen et al., op. cit.: 357, Fig. 9.19, 1986. **synon. nov.**

Plate 1. *B. elaeagnifolia*; **1:** habit, extremity with male inflorescences (x 2/3); **1a & 1b:** outline of transverse sections of top (**a**) and base (**b**) of petiole (x 8); **2:** habit with several inflorescences and lateral branch (x 2/3); **3-8:** leaf-shapes (x 2/3); **9:** male inflorescence (x 2); **10-12:** androecia, front side (x 6); **13 & 14:** front and lateral view of a distal anther (x 8); **15:** proximal anther, front (x 8); **16:** 1-flowered female inflorescence, lateral (x 2/3): **17:** idem, front (x 2); **17a:** detail of 17 showing indumentum (x 16); **18 & 19:** styles (abaxial side) (x 6); **20:** transverse section of ovary half-way along its length (x 10); **21-23:** fruits (x 1); **24:** dehisced fruit (x 2); **25:** seed with aril (x 20); **26:** leaf trichomes (x 24).

1: Breteler & De Wilde (1978)-8 (herb. and spirit) and cultivated material of the same collection; **2:** culta Breteler & De Wilde (1978)-8; **3:** Hallé & Villiers 4701 (paratype of *B. wilczekiana* N. Hallé); **4:** Arends, De Wilde & Louis 571 (herb.); **5:** Letouzey 12765 (herb.); **6:** Schultze in Mildbraed 6229 (holotype of *B. schultzei* Engl.); **7:** Mann 1651 (holotype of *B. elaeagnifolia*); **8:** Breteler & De Wilde (1978)-381 (herb.); **9:** culta Breteler & De Wilde (1978)-8; **10:** De Wilde & Jongkind 9638 (spirit); **11:** Breteler & De Wilde (1978)-8 (spirit); **12:** De Wilde, Arends et al. (1983)-179 (spirit); **13-17:** culta Breteler & De Wilde (1978)-8; **18:** Breteler & De Wilde 1978-8 (spirit) **19:** De Wilde & Jongkind 9638 (spirit); **20:** culta Breteler & de Wilde (1978)-8; **21:** De Wilde, Arends et al.(1983)-179 (spirit); **22:** Breteler & De Wilde (1978)-8 (spirit); **23:** De Wilde & Jongkind 9638 (spirit); **24:** Breteler & De Wilde (1978)-8 (spirit); **25 & 26:** culta Breteler & De Wilde (1978)-8.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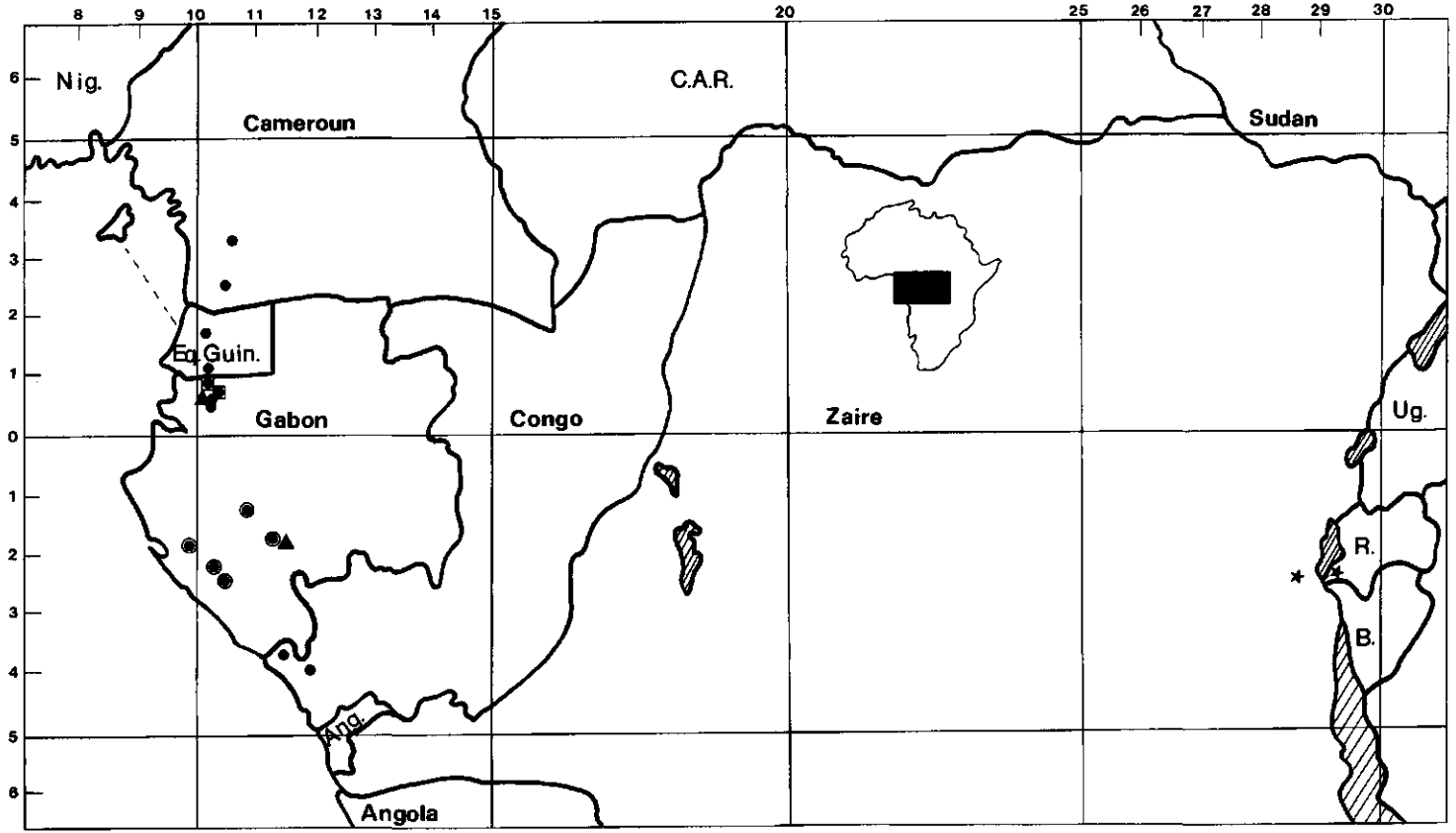


Map 1. Localities where specimens of *B. elaeagnifolia* (●), *B. karperi* (▲) and *B. rwandensis* (★) were collected; ◉: plants with a known diploid and ▣ with a known tetraploid somatic chromosome number.
B. = Burundi, C.A.R. = Central African Republic, Eq. Guin. = Equatorial Guinea including Fernando Poo, Nig. = Nigeria, R. = Rwanda, Ug. = Uganda.

Type: Gabon, Crystal Mts, Kinguélé road, *Hallé & Villiers 4531* (holotype P); a note in BR states 'isotype apparently does not exist in Brussels'.

misapplied names:

B. elaeagnifolia auct. non Hook.f., De Wild. & Th. Durand, Ann. Mus. Congo, Bot., sér. 2, I (2): 25, 1900; Th. & H. Durand, Sylloge Fl. Congol., 234, 1909; Mildbraed, op.cit.: 97, 1922; Wilczek, Fl. Congo, Rwanda, Burundi, Begoniaceae: 20, 1969.

B. schultzei auct. non Engl., Wilczek, Bull. Jard. Bot. Nat. Belg. 39: 88, 1969, p.p., Van Roeckhoudt 12 only (superfluous validation also); ibid., Fl. Congo, Rwanda, Burundi, Begoniaceae, 16, 1969; Troupin, Fl. Rwanda, II: 450, 1983.

Description: Monoecious, succulent, lepidote, epiphytic plants with creeping stems, rooting at the nodes, the roots c. 0.5 – 1 mm in diam. Dentate scales on stem, abaxial surface of stipules, petioles, lower surface of blade, peduncle, all bracts, perianth cylinder, pedicellate ovary and abaxial surface of the outer perianth segments.

Stems up to 2.5 m long, occasionally branching, terete and solid, the younger part succulent, the older part woody, dried stems light to dark brown, 1 – 3 mm in diam., living stems dark red-brown, up to 3.5 mm in diam., internodes (1.5) 2.5 – 7 (8) cm long (ratio of blade- and internode-length 1 – 5). Stipules remaining for some time at the herbaceous extremity of the stem, narrowly triangular-ovate, 6 – 15 x 1 – 5 mm, apex acute.

Leaves attached to the side of the stem away from the substrate (leaf scars may be absent on some nodes as leaves do not always develop on each node); petioles usually terete, occasionally somewhat flattened on the upper side, tapering from their base towards the blade, in transverse section circular to ovate, up to 3 (5) mm in diam. at their base, up to 2 (3) mm in diam. at the apex, 2.5 – 20 (25) cm long, green to dark brown-red; blade almost symmetrical, quite flat, hardly trough-shaped, 0.7 – 0.9 mm thick when fresh, (narrowly) ovate, 1 – 15 (20) x 1 – 11 (13) cm, base nearly cuneate, obtuse or subcordate, apex acute to acuminate, upper surface yellowish to dark green, more or less glossy, lower surface sometimes paler, but usually darker than the other surface, pale to dark green or (greenish) brown to dark red-purple, dull to more or less glossy; margin smooth to slightly sinuate with minute teeth where the secondary veins and their branches terminate in the margin; venation pinnate, of the simple craspedodromous type, and inconspicuous on the upper surface, primary vein moderate in size, usually straight and prominent on the lower surface, secondary veins (3) 4 – 7 (8) on each side diverging from the primary vein at narrow or moderate angles, of moderate size and straight or slightly curved, usually not or only partly prominent on the lower surface.

Inflorescences unisexual, axillary, usually produced at the extremity of the stem where the leaves may not have developed yet.

Male inflorescences (1-) 2- or 3-, very rarely 4- or 5-flowered; peduncle pinkish brown and terete, (5) 10 – 30 (-50) x (0.5) 0.8 – 1.2 (1.6) mm; terminated by 2

bracts, these pale greenish brown, free from each other, very rarely unilaterally fused or wanting altogether, (narrowly) triangular, up to 4 (5) mm long and up to 3 (4) mm wide; axes of the 1-st (and 2-nd) order very much reduced in length, up to 1 (1.5) mm long or quite absent; superior bracts when present (partly) concealed by the bracts, narrowly triangular, up to 3 x 0.5 mm, occasionally absent or vestigial.

Male flower with a pink perianth cylinder, terete, 5–11 (13) x 0.3–1 mm; perianth segments 4 in two opposite pairs forming a cross, white to (dark) pink, usually variegated, rarely pure white, outer segments (broadly) elliptic-obovate, apex obtuse, 6–10 x 3–9 mm, 0.3–0.5 mm thick when fresh, inner segments narrowly elliptic-obovate, apex obtuse, 4–9 x 1.5–2.5 (3) mm, c. 0.2 mm thick when fresh, sometimes reflexed; androecium a zygomorphic fascicle of (15) 20–40 (60) stamens, filaments pink, fused at their base, free parts c. 0.3–1.5 mm long; anthers yellow, basifixed, narrowly oblong, usually widening towards the apex, 1–1.8 x c. 1 mm, dehiscing by two apical pores which are more or less hidden by the cucullate anther apex, orientation of the front side of the anthers in relation to the proximal side of the androecium variable.

Female inflorescences 1-, (2-)flowered, in cultivated plants up to 3-flowered, peduncle usually absent, rarely up to 4 x 1 mm, bracts narrowly triangular, up to 2 x 0.5 mm, or absent.

Female flower with 4 perianth segments in two pairs, white to pink, similar to those of the male flower, outer segments 6–10 x 6–9 mm, inner segments 5–7 x 2–3 mm; styles in general 2 or 3 (but 3 or 4 in plants from the Chaillu Mts, Gabon), usually pink, sometimes white, fused at their base, each with two spreading arms, fused part c. 0.5 mm, free part 0.7–2 mm and the style arms (0.4) 1–2.5 mm long; stigma a yellow, papillose and horse shoe-shaped band embracing the style arms, each end of the band coiling once or less frequently almost twice around the apex of the arm. The ovary continuous with the pedicel, fusiform and curved, (7) 11–21 x 2–4 mm, reddish brown, occasionally with some greenish lenticels; multi (2-4)-locular with axile placentation in the lower part and unilocular with parietal placentation in the upper part, each septum with the placentae more or less arrow-shaped in transverse section; the ovules anatropous, ovule position in the locules epitropous, the raphe situated away from the axis of the ovary.

Infructescences with 1 (2), more or less sessile fruit, dark brown-red, fusiform, more or less curved, 20–30 x 3–4 mm, tapering towards the apex.

Mature fruits dehiscing by 1–3 longitudinal slits and soon disintegrating. Seeds botuliform with a funicular aril, c. 1 x 0.5 mm.

Pollen grains perprolate with concave to straight sides, c. 27–36 x c. 10.5–12.5 µm.

Somatic chromosome numbers 2n = 36–39 (diploid) and 2n = 72–76 (tetraploid).

