R. H. Cobben

Evolutionary trends in Heteroptera
Part I Eggs, architecture of the shell, gross embryology and eclosion

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen
op gezag van de Rector Magnificus, Ir. F. Hellinga,
hoogleraar in de cultuurtechniek,
te verdedigen tegen de bedenkingen van een commissie uit de
Senaat van de Landbouwhogeschool te Wageningen
op vrijdag 21 juni 1968 te 16 uur

1968 Centre for Agricultural Publishing and Documentation

Wageningen

Voorwoord

In deze fase van mijn entomologische activiteit, waarin een werkstuk de titel van 'proefschrift' wordt meegegeven, is het mij een behoefte dank te zeggen aan hen, die een ideale werksfeer mogelijk maakten.

Met gevoel van dankbaarheid gedenk ik mijn leermeester in de entomologie, wijlen Professor Roepke. Reeds als eerstejaarsstudent mocht ik gastvrijheid in zijn laboratorium genieten, hetgeen bepalend is geweest voor mijn gebondenheid met Wageningen.

U, Professor De Wilde, hebt mij de onafhankelijkheid gelaten, die voorwaarde is voor een vrije ontplooiing van interessen en capaciteiten. Voor de ondervonden hartelijkheid en voor het kritisch doornemen van het omvangrijke manuscript ben ik bijzonder erkentelijk.

In mijn dank wil ik de hele laboratoriumgemeenschap betrekken, waarvan ik mij gelukkig prijs lid te mogen zijn.

Veel van mijn wetenschappelijke creativiteit is in de huiselijke kring ontstaan, zonder dat dit tot afzondering behoefde te leiden. Wies, temidden van een druk gezin heeft jouw levenskunst en gevoel voor harmonie dit mogelijk gemaakt. Ik denk ook met grote dankbaarheid aan mijn familie, waarin ik ben opgegroeid; zij vormde de gunstige voedingsbodem, zonder welke dit proefschrift niet onstaan zou zijn. Ik betreur het zeer, dat mijn vader deze feestdag niet meer mocht beleven.

Allen, die op enigerlei wijze direkte steun verleenden aan mijn onderzoek, alsmede die personen en instellingen die de technische uitvoering en het in druk verschijnen mogelijk hebben gemaakt, worden met erkentelijkheid genoemd op p. 384–385 (Acknowledgments).

Contents

PREFACE 1

MATERIAL AND METHODS 3

1 STRUCTURE AND BIOLOGY OF THE LEPTOPODOID EGG 7
1.1 *Saldidae* 7
1.1.1 Literature 7
1.1.2 Material 7
1.1.3 Egg-shape and mode of oviposition 8
1.1.4 Architecture of the chorion 12
1.1.5 Gross study of the embryogenesis 22
1.1.6 Posture of the fully grown embryo and the hatching mechanism . . 36
1.2 *Leptopodidae* 40
1.3 *Omania* 42

2 STRUCTURES AND BIOLOGY OF THE EGGS OF OTHER FAMILIES 44
2.1 *Amphibicorisae* 44
2.1.1 Hebridae 44
2.1.2 Mesoveliidae 48
2.1.3 Hydrometridae 54
2.1.4 Veliidae and Macrovelia, Oravelia, Chepuvelia 61
2.1.5 Gerridae 66
2.2 *Pentatomomorpha* 74
2.2.1 Aradidae, Idiostolidae, Thaumastellidae 75
2.2.2 Piesmatidae, Malcidae, Berytinidae, Lygaeidae, Stenocephalidae . . 80
2.2.3 Pyrrhocoridae, Largidae, Colobathristidae 94
2.2.4 Coreidae 96
2.2.5 Alydidae 102
2.2.6 Rhopalidae 104
2.2.7 Cydnidae, Acanthosomatidae, Urostylidae 106
2.2.8 Scutelleridae 109
2.2.9 Dinidoridae, Tessarotomidae 112
2.2.10 Pentatomidae 116
2.2.11 Plataspidae, Aphylidae 122
2.3 *Cimicomorpha* 124

2.3.1 Nabidae, Velocipedidae, Pachynomidae 125
2.3.2 Anthocoridae, Cimicidae, Microphysidae, Plokiophilidae 132
2.3.3 Tingidae, Vianaididae 140
2.3.4 Miridae 141
2.3.5 Thaumastocoridae 166
2.3.6 Reduviidae 168
2.4 *Hydrocorisae* 184
2.4.1 Corixidae 185
2.4.2 Nepidae 200
2.4.3 Belostomatidae 206
2.4.4 Naucoridae 209
2.4.5 Notonectidae 218
2.4.6 Pleidae, Helotrephidae 230
2.4.7 Ochteridae 234
2.4.8 Gelastocoridae 238
2.5 *Dipsocoroidea, Enicocephaloidea* 240
2.5.1 Dipsocoridae 240
2.5.2 Schizopteridae 246
2.5.3 Enicocephalidae 248

3 COMPARATIVE EVALUATION OF DATA. APPRAISAL OF ANAGENESIS AND CLADOGENESIS 250
3.1 *Chorion* 250
3.1.1 Architecture and aeropylar system 251
3.1.2 Micropylar system 265
3.1.3 Eclosion rupture 272
3.1.4 Discussion 278
3.2 *Gross embryology* 290
3.2.1 Incubation time, diapause 290
3.2.2 The main features of embryogenesis and their supposed phylogeny . . 298
3.2.3 Other embryonic features varying between taxa 302
3.2.4 Discussion 305
3.3 *Dynamics of eclosion* 312
3.3.1 The persistent serosal plug 312
3.3.2 Embryonic envelopes 313
3.3.3 Tools for breaking membranes and chorion 316
3.3.4 Discussion 322
3.4 *Bilateral asymmetries. Problems arising from the determination of the polarity of the egg system* 327
3.4.1 Asymmetries, in particular the folding of the embryo's appendages 327
3.4.2 Position of released eggs 331
3.4.3 The first evidence of egg rotation 334

3.4.4 Comparison of embryonic types in standardized eggs in position as laid . . . 338
3.4.5 Dorsoventral polarity of the egg system . . . 340
3.4.6 Discussion . . . 344

4 A PRELIMINARY DISCUSSION OF THE PHYLOGENY OF THE SUBORDER . . . 350
4.1 The data and their bearing on classification above generic level . . . 350
4.2 The relation between the major subdivisions of Heteroptera . . . 360
4.3 A preview of other investigations . . . 363

5 SUMMARY AND CONCLUSIONS . . . 379

ACKNOWLEDGMENTS . . . 384

SAMENVATTING . . . 386

REFERENCES . . . 404

EXPLANATION OF FIGURE LETTERING . . . 426

PHOTOGRAPHS . . . 429

AUTHOR INDEX . . . 461

SUBJECT INDEX . . . 465

"In its best practice, taxonomy is a wonderfully promising area of synthesis for all biological knowledge"

Fox and Fox, 1964

DRUK: H. VEENMAN EN ZONEN N.V. – WAGENINGEN

Preface

In 1958, the author undertook the study of the Saldidae on a world-wide basis. The systematic position of this family has been a vexing question for a long time. Saldidae has been considered by several authors as one of the most primitive taxa within the Heteroptera. Therefore the objective of our study of the Saldidae was to investigate the comparative morphology of all species available for study and to trace intrafamilial relationships. For the analyses of the relations between this family and others, it was planned to rely wholly upon data from the literature. It soon appeared that our findings and interpretations of structures were often not in accordance with the statements made in the voluminous literature. Consequently we started with a blank card and extended the comparative analyses over all families of Heteroptera of which material could be obtained. It then became our objective to unravel evolutionary trends in Heteroptera in order to elucidate the phylogeny of the supra-generic categories. The results are presented here in a series of three Parts of which this book is the first. The originally prepared world-wide revision of Saldidae (Leptopodoidea) will appear as a separate publication, but the importance we originally attached to this family is still to be seen in the present work. The family has thus become our standard in testing the assumption of CHINA (1955a) that the ancestors of the Amphibicorisae were saldid-like bugs.

As well as developing the study of conventially used characters, mainly of the adult, we made an intensive search for new characters. A whole crop of these is described in this first publication on the egg system. The second Part of this series is concerned with the evolution of the reproductive and genital systems. In the third and last Part, various subjects will be treated, a selection of which has been reviewed in a preliminary manner on p. 363–378 of the present Part. All the collected data will be integrated in the final discussion of the phylogeny and major classification of the Suborder.

The study of structural evolution starts from the principle that evolutionary changes have been continuous; the changes involve the gradual appearance of new structures or, more often the modification, multiplication, displacement, fusion, regression or loss of pre-existing structures. Evolution has not affected all structures simultaneously, in the same manner, or at the same rate. Moreover, the phylogeny of a group may be the resultant of various phylogenies. The structural change of each single or compound character has, therefore, first to be analysed separately. These principles were applied to the data from our studies of gross embryogenesis and lead to a phylogenetic scheme (fig. 276), which may be considered as our concept of the basic pattern of heteropterous evolution. The picture brought to light is of extreme interest in that it

shows both a great diversity in character-complements and a clear radial ramification and progressive development of the types along well defined lines. The direction of evolution as it is revealed from this surveyable scheme could not have been presented in a reverse direction. Our decisions whether structures apart from the egg, which are more intricate, are more primitive or more evolved, generally run parallel with the data on embryogenesis; we therefore feel that our interpretations are fairly reliable, despite the absence of palaeontological evidence.

This study is a biotaxonomic one, but it is hoped that it may also improve our insight into the theory of insect evolution.

Material and methods

Material

Some 400 species representing almost all families of Heteroptera, have been investigated in this study. When supplemented by the data from the literature, the eggs of approximately 1100 species are now known, though most of them have been studied in an inadequate way. This is only a small proportion (about 3.5%) of the total number of species described up to the present. Assuming this relative paucity, it is the choice of the species which counts in such a study as this. Own experience and knowledge of the literature help the specialist to predict, which taxa may be worthwhile for investigation and how large the sample of species must be to characterize a given taxon. In large homogeneous families (*e.g.* Pentatomidae) a few species (some taken at random and others not) may be sufficient to define the family egg type. More representatives have to be studied when the families are heterogeneous. This applies in particular to small families whose members are often of limited geographical distribution and have special adaptations. Aberrant relict forms are very important and fortunately there has been much opportunity to study these. The conclusions from the material are gathered into several pictorial schemes demonstrating the evolution of egg characters, often step by step. This is more than we could have hoped from the original objective. We believe that our success is due largely to the species selected. There remain, of course, some gaps which may be filled in future. For some families too little material has been available.

The material from which the eggs were obtained has been collected by the writer in the Netherlands, South of France, the Netherlands Antilles and the Ivory Coast. Additional material from other territories was loaned from many colleagues and museums; they are listed under the acknowledgments. In the descriptive part, the new data on the eggs are presented by family and each of these sections is concluded with a survey of the literature. The book is thus a compendium of our knowledge of the eggs of Heteroptera for ready reference by the specialist.

Methods

Most chorionic structures were studied on eggs from dried females in systematic collections. Females with swollen abdomen were selected for this purpose, and the eggs were dissected and heated (80 °C) for some hours in lactic acid. One female provides several, often many, shells of different age. It is important for a good analysis

of structures to make simultaneous use of shells preserved at various stages of their formation. The chorion is readily cleaned in lactic acid of rudiments of ovarial tissue and of yolk; the general structure of the shell was studied in the same solution in embryo blocks. The finer structures and stratification were studied (magnification up to × 800) in mounts, for which fragments of the shell were used. Besides euparal and Faure solution for permanent preparations, lactic acid served as a temporary embedding material. The amount of fluid on the slide must be sufficient during observations for the enclosed small shell fragments to be turned over in the position desired by a slight push of the coverslip. Such pieces judiciously torn off around or through the structures to be investigated, can thus be studied from the surface, the fracture sides and in optical sections. With some experience most fine structures could be resolved rapidly in this way, whereas the cobalt sulphide injection technique (WIGGLESWORTH, 1950) and the time-consuming method of serial sectioning often gave inadequate results. The difficulties found in cutting insect chorion can be largely conquered in using water as a lubricant agent (HARTLEY, 1964). Serial sections were made of deposited eggs for studying chorionic and embryonic structures. The chorion and the serosal cuticle, if present, were punctured after placement of the eggs in Bouin's fluid. The shell structure was preserved by omitting previous treatment with diluted caustic potash. Sections were prepared by normal embedding in paraffin and double embedding with celloidin.

Microsections for the transmission electron microscope have been made of ovarian and of deposited eggs. Eggs were halved transversely and embedded in methacrylate after dehydration in alcohol. Shells weakened in hot lactic acid were easier to section; the shell architecture in the resulting micrographs was identical with that of untreated shells of the same egg batch. Vestopal appeared less suited as embedding material since its attachment to the chorion is not strong enough. Microsections, stained with $KMnO_4$ or unstained, were examined with a Siemens Elmiskop I electron-microscope (micrographs fig. 286–305).

The chorionic architecture of several species was studied with the scanning electron microscope. Dehydrated ovarian or laid eggs were first coated in an evaporating unit with gold or with carbon-aluminium-carbon. Scanning-electronmicrographs of eggs *in toto* or of fracture planes of the chorion were made with the Stereoscan apparatus (Münster, Germany, fig. 306, 308–310, 313–315A-D, F) and with the Jeol scanning microscope (Paris, France, fig. 307, 311, 312, 315E).

Living deposited eggs for embryological studies were mostly from insects reared in the laboratory. Polystyrene foam was readily accepted by Amphibicorisae and Hydrocorisae as a substrate for egg deposition. The vulnerable eggs when freshly inserted in the foam, could easily be detached from it undamaged. Only *Plea atomaria* refused to deposit in the artificial substrate and needed waterplants. Saldidae readily embedded the eggs in moist filter paper, cotton or wads of cheesecloth. All kinds of substrates were accepted by terrestrial species as long as the eggs are laid in wholly exposed position. Supply of natural substrate (soil, litter, wood, dead or living plant tissue) was necessary for those species of Geocorisae which insert

their eggs wholly or partly. In general, we have let the females oviposit at room temperatures (about 18 °C) for Dutch species, about 28°C for the species collected in the Ivory Coast and in the south of France. The study of embryogenesis is greatly facilitated in species producing egg batches because of the availability of many eggs of the same age. Other species deposit a few eggs at intervals. A number of eggs of similar age can be obtained from these by subjecting laying females to high temperatures (above 30 °C). Most species react under such conditions with a rapid discharge of their eggs. Some species, however, are stimulated to deposit only by a fall of temperature *(e.g. Himacerus apterus)*. They die at high temperatures without discharging the eggs. Other species go in diapause when the ovarioles contain ripe eggs.

The oviposition stance of the female and the dorso-ventral orientation of the egg during and after it is released were carefully observed because of their use in determining the polarity of the egg system afterwards, when the embryology is known.

For incubation, a part of the egg sample of terrestrial species was isolated from the substrate and transferred into egg dishes containing moist sterile sand. The eggs were placed on blotting paper covering the sand. Humidity conditions in the dishes were maintained according to the demands of the respective species. Eggs were incubated and studied at room temperature, unless otherwise stated. The remaining part of the egg sample was left in the original state of deposition. Comparisons of the embryogenesis of these eggs with those of the isolated ones were made in order to establish whether isolation of the eggs had affected embryonic processes or not. For example, the degree of protrusion of the persistent serosal plug in the Miridae may be influenced by the oviposition site. Furthermore, a regular check has to be made of the orientation of the egg *in situ* and the orientation of the enclosed embryo. Eggs of waterbugs (except for Nepidae) must be continuously kept and studied under water to guarantee a normal development. The eggs of surface bugs and Saldidae likewise develop quite normally when continuously submerged.

The first half of the embryonic development (until the evagination and revolution of the embryo) has been studied mostly in freshly preserved and stained eggs. Observations *in vivo* of the gross embryogenesis are likely to lead to wrong interpretation of the internal processes, even when the chorion is translucent. This is due to the faint contrasts between blastoderm thickenings, germ-band tissue and the remaining egg contents (compare fig. 54A–D, drawn from living eggs, with fig. 63, embryo fixed and stained). Eggs were killed by placing in boiling alcohol (70%) for one minute or fixed in hot Bouin's fluid; the chorion was punctured shortly after the fluid was cooled. The prick must be deep enough to pass through the serosal cuticle if this is already present (from about one fourth of the total incubation period onwards). Eggs of different ages were stained in bulk and *in toto* with borax carmine. After one to three days (dependent on the egg size) the yolk body was cleared with acid alcohol. It appeared that the wine-red of the germ band and of the blastoderm nuclei intensifies into a brilliant colour if the eggs are subsequently transferred into lactic acid.

Later embryogenesis was studied mainly *in vivo*. To trace the general shape, growth, and displacement of the embryo and the posture and behaviour of the prolarva (*i.e.*,

the fully grown embryo still enveloped by the embryonic cuticle) eggs were placed under water in black embryo-blocks and studied with reflected light. Typical terrestrial eggs survive submersion for only a limited period. Small eggs were mounted in water and viewed under high power in transmitted light. The same method was used with larger eggs to trace such processes as the behaviour of the hydropyle, the embryonic envelopes, the yolk system, the formation of the secondary dorsal organ and the details of emergence. Thick, non-transparent chorions and darkened serosal cuticles may hinder direct observations. There is some individual variation in the translucence of these coverings, so that a composite picture of the internal developments must sometimes be reconstructed. For instance, some stages during the disruption of the serosal hydropyle in *Gerris* (fig. 64) were investigated *in vivo* in intact eggs despite the moderate translucence of the chorion and serosal cuticle. Solvents or bleaches (*e.g.* NaOCL, hair bleach) were tried but were not satisfactory for making the inside of the egg visible, because of the risk of affecting the course of embryonic events. The blackening of the chorion *(Hydrometra)* and of the cement layer (Asopinae) shortly after egg release is prevented if the egg is taken straight from the ovipositor and temporarily submerged. With practice it was possible to remove the chorion of living eggs of the larger waterbugs with fine but fairly blunt forceps after the secretion of the serosal cuticle. Peeling is facilitated if the laid eggs are allowed to dry for 5 to 10 minutes. Care must be taken that the black outer layer of the serosal cuticle is not scraped off, since the underlayer will bulge out later at such points. Eggs peeled during blastokinesis did not live long; later dechorionation did not affect development over a reasonably long period. Such processes as in fig. 246, 247 can thus be followed very clearly. This routine was used in Notonectidae, Naucoridae and Nepidae, but in Corixidae peeling invariably caused puncture of the serosal cuticle.

To analyse the eclosion mechanism, the posture of the fully grown embryo within the egg and the behaviour of the serosal cuticle, the embryonic cuticle and the larva proper must be examined. The embryonic cuticle should be studied before it is shed, so that the structures of the head in the embryonic cuticle can be related to those of the underlying larval cuticle and so that their morphological origin can be easier defined. Study of the embryonic cuticle after it is shed has often led to false interpretations, because it is so crumpled. The difficulty was averted by transferring the eggs into a water film when eclosion was imminent, and then to raise the temperature. Waterbugs, surface bugs and Saldidae hatched in the normal way; the embryonic cuticle was left, spread out and completely separate from the empty shell. However eggs of typical terrestrial species often did not completely hatch; the larva usually succeeded in getting rid of the shell and most of the embryonic cuticle. Further dissection yielded a completely distended empty cuticle (*e.g.*, fig. 90).

All illustrations are free-hand. In the series of drawings depicting the consecutive steps of gross embryogenesis, the gradual but often distinct increase in egg volume has not been illustrated.

1 Structure and biology of the leptopodoid egg

1.1 Saldidae

1.1.1 Literature

The following authors have described the exterior of saldid eggs: HUNGERFORD (1919, *Salda anthracina, crassicornis*), WILEY (1922, *Salda lugubris, Saldula pallipes* (?)), POISSON (1923, *Aepophilus bonnairei;* 1933, *Salda littoralis, Saldula saltatoria*), EKBLOM (1926, *S. saltatoria*), BRINDLEY (1934, *S. littoralis*), JORDAN and WENDT (1938, *S. littoralis*), RIMES (1951, *Pentacora leucographa, Saldula brevicornis, coorongensis, psammobia*). Generally these eggs are described as being simply oval-shaped, without micropylar processes or a distinct cap. The eggs are preferably inserted into the stems of plants near the soil surface or into an algal layer. None of the authors succeeded in discovering micropyles. BRINDLEY and JORDAN & WENDT noticed a striated area, restricted to that part of the shell which is exposed from the substratum and which they termed erroneously the micropylar region. RIMES wrongly interpreted this area as having resulted from wrinkling after oviposition. JORDAN and WENDT found further that the chorion in *S. littoralis* is beset with fine pores and that a single median egg-burster splits the chorion longitudinally.

1.1.2 Material

The eggs of 39 species were examined. These include representatives of the three subfamilies and of 11 genera, recognized in the present study.

Aepophilus bonnairei Sign. (ov.) (origin France)
Chiloxanthus pilosus Fall.
Chiloxanthus stellatus Curt. (ov.) (origin Alaska)
Pentacora signoreti Guer. (ov.) (origin Neth. Antilles)
Pentacora hirta Say (ov.) (origin N. America)
Pentacora ligata Say (ov.) (origin N. America)
Pentacora sphacelata Uhl. (ov.) (origin Neth. Antilles)
Pentacora leucographa Rim. (ov.) (origin Australia)
Pentacora mexicana Van Duz. (ov.) (origin Mexico)
Orthophrys pygmaeum Reut. (ov.) (origin Morocco)
Pseudosaldula sp. (ov.) (origin Chile)

Halosalda lateralis Fall.
Saldula saltatoria L.
Saldula C-album Fieb.
Saldula fucicola J. Sahlb.
Saldula pallipes Fabr.
Saldula palustris Dougl.
Saldula arenicola Schltz.
Saldula marginalis Fall.
Saldula orthochila Fieb.
Saldula politus Uhl. (ov.) (origin N. America)
Saldula scotica Curt.
Saldula madonica Seidenst. (ov.) (origin Sicily)
Saldula rivularia Sahlb. (ov.) (origin Alaska)
Saldula variabilis variabilis H.-Sch. (ov.) (Germany)
Saldula sp. n. (ov.) (origin Turkestan)
Saldula jihafana Brown (ov.) (origin Aethiopia)
Chartoscirta cocksi Curt.
Saldula aberrans White (ov.) (origin St. Helena)
Chartoscirta cincta H.-Sch.
Chartoscairta elegantula Fall.
Saldoida armata Horv. (ov.) (origin Japan)
Saldoida slossoni Osb. (ov.) (origin N. America)
Calacanthia alpicola J. Sahlb. (ov.) (origin Lapland)
Calacanthia trybomi J. Sahlb. (ov.) (origin Russia)
Salda littoralis L.
Salda morio Zett. (ov.) (origin Sweden)
Salda sahlbergi Reut. (ov.) (origin Austria)
Salda crassicornis Uhl. (ov.) (origin N. America)

Released, living eggs were available from fifteen species. Mature ovarian eggs of the remaining species (indicated with ov. in the list above) were dissected out of dry museum specimens or alcoholic material. Conventional serial sections were made of laid eggs of *Ch. pilosus*, *S. saltatoria* and *S. littoralis*. Sections for investigation of the shell with the electron-microscope were prepared from deposited eggs of *S. palustris*, *S. littoralis* and of ripe ovarian eggs of *P. signoreti*, *O. pygmaeum* and *A. bonnairei*. Embryogenesis and eclosion were studied in *Ch. pilosus*, *S. saltatoria*, *fucicola*, *c-album*, *pallipes*, *marginalis*, *orthochila*, *scotica*, *Ch. cincta*, *elegantula*, *H. lateralis* and *S. littoralis*.

1.1.3 Egg- shape and mode of oviposition

The normal saldid egg is ellipsoid, the anterior pole being more tapered than the posterior pole. The aft side is convex, the fore side straight or slightly concave (fig. 1).

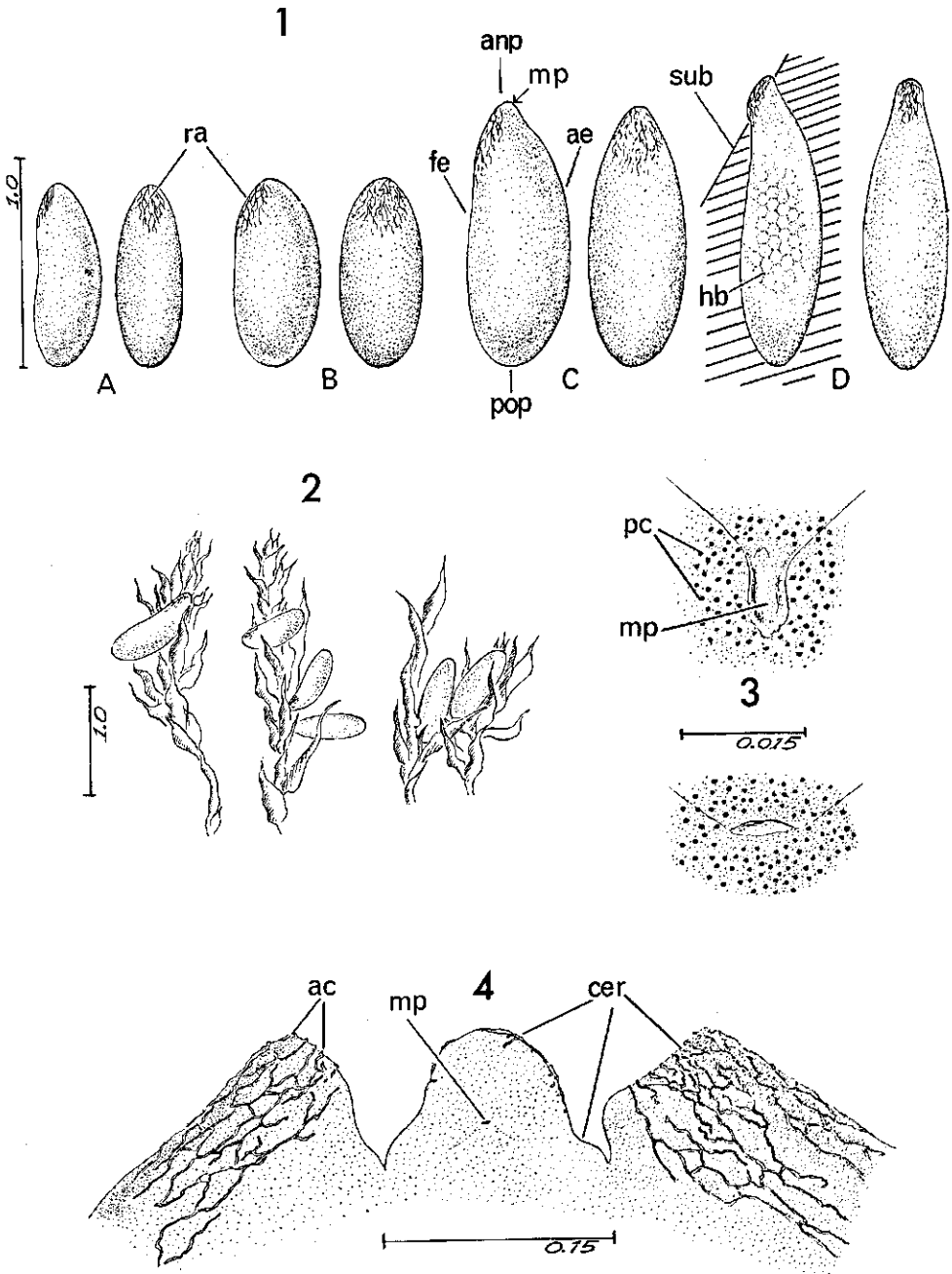


Fig. 1–4. Saldidae 1. Outline of eggs; A: *Saldula fucicola;* B: *Halosalda lateralis;* C: *Chiloxanthus pilosus;* D: *Salda littoralis.* 2. Eggs of *Saldula orthochila* in moss. 3. *S. palustris*, micropyle, exterior surface view. 4. *S. palustris*, flattened top region of vacated shell, obliquely from behind.
(For Key to lettering of figures see pp. 426–428.)

The term 'aft' (ae in fig. 1C) represents the side which is most closely associated with the substrate and is preferred here to the morphological implication of the term 'dorsal'. In entomological literature it is common to refer to that side of the egg, which corresponds with the dorsum of the mature embryo, as the dorsal side. Applying this usage to the saldid egg, the aft convex side indeed covers the prolarval dorsum. However, such a determination is founded only on practical grounds and lacks a sound morphogenetic motive. The many problems involved in the determination of the dorsoventral polarity of the heteropteran egg are discussed sub 3.4.5. It will be shown there that the morphological sides of the saldid egg are just the reverse of what is expected on first sight.

The mode of oviposition in saldids is exceptional. The ovipositing female, in bending its abdomen vertically to the substrate, points the ovipositor forward. This suggests that the base of the released egg points forward, that is towards the head of the mother. Our observations, in which the axis of the depositing female and the delivered eggs were checked, confirmed this mode of oviposition, which is also found in *Mesovelia* (see p. 48). In most other ovipositor-bearing Heteroptera the eggs are deposited in the opposite longitudinal direction. However, in both saldids and the latter group, the orientation of the fully grown embryo in relation to the substrate is the same (see further p. 331 etc.).

The ratio of length to greatest width of saldid eggs fluctuates around two and a half; the ratio decreases with the growth of the embryo. Some measurements are given in Table 1.

The greatest deviation from the standard shape occurs in *Calacanthia* and species of the *S. scotica* and *S. rivularia* group. These species have cylindrical eggs with the

Table 1.

Species	Number of eggs	Length mean ↓	Greatest width mean ↓	l/w
Ch. pilosus	6*	1.12 – *1.14* – 1.15	0.35 – *0.36* – 0.40	3.17
	8**	1.19 – *1.21* – 1.23	0.40 – *0.41* – 0.42	2.95
S. fucicola	19*	0.65 – *0.70* – 0.80	0.25 – *0.28* – 0.35	2.50
	16**	0.70 – *0.75* – 0.82	0.32 – *0.33* – 0.35	2.30
S. c-album	10**	0.86 – *0.89* – 0.92	0.35 – *0.36* – 0.39	2.47
S. palustris	9**	0.77 – *0.84* – 0.90	0.35 – *0.39* – 0.43	2.15
S. orthochila	7*	0.90 – *0.92* – 0.94	0.34 – *0.35* – 0.35	2.63
	6**	1.00 – *1.00* – 1.03	0.39 – *0.40* – 0.40	2.50
S. scotica (Dutch population)	5**	0.85 – *0.89* – 0.91	0.40 – *0.43* – 0.45	2.07
H. lateralis	8**	0.87 – *0.89* – 0.90	0.35 – *0.35* – 0.37	2.55
S. littoralis	11*	1.15 – *1.22* – 1.30	0.37 – *0.38* – 0.42	3.21

* Without eye spots
** With eye spots

cephalic pole as blunt as the basal pole. Probably all these species do not insert their eggs into the substrate, but glue them superficially despite the fact that they have well developed and serrated ovipositor-blades. We were able to ascertain this behaviour in a Dutch population of *S. scotica* in which the practice was very constant. In rearing experiments, the eggs were laid in an exposed manner against stones. Even when only filter paper was provided (material in which other saldids readily insert their eggs) the eggs of *S. scotica* are still glued to the surface.

Although the egg of *Aepophilus* is bent bean-like, it also has a broadly rounded front pole. The egg of *Salda* species *(littoralis, morio, crassicornis)*, on the other hand, is distinctly constricted at the top, so as to form a curved neck, obliquely cut off and thus exteriorly resembling the cimicomorphous type of egg. Both the cylindrical and the bottle-necked types differ from the average saldid egg in the differentiated area on the front pole. The reticulated field in Saldidae varies to some extent (fig. 1), but, the area is lacking on cylindrical eggs and in *Aepophilus*. The reticulation is well-marked, though restricted to the oblique extreme top in *Salda* species. Embedded in plant-tissue or mud, only the extreme front portion of the cephalic pole lies uncovered and just this region bears the typical chorionic reticulation. A study of ovarian eggs of species which could not be studied in life, revealed a failure of reticulation in all five *Pentacora* species checked. The eggs of those species, however, are of the normal saldid type, as regards their outline, namely tapering cephalad. RIMES (1951) showed that *P. leucographa* bores its eggs into plant tissue. Thus, the conclusion seems to be justified that only the outline of the egg in Saldidae is correlated with the mode of oviposition. The lack of a distinct reticulated area should indicate that the egg is not embedded only when the anterior pole of the egg is not obviously tapered. The egg-shape of the aberrant coastal *Aepophilus* suggests a semi-exposed oviposition in already existing crevices. *Saldula* species affix their eggs on moss-leaves in all arbitrary positions (fig. 2), if no other material is offered. This way of depositing the eggs is to be considered as anomalous. In general it may be said that most saldid species insert their eggs in such a way that only a small anterior part of the egg is exposed to free air or water. Generally this chorionic part is reticulated and the function of this structure could be respiratory. A second or a complementary possibility is that it might facilitate eclosion of the prolarva. The fine structure of the area in question will be described below and its morphology will enable us to make a decision about its function.

The saldid chorion, other than the reticulation mentioned, is smooth, shiny or mat. The hexagonal print, marking the boundaries of the follicle cells, can only rarely be traced on the shell body *(S. littoralis; S. marginalis; O. pygmaeum)*. The tint of the egg is whitish or greyish. The somewhat shaded appearance occurring later is due to colouring of the growing embryo. *Chartoscirta* eggs become pink as they mature.

1.1.4 Architecture of the chorion

External view

In surface view (720 × magnification), the shell of all saldid eggs studied (except *Aepophilus*) has a greyish granulated appearance (fig. 4, 8, 10). What seems to be granulation is, in fact, a densely packed arrangement of fine pores on a plain surface. A distinct honeycomb pattern in present in *O. pygmaeum*. In this species, the characteristic pores are absent on the broad pathways between the hexagons, which originate from the margins of the follicle cells (fig. 10). There is, however, no sculpturing and the follicular pits are very shallow. The regularly arranged pores, which are the entrances to sheer canals, cover the whole circumference of the saldid egg. They are rarely found unchanged in density and size along the fore side of the anterior pole *(P. leucographa, S. politus, S. aberrans, Calacanthia)*. Normally the number in this area is reduced and the pores often are altered into deep pits (fig. 12B). For matter of convenience the area in question, with or without reticulation, will be called the '*respiratory area*', the detailed structure of which is dealt with on pages 16–22. The egg of *Aepophilus* deviates greatly in chorionic structure. There are no pores at all and the chorion in surface view appears as a bare transparent layer to which is attached exteriorly a fine, irregular reticulation (fig. 9). This sculpturing occurs over the whole outline of the egg, except for the small circular micropylar region.

The micropyle

All 39 species studied have only a single micropyle situated in the centre of the cephalic pole in the freely deposited eggs (fig. 5) and slightly backwards from the top in the embedded eggs (fig. 1C, 4). In *Aepophilus*, it has a more distinct position on the aft side. Earlier workers failed to discover the micropyle in Saldidae. Indeed, it can only be traced with certainty when the extreme anterior top of the egg is removed and flattened in an euparal-preparation. It represents merely a slit obliquely crossing the chorion and tapering towards the inside (fig. 3, 16B). There is no micropylar process or chorionic differentiation on either the outer or inner surface of the shell. In eggs having a well-developed respiratory area, the location of the micropyle is always just beyond the anterior margin of the chorionic striation. The outer slit-like opening of the micropyle in, for instance, *S. palustris* measures about 7.5 × 2.5μ.

The structure of the chorion beyond the respiratory area

The thickness of the complete shell amounts to 3 μ in *S. jihafana*, 5 μ in *Ch. pilosus* and 7.5 μ in *S. littoralis*. The eggs of these species are of about the same size. The chorion is distinctly two-layered (fig. 15, 16B). The relatively thin and solid inner layer covers 1/8–1/12 of the thickness of the complete shell. Its thickness in a given species remains unaltered in the posterior pole, but increases slightly in the anterior

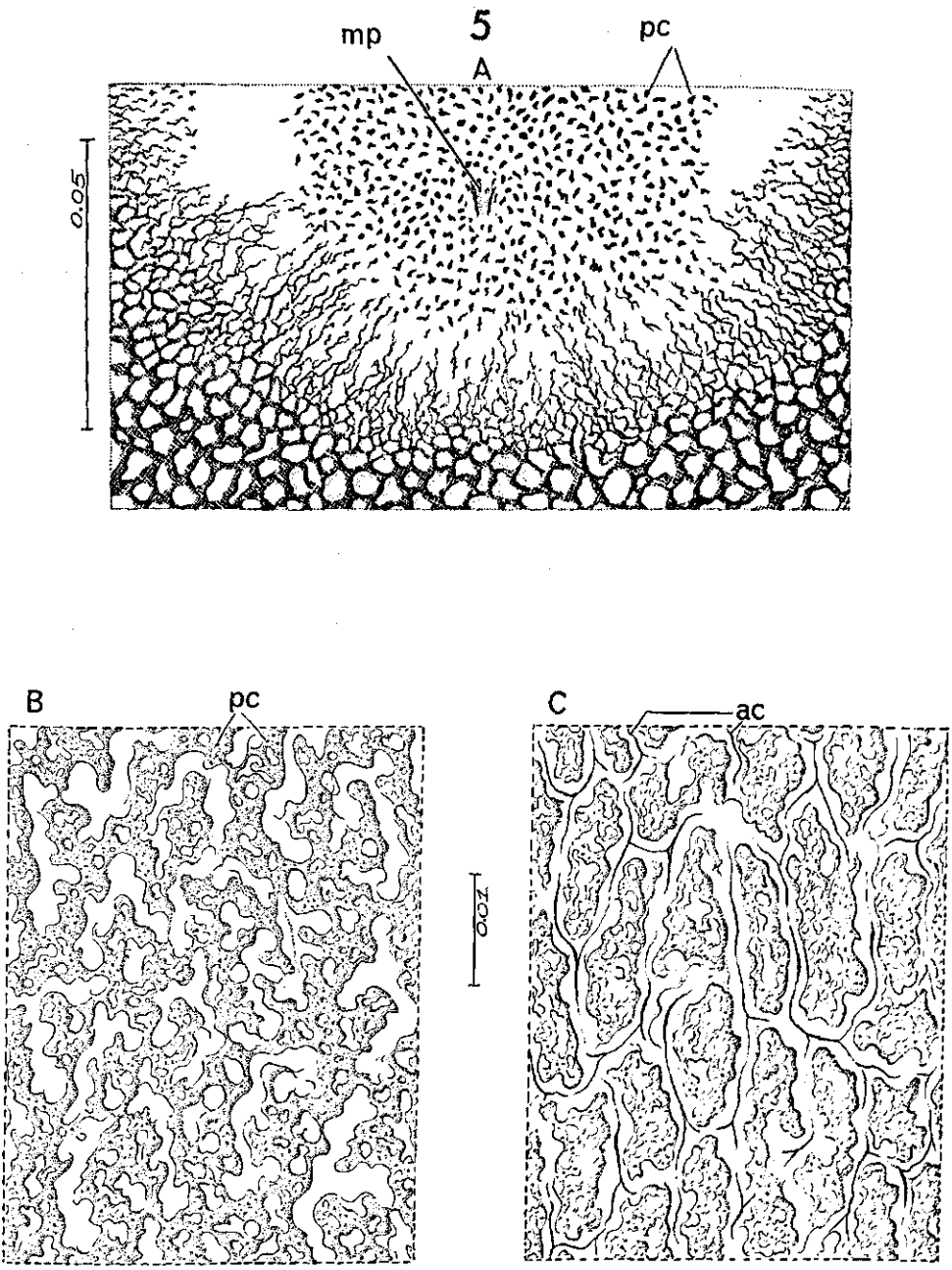


Fig. 5. Saldidae, surface view of shell structure; A: *Saldula rivularia*, anterior pole from above; B–C: *Saldula scotica*, fore side of anterior pole; B: Dutch population; C: French population (see text).

one. The thicker outer layer retains an almost equal thickness over the whole surface of the egg except at the extreme part of the posterior pole, where it is twice the diameter in *S. littoralis* (fig. 13). Where the two layers have loosened from each other, their opposing surfaces seem to be very minutely notched when observed by the high power of a light microscope (fig. 16A). Electron micrographs (fig. 17, 287C) show that the inner and outer chorionic layer are separated from each other by a thin sheet of what looks like a loosely packed marbling, if the section is somewhat oblique. The fine spongy sheet has arisen from short props extending from the inner surface of the outer layer. From the micrographs one would conclude that the props rest directly on the inner layer of the chorion. The mesh surrounds the whole egg, but the spaces in the network are smaller and fewer at the posterior pole.

As previously noted nearly all saldid eggs have minute pores (0.5–1.5 μ), densely distributed all over the shell. In *Ch. stellatus* the pores are irregular, forming undulating slits. In normal serial sections the chorion appears cross-striated.

Thus, it is supposed that the pores give entrance to canals which are in continuity

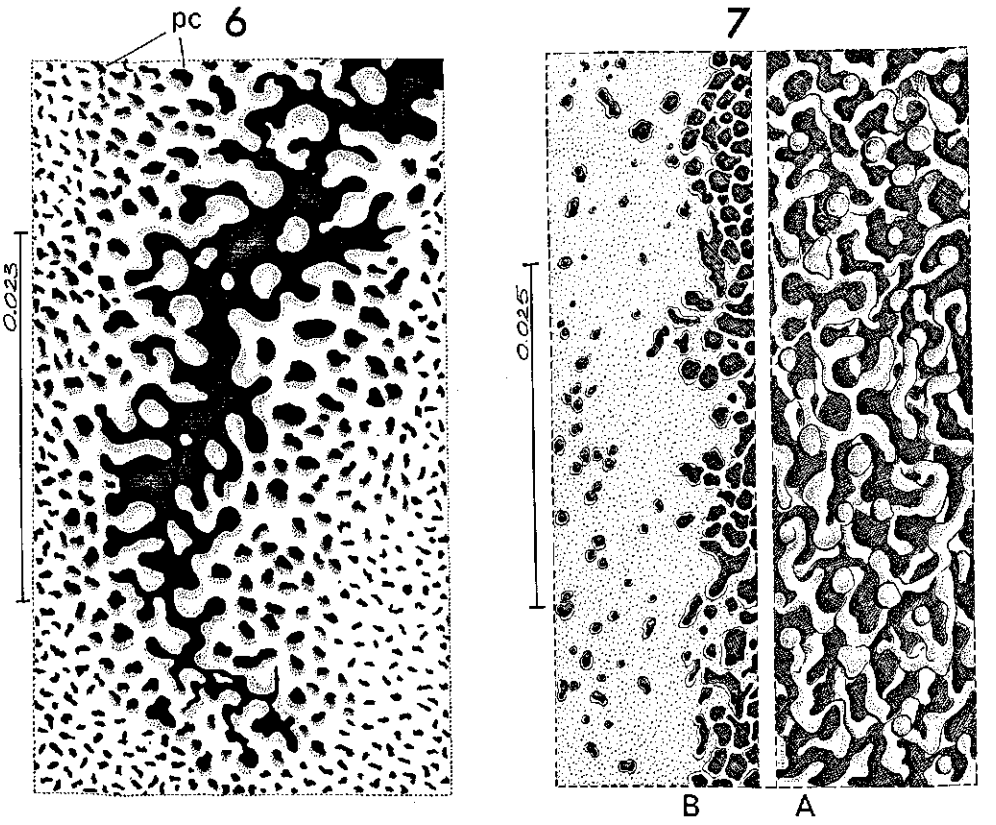


Fig. 6–7. Saldidae, surface view of shell structure 6. *Pentacora signoreti*, fore side of anterior pole with irregular porosity. 7. *Saldula madonica;* A: plastron-like area, medially on fore side; B: lateral margin of the strip figured in A.

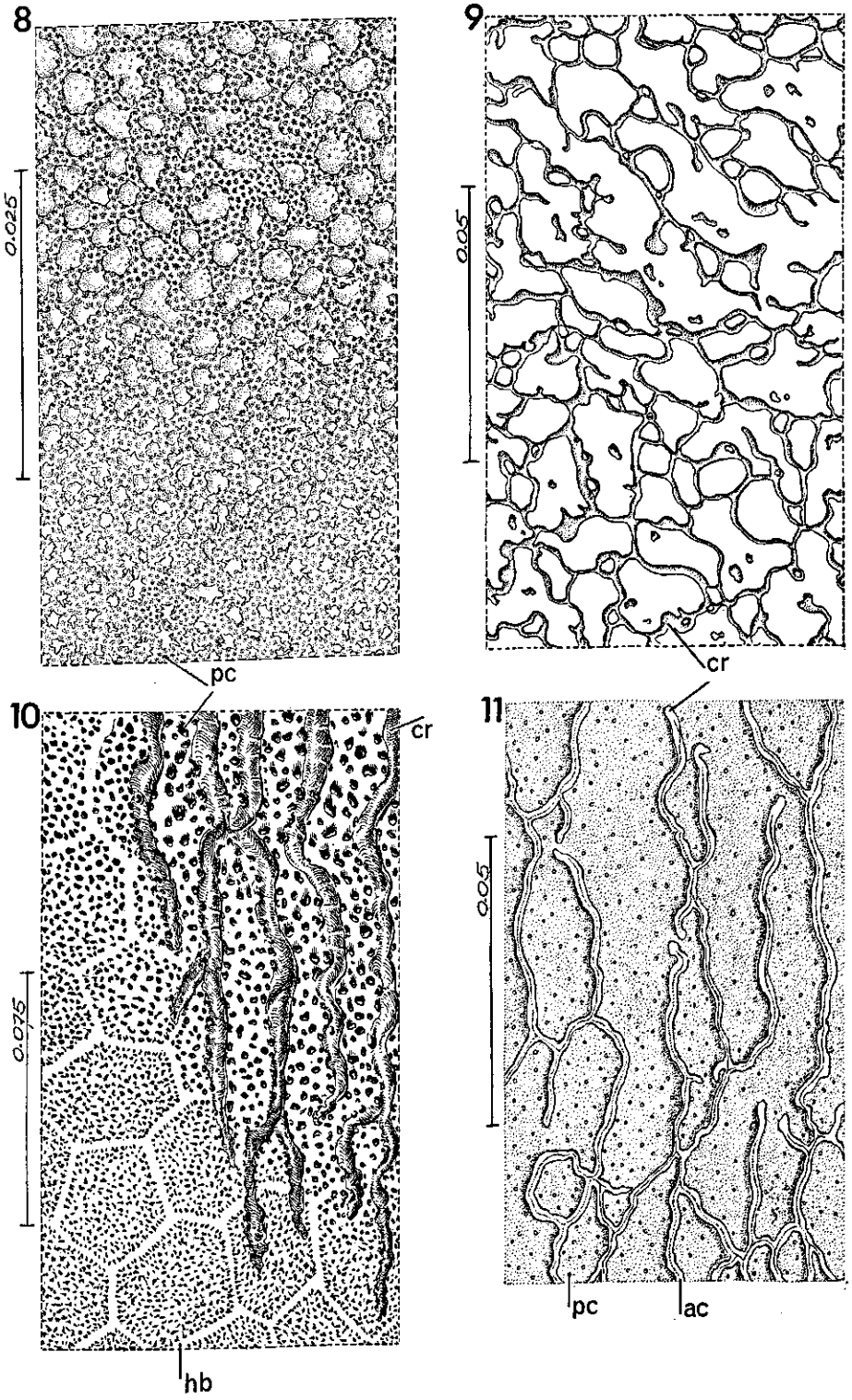


Fig. 8–11. Saldidae, surface view of shell structure, fore side of anterior pole 8. *Pentacora leucographa*. 9. *Aepophilus bonnairei*. 10. *Orthophrys pygmaeum*. 11. *Chartoscirta cincta*.

with the inner meshwork layer. Electron micrographs of eggs of *Saldula palustris* (fig. 287C), *Salda littoralis*, *Pentacora signoreti* (fig. 289) and *Orthophrys pygmaeum* (fig. 287B) strengthen this opinion, although most often the complete pathway of the canals is not presented due to the thinness of the section. The pore-canals, however, do not penetrate deeply at the posterior pole (fig. 13), or at the micropylar region. In *S. littoralis*, the sections viewed with the optical microscope reveal a zone of granular substance in the thickened posterior pole (fig. 13). Canals of the exterior pores reach the borderline of the granular zone, which most probably serves for water uptake, since a serosal hydropyle is found in this region. Finally, it is noted that apparently the whole circumference of the egg is covered with a 0.1 μ thin film of material, which is stretched also over the pore canals (fig. 17, 286). Since this layer is absent in most of the ripe ovarian eggs, we studied, it probably forms no part of the chorion proper. The ovarian egg of *O. pygmaeum*, however, shows an irregular outer coating (fig. 288). This coat is thus secreted already in the ovarioles, and this may also apply to the thin film of other Saldidae. In other heteropterous eggs such a cover has been termed the cement layer. We will introduce the term: 'suprachorionic layer' and not consider its homologous nature, because its origin and function may vary in other groups.

The chorion of *Aepophilus* is atypical. There are no pore-canals and a porous layer is lacking in micrographs. The chorion, about 4 μ thick (without the ribs), is compact but still of a two-layered composition. The inner layer is about three times the diameter of the outer layer and is thus considerably thickened when compared with other saldid eggs. Of great interest is the irregularly undulating or rather droplet-like border by which both layers are welded together (fig. 287A). The picture suggests that in the past the shell might have had a porous interspersed layer, the interstices being now filled up by material from the inner chorion (compare fig. 287A with fig. 287C). That both layers in the marine *Aepophilus* are homologous with those of other saldid eggs is, moreover, strongly suggested by the similar dark intensities of the chorionin (the sections for the electron microscope were not stained!).

The respiratory area, without extending reticulation

Within the family, species can be arranged by the development of a more or less efficient respiratory mechanism of the chorion. *Aepophilus bonnairei* has no special respiratory apparatus; the whole surface of the egg is of the same close consistency.

In *Pentacora leucographa* there is a slight differentiation of the area exposed to air in the deposited egg. The anterio-fore face of the shell bears small irregular patches of thickened chorion (fig. 8), roughly measuring around 3 μ. The regular pattern of the micro-pores, which cover the whole egg as in most saldids, is more clearly indicated in the area in question. The diameter of the pores is about 0.5 μ. The chorionic patches seem to facilitate the holding of a film of air during flooding; the pores seem to be connected with the meshwork within. The patches gradually fade away off the respiratory area due to their decrease in outline and height. An almost similar shell structure is found in the two *Calacanthia* species studied. These have a blunt anterior

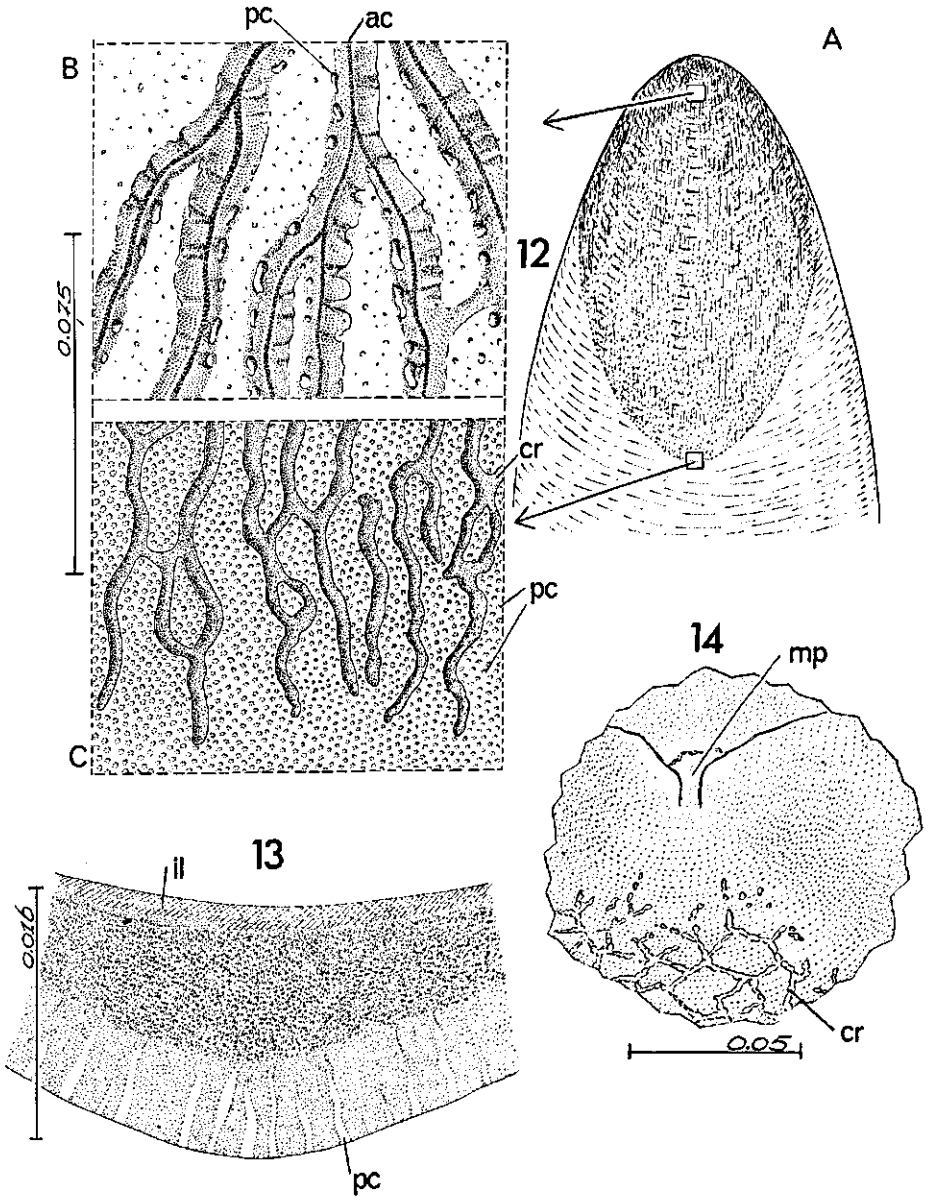


Fig. 12–14. Saldidae, shell structures 12. *Saldula jihafana;* A: fore side of anterior pole with respiratory area (shaded); B: area with airclefts; C: area with solid reticulation and aeropyles. 13. *Salda littoralis*, posterior pole, transverse section. 14. *Saldula variabilis variabilis*, anterior pole.

pole, and the protruding chorionic patches are rivet-like.

The adaptation for trapping air in a restricted area of the shell is more striking in *P. signoreti.* Here it is seen, even in surface view, that the chorion of the fore side of the anterior pole is considerably thicker than elsewhere. The pores are distinct, mostly

slit-like, and in certain places enlarged so much that they have the form of wide clefts (fig. 6). These irregular clefts run in a longitudinal direction towards the top of the egg. Electron micrographs (fig. 289) confirm the impression gained with the light microscope. The lumina of the isolated and the fused pores go down into the meshwork within. Fig. 289A and B show that the chorion in the respiratory area is two and a half times thicker than on the sides of the egg in the same transverse section.

The eggs of other *Pentacora* species studied are more or less intermediate between the *signoreti* type and the *scotica* type to be mentioned below. In *P. hirta* and *P. sphacelata*, the chorion is broken up into a homogeneous, spacious meshwork, resembling the coarsest respiratory strips of *P. signoreti*. The anterior area in question is much more finely sculptured in *P. ligata*. In the latter three species, the area for gas exchange is not only restricted to the anterior fore face of the egg, but more or less surrounds the pole. The egg of the coastal *Pentacora mexicana* has fine pores all over. The pores become coarser and more densely packed near the anterior fore face of the egg. A distinct hexagonal reticulation over the concave egg-side is superimposed upon the pored outer layer.

In *Saldula scotica* and *rivularia*, which produce blunt eggs, the respiratory area extends further in a zone around the top (fig. 5A). Near the micropylar area with more distinct pores than elsewhere fine cracks arise. These run out radially and widen to form a network of broad grooves and enclose patches of thick chorion. In between the micropylar and respiratory area, a field of chorion is separated on the left and right lacking any sculpturing. The cylindrical form of the eggs suggests that they are laid wholly exposed and for *S. scotica* (origin southern Limburg, The Netherlands, pebble banks by the Meuse), this method of deposition was confirmed. Of fundamentally different nature was the chorionic structure of a population of *S. scotica* from southern France (Puy, weir in the Loire). Instead of gluing the eggs superficially to the filter paper, females of the French population invariably inserted the eggs, as do typical members of the genus *Saldula*. In contrast to the Dutch populations, the eggs have the aft side more convex; the fore side of the exposed anterior pole, bears a specialized respiratory area. There are outer chorionic ridges which form a reticulate pattern, and the ridges are lengthwise split, down to the inner porous layer of the shell. Fig. 5B and 5C contrast the same area of the shell of both populations. They show that the single, but important difference resides in the pattern of the split ridges which can be derived from the irregular, not split external chorionic sculpture in the Dutch population. The areas enclosed by the reticulation in the French population is like the general structure in the Dutch population. The type of respiratory system occurring in the French population is further progressed in other Saldidae. A fuller account of these structures will be given on p. 20–22. The variation of egg structures within one species, *Saldula scotica*, must be checked over a wider range of geographical situations, before taxonomic conclusions can be drawn. So far, no morphological differences between the adults of the two types could be determined.

It is unrealistic to assume a constant pattern of egg-structure within a given taxonomic group. For example *S. madonica*, whose imaginal characters certainly placed it

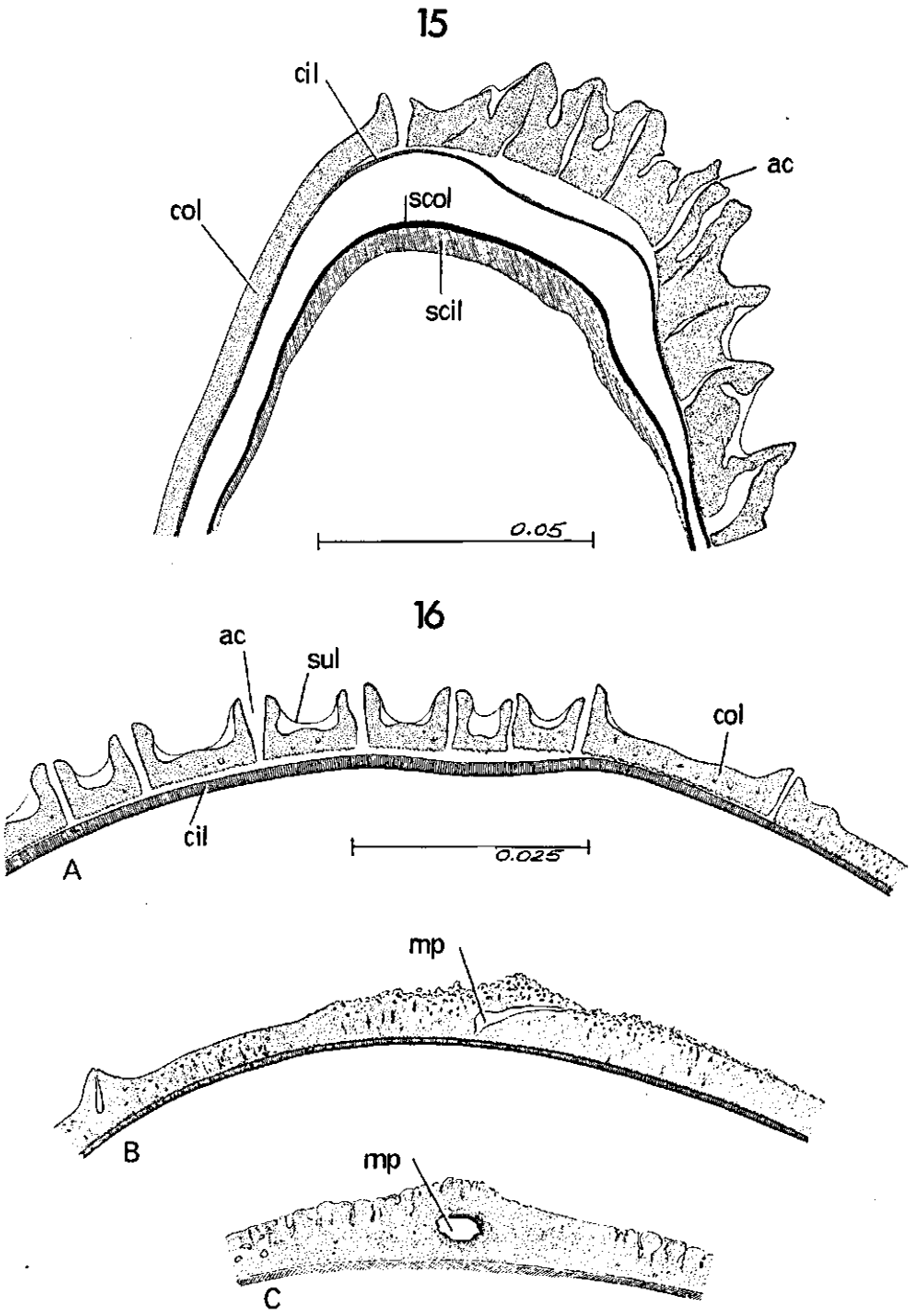


Fig. 15–16. Saldidae, sections of chorion 15. *Salda littoralis*, anterior pole; slightly oblique, dorso-ventral section, diapausing egg. 16. *Chiloxanthus pilosus;* A: transverse section of respiratory area; B: median section of micropyle; C: transverse section of micropyle.