Specimens examined:

CAMEROUN: Bikeligi, Lolodorf region, 03 14N-10 44E, *Annet 417* (P); Mt. Ngoyang, 12 km

N of Lolodorf, 03 20N-10 40E, Alt. 600-1000 m, *Letouzey 12765* (P); Ngovayang Mts, 14 km W of Lolodorf, 03 15N-10 36E, Alt. 630 m, *Satabié & Letouzey 343* (P, WAG, YA); Nkolumbimbe, promontory between Ebolowa and Campo, c. 02 30N-10 30E, *Schultze in Mildbraed 6208* (B); mountain near the falls in the Kom River, promontory between Ebolowa and Campo, c. 02 30N-10 30E, Alt. 672 m, *Schultze in Mildbraed 6229* (B: holotype of *B. schultzei* Engl. HBG: isotype);

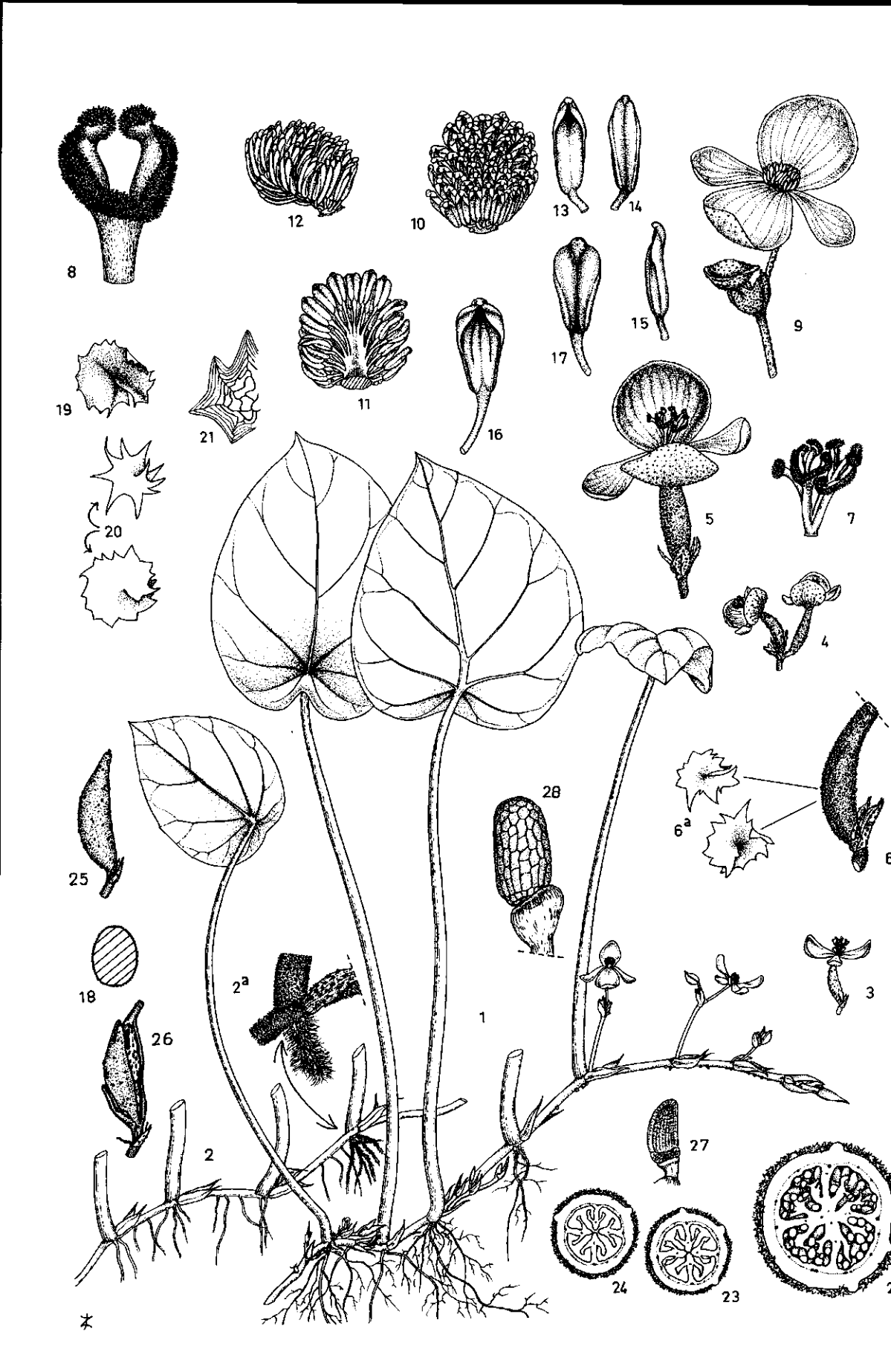
EQUATORIAL GUINEA: Crystal Mts, 10 km ENE of Okuamkas, 01 09N-10 13E, *Wilks 1750* (WAG); 52 km from Bata, Rio Benito road, Metom River, 01 45N-10 10E, *Sanford 5800* (IFE, K), *5860* (K);

GABON: Chaillu Mts, Mouila-Yeno, 42-43 km, 01 40S-11 20E, Alt. 400 m, *Arends, De Wilde & Louis 559, 571*(WAG); western flank of Doudou Mts, 02 15S-10 20E, Alt. 500 m, *Arends, De Wilde & Louis 670, 681* (WAG); Crystal Mts, Asok-Tchimbélé, 3 km, 00 41N-10 23E, Alt. 600 m, *Breteler & De Wilde (1978)-8* (WAG); id., slope near the falls of the Mbei river at Tchimbélé, 00 38N-10 24E, Alt. 500 m, *Breteler & De Wilde (1978)-38* (WAG); id., Asok-Tchimbélé, 13 km, 00 40N-10 23E, Alt. 600 m, *Breteler & De Wilde (1978)-381* (WAG); Chaillu Mts, Mouila-Yeno, 50 km, 01 40S-11 24E, Alt. 700 m, *Breteler, Lemmens & Nzabi 8248* (WAG); Rabi-Kounga oil field, 01 55S-09 50E, *Breteler, Jongkind et al. 9568* (WAG); Crystal Mts, slope near the falls of the Mbei river at Tchimbélé, 00 38N-10 24E, Alt. 420 m, *De Wilde, J.J. et al. (1983)-12* (WAG); id., Tchimbélé-Kingélé, 7 km, 00 37N-10 22E, 500-600 m, *De Wilde, J.J. et al.(1983)-31, 35, 43* (WAG); id., E of Mela, Mytsibe-Zang Rivers, Alt. 250 m, 00 35N-10 16E, *De Wilde, J.J. et al.(1983)-157* (WAG); id., Tchimbélé-Kingélé, 10 km, 00 38N-10 21E, Alt. 570 m, *De Wilde, J.J. et al.(1983)-179* (WAG); id., 20 km NW of Asok, 00 53N-10 12E, Alt. 600 m, *De Wilde, J.J. et al. (1983)-262* (WAG); Doudou Mts, Ndongo River, 02 14S-10 14E, Alt. 150 m, *De Wilde, Arends & de Bruijn 9127* (WAG); id., 35 km NW of Doussala, c.02 15S-10 20E, Alt. 530 m, *De Wilde & Jongkind 9444* (WAG); Chaillu Mts, Mouila-Yeno, 47 km, 01 40S-11 25E, *De Wilde & Jongkind 9638, 9648* (WAG); Rabi-Kounga oil field, 01 55S-09 50E, Alt. 10 m, *De Wilde, Arends et al. 9717* (LBV, WAG); 30-35 km S of Rabi-Kounga oil field, Echira River, 02 05S-09 50E, Alt. c. 20 m, *De Wilde, Arends et al. 9754* (LBV, WAG), *9758* (WAG), *9777, 9810* (LBV, WAG); Crystal Mts, Tchimbélé-Asok, 10 km, 00 40N-10 21E, Alt. 580 m, *De Wilde & Sosef 10133* (WAG); id., 2 km S Kinguélé, Mbei River, 00 27N-10 16E, Alt. 100 m, *De Wilde & Sosef 10201* (WAG); Chaillu Mts, Mouila-Yeno, 46 km, Alt. 450 m, *De Wilde & Sosef 10389* (WAG); Crystal Mts, falls of the Mbei River at Kingélé, 00 27N-10 16E, *Hallé & Villiers 4452* (P); id., Kingélé road, 00 28N-10 18E, *Hallé & Villiers 4531* (P: holotype of *B. wilczekiana* N. Hallé), *4560* (BR, P: paratype of *B. wilczekiana* N. Hallé); id., 6 km S of Asok, 00 41N-10 23E, *Hallé & Villiers 4701* (BR, P: paratype of *B. wilczekiana* N. Hallé); id., W of the Balakaba river, 00 33N-10 08E, *Hallé & Villiers 5327* (P); id., 12 km SW of the Kingélé falls, 00 25N-10 15E, *Hallé & Villiers 5374* (P: paratype of *B. wilczekiana* N. Hallé); Chaillu Mts, falls in the Waka river, 32 km SE of Sindara, 01 18S-10 57E, Alt. 250 m, *Louis, Breteler & de Bruijn 1267* (WAG); id., Mouila-Yeno, 13 km, Alt. 500 m, *Louis, A.M. 2725* (WAG); Crystal Mts, c. 01 00N-10 00E, *Mann 1651* (K, holotype); Doudou Mts, 30 km SW of Doussala, 02 32S-10 29E, *Reitsma 1958* (WAG); Crystal Mts, 0.5 km SW of Tchimbélé, 00 37N-10 24E, Alt. 520 m, *Wieringa* 473, 933 (WAG);

CONGO: Kouilou, Mayombe, Koubala Forest near Ngongo, c. 04 00 S-12 00E, *Attims 408*, (IEC); Louvandzi-N'Dindi, 03 45S-11 20E, *Sita 3670* (IEC).

2. B. karperi J.C. Arends, **spec. nov.** **Plate 2 (p. 192), Map 1 (p. 188)**
Figs. 4-6, 5-2d, 5-5, 5-7B, 5-14a, 8-16, 8-17.

Planta epiphytica, caulis longis gracilibusque (in sicco diam. c. 1.5–2 mm), habitu inflorescentiisque facie *B. elaeagnifoliae* tamen differt foliis peltatis superne lamina in vivo squamis argenteo-canis dispersis munita. Stipulae plus minusve persistentes, anguste triangulares, folia succulenta, in vivo c. 1 mm crassa. Inflorescentia mascula uni-aut diflorata, *B. rwandensis* similis conspectu parum accurata tamen differt pedunculo brevi, c. 10–15 mm longo ferente apici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duas bracteas unilateraliter connatas instar cupulae parvae late ovatae (c. 3.5 x 2 mm). Axes primi reducti vel desunt. Floris masculae perianthium cylindriforme c. 5 mm longum, tepalis exterioribus late ovatis aut orbiculatis, usque ad c. 6 x 6 mm, tepalis interioribus anguste ellipticis, usque ad c. 5 x 2 mm. Androecium c. 45 stamina continens, antheris c. 1.5 mm longis. Granum pollinis perprolatum, latere rectum aut leviter concavum, c. 29 x 12 μm.

Type: Gabon, Crystal Mts, just S of Mela, *Breteler & De Wilde (1978)- 335* (holotype WAG).

Description: Monoecious, succulent, lepidote and epiphytic plants with creeping stems, rooting at the nodes, the roots c. 0.5 – 1 mm in diam.; with a more or less dense indumentum of dentate scales present on stem, abaxial surface of stipules, petioles, lower and especially on the upper surface of the blade, peduncle and all bracts, perianth cylinder, pedicellate ovary and abaxial surface of the outer perianth segments.

Stems up to 2 m long, occasionally branching, terete and solid, the younger part succulent, the older part woody, dried stems brown, c. 1.5 – 2 mm in diam., internodes (2) 3 – 6.5 cm long (ratio of blade- and internode-length c. 2). Stipules remaining for some time at the herbaceous extremity of the stem, narrowly triangular, 9 – 15 x 2 – 5 mm.

Leaves attached to the side of the stem away from the substrate; petiole terete, circular to ovate in transverse section, 6 – 16 cm long, blade 0.7 – 1 mm thick when fresh, nearly symmetrical and peltate (the petiole attached 4 – 16 mm from the base), ovate, 5.5 – 15 x 3.5 – 11 cm, base rounded or, in cultivated plants occasionally subcordate, apex acuminate, upper surface more or less dull green when living, carrying scattered scales, these scales on the living blade silvery-grey and conspicuous, lower surface green or dark purplish green, margin smooth with minute teeth where the primary and the secondary veins terminate in the margin; venation actinodromous with 5 primary veins, the median vein straight and prominent on the lower surface, the others straight to somewhat curved and partly prominent.

Plate 2. *B. karperi*; **1:** habit, extremity with male inflorescences (x 1/2); **2:** sterile stem part (x 1/2); **2a:** detail of 2, showing indumentum (x 1); **3:** 1-flowered female inflorescence (x 1/2); **4:** 2-flowered female inflorescence (x 1/2); **5:** 1-flowered female inflorescence (x 3/2); **6:** ovary (x 2); **6a:** ovary trichomes (x 30); **7:** top of gynoecium (x 3); **8:** style, abaxial side (x 10); **9:** male inflorescence (x 1.5); **10:** androecium, front side (x 5); **11 & 12:** idem, reverse and lateral; **13, 14 & 15:** proximal stamen, front, rear and lateral (x 10); **16 & 17:** distal stamen, front and rear (x 10); **18:** transverse section of top of petiole (x 3); **19:** petiole trichome (x 30); **20:** lamina trichomes (x 30); **21:** detail of 20; **22:** transverse section of ovary half-way along its length (x 8); **23 & 24:** idem, towards the apex; **25:** mature fruit (x 1); **26:** dehisced fruit (x 1); **27:** ovule with funicle (x 20); **28:** seed with aril (x 20).

All drawn from cultivated material of Breteler & De Wilde (1978)-335, except for 25, De Wilde, Arends et al.(1983)-158.

Inflorescences unisexual, axillary, usually produced at the extremity of the stem where the leaves may not have developed yet.

Male infloresences 1- or 2-flowered, peduncle 8–15 mm long, c. 1 mm in diam., terminated by 2 bracts, these pale greenish brown and unilaterally fused, collectively ovate in outline with two small and more or less acute apices, c. 3.5 x 2 mm, axes of the 1-st order vestigial, the superior bracts on these axes absent or vestigial.

Male flower with a white or pink perianth cylinder, terete, c. 5 x 1 mm; perianth segments 4 in two decussate pairs forming a cross, white or slightly pink, outer segments broadly ovate to orbicular, 5–6 x 5–6 mm, inner segments (narrowly) elliptic, 4–5 x 2 mm; androecium a zygomorphic fascicle of c. 45 stamens, filaments white to pink, fused at their base, free parts c. 0.3–1 mm long, anthers yellow, basifixed, c. 1.5 mm long, widening towards the apex, dehiscing by two apical pores which are more or less hidden by the cucullate anther apex, front side of all anthers oriented towards the proximal side of the androecium.

Female inflorescences 1-flowered, peduncle 2.5–7 x 1 mm, bracts absent or, when present, unilaterally fused and ovate in outline with two minute more or less acute apices, superior bracts 2, narrowly oblong, 1 x 0.2 mm, or absent.

Female flower with 4 perianth segments, similar to those of the male flower, outer segments broadly obovate to orbicular, 5 x 5 mm, inner segments elliptic, 3 x 1.2 mm; styles 2 [in cultivated plants (2), 3 or 4], fused at their base, each with two spreading arms, fused part c. 0.5 mm, free part c. 0.7 mm and the style arms c. 1–2.5 mm long; stigma a yellow, papillose and horse shoe-shaped band embracing the style arms, each end of the band coiling once around the apex of the arm. The ovary continuous with the pedicel, fusiform and curved, green to reddish brown, c. 10–12 x 3 mm, multi (2-4)-locular with axile placentation in the lower part and unilocular with parietal placentation in the upper part, each septum with the placentae more or less arrow-shaped in transverse section, the ovules anatropous, ovule position in the locules epitropous, the raphe situated away from the axis of the ovary.

Infructescence with 1 fruit, fusiform and slightly curved, c. 20 x 6 mm, mature fruits known from cultivated plants only, dehiscing by 1 or 2 longitudinal slits, soon disintegrating. Seeds botuliform with a funicular aril, c. 1 x 0.5 mm.

Pollen grains perprolate with straight to weakly concave sides, c. 27–31 x c. 11.5–12.5 μm.

Somatic chromosome numbers $2n = 36 - 38$ (diploid)

Etymology: the species is named in honour of Mr J.J. Karper who was in charge of the splendid collection of living *Begonia* plants of the Department of Horticulture, Agricultural University in Wageningen until 1986, when he retired, and the *Begonia* collection was dispersed to several institutions. In 1983 Mr Karper was the senior member of a group of botanists (with J.J.F.E. de Wilde, F. Bouman, A.M. Louis and the present author) exploring various regions in Gabon. Due to his outstanding success in growing begonias all the living specimens survived their transfer from the tropical rainforest to the greenhouse. In conse-

quence, details of features which can only be studied from living plants are now known. Moreover, in cooperation with Professor J. Doorenbos, Mr Karper bred several *Begonia* hybrid cultivars which greatly contributed to the importance of these ornamentals for the floriculture industry in the Netherlands and elsewhere.

Specimens examined:

GABON: Crystal Mts, S of Mela, along the Mela River, 00 35N-10 16E, Alt.250 m, *Breteler & De Wilde (1978)-335* (WAG); id., E of Mela, Mytsibe-Zang Rivers, 00 35N-10 16E, Alt. 250 m, *De Wilde, J.J. et al.(1983)-158* (WAG); 10 km S of Mela, Essia River, c. 00 35N-10 15E, *Hallé & Villiers 4885* (P); Chaillu Mts, Massika, between Mouila and Yeno, 01 40S 11 15E, Alt. c. 550 m., *Louis & Nzabi 2952* (LBV, WAG).

3. B. longipetiolata Gilg **Plate 3 (p. 196), Map 2 (p. 198)**

Figs. 4-3 to 4-5, 5-2a, 5-3, 5-6B,5-9, 5-13b, 6-2, 6-3, 6-5, 6-7b, 6-9d to 6-9f, 6-11a & b, 7-1 to 7-4, 8-1, 8-7 to 8-9.

B. longipetiolata Gilg in Engl. Bot. Jahrb. 34: 92, 1904; Engler in Engl. & Drude, Veg. Erde, 9 (3.2): 620, 1921, in synonomy of *B. squamulosa*, p.p., specimens from Kribi region only; Mildbraed, Wiss. Ergebn. Zweit. Deutsch. Zentr.-Afr.-Exp., 1910-1911: 89 and 98, 1922; Hutchinson & Dalziel, Fl. West Trop. Afr., ed.1 (1.1): 186, 1927; Keay, Fl. West Trop. Afr., ed.2 (1.1): 220, 1954, in synonomy of *B. squamulosa*; Hallé & Raynal, Adansonia, nouv. sér., 6 (1): 113, 1966, p.p., except Mann 1654 (= type of *B. squamulosa*).
Type: Cameroun, E of Kribi, *Dinklage 1499* (holotype B, isotype HBG).

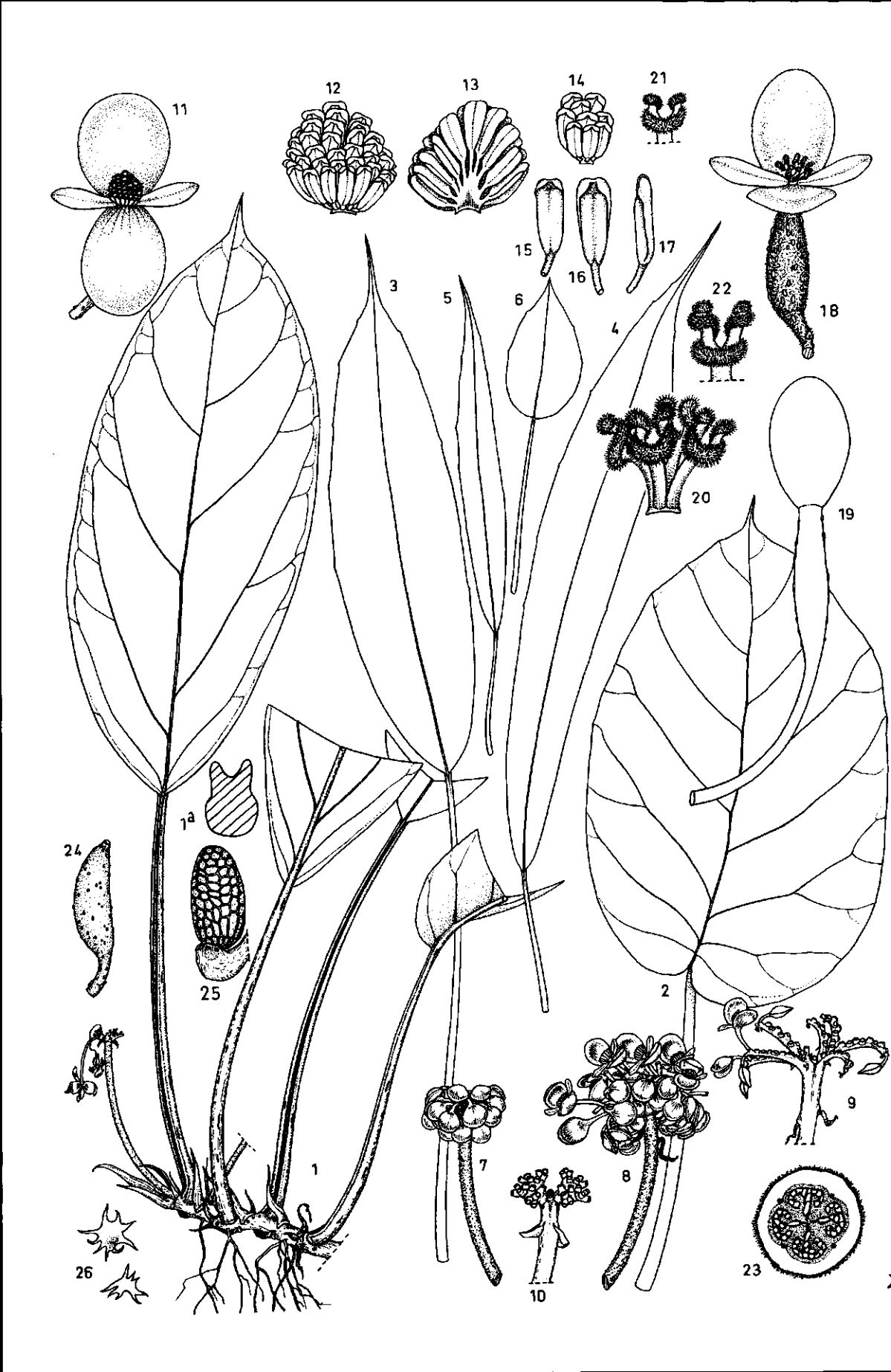
heterotypic synonyms:

B. macrura Gilg in Engl. Bot. Jahrb. 34: 92, 1904; Engler in Engl. & DruDe, op.cit., 619, 1921; Mildbraed, op.cit.: 98, 1922; Smith, Wasshausen et al., Phytologia, 54: 468, (in synonomy of *B. squamulosa*), 1984; ibid., , Begoniaceae, Smithsonian Contr. Bot. 60: 386, Fig. 14.31 (as *B. squamulosa*), 1986. **synon. nov.**
Type: Cameroun, between Mafura and Mundame, *Schlechter 12918* (holotype B).

B. gracilipetiolata De Wild., Ann. Mus. Congo, sér. 5, 2: 319, 1908; Th. & H. Durand, Sylloge Fl. Congol.,234, 1909; Engler in Engl. & Drude, op.cit.: 619 (in clavi), 1921; Mildbraed, op.cit.: 89, 1922; Wilczek, Fl. Congo, Rwanda, Burundi, Begoniaceae: 22, 1969; emend. Fernandes, Bol. Soc. Brot., sér. 2, 44: 9, pl. 3, 1970; ibid., Consp. Fl. Angolensis, 4: 293 and 364, 1970; Smith, Washausen et al., op.cit.: 381, Fig. 14.11, 1986. **synon. nov.**
Type: Zaire, Injolo, *Laurent 1702* (holotype BR, isotype B).

B. crassipes Gilg ex Engler in Engl. & Drude, op.cit.: 619 (in clavi), 1921; Mildbraed, op.cit.: 89, 1922; Smith, Wasshausen et al.,op.cit.: 382, Fig. 14.17, 1986. **synon. nov.**
Type: Cameroun, Bipindi, *Zenker 3152* (holotype B, isotypes BM, BR, G, E, HBG, K, LY, W, Z).

B. bipindensis Gilg ex Engler in Engl. & Drude, op.cit.: 619 (in clavi), 1921;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Hallé & Raynal, op. cit.: 116, 1966 (in synonomy of *B. squamulosa*). **synon. nov.**
Type: Cameroun, Bipindi, *Zenker 3098* (holotype B, isotypes BM, E, G, K).

B. squamulosa Hook. f. var. *bipindensis* (Gilg ex Engl.) N. Hallé, Adansonia, sér. 2, 12: 366, 1972 (invalid combination)

B. gladiifolia Engler in Engl. & Drude, op.cit.: 619 (in clavi), 1921; Mildbraed, op.cit.: 188, 1922; emend. Wilczek, Bull. Jard. Bot. Nat. Belg., 39: 84, 1969 (superfluous validation also); ibid., Fl. Congo, Rwanda, Burundi, Begoniaceae: 19, 1969; Smith, Wasshausen et al., op.cit.: 172, Fig. 14.16, 1986. **synon. nov.**
Type: Fernando Poo, Mt. St. Isabel, above Basilé, *Mildbraed 6394* (holotype B).

B. nicolai-hallei Wilczek, Bull. Jard. Bot. Nat. Belg. 39: 86, 1969; Smith, Wasshausen et al., op.cit.: 204, Fig. 14.13, 1986. **synon. nov.**
Type: Gabon, Crystal Mts, 12 km SW of Kinguélé, Hallé & Villiers 5381 (holotype P).