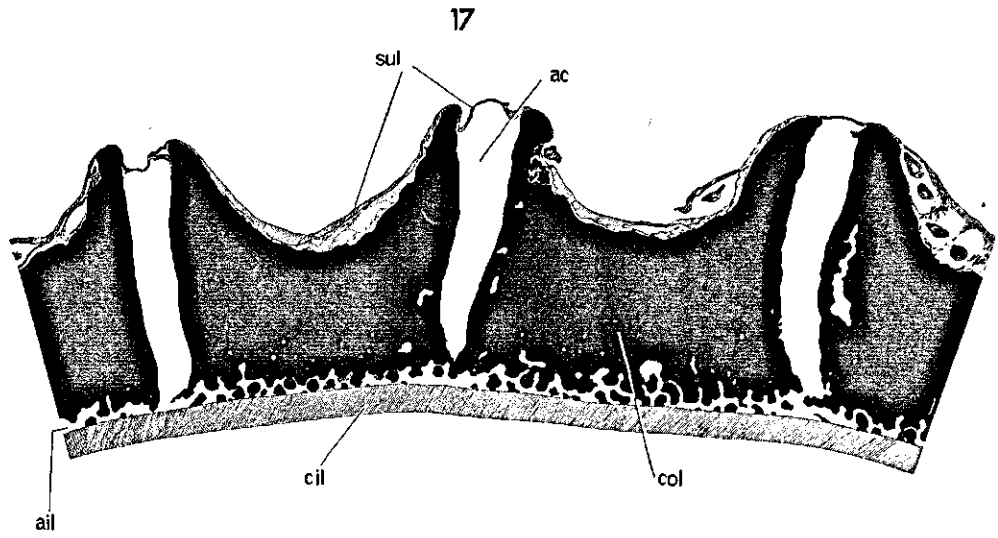


Fig. 17. Saldidae, section of chorion; *Saldula palustris*, transverse section of respiratory area, as seen with the electron microscope.

in the *scotica* group, has a broad longitudinal zone over the fore side of the egg. The sculpturing of this zone resembles that of *Pentacora* spp. The zone looks felty and with high magnification a more plastron-like modification of the chorion is observed (fig. 7). Instead of a simple break in the outer layer to achieve direct contact between the air and the inner network, the outer chorion in *S. madonica* is fractioned into a basketwork of irregular struts. In S. *horvathi* and *S. variabilis*, on the contrary, the chorion has normal tiny pores and an adjacent faint reticulation. The latter consists merely of a string of chorionic beads which is a first step towards the characteristic respiratory type to be discussed below.

The respiratory area with extended reticulation

All saldid species studied (list on p. 7,8), except species of *Aepophilus*, *Pentacora*, *Calacanthia* and *Saldula* species of the *scotica* group, have a distinct network adjacent to the outer chorionic surface. The retiform region is located on the cephalic pole on the frontal, exposed side of the shell. The general aspect of the network is seen in fig. 1, 4, 32. At first sight and even with high magnification the network looks like an arrangement of simple solid ridges serving to strengthen the chorion. But cross sections reveal the ridges to be split up to the inner spongy layer (fig. 16A, 17).

The clefts run the length of the ridges and are seen, in surface view, as a dark line (fig. 11, 12). Thus, the interior of the shell seems sure of an ample supply of air. One deposited egg of *S. palustris* and one of *S. littoralis*, used for electron-microscopic sections show that the air clefts are covered outwardly by a thin sheet (fig. 287C). This is the same layer which we considered on p. 16 as the suprachorionic layer, which

envelopes the whole chorion. Several eggs of *Ch. pilosus*, sliced in the normal way, revealed completely open traverses. These eggs too had already been deposited and bore the suprachorionic layer everywhere over the shell. With the optical microscope, the latter is clearly seen in the areas between the ridges (fig. 16A). Thus, the clefts are in fact open. From ovarian eggs it is not always possible to decide with certainty whether the ridges are split or not, without slicing them. However in most of those eggs the dark band marking the line of the split could be traced in surface view. Therefore we conclude that in most, if not all, species the distinct reticulation is connected with a type of air trap, not previously found among Heteroptera. We have not ascertained whether the ridges split lengthwise along the visible median line before or after the release of the eggs, when the shell is forced to stretch. Micrographs of the *Orthophrys* ovarian egg (fig. 288) might favour such an opinion, as we see here only faint lines, passing straight the chorion from the top of each outer ridge onto the meshwork within. However the light microscope shows no dark line (fig. 10), which would be present in ovarian eggs of other saldids. If the cleft in those saldid eggs results from subsequent swelling, we must assume at least a more distinct origin for the clefts than in *Orthophrys*. Because we consider the monotypic *Orthophrys* to be the most primitive member of the Saldinae its egg structure may represent the basis of development of the more effective air clefts of more evolved Saldinae.

The form of the respiratory system varies. The area occupied by it is very extensive in, *e.g.*, *S. aberrans, jihafana, politus* and *S. slossoni*. Generally the course of the fine ridges in those species is rather spacious. In *Salda* spp. the area is more restricted and has compactly and irregularly arranged high ridges (fig. 15). Normally the flat adjacent chorionic parts which are enclosed by the ridges, are perforated with evenly spaced pores of a uniform diameter, but less densely than in other areas of the egg surface. Only occasionally *(S. politus, aberrans)* is the density of the pores unchanged. In *S. slossoni*, a square in the middle of the reticulated field bears pores, which are much wider than elsewhere. These pores are not part of the ridge system, but in *S. jihafana* and *O. pygmaeum* the equally enlarged pores form part of the system of air clefts. In the latter species (fig. 10) the wide pores become even more enlarged towards the anterior of the egg and are distributed all over the spaces between the ridges. But where they border the ridges, they penetrate obliquely into the latter. In *S. jihafana* (fig. 12B), the pores are wide irregular gaps and are confined to the sides of the ridges proper. They excavate the thresholds of the slopes of the ridges in a horizontal plane and their canals apparently communicate with the air clefts. The peripheral offshoots of the reticulation have no clefts lengthwise and no pores entering from the sides (fig. 12C). It is important to note that the ridges of the reticulation do not coincide with the boundaries of the follicle cells. This is clearly demonstrated in *O. pygmaeum* (fig. 10), the chorion of which is distinctly honeycombed.

Saldid eggs are primarily deposited above the water level, although in a moist atmosphere. The presence of an inner open chorionic layer which communicates with the outside by a specialised system of clefts or pores can hardly be otherwise explained except as providing an access for atmospheric air. The lumina indeed are air-filled. On

the other hand, eggs of some *Saldula* and *Chartoscirta* species developed and hatched without any retardation or injury when held continuously under water immediately after their deposition. It seems unlikely that the original air-content of the shell is sufficient for respiration, since it is not held in a plastron-structure. When saldids were forced to lay eggs in blotting-paper just below water level and those eggs were held submersed continuously, normal incubation and eclosion followed. From the beginning, no air could be traced in the chorion of these eggs which apparently can function as true water-eggs too. Although the physics of the saldid egg-shell needs more exact and experimental investigation, we may provisionally conclude that the amphibious ambivalency of the saldid egg is even more striking than eggs of the true Amphibicorisae to be dealt with in the next chapters.

1.1.5 Gross study of the embryogenesis

The following schemes (fig. 18–25) outline the embryonic development of *S. saltatoria*. The embryonic processes of other saldids of different genera (mentioned sub 1.1.2) did not show deviations from the account given below. The method used permits only a rough analysis, the data being derived from dissections and staining of the germ-band at the outset and from direct observations on the living egg in the later phases of the embryogeny. These methods give criteria enough and provide an important routine for use in major systematics of the Heteroptera. The shell of saldid eggs under water is reasonably transparent although there is some variability in its translucence between specimens. The study of many eggs has given a complete picture of the gross development of the embryo.

Early embryogenesis up to blastokinesis s. str. (fig. 18–23).

The whole period of incubation takes only four days at 30 °C in the *saltatoria* group of *Saldula* and the period described under this heading covers about two days.

The saldid germ band develops in an entirely immersed invaginated position. The pit which marks the invagination at its start is located slightly above the posterior pole. Two thickenings in the blastoderm are visible as faint lateral plates. The germ band gradually rises into the yolk upwards as a straight ribbon, tail-end first. Its pathway almost coincides with the polar axis. At its base, that is the posterior pole, the sides of the germ band turn upwards to form the cephalic lobes. Before reaching the anterior pole, the germ band starts the caudal curve. The whole embryo now has a ladle-shaped appearance (fig. 18E, 20E') and moves a bit further from the posterior pole. Until this stage an isolated cluster of cells lies on the top of the germ band. This cluster probably represents the germ cells. They migrate into the abdominal segments when the caudal flexure becomes more distinct.

In the next stage (fig. 20H'), the germ band flattens out transversely. Metamerism becomes visible first in the thoracic region, and shortly afterwards in the gnathal and abdominal subdivisions. The paired thoracic and gnathal appendages are visible

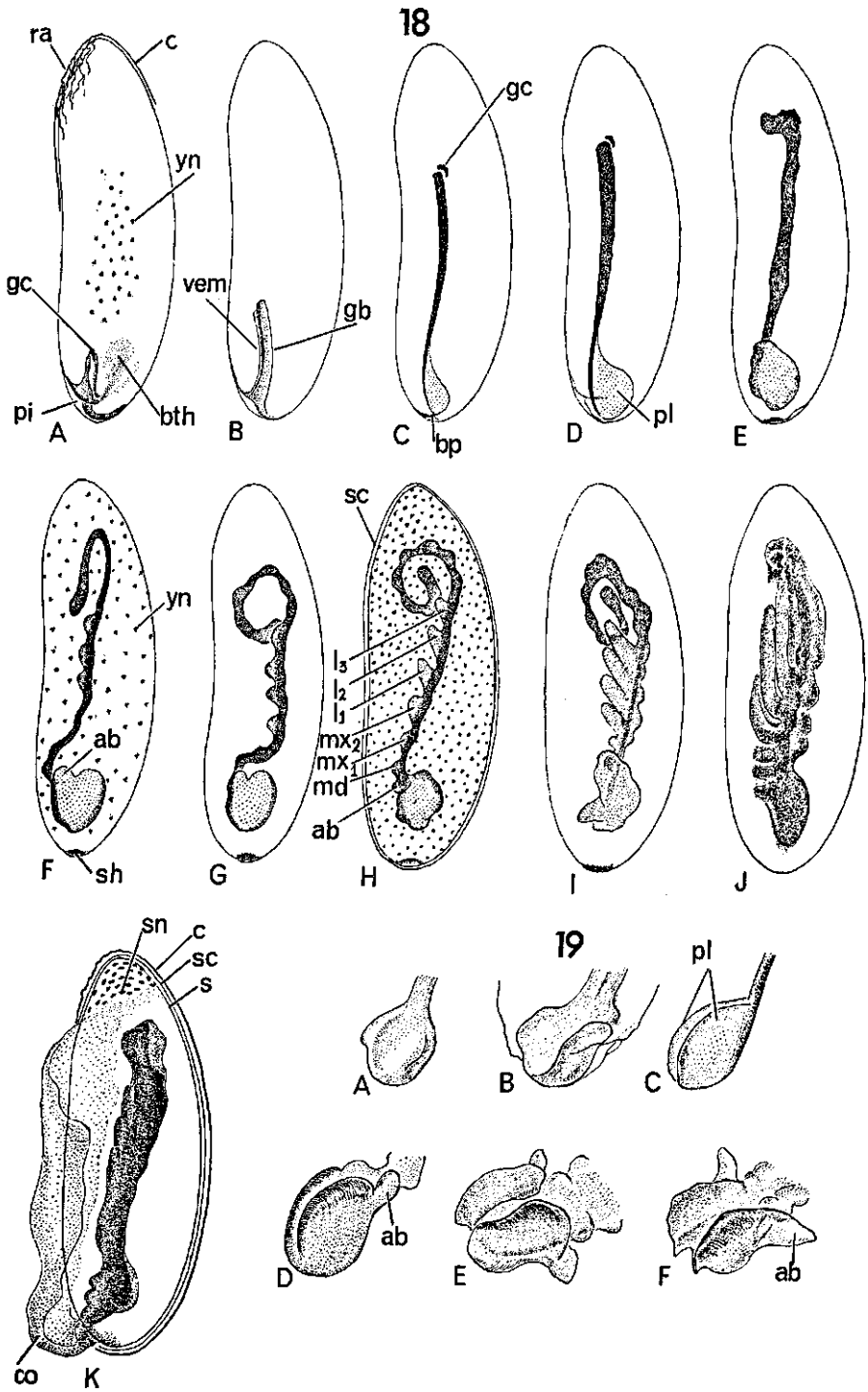


Fig. 18–19. Saldidae, embryogenesis 18. A–K: *Saldula fucicola*, embryogenesis before revolution, lateral view; A: invagination of germ band; K: condensed phase, serosal cuticle and chorion partly removed to show the extent of the cephalic organ. 19. A–F: *Saldula fucicola*, development of the protocephalon.

earlier than the transverse metameric furrows. The primordium of the stomodaeum appears simultaneously as a pit-like invagination, even before the labral swelling becomes distinct. The lateroventral outgrowths indicate that the ventral side of the germ band faces the fore side of the egg. The completely invaginated germ band (fig. 18F, G) has a circular caudal flexure ventrally and a distinct bend between the protocephalon and the protocorm. This posture is soon remodelled into a more regular ʔ -shape (fig. 18H).

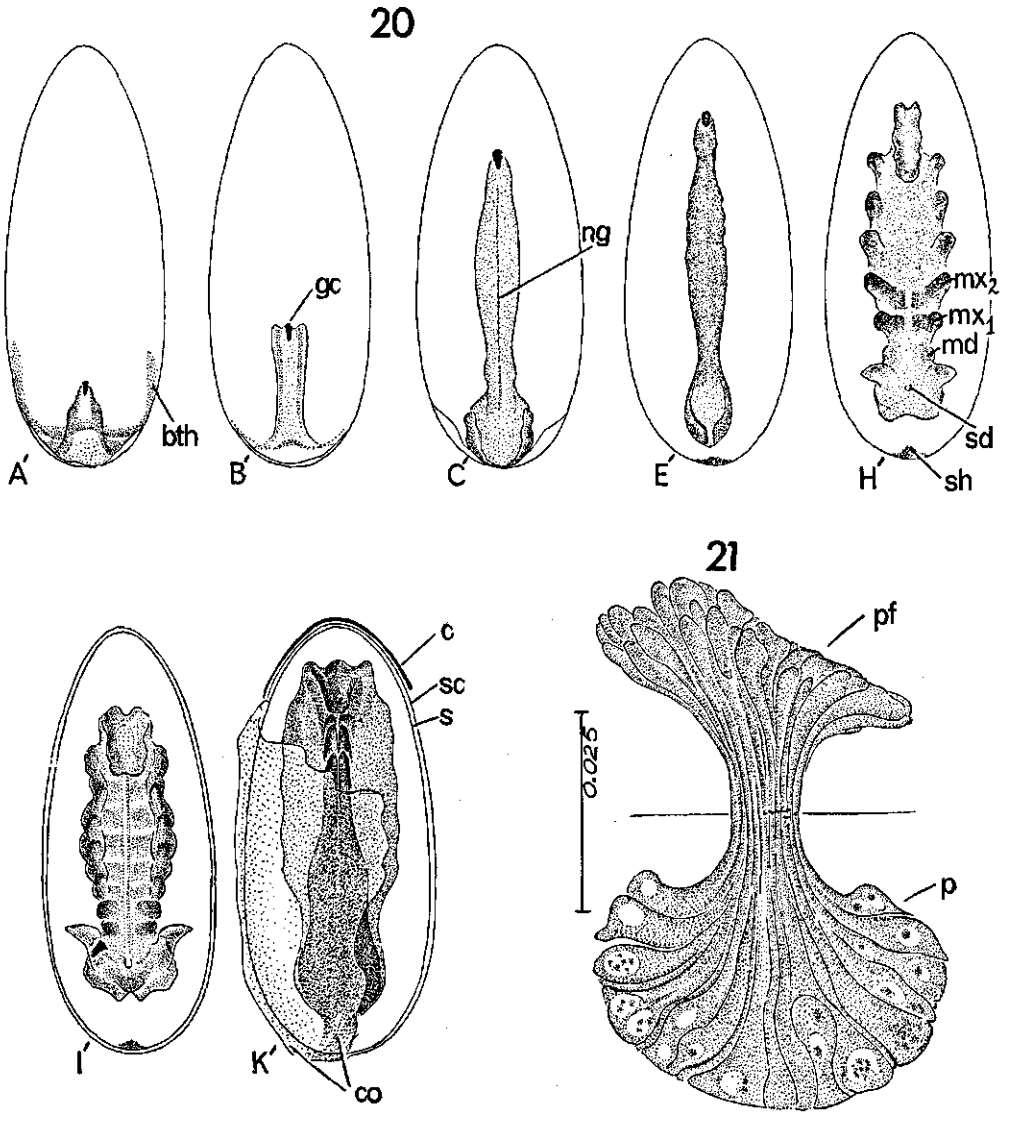


Fig. 20–21. Saldidae, embryogenesis 20. A′–K′: *Saldula fucicola*, embryogenesis before revolution, fore side of egg; stages similar as those correspondingly labelled in fig. 18. 21. *Salda littoralis*, pleuropodial gland, just before the revolution of the embryo.

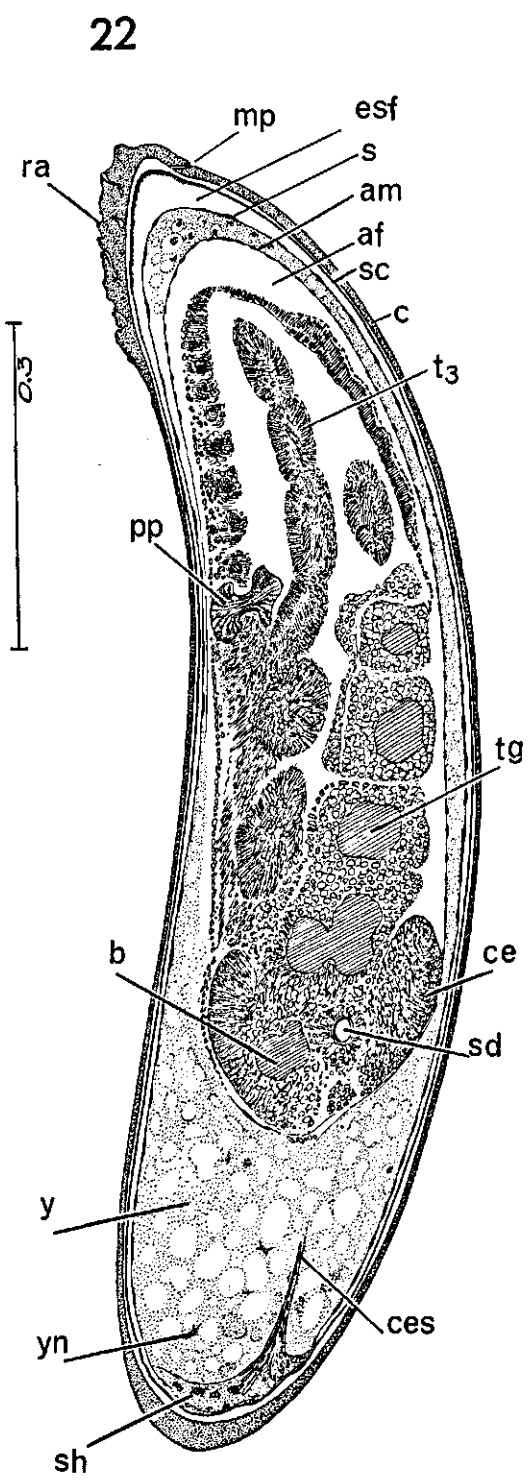


Fig. 22. Saldidae, *Salda littoralis;* slightly oblique, dorsoventral section of diapausing egg.

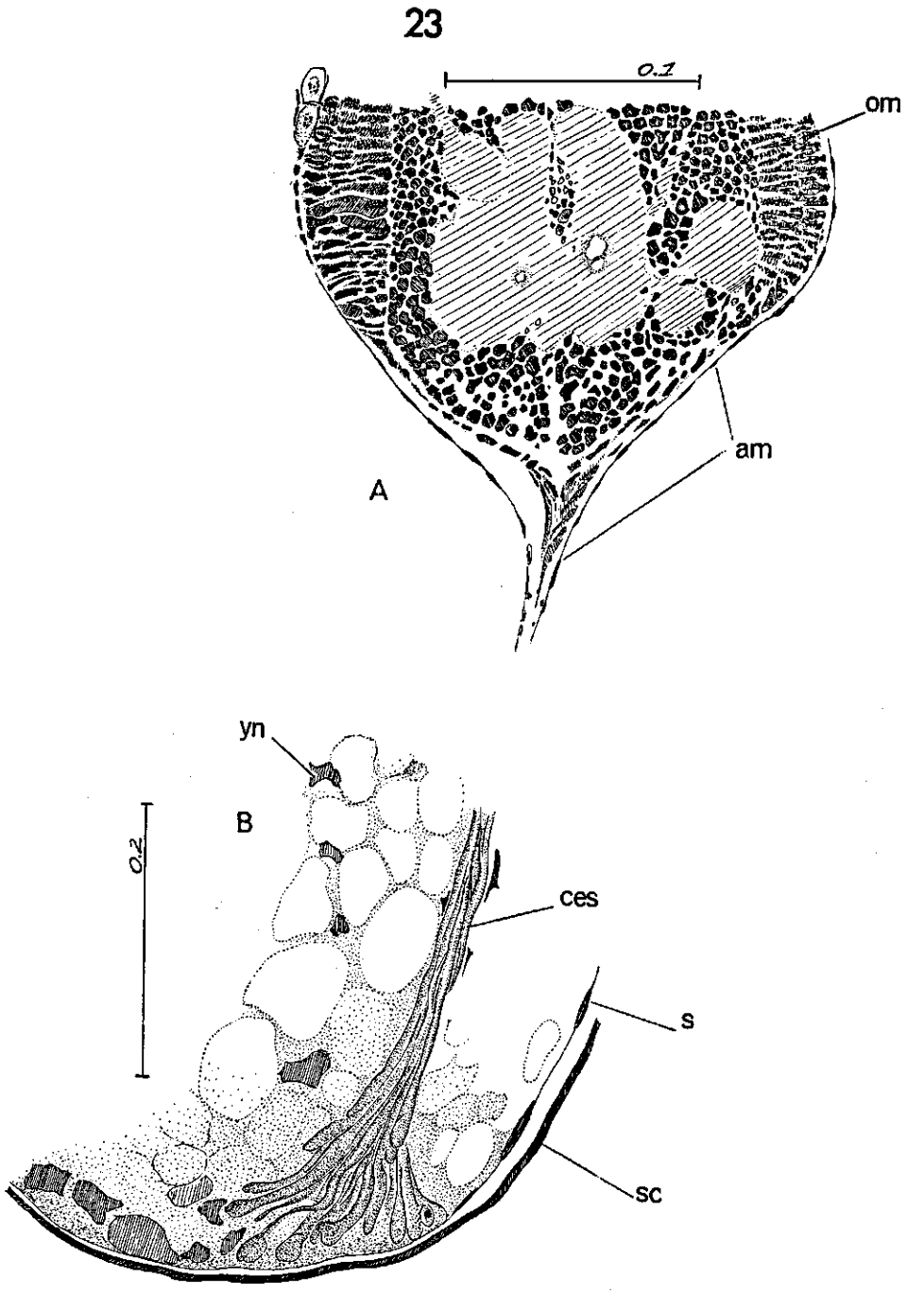


Fig. 23. Saldidae, *Salda littoralis*, diapause; A: base of cephalic strand; B: penetration of cephalic strand in serosal hydropyle.

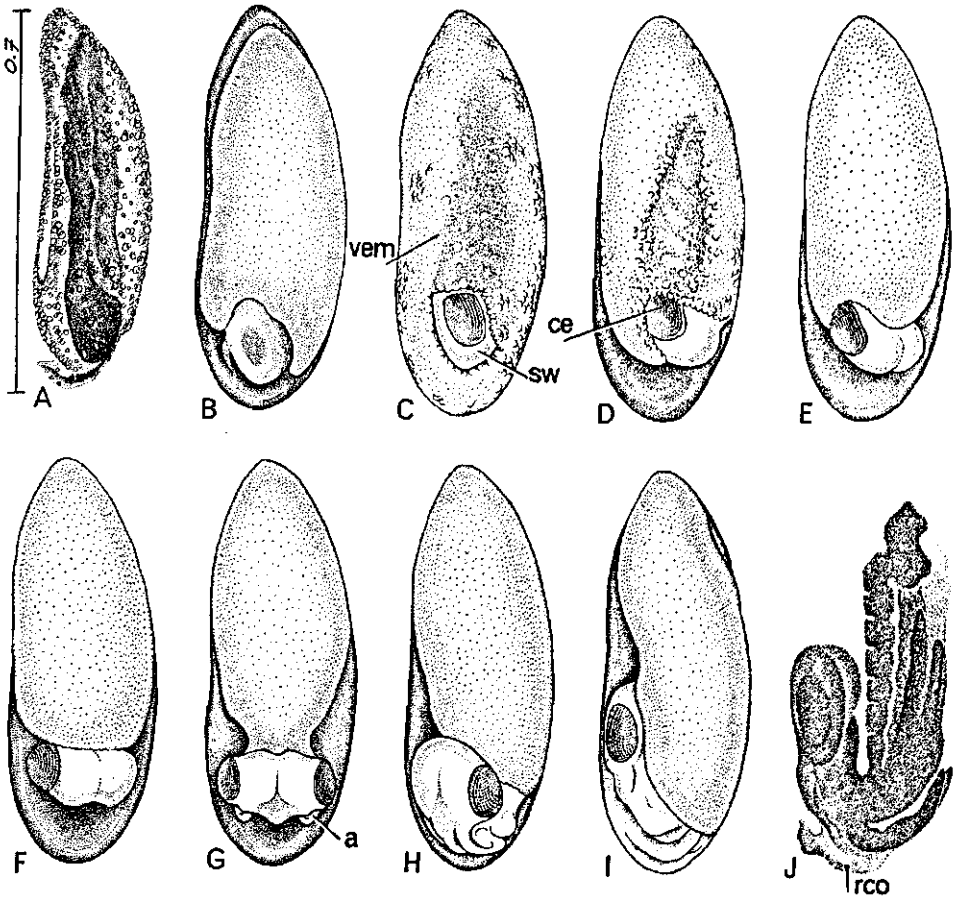


Fig. 24. Saldidae, embryonic rotation and start of revolution, left lateral view; A–I: *Saldula fuscicola;* J: *Chiloxanthus pilosus.*

It is during this remodelling that the serosal cuticle is formed. The content in the egg with only the chorion punctured cannot now be stained by borax carmine, since the serosal cuticle is impermeable to it. The total dimensions of the egg increase considerably during the latter three phases. The internal pressure and the serosal cuticle make the egg firm. Later steps until blastokinesis are the reflexure of the head region and the elongation of labial and trunk appendages. The whole embryo 'condenses'; the legs contract closely against the mid-ventral line. The entire external morphology, especially of the head, of the embryo is difficult now to visualize (fig. 18K, 20K'). In the preceding phases the formation of the cepahlic lobes and antennae and their respective positional changes had already become clear (fig. 19). In contrast to other heteropterans, the antennal buds of the saldid embryo point out from the side of the head. Rotation of the embryo is now imminent. Before dealing with this process, we must refer to other phenomena which will later be shown of great im-

portance in taxonomy. During condensing of the embryo, the whole of the large eye discs become dark red. Moreover the eye-elements are quite well demarcated. In sections, each ommatidium is recognizable and has the cone and retinal cells, although they are not yet wholly differentiated and lack a corneal lens. But the complex larval eye is almost completely differentiated before revolution, a most unusual condition amongst Heteroptera. The next phenomenon to be mentioned is intriguing although we were not able to solve unequivocally its real nature and function. From phase E onwards (fig. 18), a circular mass of thickened serosal cells is seen at the caudal pole of the egg. From its location and structure, this cluster represents the hydropyle. In the condensed phase (fig. 18K), the frontal region of the head is connected with this cushion of serosal cells. The connective strand goes across the serosal cuticle and extends into a substantial layer of tissue below the chorion. This sheet reaches its greatest thickness on the fore side and the dextral side of the egg, fading out towards the other side and the anterior pole. The lobe becomes disconnected from the embryo

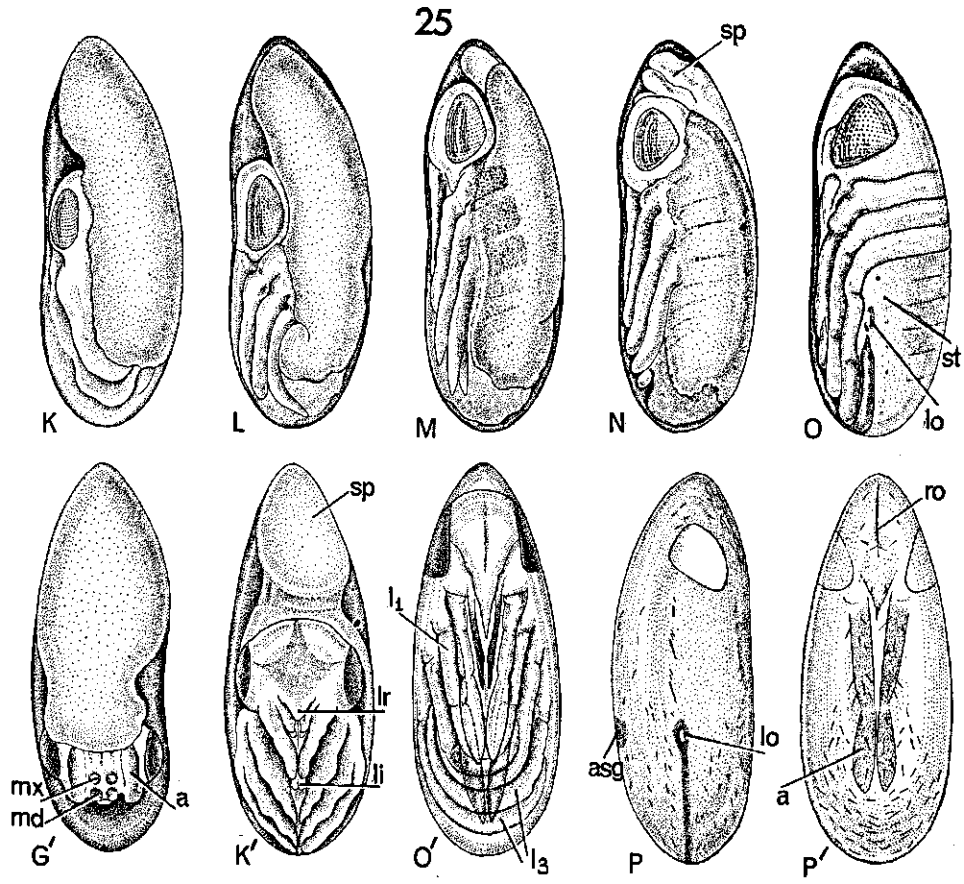


Fig. 25. Saldidae, completion of revolution, uptake of yolk, pose of full-grown embryo. K–P′: *Saldula fucicola;* K–O: as seen in submerged eggs; P,P′: eggs in dry conditions; G′: right view of G; K′, O′: fore side of stage K and O.

before blastokinesis and it persists for a time after the latter process is finished. The original hydropylar cells, however, are carried on by the retracting serosa during revolution. The study of sagittal serial sections of eggs in the condensed stage did not adequately clarify the origin and histology of the cephalic structure. We had only a few sectioned eggs of *Salda littoralis*. These eggs were in diapause and the embryonic growth appeared to be arrested in the 'condensed' phase. In these preparations the head of the embryo too is connected with the serosa, but the connective strand has probably not yet penetrated the serosal cuticle (fig. 22, 23). Although the interpretation of these few sections cannot be conclusive, it seems that they are cells of the embryos

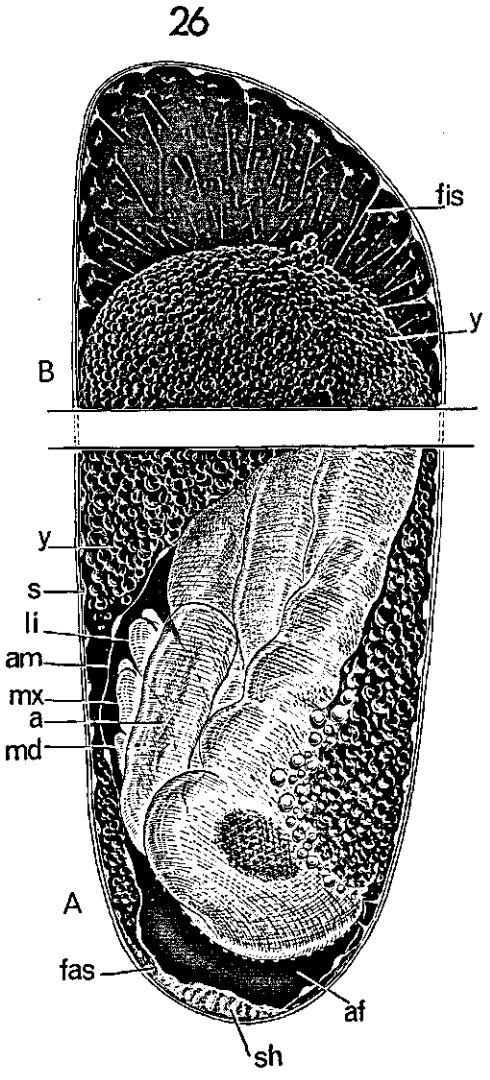


Fig. 26. Saldidea, *Chartoscirta cincta*, shortly before revolution; A: fusion of amnion and serosa B: anterior part with contracted yolk system, stage somewhat later as A.

head region which are extremely elongated to meet the serosal cells. These prolonged cells with their nuclei in the proximal half, are arranged in a cylinder with an open lumen. This lumen seems to go some distance into the cephalon till it is close to the brain. Around the basal half of the protruding bundle the amnion is pushed outwards. The amnion is probably perforated by the cephalic strand and the opening thus made is closed again afterwards, when the connection between strand and head is broken. This supposition is based on the fact that, later on, the rupture of amnion and serosa, incipient to blastokinesis, appears to occur in the normal way. The account given here of the cephalic strand and outer serosal lobe is only a rough assessment for the taxonomist's use. It merits more detailed study by embryologists and physiologists. Its function is probably as an auxiliary device for water uptake. The saldid egg can pass successfully through embryonic life and hatching procedure when placed under water. The total time of development is as long as the incubation period in a humid atmosphere. However, this also accounts for amphibicorisous eggs, but the latter lack such an embryonic cephalic organ. On the other hand, eggs of true waterbugs, which absorb large amounts of water, have one restricted serosal hydropyle. The strand-like device appears to be characteristic only for Saldidae and one might think that its growth out towards the subchorionic region may have something to do with uptake of oxygen from an extensive area of the chorion.

Blastokinesis

Beginning with this phase of development, the progress in embryonic life has been studied on submerged eggs *in vivo* (fig. 24). At the commencement of blastokinesis the yolk becomes retracted from the posterior pole so far that the head of the embryo emerges partly free out of it. Only a longitudinal strip of yolk remains, covering the ventral side of the head. The embryo now begins a 180°rotation around its longitudinal axis. The turning movement is always in the same direction, clockwise when seen from the anterior pole. Half way through the rotation, which is complete in about a quarter of an hour at room temperature, the yolk is seen to be further constricted around the neck region of the embryo. Just before the completion of rotation, the embryo sinks out of the yolk and, shortly afterwards, revolution begins. The embryo moves head first around the lower end of the egg to the anterior pole and its ventral side thus becomes conterminous with the fore side of the egg.

In fig. 24, the mass of yolk has been drawn as a more or less static body. The process of blastokinesis can be investigated continuously in more detail under high power (160 ×) and with transmitted light. Such observations show that, before the movement of the embryo, the serosa-yolk system is very active. At the anterior pole, the serosa contracts and loosens itself from the serosal cuticle. Its shrinking causes the yolk to be compressed. Next the serosa regains its original position but the yolk body remains condensed. Initially the peripheral yolk globules remain connected with the serosal cells by means of strands, cytoplasmic filaments originating from the latter (fig. 26B). It may be that the yolk retraction initiated by the serosa increases the pressure against

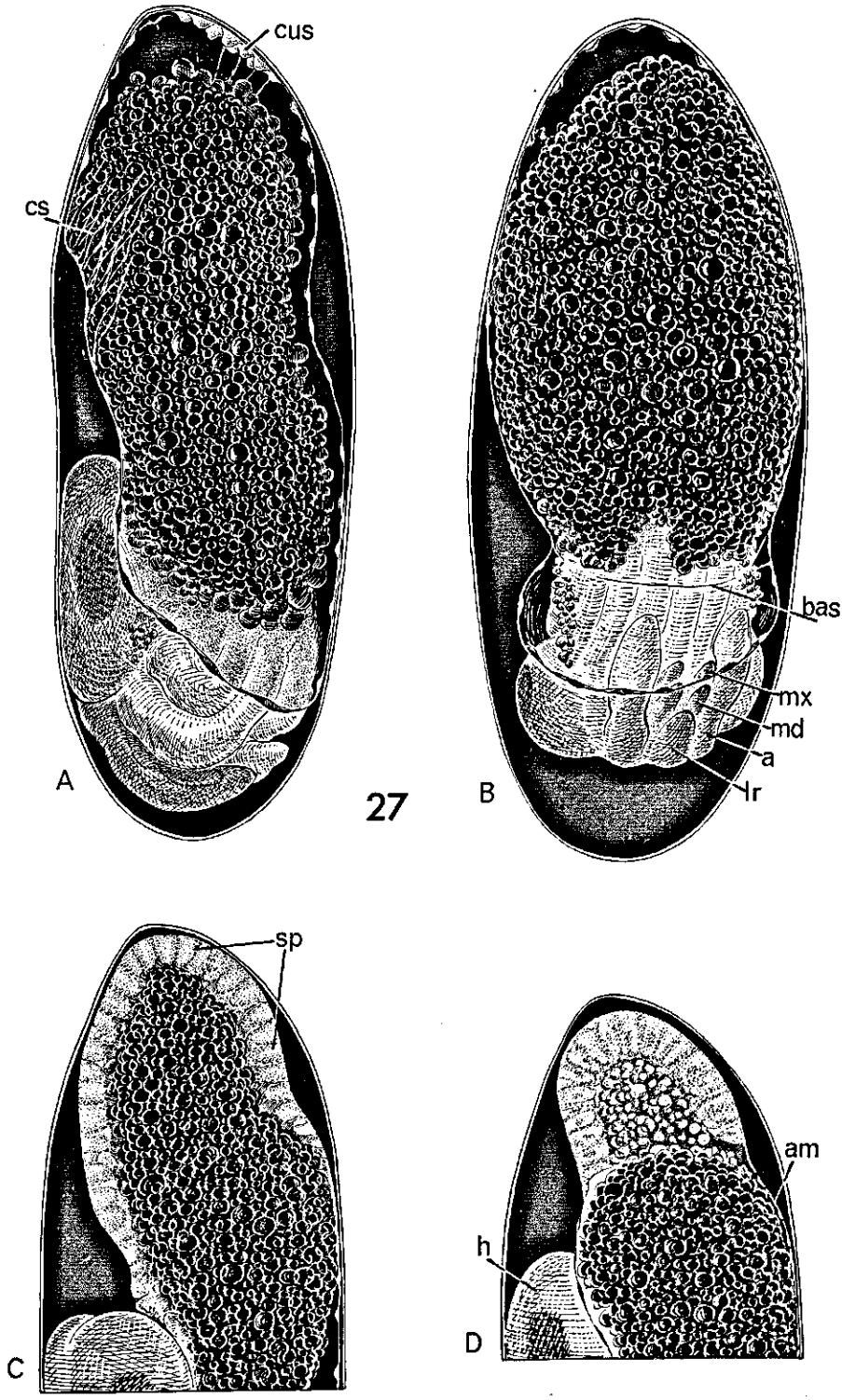


Fig. 27. Saldidae, revolution and formation of serosal plug; A–D: *Saldula fucicola;* A, C, D: left lateral view; B: aft side.

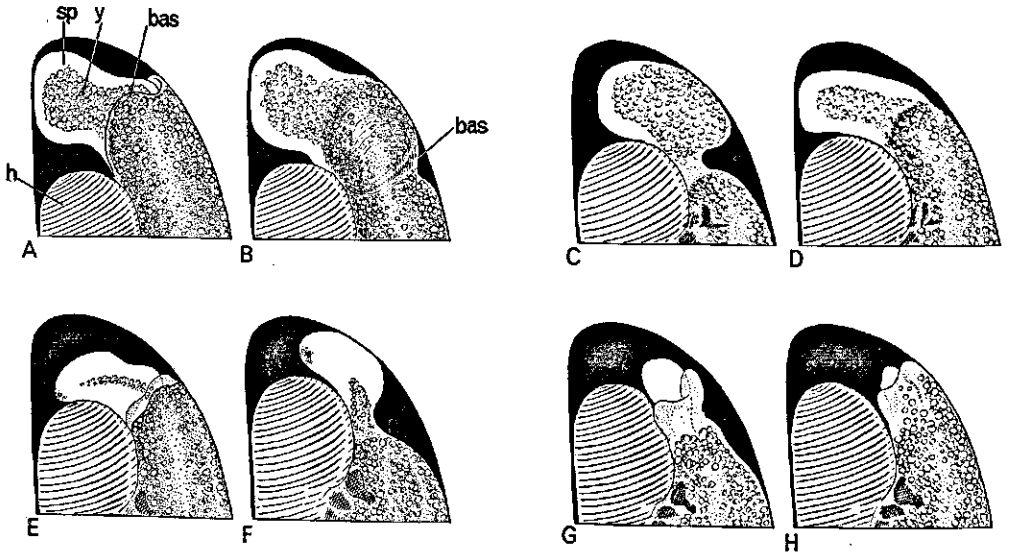


Fig. 28. Saldidae, pulsations of serosal plug resulting in the formation of the secondary dorsal organ (see text); A–H, *Chartoscirta cincta.*

of the final involution of the serosa within the amnion. The method employed is very characteristic and can be described as a series of extra-embryonic pulsations. Let us start filming the process in the *Chartoscirta cincta* egg in the period after six hours, when the beats follow in more rapid succesion. Estimates of time refer to one observed individual egg only. The serosal plug fits in a weak excavation of the anterior end of the amniotic cell layer (fig. 28A). Consequently the plug is thinner and the enclosed yolk is less dense than in the amniotic sac. The exterior border of the fold (fig. 28, bas), apparently representing the limit between amnion and serosa, is provided with large cells. Especially along the head region these cells are seen in profile to be coniform. When the next pulsation starts, the situation shown in fig. 28B quickly follows that in fig. 28A. The amnion-serosal borderline is contracted and has shifted towards the posterior, thus flattening out the serosal fold. This situation is maintained for some minutes. Then the junction of the envelopes relaxes very slowly. The dorsal constriction, seen from the side, flows out backwards in such a way that it is transmitted wave-like along the amnion. It was not determined whether this wave originated from subsequent contraction of the next amniotic cells or whether it was due to transport of fluid pressed backwards by the relaxing junction. However, contraction and the wave result in a pressure on the yolk column and consequently upon the embryo as a whole. After some minutes, the starting-point is readjusted. The situation is as in fig. 28A, but the embryo's head has reached a slightly higher level. After five minutes the contractive beat and slow relaxation begins anew. We pass over three pulsations and pay attention to the next one (fig. 28C). The incision made by the shrinking amnion-serosal junction grows deeper and proceeds at visible speed. The transformed

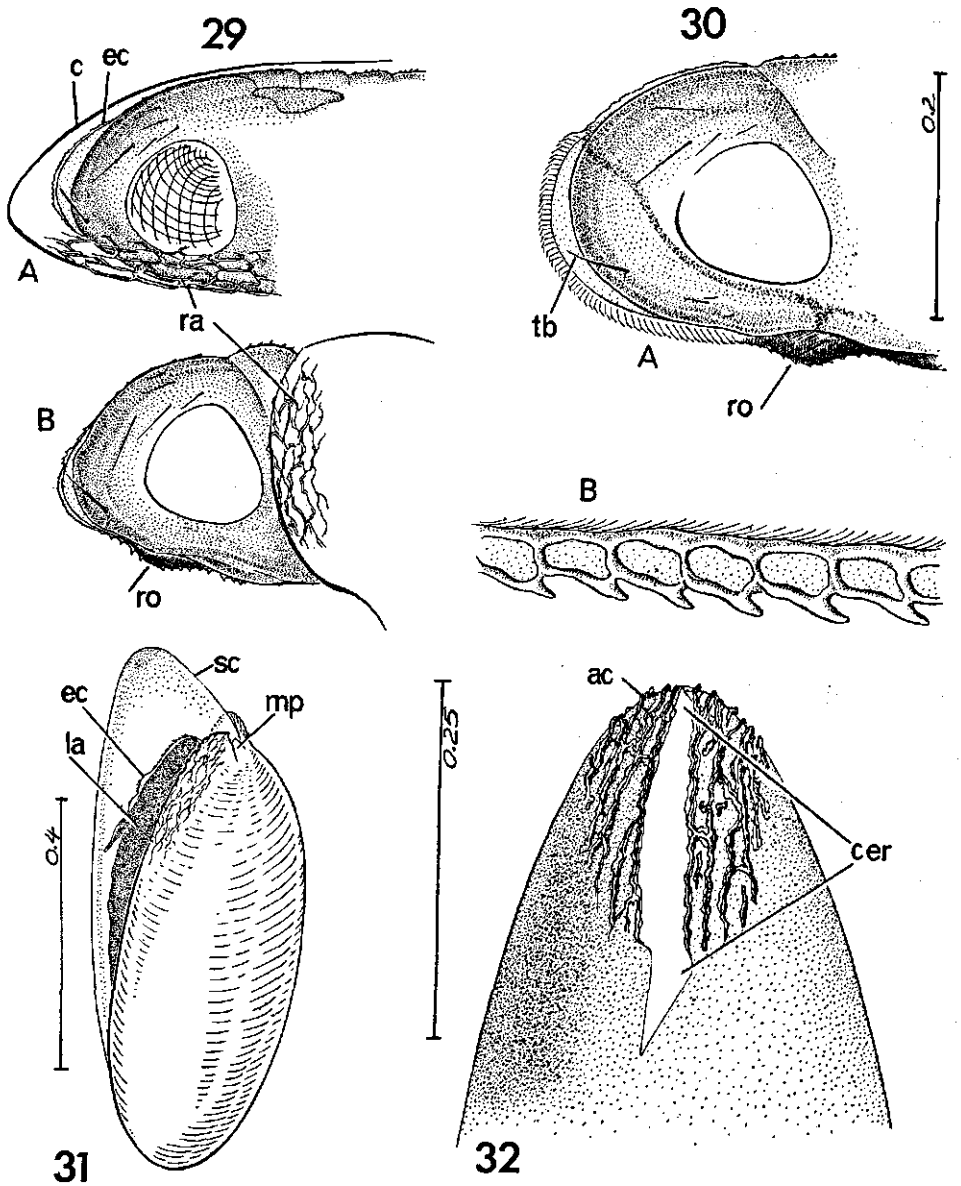


Fig. 29–32. Saldidae, structures concerned with hatching 29 *Chartoscirta elegantula*, anterior part of egg, lateral; A: before eclosion; B: after fracture of chorion and serosal cuticle. 30. *Chiloxanthus pilosus;* A: head of prolarva dissected from the shell; B: part of egg-burster. 31. *Saldula palustris*, shell artificially opened. 32. *Salda littoralis*, vacated shell.

serosal plug is loosened from the serosal cuticle, its yolk content flows out of it into the amniotic sac and the embryo's head is pushed slightly but unmistakably upwards. The releasing phase (fig. 28D) causes part of the yolk to flow back again and the serosal plug to straighten out over the head capsule. The latter on its turn sinks back again by

this process, thus making only partial use of the forward movement just gained. For the next half an hour, contractions become even more frequent and intensive. After that time they become less frequent, but their effects are radical. The situation as given in fig. 28E, is choosen now as the starting-point. This stage is reached about one hour after the beat noted in fig. 28A, B. The serosal plug is flattened, so that the cavity enclosed by the serosal pad is severely restricted and little yolk is retained in it. The next contraction pulls the plug far back and squeezes the head to such an extent that it moves forward perceptibly. The result is that on release, the yolk is completely pressed out of the plug, since the inner margins of the opposite cell layers touch each other and the plug is sunk into the amnion for one third of its length. The next effective beat is not for at least twenty minutes. In one single stroke the plug is swallowed (fig. 28G, H); only its top protrudes out of the amniotic sac and its walls are folded double within the latter. Some later beats accomplish the complete invagination of the serosa and provisional dorsal closure by the amnion. Meanwhile the sides of the definitive body wall have made progress in growing upwards, both halves meeting each other first in the caudal region.

The mechanism described above leads to a threefold effect: elimination of the serosa, filling in the mass of yolk into the upgrowing body walls and facilitating the passive forward movement of the embryo. We studied blastokinesis and serosal intake in ten saldid species of five genera: *Chiloxanthus*, *Saldula*, *Halosalda*, *Chartoscirta*, *Salda* and found no essential difference. Of several hundred eggs, only one egg of *H. lateralis* behaved abnormally; its embryo after blastokinesis faced the aft side of the egg.

When observations had to be interrupted for 15 hours or longer, eggs were transferred from room temperature to +4°C, and *vice versa* when continuing the studies. Only embryos at a stage preparatory to blastokinesis were sometimes injured by this temperature shock. With abrupt cooling after the start of revolution, processes were normally resumed and completed after raising the temperature. The diapause of the embryo, which is passed in the condensed stage before blastokinesis, has been found to be obligatory in *S. littoralis* and facultative in *S. marginalis* and other species (see further p. 297).

1.1.6 Posture of the fully grown embryo and the hatching mechanism

In eggs exposed to air the prolarva ready for hatching is recognizable through the shell by the large dark eyes, the antennae and the darkened hairs (fig. 25P, P'). Dorsally, an orange spot marks the single abdominal scent gland. An oval ring on the sides represents the larval organ if present (COBBEN, 1957). The mediofrontal egg-burster and the outline of the legs become visible when the egg is submerged. The position of the individual appendages of the prolarva reveals some unexpected aspects of great interest; other families were also checked and will be dealt with below. The arrangement of the extremities in Saldidae follows a reasonably constant pattern (fig. 25O'). The antennae lie superficially and converge with the last segment adjacent to one another. The anterior legs run laterally and then pass beneath the antennae

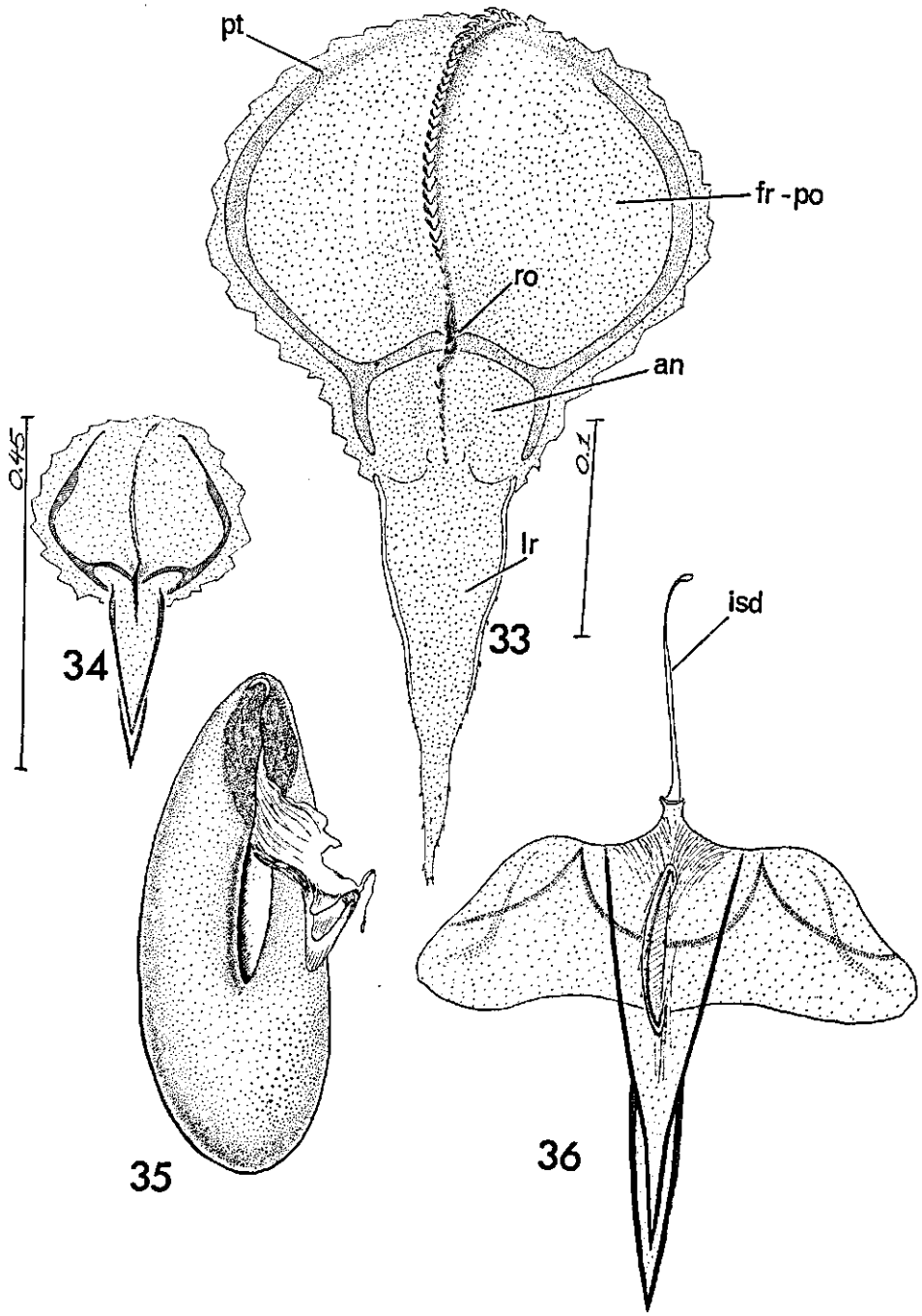


Fig. 33–36. Saldidae, structures concerned with hatching 33. *Saldula palustris*, cephalic part of embryonic cuticle *in situ* showing structure and position of the ruptor ovi. 34. *Salda littoralis*, the same. 35. *Saldula saltatoria*, vacated shell with cast embryonic cuticle. 36. *S. saltatoria*, ruptor ovi as revealed by the cast embryonic cuticle.

converging in a straight line posteriad. Both fore legs and antennae cover the labium for the greater part. The maxillary and mandibular stylets are still fairly short and rest upon the labium, completely exposed. The middle and hind legs lie superficially and are behind the antennal apices flexed parallel to the curve of the posterior pole of the egg. There are four different patterns of intertwining which can be assumed by these two pairs of legs. The patterns are presented in the following scheme showing the legs sequence behind each other.

←2L	2R →	2R →	←2L
2R →	←2L	←2L	2R→
3R →	←3L	3R →	←3L
←3L	3R →	←3L	3R →
A	B	C	D

2R → means: the distal end of the right middle leg pointing to the right as observed in ventral view. ←3L represents the curvature of the left hind leg. Ninety-four embryos of *S. saltatoria* were compared, originating from one small adult population and reared under similar conditions. As regards the flexing of the legs 33% of the sample behaved as A, 46% as B, 8% as C and 13% as D. Thus, the combinations A and B in which the legs 2 and 3 of one side run side by side tends to occur markedly more often than C and D with regularly alternating legs. Moreover there are slightly more B and D, than their mirror images. This indicates that there is a slight polarity in the bilaterally asymmetrical folding of the legs. Flexing of the legs does not occur until some time after revolution is complete, so that the polarity does not seem to be connected with the direction of rotation before revolution. Twenty-two eggs of the same population were abruptly cooled several times. Two embryos behaved later as situation A, 6 as B, 2 as C and 6 as D. The remainder six embryos were anomalous and had twisted limbs. Though numbers are too small for a final conclusion, unfavourable conditions seem to effect a proportional shift in the patterns considered.

The acts preparatory to eclosion, which we have observed only in submerged eggs, start several hours before the chorion finally breaks. The clypeo-frontal part of the head begins to throb steadily, the rate corresponding with the heart beat. Independent from this beat is the movement of the most anterior rounding of the head and of the vertex which vibrate simultaneously and vigorously. The apex of the head performs notable 'sniffing' action, which is maintained after the chorion breaks when the larva is still within the embryonic cuticle. This action is therefore most probably a symptom of swallowing of water. We did not closely compare the behaviour of submerged hatching with that of eggs exposed to air. Saldidae form an ideal group in that they have almost transparent shells and in that they incubate and hatch in both media equally easily. The effect of the presumed water or air intake could be reflected in different eclosion behaviour. Besides the local movements described, there is a third category of internal movement which now and then sets the whole insect into violent vibration and turbulation.

The forces involved serve to drive the fluid contents into the region of the head,

aided by the highly distended gut which shows strong anti-peristaltic convulsions. These latter activities occur periodically, accompanied by trembling of the body-walls and contractions of the coxae. At those periods it is clearly seen that the larva exerts pressure on the anterior egg-pole.

The shell splits open along a longitudinal median line, reaching from the anterior top over the fore side up to the posterior half (fig. 35). Anteriorly it is forked, embracing the micropylar area (fig. 4). It is obvious that this line is not actively cut by the ruptor ovi. It represents a line of weakness, because the shell splits always in the same way when weakened in potash. Structurally, this line is not recognizable in the intact chorion. In eggs stored in diluted alcohol internal pressure sometimes causes the shell to cleave, but the tough serosal cuticle remains unbroken (fig. 31). This envelope is transparent throughout but dull at the anterior pole. A black spot sometimes marks the area where it has been contiguous with the micropyle of the chorion. Though we have observed the eclosion several times it appeared us impossible to settle exactly which of the two egg-envelopes are opened at first. From what we will learn in Hydrocorisae it seems likely that first the chorion splits open by general internal pressure. Next, the serosal cuticle should be cut open by the blade of the egg-burster. This egg-burster is part of the embryonic cuticle and consists of a longitudinal ridge running from the base of the labrum up to the vertex (fig. 29, 33). The ridge bears one row of forward-pointing small teeth which are 'unicellular' vertical outgrowths (fig. 30). The actual cutting blade is a more solid extension of the ridge in the clypeal region and also is provided with some minute teeth. The blade is crossed by a weakly sclerotized strip which in turn is connected with longitudinal strips on each side. These lateral strips run in a bow along the inner margin of the eye and converge again in the dorsal mid line further towards the posterior. The pathway followed corresponds with the forks of the epicranial suture of the underlying larva. The area enclosed by the frame above the blade thus includes the frons and postclypeus. The blade and the transverse strip mark the boundary between postclypeus and anteclypeus. The configuration of the cephalic strengthening of the embryonic cuticle is shown in fig. 33, 34. The structure as a whole as well as the location of the blade are important in speculation about its phylogenetic significance in other groups. The structures must be studied *in situ* and not after they have been shed, as the real picture then becomes deformed by folding (fig. 36). The armature mentioned varied only slightly among the species studied (*cf.* fig. 29, 30, 33, 34).