Nomina nuda:

B. kribensis Engler in Eng. & Drude, op.cit.: 619 (in clavi), 1921, attached to *Schultze in Mildbraed* 6189 (B), Cameroun, between Ebolowa and Campo; Mildbraed, op.cit.: 97, 1922.

B. ludwigsii Gilg ex Wilczek, Bull. Jard. Bot. Nat. Belg., 39: 84, 1969, in synonomy of *B. gladiifolia*, attached to Ludwigs 600 (B), Cameroun, Victoria.

Description: Monoecious, succulent, epiphytic plants, sometimes growing on rocks, with creeping stems, rooting at the nodes, the roots c. 0.5 – 1 mm in diam; with a more or less dense indumentum of dentate scales, rarely completely glabrous, scales may be present on stem, abaxial surface of stipules, petioles, lower surface of the blade, peduncle, axes of the 1-st and higher orders, all bracts,

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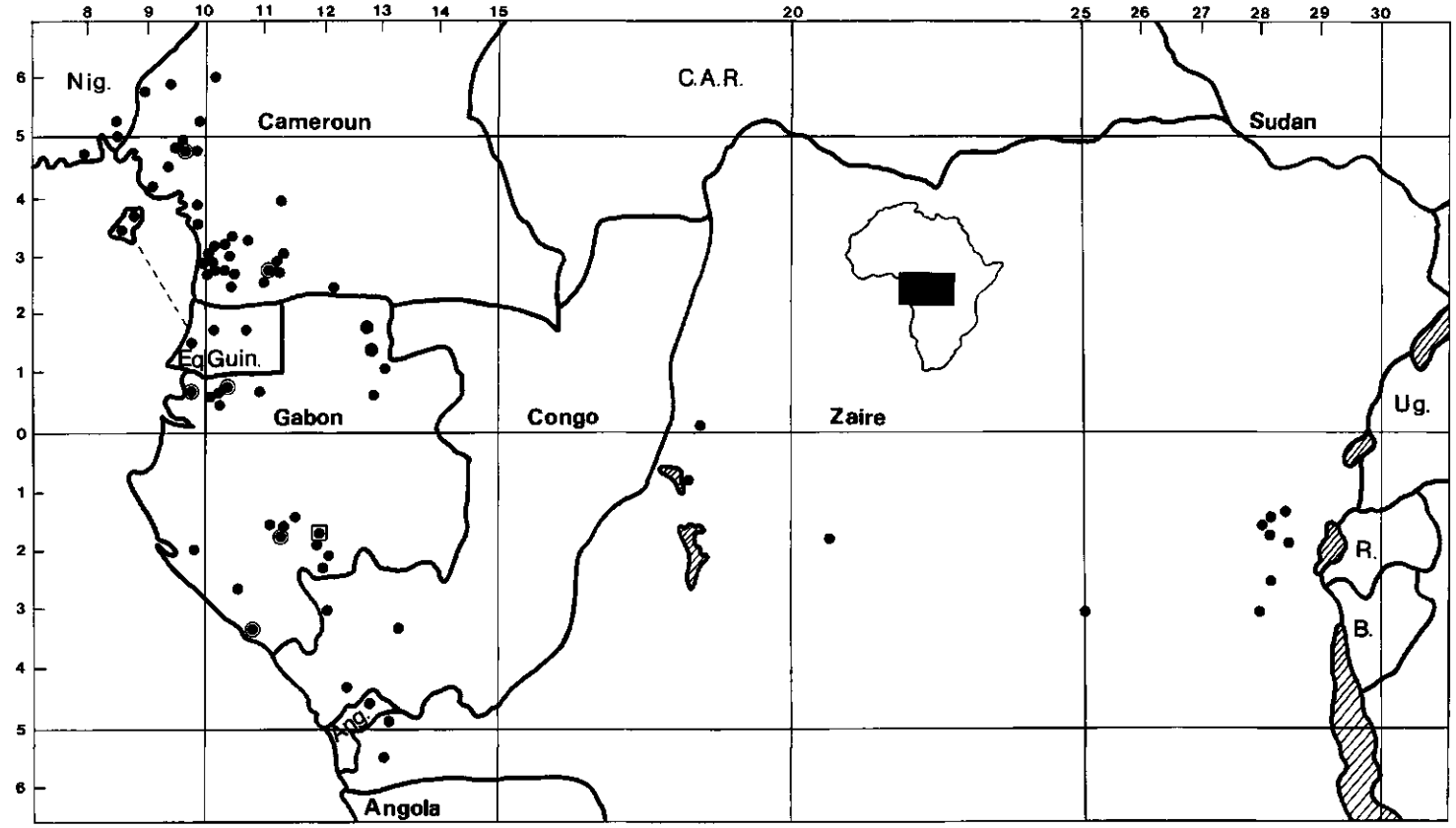
Plate 3. *B. longipetiolata*; **1:** habit, extremity with old male inflorescence (x 1/2); **1a:** outline of transverse section of top of petiole (x 2); **2-6:** leaf-shapes (x 1/2); **7:** male inflorescence before anthesis (x 1); **8:** male inflorescence (x 1); **9 & 10:** old male inflorescences (x 1); **11:** male flower (x 2); **12:** androecium, front side; **13:** idem, reverse (x 6); **14:** androecium with fewer stamens, front (x 6); **15** and **16:** proximal and distal stamens of androecium shown in 12, front; **17:** stamen shown in 16, lateral (x 8); **18:** 1-flowered female inflorescence (x 2); **19:** female flower with elongated pedicellate ovary (x 2); **20:** top of gynoecium (x 8); **21 & 22:** two styles (abaxial view) from a single collection (x 4); **23:** transverse section of ovary half-way along its length (x 5); **24:** mature closed fruit (x 1); **25:** seed with aril (x 20); **26:** trichomes of ovary (x 20).

1: De Wilde, Arends & de Bruijn 8848 (herb.) and De Wilde 7724 (spirit); **1a:** De Wilde, Arends & de Bruijn 8841 (spirit); **2:** Letouzey 15136 (herb.); **3:** Leeuwenberg 9294 (herb.); **4:** Mildbraed 6394 (holotype of *B. gladiifolia* Engl.); **5:** Mildbraed 6183 (herb.); **6:** Laurent 1702 (holotype of *B. gracilipetiolata* De Wild.); **7 & 8:** De Wilde, Arends & de Bruijn 8841 (spirit); **9 & 10:** culta Arends, De Wilde & Louis 483 and De Wilde 7724 respectively (spirit); **11-13:** De Wilde 7724 (spirit); **14:** De Wilde, Arends et al.(1983)-180 (spirit); **15-17:** De Wilde 7724 (spirit); **18:** De Wilde, Arends & de Bruijn 9270 (spirit); **19:** culta De Wilde, Arends et al.(1983)-483; **20:** De Wilde, Arends & de Bruijn 9270 (spirit); **21-26:** De Wilde 7724 (spirit).



Map 2. The localities where specimens of *B. longipetiolata* were collected; ◉: plants with a known diploid and ▣ with a known tetraploid somatic chromosome number .
For abbreviations see Map 1.

perianth cylinder, pedicellate ovary and abaxial surface of the outer perianth segments.

Stems usually up to 40 (50) cm, but in Belinga, Gabon, up to c. 100 cm long, straight or slightly to distinctly zig-zag, occasionally branching, terete and solid, the younger part succulent, the older part woody. Dried stems light to dark brown, 2–5 (6) mm in diam., when living pale green or brown to dark brownish green, 5–7 mm in diam., internodes up to 1.5 (3) cm long; stipules remaining for some time at the herbaceous extremity of the stem, narrowly triangular-lanceolate, 7–17 (25) x 3–6 mm, the apex acute.

Leaves attached to the side of the stem away from the substrate (leaf scars my be absent on several successive nodes as leaves do not always develop on each node), almost symmetric to slightly asymmetric; petioles more or less canaliculate to flattened on the upper side, very rarely terete, (1 -) 2–15 (-29) cm long, tapering from the node towards the blade, at the base up to 7 x 7, at the apex up to 7.5 x 5 mm; (pale) green to dull dark red, usually with linear to narrowly oblong pale green lenticels; blade 0.7–0.9 mm thick when fresh, lanceolate-narrowly elliptic to ovate-elliptic, sometimes slightly falcate, slightly trough-shaped to flat, 4–27 x 1–15 cm, base nearly cuneate, obtuse or subcordate, apex acute to acuminate, upper surface glossy, very rarely dull, (very) pale to dark green, lower surface dull, occasionally glossy, very pale (milkish) to darker green or (brownish) red-purple, sometimes green with red veins and margins, margin nearly smooth or weakly to distinctly sinuate with minute teeth where the secondary veins and their branches terminate in the margin, the teeth often disappearing with age; venation pinnate, of the simple craspedodromous type, and inconspicuous on the upper surface of the blade, primary vein moderate in size, straight or slightly curved, usually prominent on the lower surface, secondary veins 4–9 on each side diverging from the primary vein at narrow or moderate angles, of moderate size and straight or slightly to distinctly curved; not, only partly or entirely prominent on the lower surface.

Inflorescences unisexual, axillary, usually produced on the herbaceous extremity of the stem.

Male inflorescences when expanded lax, many-flowered with up to c. 70 flowers, depauperate inflorescences may have as few as 2 or 3 flowers; peduncle (pale) green to reddish or brownish green, terete, 10–(15–90)–100 x 1.5–3 mm, terminated by 2 bracts, these green, initially unilaterally fused and clasping the apex of the peduncle, usually separating, when fused widely depressed ovate, occasionally with two apices, 1.5–10 (15) x 1.5–11 (15) mm, when free broadly to narrowly triangular-ovate with a more or less acute apex, 1–7 x 1–4 mm, often not opposite each other and inserted at different vertical levels, peduncle usually extending above the fused bracts or the uppermost bract, the extension (0.5 -) 2–7 mm long up to the first branching, the main axis usually slightly continuing above this branching and terminating in the top flower, axes of the 1-st order c. 2–4 mm long, those of the higher orders gradually shorter, the final axes c. 0.5 mm long, superior bracts inserted on the axes of the 1-st and 2-nd order, broadly to narrowly triangular-ovate with a more or less acute apex,

0.5 – 4 mm long and up to 1.5 mm wide, vestigial or absent on the axes of the 3-rd and higher orders.

Male flowers pendulous in bud becoming erect at anthesis, more or less flattened, buds less than 4 mm thick when fresh, with a greenish white to pink perianth cylinder, terete, (3) 4 – 10 (11) x 0.5 – 1 mm at anthesis; perianth segments 4 in two opposite pairs forming a cross, very rarely the inner pair absent, white and (dark) pink, usually variegated, rarely pure white, outer segments rarely narrowly elliptic-obovate, usually elliptic-obovate, sometimes nearly orbicular, the apex obtuse, (3 -) 5 – 8 (-10) x 3 – 8 (10) mm, 0.3 – 0.6 mm thick when fresh, inner segments usually (narrowly) elliptic-obovate, rarely wider, the apex obtuse, 2.5 – 7 (8) x 1 – 2 (2.5) mm, c. 0.2 mm thick when fresh, sometimes reflexed; androecium a zygomorphic fascicle of (8) 11 – 34 (40) stamens, filaments (dark) pink, fused at their bases, free parts c. 0.1 – 0.7 mm long, anthers yellow, sometimes orange, basifixed, narrowly oblong, usually widening towards the apex, 1 – 1.8 x c. 1 mm, dehiscing by two apical pores which are more or less hidden by the cucullate anther apex, orientation of the front side of all anthers towards the proximal side of the androecium and the axis of the inflorescence.

Female inflorescences 1-(2-)flowered, up to 3-flowered in cultivated plants, peduncle (0.5) 2 – 5 (8) x c. 1.5 mm, bracts sometimes unilaterally fused, narrowly triangular-ovate, up to 1.2 x 0.3 mm or absent.

Female flower with 4 perianth segments, similar to those of the male flower, outer segments 7 – 10 x 5 – 7 mm, inner segments (3) 5 – 7 x 1.5 – 4 mm; styles (2, 3) 4 (5), white to pink, fused at their base, each with two spreading arms, fused part 0.1 – 0.5 mm, free part 1 – 2 mm and the style arms c. 1.5 (2.5) mm long, the free style parts more or less papillose, stigma a yellow, sometimes orange, papillose and horse shoe-shaped band embracing the style arms, each end of the band coiling once or rarely twice around the apex of an arm. The ovary continuous with the pedicel, in the terminal flower the pedicel proper usually distinct and elongated, (pinkish) green with pale green lenticels, fusiform, usually curved, 10 – 18 (24) x 2.5 – 5.5 mm, multi (3-5)-locular with axile placentation in the lower part and unilocular with parietal placentation in the upper part, each septum with the placentae cross-shaped in transverse section, ovules anatropous, ovule position in the locules epitropous, the raphe situated away from the axis of the ovary.

Infructescences with 1 (2) fruit, fruiting peduncle 2 – 7 x c. 2 mm, fruit fusiform and slightly curved, very rarely obpiriform, (reddish) green to brown red with some pale green lenticels, 11 – 30 (-40) x 3 – 7 mm, tapering towards the apex or cylindric.

Mature fruit known from cultivated plants only, dehiscing by 1 – 3 longitudinal slits and soon desintegrating. Seeds botuliform, c. 1 x 0.5 mm, with a funicular aril.

Pollen grains perprolate with straight, convex or weakly concave sides, c. 23 – 31 x c. 10 – 13 μm.

Somatic chromosome numbers 2n = (34) 36 – 38 (diploid) and 2n = 71 – 73 (tetraploid).

Vernacular name: sang-mongongo (Fang).

Specimens examined:

NIGERIA: Unyene, Stubbs Creek Forest Reserve, c. 04 40N-08 00E, *Keay in FHI 37714* (FHI,K); Oban, Aningeje, falls in the Kwa River, 05 17N-08 33E, *Onochie in FHI 34803* (FHI,K); s. loc., *Sharland s.n. (1950)* (K); s. loc., *Talbot 1568* (BM); Oban, 05 17N-08 33E, *Talbot 1741* (BM); Ekinta River Forest Reserve, 05 00N-08 30E, *Van Meer 1168* (FHI,WAG);

CAMEROUN: Lolodorf (region), Mt. Ngovayang, 03 14N-10 44E, *Annet 223* (P); id., Mt. Finde, 03 14N-10 44E, Alt. 1000 m, *Annet 276* (P); id., 03 14N-10 44E, *Annet 287* (P); id.; Mt. Findé, 03 14N-10 44E, *Annet 308* (P); id., Bikeligi, 03 14N 10 44E, *Annet 424* (P); Bule country, Efulen, 02 47N-10 32E, *Bates 300* (BM, G, K, Z); Kribi-Lolodorf, 18 km, 03 00N-10 02E, *Bos 4070* (WAG); Melen Forest, Kribi-Ebolowa, 27 km, 02 51N-10 05E, *Bos 6194* (K, P, WAG); Nkolbewa, Kribi-Ebolowa, 34 km, 02 49N-10 05E, *Bos 6239* (MO, WAG); 4 km N of Ekekam, 03 55N-11 22E, *Dang 655* (P, WAG, YA); Nkol Djobe, Mbaminkom Mts, 03 57N-11 22E, *Dang 675* (P, WAG, YA); Akoakas, N'Koemvone-Ambam, 24 km, 02 43N 11 16E, 650 m, *De Wilde, J.J. 7463* (WAG); N'Koemvone-Akoakas-Ambam, 3.5 km, 02 48N-11 10E, *De Wilde, J.J. 7538* (WAG); Ekouk, Ebolowa-Mbalmayo, 23 km, 03 00N-11 15E, *De Wilde, J.J. 7724* (WAG, YA); 15 km S of Ebolowa, 02 52N-11 05E, *De Wilde, W.J. & B. de Wilde-Duyfjes 2020* (BR, MO, WAG); E of Kribi near the Kienke River, c. 02 55N-09 55E, *Dinklage 1499* (B: holotype; HBG isotype); Bamenda district, c. 06 00N-10 00E, *Jackson in Keay in FHI 46309* (FHI); Lolodorf, Mt. Minn, 01 14N-10 44E, *Jacques-Felix 9173* (P); Cameroum Mts, Mapanja, 04 07N-09 07E, *Kalbreyer 155* (B, K); Mbo Forest Reserve, Kumba-Mamfe, 75 km, 05 14N-09 58E, *Keay in FHI 37551* (BR, FHI, K); Akonetye, Ngongonjie hill, 02 30N-10 00E, *Koufani 45* (YA), *149* (WAG, YA); Nkolembonda, 02 50N-10 00E, Alt. 200 m, *Ledermann 846* (B); Mbule, western slope of Mt. Koupé, 04 47N-09 41E, Alt. 800-1000 m, *Leeuwenberg 9288, 9294* (WAG); Bella, 45 km NE of Kribi, 03 16N-10 13E, *Letouzey 4121* (P); Mvan, 5 km SW of Oveng, 02 25N-12 12E, *Letouzey 8201* (BR, P, WAG); 10 km SSE of Zingui, 45 km SE of Kribi, between the rivers Niete and Minsomo, 02 42N-10 06, *Letouzey 9005* (P); 15-20 km SW of Zingui, 45 km SSE of Kribi, 02 43N-10 07E, *Letouzey 9123* (P); Akoakas, 25 km SE of Ebolowa, 02 43N-11 16E, *Letouzey 9993* (P); Log Mbo, 25 km ESE of Yingui, 05 14N-09 58E, *Letouzey 10982* (BR, K, P, WAG); Nkol Tsia, 18 km NW of Bipindi, 03 15N-10 05E, Alt.488 m, *Letouzey 12704* (P); near Nsola, 20 km N of Bipindi, 03 15N-10 25E, *Letouzey 12808* (K, P); near Nyang, Akwaya-Mamfe trail, 25 km NNE of Mamfe, 05 50N-09 20E, *Letouzey 14146* (P, YA); western slope of Mt. Nlonako, 5 km SSE of Nkongsamba, 04 58N-09 57E, Alt. 1000 m, *Letouzey 14450* (P, WAG); hill NW of Ngouti, 15 km NNW of Tombel, 04 52N-09 40E, Alt. 930 m, *Letouzey 14665* (P); Korup Forest Reserve, 05 00N-08 50E, *Letouzey 15115* (P, WAG); *15136* (P, WAG, YA); Victoria (Oeckelhausen), c. 04 00N-09 00E, Alt. 250 m, *Ludwigs 600* (B; = *B. ludwigsii* Gilg, nomen nudum); Ebolowa station, 02 54N-11 08E, Alt. 650-900 m, *Mildbraed 5636* (B, HBG); Ekouk, 22 km E of Ebolowa, 03 00N-11 15E, Alt. 700 m, *Mildbraed 5727* (B, HBG); Fenda, 58 km E of Kribi, c. 03 00N-11 30E, Alt. 200 m, *Mildbraed 5925* (B, HBG), *Mildbread 5973* (B); Besou, 45 km E of Batanga, 02 50N-10 30E, Alt. 100-140 m, *Mildbread 6068* (B, HBG); Akoakas, 27 km SE of Ebolowa, 02 43N-11 16E, *Raynal, J. & A. 9709* (P); Ebolowa, 02 54N-11 08E, *Raynal, J. & A. 10349* (P); Djabilobe, 54 km ESE of Kribi, 02 48N -10 19E, *Raynal, J. & A. 10391* (P); Mokoko River Forest Reserve, 04 26N-09 24E, Alt. 280 m, *Satabié 295* (P); between Mafura and Mundame, c. 04 30N-09 30E, Alt. 300 m, *Schlechter 12918* (B: holotype of *B. macrura* Gilg); Sebito, promontory between Ebolowa and Campo, c. 02 30N-10 30E, *Schultze in Mildbraed 6168* (B, HBG); Sogebafam, NE of Campo, promontory between Ebolowa and Campo, c.02 30N-10 30E, *Schultze in Mildbraed 6183* (B, HBG); Nkolumbimbe, promontory between Ebolowa and Campo, c. 02 30N-10 30E, *Schultze in Mildbraed 6189* (B: = *B. kribensis* Engl., nomen nudum); falls in the Kom River, Kribi-Campo region, c. 02 30N-10 30E, *Schultze in Mildbraed 6214* (B); Douala/Edea Forest c. 03 55N-09 50E, *Thomas 181* (K); Korup Nat. Park, 05 03N-08 48E, Alt. 50 m, *Thomas 3176* (WAG); Mundemba town, forest relicts, 05 58N -8 55E, Alt. 100 m, *Thomas & Mambo 4203, 4242* (WAG); Korup Nat. Park, Ndian River at Pamol field 69, 05 01N-08 50E, Alt. 50 m, *Thomas 4318* (BR, WAG), *5573* (WAG); Nkol Tsia, 18 km NW of Bipindi, 03 10N-10 16E, Alt. 500 m, *Villiers 781* (P); Nuanbong, 26 km NNE of Tombel, 04 55N-09 45E *Villiers 1481*

(YA); Bipindi(hof), 03 05N 10 25E, *Zenker 3080* (B), *3098* (B: holotype of *B. bipindensis* Gilg ex Engl., isotypes B, BM, E, G, K); *3152* (B: holotype of *B. crassipes* Gilg ex Engl., isotypes B, BM, BR, E, G, HBG, K, W, Z); *3666* (B, BM, E, G, K); *s.n., 1918* (P);

EQUATORIAL GUINEA: Alen, 15 Miles from the mouth of the Benito River, 01 35N-09 35E, *Bates 594* (P, G); Mallico Bahunguy, Benito River, 80 km E of the ocean, 01 50N-10 50E, *Guiral s.n., 29-7-1885* (P); 52 km from Bata, Rio Benito road, River Metom, 01 45N-10 10E, *Sanford 5801, 5825* (K), *5848* (IFE, K); Fernando Poo, Balacha-Ureka, 03 20N-08 35E, *Guinea 2283* (MA); id., northern slope of Mt. St. Isabel, above Basilé, 03 45N-08 25E, Alt. 600-800 m, *Mildbread 6394* (B: holotype of *B. gladiifolia* Engl.); id., Caldera, San Carlos, Ruiche trail, 03 45N-08 25E, *Sanford 4426* (K);

GABON: Chaillu Mts, Mouila-Yeno, 37 km, 01 40S-11 20E, Alt. 170 m, *Arends, De Wilde & Louis 483* (WAG); Crystal Mts, Tchimbélé, Mbei River, 00 37N-10 25E, Alt. 400 m, *Breteler & De Wilde (1978)-40* (WAG); id., Asok-Tchimbélé, 13 km, 00 38N-10 23E, *Breteler & De Wilde (1978)-43* (WAG); id.,9 km W of Asok, 00 43N-10 20E, Alt. 310 m, *Breteler & De Wilde (1978)-154*, in part, mixed with *B. squamulosa* (WAG); id., 15 km NE of Asok, 00 45N-10 26E, Alt. 600-700 m, *Breteler & De Wilde (1978)-196* (WAG); id., Asok-Tchimbélé, 5 km, 00 41N-10 25E, Alt. 750 m, *Breteler & De Wilde (1978)-204* (WAG); id., Asok-Tchimbélé, 3 km, 00 41N-10 23E, Alt. 500 m, *Breteler & De Wilde (1978)-297* (WAG); id., Mt. Mela, c. 00 35N-1 15E, Alt. 580 m, *Breteler & De Wilde (1978)- 323* (WAG); id., Kinguélé, Mbei River, 00 27N-10 17E, Alt. 70 m, *Breteler & De Wilde (1978)-356* (WAG); Bélinga, Babiel-Nord, southern slope, 01 15N-13 10E, Alt. 900 m, *Breteler & De Wilde (1978)-600* (WAG); Rabi-Kounga oil field, 01 55S-09 50E, *Breteler, Jongkind et al. 9479* (WAG); Crystal Mts, E of Mela, Mytsibe-Zang Rivers, 00 35N-10 15E, Alt. 250 m, *De Wilde, J.J. et al.1983)-156, 159* (WAG); id., Tchimbélé-Kinguélé, 10 km, 00 38N-10 21E, *De Wilde, J.J. et al. (1983)-180* (WAG); id., Tchimbélé-Kinguélé, 23 km, 00 37N-10 21E, Alt. 380 m, *De Wilde, J.J. et al.(1983)-216* (WAG); Chailu Mts, near Mouyanama, 15 km of the road Mimongo-Mbigou, 02 38S-11 45E, *De Wilde, J.J. et al.(1983)-326, 483* (WAG); Ntoum-Akok-Cocobeach, 70 km, 00 50N-09 25E, Alt. 15 m, *De Wilde, J.J. et al.(1983)-s.n.* (WAG); Crystal Mts, Kinguélé, Mbei river, 00 27N-10 17E, Alt.100 m, *De Wilde, Arends & de Bruijn 8840, 8841, 8848* (WAG); Doussa River, 10 km S along forest exploitation road, Mayumba-Tchibanga, 22 km, 03 22N-10 44E, Alt. 10 m, *De Wilde, Arends & de Bruijn 9215, 9270* (WAG); Rabi-Kounga oil field, 01 55S-09 50E, Alt. 10 m, *De Wilde, Arends et al. 9853* (WAG); Crystal Mts, Tchimbélé, Alt. 600 m, *De Wilde, Arends et al. 10037* (LBV, WAG); id., 2 km S Kinguélé, Mbei River, 00 27N-10 16E, Alt. 100 m, *De Wilde & Sosef 10195* (WAG); id., Tchimbélé-Kinguélé, 23 km, 00 32N-10 17E, Alt. 450 m, *De Wilde & Sosef 10229* (WAG); Bélinga, Babiel-Nord, eastern slope, 01 07N-13 10E, Alt. 800 m, *Elias & Sterck in A.M. Louis 2334* (WAG); id., Mebem River, 01 05N-13 11E, Alt. 580 m, *Elias & Sterck in A.M. Louis 2360, 2383* (WAG); Makokou, Ivindo River, 00 34N-12 52E, Alt. 480 m, *Gentry 33019* (MO); Crystal Mts, Abanga River, c.01 15N-13 10E, *Hallé 2193, 2194* (P); Bélinga, 01 15N-13 10E, Alt. 750-800 m, *Hallé 2992, 3246, 3363, 3372, 3781* (P); *4011* (K, P); Chaillu Mts, Etéké River, 01 25S-11 30E, Alt. 670 m, *Hallé & Cours 5899* (P); Crystal Mts, Kinguélé road 00 28N-10 18E, *Hallé & Villiers 4527, 4558* (P); id., 6 km S of Asok, 00 42N-10 23E, *Hallé & Villiers 4723* (P); id., Sanga River, 00 33N-10 08E, *Hallé & Villiers 5297* (P); id., 12 km SW of Kinguélé, 00 26N-10 16E, *Hallé & Villiers 5381* (P: holotype of B. nicolai-hallei Wilcz.); Chaillu Mts, Massika, between Mouila and Yeno, 01 40S 11 15E, Alt. c. 550 m., *Louis & Nzabi 3044* (LBV, WAG); id., Piti Massango, 01 35S-11 18E, *Le Testu 5265* (BM); id., between Ngoumbi and Ighouma, 01 40S-11 06E, *Le Testu 5275* (BM); id., falls in the Mboumi River near Mbigou, 01 54S 11 56E, *Le Testu 5409* (BM, BR); id., Bangondji Badouma, 02 17S-12 00E, *Le Testu 5429* (BM); Chaillu Mts, falls in the Nyanga River near Mouvounga, 02 50S-12 00E, *Le Testu 5454* (BM, BR, LISC); id., Itava ?, April 4, 1925, 02 01S-12 01E, *Le Testu s.n.* (BM); Nouna River, 01 28N-13 00E, Wilks, *MINK-W 611* (WAG); id., 01 49N-12 50E, Wilks, *MINK-D 55* (WAG); Nyanga River ?, s. loc., *Pobeguin s.n., (Lever Brothers Exped. 1913)* (P); Doudou Mts, 60 km SSW of Doussala, 02 37S-10 35E, *Reitsma 3246* (WAG); Gabon/Congo: s. loc., c. 03 00S-12 00E, *Thollon s.n.* (P); Crystal Mts, 11 km NNE of Tchimbélé, 00 42N-10 27E, *Wieringa 801* (WAG); id., 1 km WNW of Tchimbélé, 00 37N-10 23E, Alt. 460 m, *Wieringa 915* (WAG);