The blade is closely pressed against the definitive larval skin, but the envelope bearing the ridge over the frontal region runs separately from the underlying cuticle. A thin layer is left open, probably fluid-filled. In other families this space is blown out to voluminous proportions and acts as a buffer in eclosion. Except on the head, the embryonic cuticle is a filmy transparent pellicle ensheathing the body and limbs. High magnifications show a fine transverse scaly sculpturing, arranged in broad metameric bands and giving the protruding prolarva a better grip against the smooth serosal cuticle. The embryonic cuticle splits open anterio-dorsally and is left extending halfway out of the shell in air, but almost completely out of the shell under water.

1.2 Leptopodidae

We studied released eggs of *Leptopus marmoratus* (origin of material: Italy) and ripe ovarian eggs of two other species. No descriptions of the leptopodid egg are available in the literature. The egg of *Leptopus marmoratus* is of a very uncommon type for Heteroptera and resembles a scale insect. It is extremely well adapted to be placed against dry bare stones in that it is strongly dorso-ventrally flattened (fig. 37C), its whole aft plane being in contact with the substrate (fig. 37A). The length and width amount to 0.9 and 0.6 mm, respectively. The width in the third plane is only about 0.3 mm. Since the female's abdomen is rather soft and flexible and since the tip of the ovipositor is curved downwards in another species, egg deposition in this family may well be of the saldid type (see p. 10) although the ovipositor in *L. marmoratus* is vestigial. The chorion, only 2 μ thick, remains soft and highly flexible during the whole of incubation and the egg is difficult to loosen from the stone without damage. It looks creased especially along the marginal outline, since the fully grown embryo does not completely fill the egg. Thus the sides can be pressed against small irregularities and fit surprisingly well in small rough crevices which the female selects for oviposition (fig. 37A). The chorion is white wax-like and appears faintly honey-combed by large shallow hexagonal pits.

Despite its unusual outward appearance, the chorion is saldid-like in some of its finer structures. There is one micropyle only at the anterior pole and of the saldid type. The chorion is densely covered with pores and has a network of ridges just as in most Saldidae which have been called, on p. 20, air clefts. We found these structures in *Leptopus* only after the few available eggs were sectioned, so the extent of the reticulated pattern could not be ascertained. The chorion, despite its flexibility, seems too brittle for microtome sections. Pieces are broken off and those mounted as horizontal fractions show ridges and areas enclosed by them very much like those of *Chartoscirta* (fig. 11). Cross sections indeed show the ridges to be cleft up to the open inner layer of the shell. Physiologically there must certainly be fundamental differences between the *Leptopus* and the saldid egg. Leptopodid eggs which are laid in dry conditions must have developed a water-sparing mechanism. This accounts most probably for the thick serosal cuticle which is as thick as the chorion, 1.0 μ. On the other hand, there is no trace of hydropic structure either in the serosa or in the shell. The fact that the fully grown embryo does not occupy all the available space within the egg covering is ascribed to the failure of water uptake from the environment. The dry circumstances in our rearing vessels certainly prevented water absorption by the eggs, which were deposited some 15 cm above moist soil level underneath brick fragments, heated from above by an electric light. The original habitat of the species was dry heaps of stones.

Because of the non-transparency of the chorion and the scarce material we have not studied embryonic life continuously. This is an unfortunate gap in our knowledge. It would be of great interest to see which phylogenetic characters are preserved and which are affected by the spacious conditions within the egg envelopes. The posture of the mature embryo shows clear deviations from the saldid type (fig. 39A). The labium

points to one side and all appendages are bundled into one wide loop leaving the venter free. Fore and middle legs lie two by two upon each other, but the hind legs cross and their ends are between the abdominal margin and the insertion of the legs on the opposite side (fig. 39B). The ruptor ovi (egg-burster) is of solid construction and resembles a tin opener (fig. 38); its location corresponds with that of the blade in saldids. The longitudinal median ridge is lacking except for some small pegs close to the shell-opener. The cranial frame is as in Saldidae. Because inner tension is less it is likely that the ecloding embryo is more actively involved in opening the serosal cuticle and

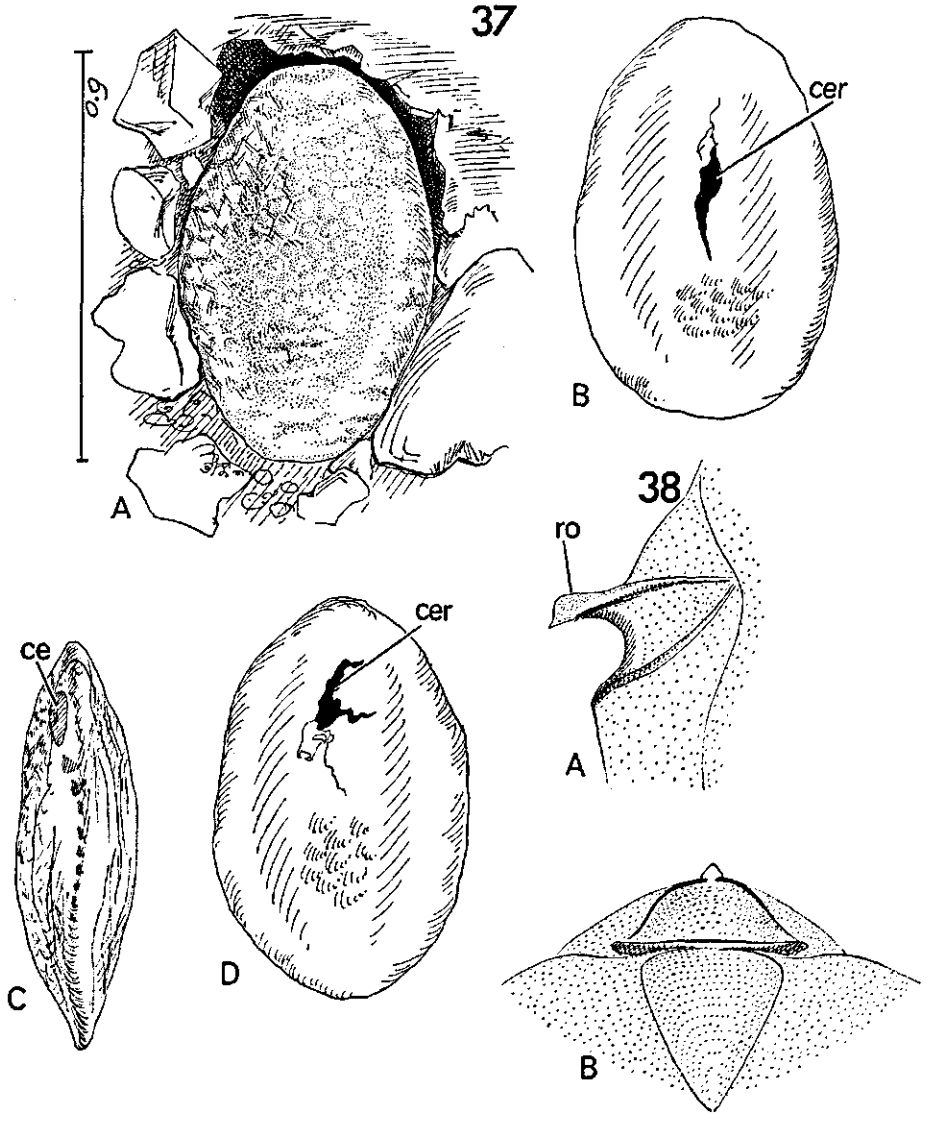


Fig. 37–38. Leptopodidae, *Leptopus marmoratus* 37. A: egg *in situ;* C: lateral side; B, D: vacated shell. 38. ruptor ovi; A: lateral; B: from above.

chorion. The variation in shape and location of the rupture of the shell in individual eggs (fig. 37B, D) indicates the difference in the action of the prolarval head.

ADDITIONAL MATERIAL *Leptopus hispanus* Ramb. (ripe ovarian eggs, origin Greece). General shape of egg is as in the preceding species, but respiratory system is different. As in some *Pentacora* species, the pore canals are much closer together towards the cephalic pole. This high density of the canals is in *L. hispanus* neatly restricted within the limits of a transverse row of hexagons.

Valleriola moesta Horv. (ripe ovarian eggs, origin Uganda). The respiratory system is a more perfected derivation of the condition in the preceding species. Some hexagons consist of a fine meshwork which suggest plastron function. The 'cells' are distributed over three areas of the flat exposed side of the egg (fig. 39C). In all five eggs studied, these three groups of spongy 'cells' were present, though the pattern they formed were irregular and varied between eggs. The only generality found is that the cells in the middle form a transverse band whereas the posterior series form a longitudinal strip. We found the same species of *Valleriola* living on rocky blocks in the river Bandama (Ivory Coast). In contrast to the eggs of *L. marmoratus* which lack plastron structures, *Valleriola* eggs are thus more exposed to the risk of long periods of flooding. The eggs split open along the anterior pole when heated in lactic acid (fig. 39C). It is doubtful whether the natural eclosion rent is along this same fracture in view of the situation in *L. marmoratus*.

1.3 Omania

KELLEN (1960) described and illustrated the egg of *Omania samoensis* from Samoa, It was very large relative to the size of the female and it had a rigid hexagonal patterns was broad in shape with blunt poles and measured around 0.7 × 0.4 mm. The eggs were laid deep in fine crevices in the intertidal rocks. We studied ripe ovarian eggs of *O. marksae* Woodw. from the type locality in Australia. Based on adult characters we believe that KELLEN's species *samoensis* is conspecific with *marksae* and thus the account given here should refer to the egg of the same species. At a magnification of × 700 the chorionic surface appears granulated (fig. 40). Small specks of extending chorionic substance are distributed over the spacious hexagonal fields, except for the rigid ribs. The hexagons are smaller towards the anterior pole where their boundaries become wholly obliterated. The top of the egg is free of any sculpture and contains a single funnel-shaped micropyle similar to that seen in the Saldidae. The shell has no visible pore canals, thus suggesting a solid chorion as in *Aepophilus* which is also intertidal.

The embryology of the species remains unknown. The average incubation period should be 16 days at an ambient temperature of 25 °C. The prehatching stage is figured by KELLEN (o.c., fig. 10). The frontal region is narrow due to the excessively large eyes. Consequently the strengthening frame on the embryonic cuticle is com-

pressed and forms a rather elaborate longitudinal structure. KELLEN's figure does not show clearly to what extent the ruptor ovi proper is developed.

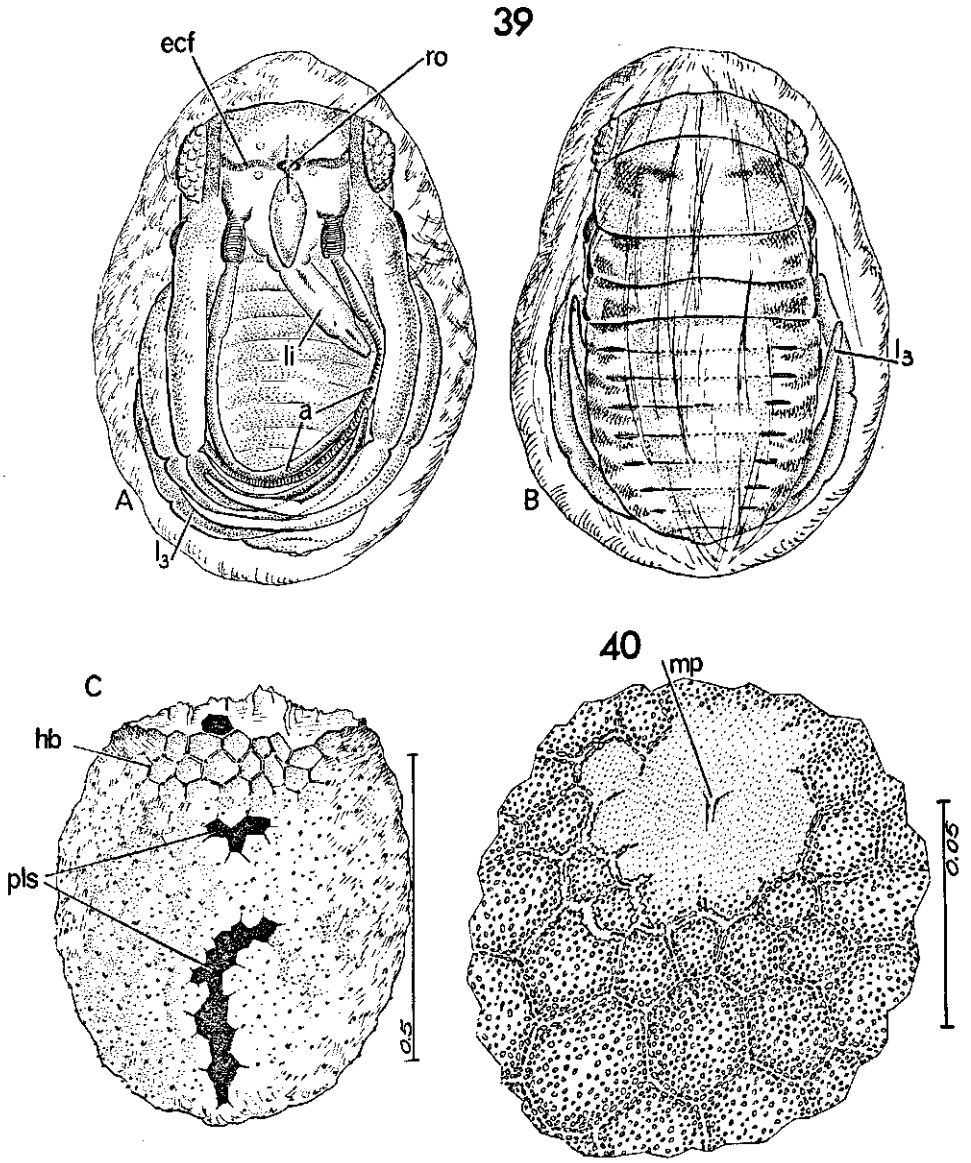


Fig. 39–40. Leptopodidae and *Omania* 39. A–B: *Leptopus marmoratus*, pose of prolarva; A: ventral; B: dorsal. 39C: *Valleriola moesta*, fore side of egg. 40. *Omania marksae*, micropylar area.

2 Structures and biology of the eggs of other families

The eggs of many Heteroptera have been described in the past. The data referring to land bugs were compiled by SOUTHWOOD (1956). This very useful study lists some 330 references. The eggs of water-surface and water bugs have interested many investigators for a long time. The outline and dimensions of the eggs to be treated below, and the method of oviposition will therefore not be described here, but we will refer entirely to the figures. At the end of each heading, earlier descriptions will be listed and necessary comments will be made. In the case of terrestrial groups, however, we cite only the compilation of SOUTHWOOD *(o.c.)* and any more recent data.

The principle areas of our investigation have received little attention in the past. Information regarding chorionic architecture, embryogenesis, polarity and hatching mechanics will be described in detail where such characters assume phylogenetic importance. The terms endo- and exochorion have been avoided, as we found much variation in stratification. At present the homology of these layers is not certain (see 3.1); closer study will be necessary for an understanding of the physiology of the shell in the different groups. All figures of whole eggs (except *Microvelia*) are drawn with the substrate side at the right (shaded) or in case of upright position with the point of attachment directed downward. For reasons given on p. 10 the right profile of the figures is termed aft side, the left profile as the fore side of the egg.

The material originates from the Wageningen area of the Netherlands unless otherwise stated.

2.1 Amphibicorisae

2.1.1 Hebridae

MATERIAL: *Hebrus ruficeps* Ths (living deposited eggs); *H. elimatus* Dr & Cb. (unripe and ripe ovarian eggs, origin: Curaçao, Neth. Ant.); *Hyrcanus* sp. (unripe and ripe ovarian eggs, origin Indonesia).

Hebrus ruficeps

Eggs, surrounded by tough coating material, are laid *in vitro* superficially to or into moist blotting-paper. The method of oviposition has not been observed but judging from the slight downward bend in the tube-like ovipositor it is possible that eggs are released as in Saldidae or Mesoveliidae (see p. 10 and 48).

CHORION The chorion is completely covered with small globules. In cross-section the optical microscope shows a single compact layer of about 3 μ without pores but with a thin outer film. The latter is attached to the globules and is often detached in sections (fig. 43B). This outer layer most probably represents the suprachorionic adhesive coating which is shrunk in fixative. Only one micropyle is present at the anterior pole (fig. 43B), situated in plug-like thickening of chorion, widening externally, projecting forwards some distance along the inner side of the shell as a solid tube of 1 μ diameter.

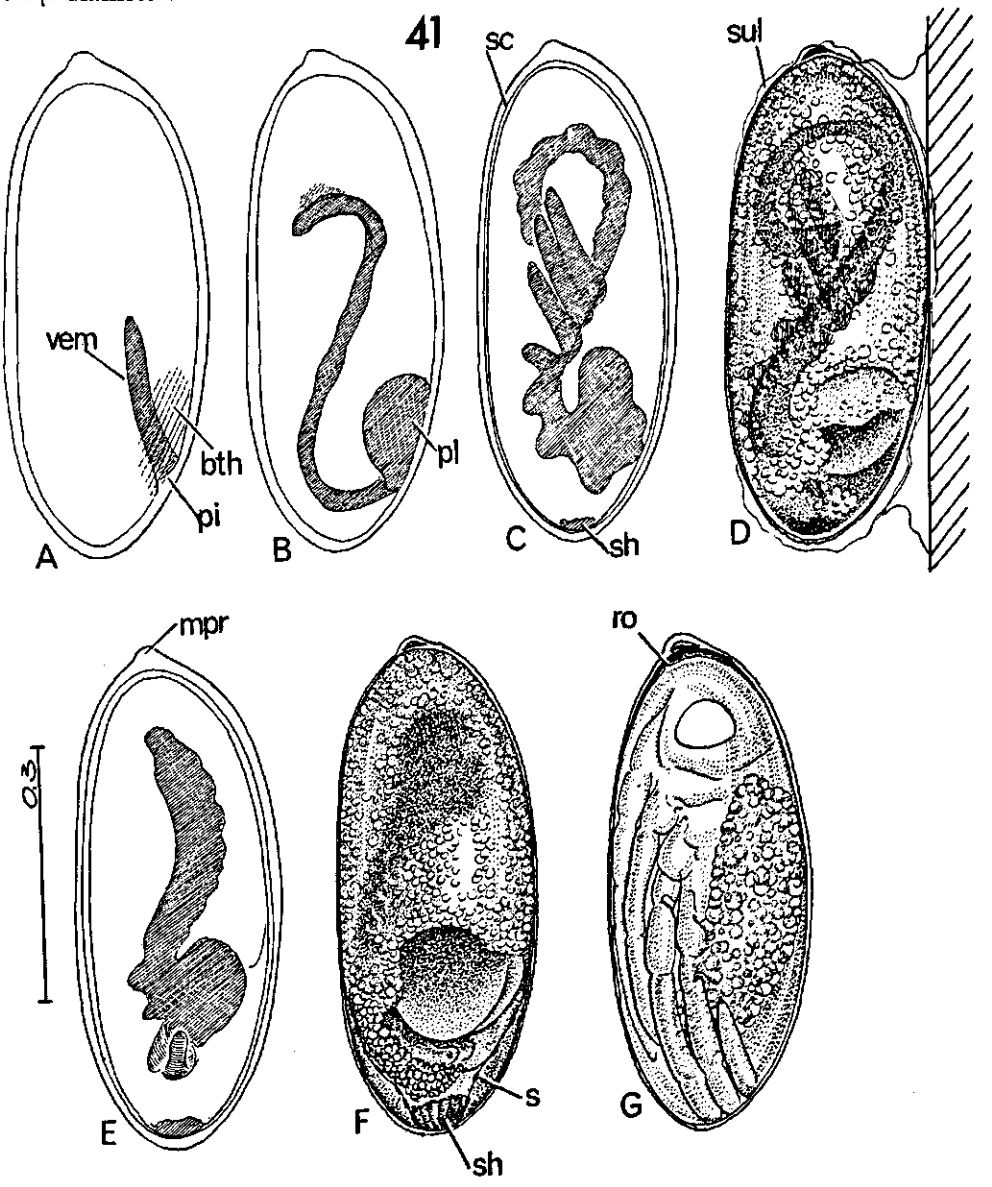


Fig. 41. Hebridae, *Hebrus ruficeps*, gross embryogenesis; D, F, G: drawn from living submerged eggs; A–C, E: germ band fixed and stained.

GROSS EMBRYOGENESIS (fig. 41A–G) The incubation period takes about 12 days at about 22 °C and six and a half days at 30°. Invagination of germ band starts aft of the posterior pole. The germ band is immersed except at the cephalic lobes, with a distinct caudal flexure pointing to the egg's foreside. A weakly defined cluster of material is pushed in front of the involuting tail of the band. A serosal cuticle is laid down and this is not submitted to any darkening later on. A large serosal hydropyle fills up the posterior pole but rises entire with the serosa during revolution (checked in six eggs). The condensed phase of the embryo is marked by the transverse folding of the antennae. Reversion of the embryo occurs along the fore side of egg and is immediately preceded by a 180° rotation. Until just before this rotation, a strand of yolk remains enclosed beneath the head in the edge between serosa and amnion in front of their point of fusion (fig. 41F). Pigmentation of eyes occurs after revolution. In all 24 eggs examined, the chorionic and serosal cuticular hydropyle is repaired with a dark plug after migration of the serosal hydropyle.

HATCHING (fig. 42) Entire incubation and successful hatching are possible when the egg is continuously under water as well when continuously in a moist atmospheric medium. The posture of the fully grown embryo is as figured (fig. 41G and diagram, fig. 279B on page 329). Unilateral polarity in the asymmetrical arrangement of the legs is strongly suggested. Of the 16 eggs checked, only one egg showed the mirror-image. The embryonic cuticle has fine cross-sculpturing throughout, clearly marking the boundaries of three thoracic and ten abdominal segments. The egg-burster is formed by a transverse sclerotized strip with one pointed peg on both sides (fig. 42A, C); rarely there is only a single tooth in the centre of the cross-strip, the latter apparently marking off the anteclypeus from the postclypeus. The further course of the cranial frame-work consists of one offshoot running on each side down to the base of the labrum (fig. 42). On these frames and also on the enclosed median area there are a few fine pegs. The most remarkable details of the embryonic cuticle are two stout bristles on the vertex region (fig. 42B, eco). It was first thought that these bristles belong to the underlying larva itself and that they traverse the embryonic cuticle. Close inspection of four eggs revealed that the outgrowth indeed belonged to the embryonic cuticle. They are lighter-coloured than the larval bristles and do not originate from a pit-like impression. Such embryonic cuticular bristles are thus far unique for Heteroptera. It is hardly conceivable that they play an important role in eclosion. It might be that they represent a preadaptation of the extremely long trichobothria of the free larva. Opening of the chorion occurs simply along a median line.

ADDITIONAL MATERIAL Ovarian eggs of *H. elimatus* show identical chorionic structures with light microscope (fig. 43A). Micrographs indeed revealed the complete absence of an inner meshwork layer and of pore canals (fig. 290). A distinct two-layered structure is also lacking. The external first quarter of the shell becomes darker coloured in stained sections than the rest, but without a clear limit. The innermost face of the shell has a black lining, but it is uncertain whether this represents the rudiment

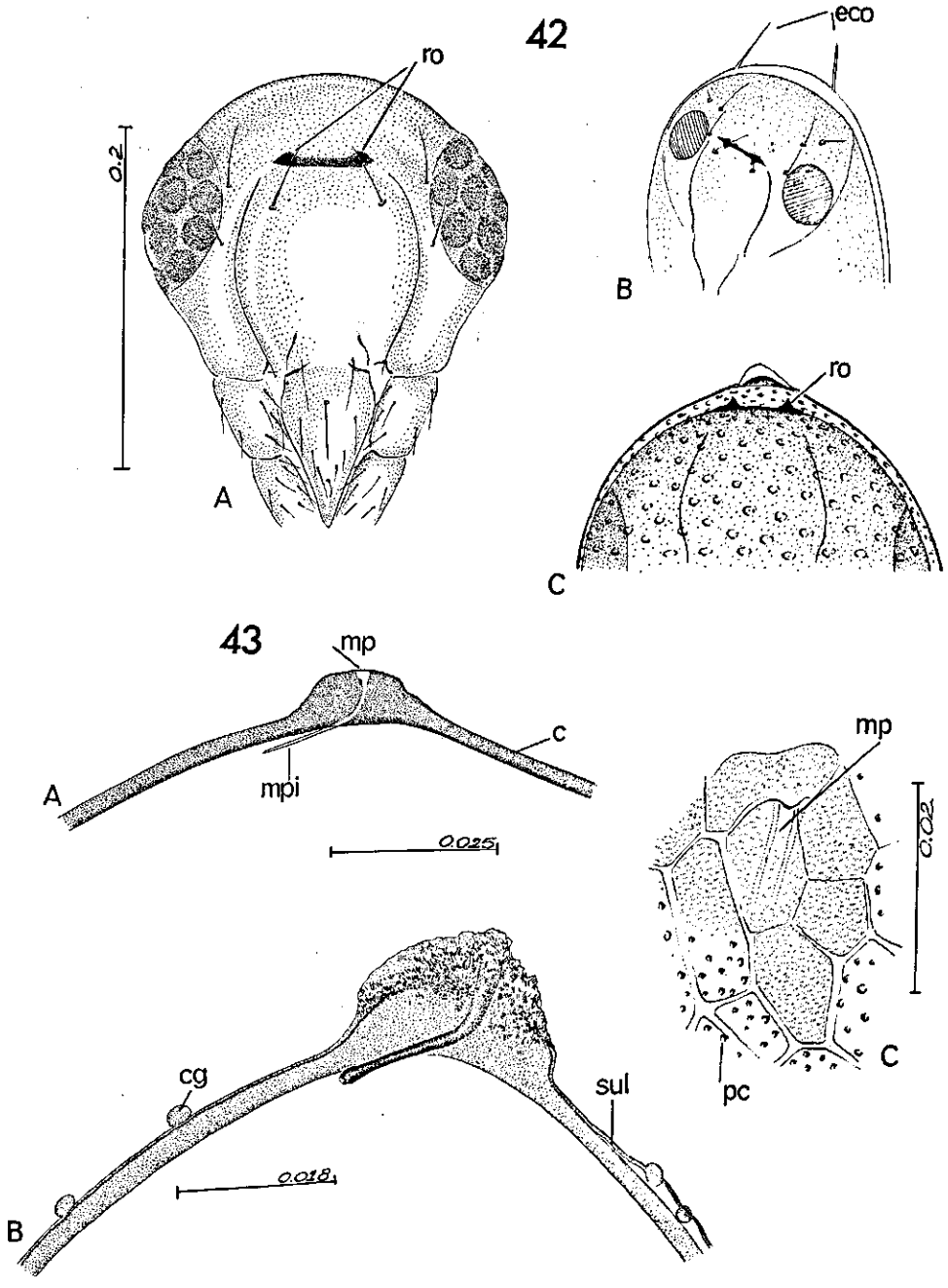


Fig. 42–43. Hebridae, structure of chorion and burster 42. *Hebrus ruficeps;* A: head of prolarva, fore side; B: the same, obliquely from above to show outgrowths of the embryonic cuticle; C: position of burster beneath the shell. 43. A: *H. elimatus*, anterior pole of unripe egg, median section; B: *H. ruficeps*, the same, deposited egg; C: *Hyrcanus* sp., micropylar area from above.

of the inner layer which occurs in the gerrid-veliid eggs. The outer surface shows the marbling, also seen with light microscope in *H. ruficeps*. Moreover, the thick supra-chorionic coat, supported by the chorionic globules, is present, which thus appears to be secreted in the ovarioles. The very thin coat, which covers the solid chorionic surface below the jelly coat in *Gerris* and *Microvelia*, is not discernable here.

Hyrcanus sp. This is unlike the *Hebrus* egg. Its shape and the difference in chorion structure fore and aft suggest that the egg is deposited more or less exposed. There is one micropyle pointing obliquely downwards and forewards beneath the shell, but an external upgrowth is lacking. The micropylar area is thin and its felty appearance possibly indicates a fine porosity (fig. 43C). The exposed side of the egg is plastered with another chorionic layer bearing hexagonal ridges and deep pits on the hexagons' surface.

PREVIOUS DESCRIPTIONS HUNGERFORD, 1919 (*H. concinnus*, outline); JORDAN, 1935 (*H. ruficeps*, outline); LEBRUN, 1960 (*H. ruficeps*, *H. pusillus*, outline of egg, absence of ruptor ovi claimed erroneously).

2.1.2 Mesoveliidae

MATERIAL: Mesoveliinae: *Mesovelia furcata* Muls. & Rey (living deposited eggs); *M. mulsanti* White (ripe ovarian eggs, origin Curaçao, Neth. Ant.); *M. horvathi* Lundbl. (ripe ovarian eggs, origin Sumatra). Mesoveloideinae: *Mesoveloidea williamsi* Hungerf. (ripe ovarian eggs, origin Surinam).

Mesovelia furcata

The ovipositor, which is held out normal to the substratum, is directed with its extreme tip somewhat anteriad. This curve in the ovipositor thus suggests the condition in Saldidae and one would expect a similar mode of oviposition. It has been confirmed that the dorso-ventral orientation of the egg during laying is indeed the same as in saldids. The fore side of the laid egg is faced to the females venter, in contrast to the orientation in Cimicoidea, which is the reverse. In captivity, *Mesovelia* always laid eggs above water level, either in floating polystyrene foam or in grass stems above the water.

CHORION The shell is smooth with a pseudoperculum and thin (2.5 μ), but four times thicker in the lid and about three times thicker at the posterior pole. No differentiation in the chorion was detected with an optical microscope except for a very faint hexagonal pattern. The lid shows some superficial roughness; cross-sections show scattered fine holes and a faint trace of what could be fine traversing canals. Electron micrographs made from sections across the lid (fig. 291B) reveal, however, that the chorion is without any sign of porosity and an inner mesh-work layer is

lacking altogether. The single micropyle is located in the aft half of the lid. It penetrates the chorion obliquely forwards and extends internally more than half its length beyond the lid, being well-marked as a blackish conduit (fig. 46L, M) of 2 μ diameter with an outer aperture of about 5 μ.

GROSS EMBRYOGENESIS (fig. 44A–J) Incubation takes ten and a half days at 30 °C. Invagination of germ band starts aft of the posterior pole. The germ band is immersed within the yolk, assuming an elongated ϱ -shape, ventral side directed towards the fore side of the shell. A small frontal area of the head remains in contact with serosa. No isolated group of germ-cells are visibile at the tail end of the early germ band. Blastokinesis involves a slow 180° rotation, followed directly by revolution along the concave egg side. The rotation is often incomplete if the egg is at that time subjected

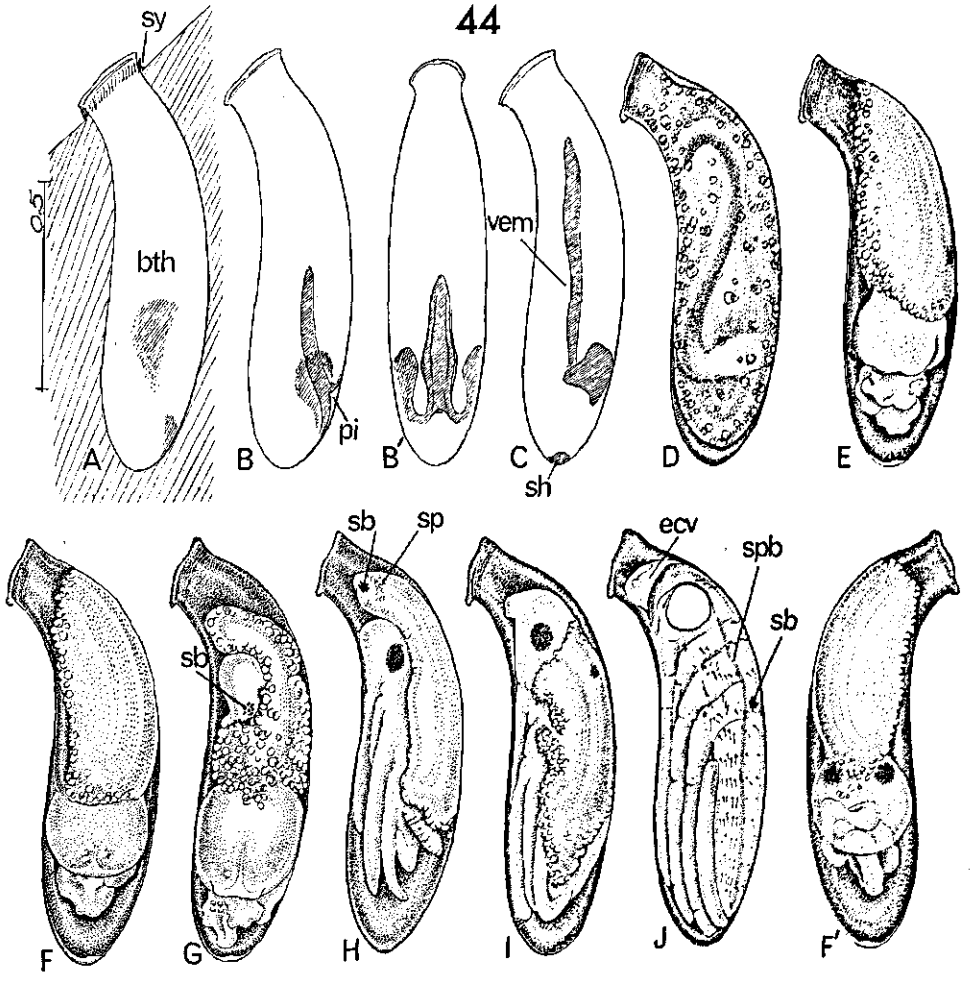


Fig. 44. Mesoveliidae, *Mesovelia furcata*, embryogenesis; A–C: fixed and stained; D–J: living eggs; E, F, F', G: showing an abnormal rotation resulting in death of the embryo.

to cold; the end result is anomalous development without revolution (fig. 44G, F').

A distinct serosal hydropyle is formed during stretching of the invaginating embryo and the hydropyle soon fills up the whole posterior curve of the egg (fig. 45A). The behaviour of the hydropic cells have been studied in about twenty eggs; all showed the following picture (fig. 45A–E). With the first appearance of the protocormic appendages, the yolk lies close to the hydropyle. The next day the boundary of the yolk is considerably retracted from the organ, although still joined the latter by long, thin cytoplasmic filaments of the individual serosal cells. It might be that the lumen thus developed is filled with water, which has been taken up before formation of the serosal cuticle is complete. This general picture remains until the embryo commences to rotate around its polar axis. Then the posterior of the serosa contracts and finally draws the hydropic cells aftwards from the posterior pole. Before the rotation is complete, the 'knees' of the antennae push through the amnion-serosal junction and the head is slowly delivered from the envelopes. The serosa is discarded and moves up to the anterior pole to form the serosal plug. At the left side of the base of this plug, the serosal hydropyle can still be traced for an hour after it has been transported anteriad as a lump, constricted basally from the serosa. Partial pigmentation of the eye starts before blastokinesis; five to eight ommatidia near the centre of the eye disc are coloured red before revolution; pigmentation spreads centrifugally after revolution. Once the serosal plug is formed, it occupies the whole space beneath the lid. By alternating contractions of the amnion-serosal junction, almost as in Saldidae (p. 34), the plug sinks into the prothorax, the complete process taking four to five hours at 27 °C.

The uptake of the serosa in this species is accompanied by an interesting new phenomenon. During withdrawal of the plug from beneath the operculum, a red spherical body becomes visible in the top of the yolk (fig. 44H). It migrates through the yolk towards the dorsal side within the presumptive prothorax (fig. 44I) at a speed which is slightly greater than that with which the plug is withdrawn. Once arrived in the dorsal organ, the ball moves posteriad through the thorax (fig. 44I, 46A) and at the time of eclosion it has reached the height of the first abdominal segment. Dissections reveal that the red body is enclosed in the anterior part of the stomach. During hatching, when the air-filled gut is in great turmoil, the sphere breaks up into many fractions and these fractions move about. In the free larva, however, the fractions at first recombine to form a single body in the hind part of the mid gut. Later on we lost sight of it so that its fate remains obscure during larval life. The spherical body appears to consist of dark granules embedded in a red substance and we can only conclude that they are symbiotic organisms (COBBEN, 1965b). This is the first record known of symbionts in Amphibicorisae and, even more important, the first data on micro-organisms in such a relation to an entirely carnivorous species. At least, all information to hand reveals that *Mesovelia*, as all other semi-aquatic bugs, is carnivorous, but careful observations are still needed to decide to what extent *Mesovelia* happens to suck vegetable food. The mode of transmission of the symbionts within the egg is unparalleled in Heteroptera. Infection of the interior is probably transmitted through the micropyle. Freshly laid eggs appear to have the same organisms, but now

rod-shaped (1 × 2 μ), externally under the extending margin of the cap embedded in a collar of cement (fig. 46M). Some time before blastokinesis, a brown ring appears against the inner surface of the lid, running concentric with the latter (fig. 46L). After withdrawal of the serosal plug, the lid again is uniformly transparent. The brown ring, therefore, is not a print of the serosal cuticle. Our supposition is that the ring is formed by the symbionts, after penetrating the egg through the micropyle, before the serosal cuticle is secreted. The fact that the organisms initially occur in the cement coat,

45

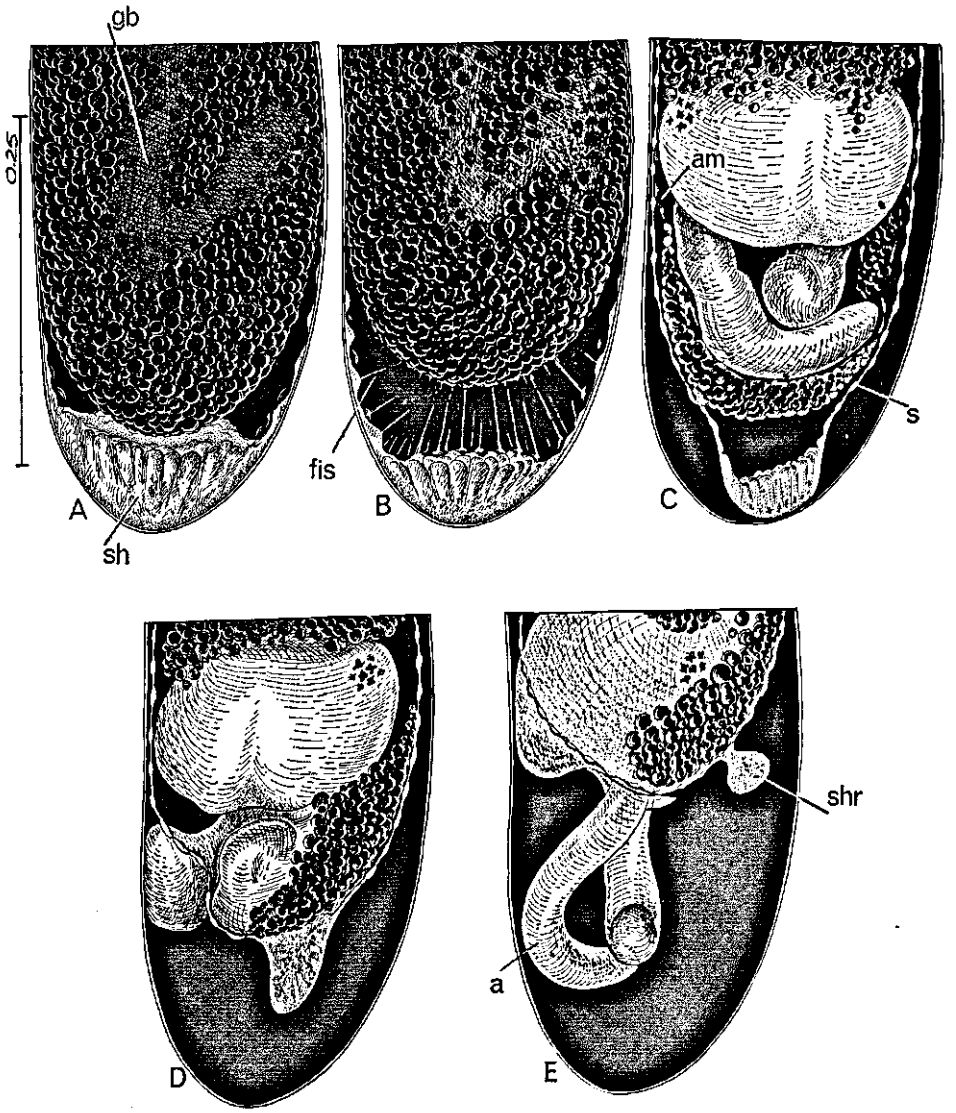


Fig. 45. Mesoveliidae, *Mesovelia furcata:* position (A) and fate of serosal hydropyle during rotation (C) and revolution (E) of embryo.

would suggest contamination through the genitalia rather than the intestine. However, there is clear evidence for the latter possibility. The mid gut of females with ripe eggs, has bright red spots of irregular shape and extent, corresponding in appearance with the substance of the red ball in the egg. These bodies are lodged between the cells of the gut wall, but red fragments occur also free in the gut content. It is interesting that the micro-organisms form these intercellular clusters only shortly before oviposition. Before that time no clumping of the red connective substance could be traced, but the organisms individually swim in the digestive fluid of the gut. Thus it seems most likely that after the egg is laid and the ovipositor blades are withdrawn, a drop with symbionts is delivered from the anus and is spread over the egg-cap. We have indeed observed that the female taps several times with the abdominal apex against the region where the egg has been laid.

HATCHING Complete incubation and successful hatching is possible under water as well as in moist air. The attitude of the fully grown embryo is shown in fig. 44J and the diagram, fig. 279E. The arrangement as figured seemed prevalent; only 26% of the 34 eggs were the mirror-image. The structures involved in hatching show some highly remarkable features which clearly distinguish the *Mesovelia* egg from amphibicorisous eggs. Instead of a sharply pointed and sclerotized egg-burster, *Mesovelia* develops a bladder-like outgrowth of the frontal region of the embryonic cuticle which acts as a buffer to push off the egg cap. During withdrawal of the serosal plug, the embryo's frontal region protrudes to form a trunk-like structure. Later the head proper is retracted, but the embryonic cuticle remains protruding; the space between it and the larval head fills with liquid. The frontal ampulla thus formed has a characteristic shape, the elements of which may still be derived from the normal amphibicorisous egg-burster. The cranial frame of the embryonic cuticle is indicated by two faint black lines (fig. 46K), running from behind the eyes to the base of the labrum. The top of the ampulla has a longitudinal groove, flanked on both sides by a conical projection (fig. 46A, F). These conical papillae may be homologous with the paired egg-teeth of *Hebrus*, since they are connected with the cranial frame.

The ingenious buffering and precise fit of the ampulla becomes apparent, when the larva is ready for eclosion. The groove of the ampulla fits over a knob-like inward projection of the serosal cuticle which develops long after the chorion but long before the embryonic cuticle. The cones of the embryonic cuticle press forwards on either side of the knob-groove construction and increase the force exercised upon the serosal cuticle and the chorionic cap. In a split second the cap is shot off and the insect's head protrudes out of the neck of the egg (fig. 46D). The central knob still fits into the hole of the ampulla, but increasing swelling of the head causes the knob to slip out of the hole. The cap remains in contact with the egg-collar by means of an elastic dorsal strand (fig. 46D). The latter probably is part of the serosal cuticle of which the rest is also disrupted along a circular line. Along both sides of the embryonic cuticle a narrow strip continues from the epicranial frame and runs to the abdominal apex (fig. 46A, spb). The strip is covered with fine pegs, arranged in two or three rows. These point

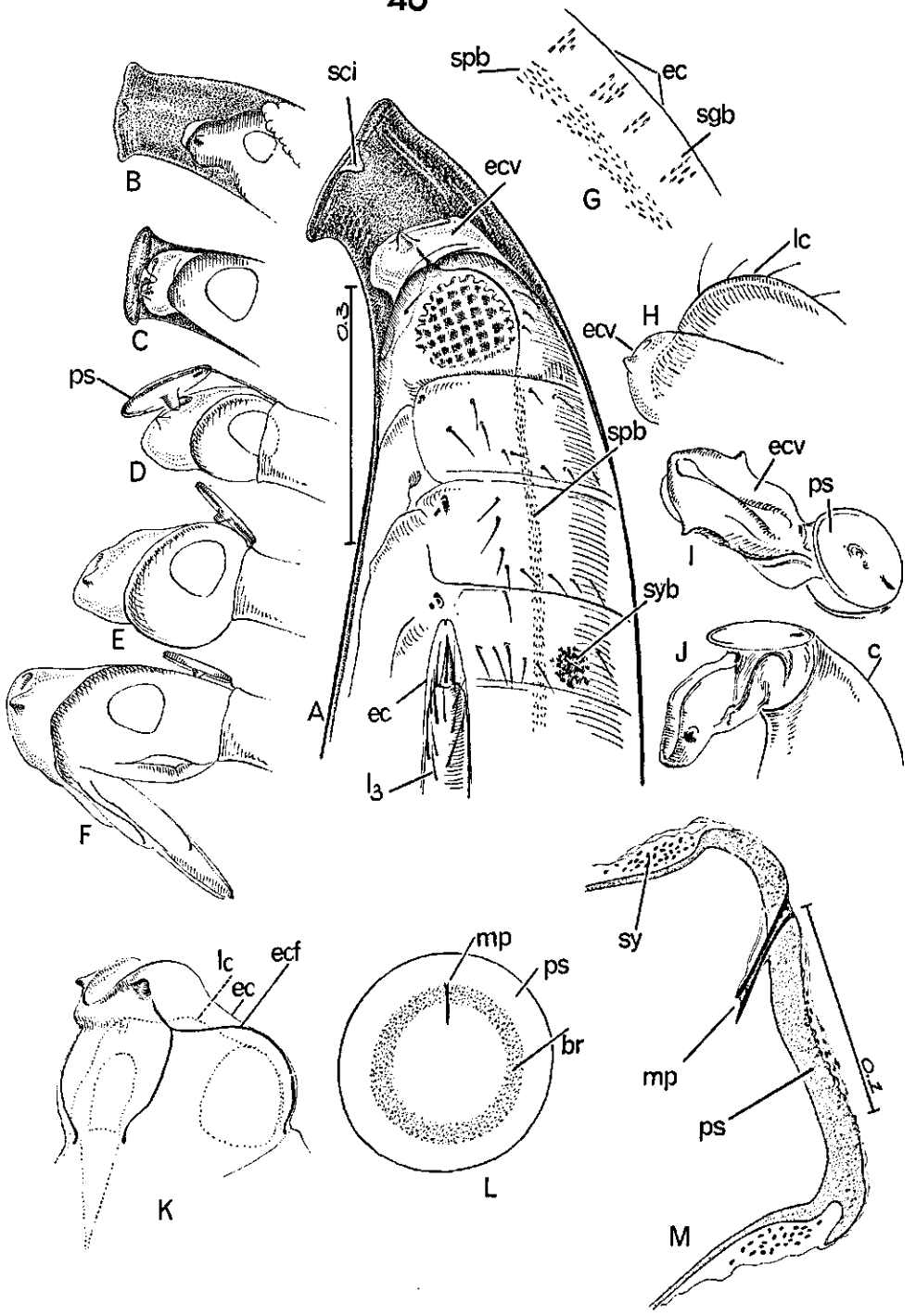


Fig. 46. Mesoveliidae, *Mesovelia furcata;* A: fully grown embryo; B: formation of frontal vesicle; C–F: eclosion act; G: abdominal part of embryonic cuticle; H: bursting of the embryonic cuticle; I, J: vacated frontal vesicle; K: head of prolarva; L: egg seen from above the cap, before revolution, with brown ring of supposed symbionts beneath serosal cuticle; M: median section of egg cap.

backwards and prevent the prolarva from slipping backwards into the shell, in the pauses of the forward pressure between the pulsations which end in freedom. The embryonic cuticle at last, splits along the dorsal side, as far forward as the ampulla (fig. 46H–J).

ADDITIONAL MATERIAL Ovarian eggs of *M. mulsanti* have identical chorionic structures. The egg of *M. horvathi*, however, has a less clearly defined cap and a distinct reticulation which approaches the type in *Mesoveloidea*. Furthermore, the very long micropyle is located further aft (fig. 48).

Mesoveloidea williamsi (fig. 49A–C). The curved egg is obliquely truncated anteriorly; it is therefore probably embedded like the *Mesovelia* egg. A pseudopercular margin is not present and it is not certain whether the eclosion split is longitudinal or, more probably, circular. The flattened anterior pole is distinctly reticulate. No internal porosity nor aeropyles could be traced in the shell. The single micropyle is a short inconspicuous tube, about two μ wide and projects inward as in *Mesovelia furcata*.

Speovelia maritima The egg is as in *Mesoveloidea* but the single micropyle (2.5 μ wide, 50 μ long) is located outside the higher lip on the aft edge of the truncate anterior pole.

A discussion of the ovarian egg of *Macrovelia* and other amphibicorisan bugs with a puzzling systematic position, placed by some authors in the Mesoveliidae, is given on p. 64, 65.

PREVIOUS DESCRIPTIONS HUNGERFORD, 1919 (*Mesovelia mulsanti* White, elaborate description of oviposition, but no mention of the characteristic forward placement of the egg; the temporary appearance of a faint ring of pink in the cap region suggests a similar transmission of symbionts as in *M. furcata*); POISSON, 1933 (*M. furcata*, sagittal section through cap, micropyle shown without inward projection).

2.1.3 Hydrometridae

MATERIAL: *Hydrometra stagnorum* L. and *H. gracilenta* Horv. (living deposited eggs); *Limnobatodes paradoxus* Huss. (ovarian eggs, origin Brazil).

The following account is of *Hydrometra stagnorum*. Differences in *H. gracilenta* are mentioned simultaneously where necessary.

Eggs are pushed out horizontally and the base which forms a distinct pedicel is glued to vertical objects (stems, glass-wall of aquarium). Less often they are deposited downwards and erect against floating material. Without exception oviposition is terrestrial, the eggs being laid at a distance of from a half up to several centimetres above water level. The released egg is white. Within a few minutes, the chorion rapidly darkens until the egg is entirely purple and later granite-blackish in *H. stagnorum* and

light brown in *H. gracilenta*. Eggs taken straight from the female and placed under water, remain whitish; this permits study of the live embryo.

CHORION The chorion is distinctly two-layered. A voluminous and highly complex meshwork ensheathes a thinner compact inner chorionic layer. There is only one micropyle which traverses a narrowly constricted tube-like anterior elongation of the egg and opens exteriorly in a protruding pellet of a finely granular substance. Posteriorly, the outer sheath seems to be absent from the basal attachment disc, the latter being connected with the inner chorion by means of a slender stalk. In *H. gracilenta*, the projections of the micropyle and pedicel are both much longer. The equally elongated spongy sheath in this species is not connected with the actual pedicel, but with a sheath of apparently porous material loosely surrounding the stalk.

The outer sheath has a surface pattern consisting of ridges separated by furrows along the actual egg and a continuous reticulate sculpturing around the micropyle and

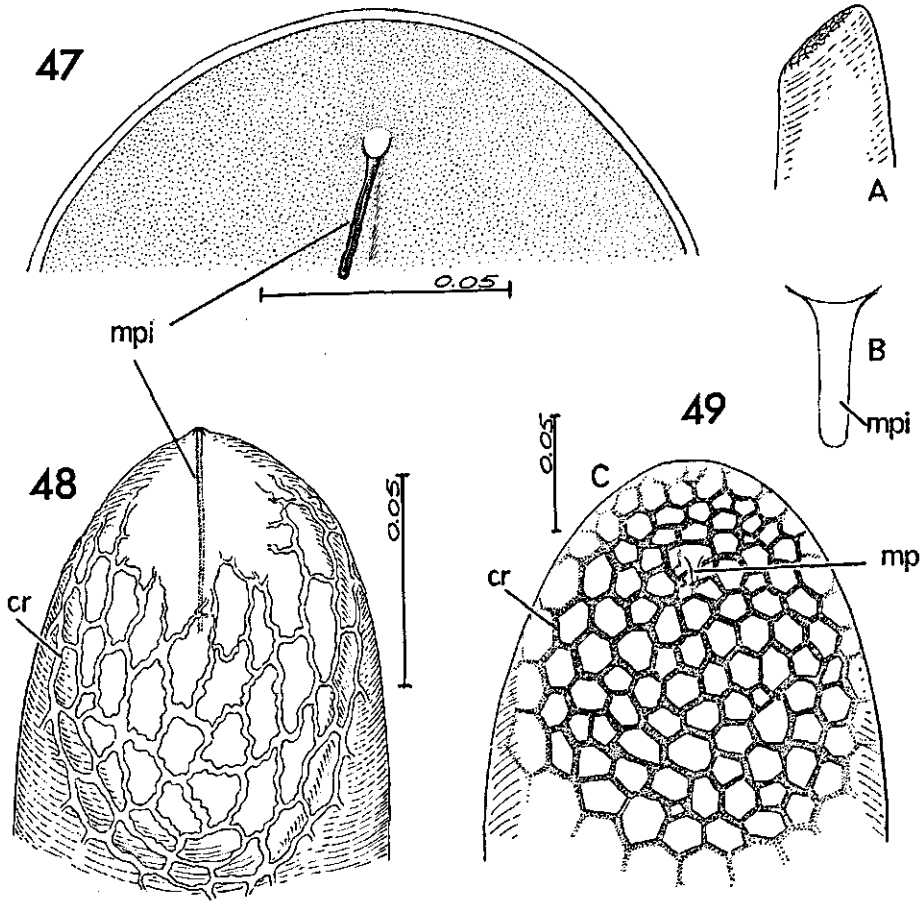


Fig. 47–49. Mesoveliidae, chorionic structures 47. *Mesovelia mulsanti*, part of pseudoperculum with micropyle, inner view. 48. *M. horvathi*, anterior pole, outer view. 49. *Mesoveloidea williamsi*, anterior pole; A: lateral view; C: outer view; B: micropyle.

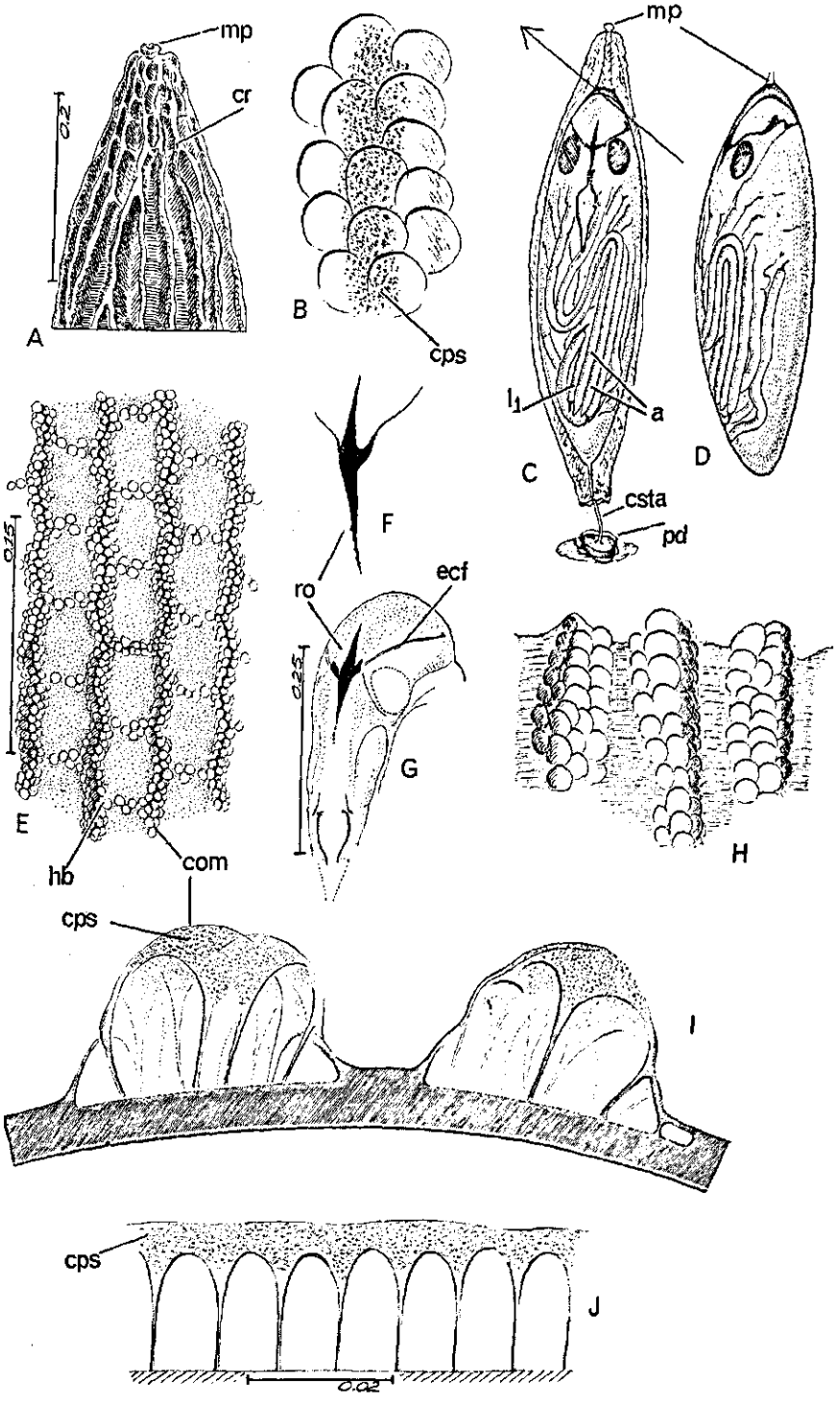
pedicel (fig. 50A, C). The luxuriant architecture of this outer sheath is best demonstrated by a close investigation of the mid egg-region. The longitudinal ridges are composed of minute blisters arranged lengthwise in four to five adjacent rows (fig. 50H). Chorion fragments mounted in euparal reveal that the ridges form a regular hexagonal pattern probably reflecting the follicular cell boundaries in that their course is a slight zigzag. The edges of the ridges are cross-connected with neighbouring ridges by indistinct blisters not protruding so far (fig. 50E).

Cross sections of this region for the optical microscope show the following picture (fig. 50I). The crests are sunk somewhat into the actual shell, which is compact in structure and is 5 μ thick beneath the crests and 7.5 μ between them. The close grouping of the blisters creates an air system, like a system of dome-shaped vaults supported by vertical columns. A greyish granular substance is suspended in the sheet-like roof of the vaults. It is difficult optically to conclude whether and to what extent the vertical columns are connected to each other to form partitions. The regular sequence of cells when a crest is seen from side-view (fig. 50J) suggests that they partly connect traversely. The electron-microscopic picture suggests that the cavities of the crests are connected with each other by holes in the radial partitions (fig. 294A, E). Scanning-electronmicrographs unequivocally show such holes (fig. 306A-D). The labyrinth is very spacious and intricate at the base and the top where the egg has no contents. Here, the structure is somewhat different in basic pattern from that of the middle of the egg. Fig. 51 shows an oblique section through the base of the micropylar region. The follicular pits are much smaller and each pit forms a single sheath element by a long column arising from its edges. The columns split at the top and the ramification supports the domes of the external, enveloping sheet. The element based upon a single follicular pit diverges outwards and is closed by only one dome. The regular grouping of these domes gives the egg proximally and distally a squamous surface. The architecture of the external sheath in *H. gracilenta* is only slightly different. The hexagonal pattern formed by the crests is less evident because the furrows are wholly made up of blisters in the chorion. On the other hand, the blister system around the egg projections are so elaborate that they give an obvious honeycomb structure superficially.