CONGO: M'Vouti, 04 15S-12 25E, *Barabé 86-99, culta MT* (MT, WAG); Komono, Bouba road, 03 15S-13 15E, *Bouquet & Sita 2345* (P); road of the new Maamar Camp, c. 03 00S-12 00E, *Sita*

3753 (P); Niari Region, Mt. Bamba, 04 14S-12 32E, Alt. 550 m, *La Croix 5016* (WAG); Nukudi, between Loambitsi and the Nyanga River, c. 03 00S-12 00E, *Sita 4094* (BR);

ANGOLA-CABINDA: Maiombe, Belize, Mbule hills, source Zanza-Lufo River, c.04 30S-12 40E, *Gossweiler 7811* (BM, COI, K, LISU);

ZAIRE: Masisi-Walikale, 01 25S-28 30E, *Bequaert 6474* (BR); INERA, Lundu, Tshela, 04 45S-13 03E, *Breyne 2751* (BR); Mayumbe, between Lukula and Boma, 05 23S-12 57E, *Cabra 115* (B, BR); Irangi, 70 km W of Lake Kivu, 01 53S-28 27E, Alt. 750 m, *Cambridge Congo Exp. (1959)-295* (BM), *318 bis* (BM, BR, LISC); Monkoto Nat. Park, Yongo River Yenge trail, 01 38S-20 39E, *Evrard 4740* (BR); Bola-Gombe, Ruki river, 00 05N-18 16E, *Gentil s.n. (June 1900)*; Bikoro, Lake Tumba, 00 45S-18 07E, *Goossens 1579* (BR); Injolo, 00 11S-18 28E, *Laurent 1695* (BR), *1702* (BR: holotype of *B. gracilipetiolata* De Wild., B isotype); between Masisi and Walikale, 01 25S-28 30E, Alt.1140 m, *Lebrun 5164* (BR); Urega (Maniema) c.03 00S-28 00E, Alt. 1200 m, *Lebrun 5595* (BR); Kampala, Walikale, 01 25S-28 03E, Alt. 700 m, *Léonard 1605, 1664* (BR); Kisanga, Shabunda, 02 27S-28 15E, Alt. 1100 m, *Léonard 3916* (BR, K); Buta-Bima, c. 03 00S-25 00E, *Séret 120* (BR); Itebero-Utu, 3 km, 01 42S-28-07E, Alt. 700 m, *Troupin 2455* (BR); Kivu, Irangi, IRSAC reserve, Luhoho River, 01 53S-28 27E, Alt. 850 m, *Van der Veken 9724* (WAG); St. Trudon, 05 04S-23 28E, *Van Kerckhoven 11* (BR).

4. B. pelargoniiflora J.J. de Wilde & J.C. Arends, **spec. nov.**
Figs. 5-2f, 5-8B, 6-6a, 8-2, 8-18 **Plate 4 (p. 204), Map 3 (p. 206)**

Planta epiphytica vel rupicola, habitu proxime aequans *B. longipetiolatae* tamen differt stipulis plerumque triangularis, laminis foliorum superne interdum squamis instructis ac inflorescentiis interdum bisexualibus. Inflorescentia similis umbelliformis 7–20 flores ferens, omnis pedunculo 2 cm excedenti femina includens, bracteis superioribus numerosis dum axes primorum et sequentium ordinum brevissimi vel desunt. Flores tepalis exterioribus late ovatis et subcordatis, saltem 20 x 15 mm, tepalis interioribus ellipticis, saltem 10 x 4.5 mm. Flores masculi antheris c. 4 mm longis, flores feminei quattuoribus stylis muniti, c. 7 mm longis (pars connata et ramuli styli includens). Granum pollinis distincte prolatum, latere convexum, c. 21 x 12 μm.

Type: Cameroun, western slope of Mt. Nlonako, 5 km SSE of Nkongsamba, *Letouzey 14448* (holotype P, isotypes WAG, YA).

Description: Monoecious, succulent, lepidote plants, growing on tree-ferns and rocks, with creeping stems, rooting at the nodes; with an indumentum of scattered dentate scales on stem, abaxial surface of stipules, petioles, both surfaces of the blade, peduncle, all bracts, perianth cylinder, pedicellate ovary and abaxial surface of the outer perianth segments.

Stems at least 20 cm long, terete and solid, usually not branched, dried stems dark brown, 3–6 mm in diam., internodes 1–4.5 cm long; stipules persistent, usually triangular, sometimes narrowly so, apex acuminate, 15–25 x 5–10 mm.

Leaves attached to the side of the stem away from the substrate (several successive nodes may not bear leaves, as leaves do not always develop on each node), petiole canaliculate on the upper side, 7–27 cm long; blade almost symmetrical, narrowly ovate to ovate, base obtuse, truncate or subcordate, apex acuminate to cuspidate, 8–30 x 6–15 cm, margin smooth, occasionally, particularly in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young leaves, slightly sinuate, with minute teeth where the secondary veins and their branches terminate in the margin; venation pinnate, of the simple craspedodromous type, primary vein straight and prominent on the lower surface, secondary veins 4–9 on each side diverging from the primary vein at moderate angles, straight or slightly curved, conspicuous and partly prominent on the lower surface.

Inflorescences axillary, restricted to the apex of the stem, unisexual, but occasionally bisexual, all inflorescences similar, 7- to 20-flowered; peduncle 2–12 cm long, up to c. 5 mm in diam., terminated by 2 bracts, these caducous and supporting the remainder of the umbelliform inflorescence; axes of the 1-st and higher orders very much reduced in length or absent, the number of superior bracts related to the number of flowers, elliptic, apex acute, up to 23 x 4.5 mm.

Male flower white with a terete perianth cylinder, 15–35 mm long, perianth segments 4, in two opposite pairs forming a cross, outer segments broadly ovate, base subcordate, apex obtuse, 20–22 x c. 15 mm, inner segments elliptic, apex acute, shallowly boat-shaped, 10–12 x 4.5–8 mm; androecium a weakly zygomorphic fascicle of 16–28 stamens, filaments fused at their very base only, similar in length, c. 1 mm long, anthers basifixed, narrowly oblong, c. 4 x 1 mm, apex cucullate with two pores, the front side of all anthers oriented in the same direction.

Female flower with 4 perianth-segments, similar to those of the male flower, caducous; styles (3) 4, fused at their very base, each with two spreading arms, fused part c. 1 mm, free part c. 2.5 mm and the arms c. 3.5 mm long; stigma a papillose horse shoe-shaped band embracing the style arms, each end of the band coiling almost twice around the apex of the arm. The pedicellate ovary slender, up to 5 cm long, the ovary fusiform, possibly with 4 faint ribs, c. 5 mm in diam., gradually tapering into the pedicel.

The single infructescence known contains 10 immature fruits, the pedicellate fruit up to 10 cm long. Mature fruits and seeds unknown.

Pollen grains distinctly prolate with convex sides, c. 21 x 12 μm.

Etymology: the specific epithet alludes to the inflorescences which superficially resemble those of cultivated *Pelargonium zonale* L'Hér.

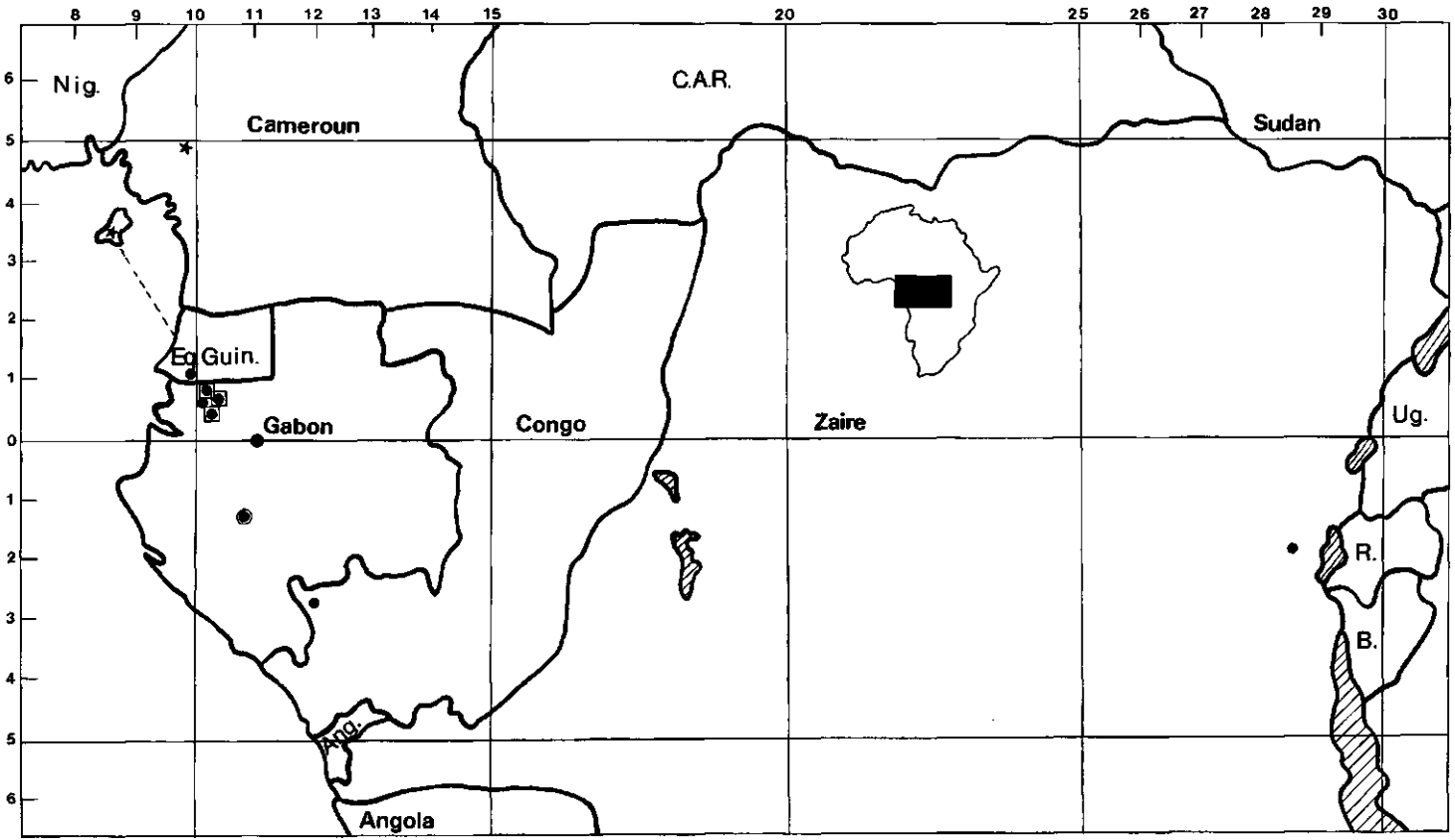
Specimens examined:

CAMEROUN: western slope of Mt. Nlonako, 5 km SSE of Nkongsamba, 04 58N-09 57E, Alt. 1000 m, *Letouzey 14448* (P, WAG, YA);

EQUATORIAL GUINEA: Fernando Poo, Caldera, San Carlos, Ruiche trail, 03 45N-08 25E, *Sanford 4440* (MO), *4442* (IFE).

Plate 4. *B. pelargoniiflora*; **1:** habit, extremity, the two inflorescences with female flowers and fruits (x 2/3); **2:** top of leaf (x 2/3); **3:** male inflorescence (x 2/3); **4:** androecium (x 6); **5:** anther, front (x 6); **6:** top of gynoecium (x 6); **7:** style, adaxial side (x 6); **8:** infructescence with immature fruits (x 2/3); **9:** leaf trichomes (x 30).

1 and **4-8:** Letouzey 14448 (herb.); **2:** Sanford 4440 (herb.); **3:** Sanford 4442 (herb.).



Map 3. The localities where specimens of *B. squamulosa* (●) and *B. pelargoniiflora* (★) were collected; ◉: plants with a known diploid and ▣ with a known tetraploid somatic chromosome number.
For abbreviations see Map 1.

5. B. rwandensis J.C. Arends, **spec .nov.** **Plate 5 (208), Map 1 (p. 188)**
Figs. 5-2e, 5-8A, 5-14b, 6-13b, 8-3, 8-19.

Planta epiphytica caulibus repentibus habitu fere *B. karperi* aequans, tamen differt caulibus crassioribus (in sicco diam. c. 2.5 – 5 mm), stipulis tamdiu persistentibus, triangularis, foliis crassioribus (in vivo c. 2 mm). Inflorescentia mascula usque ad quinque florata, pedunculo elongato longitudine c. 45 – 75 mm, gerente apici duas bracteas oppositas separatas, late triangulares vel ovatas et fere cymbiformes, usque ad 5 x 5 mm. Axes primi elongati usque ad 5 mm longi. Flos mascula periantio cylindrico usque ad 12 mm longo munita, tepalis exterioribus late ellipticis ad obovatis, interdum leviter cordatis, saltem c. 9 x 8 mm, tepalis interioribus (anguste) ellipticis, saltem c. 6 x 2 mm. Androecium c. 20 stamina continens, antheris c. 3 mm longis. Granum pollinis prolatum, lateraliter convexum, c. 25 x 13 μm.

Type: Rwanda, Cyangugu, Rangiro region, Rutabanzogera, *Bridson 380* (holotype K, isotypes BR, WAG).

Description: Monoecious, succulent, lepidote, epiphytic plants with creeping stems, rooting at the nodes; with a more or less dense indumentum of dentate scales on stem, abaxial surface of stipules, petiole, lower surface of the blade, peduncle, all bracts, perianth cylinder, pedicellate ovary and abaxial surface of the outer perianth segments.

Stems at least 45 cm long, occasionally branching, terete and solid, the younger part succulent, the older part woody; dried stems yellowish brown, c. 2.5 – 5 mm in diam., internodes (1) 1.5 – 3.5 cm long (ratio of blade- and internode-length 2 – 4). Stipules more or less persistent on the younger and marcescent on the older part of the stem, triangular, 6 – 12 x 4 – 6 mm, acute.

Leaves attached to the side of the stem away from the substrate; petiole terete, 3 – 9 cm long; blade distinctly succulent, fleshy, c. 2 mm thick when fresh, almost symmetrical and peltate (the petiole attached 2 – 3 mm from the base), ovate, 3 – 7 x 2 – 4 cm, base rounded or almost subcordate, apex acute to acuminate, upper surface bright apple green with a purplish margin, lower surface reddish, margin smooth or somewhat sinuate, with minute teeth where the primary and the secondary veins terminate in the margin; venation actinodromous with 5 primary veins, the median vein more or less straight, the others straight to slightly curved.

Inflorescences unisexual and axillary, produced on the younger part of the stem.

Male inflorescence lax, up to 5-flowered, peduncle (30) 45 – 75 x 1.5 mm, terminated by 2 bracts, these free from each other, broadly triangular-ovate, apex acute, shallowly boat-shaped, up to 5 x 5 mm, the main axis extending up to 3 mm beyond the bracts into the perianth cylinder of the terminal flower, axes of the 1-st order up to 5 mm long, extending c. 1 – 2 mm beyond the bracts on these axes, these bracts triangular, up to 2.5 x 1.5 mm.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Male flower pink with reddish veins, with a terete perianth cylinder, up to 12 mm long, perianth segments 4 in two opposite pairs forming a cross, outer segments broadly elliptic to obovate, (7) 9–12 x (6) 8–10 mm, occasionally almost subcordate, inner segmets (narrowly) elliptic, 6–10 x 2–3 mm; androecium a zygomorphic fascicle of c. 20 stamens, the filaments fused at their base, free parts up to 3 mm long, anthers basifixed, narrowly oblong, up to 3.0 (3.5) x c. 0.5 mm, dehiscing by two apical pores, apex cucullate, the front side of all anthers oriented towards the proximal side of the androecium.

Female inflorescence initially 3-flowered, but at anthesis 1-flowered by abortion of the other two, peduncle c. 1 mm long, bracts triangular, c. 3 x 2 mm, superior bracts 1 or 2, narrowly triangular, c. 2 x 0.5 mm.

Female flower more or less similar to the male flower, outer segments oblate to almost reniform, c. 6 x 8 mm, inner segments elliptic to obovate, c. 5 x 2 mm; styles 3 (or 4 ?), fused at their very base, each with two spreading arms, free style part c. 2.5 mm and the arms c. 1 mm long; stigma a papillose and horse shoe-shaped band embracing the style arms, each end of the band coiling once around the apex of the arm. The ovary continuous with the pedicel, fusiform, c. 23 x 4 mm.

Infructescence with 1 fruit, fruiting peduncle c. 7 mm long; fruit fusiform, dark reddish brown, apex flat with a circular rim, up to 29 x 6 mm. Mature fruits not known. Seeds botuliform, with a small funicular aril, c. 1 x 0.5 mm.

Pollen grains prolate with convex sides, c. 25 x 12–14 μm.

Specimens examined:

ZAIRE: Mushwere (Kabare), 02 34S-28 36E, Alt. 2000 m, *Van Roeckhoudt 12* (BR);

RWANDA: Rugege Forest, 2 km before Gisakura on the road Butare-Cyangugu, 02 30S-29 15E, Alt. 1950 m, *Auquier 3360* (LG); Nyungwe Forest near Gisakura, 02 26S-29 04E, Alt. 1900 m, *Bouxin 164* (BR,LG); Nyungwe Forest, Kamiranzovu Marsh, 02 30S-29 09E, Alt. 1950 m, *Bouxin 257* (BR, GENT, K, LG), *1122* (BR, LG); Rangiro region, Rutabanzogera, 02 28S-29 09E, Alt. 1700 m, *Bridson 380* (BR, K, WAG); Butare-Cyangugu, 100 km, 02 30S-29 10E, Alt. 2000 m, *Bridson 474* (BR, K).

Plate 5. *B. rwandensis*; **1:** habit, extremity with two mature fruits (x 2/3); **2:** young female inflorescence: **a:** bracts, **b:** superior bracts of lateral axes; **c:** end flower (x 14); **3:** idem, outside (x 9); **4:** male inflorescence before anthesis (x 2); **5:** male flower taken from the top of a lateral axis (x 2); **6, 7** and **8:** androecium, front, reverse, lateral (x 6); **9, 10** and **11:** proximal stamen, front, rear and lateral (x 12); **12:** distal stamen, front (x 12); **13:** mature female inflorescence (x 2); **14:** top of gynoecium (x 6); **15:** apex of style, abaxial side (x 12); **16:** seed (x 20); **17:** fruit trichomes (x 20).

1 and **13-17:** Bridson 380 (herb.); **2** and **3:** Bouxin 164 (herb.); **4-12:** Van Roeckhoudt 12 (herb.).

6. B. squamulosa Hook. f. **Plate 4 (p. 211), Map 3 (p. 206)**
Figs. 4-1, 4-2, 5-2b, 5-4, 5-6A, 5-11, 6-4, 6-7a, 6-8a, 6-9c, 6-10, 6-12, 7-5 to 7-9, 8-4 to 8-6.

B. squamulosa J.D. Hooker in Oliver, Fl. Trop. Afr. 2: 579, 1871; Engler in Engl. & Drude, Veg. Erde, 9 (3.2): 620 (in clavi), 1921, p.p., specimen Sierra del Crystal only; Hallé & Raynal, Adansonia, nouv. sér., 6: 113, 1966, p.p., Mann 1654 only; Wilczek, Fl. Congo, Rwanda, Burundi, Begoniaceae 21, 1969, p.p., Christiaensen 1922 only; Hausler, Begonian, 50: 65, photo of inflorescence with (monstrous) male, not female, flower, 1983.
Type: Gabon, Crystal Mts, *Mann 1654* (holotype K, isotypes B, P).

homotypic synonym:
B. squamulosa Hook.f. var. *squamulosa*, Hallé, Adansonia, sér. 2, 12: 366, 1972.

misapplied name:
B. squamulosa auct. non Hook.f., Keay, Fl. West. Trop. Afr., ed. 2, (1.1): 220, 1954; Smith, Wasshausen et al., Begoniaceae, Smithsonian Contr. Bot. 60, 1986: 377, Fig. 13.17 depicts the cultivated specimen Raynal 9707 (= *B. longipetiolata*); 386, Fig. 14.31 depicts the type of *B. macrura* (= *B. longipetiolata*).

Description: Monoecious, succulent, epiphytic plants with creeping stems, rooting at the nodes, the roots c. 0.5 – 1 mm in diam.; with a more or less dense indumentum of dentate scales present on stem, abaxial surface of stipules, petioles, lower surface of blade, peduncle, axes of the 1-st and higher orders, all bracts, perianth cylinder, pedicellate ovary, abaxial surface of the outer perianth segments and characteristically also on the styles.

Stems up to 2 m long, straight or somewhat zig-zag, occasionally branching, terete and solid, the younger part succulent, the older part woody, dried stems (3 -) 5 – 8 mm in diam., (dark) brown, 6 – 10 mm in diam. when living, brownish green and later greyish brown, internodes (2 -) 3.5 – 6 cm long [ratio of blade-

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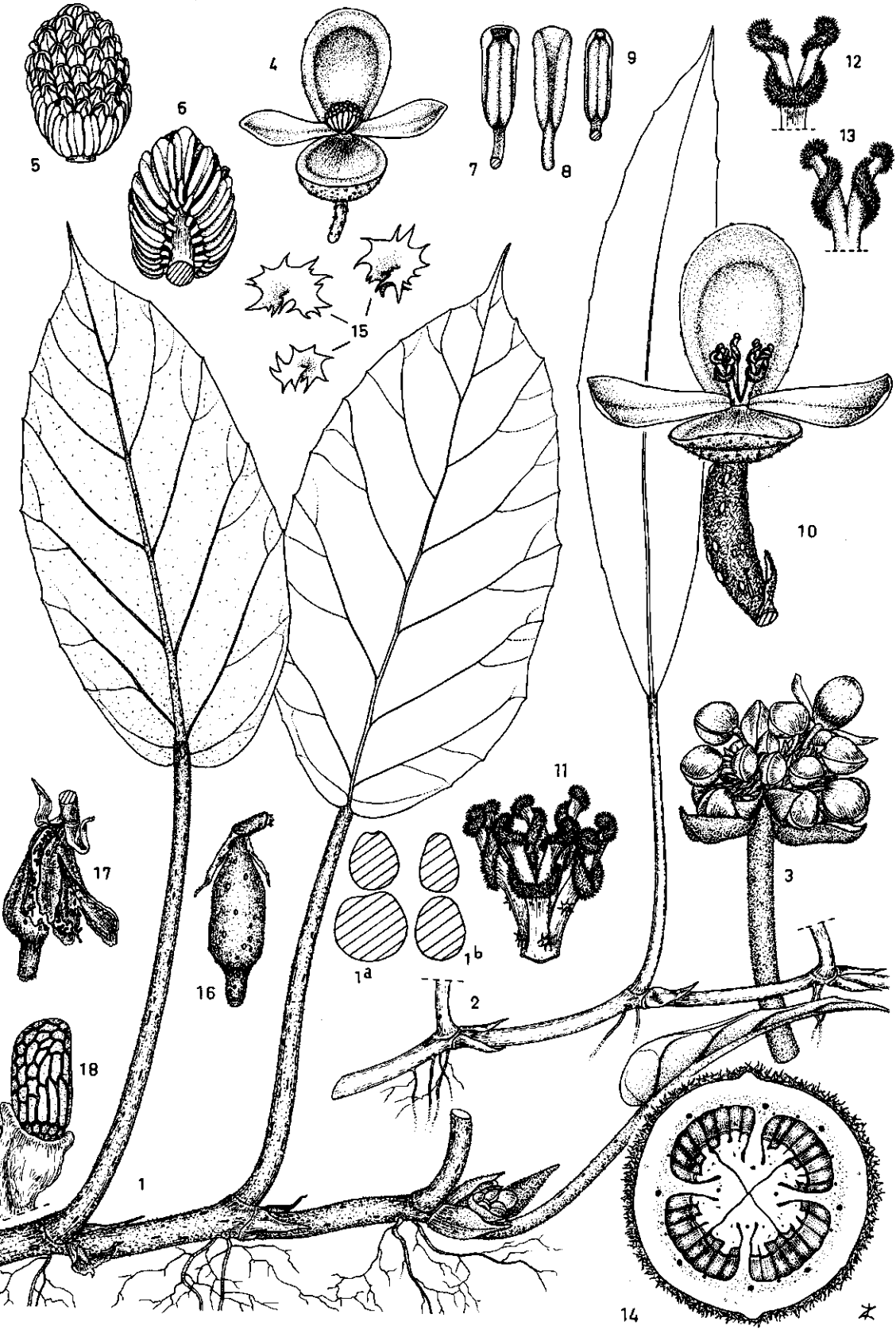
Plate 6. *B. squamulosa*; **1:** habit, extremity with young male inflorescence (x 1/2); **1a** and **1b:** outlines of transverse sections of the top and base of the petioles of a diploid (1a) and a tetraploid (1b) plant (x 2); **2:** habit, part of a narrow-leaved plant (x 1/2); **3:** male inflorescence (x 1); **4:** male flower (x 2); **5:** androecium, front side (x 6); **6:** idem, reverse (x 6); **7 & 8:** distal stamen, front and rear respectively (x 10); **9:** proximal stamen, front (x 10); **10:** 1-flowered female inflorescence (x 2); **11:** top of gynoecium, on the styles some trichomes (x 5); **12 & 13:** style, abaxial and adaxial view respectively (x 5); **14:** transverse section of ovary half-way along its length (x 10); **15:** ovary trichomes (x 20); **16:** closed mature fruit (x 1); **17:** dehisced fruit (x 1); **18:** seed with aril (x 20).