The hydrometrid shell is obviously designed to trap atmospheric air in the granular outer layer of the blisters and also in an open chorionic layer of the actual shell. Eggs placed under water as soon as they leave the female, do not contain air in the shell. Air is seen to penetrate the outer meshwork, when the egg is allowed to dry. There is no gradient from the anterior part backwards, but air enters directly and almost simultaneously all over the surface. The penetration occurs first in the top of the blisters where they are granular and afterwards in the spaces under the depressions between

---

Fig. 50. Hydrometridae, chorionic structures and burster; A–F, H–J: *Hydrometra stagnorum;* G: *H. gracilenta;* A: anterior third of egg; B, E, H, I, J: blister-like reticulation of the outer chorionic layer; B, E, H: surface view; I: transverse section; J: longitudinal section (all seen optically, compare electron micrographs of fig. 294); E: region on mid-part of egg, showing the hexagonal ground-pattern; C, D: posture of prolarva; G: embryonic cuticle covering larval head.


mp
cr
0.2
A
B
cps
mp
l1
a
C
D
csta
pd
F
ro
ecf
0.25
G
E
hb
com
H
cps
I
cps
J
0.02

blisters. The granular substance in the top of the domes, is chorionin with high porosity in transmission electron micrographs (fig. 294B, C, E). The blisters are entirely covered by a thin coat of cement.

Normally deposited eggs bear a continuous air space in the inner layer of the shell. This is clearly shown in euparal mounts of intact eggs. An initially continuous air-film beneath the level of the blisters is gradually disrupted and shrinks away. Electron micrographs actually show this air-filled inner layer (fig. 265G). The sections further reveal a three-layered structure of the shell. The outer layer, giving rise to the blisters, is marked off from the thick middle layer by a porous sheet, whose pores are probably not continuously connected.

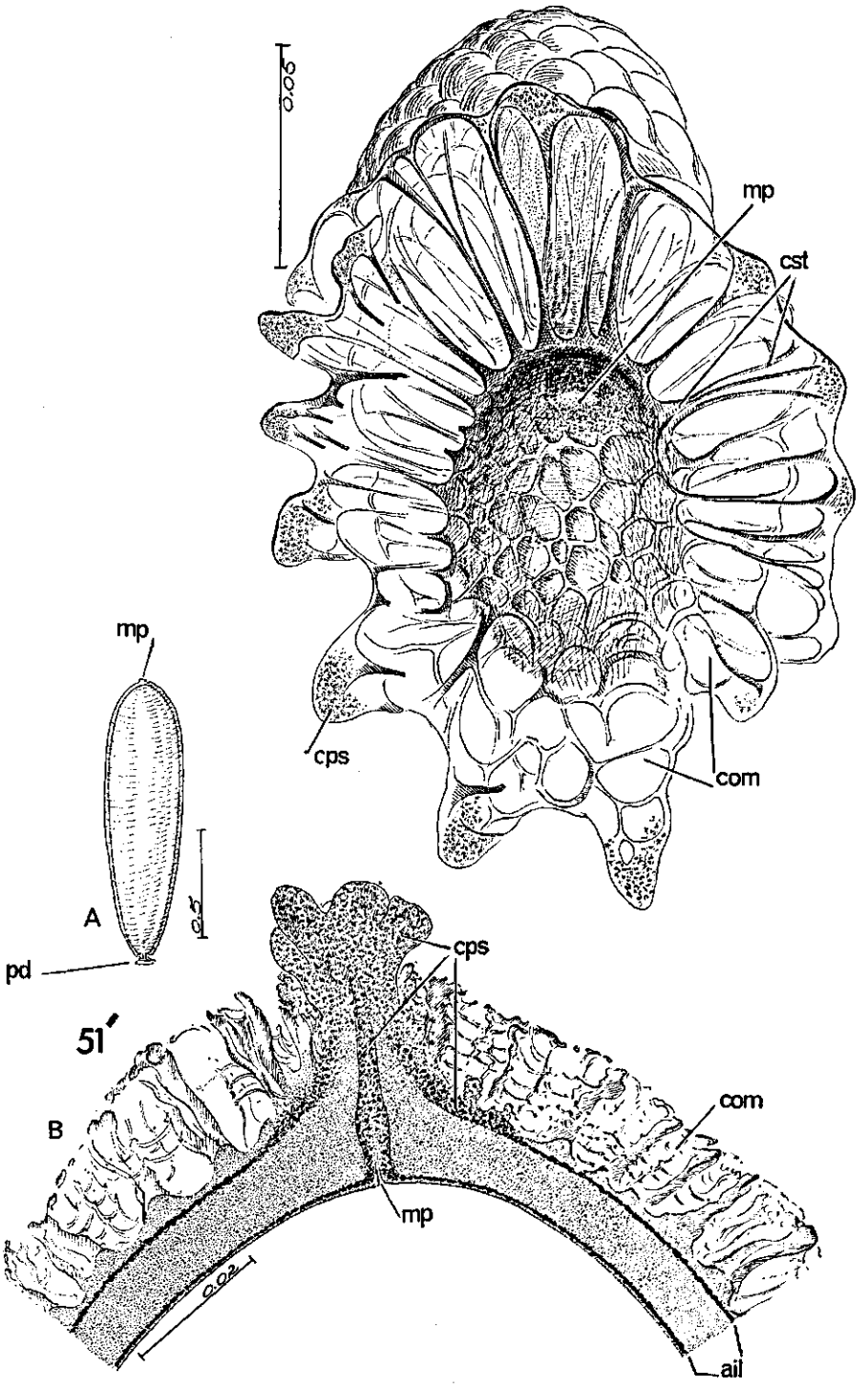
Air is probably transported to the inner chorionic zone through the micropylar tube. The wall of this tube around the extreme apex is porous (fig. 294F) and may function as a direct route for oxygen from the outer blister-layer towards the inner aerostatic layer, if the egg becomes submerged. Whether the large interface between the air and surrounding water permits the 'granular' outer layer to function as a plastron has not been tested. Nor have we verified whether the cavities of the labyrinth becomes entirely air-filled. Further exteriad the micropylar tube has a solid wall, but towards the innermost layer of the shell, the lumen is lined by an accumulation of porous chorionin. The inner aerostatic layer seems to originate in the lower part of the micropyle. The pedicel is entirely solid and there is no serosal hydropyle; therefore the stalk should not function in water absorption. The outer chorionic labyrinth normally becomes detached from the pedicel disc. Along this rupture water may readily reach the large cavities of the labyrinth ensheathing the egg. The labyrinth may therefore become waterfilled during submersion, whereas the 'granular' substance firmly holds air. This air-film would thus be enclosed externally and internally by water and consequently an extensive area for oxygen diffusion is provided. The physical properties of the hydrometrid shell should be further examined to clarify the advantages and purpose of the adaptations of the chorion. There is the contradiction that the egg developes quite normally under water without an air store in the shell. Four eggs, taken straight from the laying mother and placed under water, developed and hatched normally. Ten fresh eggs treated for one and a half hours with detergent (Triton X 100) hatched also when kept continuously under water. The main advance of the hydrometrid egg over other Amphibicorisae is probably the greater tolerance for a dry environment. The voluminous labyrinth sheath might serve predominantly for regulating fluctuations in humidity.

GROSS EMBRYOGENESIS The incubation period for both species lasts 6.5 to 7 days at 30 °C.

Eggs are not wholly isodiametric in cross section. One side is slightly more convex

---

Fig. 51–51′. Hydrometridae 51. *Hydrometra stagnorum*, inner view of anterior top, obliquely sectioned according to the arrow in Fig. 50C; external struts arising from the edges of the polygons. 51′. *Limnobatodes paradoxus;* A: lateral view of egg; B: optical section of micropylar area.


0.05
mp
cst
cps
com
mp
A
pd
0.5
51'
cps
B
com
mp
0.02
ail

than the other in fresh eggs; the shape of the egg is not influenced by the growing embryo. It is difficult te decide which is the fore side of the egg. A number of females were placed individually in narrow tubes (8 cm diameter), in which they could move freely but not turn, so that the dorsoventral orientation of deposited eggs could be related to the known orientation of the mother. Such eggs were laid flat and seemed to have left the female sometimes with their convex side upwards, at other times downwards.

The blastopore appears on the flat side, but in a few specimens we found it on the convex side. The major shifts of the embryo are not constant. The representation of embryogenesis, as given in fig. 52 gives a rather sketchy picture of the course of events. The blastopore gradually shifts anteriad. At the tail end of the invaginating germ band a substance accumulates, which is only faintly discernible and stainable and therefore probably does not represent the germ cells. The germ band is wholly immersed, but a small cephalic area retains contact with the serosa. The embryo rotates 180° along its polar axis at a variable point of time in the ♀ -stage. Individuals may be found which have already rotated in stage D (fig. 52) while others do not rotate before stage F. Whether the rotation is to the left or right could not be ascertained. Embryos are sometimes found in the act of twisting (fig. 52E'). In the serosa staining did not reveal any thickening, which might be a hydropyle. No exact measurements of increase in egg volume have been made, but the increase is not as striking as in other amphibicorisous eggs which do have a hydropyle. The fact that the eggs hatch even when they are laid about 3 cm above water level (glass wall of open aquarium in dry room), demonstrates all but independence of water. Since in nearly all other Heteroptera studied, we could trace a serosal cuticle, *Hydrometra* most probably developes such a cover too, though we could not demonstrate it by study of whole eggs. It might be extremely thin or its consistency may be quite different from the serosal cuticle in other semi-aquatic bugs. In the hydrometrid embryo, the antennae point straight forward. The eyes are pale red before revolution. A gap in our information concerns revolution of the embryo. Because of the individual variation mentioned earlier, we cannot decide from the ultimate orientation of the prolarva whether blastokinesis is accompanied by a second rotation. The majority of prolarvae leave the shell through a slit on the more convex side. Thus, rotation just before the revolution may be absent, although a prolarval backward rotation could theoretically follow a blastokinetic rotation, thus explaining the final position. In quite a number of eggs, the prolarvae face laterally or the aft side of the egg.

HATCHING Complete incubation and successful hatching is possible both under water and in the atmosphere. The attitude of the mature embryo is shown in fig. 50C, D and the diagram fig. 279E. The extremely long appendages evoke a characteristic asymmetry. There is a marked unilateral polarity in that the bundle of antennae and fore legs loop always upwards on the embryo's left side (checked in 25 eggs). The egg shell is cut open and splits along a short longitudinal line between two crests of the outer sheath. The egg burster is a longitudinal knife-like black structure.

Its location and connection with the head frame of the embryonic cuticle appears in fig. 50G.

ADDITIONAL MATERIAL *Limnobatodes paradoxus* The basic plan is as in *Hydrometra*, but the features of the shell are not so pronounced (fig. 51'). The inner porous layer is very distinct and shows a hexagonal lining along which the porosity is of a coarser nature. This porous layer covers the whole shell, even round the posterior pole. The cavities in the outer zone of the solid chorion layer are moreover continuous, where in *Hydrometra* only isolated holes could be traced. The external open blister-structure is not as elaborate as in *Hydrometra*. All three spaces of the chorion are in connection with each other around the short micropylar projection (fig. 51'B).

PREVIOUS DESCRIPTIONS Over ten authors have described the external appearance of hydrometrid eggs (references in POISSON, 1933 and SPRAGUE, 1956). The latter author elucidated the shell structure of *Hydrometra martini* Kirk. to some extent. The external chorionic sculpturing as figured by her does not deviate essentially from our European species. Both in the text and the figures, she gave the impression that the lumina of the outer sheath are filled up by minute cells arranged on top of each other, also in the cross-directions, thus giving it a spongy pattern. A similar picture would be obtained also in our species from observations made at low magnification. The vertical columns and their bifurcations at different levels suggest that the 'cells' are subdivided transversely. SPRAGUE described the posture of the fully grown embryo, which seemed to have an identical left-sided polarity as in our species. That the embryonic cuticle should split along the lines of the head frame as she claims, is incorrect. The skin cleaves along the back of the thorax.

2.1.4 Veliidae and Macrovelia, Oravelia, Chepuvelia

MATERIAL: Microveliinae: *Microvelia reticulata* Burm. (living deposited eggs). *M. longipes* Uhl., *pulchella* Westw., *signata* Uhl. (ripe ovarian eggs; origin: *longipes*, *pulchella* from Curaçao, N.A. and *signata* from Colorado, U.S.A.).

Veliinae: *Velia caprai* Tam. (ripe ovarian eggs).

Haloveliinae: *Halovelia hilli* China (ripe ovarian eggs, origin Montebello Islands).

Hebroveliinae: *Hebrovelia* sp. (deposited eggs, origin Ivory Coast).

Some aberrant velioids: *Ocellovelia germari* Dist. (unripe ovarian eggs, origin S. Africa); *Oravelia pege* Dr. & Ch. (ripe ovarian eggs, origin California, U.S.A.); *Macrovelia horni* Uhl. (ripe ovarian eggs, origin Colorado, U.S.A.); *Chepuvelia usingeri* China (ripe ovarian eggs, origin Chile).

Microvelia reticulata

Eggs are laid on the edge of the water on floating material.

CHORION The smooth chorion is entirely covered with cubical projections except around the micropylar protuberance at the anterior pole (fig. 53C). The projections vary in the various specimens; mostly they are truncate, rivet-shaped and their tops have a coat of jelly by which the egg is attached to the substrate. The jelly matrix covers more of the egg than just its aft side. Under the optical microscope the shell appears in cross-section as a single compact layer, about 2.5 μ thick (fig. 53A). With the electron microscope (fig. 293), it is finely porous. Numerous radial pore canals of 0.05 μ diameter pass through the thickest part of the shell and enter a spongeose porous inner layer, about 0.3 μ thick, which must be water-filled under normal conditions. The innermost layer of the shell within the spongy zone is solid and is 0.05 μ thick. The electron micrographs further show that the outer protuberances consist of chorion of a lower density than the main part of the shell. An extremely thin (10 Å) film covers the surface of the shell. This may be called the first suprachoral layer and bears no relation to the thick jelly layer, which is also clearly seen in the micrographs supported by the chorionic rivets. There is a group of two or three very small micropylar canals at the anterior pole, which are difficult to discover as they are masked externally by a cap which seems to be porous (fig. 53B).

GROSS EMBRYOGENESIS (fig. 54)* Incubation lasts six to seven days at 30 °C. Invagination of germ band starts aft of the posterior pole. The germ band is entirely immersed, assuming a distinct ♀ -shape, the ventral side being towards the fore side of the egg. There is a cluster of initially isolated cells, apparently germ cells, and a serosal hydropyle at the posterior pole. With the appearance of appendages, the exposed side of the egg becomes darkened due to the formation and pigmentation of the serosal cuticle. Eye plates are pale orange before revolution, but the individual optical elements are not yet discernible. The process of blastokinesis has been only once followed. Fusion and rupture of the serosa and amnion occurred without a preceding rotation. The embryo emerged from the hole in the serosa and amnion by moving first in a clockwise spiral rotation, when observed from the front. Finally it moved up towards the anterior pole with its venter towards the free side of the egg. It is not certain whether this method is the common one in this species. The fate of the hydropyle has not been traced.

HATCHING The whole development and hatching proceed successfully under water or in moist air.

The attitude of the fully grown embryo is as shown (fig. 54G, H, diagram fig. 279D). There is a distinct unilateral polarity in the asymmetrical arrangement of the limbs. Of the 33 specimens checked, 85 % show the configuration as shown and only 15 % the mirror image. There is one median egg-breaker situated on a broad sclerotized cross-

* Attention is called to the presentation of the figures, which is left-right the reverse of that used for all other families throughout this work.

band (fig. 54G, H; 55A, B). Branches of this frame pass dorsally along the inner margin of the eye-plate and to the base of the labrum anteriad. The rupture of the chorion occurs simply along a median slit, which runs most of the way down the free side.

ADDITIONAL MATERIAL Chorionic texture and micropylar system of *M. longipes* and *M. pulchella* show almost the same pattern as described above. The outward projections are round knobs as also in *Velia caprai*. Further data pertaining to this latter relatively large species are: Thickness of chorion 10 μ, finely striated in optical

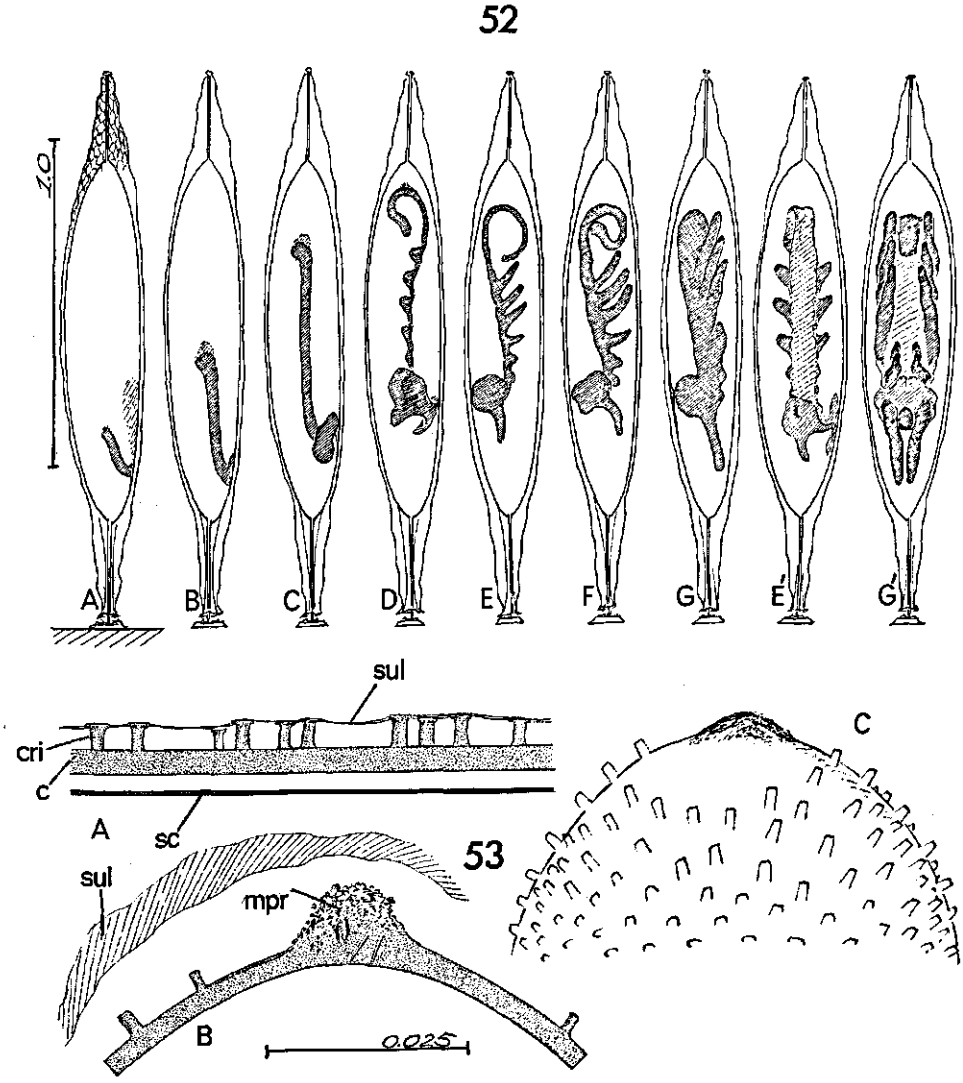


Fig. 52–53. Hydrometridae, Veliidae 52. *Hydrometra gracilenta*, gross embryogenesis before revolution; A–G: lateral side; E′: dorsal view; G′: ventral view of embryo. 53. *Microvelia reticulata*: A, B: longitudinal section of the mid part and the anterior part of the shell; C: anterior pole.

section, suggesting a porosity similar to that shown in micrographs of *Microvelia* and *Gerris;* three or four very small micropylar canals running spirally through the centre of the anterior pole, diameter of each canal measuring about 2.5–3.5 μ, each canal sometimes with a vermiform projection inside the shell, consisting of jelly-like material. In *M. signata,* the micropyles with a diameter of about 2 μ are more distinct and project inwards (fig. 56). Furthermore the knobs in this species are in a hexagonal chain with isolated ones in the enclosed areas; the rest of the chorion is without sculpturing and measures 7.5 μ in cross-section.

Halovelia hilli In contrast to all other Veliidae studied, the egg has only one micropyle. Its transverse canal runs parallel with the innerside of the shell. Externally it opens in a cup-like projection lined with porous substance.

Hebrovelia sp. The oval egg (fig. 57B) is glued lengthwise with its less convex side to the substrate (blotting paper in captivity). The 7 μ-thick chorion is very finely pored, more densely so on the hexagonal ribs. There are two or three micropyles (fig. 57A) on top of the tapering cephalic pole. These canals, 3 μ wide, curve downwards in a half circle through the shell, the arcs together producing a centrifugal figure. The canals do not seem to project within the shell. The large eyes are already clearly pigmented before blastokinesis (seen only in one egg). A blackish medio-frontal egg-burster (fig. 57B) probably causes a longitudinal split in the shell.

Ocellovelia germari Unripe eggs are typically veliid (fig. 58A). The four to six micropyles are grouped on an anterior thickening of the shell. They penetrate the plug vertically and make a short curve along the innerside of the chorion (fig. 58B).

Oravelia pege Unlike other eggs of the veliids and in complete contrast to those of *Macrovelia,* the egg of *Oravelia* is slender and spindle-shaped (fig. 60A), so that it is probably deposited in more sheltered sites. The smooth shell has a very weakly developed hexagonal pattern, the numerous hexagons being small in size. The shell has distinct and regular pores, but a continuous loose-textured inner layer could not be traced in optical sections, and so must be very thin. The anterior pole is thickened to form a knob which is traversed by three to five micropyles (diameter 2.5 μ). Deep holes between but separate from the micropyles (fig. 60B) are a distinct feature. These irregular holes do not seem to connect with the porous inner layer.

Chepuvelia usingeri The chorion (8.5 μ thick) does not seem markedly porous by optical microscope, except for a thin outer layer around the micropylar area. The four or five micropyles are grouped in a circle and the internal canals follow the same circular pattern, clockwise when seen from above (fig. 58').

Macrovelia horni The chorion of this aberrant form is of particular interest, as even the optical microscope shows a distinct inner meshwork (fig. 59B, ail). Further,

the increased number of micropyles (about 7) and their almost circular arrangement is of great importance as will become apparent later. The micropyles have lined openings (2.5 μ) and they curve inwards away from the anterior pole. The few eggs seen had irregular openings within the micropylar circle (fig. 59A, B), but we do not think they were aeropyles. The inner meshwork seems to originate posterior to the micropyles. Canaliculi reaching down to the porous inner layer were not found with the optical microscope, but as in *Microvelia* (micrograph fig. 293) they could be expected all over the egg. Except on the micropylar area there is a distinct polygonal outer sculpturing with circular elevations within the polygons (fig. 59C). The oval shape of the egg suggests that eggs are laid fairly exposed and that the chorion splits longitudinally.

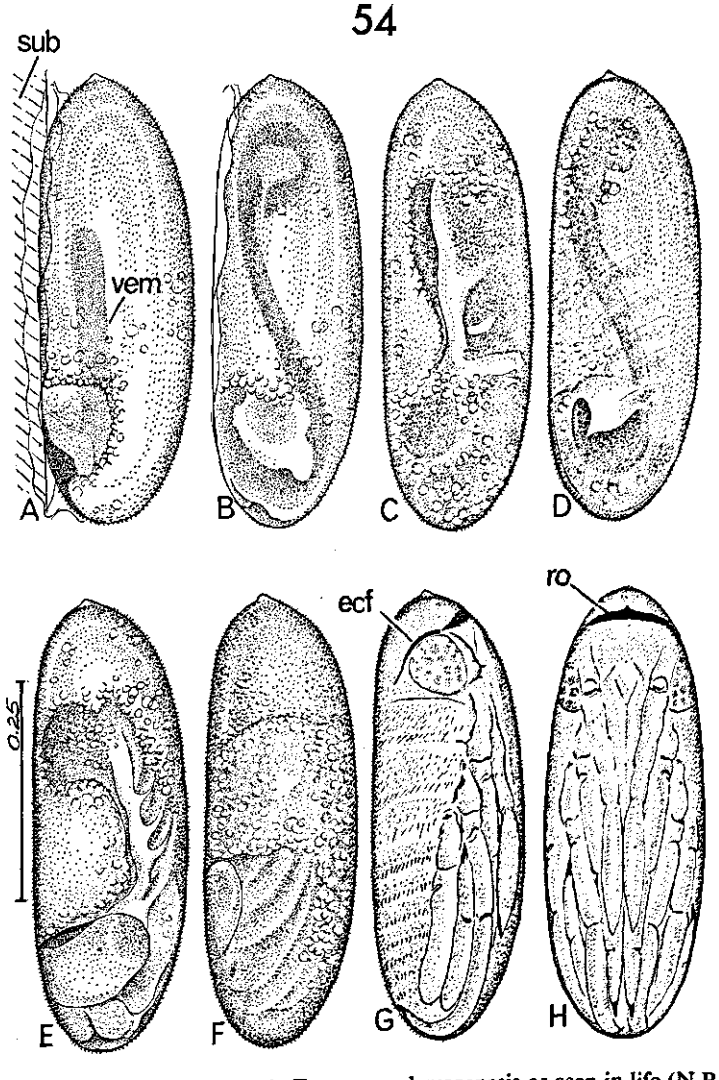


Fig. 54. Veliidae, *Microvelia reticulata;* A–F: gross embryogenesis as seen in life (N.B. substrate on left) A: process of invagination; F: halfway through revolution; G, H : posture of prolarva.

PREVIOUS DESCRIPTIONS Brief accounts of *Microvelia* and *Velia* eggs are given by LEUCKART (1855), HUNGERFORD (1919), JORDAN (1932), POISSON (1933), MIYAMOTO (1953) and LEBRUN (1960).

LEUCKART and POISSON recorded two micropyles in the *Velia* egg whereas LEBRUN showed that, in *Velia* also, the ruptor ovi conforms to our description for *Microvelia.* A short micropylar projection terminating in four minute lips is mentioned for the egg of the marine veliid *Halovelia marianarum* Us. (KELLEN, 1959). The egg-burster of this species, which attaches its eggs to rocks just above the water surface, is like that of *Microvelia.*

2.1.5 Gerridae

MATERIAL: *Gerrist horacicus* Schumm., *G. lacustris* L., *G. odontogaster* Zett. (living deposited eggs). *G. gibbifer* Schumm., *Aquarius paludum* Fabr., *Cylindrostethus hungerfordi* Dr. & C., *Trepobates taylori* Kirk., *Rhagadotarsus* sp., *Ptilomera assamensis* Hungf. & Mats., *Ventidius distanti* Paiv. (ripe ovarian eggs). Origin: *Cylindrostethus* from Surinam, *Trepobates* from Curaçao, N.A., *Rhagadotarsus* from Ivory Coast, *Ptilomera* from Laos, *Ventidius* from Malaya.

Gerris thoracicus

A special feature of oviposition adds a further complication to the determination of the egg's polarity. Eggs are attached normally longitudinally to the underside of floating weeds, one side of its long axis being glued to the substratum. The female remains in a horizontal position upon the water film and dips only the extreme tip of its abdomen under water. The small ovipositor is able to contact only the edge of a floating leaf and so rows of eggs are found only along the margins of the substrate. Such eggs are suspended from the floating material. When the latter is not available, the female takes a more oblique position in order to sink its abdomen deeper under water, searching for submerged material. In containers, eggs are deposited on the glass bottom when the water is less than a centimeter deep. When the depth is too great, eggs are placed against the vertical glass wall. The same side of the egg is exposed, regardless of the method of oviposition. Dorsal and ventral planes of the gerrid egg are readily recognized. The venter of the mature embryo always faces the convex side. In both situations, the prolarva escapes from the side of the egg away from the substrate, although the position and orientation taken by the laying animals was the same. This and also topographical data from early embryogenesis suggest that the female is able to regulate internally the dorsoventral orientation of the egg, so as to adapt their position to the oviposition-site. The type of oviposition, in which the eggs are pressed down upon the substrate, is found in most other families. Therefore, in order to be laid below an object, the egg must undergo a rotation of 180° around its polar axis somewhere in the genital tract. The stimulus for deciding whether the next egg must rotate or not may be through contact receptors on the ovipositor.

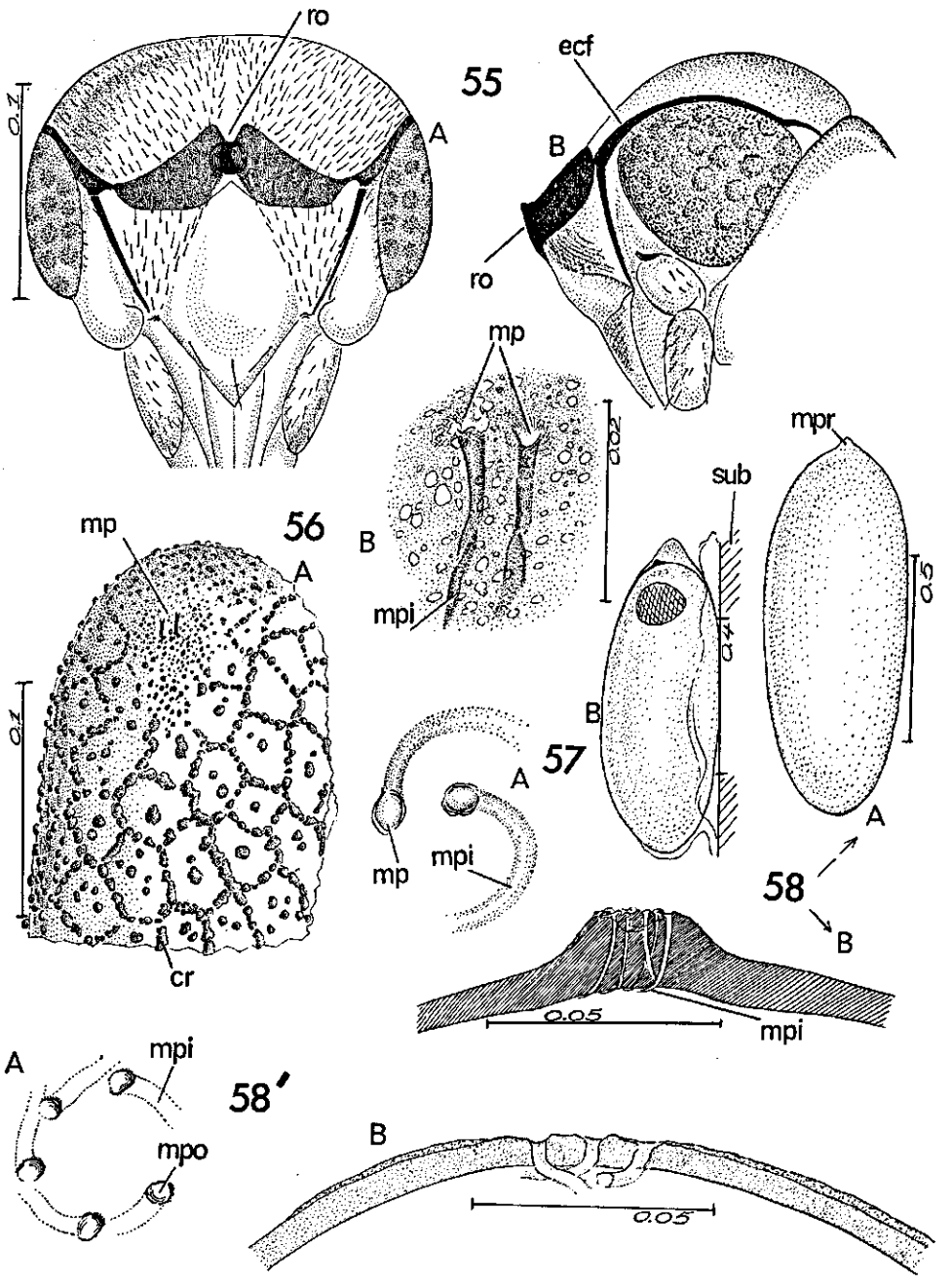


Fig. 55–58′. Veliidae 55. *Microvelia reticulata;* A, B: prolarval head with egg-burster. 56. *M. signata;* A: fore side near anterior pole; B: micropyles, surface view. 57. *Hebrovelia* sp.; A: micropyles, surface view; B: outline of egg. 58. *Ocellovelia germari;* A: lateral view of egg; B: optical section of micropylar area. 58′. *Chepuvelia usingeri;* A: micropyles from above; B: optical section of cephalic pole.

CHORION Smooth, without distinct sculpturing or hexagonal pattern, thickness about 8 μ, of double thickness at the posterior pole bearing the hydropyle. In surface view the chorion appears an even grey, which becomes coarser when the focus is lower. In optical sections, it seems cross-striated but does not show a substantial inner porous layer. Electron micrographs in fact show a fine tangled porous inner layer without sharp limitation outwards. The architecture is essentially as in *Microvelia*, except for differences in the thickness of layers (fig. 292C–E) and the presence of only very small projections. The innermost layer is only 1/100, and the subsequent spongy layer 1/20 of the total shell thickness. The narrow (0.03 μ) pore canals are grouped more densely in the inner half than in the outer half of the thickest shell layer (fig. 292). An explanation of this discrepancy is that the density of the canals right of the anterior pole is greater than just posterior to it. The micrographs are from oblique cross-sections close to the anterior pole.

The egg darkens later through irregular dark spots in the serosal cuticle on the exposed side. The blunt anterior pole bears a slight depression, through the centre of which passes a single short micropyle, which runs slightly in a transverse direction and opens inward through the shell by a short rectangular bend. After the appearance of the serosal cuticle, its location is marked with a small black spot.

GROSS EMBRYOGENESIS (fig. 63 A–F, 62A–B) Six eggs, kept under water at 30 °C were incubated for 6–7 days. Ten eggs, kept at the same temperature in moist air required 8–9 days in order to hatch. The difference in time must be checked in a greater number of eggs.

The blastopore appears aft of the posterior pole. The germ band initially forms a straight line immersed in yolk, and is covered caudally by a cluster of isolated intensely staining cells, presumably the germ cells. The band remains crosier-shaped because flexure is only caudal and not dorsal. The cephalic end too becomes completely separate from the egg wall. At the time of appearance of the protocormic buds, the mid-thoracic appendages are longer than the other buds. Later, these will give rise to the extremely long rowing legs of larvae and adults. With the further elongation of the appendages and while the serosal cuticle develops and starts to darken, the embryo starts to rotate 180° around its polar axis. The direction and rate of this movement, which is complete long before revolution, was not established. Revolution occurs, without further rotation, along the convex side of the egg and the embryo assumes the final position for eclosion. The account given here is based on a study of some hundreds of eggs of the spring generation in 1963. All eggs, whether deposited upon leaves or suspended from them, behaved in the same way. Our observations on 13 eggs of the same species from the summer generation in 1958 contrast with this. These eggs were laid almost simultaneously, probably by one female. The position before blastokinesis in all these eggs was the same, but from then on, only eight eggs behaved as above. Blastokinesis in the remaining five embryos began with a 180° rotation back, so that after revolution their venter faced aft. All embryos rotated again 180° anti-clockwise when observed from the anterior pole, thus allowing successful hatching.

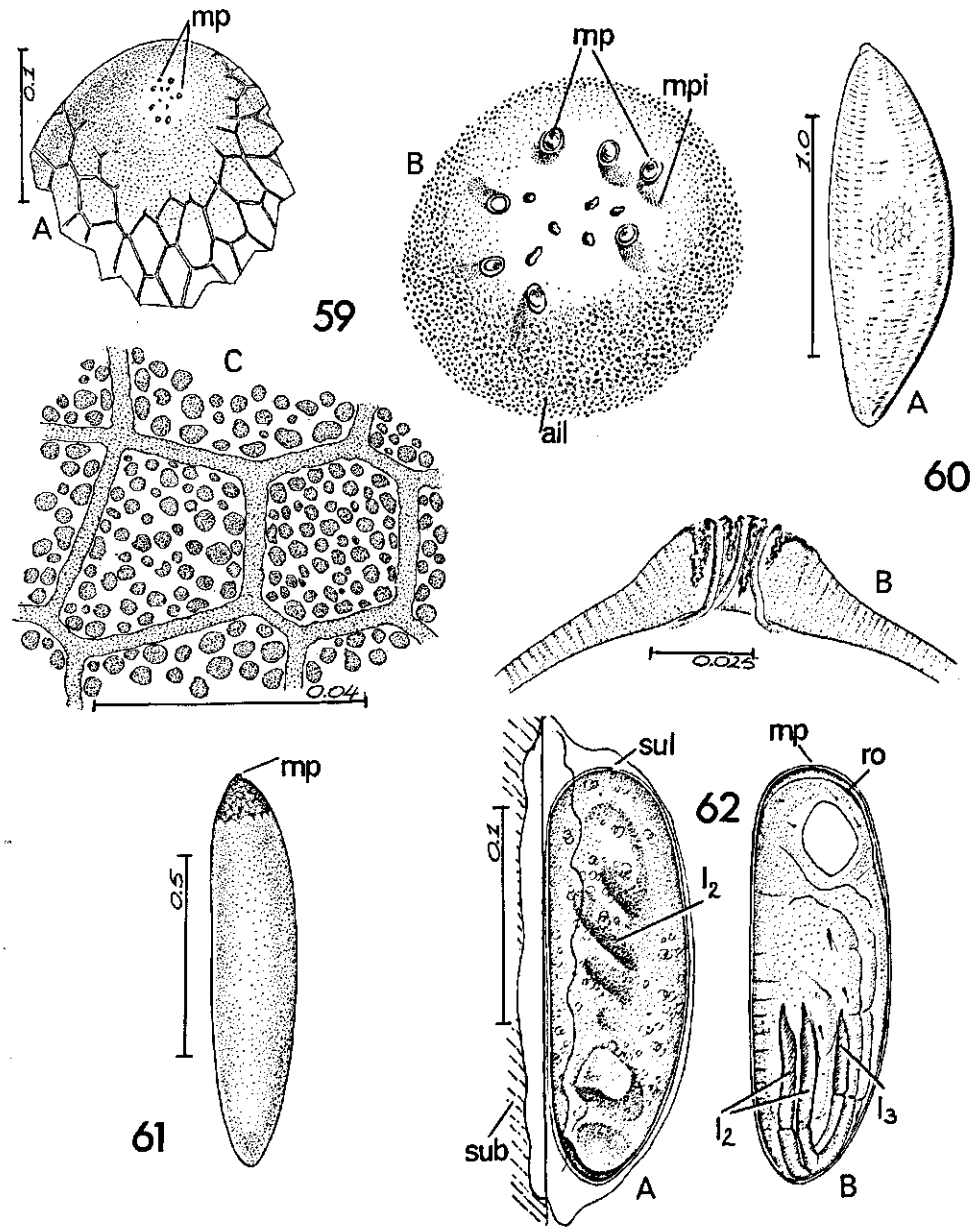


Fig. 59–62. Veliidae, Gerridae 59. *Macrovelia horni;* A, B: anterior pole, surface view of unripe egg; C: exterior chorionic pattern, mid part of ripe ovarian egg. 60. *Oravelia pege;* A: outline of ovarian egg; B: optical section of micropylar area. 61. *Rhagadotarsus* sp., outline of ovarian egg, lateral. 62. *Gerris thoracicus;* A: living egg containing young embryo; B: posture of prolarva (N.B. substrate on left).

Thus, a total of three rotations occurred in this latter sample, two before and one after revolution. The cause of all this movement is unknown, although the fact that all 13 eggs were removed from the substrate soon after they were laid, could be of influence. On the other hand, such a detachment had no apparent effect in the larger sample of spring eggs. However, the variability in egg laying, mentioned above, may indicate that the egg system has not yet reached a stable stage of evolution.

The gerrid egg has a serosal hydropyle slightly excentric at the posterior pole (fig. 63B, sh). The organ becomes detached from the serosa just before revolution (fig. 64A–F, studied in 12 eggs). The embryonic head is found in the position given in fig. 64A for a long time before revolution. A cone of yolk along its ventral side connects the hydropyle. The yolk cone is intimitely surrounded by the serosa, which is joined with fine protoplasmatic filaments to an outer envelope. The origin of this envelope is not clear. It is unlikely that it represents the inner layer of the serosal cuticle, which in other insects is said to be resorbed at a much later time. If such an attribution of the envelope is correct, it appears that in *Gerris* it is resorbed by the serosal cells, but this resorption remains restricted to the aft half of the egg. For some time after the revolution, its remnants can be traced along the convex fore half. Anteriorly it fades away aft of the pole and posteriorly it is broken just anterior to the hydropyle. The layer may be an incompletely secreted second serosal cuticle (see discussion p. 314, 315). The hydropyle is detached from the retracting serosa in a spectacular way at a visible rate (fig. 64C–F). The serosal cells at the top of the yolk cone coalesce and the formless mass is stretched out in a thick strand by the contraction of the whole serosal system. The hydropyle is now bordered by a ring-like thickening (fig. 64D). Gradually the serosal mass retracts but remains in contact with the hydropyle for a while by means of lengthening filaments arising from each individual cell of the latter. At last, contact is completely broken and the serosal mass migrates anteriad as a decreasingly thickened part of the serosa during revolution. This revolution begins 30 minutes after contact is broken. The antennal apices split open a hole through the amnion-serosal fusion and, within 20 seconds, the completely freed antennae point into the posterior lumen of the egg. It takes the embryo less than half an hour to move up to the anterior pole. The uptake of the serosal plug results in a clearly visible dorsal organ. It seems normal in this species that the serosal hydropyle is left behind. We have not followed the detailed fate of the organ in the abnormal case when revolution is preceded by a second rotation of the embryo.

HATCHING Entire incubation and hatching proceeds successfully both in water and in moist air. The posture of the fully grown embryo is of interest because the unequal length of the legs produces a characteristic asymmetrical jig-saw pattern (fig. 62B, diagram fig. 279F). The two elongated mid legs coil side by side at the posterior pole up to the metathorax at one side. In the 82 eggs checked, there was no marked polarity; left-coiling mid legs were almost as frequent as right-coiling legs. Sometimes, unilateral polarity is suggested in isolated series of eggs, originating from single females. In one series of eight eggs only one coiled to the left; in another series

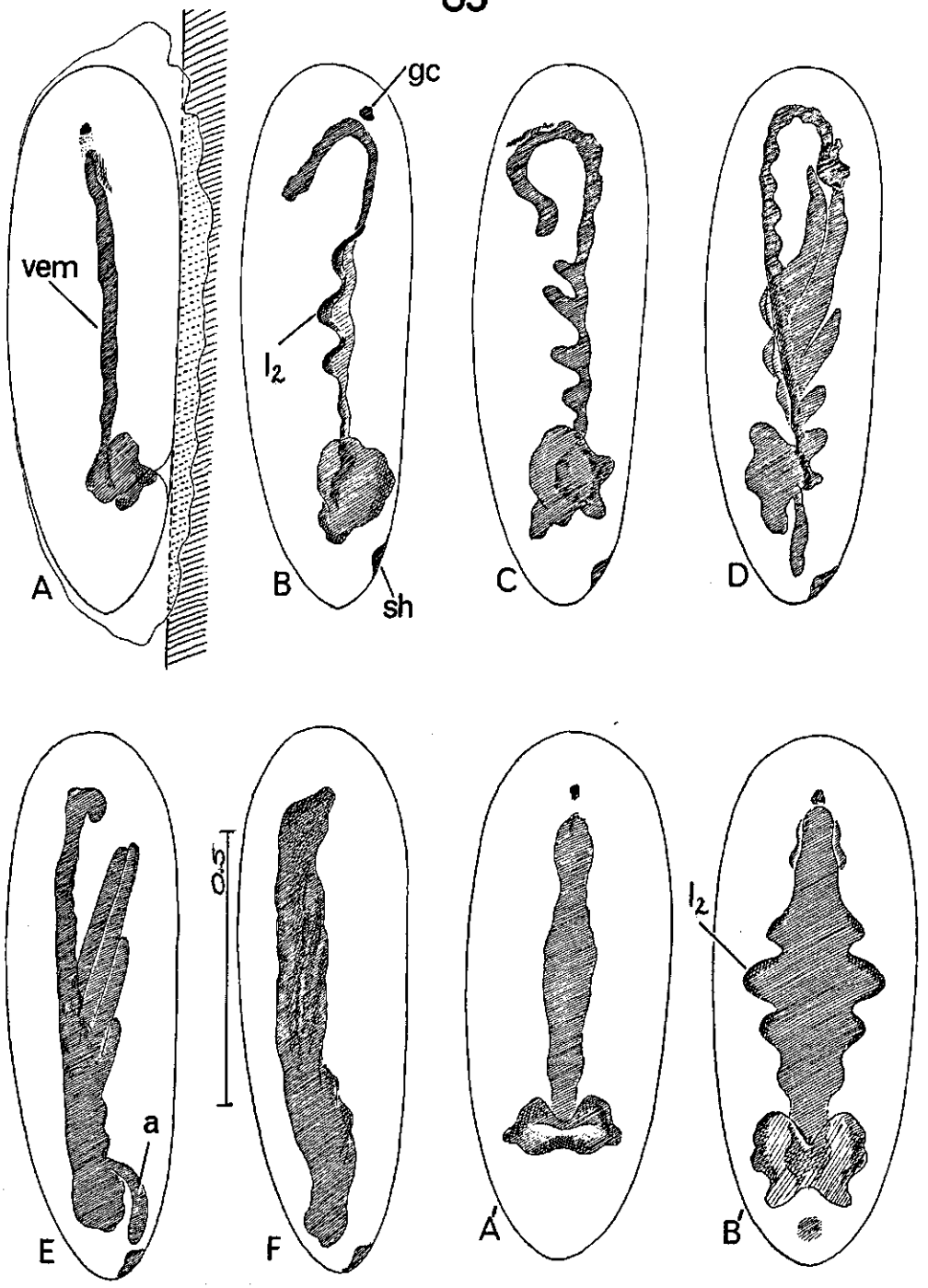


Fig. 63. Gerridae, *Gerris odontogaster;* A–F: first half of embryogenesis, lateral; F: condensed stage; A′, B′: dorsal view of embryo corresponding with stage A and B, respectively.

only one of the six coiled to the right. The arrangement of the hind legs always corresponds with the direction of the mid legs in that the right hind leg ends in the most lateral position on the left side in case the mid legs are right-coiling. With left-coiling of the mid legs, the hind legs are the mirror image.

Hatching is aided by a solid longitudinal egg-burster of the cruciform shape as in *Hydrometra*, but otherwise there is no sclerotized epicranial frame. The shell opens along a median slit from the anterior pole reaching two-thirds of the way down the convex fore side. Ten eggs treated with potash burst open laterally or aft. The egg-burster makes the actual cut, as the future eclosion slit does not develop as a weak line.

ADDITIONAL MATERIAL *Gerris lacustris* and *G. odontogaster* (ripe deposited eggs) deviate only slightly from *G. thoracicus*. *G. odontogaster* places isolated batches, containing only a few eggs arranged side by side. Differences in allometric growth of the mid legs are demonstrated in the level reached by them in the egg. In *G. odontogaster*, the coil of the mid legs extends up to the head. Whether a significant deviation from the 1:1 ratio between left and right forms occur in this species has not been checked. Chorionic structures of other gerrids show no special features. The chorion of *Cylindrostethus* is thick (17.5 μ) and without any sculpturing. The egg of *Trepobates* looks like that of a veliid as regards the presence of small protuberances on the convex side. The opposite side bears an irregular indistinct reticulation. The chorion of all species studied shows a fine even porosity, probably similar in form to that in *G. thoracicus*. The shell of *A. paludum* has been sectioned for the electron microscope, and had the same architecture (fig. 292A, B) as in *G. thoracicus*. Gerridae normally have one micropyle, but the *Ventidius* and *Ptilomera* species has two or three. These are very close to each other and their inward extensions run parallel.

The *Rhagadotarsus* egg (fig. 61) also possesses one micropyle, which is outwardly marked by a nozzle-like projection as in *Hydrometra*. *Rhagadotarsus* has a long ovipositor and eggs are believed to be embedded; it seems to be an exception in the family. The shape of the egg strengthens this supposition. The upper tenth of the egg would extend from the substratum since it has a distinct structure with fine cracks and hexagonal sculpturing. The rest of the 2.5 μ-thick shell seems entirely featureless.

PREVIOUS DESCRIPTIONS The many descriptions of gerrid eggs refer to outer appearances, egg-bursters and sometimes recognition of the micropyle (*e.g.* LEUCKART 1855, MECZNIKOV 1866, LUNDBECK 1914 *(Halobates)*, HUNGERFORD 1919 (5 American species of different genera), POISSON 1933, WESENBERG-LUND 1943, LEBRUN 1960). From all these data a very uniform picture of the gerrid egg with a single micropyle can be derived. In 1869, an outstanding and highly admirable presentation of the embryogenesis of a *Gerris* sp. was given by BRANDT. He noted that the antennal tips penetrate the amnion-serosal opening first. He mentioned further the reddening of the eye before revolution and the presence of an egg-burster and one micropyle. He stated that the allometric differentiation of the legs starts after the yolk has been taken up. Our findings show that this allometry has already occurred very early in the thoracic

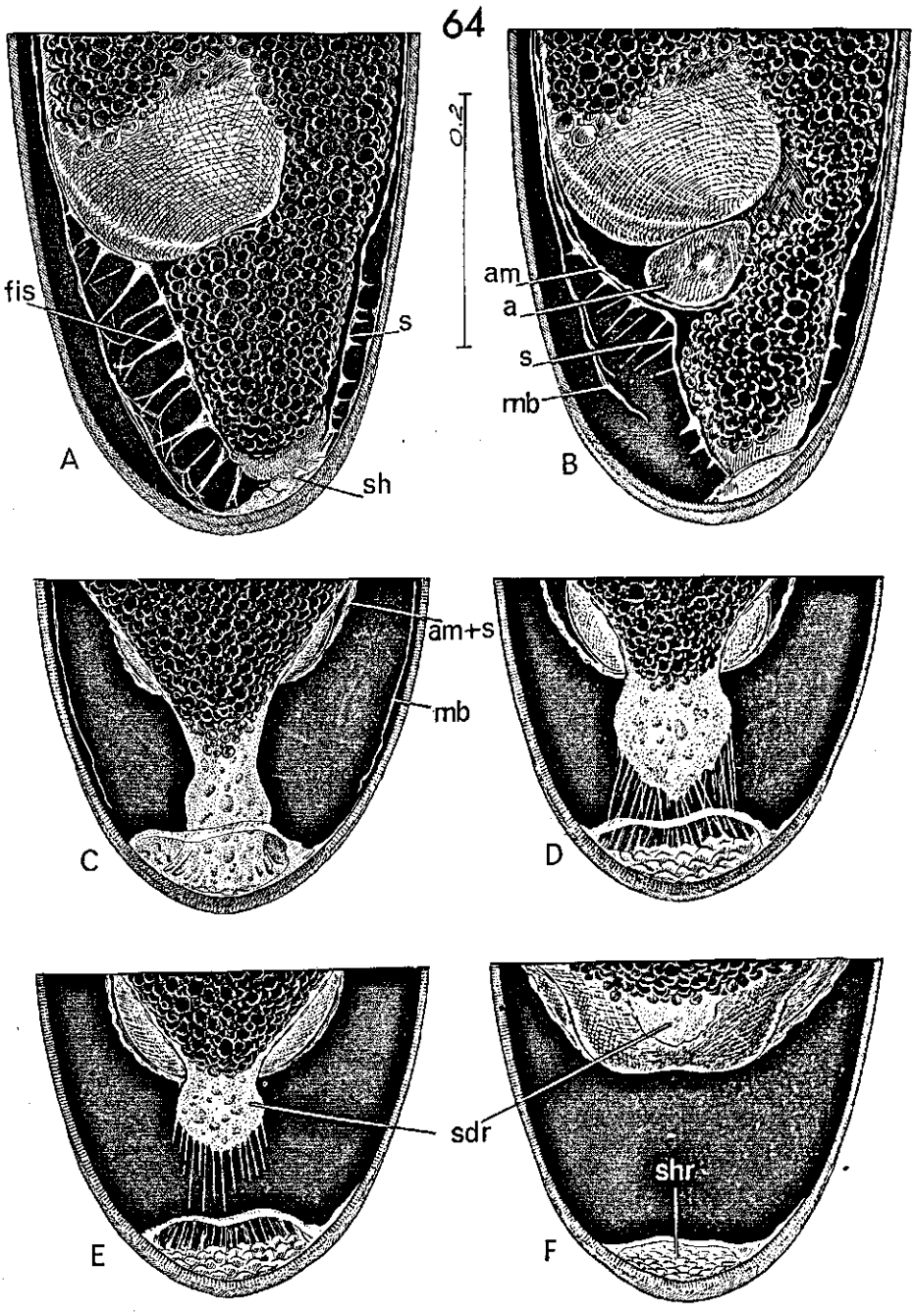


Fig. 64. Gerridae, *Gerris thoracicus*, posterior pole, some phases incipient to revolution, detachment of serosal hydropyle A, B: lateral view; C–F: ventral view of embryo.

buds. BRANDT recognized that blastokinesis is caused by contraction of the embryonic envelopes. He also studied the detachment of the thickened serosal cells, which he indicated as 'Kuchen' and which are considered by us as hydropic cells.

Aquarius najas (SATTLER 1957) has an identical arrangement of the prolarval legs as shown above in some *Gerris* species. The figure presented by BRINKHURST (1960) gives an anomalous alignment of the hind legs in *A. najas*. The mid legs in this species are relatively longer and coil back over the head. The configuration of the legs in the prolarva of *G. fluviorum* F. as shown by TONAPI (1959), is doubtless based on inaccurate observation. Contrary to our findings in *G. thoracicus*, *A. najas* shows an outstanding majority of the right-coiling embryos. SATTLER found only 22.5% of the 160 eggs coiling left. *A. najas* dives completely under water and remains there for half an hour to lay a batch of around 25 eggs. The careful observations of SATTLER suggest that eggs are preferably laid in the normal depressed way. He described how a floating leaf with a batch of nine eggs underneath was placed in a cool environment and illuminated with a lamp placed just above the object. The fact that six prolarvae were oriented venter-up and were thus unable to escape, was attributed to light. Although this may be, he did not ascertain whether the egg's polarity was adapted to the reversed oviposition-site (see our observations on p. 66).

2.2 Pentatomomorpha

In this and the following section (2.3), we have refrained from describing general chorionic structures, as the group as a whole is fairly well known as regards specific egg characters. SOUTHWOOD (1956) characterizes pentatomomorphous eggs by their micropyles consisting of a central micropylar canal surrounded by porous air-filled chorion, lack of operculum, but sometimes with a pseudoperculum, and by their median egg-burster on the vertex. This definition, however, seems rather too general and static, and the term vertex needs further comment. Sections of the shell of a few species will be presented below. Much more work on the layered structure of the shell and the structures of the embryonic cuticle(s) is needed to elucidate evolutionary divergencies and parallelisms. Some trends which become evident from this data will be discussed in Chapter 3. Our main aim here is to expand our knowledge of the embryology of this group. Detailed embryological studies of *Pyrrhocoris apterus* (Pyrrhocoridae) were made by SEIDEL (1924) and of *Oncopeltus fasciatus* (Lygaeidae) by BUTT (1949). These examples show quite different patterns from the groups already discussed. Though the figures in the papers of these two authors suggest that the embryo does not rotate during blastokinesis, this has not been specifically claimed. The eggs of the two species are recorded as being radially symmetrical so that rotation would be easily overlooked by someone not concerned with polarity. The lack of a rotation could be of phylogenetic importance, since rotation is a normal feature in Saldidae and Amphibicorisae. This problem attracts our attention in the following examples.

The species in which we studied embryogenesis failed to complete embryonic

development when the eggs were placed under water. Malformations of the germ band soon occurred when fresh eggs were submerged. If eggs with fully grown embryos were submerged, hatching was generally anomalous.

2.2.1 Aradidae, Idiostolidae, Thaumastellidae

Aradidae

MATERIAL: *Neuroctenus* sp., *Mezira rugosa* Sign. (Mezirinae). Both species were from the Ivory Coast; ovarian and some preserved stages of deposited eggs.

Neuroctenus sp.

The egg is dorso-ventrally compressed and boat-shaped (fig. 65A–C). The more convex side is thinner-walled and more delicate than the flattened side opposite. The eggs were deposited under the bark of fallen trees, always with their convex side glued to the substrate (fig. 65B).

CHORION The flat side bears characteristic sculpturing. The surface has a regular pattern of open blisters. The spaces between the blisters are filled with greyish, apparently porous, material (fig. 65D). The blistering is very thin on the aft side of the egg and is easily disrupted from the underlayer, when the egg is loosened from the substrate. There are from two to four minute truncate aero-micropylar processes, close to each other at the anterior pole. The inner chorionic layer is transparent and, when observed through the centre of the round pits or in optical sections there is no sign of an inner aeriferous layer except in the micropylar region. The presence of the aerostatic inner layer was verified with the electron microscope in transverse sections (fig. 295), suggesting that the porosity is continuous all around the egg. The cavities in this sheet are extremely fine, as the whole inner layer of chorion, of which the porous sheet forms the innermost part, measures only about 1.5 μ. The continuous chorionic film, which limits the aerostatic layer and has irregularly spaced struts towards the body of the shell, is about 0.1 μ thick. What we have seen optically as open blisters separated by porous zones, compose the outer layer of the shell, which has an anomalous structure. The first anomaly is that the outer and inner layers are not connected to each other. Yet there is no doubt that the outer layer is of true chorionic origin. The open blistering is already present in ovarian eggs. The blisters are more angular, and the boundaries form a hexagonal pattern which undoubtedly marks boundaries of the follicular cells. The outer shell consists of a vacuolate fibrous material (fig. 295), which is of higher electron-density than the inner layer. The ridges surrounding the pits of the blisters are of a coarsely flaky structure. The outer wall and the bottom of the pits are of a denser, multilayered nature. In microsections of laid eggs a smooth pavement of a pale substance is seen to cover and partly impregnate the outer surface of the shell. The summits of the ridges are always free of it. The outer pavement presumably

represents not the cement layer but chorionin which may account for the sharply defined ring-structure of the blisters, already present in ovarian eggs.

Whatever the function of the porousness of the outer shell, it is clear that it gives ample entry to air. There is, however, no continuity with the innermost aerostatic layer of the shell, unless it be in the micropylar region. The blistered structure and vacuolated ridges extend unchanged onto the micropylar processes. The cupula of the latter is fully developed before the excretion of the outer layer of the shell (fig. 65E). The cupula is only later covered with the outer chorion and it seems that its porousness extends over its upper margin to make contact with the conducting internal porosity of the aero-micropylar process (fig. 65F). Thus it may be that the outer layer of the shell stores air from which oxygen could be consumed when the bark fills with water during flooding or heavy rain.

GROSS EMBRYOGENESIS The few stages available for study show the germ band already with appendages and immersed (fig. 65A). The whole embryo is immersed in yolk, except the frontal region of the head, which remains touching the egg wall. This fact suggests that the developing organism has invaginated at the side of the egg precisely opposite to that in families already described. As a consequence, the antennal buds in *Neuroctenus* point anteriad instead of caudad and the shape of the embryo is ↄ instead of ʔ . The intermediate stages between A and B in fig. 65 show that revolution follows directly from the orientation in A, thus not after a rotation. The ventral side of the mature embryo faces the substrate side of the egg.