1 & 1a: Arends, De Wilde & Louis 371 (herb.) and cultivated material of the same collection; **1b:** De Wilde, Arends & de Bruijn 8839 (spirit); **2:** Hallé & Villiers 5272 (herb.); **3-9:** Arends, De Wilde & Louis 371 (spirit); **10-13, 15-18:** De Wilde, Arends et al.(1983)-119 (spirit), **14:** culta Arends, De Wilde & Louis 371.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Leaves attached to the side of the stem away from the substrate; petioles more or less terete, rarely flattened or scarcely canaliculate on the upper side, tapering from the stem towards the blade, usually circular at the base and ovate at the apex in transverse section, up to 9 mm in diam. at the base, up to 9 x 6 mm at the apex, (3.5 -) 6 – 23 cm long, green to dark red-brown with pale green linear lenticels; blade 0.5 – 0.9 mm thick when fresh, more or less symmetrical, narrowly ovate, sometimes ovate, trough-shaped, 11 – 23 (26) x 3.5 – 11 cm, base obtuse, sometimes nearly cuneate or subcordate, apex acute to acuminate, occasionally almost cuspidate, upper surface glossy, green, lower surface dull, very rarely glossy, green, occasionally entirely tinged with red or only so along the veins; margin smooth or slightly sinuate, with minute teeth where the secondary veins and their branches terminate in the margin, the teeth often disappearing with age; venation conspicuous on the lower surface, pinnate of the simple craspedodromous type, primary vein stout to moderate in size, more or less straight and prominent on the lower surface, secondary veins (4) 5 (6) on each side diverging from the primary vein by narrow to moderate angles, moderately in size, straight to smoothly curved and often prominent.

Inflorescences unisexual, axillary, usually present at the herbaceous extremity of the stem.

Male inflorescences when expanded dense, more than 5-flowered, in the wild c. 10 – 25, in cultivation up to 60-flowered; peduncle purplish red-brown, terete, (20 -) 30 – 60 (85) x (1.5) 2.5 – 4.5 mm; terminated by 2 bracts, these supporting the remainder of the inflorescence, (bronze)-green, initially unilaterally fused and forming a broadly ovate to kidney-shaped structure with two minute tips, clasping the apex of the peduncle, later separating and assuming an opposite position, more or less broadly ovate with an acute apex, (2 -) 4 – 11 x (2 -) 5 – 13 mm; axes of the 1-st and higher orders very much reduced in length and forming collectively an irregularly shaped dome-like structure; the number of superior bracts related to the number of axes, usually many, bronze-green, persistent, later shrivelling and becoming dark brown, narrowly to broadly triangular, somewhat boat-shaped and variable in size, the largest within an inflorescence 4 – 13 x 1.3 – 8 mm.

Male flower erect in bud, the buds more or less globose, 7 – 10 mm in diam. when fresh, with a terete, pink perianth-cylinder, 3 – 8 x 1 – 1.5 mm at anthesis, perianth-segments 4 in two opposite pairs forming a cross, white to (dark) pink, rarely red-purple, variegated; outer segments obovate, the apex obtuse, spoon-shaped, dorsally convex, the adaxial side concave with a flat margin, 8 – 12 x 6 – 9 mm, succulent, 0.7 – 1.4 mm thick when fresh, inner segments obovate-elliptic, somewhat spoon-shaped, 6 – 7 x 3 – 4 mm, more or less succulent, 0.4 – 0.6 mm thick when fresh; androecium a zygomorphic fascicle of 20 – 50 stamens; the pink filaments fused at their base, free parts 0.1 – 1 mm long; anthers yellow, basifixed, narrowly oblong, gradually widening towards the apex, (1.7) 1.8 – 2.2 (2.5) x c. 1 mm, dehiscent by two apical pores which are more or less hidden by the cucullate anther apex; the anther front of most stamens oriented towards the proximal side of the androecium and this in its turn

facing the axis of the inflorescence, but the peripheral stamens oriented towards the centre of the androecium.

Female inflorescences 1-flowered (in cultivated plants up to 3-flowered), almost sessile; peduncle up to 3 mm long and c. 1.5 mm in diam., with 2 bracts that may be unilaterally fused.

Female flower with 4 perianth segments, similar to those of the male flower, outer segments 10–17 x 8–10 mm, inner segments 8–13 x 4–6 mm; styles 4 [in cultivated plants (3), 4 and (5)], white to pink, fused at their base, each with two spreading arms, fused part c. 0.5 mm, free part 1.8–3 mm and the arms 1.8–2.5 mm long, the fused and the free style parts with 1–6 dentate scales; stigma a yellow horse shoe-shaped papillose band embracing the style arms, each end of the band coiling (almost) twice, rarely once (observed in cultivated plants), around the apex of the arm. The ovary continuous with the pedicel, fusiform and usually slightly curved, 15–17 x 4 mm, brownish green with pale green lenticels; multi (3-5)-locular with axile placentation in the basal part and unilocular with parietal placentation in the upper part; each septum with placentçal lobes in transverse section arrow-shaped, the ovules anatropous, ovule position in the locules pleurotropous, the raphe oriented towards the apex of the ovary.

Infructescence usually with 1 (-3) fruit, fruiting peduncle c. 5 (50) x 1.5–2.5 mm, occasionally with 2 narrowly triangular bracts, 6–8 x 2–3 mm; fruit dark-brown with some pale green, circular-oblong lenticels, fusiform, slightly curved, 15–20 x 6–8 mm, the apex cylindrical, sometimes tapering, c. 3 mm long, 2.5 mm in diam.

Mature fruit dehiscing by 4 longitudinal slits, soon disintegrating. Seeds botuliform, c. 1 x 0.5 mm, with a funicular aril.

Pollen grains perprolate, 27–35 µm long, 12–15 µm in diam., usually with more or less concave sides.

Somatic chromosome numbers 2n = 36, 38 (diploid) and 2n = 71–76 (tetraploid).

Specimens examined:

EQUATORIAL GUINEA: Rio Muni region, Neu-Kamerun, c. 01 00N-10 00E, *Escherich 248* (B);

GABON: Chaillu Mts, Waka river Forest exploitation, 01 18S-10 57E, Alt. 320 m, *Arends, De Wilde & Louis 371* (WAG); Crystal Mts, 9 km W of Asok, 00 43N-10 20E, Alt. 310 m, *Breteler & De Wilde (1978)- 154*, in part, mixed with *B. longipetiolata* (WAG); id., Kinguélé, Mbei River, 00 27N-10 17E, *Breteler & De Wilde (1978)-355* (WAG); id., id., 20 km NW of Asok, 00 53N-10 12E, Alt. 310 m, *De Wilde, J.J. et al. (1983)-100* (WAG); id., Tchimbélé-Kinguélé, 11 km, 00 37N-10 21E, *De Wilde, J.J. et al. (1983)-119* (WAG); id., Tchimbélé-Kinguélé, 10 km, 00 38N-10 21E, Alt. 620 m, *De Wilde, J.J. et al. (1983)-181* (WAG); id., Tchimbélé-Kinguélé, 23 km, 00 37N-10 21E, *De Wilde, J.J. et al. (1983)-220* (WAG); id., 20 km NW of Asok 00 53N-10 12E, Alt. 610 m, *De Wilde, J.J. et al.(1983)-288* (WAG); Kinguélé, Mbei River, 00 27N-10 17E, Alt. 100 m, *De Wilde, Arends et al. 8839* (WAG); id., Kinguélé-Tchimbélé, 25 km, 00 32N-10 17E, Alt. 350 m, *De Wilde & Sosef 10086, 10091, 10246* (WAG); id., 2 km S Kinguélé, Mbei River, 00 27N-10 16E, Alt. 100 m, *De Wilde & Sosef 10212* (WAG); id., Tchimbélé-Kinguélé, 11 km, 00 34N-10 19E, Alt. 700 m, *De Wilde & Sosef 10266* (WAG); 15 km NE of N'Djolé, 00 00-10 50E, Alt. 250 m, *De Wilde & Sosef 10343* (WAG); Crystal Mts, Kinguélé, 00 27N-10 17E, *Hallé & Villiers 4410*

(P); id., Sanga River, 00 33N-10 08E, *Hallé & Villiers 5272* (P); Crystal Mts, c.01 00N-10 00E, *Mann 1654* (K: holotype, B, K, P isotypes);

ZAIRE: Kivu, Kalehe, IRSAC reserve, Irangi, Kavumu-Walikale, 110 km, Luhoho River, 01 53S-28 27E, Alt. 850 m, *Christiaensen 1904* (BR), *1922* (BR, K); id., Irangi, IRSAC reserve, Luhoho River, 01 53S-28 27E, Alt. 850 m, *Lambinon 78-279* (BR, LG).

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Binnen het kader van het onderzoekproject 'Fundamenteel plantentaxonomisch onderzoek aan Afrikaanse Begoniaceae' dat geleid wordt door Dr J.J.F.E. de Wilde, ben ik verantwoordelijk voor het karyologisch onderzoek van de levende Begonia-planten.

In de beginfase van dat onderzoek (1979-1982) telde ik in de worteltopcellen van planten die behoren tot *Begonia* sectie *Tetraphila* gewoonlijk 2n = ca. 36 chromosomen; enkele andere planten bleken echter het dubbele ('tetraploïde') aantal, dus 2n = ca. 72, chromosomen te hebben. Alle tetraploïde planten werden gekenmerkt door kruipende stengels. Het omgekeerde, d.w.z. planten met kruipende stengels zouden tetraploïde zijn, ging daarentegen niet op, want sommige van zulke planten waren diploïde.

Toen ik Dr Hans de Wilde, thans mijn co-promotor, informeerde over mijn waarnemingen, konden wij slechts gissen naar de betekenis van de verschillende aantallen chromosomen voor de taxonomie van planten met kruipende stengels binnen sectie *Tetraphila*. Het is een van de verdiensten van De Wilde dat hij onmiddellijk inzag dat een taxonomische bewerking van dergelijke planten de basis zou kunnen zijn voor een proefschrift en hij suggereerde dat ik die bewerking op mij zou nemen. Ik heb geruime tijd geaarzeld voordat ik het uitdagende aanbod van De Wilde aannam, omdat het toen al duidelijk was dat een revisie van de betrokken soorten, hoewel beperkt in aantal, geen eenvoudige zaak zou zijn. Ik had nauwelijks ervaring met de 'klassiek taxonomische' aspecten van zulk onderzoek, terwijl ik me bewust was dat ik niet zonder gevoelens van, wat Van Hooff* omschrijft als 'academische twijfel' door het leven ga. Zulke gevoelens kunnen lastig zijn wanneer interpretaties niet geheel in de pas lopen met of zelfs haaks staan op die van andere onderzoekers.

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*) A. van Hooff. De academicus als een mismaakt manager. NRC/Handelsblad, 1 november 1991, p. 9.

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Index of (infra-)specific plant names.

(Names in italics are synonyms or nomina nuda, new names are in bold face, numbers in italics refer to pages with illustrations).