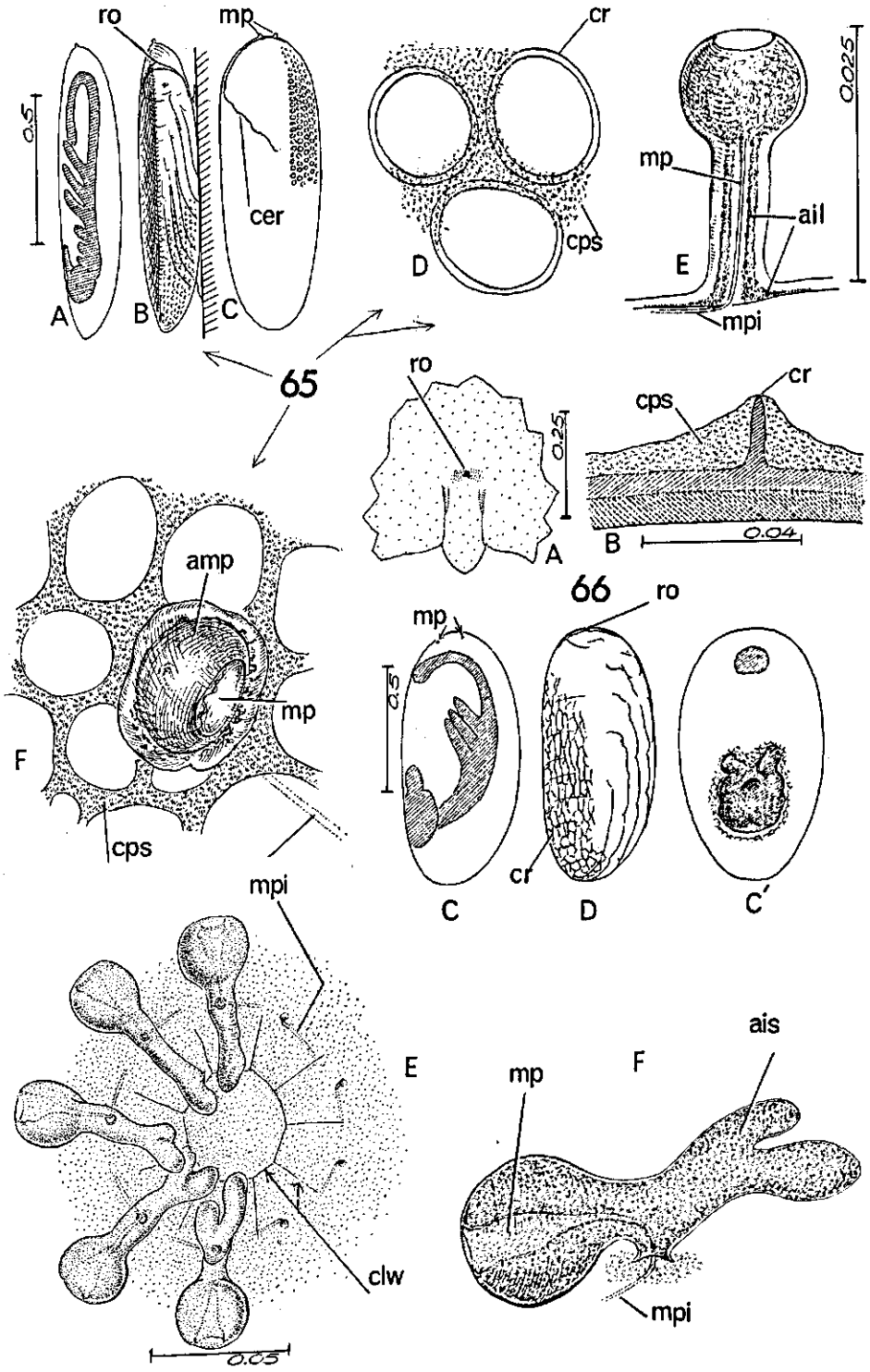
ECLOSION The egg-burster is an elevated sharp point on the frons of the embryonic cuticle. It cuts the chorion between the aero-micropylar cups. The eclosion split runs along the anterior margin of the flat side of the egg and then turns transversally across the flat surface (fig. 65C). The area demarcated by this line is thus nearly like a pseudoperculum.

Mezira rugosa

The eggs are not flattened (fig. 66D). A few were laid in a vial containing some piece of bark. Instead of being glued, these eggs were found loose on the bottom of the glass. The spherical white egg has inconspicuous reticulation. The chorionic structure is quite different from that in *Neuroctenus*, but has not been completely elucidated. Fig. 66B shows a faint picture of an optical section. The chorion is two-layered with

---

Fig. 65–66. Aradidae, Lygaeidae 65. *Neuroctenus* sp.; A: embryo before revolution; B: prolarva; C: vacated shell, fore side; D: fragment of shell, surface view; E: aero-micropylar cup, optical section; F: the same, from above. 66 A–D: *Mezira rugosa;* A: egg-burster; B: optical section of shell; C: invaginated embryo; D: prolarva; C′: fore side of stage C; 66 E, F: *Orsillus depressus;* E: cephalic pole from above , four aero-micropylar processes omitted to show internal canal; F: aero-micropylar process.


ro
mp
cer
A
B
C
0.5
cr
cps
D
0.025
mp
ail
E
mpi
65
ro
0.25
A
cr
cps
B
0.04
amp
mp
F
cps
66
mp
ro
0.5
cr
C
D
C'
mpi
E
clw
0.05
ais
mp
F
mpi

ridges extending from the outer layer. In fact the ridges are as thick as the solid chorion (12 μ), but the reticulation is levelled because the follicular pit is filled up with less dense material. An aeriferous inner layer could not be resolved optically along the greatest part of the shell, but presumably it is present throughout as in *Neuroctenus*. There are 3–4 very small aero-micropylar cups at the anterior pole (diameter of cup about 15 μ, micropylar canal 2.5 μ). The micropyle is inclined transversely and proceeds a short distance into the cavity of the egg.

Fig. 66C and D reveal a course of embryogenesis similar to *Neuroctenus*. Fig. 66C shows that the frons of the head remains entirely superficial. The simple egg-burster (fig. 66A) is like that of the previous species. The eclosion split is probably a longitudinal or inclined line, as no operculum boundary is formed in the intact egg.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) mentioned eight authors dealing with aradid eggs and added some of his own observations, including the egg of a termitaphidid, a family which is closely related to Aradidae. TAMANINI (1956) and USINGER and MATSUDA (1959) described eggs of more species, providing photographs of some of them. All these data yield a rather uniform outline for aradid eggs with some reticulation, a few small micropylar cups, simple egg-burster and an irregular eclosion line. The picture of the empty shells of the mezirine *Neuroctenus pseudonymus*, given by the last authors, suggests the presence of an indistinct lateral pseudoperculum.

Idiostolidae

MATERIAL: *Idiostolus* sp. (ripe ovarian eggs: the material from Chile belongs to the same series of the British Museum as studied by SCUDDER (1962) and identified by him as *I. insularis* Berg after comparison with the type. The series, however, may contain two species, one of them undescribed, so that only the genus name is applied here.

The *Idiostolus* shell is the simplest of all the Pentatomomorpha and with the egg alone its affiliation to this group would be very questionable. The shell (5 μ thick) seems entirely solid without a spongy sheath around the two micropyles. The micropyles project a long distance inwards from the shell and curve transversely as shown in fig. 66′. The external opening is only marked by a slight difference in the chorionic material. The centre of the anterior pole bears a weak irregular reticulation. As there is no further differentiation, the eclosion rent is probably longitudinal.

PREVIOUS DESCRIPTIONS None.

Thaumastellidae

MATERIAL: *Thaumastella aradoides* Horv. (ovarian egg, origin Sudan).

Although all seven females studied were captured by attraction to light, one of them

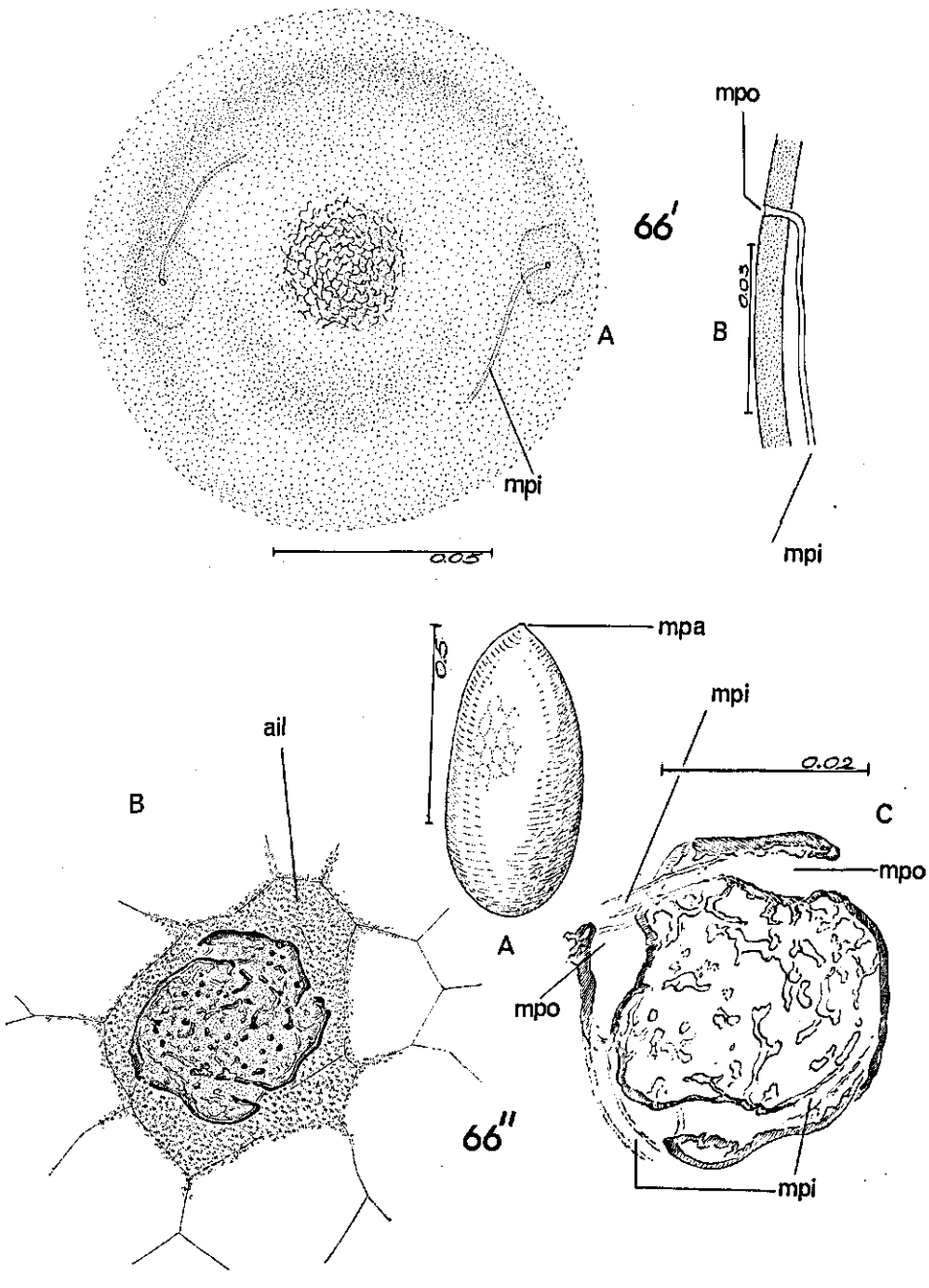


Fig. 66'–66". Idiostolidae, Thaumastellidae 66'. *Idiostolus* sp.; A: cephalic pole from above; B: optical section of micropyle. 66". *Thaumastella aradoides;* A: ovarian egg; B: rosette of cephalic pole with adjacent shell, from above; C: rosette with micropyles, inner view.

contained an egg. The egg is large, half the length of the abdomen, and atypical for a pentatomomorphan. Outwardly (fig. 66″A) it resembles the eggs of certain aquatic or semi-aquatic bugs (e.g. Hebridae, Corixidae). The shell is thin and has a faint hexagonal marking. The eclosion split is most probably longitudinal. The anterior pole bears a small projection, which looks like a rosette at high magnification (fig. 66″B). Initially we could not trace either micropyles or spongy cavities connecting the aerostatic inner layer with the atmosphere. Yet the aerostatic layer is distinct in the region round the rosette and extends by clear cavities along the margins of hexagons. Close inspection of the rosette from the inner side revealed with some difficulty, but unequivocally, the presence of micropyles (fig. 66″C). Their inner transverse deviation follows the same directions as in other lower Pentatomomorpha. The peculiar arrangement in Thaumastellidae (*Th. aradoides* is the only species known) is however that there are just three micropyles, close together and without outer projection or sponge. We could not settle whether the inlet of air occurs along the micropylar canal or elsewhere.

PREVIOUS DESCRIPTIONS None.

2.2.2 Piesmatidae, Malcidae, Berytinidae, Lygaeidae, Stenocephalidae

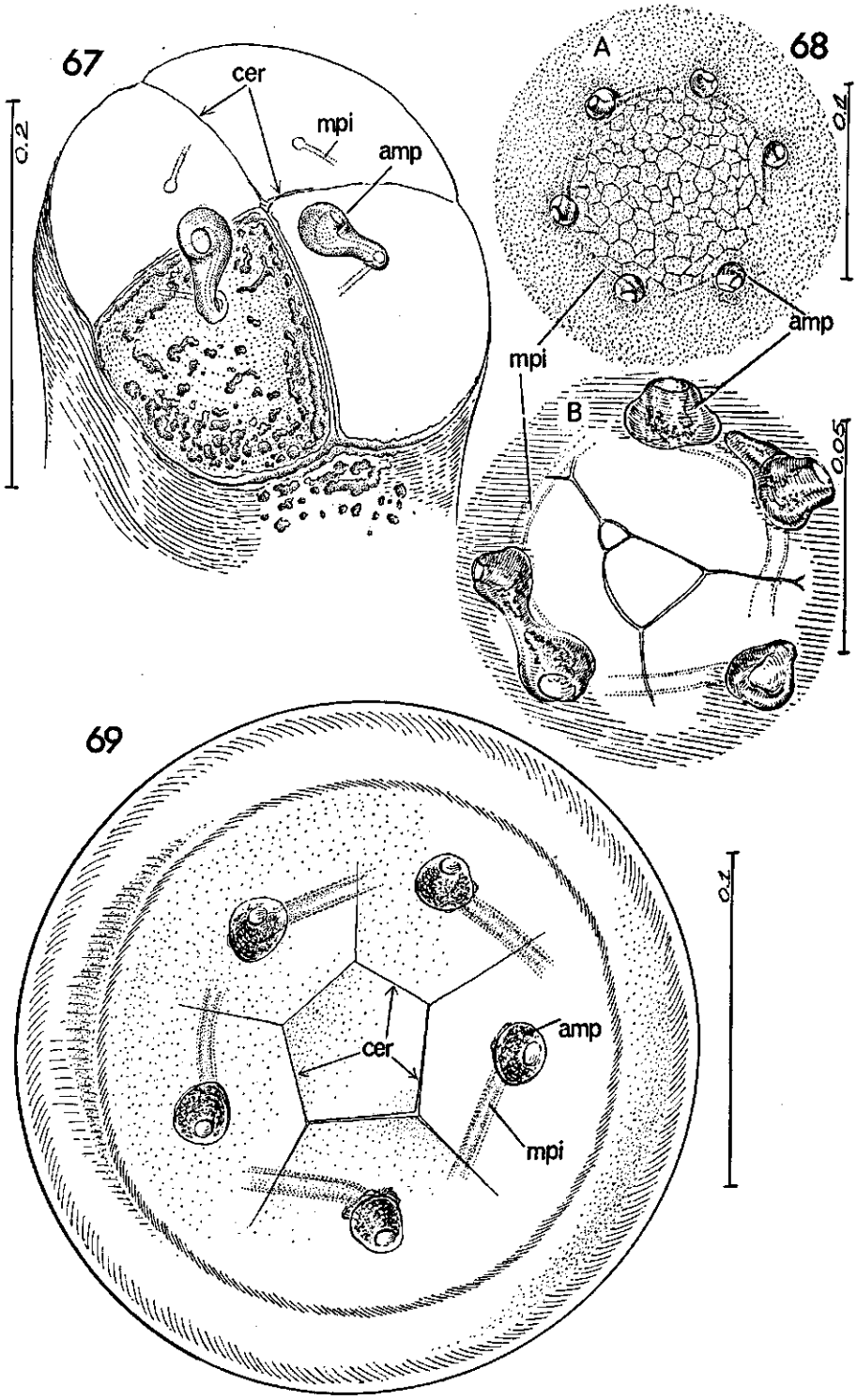
Piesmatidae

MATERIAL: *Piesma quadratum* Fieb., P. *cinereum* Say. (ripe ovarian eggs, the last species from Curaçao, Neth. Ant.); *P. maculatum* Lap. (living deposited eggs).

Piesma quadratum

The egg, which is said to be glued lengthwise to the food-plant, is truncate anteriorly. The anterior end has a thickened ring bounding the truncation, suggesting the presence of a pseudoperculum (fig. 69). However, in lactic acid all ovarian eggs opened along radial lines, starting from the edges of a polygonal plate in the centre of the pole. It is clear that the eclosion lines are formed by the boundaries of follicular cells, which thus are very large. The radial lines run equidistant between each pair of aero-micropylar cups and thus each cup is produced from the centre of one follicle-cell. The cup is short and the micropylar canal deviates in transverse direction and projects a long distance horizontally below the shell. Since the canals of the individual cups deviate in the same way, altogether they follow a circular course, running clock-wise when the anterior surface is viewed.

Fig. 67–69. Malcidae, Piesmatidae, Lygaeidae; cephalic pole from above 67. *Chauliops rutherfordi*, two aero-micropylar cups omitted to show internalcanal. 68A: *Cymus glandicolor;* B: *Beosus maritimus*. 69. *Piesma quadratum*.


67
cer
mpi
amp
0.2
68
A
amp
mpi
B
0.05
69
cer
amp
mpi
0.2

Piesma maculatum

Eggs are glued with their convex side to the underlayer. Chorionic structures are essentially as in the previous species. The polygon in the centre of the cephalic pole always has as many sides as there are micropylar processes, five to eight. The sutures radiating from the polygon are only weakly discernible, because of a reticular sculpture over the whole egg. Empty shells show that the radial sutures indeed are adapted for eclosion. The ripening egg becomes fluted longitudinally and some embryonic stages are illustrated (fig. 70A–C). Noteworthy is the sharp kink in the gnathal region in the many embryos studied in this stage. The embryo was fairly immersed; there was no 180° rotation during blastokinesis, so that the mature embryo faces away from the substrate (in contrast to *Neuroctenus*!)

The egg of *P. cinereum* is like that of both previous species. A *cinereum* female contained, among the several ovarian eggs, one with a fully grown embryo. In this aberrant case there was a median egg-burster of the type to be described for *Berytinus* (p. 84).

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) did not mention the characteristic ecdysal lines in *Piesma*, though he claimed that the eclosion fracture did not always correspond to the border ridge of the anterior pole. However, the drawing in WEBER (1930, fig. 259k, after EXT) and in PUCHKOVA (1956, fig. 27, Pl. 1), of an empty egg, show all hexagons bearing the micropyles, turned back like the flaps of a cardboard box. WILLE made the same observation in 1929.

Malcidae

MATERIAL: *Chauliopinae: Chauliops rutherfordi* Dist. (origin Ivory Coast), *C. bisontula* Banks (origin Malaya); *Malcinae: Malcus flavidipes flavidipes* Stål (origin Indonesia), *M. tuberculatus* Štys (origin Sikkim). Only ovarian eggs of the four species were studied.

Chauliops

Eggs of both species are fairly large and the abdomen contains only a few, indicating few ovarioles. The moderately elongated egg is square in cross section. The shell is brown and fairly solid (about 10 μ thick). The truncate anterior pole is divided in four quarters, each bearing an aero-micropylar cup with a stem. The outer micropylar opening measures 5 μ, the inner one 2 μ. Each micropyle projects inwards and always curves clockwise as seen from above the pole (fig. 67). The quartering of the pole undoubtedly reflects the lines of dehiscence of the shell; the margin of each quarter is sharply incised.

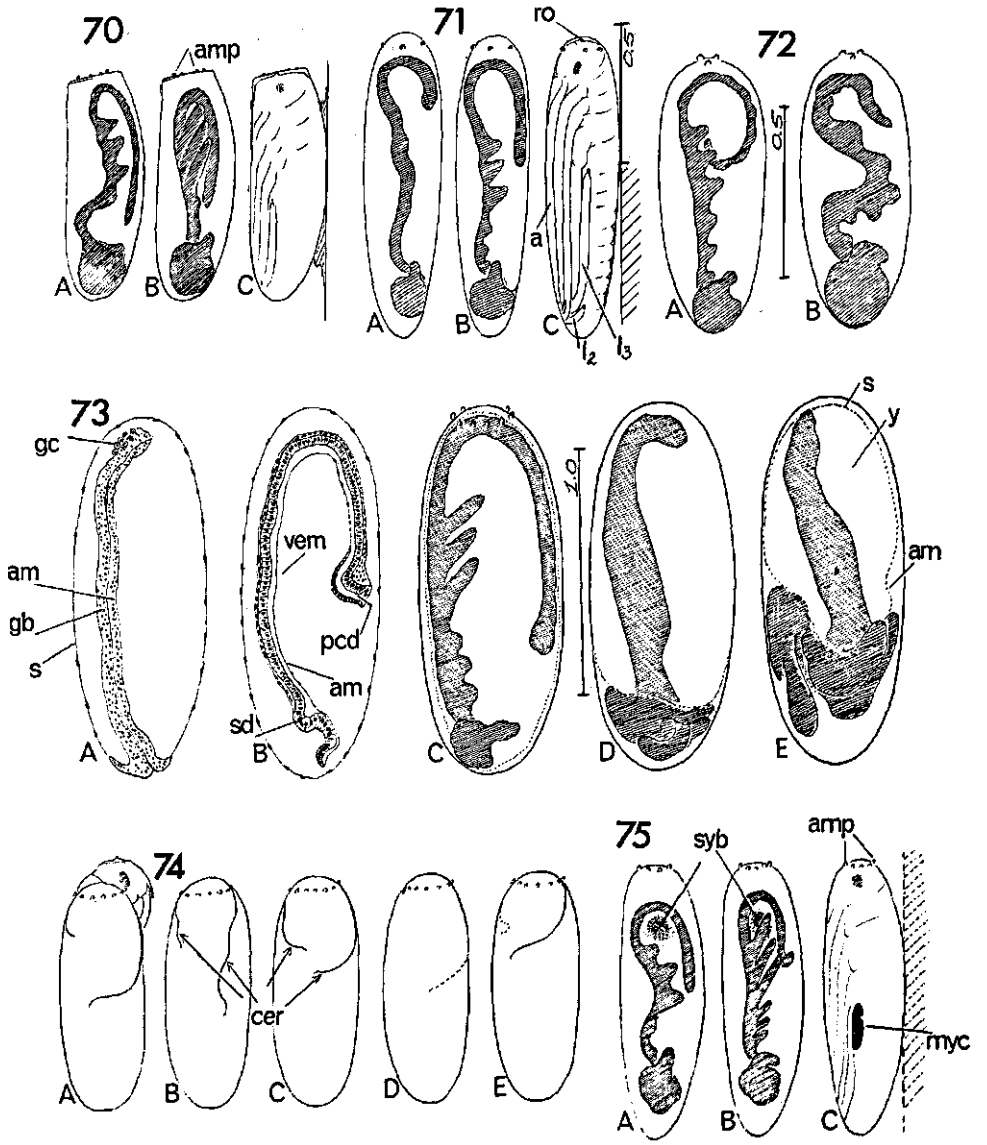


Fig. 70–75. Piesmatidae, Berytinidae, Lygaeidae; embryonic stages and eclosion rent 70A–C: *Piesma maculatum.* 71A–C: *Berytinus signoreti.* 72A–B: *Stygnocoris pedestris;* B: in diapause. 73A–E: *Oncopeltus fasciatus;* A, B: longitudinal section redrawn from BUTT (1949); E: beginning of revolution. 74A–E: *O. fasciatus,* varying types of eclosion rupture. 75A–C: *Nysius thymi;* C: prolarval diapause.

Malcus

Differing from *Chauliops* in having only three micropyles. The eclosion lines are correspondingly forming a λ- instead of a cross-figure.

PREVIOUS DESCRIPTIONS VAN DER GOOT (1929) figured the egg of the Indonesian *Chauliops* (named by him *Ch. bisontula* Banks). The line drawing show similar polar partition with four micropyles.

Eggs are glued lengthwise and confined to the underside of leaves. One female produces only 16 eggs on average and these are deposited over a period of almost two months.

Berytinidae

MATERIAL: *Berytinus signoreti* Fieb. (living deposited eggs); *B. crassipes* H.-Sch. (living deposited eggs); *Gampsocoris punctipes* Germ. (ripe ovarian eggs).

Berytinus

Egg shape and position of the few (4–6) aero-micropylar processes (micropyle not protruding within the egg cavity) are indicated in fig. 71A–C, which show some embryological phases. Invagination occurs posteriorly at the side of the shell to which the ventral side of the band faces before revolution. The band remains immersed, and lies for some time along the longitudinal axis of the egg. With further elongation, only the tail approaches the outside of the yolk. There is no rotation and after revolution the embryo is situated as figured (fig. 71C), thus facing away from the substrate. The crossing of the folded long hind legs causes their extremities to lie lateralwards on both the right and left side. The egg-burster is a transparent helmet with a projecting sharp knife (fig. 77″A, B), pressing against the centre of the anterior pole. The eclosion rent starts as a straight line from the anterior pole and curves soon to one side; it has not been established whether the longitudinal rupture is median or transverse.

The egg of *Gampsocoris* bears only 3–4 aeromicropyles, which have a transverse micropylar canal projecting within the egg cavity (contrast *Berytinus*). The polar area between the micropyles bears no large hexagon.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) listed six other authors who had dealt with berytinid eggs and HERTEL (1955) must be added to the list. All the data do not show major variation in the gross structure of the berytinid egg, except that the *Metatropis* egg is attached by its base to stems.

Lygaeidae

MATERIAL: Geocorinae: *Geocoris grylloides* L., *G. dispar* Wg. (origin southern

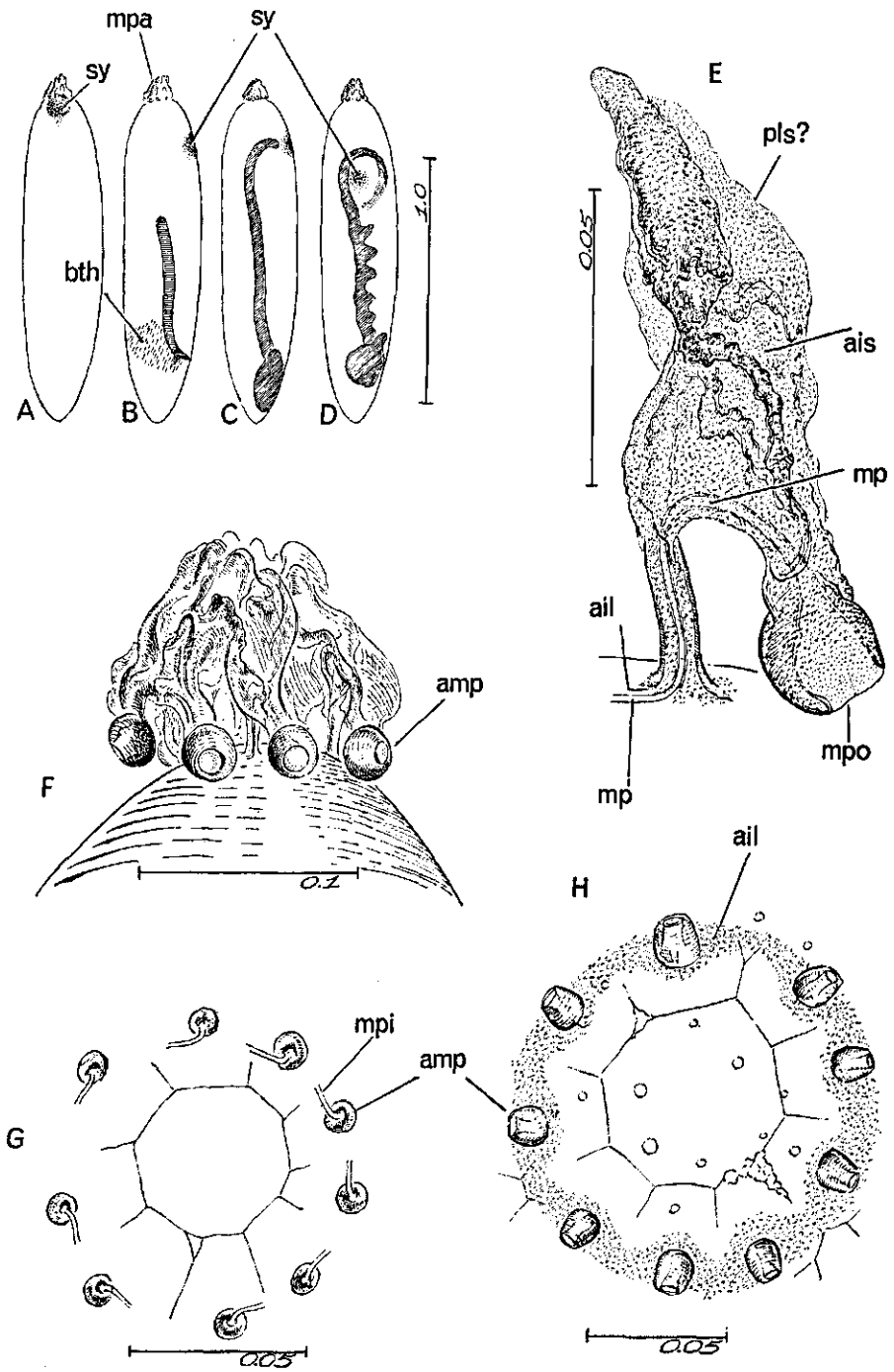


Fig. 75'. Lygaeidae A–G: *Ortholomus punctipennis;* A–D: early embryogenesis; E: aero-micropylar process; F: anterior pole from the side; G: anterior pole, inner view; H: *Geocoris dispar*, anterior pole from above.

France), *G. punctipes* Say (origin Curaçao, Neth. Ant.), *Piocoris erythrocephalus* Lep. & Serv. (origin southern France).

Henestarinae: *Henestaris laticeps* Curt. (origin southern France).

Artheneinae: *Chilacis typhae* Perr.

Heterogasterinae: *Heterogaster urticae* Fabr.

Blissinae: *Blissus leucopterus insularis* Barb. (origin Curaçao, Neth. Ant.); *Ischnodemus sabuleti* Fall.

Oxycareninae: *Metopoplax ditomoides* C., *Macroplax fasciata* H.-S., *Oxycarenus pallens* H.-S. (all from southern France).

Orsillinae: *Nysius thymi* Wlff., *N. helveticus* H.-S., *N. californicus* Stål (origin Curaçao, Neth. Ant.), *Ortholomus punctipennis* H.-S. (origin southern France), *O. jamaicensis* Dall. (origin Curaçao, Neth. Ant.), *Kleidocerys resedae* Panz., *K. championi* Dist. (origin Curaçao, Neth. Ant.), *Orsillus depressus* Dl. (origin southern France).

Rhyparochrominae: *Peritrechus geniculatus* Hahn, *Beosus maritimus* Scop., *Graptopeltus lynceus* Fabr., *Megalonotus chiragra* Fabr., *Trapezonotus arenarius* L., *Aphanus rolandri* L., *Stygnocoris pedestris* Fall.

Cyminae: *Cymus glandicolor* Hahn.

Lygaeinae: *Oncopeltus fasciatus* Dall. (laboratory stock), *Lygaeus equestris* L. (origin southern France), *Melanocoryphus albomaculatus* Gz. (origin southern France).

For all these species chorionic structures were studied. Embryonic stages were available of *Geocoris dispar, Metopoplax ditomoides, Nysius thymi, Ortholomus punctipennis* and the Rhyparochrominae and Lygaeinae listed.

Oncopeltus fasciatus

CHORIONIC STRUCTURES Fig. 297B shows an electron micrograph of a transverse section within the micropylar ring, close to a micropyle. The air-filled inner layer is 1/6–1/10 of the total shell thickness of about 4.5 μ. The solid chorion is divided into three layers of increasing electron density. The pale inner layer, next to the air-filled meshwork, has fine striation. These are bands of higher density alternating with narrower lines of lower density running perpendicular to the plane of the shell. The striate layer, or at least its striation, is absent around the aero-micropyles, where the inner meshwork forms nearly a third of the shell's thickness (fig. 297A). The outer layer is somewhat fibrous and, since it has a high degree of electron density, it may be homologous with the flocculent cover of the *Neuroctenus* egg. The three basic layers of the shell are still discernable in the aero-micropylar clubs (fig. 297C–F). The wall of the processes has two solid chorionic covers of equal thickness. At the mouth of the cup, the wall continues as an invagination, but the internal canal is lined only by the mid chorionic layer. The configuration suggests that the follicular cell or cells had cylindrical processes which are invaginated for some time along the axis of the micropylar process. The secretory sites of the outer and of the invaginated follicle face each other. The spongy air-filled inner layers, deposited thus from opposite directions,

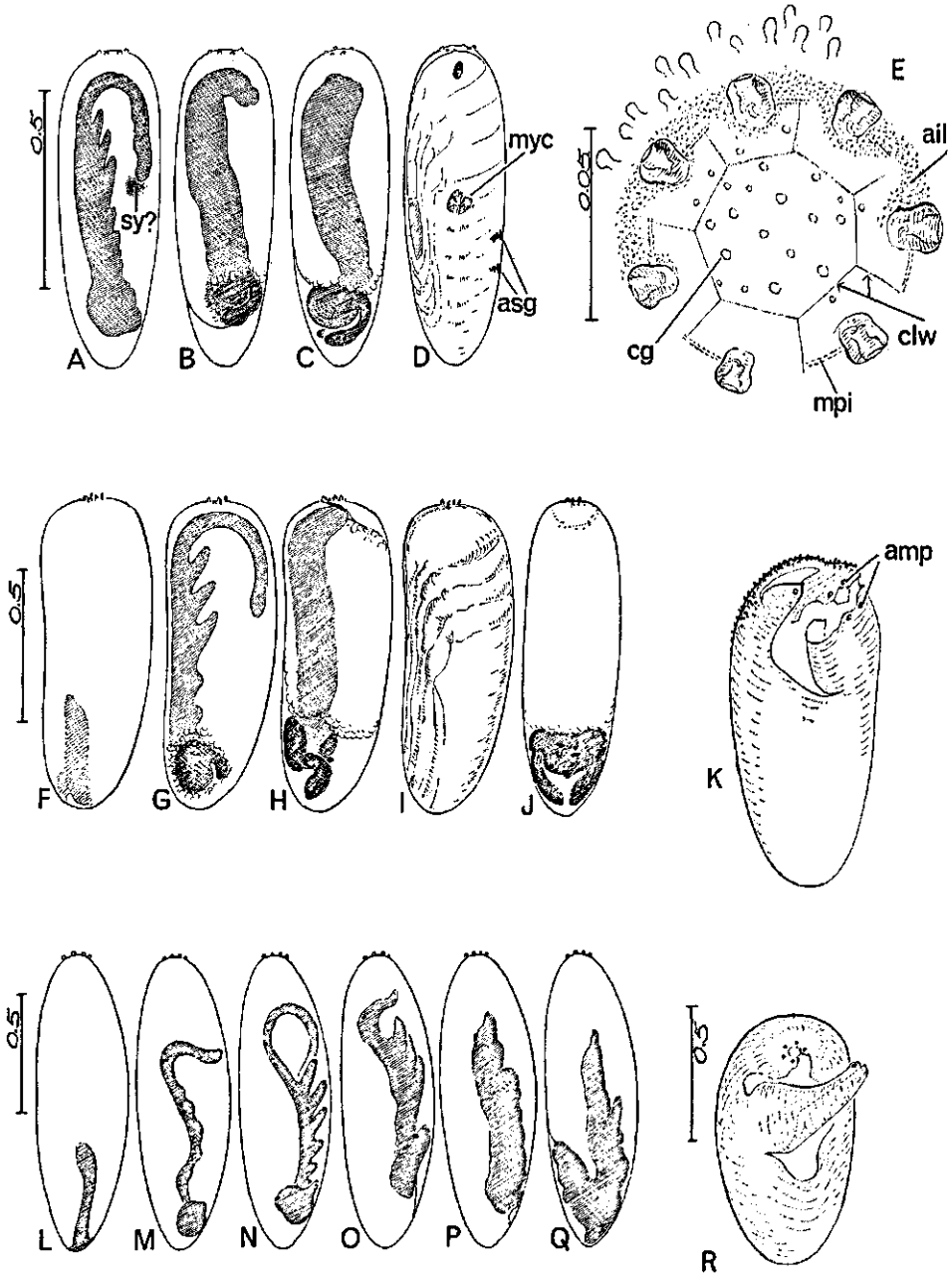
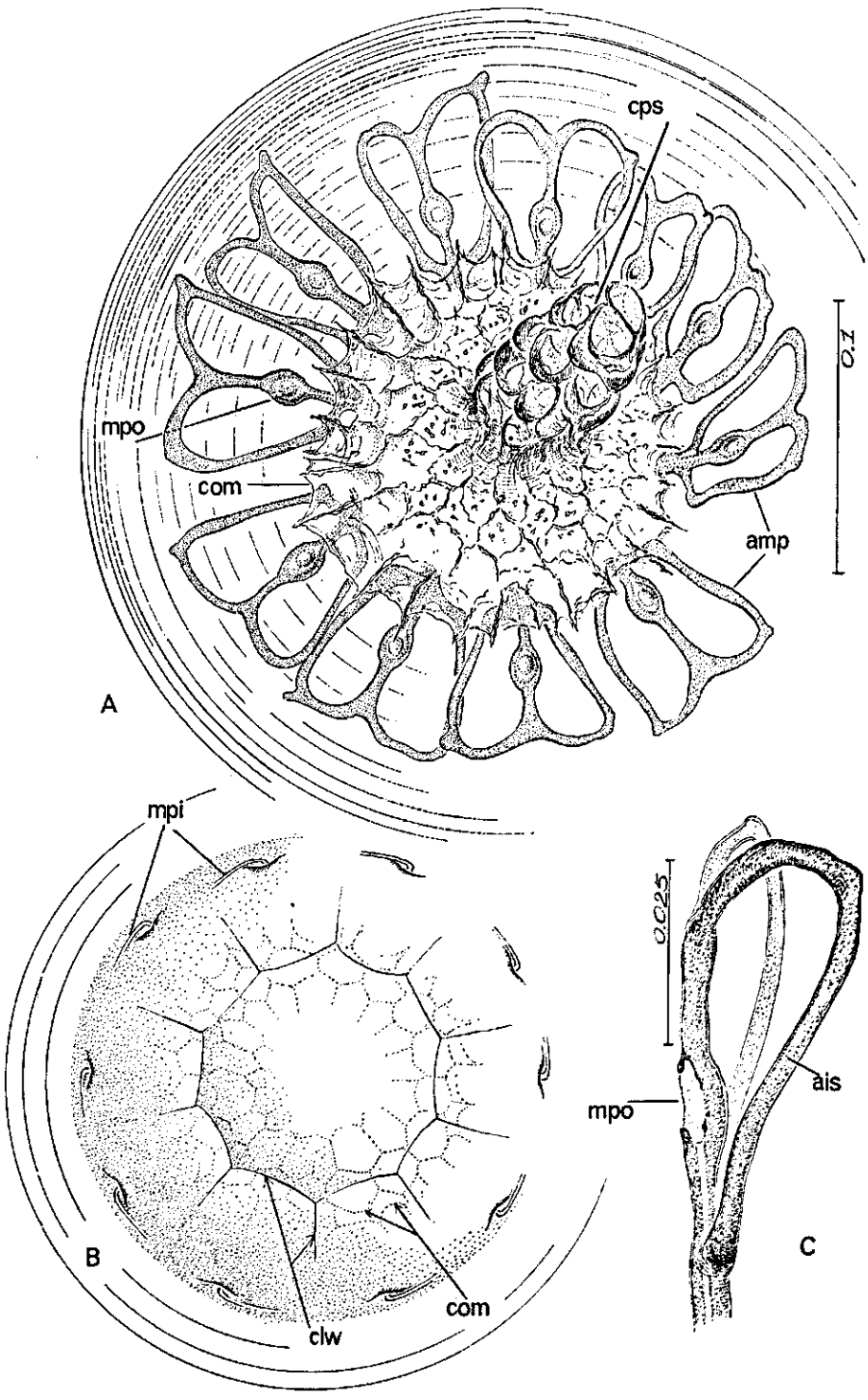


Fig. 76. Lygaeidae A–D: *Metopoplax ditomoides*, later embryogenesis; E: *Trapezonotus arenarius*, anterior pole from above; F–K: *Aphanus rolandri;* F–J: embryogenesis; J: aft side of stage H; K: vacated shell; L–Q: *Geocoris dispar*, early embryogenesis; R: *Megalonotus chiragra*, vacated shell.

contact each other to form a foamy lumen between the outer wall of the cup and the central micropylar core. Openings in the very thin diaphragms of the foam and locally in the wall lining the funnel-shaped cups conduct air directly to the interior.

GROSS EMBRYOGENESIS To clarify the polarity of the transversely isodiametric eggs the shells were marked. The shell is rather opaque but there is some individual variability. In those eggs, where the germ band could be located, no rotation was observed. Many eggs are slightly dorsoventrally asymmetric; the ring of micropylar processes is not completely concentric round the anterior pole. Despite this landmark, young and older eggs with stained embryo did not reveal rotation of the embryo. The embryogenesis is roughly as in the pictures (fig. 73A–E). Invagination starts almost axially at the posterior pole. The germ-cells lie at the caudal end attached to the germ band (BUTT, 1949) and thus do not form an isolated cluster in entire preparations. The very long caudal flexure and the protocormic outgrowths show that the venter faces aft. Further, the dorsal side of the band runs along the membrane, separated from the serosa only by a small film of yolk. In the shortened or 'condensed' phase, the cephalothoracal part of the embryo becomes more immersed within the yolk and is thus more suitably placed ready for revolution. Pigmentation of the eye spots starts after blastokinesis. In the detailed description of embryonic development given by BUTT (1949), there is no mention of the serosal cuticle. Since we found such a membrane in all other heteropterous eggs studied, its presence in *Oncopeltus* is likely. The dorsal organ is a large disc, marked in stained entire preparations as a wide circular band with a central pit. The posture of the fully grown embryo is as shown (diagram fig. 279I). This posture and the mirror-image are realized in a ratio close to 1:1. A triangular area of the embryonic cuticle is raised into a rather conical egg-burster. The single structure is not pigmented and is therefore easily overlooked. It is medial on a line between the posterior edge of the eyes (fig. 79). This region does not represent the vertex, but the fronto-postclypeus judging by the underlaying epicranial sutures of the larval skin. This can best be seen when the mature egg is held under water until the prolarva darkens, while still within the shell. An epicranial lining on the embryonic cuticle cannot be traced. The chorionic split through which the larva escapes from the egg is irregular only at its beginning and its end. The break of the chorion, brought on by the burster, always lies near the centre of the anterior pole and divides the circular area between the micropylar processes by a straight line, often corresponding with the head axis of the enclosed larva. In a few cases, the initial break occurs across this axis. The extent of the slit in both directions is variable, but the ends most often approach each other on one side of the egg and make a flap-like structure (fig. 74A–E). This arrangement is important for deriving the operculum from a longitudinal slit as will be discussed later.

Fig. 77. Lygaeidae, *Kleidocerys championi*, A: anterior pole from above; B: anterior pole, inner view; C: aero-micropylar process, lateral.


cps
mpo
com
amp
0.1
A
mpi
B
clw
com
0.025
ais
mpo
C

The remaining 30 lygaeid species studied

GROSS EMBRYOGENESIS The data on embryogeny, though fragmentary, reveal some variety within the family. The development of *Melanocoryphus* and *Lygaeus* is like *Oncopeltus*. In all others there is a greater immersion of the embryo, particularly in *Ortholomus* (fig. 75'B–D) and *Geocoris* (fig. 76L–Q). Whereas the germ band generally invaginates just at the distal pole, in *Ortholomus* this occurs quite remote from it on the aft side. In none of the Lygaeidae was an embryonic rotation observed. Beginning of revolution is afforded by the tips of the antennae. Ripe ovarian eggs of all Orsillinae studied had a symbiont ball beneath the anterior pole. These symbionts can even be traced in eggs dissected from dried museum material after softening in hot lactic acid (fig. 75'A). The symbionts migrate in a ball slightly aftwards when the egg is fertilized (fig. 75'B). The tail of the upgrowing germ band makes contact with the symbionts which move later into the venter of the embryo (fig. 75A, B; 75'C, D). The symbionts are recombined in two red mycetomes left and right in the abdomen after revolution (fig. 75C). Such mycetomes were also traced in the oxycarine *Metopoplax*, but it has not been verified whether the early migration of the symbionts follows the same path as in Orsillinae, thus from the anterior pole. In the blissine *Ischnodemus* the original position of the symbionts is at the posterior pole (SCHNEIDER, 1940).

Some of the lygaeids went into embryonic diapause. *Ortholomus punctipennis* and *Geocoris dispar* stopped development in stage fig. 75'D and 76P, respectively (oviposition end of July, Upper-Loire, 1000 metres elevation). *Nysius thymi* from the Netherlands (eggs deposited early August) overwintered in an uncommonly late stage of development, namely as prolarva.

AERO-MICROPYLAR SYSTEM Lygaeid eggs are characterized by a limited number of micropyles, mostly below ten, close to the anterior pole and provided with an internal projection deviating transversely beneath the shell in a clockwise direction (egg seen from above, fig. 68A, B). There are a few exceptions. In *Heterogaster* the 9–11 micropylar tubercles form a ring a quarter of the egg's length from the anterior pole. These micropyles have only a short internal canal which does not point transversely but longitudinally forewards.

The second exception refers to Blissinae. *Blissus leucopterus* has 4 or 5 micropyles situated on the truncate anterior pole; their internal canals deviate radially and centrifugally from the pole. Only the apical part of the canal has a weak transverse curvature. An entirely radial course of the internal canal occurs in the second blissine, *Ischnodemus sabuleti*, though the anterior pole is quite otherwise constructed. The pole is not truncate, but tapering and bears a dense calyx of 7–10 micropyles on top.

In general the lygaeid aero-micropyles are sessile and uniform but in all eight Orsillinae studied they are stalked and often transformed into peculiar structures. Such transformations are concerned with enlargement of the air sponge around the external micropylar canal. The aero-micropyles in *Orsillus* have each a radial extension which is filled with air sponge, surrounded by an apparently impervious wall (fig. 66E, F).

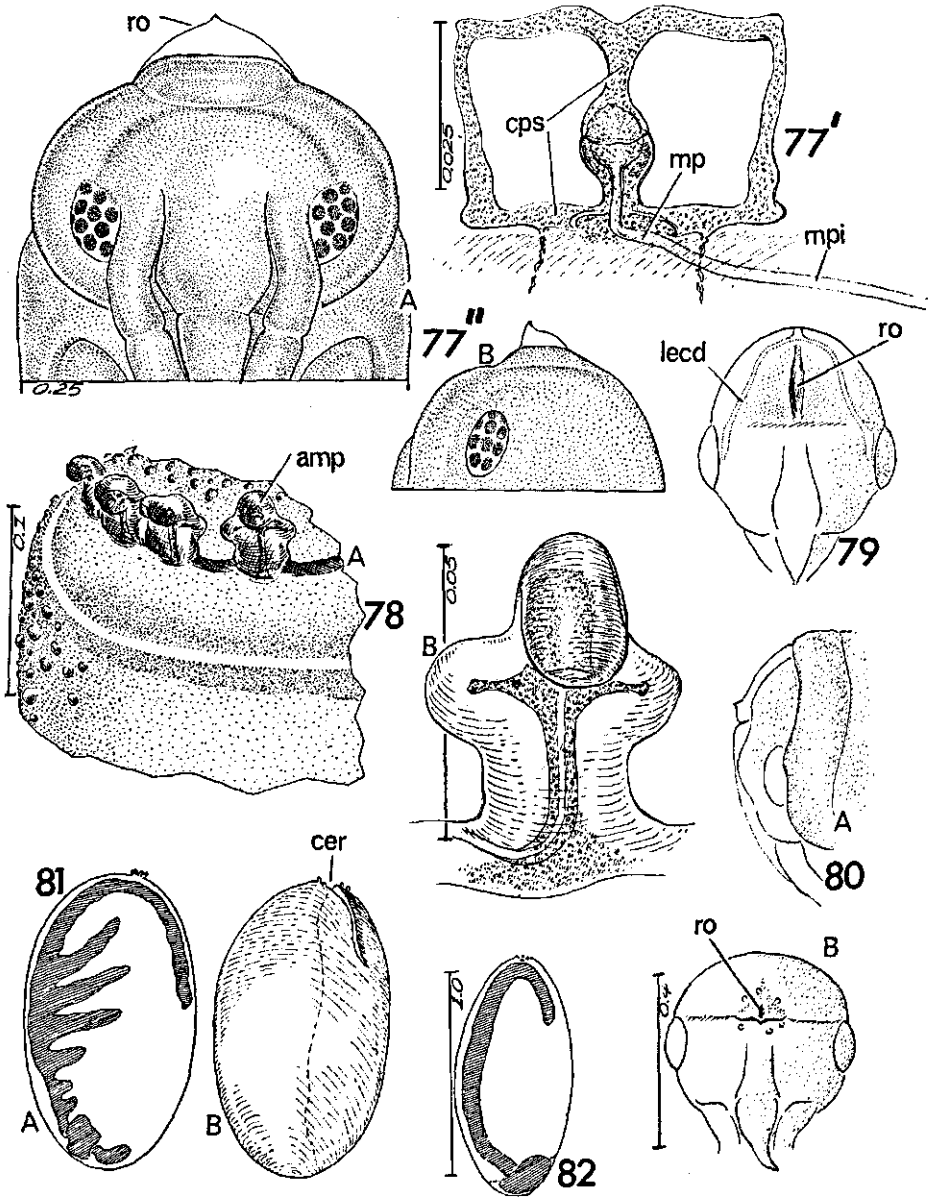


Fig. 77'–82. Berytinidae, Lygaeidae, Pyrrhocoridae 77'. *Kleidocerys resedae*, lattice-like aero-micropylar process. 77"A–B: *Berytinus crassipes*, head of prolarva. 78A–B: *Cosmolestes annulipes;* A: fragment of cephalic pole; B: aero-micropyle. 79. *Oncopeltus fasciatus*, prolarval head. 80A–B: *Pyrrhocoris apterus*, prolarval head. 81A–B: *P. apterus;* A: position of embryo; B: vacated shell. 82: *Dermatinus* sp., early embryonic stage.

Noteworthy are the processes in both *Kleidocerys* spp. grown out as they are in the form of separate links of a chain (fig. 77A, 77'; scanning-electronmicrographs fig. 309A–D). The original cup is recognized in the centre of each link, where there is the only entrance to the structure. The opening (fig. 77C) is directed away of the pole. The chain seems to be completely closed externally and, as it is filled with porous material, it certainly serves to enlarge the air-filled meshwork without functioning as a plastron. An elevation arises from the centre of the polar area within the ring of micropyles. In the European *K. resedae* this projection seems amorphous, but in the Nearctic *K. championi* it consists of coarse foamy chorionic material (fig. 77A, cps). Some of the internal partitions between the blisters are porous, but the base of the entire projection seems not to penetrate the polar shell. The structure rather serves for superficial retention of air between itself and the marginal aeropylar openings. The central process belongs to a chorionic layer superimposed on the actual shell. This additional layer extends in a thin reticulate film up to the aero-micropylar chains (fig. 77A, com).

The anterior pole of *Ortholomus* (both the European and Nearctic species) bears a wig-like structure formed through an elaborate transformation of the aero-micropyles. There are 7–10 of them; each bears a stalk which makes a wide loop so that the terminal cup suspends radially from the anterior pole (fig. 75'E; scanning-electronmicrographs, fig. 310A–F). The wig-structure is an external proliferation of the air sponge (fig. 75'D). Optically it seems that the outer wall of the proliferation is finely perforated so that a plastronic function is suggested. There is no contact of the air-sponge outgrowths between adjacent micropyles but the structures intercommunicate by solid chorionic sheets.

The aero-micropylar processes are simple in the subfamilies other than Orsillinae, but in *Beosus* (fig. 68B) and in *Chilacis* the cups are often anastomosed, particularly of the pneumatic lumina.

ACTUAL SHELL STRUCTURE OF ANTERIOR POLE The eclosion rupture in Lygaeidae is said to be irregular, but some noteworthy points about regularity in the ruptures have been mentioned above for *Oncopeltus; Melanocoryphus* and *Lygaeus* conform to this. The prints of the follicular cells in these Lygaeinae reveal many 'cells' in the polar area between the ring of micropyles. A similar condition prevails in *Cymus, Chilacis, Blissus, Ischnodemus* and *Heterogaster*,

Quite different is the situation in all other species studied. The shell of the anterior pole bears only a few cell boundaries. When only few micropyles are present there is a striking analogy with *Piesma* (fig. 68B). In these lygaeids there is a strong tendency for retention of the original single hexagon on the pole. With increase of micropyles the original hexagon changed into a polygon with as many sides as there are micropyles (fig. 66E, 75'G, 76E). This central polygon persists even when the aero-micropyles form an elaborate structure over it (*Ortholomus*, fig. 75'F, G). This is even so in the peculiar egg of *Kleidocerys*, which superficially resembles cimicomorphous conditions, and thus an operculum would be expected (electron micrograph fig. 309). However, the central polygon in *Kleidocerys* is still traceable when the shell is viewed from

beneath. The picture is confused by the additional reticulate layer (p. 92), which covers the anterior pole (fig. 77B, com).

In none of the lygaeid eggs treated with lactic acid, did the egg splay out as in *Piesma*. In the actual process of eclosion only one or a few sides of the polygon participate in the rupture which extends over one side of the egg in an irregular but rather constant pattern for each species (fig. 76K, R). A further important difference contrasts the egg type with the single polar polygon from the type with many polar 'cells.' The inner chorionic meshwork, the aerostatic layer seems to continue throughout the whole polar area in the latter type. But in the type with the single polygon this layer apparently is absent in the pole, or at least diminished to such an extent that it is not detectable optically (fig. 75'G, 76E).

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) cited 29 investigators of lygaeid eggs and he himself contributed some original data. In the same year PUCHKOVA described, illustrated and keyed the eggs of numerous species. Her extremely important survey shows that micropylar and eclosion structures are very diverse. Further, this family shows a trend towards the development of a true pseudoperculum and may be already achieved in a few cases. The remarkable structures of the orsilline eggs have been studied by her but apparently not in detail, so that the exact micropylar and aeropylar constituents remained obscure. Unfortunately the work of PUCHKOVA is entirely in Russian so that we cannot consider her final ideas on the evolution of structures. The results of her work are briefly summarized by SWEET (1964), who himself gathered valuable data on the Rhyparochrominae eggs of New England. CORBY (1947) and PUCHKOVA *(op. cit.)* already discovered the radial cleavage from a central polygon in some lygaeoid eggs. SWEET *(op. cit.)* grouped the eggs of 39 Rhyparochrominae according their shape and chorionic texture into 'piesmoid' and 'aphanoid' types, each with two subtypes. It is not clear whether eclosion fractures are considered in this grouping. As pointed out by SWEET, similar shape and chorionic investiture may reflect parallel adaptations. The morphology of the anterior pole, however, is of phylogenetic importance, although anagenesis to a high degree masks the true relationships. SWEET *(op. cit.)* (p. 75) states: "The piesmoid type reappears independently in the Myodochini, Rhyparochromini, Stygnocorini and Drymini". If the piesmatoid type coincides with radial cleavage of the chorion, we are inclined to consider this the original type in those tribes (see also the discussion on p. 275).

Our account of the lygaeid eggs has shown that a detailed study may reveal more important characteristics of the shell than were recognized in the past. Such new characters may not be omitted in future analyses of evolutionary events. Otherwise wrong taxonomic conclusions may be drawn. For instance, on superficial comparisons, the *Blissus* egg would represent the piesmatoid type. We pointed out however that the shell structure at the pole and the course of the micropylar internal canal in *Blissus* is very unlike that in *Piesma*. The remarkable lattice-like processes on the *Kleidocerys* egg was first described by JORDAN (1933). Erroneously, he thought the micropyle was situated in the centre of the pole on top of the conical elevation. As shown above the

micropyle is in fact found in the centre of each lattice, which JORDAN thought to be a closed cell.

The egg of *Oncopeltus* has been studied by ANDRE (1934) and SOUTHWOOD (1956, p. 169, 192). SOUTHWOOD analysed the structure of the micropylar process and called attention to the basal bend in the canal, which he called the 'transverse canal'. In his figure 3A this canal runs parallel with the outer surface of the inner meshwork layer of the shell before penetrating it. Thus the canal would not project into the egg cavity. In our opinion this observation needs confirming. Although we have no direct proof from serial sections, optical sections and surface views suggest that the canal penetrates directly through the shell and proceeds transversely along the inner margin of it. This would accord with the condition in some pentatomoid and in some (semi)aquatic groups, where the canal certainly projects into the egg-lumen. SOUTHWOOD may have cut only the beginning of the transverse canal, which might run as shown by him, and so he missed the contamination of the tube into the egg. The whole transverse canal is considerably longer than would appear from SOUTHWOOD's fig. 3A.

Other than *Oncopeltus* (BUTT, 1949), the early embryology of *Ischnodemus* is only partly clarified by SCHNEIDER (1940) in his study on transmission of symbionts. His figures are suspect as they suggest a rotation after the early stage of invagination. A mistake in ascertaining the orientation of the egg may have lead to a false conclusion.

Stenocephalidae

MATERIAL: *Dicranocephalus medius* Muls. & Rey (ovarian eggs).

The polygonal line of dehiscence in the centre of the anterior pole and the regular arrangement of the aero-micropyles beyond and opposite the sides of the central polygon are like those in Piesmatidae. The internal micropylar canals, however, are not parallel, but deviate centripetally by about 60° (fig. 269E″).

PREVIOUS DESCRIPTIONS The descriptions by BUTLER (1923), PUCHKOVA (1955, 1957) and SCUDDER (1957) are limited to the egg outline and the number of micropyles.

2.2.3 Pyrrhocoridae, Largidae, Colobathristidae

Pyrrhocoridae, Largidae

MATERIAL: *Pyrrhocoris apterus* L. (living deposited eggs), *Dermatinus* sp. (living deposited eggs, origin Ivory Coast), *Dysdercus* sp. (ovarian eggs, origin Sumatra). *Largus fulvipes* Blöte (ovarian eggs, origin Curaçao, Neth. Ant.).

Pyrrhocoris apterus

The micropyle protrudes only slightly inside the egg. The transverse part of the

canals forms a circle. The images of follicular cells in the shell area enclosed by the micropylar cups are spacious, but they do not exhibit a characteristic hatching pattern.

Because the ring of micropylar processes on the egg's cap is slightly excentric, the fore and aft of the egg are distinct in the fresh egg (fig. 81A). The embryo does not rotate and develops like *Oncopeltus*. However, the lateral thickenings of the blastoderm at the onset of invagination are large and well defined in *Pyrrhocoris*. The posture of the mature embryo shows the legs regularly alternating, those of the left and right side meshing into each other (pattern resembling fig. 279H). Prolarvae with left- and right-sided pattern are almost equally frequent. The egg-burster (fig. 80A, B) has the same location and is of almost similar construction to that in *Oncopeltus*. The shell usually splits along a lateral longitudinal line over the pole (fig. 81B) by a straight line. The rent runs from nearly half way down one of the lateral sides over the micropylar ring to the posterior region of the opposite side of the egg. Occasionally the fracture runs medially over the most convex side.

ADDITIONAL MATERIAL The internal micropylar canal in *Dysdercus* is longer than in *Pyrrhocoris* and *Dermatinus*. There are about 18 micropyles in *Largus;* the faint internal canals are arranged as in Pyrrhocoridae.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) quoted 12 authors on pyrrhocorid and largid eggs. He himself first noted the egg-burster, and said that the chorion split irregularly at eclosion, but this is not entirely true. KÖHLER (1903) studied the formation of the chorion and SEIDEL (1924) the embryogeny of *P. apterus*. A remarkable discovery by SHARAN and SAHNI (1960) was that the *Dysdercus* embryo produces two embryonic cuticles. As such a phenomenon certainly is not restricted to one small taxon, it will be discussed in a wider connection later (p. 315).

Colobathristidae

MATERIAL: *Cosmolestes* sp. (ripe ovarian eggs, origin Sumatra).

The spindle-shaped egg is distinguished by a ring of 20 unusual aero-micropyles and a circular transparent line, marking the weakness of the pseudoperculum (fig. 78A). The cap does not correspond with the ring of micropyles, which are beyond the cap along the aft side of the egg. The micropylar projections, being connected with each other by a solid ridge, are of a characteristic cruciform shape (fig. 78B). The hollow of the cross-bar connects with the aeriferous sheath around the micropyle, which projects interiad by a short transverse canal.

PREVIOUS DESCRIPTIONS ILLINGWORTH (1921), BOLLE and STAMMESHAUS (1929) and MILLER (1956) figured or described roughly the egg of the colobathristid *Phaenacantha* sp. These eggs, which are laid in or near the soil surface, bear only about 10 micropyles, but are otherwise like *Cosmolestes*.

2.2.4 Coreidae

MATERIAL: This is divided here for convenience into sections A–E according to egg types.

A. Coreinae: *Coreus marginatus* L., *Homoeocerus paleus* F., *H. schoutedeni* Vill., *Cletus unifasciatus* B., *Acanthocoris* sp., *Sulpicia distincta* Sign., *Mictis metallica* Sign., *Cossutia* sp., *Haploprocta sulcicornis* F., *Spathocera laticornis* Schill., *S. dalmani* Schill., *Dalader acuticosta* Am. & Serv.

B. Coreinae: *Anoplocnemis* sp., *Leptoglossus membranaceus* F.

C. Coreinae: *Catorhintha selector* Stål.

D. Coreinae: *Hydara tenuicornis* Westw.

E. Pseudophloeinae: *Mevaniomorpha hystrix* Gerst., *Acanthomia hystrix* Dall., *Ceraleptus gracilicornis* H.-S.

Except *Coreus*, *Ceraleptus*, *Haploprocta*, *Spathocera* (France), *Catorhintha* (Curaçao, Neth. Ant.), and *Dalader* (Indonesia) all material originated from the Ivory Coast. Embryonic stages of all species were studied except *Dalader*.

A. Coreus marginatus

Eggs are usually deposited in groups of 3–4. The middle of the flat aft side of the egg is attached to the food plant (fig. 97F). This part of the chorion is delimited by a contraction of the surrounding chorion which seems to occur during or shortly after its deposition by the follicular cells. We concluded this from the meandering course of the hexagonal lines around the adhesive pad (fig. 97G). There is a ring of widely separated aero-micropylar tubercles round the anterior pole. The micropyles do not project inward. The pseudoperculum is already formed as a white band in the otherwise smooth and brownish chorion. Its boundary intersects the ring of aero-micropyles.

Just before invagination of the germ band, two voluminous lateral plates of blastoderm fill the posterior aft side (fig. 97A). The irregular plates are fused along the median line. They have a sharp outline, but lack bilateral symmetry. Invagination starts just aft of the basal pole. At first the band projects obliquely into the yolk and bends sharply forwards. It then grows up the fore side and round the cephalic pole. Later the blastopore shifts gradually forwards (fig. 97B–E). The cephalic lobes remain in contact with the serosa. As the thoracic appendages elongate, a serosal cuticle is laid down. This membrane is so closely associated with the shell that the pseudoperculum is imprinted on it. In the condensed phase, the embryo is still rather superficial with its venter facing inward. Revolution follows without rotation round the polar axis. The posture of the larva is as for pentatomids (diagram, fig. 279H). The left- and the right-sided positions are equally frequent. The egg-burster is a triangular plate just above the transverse ocular line. Although this plate is transparent, it is distinctly thicker than the rest of the embryonic cuticle. The actual burster is a Ω-shaped sclerotized ridge upon the plate (fig. 92C). The structure fits against the mid-aft edge of the pseudoperculum, where the lid first lifts (fig. 97F). The free larva retains a clear print of the

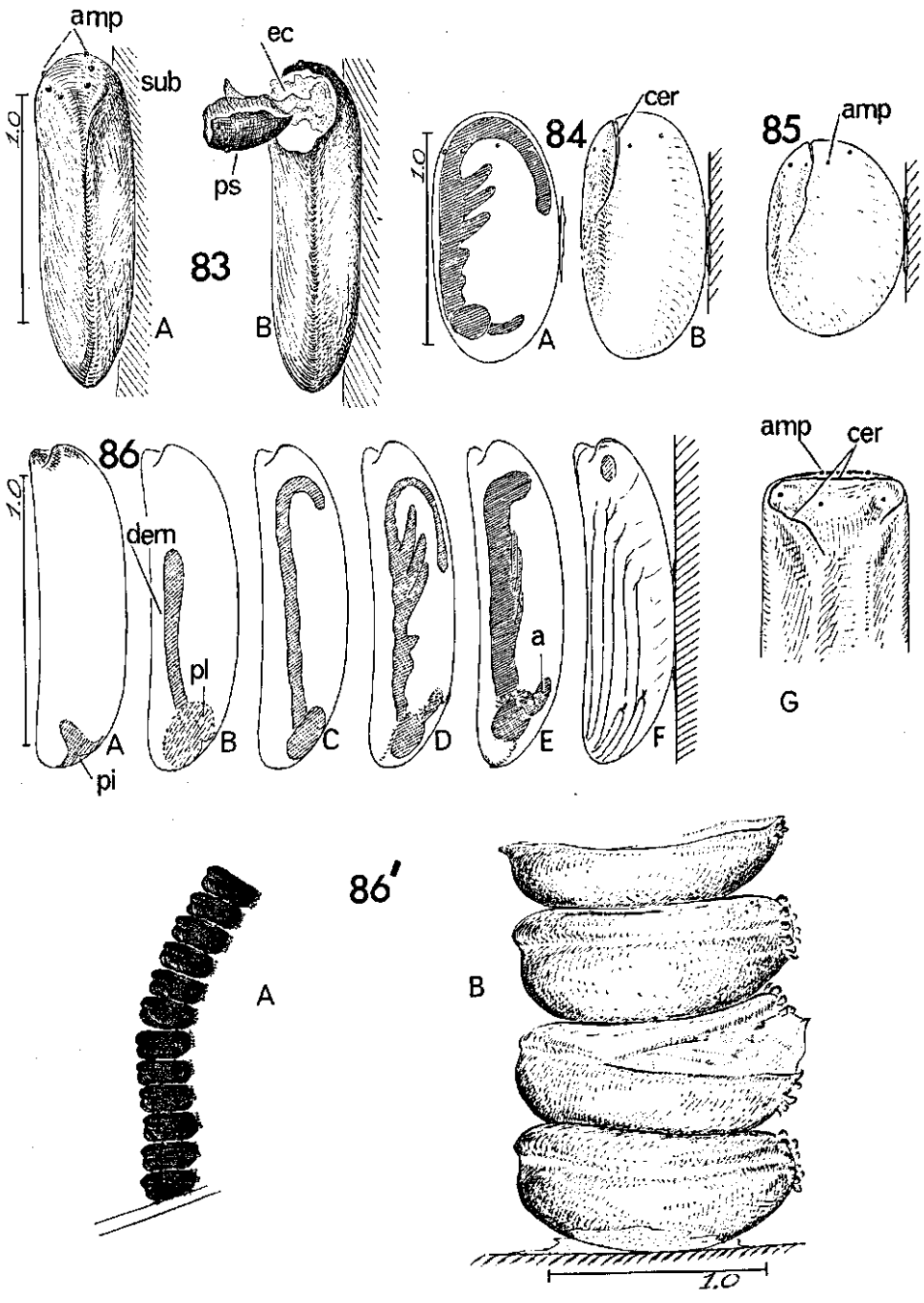


Fig. 83–86′. Alydidae, Coreidae, embryonic stages, eclosion rent 83A–B: *Leptocorisa* sp. 84A–B: *Mevaniomorpha hystrix*. 85. *Acanthomia hystrix*. 86A–G: *Hydara tenuicornis;* A–F: embryogenesis, lateral view of egg; G: fore side of cephalic pole, hatched egg. 86′. *Ceraleptus gracilicornis;* A: egg batch; B: remnant of egg batch after some larvae have been hatched; second egg from below during hatching; only the aft half of the vacated shell on top is left.

egg-burster on its integument, so that it aids the positioning of this embryonic structure on the head. A comparison of fig. 92A with fig. 92B shows that the part between the epicranial fork has contributed to the origin of the burster.

ADDITIONAL MATERIAL There are only small specific differences in the shell of species listed under A; embryogenesis and eclosion are constant. The number of micropyles in *Sulpicia* is about 60, the most so far in coreids. The aero-micropylar ring approaches the lower edge of the pseudoperculum medially (fig. 99). The egg of *Mictis* (fig. 91) is no larger than that of *Anoplocnemis* (sub B), but has the thickest chorion of any Heteroptera, about 100 μ.

B. Anoplocnemis sp.

The cylindrical eggs are deposited lengthwise in chains. The 30–45 aero-micropylar tubercles are in an acentric ring round the anterior pole. The tubercles are about 12.5 μ thick, the central canal 2.5 μ wide. The solid chorion is 50–60 μ thick; the inner layer is four times as thick as the outer layer. Inwards the micropyles again form tubercles, which are imprinted on the serosal cuticle. No attempt was made to trace any aerostatic layer around the inner surface of the massive chorion.

Incubation takes 9–10 days (25°–30°C). Group B is distinguished by striking asymmetry in early embryogenesis. Invagination takes place at the posterior end of the left side of the egg (fig. 100A). The band elongates from the aft side towards the fore side simultaneously bending to the right (fig. 100A″, B). When the tail reaches the sagittal plane, the blastopore too moves into this plane, so that ultimately the band becomes entirely symmetric in the egg. Protocormic segmentation is already clear before the band has fully elongated (fig. 100C). The serosal cuticle starts to form at this time. The embryo reaches just up to the upper edge of the aft side of the egg. It is superficial except for a narrow zone behind the head and at the tail, where there is a thin layer of yolk between the serosa and the embryo. The head remains visible through a clear area, the serosal window, free from yolk globules; amnion and serosa do not seem to dissociate in that region. Fig. 100E and F show that the posture of the antennal rudiments determines the shape of the window. The revolving embryo ascends along the side of the egg to which the dorsum had faced (fig. 100G) and thus no rotation has occurred. Red pigmentation of the eye occurs after blastokinesis. The attitude of the mature embryo is shown in fig. 100I, I″. A thinner spot at the zenith of the opercular ring exists to receive the tooth of the otherwise normal coreid egg-burster.

ADDITIONAL MATERIAL Egg and egg-life of *Leptoglossus* are almost similar to those of *Anoplocnemis*.

C. Catorhintha selector

The cubical egg has two interesting features. It has four flattened sides, which do not

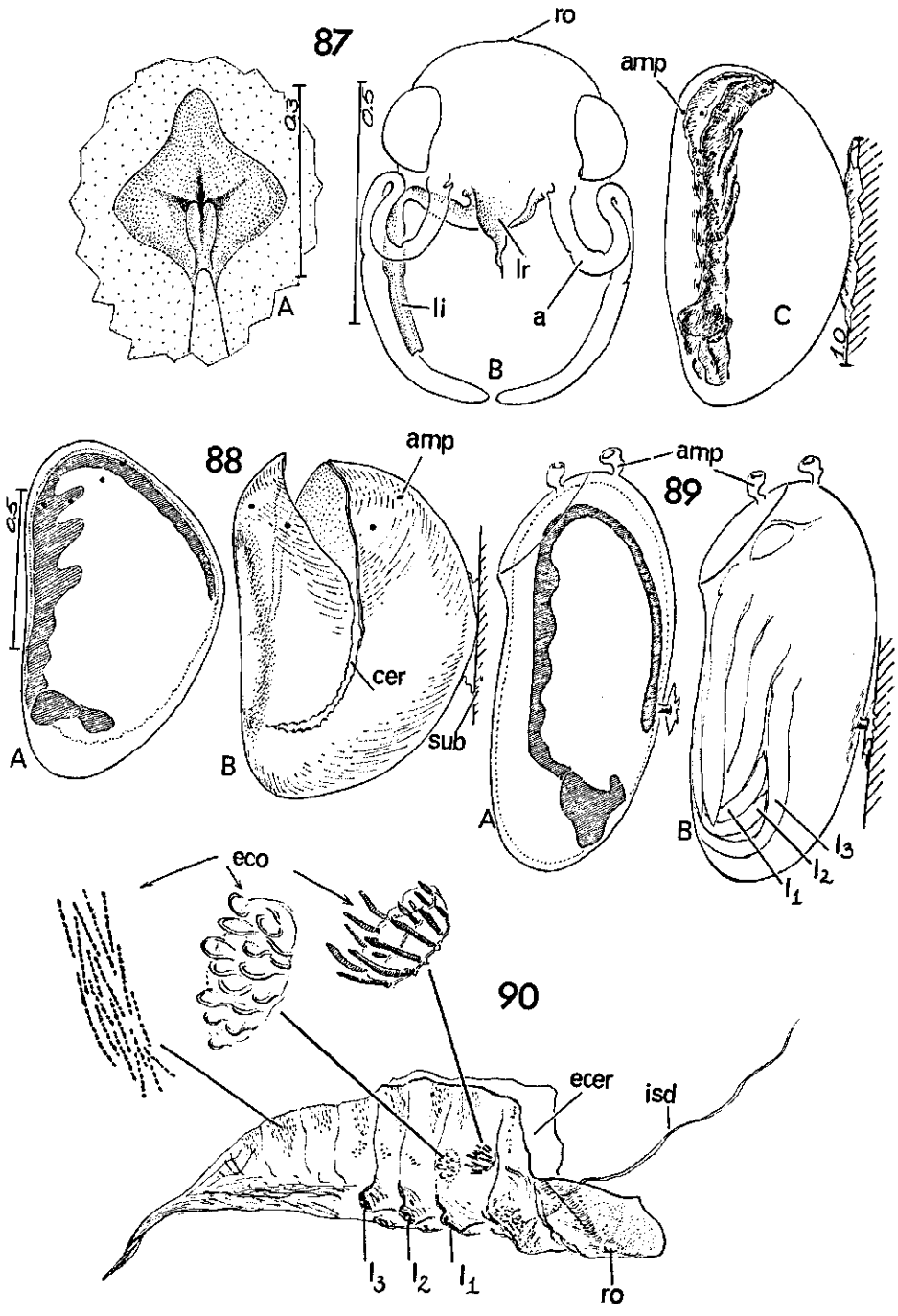


Fig. 87–90. Alydidae, Rhopalidae 87. *Camptopus lateralis;* A: ruptor ovi; B: head of prolarva; C: egg with embryo, condensed phase, lateral. 88. *Alydus calcaratus;* A: early embryo; B: hatched egg. 89. *Chorosoma shillingi;* A: embryo in diapause; B: posture of prolarva. 90. *Myrmus miriformis,* shed embryonic cuticle.

coincide with the morphological sides of the underlying fully grown embryo (fig. 95). If the egg were deposited lengthwise in the normal way, it would balance on the substrate resting upon one edge. However the egg tips sideways through about 45° and so rests stable on a flat side. The laying female probably tips the egg after it is delivered from the genital valves in the normal orientation. Eggs are arranged in long rows alongside one another (fig. 95). The direction in which they have tipped is mostly the same in all eggs of one row; rows tipped to the left and right are found among each other. The second feature is coincidence of the pseudopercular and micropylar rings (fig. 96), a rare feature in coreids.

D. Hydara tenuicornis

This species, when keyed out with the table of families of CHINA & MILLER (1959) should belong to the Coreinae. The egg, both structurally and in embryogenesis, is less evolved than the previous species from sections A–C. It is more alydid-like and shows the importance of studying a wide series of species, as the range of progression within one family is much greater than expected.

The oblong boat-shaped eggs (fig. 86) are deposited mostly in small groups alongside each other or end to end. The anterior pole has a saddle fore-aft and bears 4–6 aeromicropylar tubercles. Incubation takes 9 days at 25°–30°C. The gross embryogenesis is shown (fig. 86A–F). The germ band remains immersed. Note that the antennal rudiments point anteriad (fig. 86D, E, opposite to *Anoplocnemis*). The eclosion split forms a characteristic flap. The line of rupture is somewhat irregular, but it follows the same transverse path through the micropylar ring as in species with a well differentiated pseudoperculum (fig. 86G).

E. Pseudophloeinae

The egg characters of these pseudophloeines (fig. 84 and 85) are typically alydid (*vide* sub 2.2.5): the most convex side faces the substrate, a few circumpolar aeromicropyles and a crescent-shaped eclosion fracture. Embryogenesis is as in *Coreus*.

Ceraleptus gracilicornis has the very unusual habit of laying the eggs one above another. The first laid egg is stuck to stalks of leguminous food plants. The aft side of each consecutive egg is glued to the fore side of the preceding one. The egg stack thus formed extends generally at an oblique angle from the substrate (fig. 86'A). The stack shows a striking resemblance to the ripe pods of some Papilionaceae, such as *Ornithopus*. Though the biological significance of a supposed mimicry is obscure, the illusion is strengthened by the colour of the eggs, which soon turn black, and by their shape which gives the whole batch a wavy outline.

The *Ceraleptus* egg differs from other Pseudophloeinae and from the Alydidae in that there are numerous aero-micropyles close together around the top of the anterior pole. It would be expected that rupture of the shell to release the larva would be con-

fined to the anterior pole, because the fore side of the egg where in other pseudophloeines the rupture occurs, was blocked by the adjacent eggs. However this is not so. The line of the future dehiscence is laid out already in the ovarian egg and is marked as a white band around the lateral sides of the egg. The actual eclosion rupture starts at the anterior pole (fig. 86'B) and proceeds right along the flanks of the egg, the left and right ruptures meeting each other at the distal pole. As a consequence the fore half of the shell is completely dislodged from the aft half. There is no regular sequence in hatching of the eggs from the first laid upwards. So it may happen that one egg in the middle of the stack hatches first. Since this egg is halved (fig. 86'B, upper egg), its fore side bearing the remote part of the egg stack falls downward. The two parts of the original pile fragment further when other eggs hatch.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) referred to 25 papers dealing with coreid eggs and PUCHKOVA (1957) contributed much. It appears that the egg is variable in shape as well as in the placing of eggs singly, in small or larger groups or in long chains end to end or side by side. The dorsum of the prolarva always seems to face the

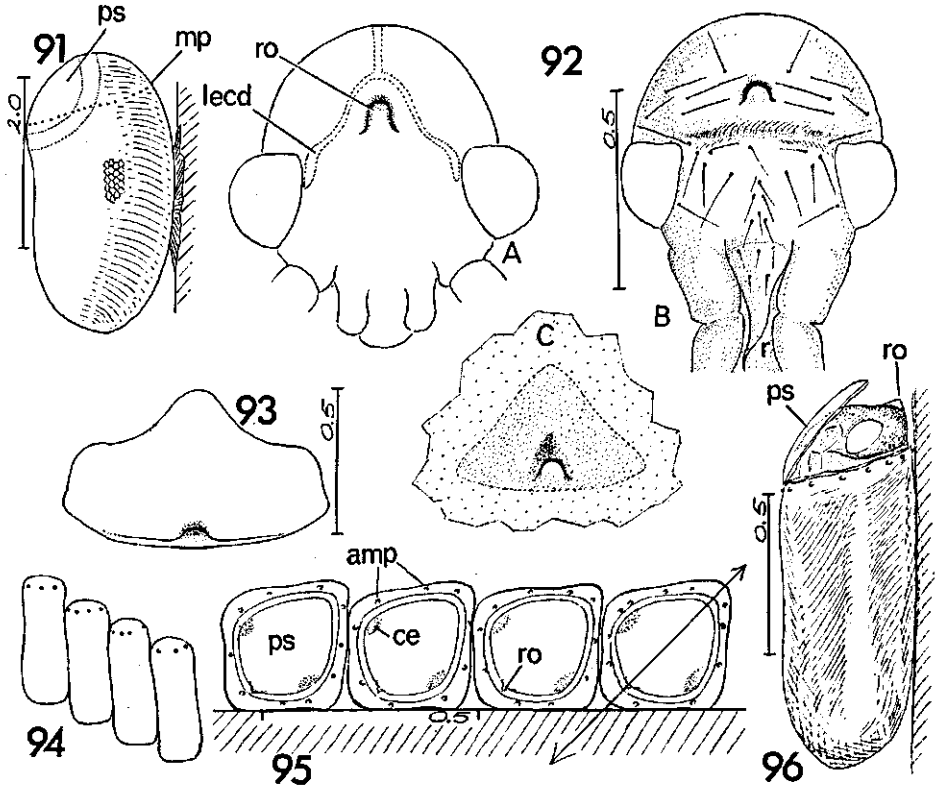


Fig. 91–96. Coreidae 91. *Mictis metallica;* egg, lateral side. 92. *Coreus marginatus;* A: head of first instar larva, position of egg-burster of the embryonic cuticle (B) indicated; C: ruptor ovi. 93. *Anoplocnemus* sp., ruptor ovi. 94. *Leptocorisa* sp.; part of egg batch, from above. 95. *Catorhintha* sp.; part of batch, seen from the head end. 96. *Cathorhintha* sp.; hatching prolarva, lateral view.

side of the egg on the substrate. The pseudoperculum varies slightly in form but is typically a well defined circular cap, which is sometimes confined to the free fore side of the egg. The indistinct micropylar processes are numerous and form a ring intersecting the pseudoperculum. However, sometimes both rings coincide so that the processes lie along the line of eclosion as we found in *Catorhintha* (section group C above). SOUTHWOOD *(op. cit.* p. 189) cited a similar condition in a *Dalader* sp. and in *Spathocera dalmani* Schill. found by ANNANDALE (1905) and JORDAN (1933), respectively. We found the egg of the latter species was the same as *Coreus*, with the micropylar ring intersecting the pseudoperculum. JORDAN himself did not indicate the coincidence of micropyles and cap either in his text, or in his figure. But ANNANDALE did indeed claim such a coincidence in what he called *Dalader*, the egg of which was *Coreus*-like. We studied ovarian eggs of *Dalader acuticosta* Am. & Serv. and, indeed, the pseudoperculum and micropylar ring are not coincident. The isolation of the Pseudophloeinae, which might be removed from Coreidae, is expressed too among the species which PUCHKOVA *(op. cit.)* studied and which completely conform to the type given by us.

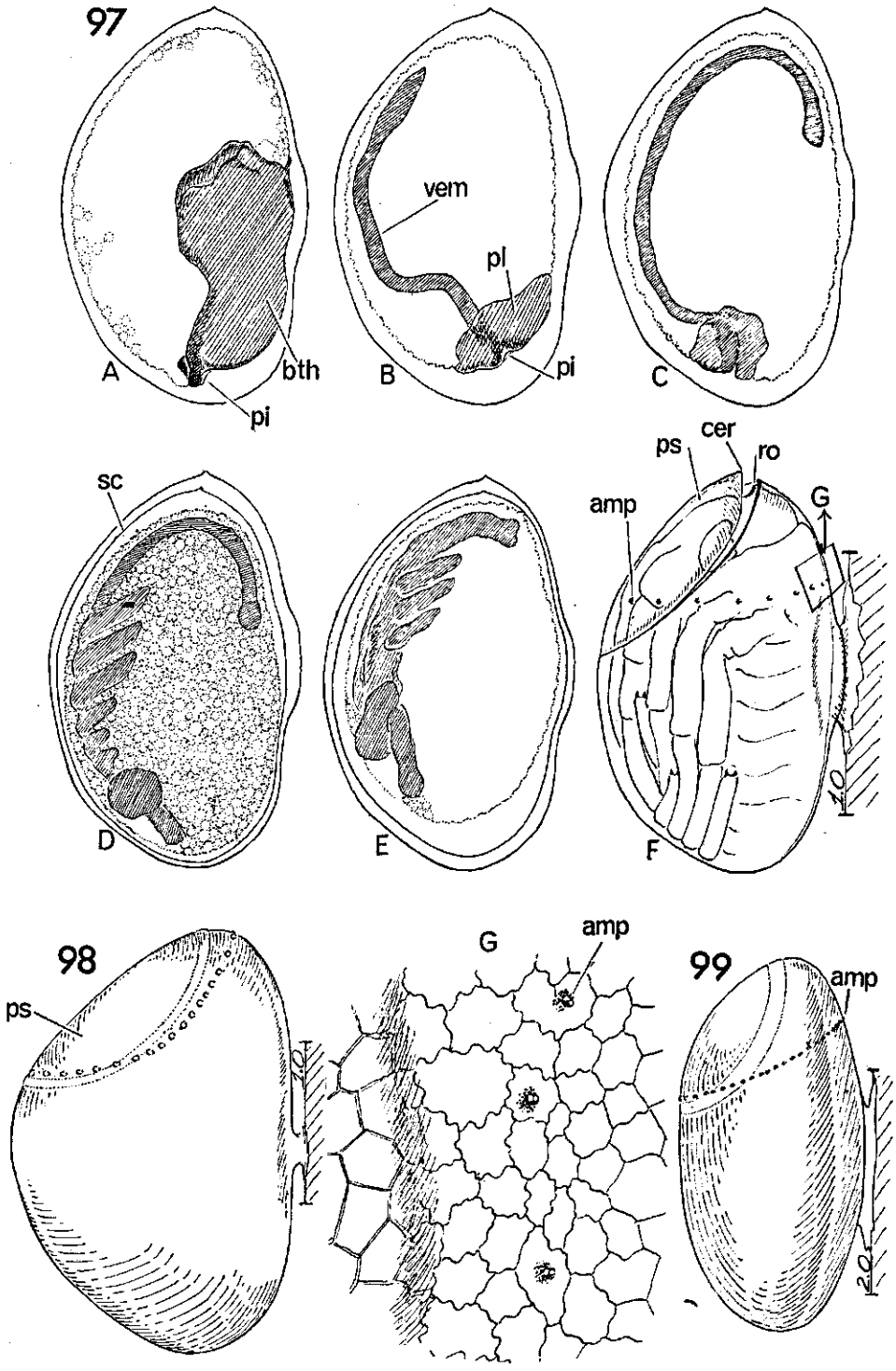
2.2.5 Alydidae

MATERIAL: *Alydus calcaratus* L., *Camptopus lateralis* Gm. (living deposited eggs, origin South of France); *Mirperus jaculus* Thunb. (living deposited eggs, origin Ivory Coast); *Leptocorisa* spp. (dried eggs *in situ*, origin Curaçao, Neth. Ant. and Ivory Coast).

Alydus calcaratus

The egg shape (fig. 88) resembles that of *Coreus*, but the flat side is attached to the substrate, the reverse of most coreids. Unlike other coreoids the few micropyles penetrate the shell along a helical line and have a short transverse projection within the shell. Embryogenesis is as in *Coreus*. Because of the flat fore side of the egg the posture of the larva before eclosion is very characteristic. The antennae make a sharp bend laterad, leaving the venter free. The labium is pushed to one side (fig. 87B). The alternation of the legs is not constant. The egg-burster is a square transparent plate with a sharp opener in its centre (fig. 87A). It is in the same place as in *Coreus* but there is no imprint left on the larval cuticle. The chorion splits along a longitudinal lateral line which nearly separates the whole of the flat fore side from the rest of the shell (fig. 88B). At the anterior end the split is smooth, but posteriad it is frayed, suggesting that the chorion there has no weak line. However, the complete split followed a reasonably constant pattern in many shells investigated.

Fig. 97–99. Coreidae 97. *Coreus marginatus;* A–E: early embryogenesis; F: prolarva ready to hatch; G: fragment of chorion outlined in F. 98. *Dalader acuticosta;* egg, lateral view. 99. *Sulpicia distincta;* egg, lateral view.


97
A
bth
pi
B
vem
pl
pi
C
sc
D
E
ps
cer
ro
amp
G
F
98
ps
G
amp
99
amp

ADDITIONAL MATERIAL The *Camptopus* and *Mirperus* eggs are the same as that of *Alydus calcaratus*. The *Leptocorisa* eggs are placed in rows end to end (fig. 94) and, although more elongated and slender, they too have the fore side free and flat. In its eclosion, however, the egg is more advanced. Both ends of the crack meet each other on the fore side near the anterior pole. The cap thus formed is completely separate from the shell. It is a pseudoperculum as its boundary hardly varies in the many hatched eggs studied, although not visible in the intact egg. The zenith of the cap transects the ring of micropyles (fig. 83B).

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956, fig. 10K) showed the egg of *Riptortus tenuicornis* Dall. as though it were deposited with the flat side to the substrate, thus obscuring the principal difference between alydid and coreine eggs. The same mistake seems to have been made by PUCHKOVA (1957) judging from her figures of the eggs of three other species. KALSHOVEN (1950, fig. 99) shows *in situ* the egg of *Leptocorisa acuta* Thunb. which is more circular in outline, when seen from above.

2.2.6 Rhopalidae

MATERIAL: *Myrmus miriformis* Fall., *Chorosoma shillingi* Schumm. (living deposited eggs); some unidentified species from the Netherlands Antilles (dried laid eggs); *Leptocoris* sp. (ovarian eggs, origin India).

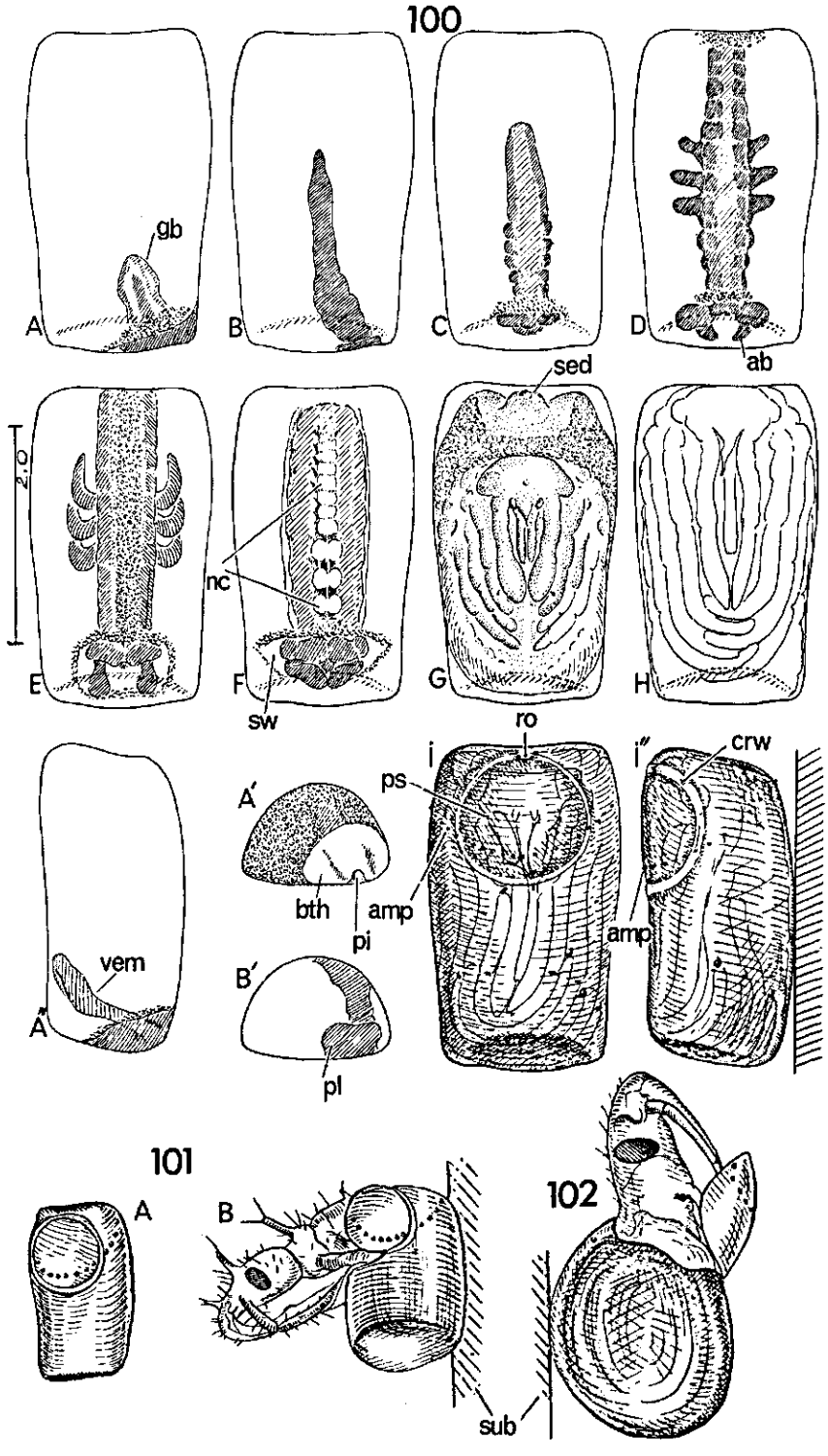
Myrmus and Chorosoma

Characteristic for both species (fig. 89) and other rhopalids are shape of egg, presence of only two distinct aero-micropylar processes (one upon the well defined pseudoperculum, the other aft of the latter) and a small stalk for attachment equatorially on the aft side. Gross embryogeny is as in *Coreus*, but the germ band remains more submerged in yolk at first (fig. 89A). In the Netherlands, both species cease development when the thoracic appendages show indistinctly. This winter diapause starts in August–September, the species being univoltine. In the south-east of France (Argelès), the life-cycle may be different at least for *Ch. shillingi*. Eggs were laid in July, and developed without diapause. *M. miriformis* however diapaused in Upper Loire (1000 metres elevation) in exactly the same embryonic stage as in the Netherlands.

The posture of the fully grown embryo of *Chorosoma* is as shown (fig. 89B and diagram, fig. 280M), the mirror-image occurred only in one of six specimens studied. Despite the smaller length-width ratio of the larva of *M. miriformis*, the prolarva is folded exactly the same as in *Chorosoma*. Four eggs showed a mirror -image of that of

---

Fig. 100–102. Coreidae 100A–I: *Anoplocnemis* sp., embryogenesis; A–I: fore side of egg; A″, I″: lateral view; A′, B′: view normal to the flattened posterior pole (note the asymmetric invagination). 101. *Phtyia* sp.; A: egg obliquely from the side; B: hatching larva, embryonic cuticle already discarded. 102. hatching egg of unidentified species (Neth. Ant.).


100
gb
A
B
C
D
ab
sed
2.0
nc
E
F
G
H
sw
ro
i
i''
crw
ps
A'
bth
amp
pi
amp
vem
A
B'
pl
101
A
B
102
sub

another five eggs, thus neither left nor right asymmetry seems dominant in *Myrmus*. The egg-burster consists of a shield-like transparent plate with a small unsclerotic central projection (fig. 90, ro), which forces the zenith of the pseudoperculum open. The embryonic cuticle bears laterally further special structures, especially on the prothorax, which increase friction during hatching (fig. 90).

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956), in his survey of the group, quoted 14 references and PUCHKOV and PUCHKOVA (1956), PUCHKOVA (1957, 1962) investigated species of other genera. All these data present a uniform egg type in *Rhopalidae*, but the eggs of *Brachycarenus tigrinus* Schill. and *Stictopleurus abutilon* R. are elongate and are flat aft without a stalk. Another exception is the egg of *Leptocoris (Serinetha) augur* F., whose pseudoperculum bears a ring of 14–22 processes; the aft side bears anteriorly a similar ring of processes (MALHOTRA, 1958). Otherwise the egg of *Leptocoris* is typical of the rhopalid type. MALHOTRA suggested that only the processes on the pseudoperculum have a micropylar function. In eggs of this species from India we found that both rings have the double function of aeropyles and micropyles. Perhaps each ring has evolved from one process, as the basic number is two in typical rhopalids.

2.2.7 Cydnidae, Acanthosomatidae, Urostylidae

Cydnidae

MATERIAL: Sehirinae: *Sehirus biguttatus* L. (living laid eggs). Corimelaeninae: *Thyreocoris scarabaeoides* L. (ovarian eggs).

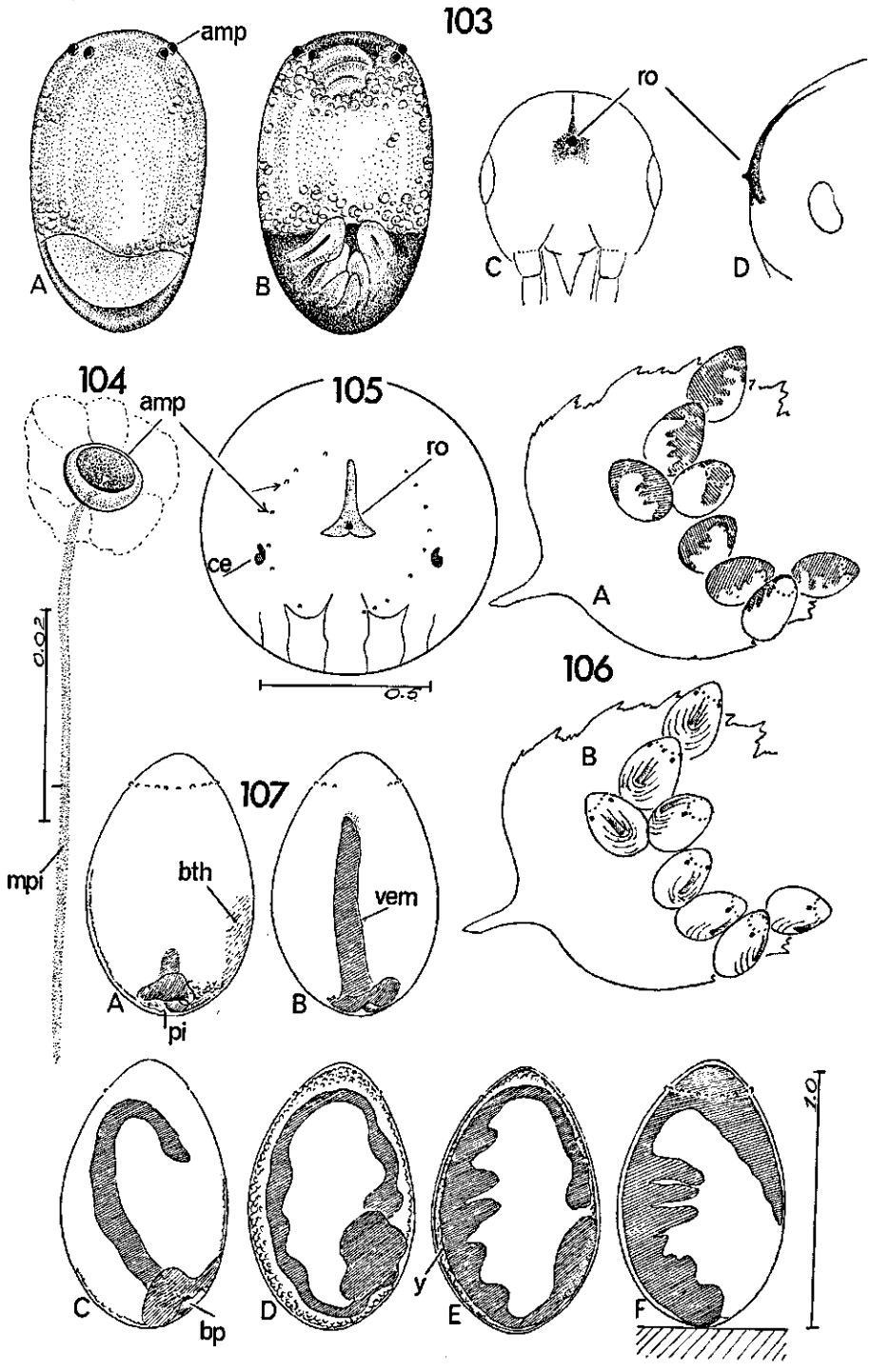
Sehirus biguttatus

The notes on this species are only fragmentary and not as adequate as for most other material. We would stress the need for the complete embryology of cydnids, because of their great phylogenetic importance.

Like other Sehirinae, *S. biguttatus* guards its egg mass, which is laid in the soil. The chorion is thin, rather transparent and bears a circle of a few aero-micropylar knobs. The central canal of each knob protrudes thread-like far beneath the inner surface of the shell. All canals have an oblique clockwise course interiad. Revolution seems to be preceded by 180° rotation (fig. 103A, B). The eye pigment does not become visible until long after revolution. The posture of the mature embryo is as shown (diagram, fig. 279G). The weakly sclerotic egg-burster is developed mainly as a longitudinal ridge

---

Fig. 103–107. Cydnidae, Acanthosomatidae 103. *Sehirus biguttatus;* A: early embryo; B: shortly before revolution (egg similarly orientated as in A); C, D: prolarval head, fore and lateral side, respectively. 104. *Acanthosoma haemorhoidale*, aero-micropylar cup. 105. *Elasmostethus interstinctus*, anterior pole from above with prolarval head. 106. *E. interstinctus*, egg batch, orientation of embryo before (A) and after (B) blastokinesis. 107A–F: *Elasmucha grisea*, embryogenesis before revolution.


103
amp
A
B
ro
C
D
104
amp
mpi
0.02
105
ro
ce
0.5
A
106
B
107
bth
vem
A
pi
B
C
bp
D
y
E
F
1.0

(fig. 103C, D). Anteriorly it approaches the transverse ocular line where it bears a small tooth. The shell splits by a straight line anterio-ventrally over the prolarva.

Thyreocoris scarabaeoides

The chorionic surface is rough and beset with pegs, suggesting that the egg is deposited in a less protected way. Seven micropyles are arranged in a wide ring round the anterior pole. The micropylar internal canals are directed according a circle. This is in contrast with Sehirinae where the canals turned somewhat centripetally.

PREVIOUS DESCRIPTIONS The surveys given by SOUTHWOOD (1956) and PUCHKOVA (1959) now cover about 15 species from the three subfamilies, all giving a reasonably stable family pattern of shell structure. The egg of *Stibaropus* has been described by WILBRINK (1912). Two species of Corimelaeninae (considered by FROESHNER, 1960, as a family) laid eggs laterally attached to plants (LATTIN, 1955; SOUTHWOOD, 1956). *Brachypelta aterrima* Först. seems to be more evolved in eclosion as the shell breaks either sagitally or transversely (SCHORR, 1957).

Acanthosomatidae

MATERIAL: *Elasmostethus interstinctus* L., *Elasmucha grisea* L., *E. fieberi* Jak. (living deposited eggs), *Acanthosoma haemorrhoidale* L. (ovarian eggs.)

The form of the egg and arrangement of the flat aero-micropylar processes follow from fig. 107A. The micropyle protrudes inward as a long fine filament which is difficult to trace (fig. 104). The fine structure of the shell of *E. grisea* is shown in fig. 298A, B (deposited egg, stained with KMnO4). The main layer of the *Elasmucha*-shell is much thicker than in *Oncopeltus* and *Neuroctenus*. The outer layer, if homologous with that of the lygaeid and aradid, is reduced to a thin dark coat, which is not clearly separated from the main layer. The air-filled inner part of the shell consists of two superposed laminae with cavities, of which the innermost represents the aeriferous system proper (section is close to the ring of aero-micropyles). The *Elasmucha* spp. lay confined batches of about 40–50 eggs which are usually placed in an upright position. The batches are continuously guarded by *Elasmucha*, but not by *Elasmostethus* which deposits groups of 8–40 eggs. *Elasmostethus* eggs are often all attached lengthwise. This allows easier assessment of orientation in these isoradial eggs. Comparing orientation before and after blastokinesis (fig. 106A, B) there seems to be some rotation, although not always as much as 180°. The early embryogeny has some plesiomorph features, when compared with following pentatomoids. Fig. 107A–F shows invagination at the posterior pole, an entirely immersed upward growth of the band, a later slight shift of the C-shaped embryo towards the yolk boundary and a shift of the blastopore to the aft side. The upmoving tail end of the band bears a faint shadow, which is probably not the cluster of germ cells because it does not stain. The

picture, just before eclosion of the egg (fig. 105), shows the tooth of the egg-burster exactly at the anterior pole and not close to the micropylar ring, in contrast to operculate pentatomoid eggs. The eclosion crack in the three species is a straight longitudinal line from the anterior pole down the fore side. The rent continues aft a short distance, either lengthwise or curving transversely laterad.

PREVIOUS DESCRIPTIONS Reviews on acanthosomatid eggs are given by SOUTHWOOD (1956), PENDERGRAST (1958), JORDAN (1958) and PUCHKOVA (1959). Description is confined to egg-shape, eclosion fracture and to the recognition of the egg-burster.

Urostylidae

MATERIAL: *Urochela nigropunctata* Blöte (origin Laos); *Urostylis flavomaculata* Stål (origin Korea); *Tessaromerus licenti* Yang (origin China). All were ripe ovarian eggs.

A consistent pattern is revealed by the three species, of egg shape, chorionic structure and the three stalked aero-micropyles (fig. 113B). YAMADA showed (1914, 1915) that the two rows of eggs of *Urostylis westwoodi* and *U. striicornis*, overwintering in crevices of bark, are covered with a dark secretion, except for the apices of the three, rarely four, processes. The micropylar canals are very distinct throughout and extend far transversely within the shell in a clockwise direction (anterior pole faced to the observer) (fig. 113B). Externally the swollen tip of the stalked process, has a pore well differentiated from the surrounding concentric inlet for the air. There are small differences between species: In *U. nigropunctata* and *T. licenti*, the external pore of the micropyle is sunk within the cup, and the processes are longer; the internal transverse canals are shorter in the latter than in the former species. In *Urostylis flavomaculata*, the external pore of the micropyle extends as a tube out of the cup (fig. 113A). In all the many ovarian eggs of the three species, only three micropyles per egg were observed. The egg shape is like Acanthosomatidae; like them and the Cydnidae, Urostylidae must have a longitudinal eclosion rent, since we observed no previous line of weakness.

PREVIOUS DESCRIPTIONS Besides YAMADA cited above, only MILLER (1953, 1956) described the exterior of the ovarian eggs of two more species. The suggestion of MILLER (1956) that the eggs would be inserted into decaying vegetable matter, into shoots of plants or into the soil, contradicts the earlier observations of YAMADA (1914, 1915).

2.2.8 Scutelleridae

MATERIAL: *Hotea subfasciata* Westw., *Procilia morgani* White, *Steganocerus multipunctatus* Thunb., *Sphaerocoris annulus* F., *Calidea hutereanae* Schout. (living deposited eggs, origin Ivory Coast), *Hotea curculionoides* H.-S. (ripe ovarian eggs,

origin Indonesia); empty shells of several species of *Agonosoma*, *Odontoscelis*, *Odontotarsus*, *Eurygaster*, *Symphylus* and *Elvisura*.

Hotea subfasciata

The white eggs are subspherical, slightly longer than wide, and are always placed in batches of three adjacent rows. The orientation of the eggs when leaving the mother is shown in fig. 108E (laying female on right, delivery of egg in direction of arrow).

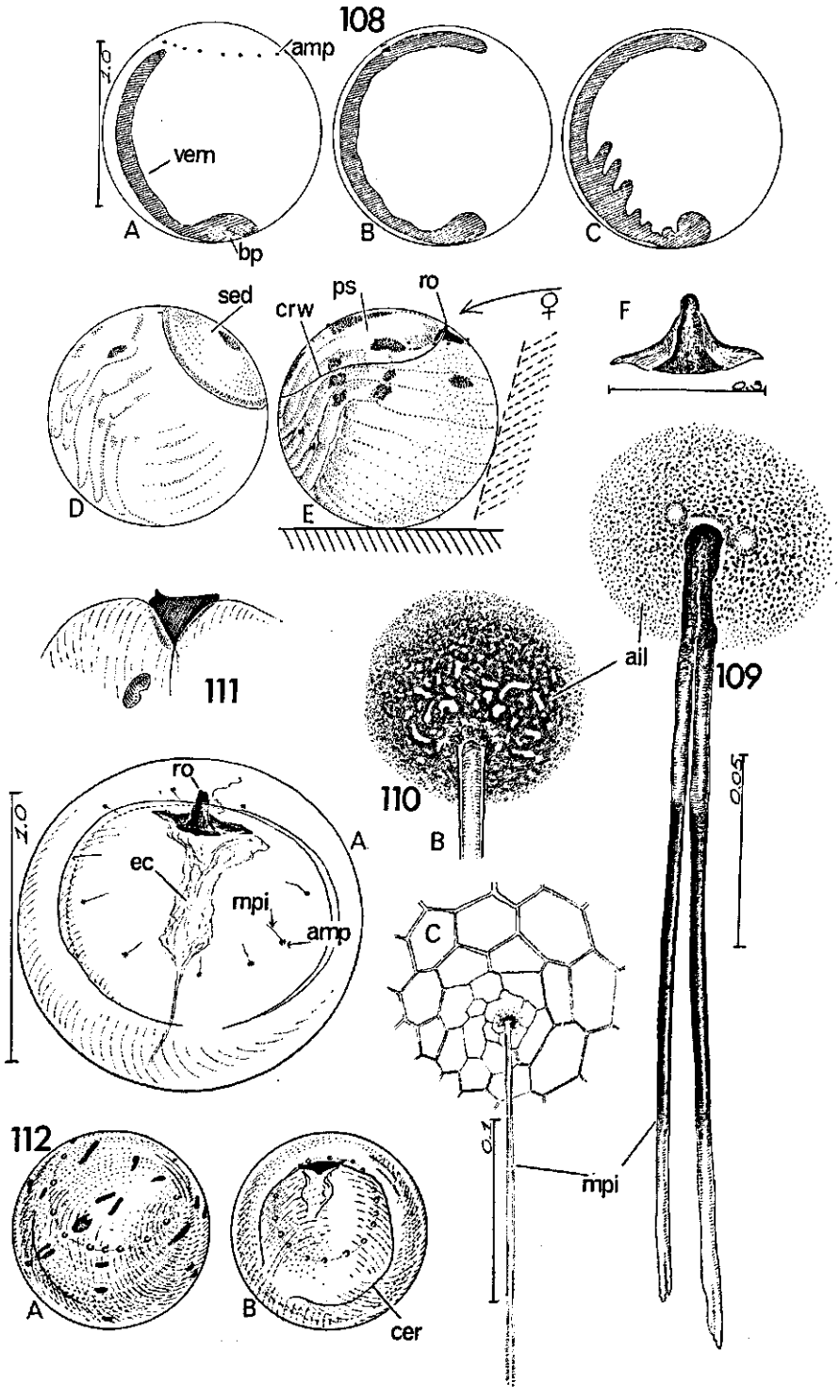
There are about 20 aero-micropylar processes, arranged in a large ring round the anterior pole. Externally they are minute knobs, but on the inner surface of the shell, they form long ducts, partly dark-pigmented (fig. 109 of *H. curculionoides*) and separate from the shell; the internal canals have a centripetal course.

Fig. 108A–E clarifies gross embryogeny and reveals the pentatomoid type: an almost superficial band, the dorsum facing outwards and no rotation before blastokinesis. The small triangular burster has an anterior tooth which penetrates the thin chorion just within the micropylar ring (fig. 108E). The cap, which then lifts, varies little in form, and slopes down the fore side of the egg. The burster is dorsal between head and pronotum; the morphology of this region will be discussed on p. 319).

The other species studied, belonging to various subfamilies, show no important deviations (fig. 110, 112, 118). The long internal projection of the micropylar canal is always present as a faint pale stripe (fig. 110A–C); the canals run inwards centripetally. The shell of *Odontoscelis fuliginosa* is rough, with fine interrupted ridges bordering the hexagons and with globules of chorionin inside the hexagons. About eight micropyles form a wide oblique ring round the middle of the egg. The shell of *Elvisura* sp. is about 40 μ thick, but otherwise reveals all typical characters of the family.

PREVIOUS DESCRIPTIONS Some information on scutellerid eggs is given and compiled by SOUTHWOOD (1956) under the heading Pentatomidae. He speaks of an irregular split of the chorion at eclosion, but we and PUCHKOVA (1959) found constant fracture. PUCHKOVA (1959) added much to information on 12 species from 6 genera. VODJDANI (1954) stated that the long inner duct of the micropyle in *Eurygaster integriceps* is entirely within the chorion. The labelling of the egg coverings in a cross-section (his fig. 12), however, hints that his endochorion represents a subchorionic layer.

Fig. 108–112. Scutelleridae 108A–F: *Hotea subfasciata*, position of germ band and prolarva (arrow indicates the site of the depositing female; the slightly oval egg is outlined as a circle for convenience); F: ruptor ovi. 109. *H. curculionides*, inside of shell with two partly fused aero-micropyles. 110. *Odontotarsus* sp.; A: vacated shell; B, C: aero-micropyle, inner view of shell. 111. *Eurygaster integriceps*, prolarva with egg-burster. 112. *Symphylus* sp.; A: egg with embryo after revolution; B: vacated shell.


108
amp
vem
bp
A
B
C
sed
ps
ro
crw
♀
D
E
F
111
ail
109
110
B
ro
ec
mpi
amp
A
C
112
A
B
cer
mpi

2.2.9 Dinidoridae, Tessarotomidae

Dinidoridae

MATERIAL: *Aspongopus* sp. (living laid eggs, origin Ivory Coast); *Megymenum subpurpurascens* Westw. (ripe ovarian eggs, origin Borneo).

Aspongopus sp.

Eggs are laid in chains of up to 20 eggs touching end to end, and glued to the substrate (fig. 114A). A ring of about 50 minute aero-micropylar cups runs excentrically around the egg, with its nadir on the free fore side below the equator. The micropyle has a long but faint tube-like projection inside the egg. Although we missed the early embryogeny, development is normal for the pentatomoid group: almost superficial band and no rotation during blastokinesis. The legs and venter of the mature embryo face the free side of the egg and the burster points to the anterior fore edge. There a flap lifts, which consists of almost the whole fore side of the egg (fig. 144A, ps). The egg-burster is like a pickaxe. It consists of the usual ⊥ trunk, which is heavily sclerotized and bears the actual opener at eye level. Its stem is elongated posteriad, where it is flattened out into a more transparent triangular plate, which protects the underlying enclave in between the head and pronotum of the larva (fig. 114B).

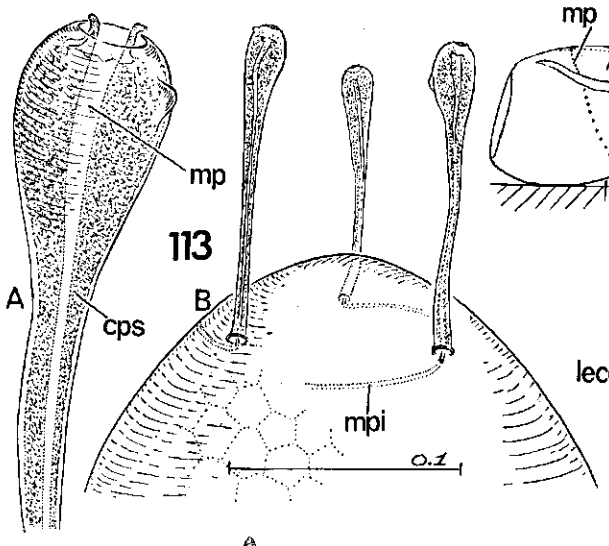
Egg shape and shell structure of *Megymenum* is like *Aspongopus*, but the number of micropyles averages 30.

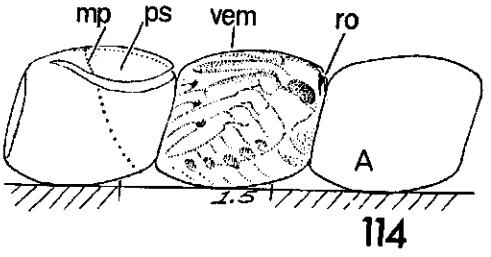
PREVIOUS DESCRIPTIONS LESTON (1955) in describing the eggs of *Coridius cuprifer* Westw. stated: "The chain formation suggests that eggs laid first eclode last", apparently because he erroneously thought the pseudoperculum of a given egg should face to the bottom of the adjacent egg. This should be an unprofitable step in evolution. It is probably due to inaccurate observation that LESTON concluded: "Egg-burster situated beneath the centre of the upper pole". Comparing our fig. 114A, it appears that the part of the burster, which is responsible for punching out the cap, reaches up to the fore edge of the flat anterior pole. He misidentified the micropyles, which he thought were located on the rim of the anterior pole.

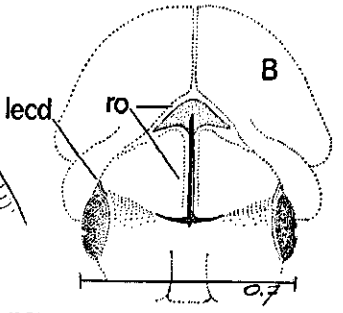
Tessarotomidae

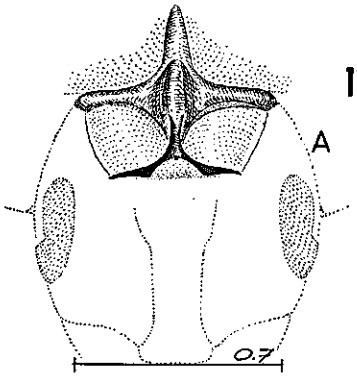
MATERIAL: Egg-batch of unidentified species (origin Ivory Coast); *Agapophyta viridula* Blöte (origin West Irian), *Tessarotoma javanica* Thunb. (origin Java), *Siphnus*

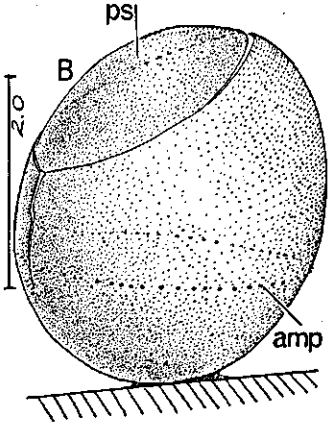
Fig. 113–117. Urostylidae, Dinidoridae, Tessarotomidae 113A: *Urostylis flavomaculata*, apex of aero-micropyle; B: *Urochela nigropunctata*, anterior pole. 114: *Aspongopus* sp.; A: part of egg batch; B: prolarva, anterior view. 115. tessarotomid sp.; A: prolarval head; B: vacated shell. 116. *Siphnus alcides*, ovarian egg. 117. *Agapophyta viridula*, surface view of chorion.

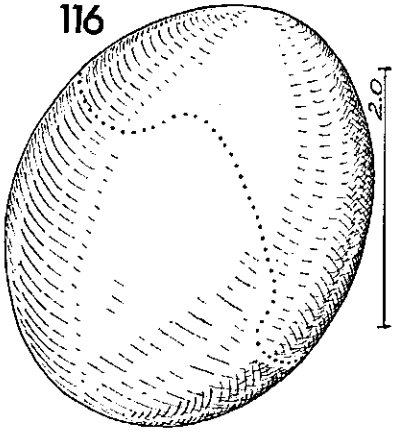

mp
113
A
cps
B
mpi
0.1

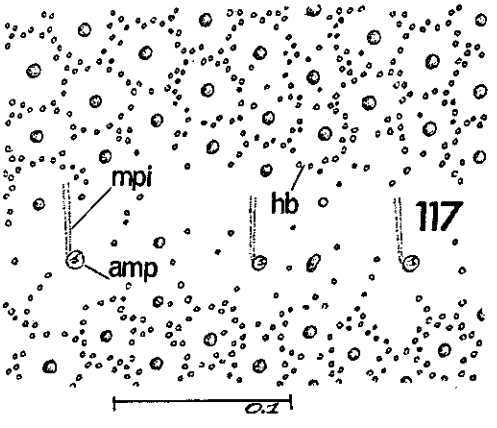

mp
ps
vem
ro
A
1.5
114


B
lecd
ro
0.7


A
0.7


115
ps
B
2.0
amp


116
2.0


mpi
hb
117
amp
0.1

alcides Stål (origin Vietnam). Of the latter three species only ripe ovarian eggs were studied.

An isolated cluster of eggs we found in the Ivory Coast without their depositor doubtless belongs to a representative of this family. The subspherical eggs are more than 3 mm in diameter an the egg-burster is of the type which has been described as characteristic for these pentatomoid bugs. The form of the first larval instar which hatched from these eggs, reinforces our conclusion that this batch of eggs belonged to a tessarotomid.

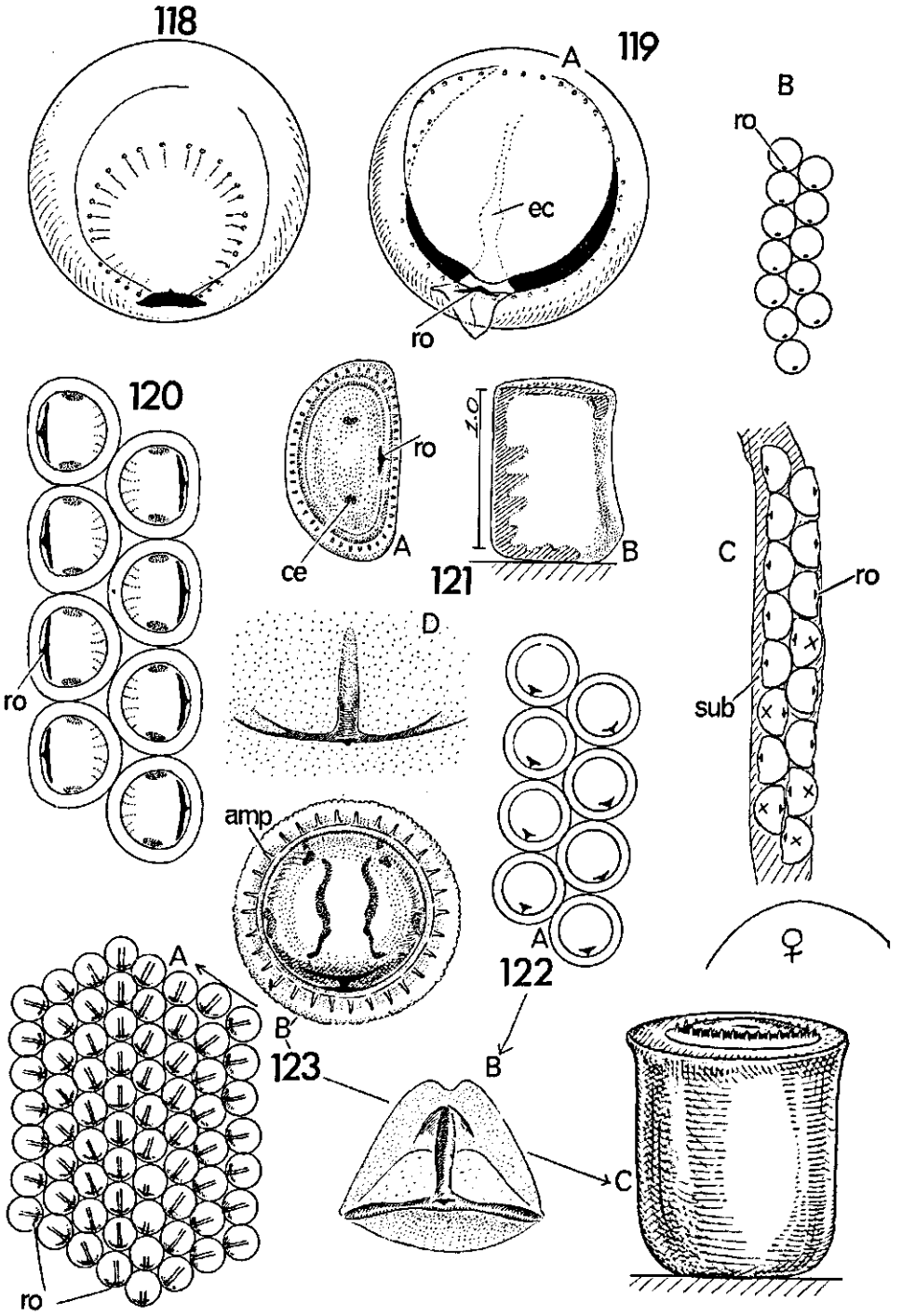
Eggs are glued almost perpendicularly upright (fig. 115B) and the deposition of these eggs on a very thin branch is probably the cause of their unusual arrangement in two irregular rows. Several eggs were even placed on top of the others. The aeropyles are entirely on the posterior half in a circle of more than 60. Exteriorly they are minute knobs (⌀ 12 μ). The micropylar canal, 3 μ wide, passes vertically through the 40 μ thickness of the chorion but does not seem to project inwards.

The fully grown embryo lies with its venter facing the more convex side of the shell. The anterior tooth of the complex egg-burster (fig. 115A) perforates the anterior pole precisely in the centre and an oval cap lifts from the more convex side. The main part of the large burster is a projection backwards covering the cephalo-pronotal suture.

ADDITIONAL MATERIAL The eggs of the other three species do not differ in shape, but in chorionic texture, location and number of micropyles. *Agapophyta* and *Siphnus* have a characteristic hexagonal design (fig. 117) which is also present in *Tessarotoma* but without a knob in the centre of each hexagon. The micropyles have a transverse inner projection (fig. 117, mpi). There are around 50 micropyles in *Agapophyta* and *Tessarotoma*, and about 100 in *Siphnus*. The ring of micropyles is not so far posterior as in the unidentified species, and very peculiar is the lateral deviation of the ring in *Siphnus* (fig. 116).

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) listed 11 papers with data on egg outline and bursters. He concluded, apparently from figure 4 in LESTON (1955), that the tessarotomid micropylar process is stalked and contrasts this with the stalkless condition in scutellerid eggs. In our species, it is certainly not stalked and it could be that the so-called stalk in LESTON's drawing represents the intra-chorionic passage of the canal. In no eggs previously described has a posterior ring of micropyles been reported. MILLER (1934) found that the egg of *Eusthenes robustus* and *Pycanum ruber*

Fig. 118–123. Scutelleridae, Pentatomidae 118. *Agonosoma trivittata*, vacated shell. 119. *Edessa* sp.; A: vacated shell B: egg batch. 120. *Aeliomorpha* sp., part of egg batch (note inversed orientation of left and right eggs with unchanged orientation of the depositing female). 121. *Macrina juvenca;* A: egg from above with prolarva; B: germ band; C: egg batch; D: egg-burster. 122. *Tantia* sp.; A: egg batch; B: egg-burster. 123. *Arvelius atropunctatus;* A: egg batch; B: egg from above; C: from the side.


118
119
A
ec
ro
B
ro
120
ro
ro
A
ce
1.0
121
B
C
ro
sub
D
amp
A
122
♀
A
B
123
B
C
ro

had an equatorial stripe. To judge from his figures, this stripe may represent the ring formed by the micropyles.

2.2.10 Pentatomidae

MATERIAL: Pentatominae: *Sciocoris cursitans* Fabr.; *S. distinctus* Fb. (origin southern France); *Carpocoris pudicus* Poda, *Eurydema cyaneum* Fb. (origin South of France); *Aeliomorpha* spp. (origin Ivory Coast) (a continuous series of embryonic stages of the four species was available). Egg shells closed and hatched, of many species (*e.g.*, *Arvelius*, *Nezara*, *Edessa* and unidentified species from the Caribbean region and the Ivory Coast).

Graphosominae: *Ancyrosoma albolineatum* F. (vacated eggs *in situ*, origin Portugal).

Phyllocephalinae: *Gellia dilatata*, *Tantia striata* Sign., *Macrina juvenca* Burm. (origin Ivory Coast, embryonic stages preserved).

Eumenotinae: *Eumenotes obscura* Westw. (ovarian eggs, origin Indonesia).

Discocephalinae: *Antiteuchus mixtus* F. (ovarian eggs, origin Surinam).

Asopinae: *Dorycoris pavoninus* Westw., *Afrius figuratus* Germ., and two not identified species (living deposited eggs, origin Ivory Coast); *Picromerus bidens* L.; *Perillus bioculatus* Fab. (living deposited eggs).

Sciocoris cursitans

This species is treated separately because the structure, deposition and orientation of the egg deviates from the family pattern. Eggs are laid singly with their convex side along the substrate (in captivity filter paper) (fig. 124C). The whole chorion is remarkably sculptured with various incrustations and outgrowths. It resembles a microfloral cover; a portion of this picturesque covering is shown in fig. 124D. A dark area covers the centre of the pseudoperculum and has several truncate projections, which at first sight could be micropyles, although their arrangement would be exceptional. However, as in other pentatomoids with a well defined pseudoperculum, the aero-micropylar canals occur in *Sciocoris* along the opercular margin. They are extremely difficult to trace amongst the horns resembling aeropyles which project from the whole chorion (fig. 124D).

Embryogeny is almost typical with the embryo nearly superficial, venter facing into the yolk, and blastokinesis without 180° torsion. But the orientation of the germ band and consequently of the fully grown embryo towards the substrate (fig. 124C) is a distinct feature which will be discussed later (p. 344).

S. distinctus did not show essential differences.

ADDITIONAL MATERIAL

ORIENTATION OF DEPOSITED EGGS IN SITU The other species which have been listed at the head of this section (except most probably *Eumenotes*), lay eggs upright.

The orientation of these eggs in relation to the depositing female is just the reverse of *Sciocoris*. If attached by the aft side the prolarval legs would point to the foie side like *Hotea* (fig. 108E, substrate as it would be if attached aft indicated by interrupted shading at right). The lateral sides of the eggs concur with those of the mother when the batch consists of only a few rows. This fact is difficult to ascertain, because most of the eggs are spherical; at hatching egg orientation can be traced by the position of the burster. Sometimes there is a slight left-right deviation of double-rowed eggs, as in *Tantia* (fig. 122A). This deviation may be caused by the slight movements side to side of the mother's axis during deposition. In the two-rowed batches of *Edessa*, the left and right eggs have exactly the same orientation (fig. 119B). A similar situation was common in two-rowed batches of other species. In eggs clustered in many rows, as in *Arvelius*, where clusters contain up to 80 eggs, the orientation of the mature embryos

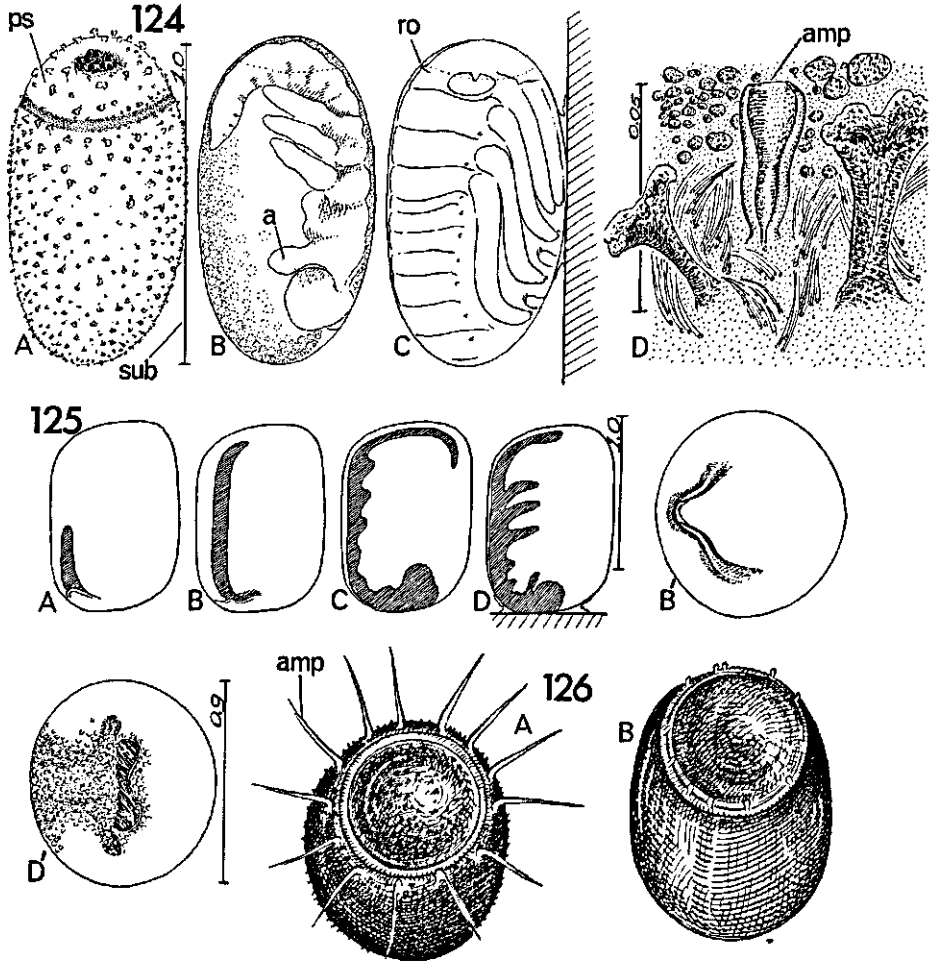


Fig. 124–126. Pentatomidae 124A–D: *Sciocoris cursitans;* D: chorionic fragment with one aeromicropyle. 125A–D: *Perillus bioculatus*, early embryogenesis; B', D': normal to the basal pole. 126A, B: eggs of unidentified species (Neth. Ant.), obliquely from above.

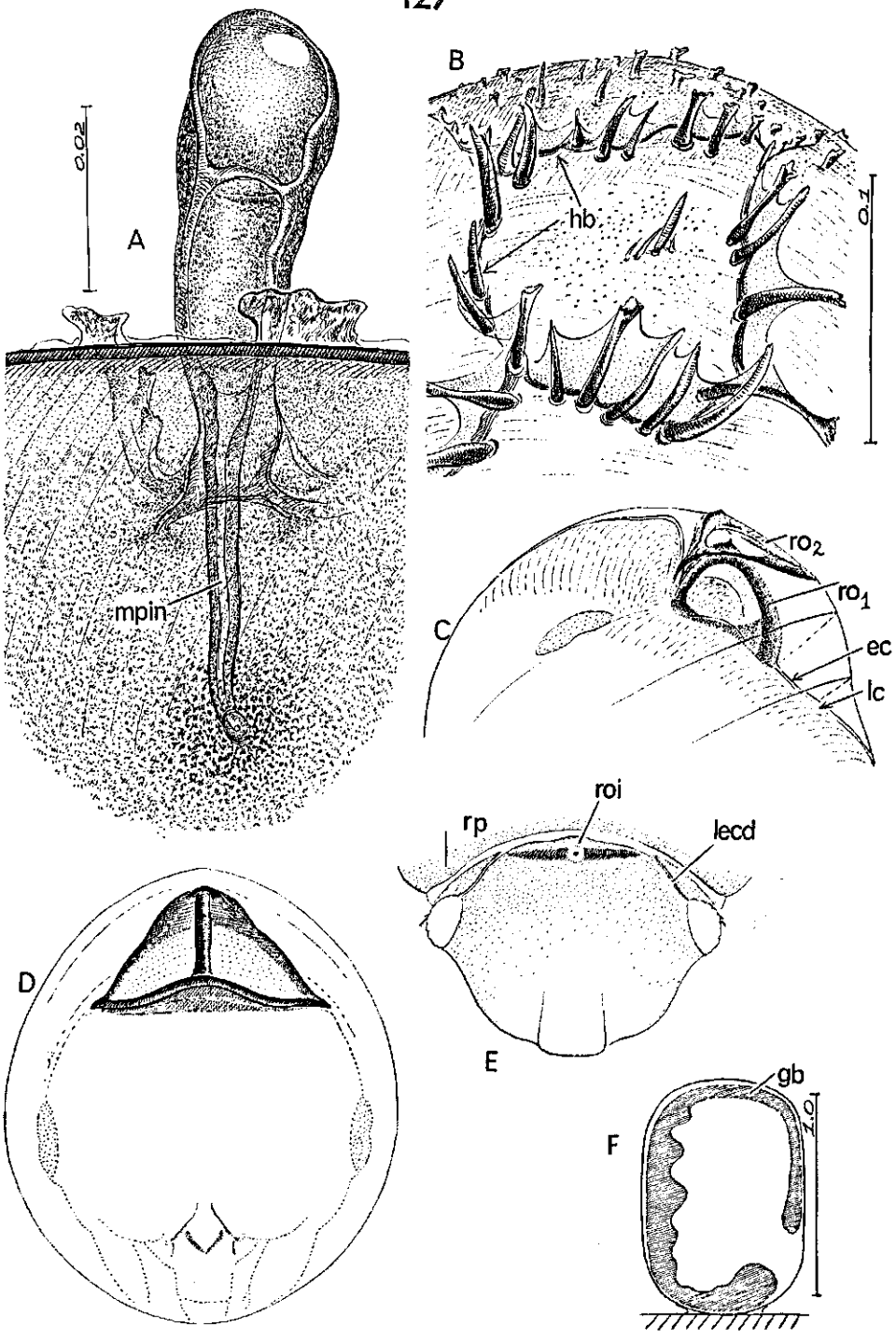
show that there is a gradual turn of the eggs from the middle row towards the side rows (fig. 123A). The mother, walking forwards along a straight line, has to turn her longitudinal axis over half a circle, each time that a transverse row is deposited. The result is that the eggs of the left and right outer row are almost opposed to each other in their dorsiventrality. A similar but complete inversion of the eggs has been encountered in two-rowed eggs of *Macrina juvenca* and *Aeliomorpha* sp., each belonging to a different subfamily. However inversion here has another reason. The dorsiventrality of the prolarva can at once be derived from the position of the black egg-burster, which marks the anterior dorsal region of the larva. In these two species, the egg-bursters in each row point outwards (fig. 120, 121C). This means that the venters of the prolarvae face each other. The eggs are deposited in two rows along grass stems, and the position of the female along the grass cannot be changed during laying. Thus the eggs leave the genital tract rotated through 90°; the possibility of the eggs being re-arranged by the female's legs may be excluded. Those eggs which come to belong to a given row, are glued to the substrate turned through 180° when compared with the eggs of the adjacent row. Since the eggs are delivered alternately one for the right and one for the left row, we suppose that they originate consecutively from the right and from the left ovary and that alternate eggs are rotated 90° in each direction. The reversed grouping of the left and right eggs is easily recognized in *Macrina* because of the different convexity of the fore and aft side of the egg. This unusual behaviour is not invariable in the three batches of *Macrina* studied (fig. 121C), but the many series of *Aeliomorpha* only rarely showed misrotations (fig. 120).

SHELL STRUCTURE In the typical pentatomid egg the aero-micropylar system, with a varying number of projections, is arranged around the rim of a well defined cap (fig. 121, 123B, 126). *Edessa* and *Antiteuchus*, however, have retained the excentricity of the micropylar and the opercular rings (fig. 119A), a condition which is normal in scutellerids. In contrast to scutellerids, *Edessa* and *Antiteuchus* have no projections of the micropyles inward and none of the pentatomid eggs studied possess them. The aero-micropylar outer projections tend to be prolonged in the Asopinae, where they conform to a constant type: skittle-shaped, glossy and smooth. Asopine eggs are not quite spherical; the anterior pole and pseudoperculum slope down slightly towards the fore side (fig. 125). Details of the micropylar processes may be useful for taxonomic grouping. In many spp. the shell has a characteristic sculpturing and the remarkable texture in *Ancyrosoma* resembles that of *Sciocoris* described above.

The allotment of the Eumenotinae to the Pentatomidae seems doubtfully correct, when the quite deviative type of the egg of *Eumenotes obscura* is considered. The pseudoperculum of this species is displaced entirely to the lateral side. This condition

---

Fig. 127. Pentatomidae, *Carpocoris pudicus*. A: aero-micropyle, optical section; B: fragment of chorion, outer view; C: lateral view of prolarval head, larva enveloped by two membranes with bursters, artificially separated (see text); D: same as C, front view; E: head of prolarva; F: early embryo.


A
0.02
mpin
B
hb
0.2
C
ro2
ro1
ec
lc
roi
rp
lecd
D
E
F
gb
0.2

and the egg shape is exactly paralleled in the *Anoplocnemis* group (Coreidae), which lay the eggs in chains. The ring of micropyles is not concentric with the cap, but its precise course has not been verified in *Eumenotes*.

The shell of *Macrina* was studied with the electron-microscope. Fig. 298C reveals a solid unlayered section. The only sign of a transition between two layers is given by a zone of square holes, which separates the inner third of the shell. The pseudoperculum has the same structure as the rest of the shell and its margin is indicated only by a deep constriction. The thin aerostatic inner layer passes uninterrupted through this border. The layer is almost twice as thick along the square anterior edge of the egg, which carries the outer aero-micropylar processes.

EMBRYOGENESIS This follows almost the same pattern as for scutellerids. Invagination, elongation and the beginning of differentiation are shown for *Perillus* (fig. 125A–D). The maximum length of the band in the Asopinae is less than in the Pentatominae studied (fig. 121B, 127F). *Picromerus bidens* overwinters as the egg. Morphogenesis stops early in elongation of the band, before protocormic outgrowths appear.

HATCHING The posture of the prolarva within the egg is normally as in diagram fig. 279H; this picture is as frequent as its mirror-image. The pseudoperculum is first loosened medially aft by a strong opener (fig. 111, 121D, 122B). It has been known for a long time that the solid pentatomid egg-burster is enclosed on the neck of the larva (fig. 111). This region is morphologically the same part of the head, which carries the more anterior burster in other pentatomomorphous groups and is not the vertex. The epicranial sutures of the hatched larva show this; the vertex in pentatomids and scutellerids has disappeared, because the lateral epicranial arms run straight back into the neck (fig. 127E). The last medio-dorsal part of the head therefore represents the frons. It is this element and a small area of the pronotum which are enclosed by the egg-burster. The egg-burster of *Carpocoris* (fig. 127) has some features not reported in the past. After removal of the chorion the picture is as drawn in fig. 127C. It seems that two bursters are superimposed and each forms part of a separate membrane. The outer membrane is a smooth sack surrounding the whole larva without enveloping the individual appendages separately. Therefore it may be the serosal cuticle, but the burster and the lines marking the larval segments and appendages make epidermal origin more likely. This problem will be discussed further on p. 315. The egg-burster of the outer pellicle is not merely a strengthened plate, but it is sharply and characteristically delimited in three dimensions (fig. 128), rising vertically at the front. A transverse line connects the epicranial arms. Thus the anterior border of the triangular structure exactly marks the suture between postclypeus and frons. The lines are completely absent on the inner embryonic cuticular membrane which bears the egg-burster proper. The front of this pyramid is a solid vertical plate which presses the clypeo-frontal suture down as in fig. 127C, where the situation is artificially exaggerated because preservation fluid has separated the two membranes. In the free larva,

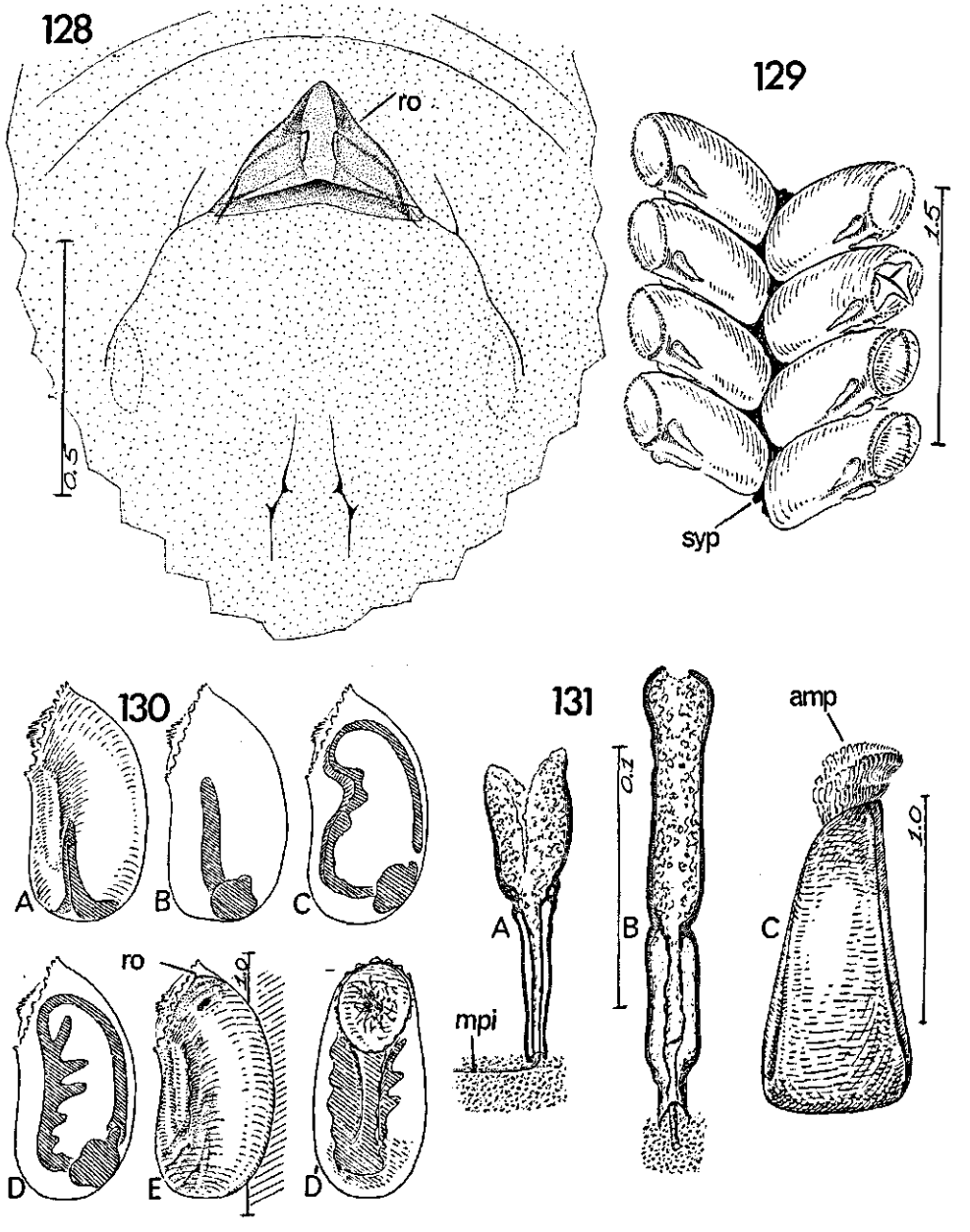


Fig. 128–131. Pentatomidae, Plataspidae 128. *Carpocoris pudicus*, second embryonic membrane, flattened out. 129. plataspid species (Ivory Coast), egg batch. 130A–E: plataspid species (Ivory Coast), gross embryogenesis. 131A–C: *Ceratocoris bucephalus;* A, B: aero-micropylar process from fore and aft sides, respectively.

the projection of the egg-burster remains anteriorly as a transverse dark ridge with a white circle in the centre (fig. 127E). Two bands of fine denticles are found on the head, which become visible on the embryonic cuticle left by the larva. In all the other pentatomids, whose mature eggs have been studied, there was only one burster.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) dealing with available information on the pentatomoid eggs, cited about 100 papers, most of them referring to Pentatomidae. PUCHKOV and PUCHKOVA (1956) and PUCHKOVA (1959) added much new data. The embryonic membranes and the position of the egg-breaker on the head need further study. From our account in the previous sections, the ruptor seems to move posteriad along the head during phylogenesis. This shift is topographical and not morphological. SOUTHWOOD *(op. cit.)* thought that the pentatomomorphous egg-burster was associated with the vertex. Yet in 1925, VAN EMDEN recognized that it had other origin and we can confirm this. The burster is always attached to the frons.

2.2.11 Plataspidae, Aphylidae

Plataspidae

MATERIAL: *Coptosoma*, five unidentified spp. from the Ivory Coast (living deposited eggs); *Ceratocoris bucephalus* White (ripe ovarian eggs, origin Ivory Coast).

Deposition and chorion structures

The characteristic plataspid clutch of eggs, known from the literature, is produced by the *Coptosoma* spp. we studied. Fig. 129 shows that the two rows of eggs are pressed down sidewards, each row to the opposite side. Sagitally the eggs are almost in the same plane and thus no rotation of the type as shown, for instance, in *Aeliomorpha* (p. 118) has occurred. In all species, black pellets containing symbionts are attached to the substrate between the eggs. In the group of true ootheca-builders the deposition is different as in some *Plataspis* spp. and, judging from the shape of ovarian eggs also in *Ceratocoris* (fig. 131C). CARAYON (1949) drew the ootheca of *P. flavosparsa* Mont. in which the two rows of eggs adhere to the substrate by their aft sides. Deposition is not likely to be as in *Aeliomorpha* and *Macrina* (see p. 118), if eggs are pressed down as in *Plataspis*. Perhaps one row is laid and then the other is laid in the opposite direction.

Coptosoma eggs are distinguished by left-right asymmetry (see cross-section in fig. 132A). This is an adaptation to the oblique arrangement in pairs; the shape makes them firmer. In eggs of the species illustrated (fig. 129), two transparent solid outgrowths, one in each lateral groove, serve the same purpose. In the typically hod-shaped egg of *Ceratocoris* (fig. 131C), the greatest economy in space occupied by the batch is reached by the flattening of all surfaces. The chorion structure in these protected eggs, is simple, but the exposed eggs of smaller species have a sculpturing, characteristic for the species, although based on the same plan. In one of the *Copto-*

soma species studied, the sculpturing of the outer layer reaches the form of a spacious structure supported by struts. The struts are simple columns along the edges of the follicular polygons (fig. 132B). In the centre of each follicular pit a massive strut arises. This branches upwards to support the thin chorionic outer film (fig. 132D). This film is lacking in the median strip along the fore side (fig. 132A) allowing air into the spaces all round the egg. The varying size of the cavities of the outer layer is revealed by the section drawn (fig. 132). The seemingly solid inner layer of chorion is almost constant in thickness (20 μ). An aeriferous inner layer is obviously present in the anterior part of the shell, judging from surface observation ('felty' aspect when sharply focused on the inner chorion). The few adequate microsections (fig. 296) show this open inner layer very clearly. It now appears that what was seen in hand sections as compact chorionin, consists mostly of spongy material. The solid lamina inwards from the

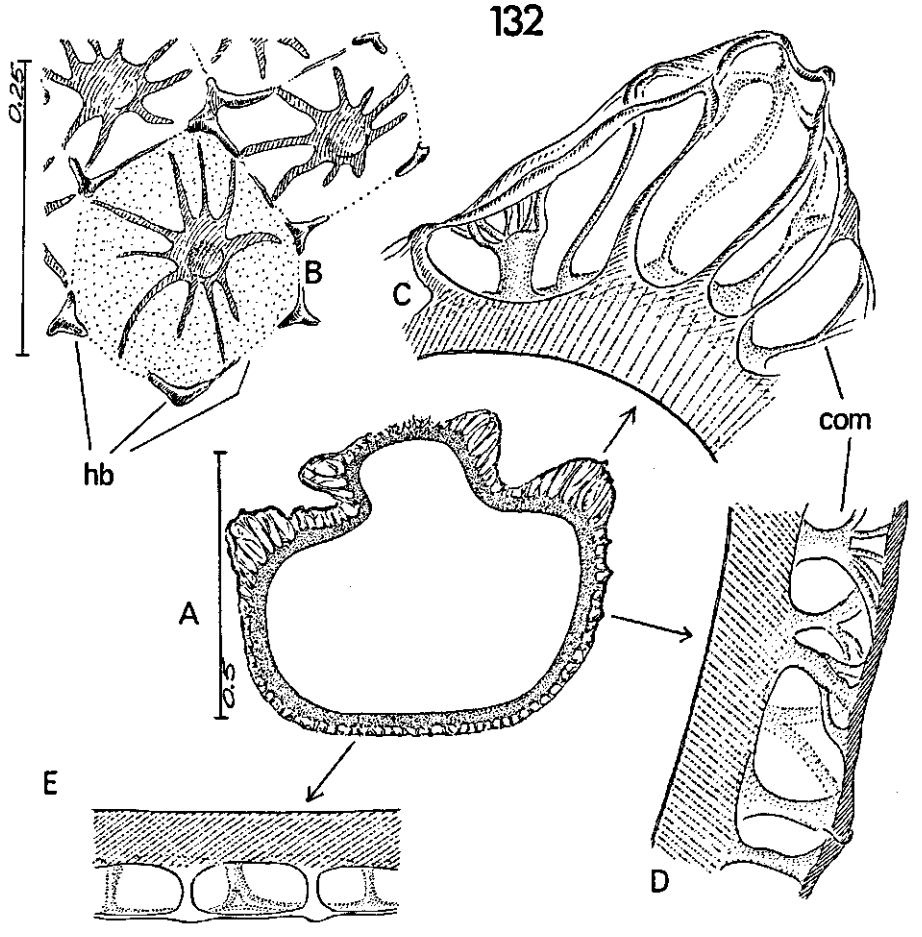


Fig. 132. Plataspidae; A–E: plataspid species of fig. 130; A: transverse section of the egg's waist; B: surface view of chorion, lateral side of egg; C–E: transverse sections from the shell regions as indicated by arrows.

aeriferous inner layer is only 0.5 μ thick. The *Coptosoma* shell is thus highly porous externally and internally. An experimental analysis of its respiratory capacity is needed.

The many aero-micropylar processes vary in complexity and form between species. Those of the large eggs placed in ootheca, are long. This elongation of the processes probably ensures adequate aeration of the egg in the ootheca. The processes on the side attached to the substrate are longer. In *Ceratocoris*, this is due to the distal compartment of the processes, being longer than on the opposite side (fig. 131A–C). In contrast, the micropylar canal in the short process is longer and makes a sharp bend inside the egg.

EMBRYOGENESIS This has been studied in the *Coptosoma* spp. Invagination occurs at the posterior pole, but the blastopore gradually shifts aftwards (fig. 130A–D). The band is not entirely superficial and when fully elongated the tail touches the cephalon. The asymmetric constriction along the fore side of the egg creates a bilateral asymmetry of the germ band (fig. 130D'). Blastokinesis occurs without rotation. The opener of the pentatomid-like T-shaped burster presses against the zenith of the opercular rim.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) listed nine papers with data on plataspid eggs. He discussed sections of shell and micropyles of some species. SOUTHWOOD claimed that the follicular pits are lined with a coat of cement during oviposition. In our studies, the roof over the struts consisted of chorionic material.

Aphylidae

MATERIAL: *Aphylum bergrothi* Schout. (ovarian eggs, origin Australia).

The egg resembles the small plataspid eggs (lateral sides somewhat indented, pseudoperculum sloping). The chorion (45 μ thick), however, is not markedly vacuolated, except for the thin aerostatic inner layer. There are about 20 short aero-micropyles, whose central canals do not protrude inward. The boundary of the cap is well marked.

PREVIOUS DESCRIPTIONS None.

2.3 Cimicomorpha

SOUTHWOOD (1956, p. 198) characterized cimicomorphous eggs as follows: "Eggs with micropylar apparatus consisting of canals running in the rim of the chorion and surrounding the operculum, which is always present; the canals of two types, true micropyles (for sperm passage) and pseudomicropyles (for gaseous exchange), but one type may be absent; operculum strongly differentiated from the rest of the chorion with deep follicular pits; median egg-burster absent". Because of the general appli-

cation of this definition, eventual exceptions should have phylogenetic significance. There are some striking exceptions and they will be presented. SOUTHWOOD, and earlier workers, could not trace true micropyles in Nabidae, Microphysidae and Miridae, but he was aware that he might have overlooked them. Their absence in Cimicidae and Anthocoridae is more understandable, because in these families fertilization occurs before chorion formation. More recently HINTON and HARTLEY (HINTON, 1962) found two micropyles in Miridae. We confirmed their presence in all Miridae eggs studied, and in some Nabidae and Microphysidae. According to SOUTHWOOD *(op. cit.)* the canals in Tingidae could be all micropylar. Yet, LIVINGSTONE (1962) considered the canals as aeropyles. We concluded that tingid eggs possess two micropyles besides the many aeropyles. Micropyles are always clearer distinguishable from aeropyles, when observed in fragments of the untreated shell by the classical optical method, than by the cobalt sulphide treatment and serial sections.

Whereas the chorionic structures are rather uniform in this major group, the embryogeny is more varied. In embryology the Reduviidae are remote from the typical Cimicomorpha.

2.3.1 Nabidae, Velocipedidae, Pachynomidae

Nabidae

MATERIAL: *Nabis rugosus* L. (living deposited eggs), *Himacerus apterus* Fabr. (preserved eggs with young embryos), *Stalia boops* Schdte (deposited eggs); ovarian eggs of *Gorpis deliensis* Naez. and *Lorichius umbonatus* Dist. (origin Sumatra), *Prostemma* sp. (origin Curaçao, Neth. Ant.), *Arachnocoris dispar* Scott (origin Brasil).

Nabis rugosus

The posterior pole of the egg points away from the mother's anterior when having left the ovipositor; the egg thus is placed in a direction opposite to that of saldids and mesoveliids. The nabid mode of oviposition is the most widely practiced and occurs in all those cimicomorphans which insert their eggs.

AERO-MICROPYLAR REGION The fine striation along the cylindrical prolongation of the egg's anterior end consists of the numerous aeropylar canals (fig. 136A). The canals open by minute pores of about 1 μ diameter into the inner meshwork layer of the shell. This aeriferous layer is most developed in the anterior aft of the egg. There is one micropyle which, noteworthily, is off-centre to left or right in the elliptical rim and slightly aft. The micropylar canal is about the same diameter as the aeropyles, but it is easily distinguished by its shortness (fig. 134). The canal opens in the shell above the upper limit of the aerostatic inner layer. The operculum bears an elaborate meshwork which is air-filled. Light-optically its inner layer seems to be porous all over. Scanning-electronmicrographs reveal that the aerostatic inner layer of the actual

shell body extends up to the fracture plane where the operculum is pushed off (fig. 314). It is thus likely that this layer continues uninterrupted through the operculum.

GROSS EMBRYOGENESIS (fig. 133A–I) Incubation lasts about eight days at 30 °C. Invagination occurs aft posteriorly. The blastopore gradually shifts anteriad as the band's tail grows anteriad. An isolated cluster of cells (presumably germ cells) is clearly visible at the upper curve of the caudal flexure. The cephalic part is flexed at a right angle to the protocorm. Although the germ band is immersed within the yolk, it remains attached to the serosa by the right side of the embryonic head. It is remarkable that this point is off the sagittal plane to the left of the egg (marked with X in fig. 133E). The venter of the germ band before revolution always faces the concave side of the egg. Only in one out of the about 150 eggs tested was the orientation reversed. Blastokinesis begins with a slow 180° degrees rotation around the embryo's long axis taking several hours. Six to eight ommatidia are usually faintly visible then. No hydropic organ has been observed. Contrary to our findings in other groups, the anterior serosal plug is already partly formed in *Nabis* long before revolution. The reversal movement is nearly always achieved along the concave fore side. The serosal plug is incorporated into the dorsal organ, but over a much longer period than in Saldidae. The rhythmic pulsing, which accompanies the mixing, is similar but less obvious. When the yolk has been squeezed entirely into the dorsum, the embryonic cuticle is lifted from the front of the head. Within seven hours at room temperature a voluminous bladder is formed like the analogous structure in *Mesovelia* (see p. 52). However, in *Nabis*, the cuticle is stretched by extra-embryonic fluid which is pressed forwards (fig. 133K–M) while in *Mesovelia* the actual head stretches and it is only when the head is withdrawn that the stiff vesicle becomes fluid-filled. The bladder in *Nabis* is initially held constant in shape but before hatching it shows its plasticity. The fluid is withdrawn and the bladder collapses in a wrinkled mass over the head (fig. 136A). The larval head then fills the whole anterior of the egg, by alternate influx of blood into the head and stretching followed by relaxation (compare fig. 136A and fig. 136B). Stretching is easier with the stretched cephalic vesicle. The filling of the subopercular space is more the result of enlargement of the head than of displacement of the larva, because the eyes remain at nearly the same level under the shell. The bladder of the embryonic cuticle then becomes a buffer for eclosion.

ECLOSION The serosal cuticle is, in fact, the first barrier and is the most resistant. At eclosion, the operculum can be easily lifted from the egg with fine pins. This suggests that widening of the neck of the egg under pressure from the pulsating head has already weakened or broken the seal of the chorion. The bursting of the serosal cuticle takes only a fraction of a second during which the head is expelled from the collar of the shell (fig. 133N). As the cephalic bladder has just before attained its greatest volume, the pressure of extralarval fluid seems to cause the break of the serosal cuticle. This cuticle is broken along an irregular circle below the egg's mouth. This serosal cuticular cap has not the distinct ring structure which in many reduviids forms

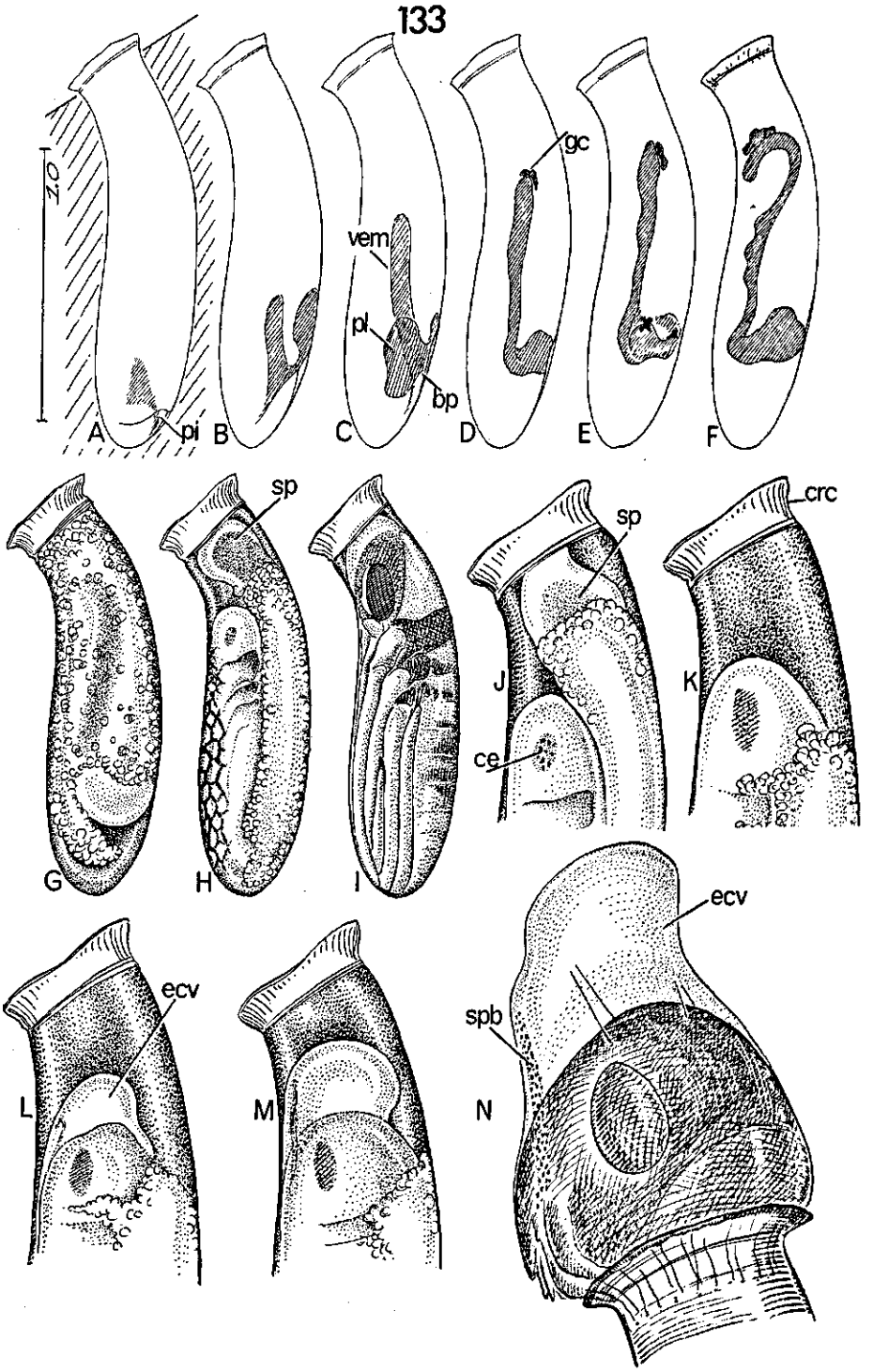


Fig. 133. Nabidae; A–N: *Nabis rugosus*, embryogenesis, before (A–G) and after (H–M) revolution; N, hatching, operculum shot off.

a tool for dislodging the operculum. On the ventral side of the cephalic bladder there are two bands of micro-denticles (fig. 133N, spb), which seem to prevent the larva from slipping back. When the larva, still enveloped by the embryonic cuticle, is two-thirds out of the shell, the fluid is suddenly evacuated from the cephalic bladder. Soon afterwards the pronotum bulges out and the embryonic cuticle splits there.

Successful development does not occur when eggs are placed under water. Freshly laid eggs *in situ* likely desintegrate when submerged, the operculum loosens and yolk is expressed. Eggs, placed in water after blastokinesis, seem to develop in a normal way but cannot hatch. Of 10 submerged eggs removed from the substrate, only one prolarva succeeded in escaping but drowned afterwards. Two forced open the serosal cuticle, but died still enveloped by the embryonic cuticle. The other seven died without breaking the serosal cuticle.

The posture of the fully grown embryo within the egg is illustrated in diagram fig. 279K. The arrangement of the appendages is as frequent as its mirror-image. A characteristic feature is the course of the two mid legs hidden from outside below the other appendages.

Himacerus apterus

The collar is very high and bears 40–50 aeropyles (fig. 135, 137). The diameter of these canals is about 5 μ. The entrance into the aeriferous inner layer is much closer to the rim than in *N. rugosus* and is marked by a spacious air reservoir. The single micropylar canal occupies about a third of the collar and is less than half the diameter of the aeropyles. The micropyle curves to the interior of the egg anterior to the level of the aeropylar reservoirs. Six eggs had the micropyle dextrally, four sinistrally and in one egg no micropyle was traced.

Eggs overwinter and diapause is passed in the ♀ -stage when the thoracic appendages are still small. Eggs are laid in autumn and a fall in temperature stimulates oviposition. The germ band, in contrast to *N. rugosus*, does not extend higher than the posterior two thirds of the egg.

The early embryogenesis differs in another respect from that of *N. rugosus*. The invagination seems to occur further lateral in the egg. We missed the first stages, but the position of the ♀ -shaped embryo is variable. In some of them the dorsum faces left of the egg as seen from anterior pole, some others face aft or are intermediate. A lateral invagination is possible as we will see in the Miridae. Development of *H. apterus* after diapause has not been traced.

THE AERO-MICROPYLAR REGION IN SOME OTHER SPECIES *Gorpis deliensis*. Much like *H. apterus*, 50–65 aeropyles of about 2.5 μ width, their course sharply defined up to the apical margin of the collar, where they open in a ring. The single latero-aft micropyle is as wide but extends up to a third of the collar's height.

Lorichius umbonatus. Aeropyles 60–80 in number and about 2 μ wide; their entrance in the aeriferous inner layer is indicated not by a circular pore, but by a long wedge-

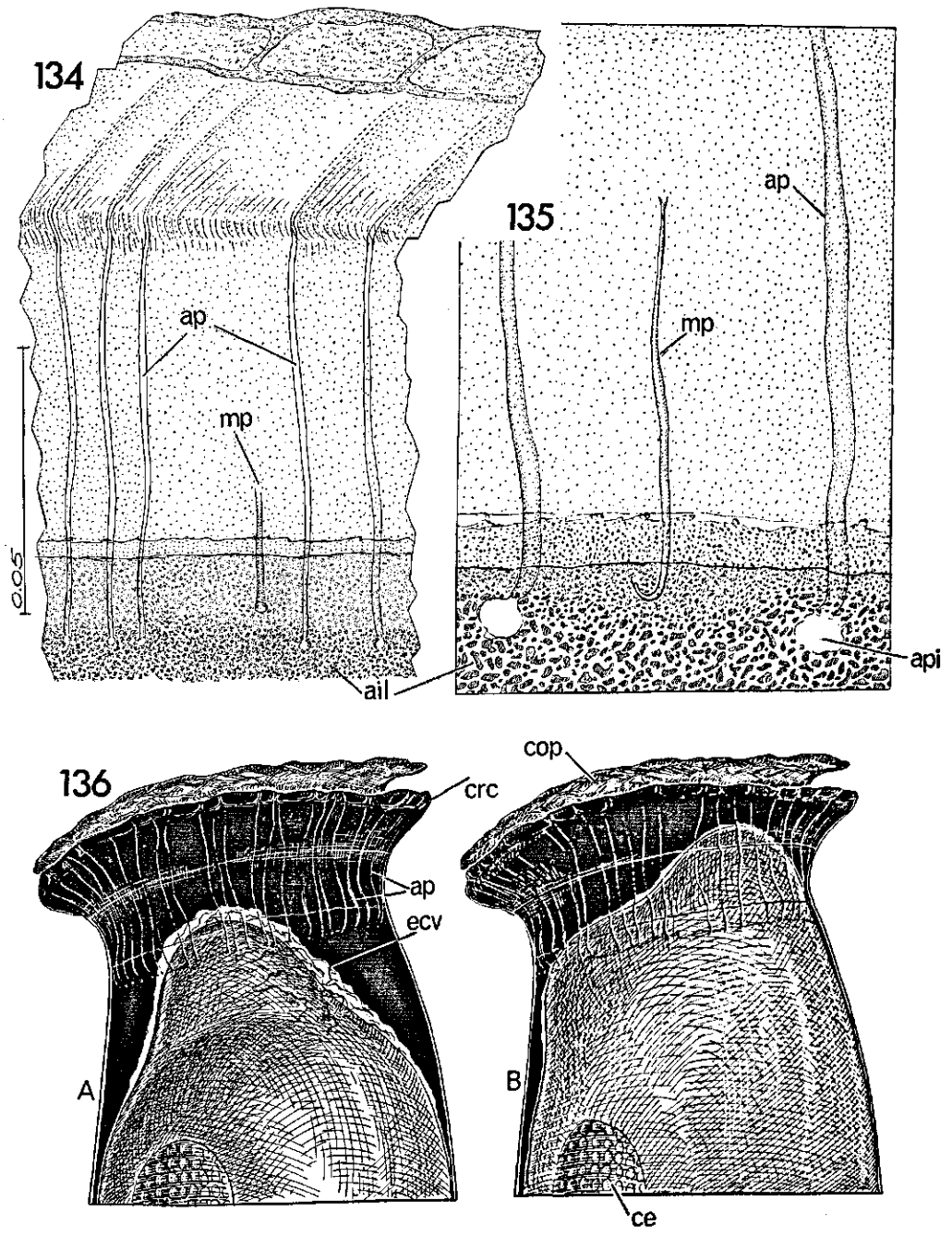


Fig. 134–136. Nabidae 134. *Nabis rugosus*, lateral part of rim collar. 135. *Himacerus apterus*, the same. 136A, B: *Nabis rugosus*, incipient to hatching, filling of the vesicle of the embryonic cuticle with the larval head.

shaped cavity in the meshwork. The single micropyle is further aft and among ten eggs investigated it occurred six times left and four times right. It is twice as wide as the aeropyles and goes only a ninth of the way up the collar.

Prostemma sp.(fig. 138). The high collar bears a regular scalariform structure, except at the base. Unlike the previous species, the wide aeropyles in *Prostemma* are short and cover only a ninth of the collar length. They have irregular openings into the outer network and their canals point deep into the aeriferous inner meshwork of the shell. The single micropyle is much narrower, its base penetrating into the rim of the shell.

Arachnocoris dispar (fig. 140). The egg bears a posterior oblique disc, thus suggesting that the egg is not embedded but attached superficially. This is certainly an adaptation to its life in spider's webs. Operculum with central elevation. Aeropyles very fine, extending far into the porous inner layer. No micropyles were observed, which could mean that fertilization is intra-ovarian.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) studied chorionic structures of two species and he cited seven other authors on external aspects of nabid eggs. None of the authors found the micropyle, which actually is present in most nabids. In those species having haemocoelic insemination the sperm-canal would be lost.

SOUTHWOOD discovered the cephalic ampulla in *D. limbatus*. He misinterpreted its origin in referring to it as the 'yolk plug' which JOHNSON (1936) applied to the retained anterior serosal strand in Miridae, for which we will propose, on p. 164, the term: 'persistant serosal plug'.

Velocipedidae

MATERIAL: *Scotomedes minor* Bredd. (ripe ovarian eggs, origin Java).

The egg-shape, the collar differentiation from the shell rim and the operculum, confirm the close relationship of this family with the Nabidae. The air-filled inner layer of the shell is voluminous and is like the hexagonal follicular pattern on the outside of many insect eggs. The inner layer has wide tunnels following the hexagon boundaries (fig. 139). These tunnels are flanked by large struts, between which air can penetrate into the hexagons which are supported by numerous fine struts. The aeropyles, about 20 in number, are in direct contact with the broad inner air tunnels and are of the same width, *i.e.*, 7 μ, but they do not reach higher up in the collar. The single micropyle on one of the sides close to the convex aft side is rudimentary. It is extremely small and seems solid, so that fertilization may be intra-ovarian.

PREVIOUS DESCRIPTIONS The outline of the egg of only one velocipedid is known, of *Scotomedes alienus* Dist. (MILLER, 1956).

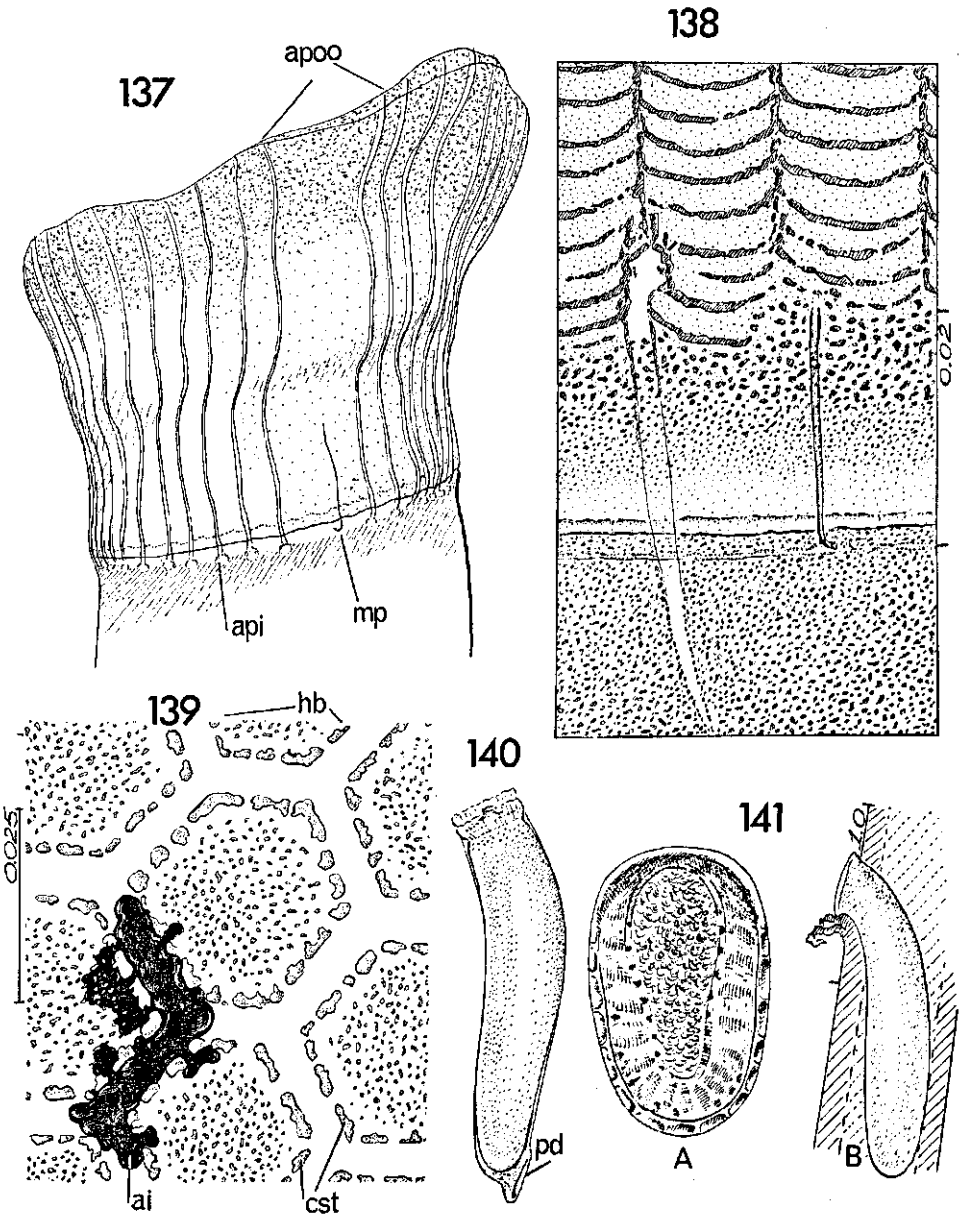


Fig. 137–141. Nabidae, Velocipedidae 137. *Himacerus apterus*, anterior pole, lateral. 138. *Prostemma* sp. (Neth. Ant.), lateral part of rim collar. 139. *Scotomedes minor*, open chorionic inner layer, partly air-filled. 140. *Arachnocoris dispar*, ovarian egg. 141. *Stalia boops;* A: operculum, external view; B: deposited egg.

Pachynomidae

MATERIAL: *Pachynomus brunneus* Latr. (ripe ovarian eggs, origin Sudan).

The egg is nabid-like (shape, structure of aeropylar and opercular region). A spur of micropyles was never traced. Micropyles are absent as in some cimicoids but not reduviids. It has still to be verified whether there were originally two micropyles as in cimicoids.

PREVIOUS DESCRIPTIONS None.

2.3.2 Anthocoridae, Cimicidae, Microphysidae, Plokiophilidae

Anthocoridae

MATERIAL: *Anthocoris nemorum* L., *Acompocoris pygmaeus* Fall. (living ovarian and deposited eggs); *Anthocoris confusus* Rt., *nemoralis* Fab., *gallarum-ulmi* De G.; *Temnostethus gracilis* Horv., *pusillus* H.-S.; *Orius* spp.; *Lyctocoris campestris* Fabr. (living ovarian eggs).

A ring of aeropyles is present, without any micropyle. Fertilization occurs before deposition of the chorion. Invagination of the germ band occurs when the chorion starts to be secreted. Oogenesis occurs in all ovarioles simultaneously (contrast *Cimex*) and more than one egg is in each ovariole just before deposition. This counts not for hibernating *Temnostethus gracilis*, whose ovarioles contain only one egg (for the extraordinary reproductive cycle of *Temnostethus*, see p. 295).

Anthocoris nemorum

EARLY EMBRYOGENESIS Fertilization and half of the incubation period takes place in the ovariole (fig. 142, 143). Invagination of the germ band starts just aft of the posterior pole (fig. 142A). When the band is still short and no spur of protocormic outgrowths is shown it assumes a pronounced ʔ -shape, the caudal end reaching only the equator (fig. 142B). When protocormic buds appear, the caudal curve advances anteriad, but the cephalic dorsal flexure becomes gentler. The next stage (fig. 143D, E) represents the ʔ -formation, typical of bugs with an immersed germ band, but here it remains far remote from the anterior pole. The condensed stage retains the ʔ -shape, but the whole embryo shrinks and folds into the basal half of the egg (fig. 143F). The egg is deposited by the female in this stage.

Isolated germ cells could only be traced in stages B and C (fig. 142, 143). The outline of the oocyte changes before chorion formation. The oocyte, surrounded by distinct binucleate follicle cells, is at first constricted posteriorly. The constriction gradually shifts anteriad and at last gives rise to the aeropylar region and operculum (fig. 143E, ra).

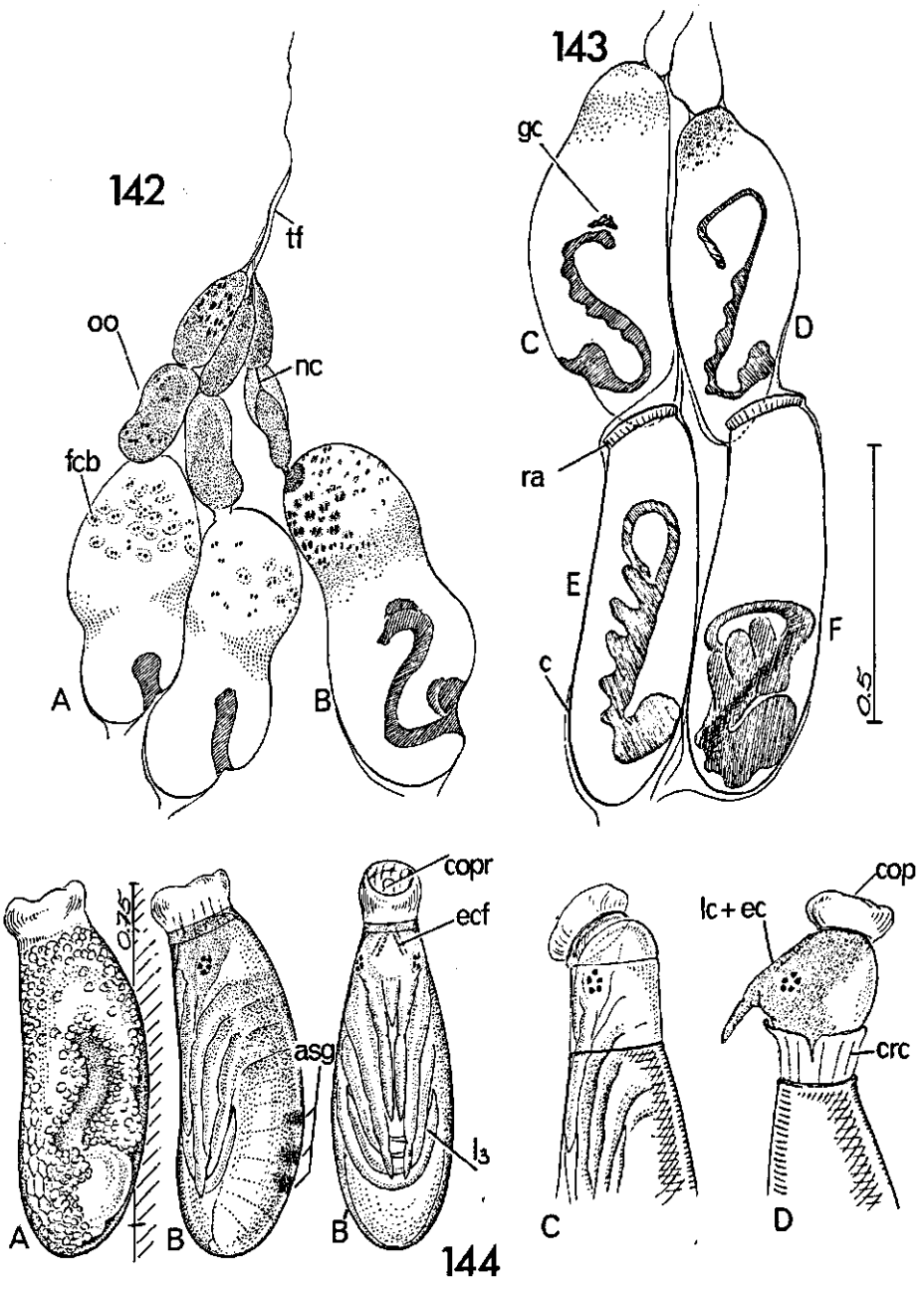


Fig. 142–144. Anthocoridae, embryogenesis 142A–B: *Anthocoris nemorum*, start of intra-ovarial embryogenesis. 143C–F: *A. nemorum*, further embryonic growth, chorion secretion after stage D. 144. *Acompocoris pygmaeus;* A: before revolution; B, B′: attitude of prolarva; C, D: hatching.

The later development and hatching have been studied in the next species.

Acompocoris pygmaeus

LATER EMBRYOGENESIS Unlike *Anthocoris*, which inserts its eggs, *Acompocoris* usually lays eggs exposed between the bases of pine needles. Eggs were only rarely inserted into the needle. When moist filter paper was provided alone, eggs were attached and not inserted.

Blastokinesis varied, but it might have been affected by the moistness in the petri dish, as several embryos died before eclosion. In six eggs the embryo moved directly along the convex aft side towards the anterior pole so that its venter faced the substrate. Five embryos behaved normally with a 180° rotation. In four eggs, the embryo moved laterally anteriad. Until blastokinesis the eye plate appears yellowish; the real pigmentation of the optic elements starts after revolution; only five isolated ommatidia are present in the first larval instar. The serosal plug becomes entirely retracted within the embryo long before eclosion.

ECLOSION The appendages (fig. 144B, B') are arranged as in *Nabis*. There is no cephalic ampulla for eclosion. The embryonic cuticle has a longitudinal crenulate ridge with two diverging arms running anteriad over the clypeal region of the head (fig. 144B'). The explosive discharge of the operculum may be effected by the simultaneous circular break of the serosal cuticle. As the prolarval head is ejected, the collar stretches considerably before its upper margin rips from the operculum (fig. 144C, D).

Cimicidae

MATERIAL: *Cimex lectularius* L. (living, from laboratory stock of Berkeley, California).

CHORION The chorion starts to be secreted when the blastoderm is formed (DAVIS, 1956). When the germ band invaginates it is complete, 15 μ thick in the neck region and about 10 μ elsewhere. The inner aerostatic layer is distinct in the anterior region. There it is 2.5 μ thick and the struts are arranged in large irregular 'cells' as seen in surface view. Posteriad the struts are finer, shorter and less spaced. The short collar above the rim has a thick solid bar round the top. The aeropyles do not reach this upper margin. They measure scarcely one micron in diameter and their number averages 150. Micropyles are absent; fertilization precedes chorion secretion.

EARLY EMBRYOGENESIS About a third of embryogeny is in the ovary (fig. 145). The development of the embryo is roughly as in other Cimicoidea with sagittal invagination: germ band immersed with only the head touching the serosa and blastokinesis involving 180° rotation. Fig. 146A–I of the first half of the development shows the following differences from *Anthocoris*. *Cimex* starts depositing the chorion much

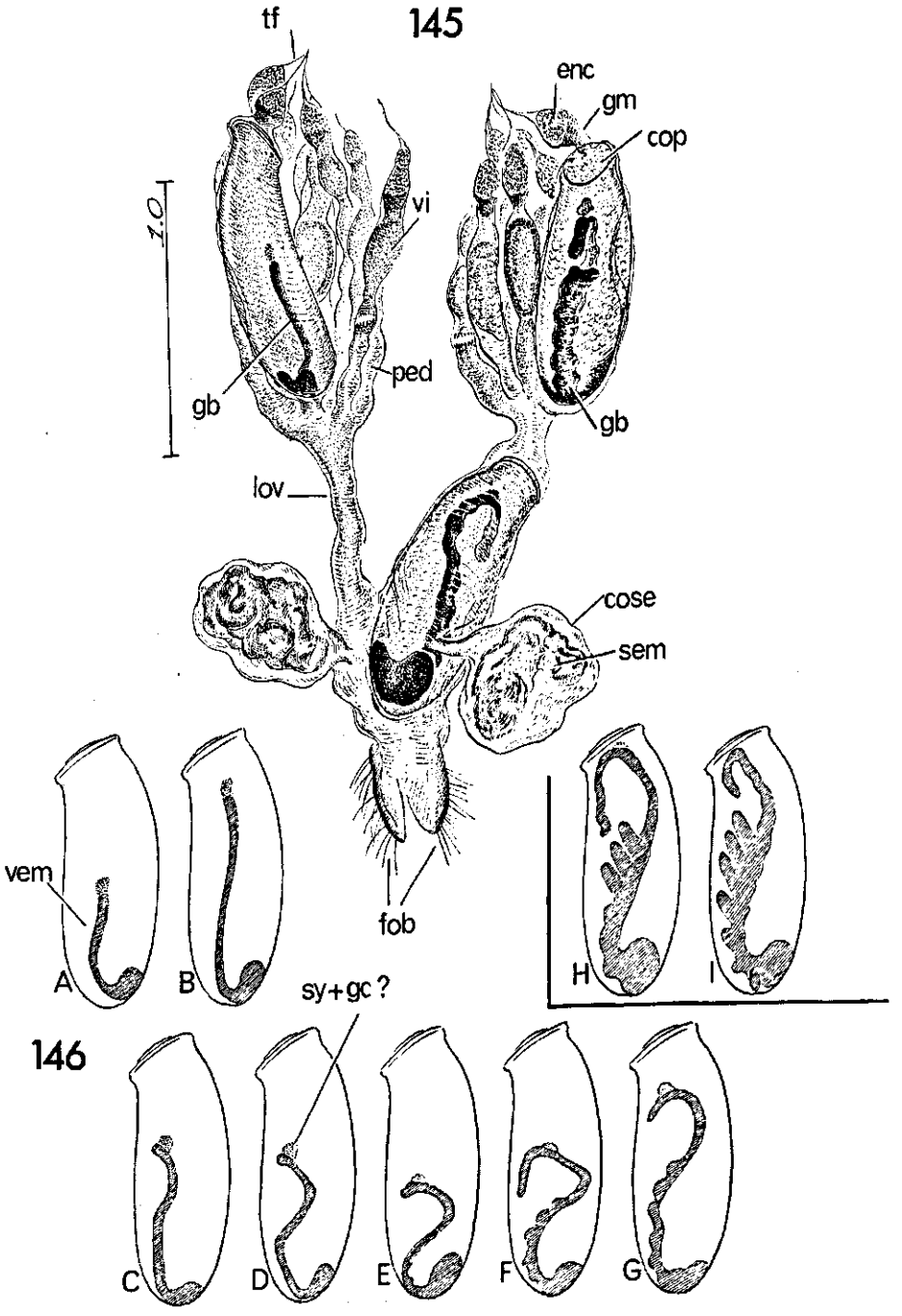


Fig. 145–146. Cimicidae, *Cimex lectularius* 145. female genital system, intra-ovarial embryogenesis, one egg passing through the oviduct. 146. early embryogenesis; A–G: within the female; H, I: after deposition.

earlier. Only one egg at a time is formed in each ovariole and at any time there is not more than one fully formed egg in each ovary (fig. 145). In *Anthocoris* the shell starts to form when the germ band invaginates and all ovarioles are producing more eggs simultaneously (fig. 143). The change in shape of the band is different. The embryo of *Cimex* invaginates in a straight line to just below the operculum. It then folds to make a ♀ in the posterior half of the egg but then stretches to a maximum length when the egg is laid. In *Anthocoris* the blastopore is further aft of the posterior pole; the caudal and gnathal flexures are distinct and have already arisen before the band reaches beyond the equator; the later lengthening of the embryo before revolution never reaches the upper pole. The *Anthocoris* embryo is folded like an accordion at egg release.

In *Cimex*, a cluster of stainable material is found on the tail of the band (fig. 146D). Its appearance, location and migration is as in *Anthocoris* and in many other species treated in this study. We referred to it as germ cells, but BUCHNER (1953) referred to it in *Cimex* as a mycetome. The embryos of *Nysius* and Aphididae have a mycetome attached to the same place; we easily recognized these structures by the same staining and dissection technique. The untreated mycetomes are very striking and coloured. Not so in *Cimex*, where BUCHNER mentions that initially the mycetocytes are only sparely infected and many cells are probably entirely free of symbionts. We think therefore that the cluster may be partly of germ cells.

As later embryonic stages and eclosion have been studied in the past, we have ommitted these aspects. We can however add that the serosal cuticle splits in a circle at eclosion.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) gives 20 references for anthocorid and the closely related cimicid eggs and HASE (1917) and SANDS (1957) should be added. Cimicid eggs and anthocorid eggs of species which live in stored products, are laid in exposed or semi-exposed situations. No micropyles were found, but as in other cimicoids they have always been overlooked, investigation was renewed. We confirmed their absence in many species. In most species embryogenesis starts within the female. We have found the ♀ -shaped embryo in ovarian eggs of several species of *Anthocoris*, *Orius* and *Temnostethus* and CARAYON (1949b) found it in many other genera and in cimicids. A superficial account of later embryogeny of *Cimex* is given by HASE (1917). He mentioned only revolution along the fore side of the egg. He, and SIKES and WIGGLESWORTH (1931) studied hatching of *Cimex* and reported denticulate ridges on the head of the embryonic cuticle as in *Acompocoris*. The embryological account by HEYMONS (1899) refers not to *Cimex dissimilis* Fab. but to a pentatomomorphan. HASE *(op. cit.)* and JOHNSON (1940) submitted *Cimex* eggs to different treatments. The period of incubation after laying lasts at least five days at 30 °C. Complete incubation probably takes twice as long. Development is inhibited when the eggs are submerged.

Microphysidae

MATERIAL: *Loricula elegantula* Baerenspr., L. *pselaphiformis* Curt., *Myrmedobia coleoptrata* Fall. (ripe ovarian and freshly deposited eggs).

Eggs are inserted in crevices amongst lichens on tree trunks and have curious long tapering and porous outgrowths like a rosette surrounding the operculum. Along the inner surface of each element is one, rarely two, groove which extends as a short

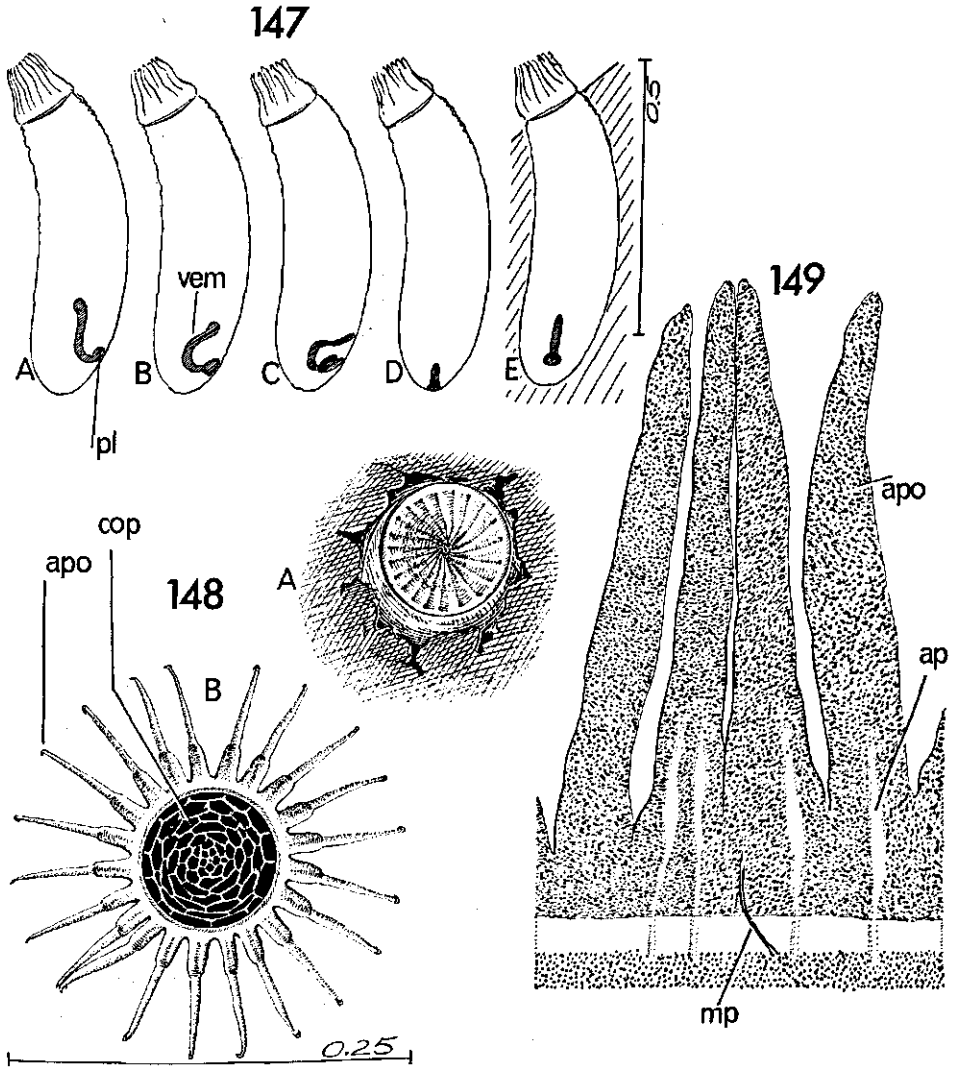


Fig. 147–149. Microphysidae 147A–E: *Loricula elegantula*, diapausing embryo in individual eggs; A is represented most often. 148. *L. elegantula*, egg observed from the anterior pole; A: under humid; B: under dryer conditions (compare micrographs, fig. 315). 149. *Myrmedobia coleoptrata*, part of chorionic rim.

aeropyle into the inner meshwork layer (fig. 149). A micropyle has been found in *M. coleoptrata* (fig. 149) but we could not ascertain its exact position along the rim nor whether there are two or only one. If present, in *L. pselaphiformis* the micropyles are very obscure.

SOUTHWOOD (1956) found that the tips of the porous 'petals' of ovarian eggs touch each other. CARAYON (1949 b) noticed that they radiate out in laid eggs. We observed that even after egg release the processes can close over the operculum in moist air. When a petri dish, containing eggs under humid conditions, is opened and a lamp is focused on the eggs, the 'petals' turn rapidly upwards and outwards as in a flower (fig. 148B, 315F). The tips again close over the egg, when the dish is closed (fig. 148A, 315E). This reversible movement implies that part of the chorion at the base of the petals is hygroscopic and study of its fine structure is needed. The effect of the mechanism is clear. With increasing humidity, the petals close and trap air for respiration. The egg thus escapes drowning if it is flooded for long periods of the winter. The porousness of the filaments suggests a function as plastron (scanning-electronmicrographs, fig. 315).

Early embryogeny was studied in *L. elegantula*. The immersed germ band diapauses in a very early stage of development. It is short, weakly ʔ -shaped but lacks any sign of bud formation (fig. 147A). There is some variation in the position of the young band in the egg, as is shown in the preserved stained series (fig. 147A–E). Each stage represents one specimen, except A, which occurred in three eggs. The lateral position of the band in fig. 147E is of interest, since lateral invagination is normally in Miridae. A greater series of eggs would elucidate the normal pattern, which could be lateral invagination followed by a 90° rotation of the band aftwards.

PREVIOUS DESCRIPTIONS CARAYON (1949 b) found no embryonic development in recently laid eggs of *L. elegantula*, *M. tenella* and *M. coleoptrata*. He cited BUTLER (1923), who dissected from *L. pselaphiformis* an egg, which already contained the embryo 'already 3/4 hatched'. This case of possibly haemocoelic fertilization 'by accident' coincides surprisingly well with our observation of an anomalous copulatory act in the same species (Chapter II of this series). Another study was by THOMAS (1938).

Plokiophilidae

MATERIAL: *Embiophila myersi* China (ovarian eggs, origin Trinidad).

Eggs, which seemed to have a completely developed chorion, were unexpectedly unspecialized. The egg is barrel-shaped; the anterior pole is blunt and wider than the posterior. The chorion is smooth, shiny and undifferentiated: no operculum or pseudoperculum and no visible aeropylar and micropylar system. Lactic acid treatment suggests that eclosion probably occurs by a longitudinal or irregular rent.

PREVIOUS DESCRIPTIONS None.

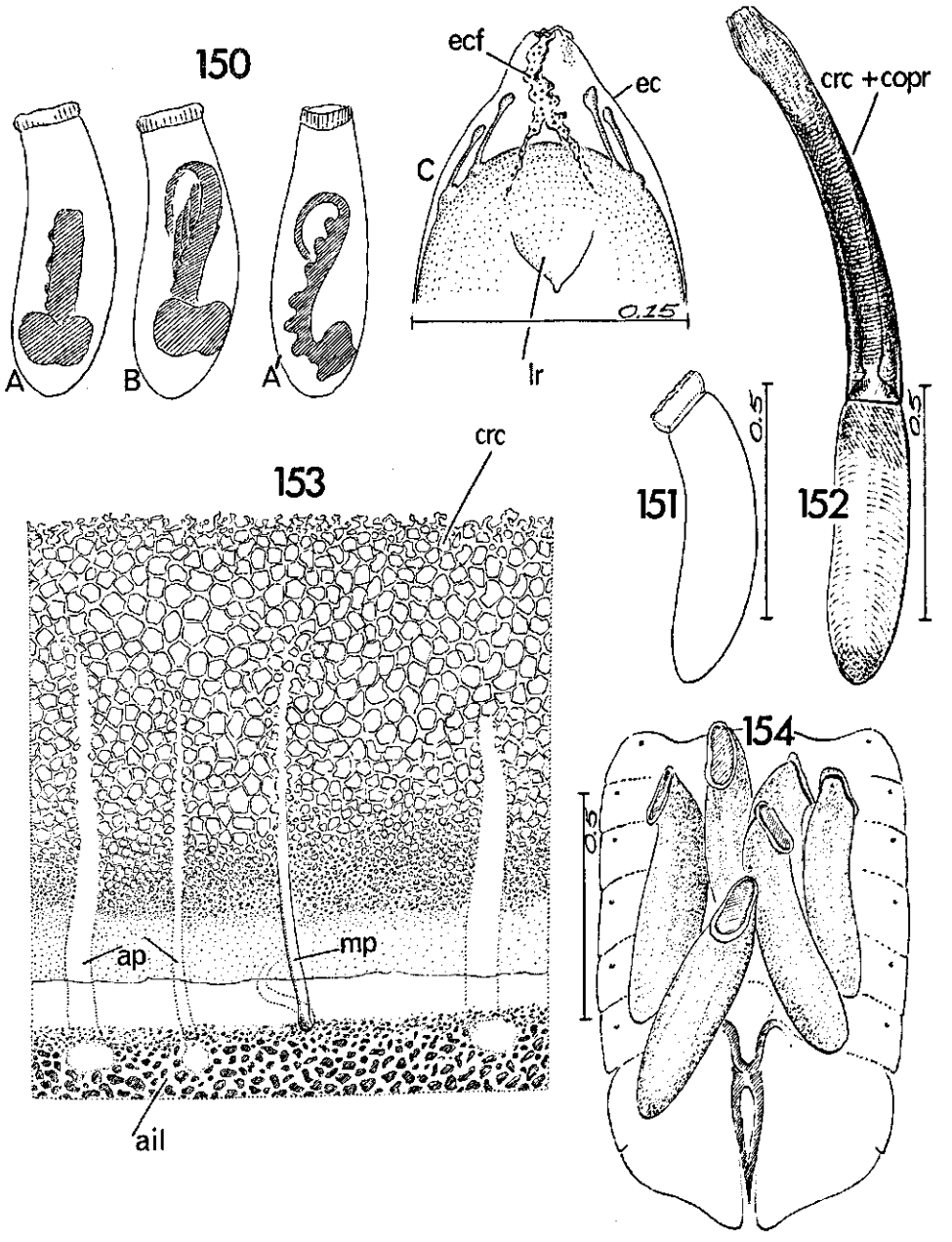


Fig. 150–154. Tingidae 150A–C: *Urentius* sp., position of early embryo, lateral invagination; A′: fore side of egg; C: prolarval head. 151. *Anommatocoris minutissimus*, ovarian egg. 152. *Sakuntula ravana*, ovarian egg with an extremely long anterior process. 153. *Dictyla symphyti*, fragment of chorionic rim. 154. *Agramma laeta*, position of eggs in abdomen (enveloping genital system not drawn).

2.3.3 Tingidae, Vianaididae

Tingidae

MATERIAL: *Urentius* sp. (some preserved stages of laid eggs, origin Ivory Coast); *Dictyla symphyti* Vall., *Acalypta platychila* Fieb., *Agramma laeta* Fall. (ovarian eggs), *Sakuntula ravana* Kirk. (ovarian eggs, origin Indonesia), *Cantacader infuscata* Dist. (ovarian eggs, origin India).

Vianaididae

MATERIAL: *Anommatocoris minutissimus* China (ovarian eggs, origin Trinidad).

All these eggs have aeropyles and micropyles, arranged as in most mirids. There are two micropyles, left and right, but in *Cantacader* they are close to the fore side. In *Agramma* and *Acalypta* they can easily be confused with the aeropyles, with which they correspond in length and diameter. However, the curve of the micropylar canal into the shell can be distinguished by close investigation. The discharge of the aeropyles into the inner meshwork layer appears as a circular space. In *D. symphyti*, aeropyles vary in width and the micropyles are easily recognized as they open more anteriorly in the shell and with a curve (fig. 153).

The egg of the aberrant *Anommatocoris* is similar (fig. 151). The rim is a coarse network on which the aeropylar pathways are not distinct. The few aeropyles curve within the shell just like the two lateral micropyles, but are wider. A clear aeriferous inner layer surrounds the whole egg.

The range of opercular structures will not be described here. What might be the climax in opercular proliferation is achieved in *Sakuntula ravana*. The outgrowth of the rim and cap has surpassed the length of the actual egg (fig. 152). At the top the collar and opercular elevation fuse so that a long double-walled respiratory cylinder with fine reticulation results.

EMBRYOGENESIS Some developmental stages are available only of *Urentius* (fig. 150A–B), which are sufficient to show a great resemblance with the mirid eggs to be described. At the stage as illustrated in fig. 150A, the embryo is always lateral. We assume also a lateral invagination of the germ band. It must be stressed that the egg of the *Urentius* species is circular in cross section and not laterally compressed as in most mirids. Before condensing, the embryo turns gradually 90° and its dorsum finally faces the convex side of the egg. Blastokinesis is accompanied by a 180° rotation according to the orientation after revolution. The serosal cuticle does not protrude out of the opercular orifice. Several prolarvae dissected from preserved eggs had a bladder-like extension of the embryonic cuticle (fig. 150C), perhaps aiding eclosion as in *Nabis*. The forked cephalic frictional band on the embryonic cuticle is as in most other cimicomorphans.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) listed 27 papers dealing with tingid eggs. Later ŠTUSÁK devoted papers to the subject (1957, 1958, 1961), introducing a Latin terminology for the anterior chorionic differentiations. SOUTHWOOD, using the cobalt injection technique, concluded that all canals in the reticulate collar were micropylar and ŠTUSÁK agreed. LIVINGSTONE (1962), on the contrary, considered all visible canals as aeropyles but mentioned no micropyles. Tingid eggs show a wealthy diversity between spp. of the extent and architecture of the chorionic rim and the operculum (ŠTUSÁK, 1962). The hatching process of *Corythaica cyathicollis* Costa has been described by KOGAN (1960), but not in sufficient detail to show the function of the serosal and embryonic cuticles.

2.3.4 Miridae

MATERIAL:

Isometopinae: *Isometopus intrusus* H.-S.

Mirinae: *Pantilius tunicatus* Fabr., *Miridius quadrivirgatus* Cost., *Phytocoris ulmi* L., *Calocoris roseomaculatus* De G., *Polymerus holosericeus* Hhn., *Capsus ater* L., *Capsodes gothicus* L., *Liocoris tripustulatus* Fabr., *Exolygus rugulipennis* Popp., *Megacoelum beckeri* Fieb., *M. infusum* H.-S., *Notostira elongata* Fabr., *Megaloceraea recticornis* Geoff., *Leptoterna ferrugata* Fall., *L. dolabrata* L., *Pithanus maerkeli* H.-S.

Phylinae: *Macrotylus paykulli* Fall., *Orthonotus rufifrons* Fall., *Harpocera thoracica* Fall., *Hoplomachus thunbergi* Fall., *Oncotylus punctipes* Reut., *Megalocoleus molliculus* Fall., *Chlamydatus evanescens* Boh., *C. saltitans* Fall., *Plagiognathus arbustorum* Fabr., *P. chrysanthemi* Wlff., *Monosynamma maritima* Wgn., *Sthenarus roseri* H.-S., *Systellonotus triguttatus* L.

Orthotylinae: *Strongylocoris luridus* Fall., *S. leucocephalus* L., *S. obscurus* Ramb. (origin France), *Orthocephalus mutabilis* Fall., *Halticus apterus* L., *H. major* Wgn. (origin France), *Cyllecoris histrionicus* L., *Globiceps sphegiformis* Ross., *Orthotylus marginalis* Reut., *O. virescens* D. & Sc., *O. diaphanus* Kirschb., *O. ericetorum* Fall., *Heterotoma planicornis* Pall., *Fieberocapsus flaveolus* Reut., *Pseudoloxops coccineus* M.-D., *Malacocoris chlorizans* Panz.

Deraeocorinae: *Termatophylidea opaca* Carv., *Deraeocoris ruber* L., *D. olivaceus* Fabr., *D. cordiger* H., *D. serenus* Dgl. & Sc., *Alloetomus germanicus* Wgn.

Dicyphinae: *Dicyphus pallicornis* M.-D., *D. pallidus* H.-S., *D. epilobii* Reut., *D. globulifer* Fall., *D. annulatus* Wlff., *Macrolophus nubilus* H.-S., *Campyloneura virgula* H.-S., *Hyaliodes* sp. (origin Saba, Neth. Ant.).

Bryocorinae: *Bryocoris pteridis* Fall., *Monalocoris filicis* L., *Helopeltis antonii* Sign. (origin Java), *Sahlbergella singularis* Hagl. (origin Ivory Coast).

Cylapinae: *Peritropis* sp. (origin the Philippines); *Teratodella brevicornis* Reut. (origin Africa).

The whole embryonic cycle was studied of *Liocoris tripustulatus, Chlamydatus evanescens, Dicyphus pallicornis, Bryocoris pteridis* and *Sahlbergella singularis.* Of *Pantilius, Notostira, Megaloceraea, Leptoterna, Macrotylus, Megalocoleus, Plagiog-*

nathus, *Stongylocoris*, *Orthocephalus*, *Halticus*. *Heterotoma* and *Macrolophus* early embryogenesis was followed and of the remaining species chorionic structures of ovarian eggs were examined. First a survey of the eggs and embryology of the five species will be given; the order of treatment corresponds to the increasing importance of the serosal cuticle in eclosion. As well as live eggs early developmental stages of stained embryo were studied. The eggs, dissected from the plant, were examined under water. Incubation is possible during continuous submergence; the eclosion procedure, however, was never complete.

Chlamydatus evanescens

AERO-MICROPYLAR REGION The elliptical rim around the operculum, is covered with a short upright collar of thin, evenly porous substance. The collar contains about 70 aeropylar canals of variable width. They open outwards below the top of the collar, where they are widened. The two micropyles, on the right and left, are slightly narrower and open outwards lower down the collar. The micropyle enters the chorion about the same level transversely as the aeropyles but, unlike them, bends by a right angle and fades away in the cross direction as in *Ch. saltitans* (fig. 156).

EARLY EMBRYOGENESIS Invagination has not been observed in this species. Judging from the embryogenic steps being at hand (fig. 155A), and from the other mirids studied, the point of invagination probably lies on the left some distance from the posterior pole. Such an unilateral origin of the germ band with its median plane at right angles to the sagittal plane of the egg, was unexpected in embryology. As mentioned before, something similar is suggested to occur in tingids and some nabids. The subsequent changes in the band (fig. 155A–F) were deduced from the study of about thirty eggs.

The embryo soon rotates 90° anti-clockwise when seen from the anterior. When the tail flexes, the orientation of the embryo is as in most other groups mentioned. Features in the development of the germ band are the three-kink stage (fig. 155D) and the condensed stage in which the ♀ -form is still apparent (fig. 155F). Both features are as in *Anthocoris*. We saw no isolated germ cells nor specialized hydropic cells.

LATER EMBRYOGENESIS Blastokinesis follows a retarded rotation of 180° which takes some hours at 22 °C. The rotation is not immediately followed by the revolution, but there is a stop of varying length (fig. 155G–J). The serosa with the yolk included retracts from the posterior pole. The chorion of this empty chamber shows the hexagonal sculpturing clearly. The surface of the ribs seems to be porous, quickly trapping air but equally quickly replaced by water if the egg touches a drop of water. The hexagonal pattern turns black as soon as the air in the pores is replaced. In no fixed relation to the hexagons, the chorion contains oval rings (fig. 157A). These rings are scattered all over the shell; their exact structure and function remains unsolved. The process of emergence from the amnion is shown in fig. 157B and C. The retracted

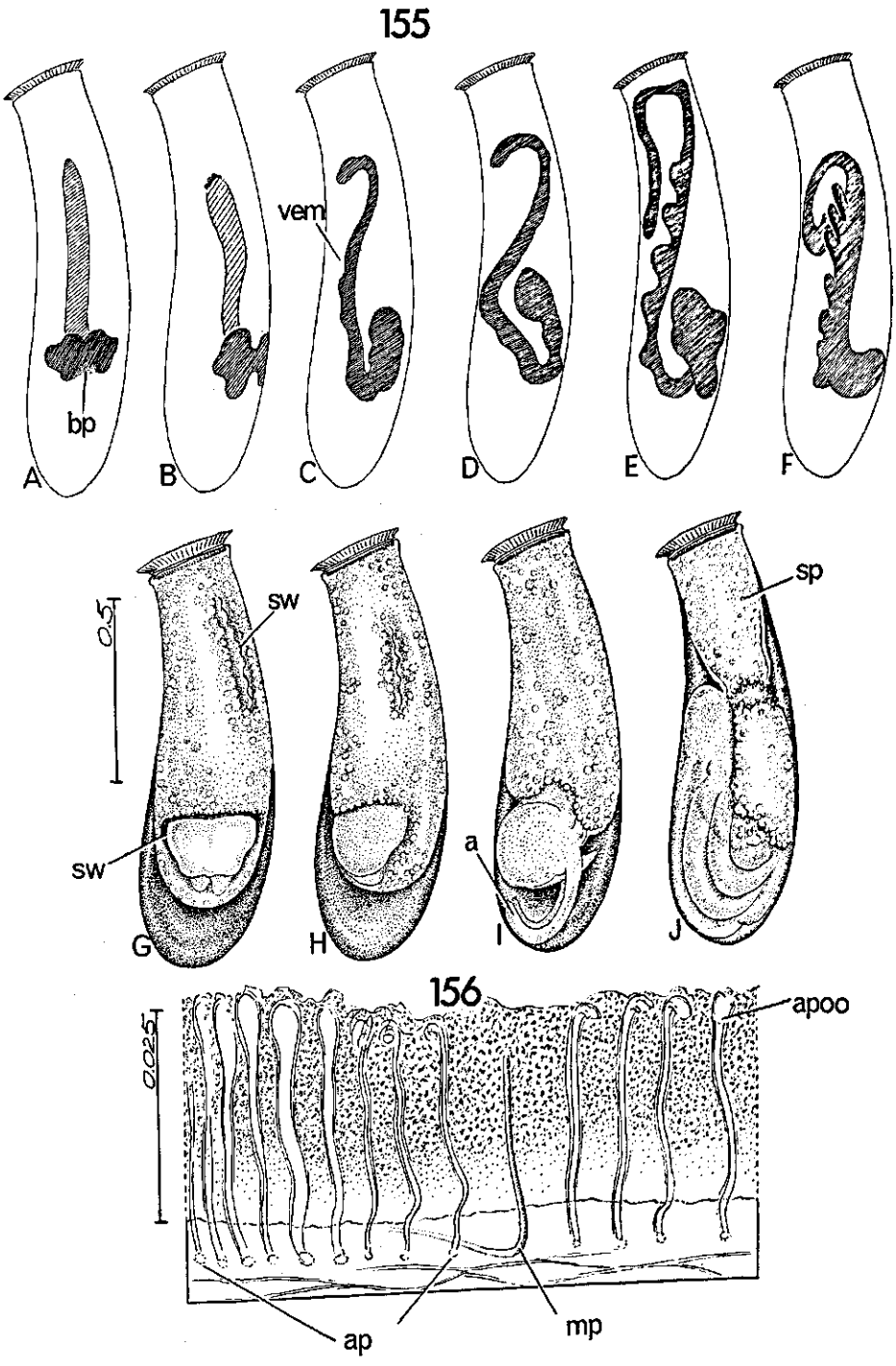


Fig. 155–156. Miridae 155. *Chlamydatus evanescens;* A–F: early embryogenesis; G–H: embryonic rotation; I: break of envelopes; J: revolution. 156. *C. saltitans,* lateral part of chorionic rim collar.

serosa presses against the antennae, which are enclosed by a film of yolk, and the front of the head becomes depressed.

The boundary of the amnion slips over the head and the antennae. The tips of the antennae point dorsad and they are pushed through the slit. The whole head then sinks posteriad but the antennae remain initially bent dorsad. During revolution they become folded the opposite way. Pigmentation of the eyes occurs after revolution. The yolk is pressed out of the calyx-like serosal plug earlier than in other mirids to be described. The serosal cuticle does not protrude from the chorion before eclosion. The general attitude of the fully grown embryo is as in other mirids (described in *Dicyphus*, p. 146); the front legs are shorter and do not turn around the posterior pole.

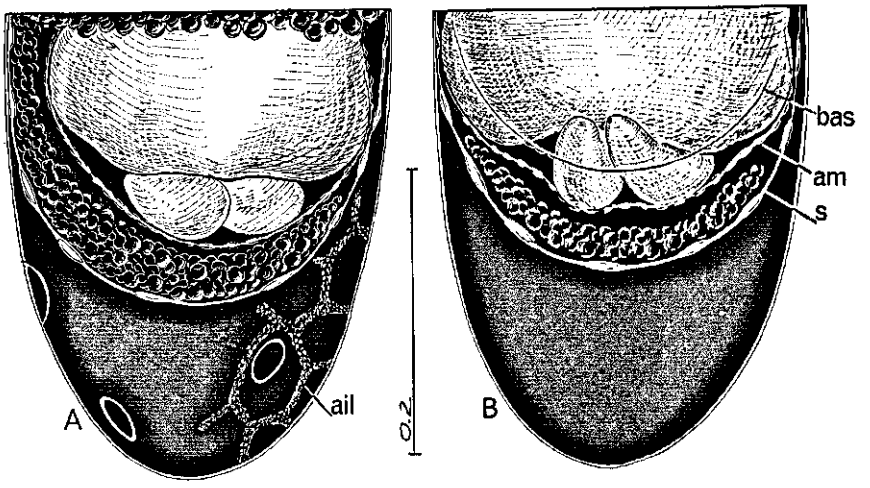
Dicyphus pallicornis

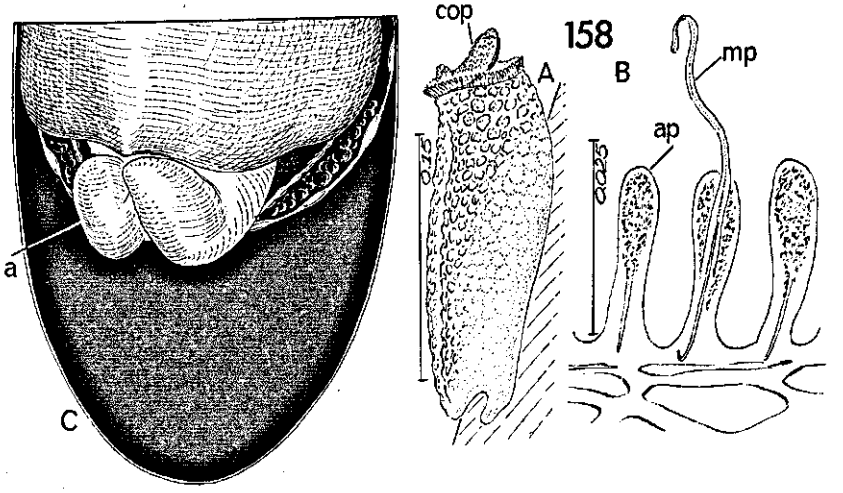
AERO-MICROPYLAR REGION There is no cylindrical elevation of the rim and the aeropyles are restricted to the fore and aft edges of the egg's neck. There a white scaly outgrowth is surmounted by three to five wide aeropylar openings (fig. 159). Aeropylar canals, however, could not be traced. It seems rather that the outgrowth forms a direct and unchanged continuation of the shell, whose inner meshwork layer is thus in direct contact with atmospheric air through the wide pores. Two micropyles are present, on the left and right side of the anterior margin of the shell. Rarely there are three, of which two are close together. The sperm-transmitting canal is 2–3 μ wide and traverses the shell just under the rim. The canal extends inwards some distance, parallel with the rim. The inner curve of the left micropyle points towards the fore side, but the right micropyle aft. Outwardly the micropyle extends as a tube with a dilated apex. The aeriferous inner layer of the shell is absent round the micropyle. The hexagonal print of the follicular cells are marked only in the neck region and these cells are more compact towards the rim region as in *D. pallidus* (fig. 159). Another hexagonal lining around the whole egg is the inner repiratory layer of the shell. The vertical struts of this layer are higher, thicker and more widely dispersed along those lines which seem to follow the outlines of the follicular cells. The spaces of the inner respiratory layer which are enclosed by these hexagons, are lower and supported by smaller, densely packed struts.

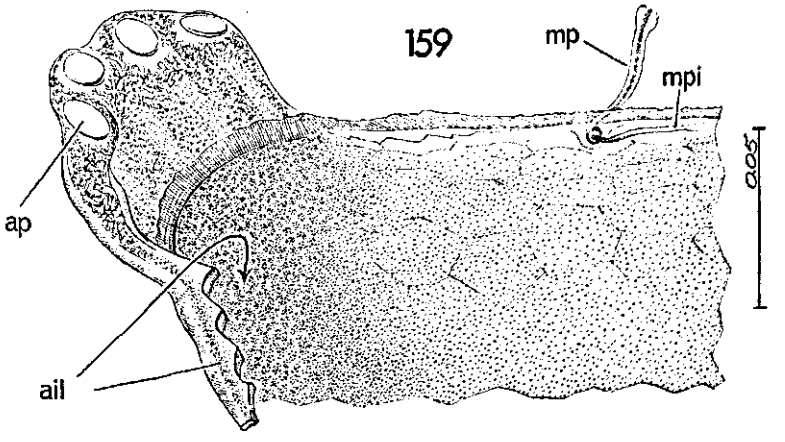
GROSS EMBRYOGENESIS Fig. 160A–H presents embryogenesis up to and including revolution. Invagination starts laterally and the position off centre in the egg is normally retained during the first half of the incubation. Revolution, preceded by a slow 90° rotation, occurs along the concave fore side. Red pigmentation of the eyes appears after this process. Waves of contraction in the junction of serosa and amnion

---

Fig. 157–159. Miridae 157A–C: *Chlamydatus evanescens*, posterior pole, embryo just before revolution, antennae pushing through the slit membranes. 158. *Pseudoloxops coccineus;* A: egg, lateral, operculum somewhat lifted; B: lateral part of chorionic rim. 159. *Dicyphus pallidus*, one edge of the anterior pole, inner view; operculum and one lateral side removed.


A
ail
0.2
B
bas
am
s


a
C
cop
A
0.15
158
B
mp
ap
0.025


159
mp
mpi
ap
ail
0.05

are vigorous, but only very late do they result in uptake of the serosa by the larva. The process of uptake of yolk and serosa, is as will be described in *Liocoris*.

ECLOSION The attitude of the mature embryo is shown in diagram fig. 279L. The long fore legs run parallel and close to each other around the posterior pole, and extend forwards aft. The serosal plug is still present just before hatching. It is cup-shaped and filled with yolk under the opercular region and a slender clear strand connects it with the yolk column in the larval body. Fractions of the anterior yolk mass are periodically pressed posteriad traversing the strand (fig. 161A), so that before eclosion the whole serosal plug is clear of yolk but still persists. At this time the opercular region has lengthened somewhat (fig. 161B). This is caused by stretching of the serosal cuticle, which extends now a short distance beyond the collar and has loosened the operculum from the rim. From now on the serosal plug and strand are rapidly displaced and the prolarva penetrates upwards into the constricted neck of the shell. The lengthwise deformation of the eyes (fig. 161C) shows that this must be accomplished with considerable efforts. With further protrusion of the prolarva, the operculum separates from the serosal cuticle and the boundary of the latter becomes clear and shows a median impression on its fore side, the so-called stenopyle. The embryonic cuticle is lifted from the larval cuticle apparently by extra-embryonic fluid, and presses against the stenopyle (fig. 161C, D). The serosal cuticle is filled by the head with increasing inner pressure and the stenopyle flattens and bulges out (fig. 161E). At this stage bubbles of air appear trapped between the serosal and embryonic cuticles. This air seems to be squeezed from the mid-anterior differentiation of the serosal cuticle by the pushing head. At last the serosal cuticle bulges out until it bursts and slips back along the embryonic cuticle to form a sleeve around the mouth of the egg (fig. 161F). The embryonic cuticle is shed later by the head swelling after the larva has swallowed air. No cutting egg-burster is necessary because the operculum is lifted primarily by the serosal cuticle. The λ-shaped ridge on the clypeo-frontal region of the embryonic cuticle helps to burst the latter envelope.

Liocoris tripustulatus

AERO-MICROPYLAR REGION The many aeropyles are situated in a circle, round the top of the collar-like prolongation of the rim. They project like stalked cups from the collar traversed by the funnel-shaped aeropylar canal. The canals are only about 1 μ wide where they enter the aerostatic inner layer and 5–7 μ at the outside opening. There are two micropyles, on the right and left sides of the rim at the same level as the aeropyles. The micropyles are half as long as the aeropyles and form pyramidal projections with a central canal less than one μ wide. The situation is almost like that in *Exolygus* (fig. 176A, B). The inner meshwork layer of the shell in the ripe egg is not visible in surface view, because of the thick secondary deposition of chorionic material. In early stages of chorion secretion (fig. 176A), the 'felty' layer is apparent, while the anterior margin of the shell shows a sharp hexagonal pattern. The follicular cells are

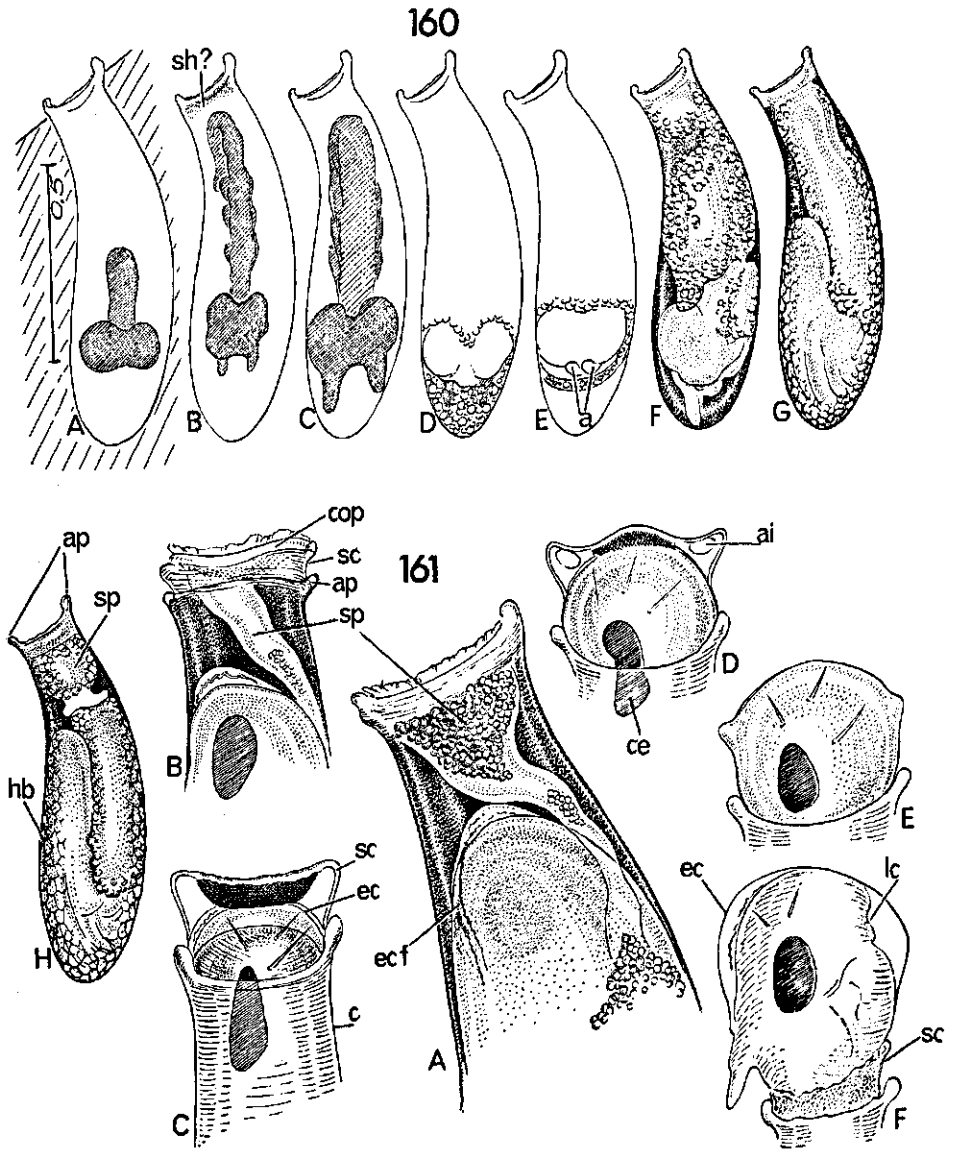


Fig. 160–161. Miridae, *Dicyphus pallicornis* 160. early embryogenesis (A–E) and revolution (F–H). 161. eclosion act (A–F).

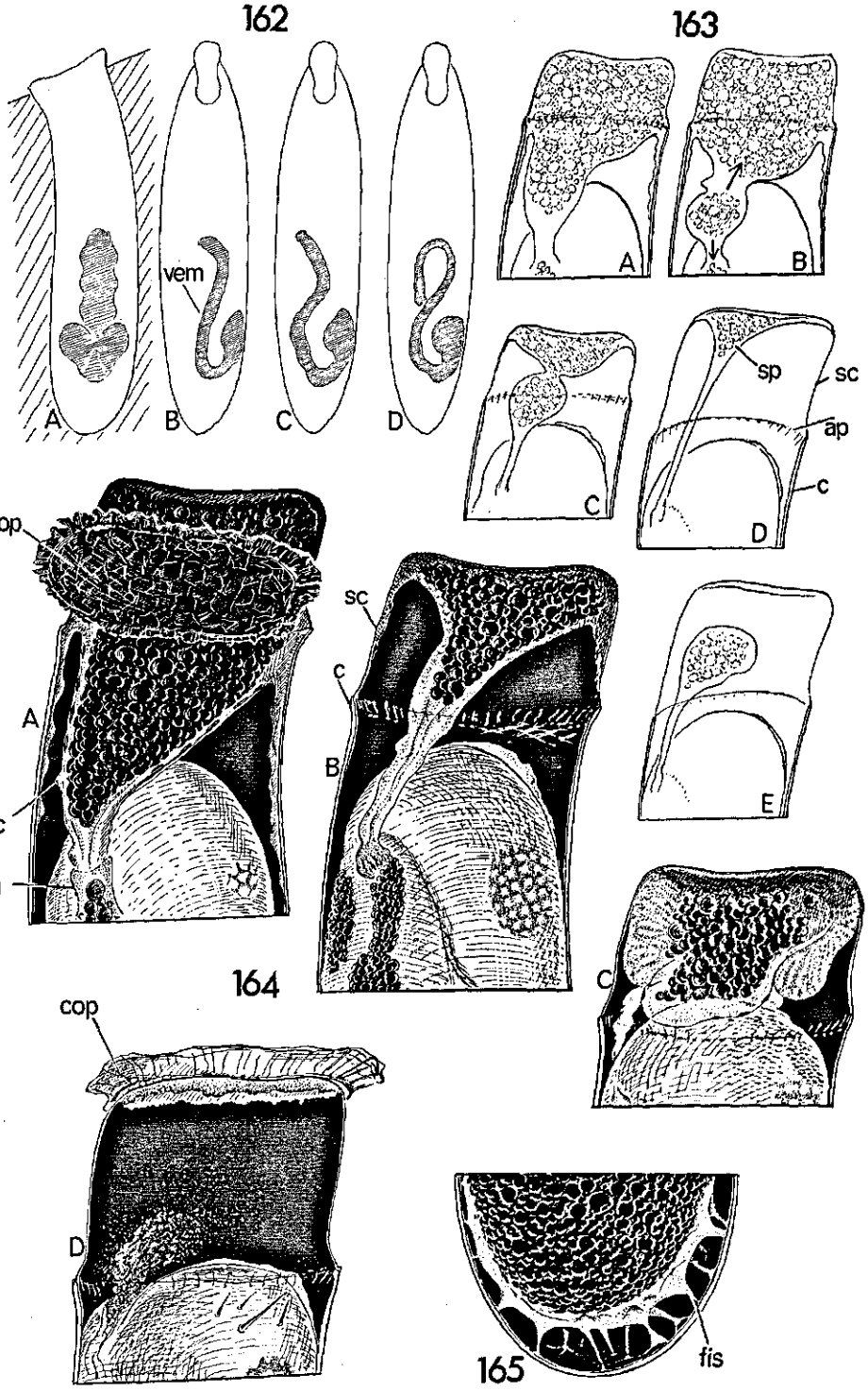
evidently more compact and cross-constricted in the micropylar region. Later the follicular pits on the chorion become partly filled by chorionic deposits. In unripe eggs the micropylar canal curves inside the shell (fig. 176A). While at this stage, the aeropylar and micropylar processes are already fully developed, the collar of the rim is not yet laid down. Fig. 176A and B show that the spongy, irregularly shaped collar originates from conical elements almost like those which have given rise to the formation of the aero- and micropylar projections.

GROSS EMBRYOGENESIS Incubation at 30 °C takes 7–8 days. Invagination occurs on the left side at some distance from the caudal pole. In five eggs investigated, this position was retained at least up to the stage in which the protocormic outgrowths began to develop (fig. 162A). The nearly 8-shaped embryo is less than half the egg's length. Hydropic cells and isolated germ cells were not noticed. In another five eggs, blastokinesis comprised the normal 180° rotation followed by revolution along the concave egg-side. Pigmentation occurs after revolution and spreads gradually from the centre of the eye disc (fig. 164A, B). The uptake of yolk and the fate of the serosal plug has been followed more closely than in other mirids. The serosal cuticle in *Liocoris* is so elastic that it often protrudes from the neck before revolution. The operculum is pushed up but remains attached by the top of the stenopyle (fig. 164D) or it hinges down on one side (fig. 164A). The serosal plug becomes constricted at the base shortly after revolution, but most of it remains closely attached to the whole circumference and the apex of the protruding part of the serosal cuticle. It forms a voluminous funnelled organ, whose narrow stem fits in a short tubular projection of the amnion in the pronotum. This situation is outlined in fig. 164A where the amnion forms the provisional dorsal closure. The thick serosal wall of the plug seems to flex back along the serosal cuticle before filling the top of it (fig. 163A). Sections have not shown whether the serosa itself is double-folded backwards or whether the serosa joins rudiments of an extra outer serosal layer. The latter possibility seems more probable, since it was observed that during blastokinesis material in the form of drops was affixed against the innerside of the serosal cuticle. These drops may also be protoplasmic rudiments of the serosa itself, left behind some time before the latter was withdrawn from the enveloping layers. The retraction of the serosa from the posterior pole in the phase before blastokinesis is accompanied by the same phenomenon as in gerrids and saldids. The serosa is seen to be thickened into a creamy granular layer. Although it has loosened from the egg-wall, protoplasmic strands remain connected to the wall for a long time (fig. 165).

Despite the fact that the serosal plug is fixed in the stenopylar region, its funnelled base is continually changed by beat-like contractions which initially behave as in

---

Fig. 162–165. Miridae, *Liocoris tripustulatus* 162A–D: early embryogenesis; A: lateral side of egg; B–D: fore side of egg (note lateral invagination of germ band). 163A–E: contractile behaviour of the serosal plug. 164A–E: transformation, contraction (C) and disintegration (D) of serosal plug. 165. posterior pole before revolution.


162
vem
A
B
C
D
163
A
B
C
sp
sc
ap
c
D
cop
A
scc
am
sc
c
B
E
C
164
cop
D
165
fis

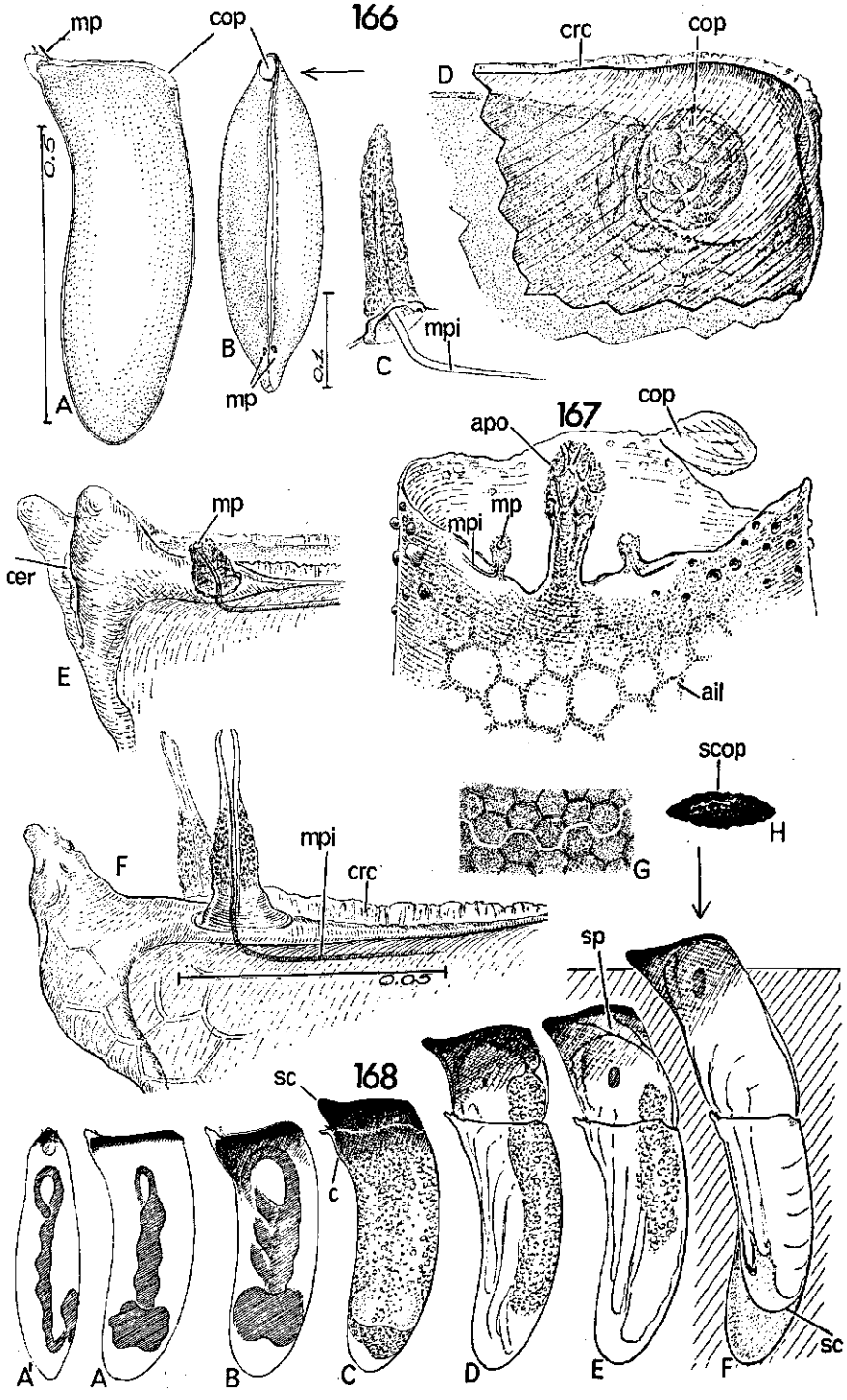
other families (see p. 34 and 224). Shortly after the plug has formed, convulsions are infrequent and they occur only in the base of the plug, which seems to represent the serosa-amnion junction. A contraction occurs extremely rapidly. The tension is held for several minutes, while part of the stringed yolk flows slowly posteriad into the amnion and the embryo as a whole moves a short distance forward. Relaxation is gradual so that later a slightly different starting point is again reached and a longer period of complete rest begins. After the appearance of the eye elements, the serosal contractions become more vigorous (fig. 163B, 164C), the two beats illustrated immediately follow the situation in fig. 163A and 164B, respectively. There also seem to be some cone-shaped serosal cells which are involved in the contractile activity (fig. 164A, scc). The course of later events is as follows: the basal half of the serosal plug becomes transformed into a long strand with a narrow central passage and a thickened serosal wall (fig. 164B, 163D). Yolk globules are confined to the apical compartment of the plug which is still distended. In the area where contractions take place, the cord of the plug shifts more anteriad (fig. 163C). These contractions now have almost no effect on yolk transport downwards, although small secondary waves tend to push the yolk through the central canal. Although the normal contractions continue, the rest of the yolk remains in the upper part of the plug. In four of the five eggs studied in this phase, the serosal plug was eventually detached from the stenopyle (fig. 163E). The feathery serosal structure was occasionally swept fore and aft over the head because contractions of the serosa still persisted but without moving the yolk. At last the entire plug, up to its entrance in the pronotum, vanishes. This demolishing process does not always occur in the same way. In some eggs the apical portion of the plug breaks off and the yolk mass may float into the anterior cavity of the egg. In others, the whole plug disintegrates into a cloudy mass which is soon absorbed in the extra-embryonic fluid (fig. 164D). In one egg, which was cooled during yolk uptake for three days at 3 °C, the process was anomalous. The prolarva pushed forwards against the serosal plug, while the plug was still substantial and was contracting vigorously. The serosal cuticular cap, inclusive of the plug, at last slipped off sideways from the protruding head of the larva. As a result, the larva escaped not through the stenopyle. The bug died in this semi-hatched condition. The embryonic cuticle bears a λ-cephalic ridge as in other mirids. The attitude of the mature embryo follows the pattern of other mirids.

Bryocoris pteridis

Some features of the shell of this fernicolous mirid which have previously been overlooked are unexpected and quite atypical for the family. In contrast to all Cimi-

---

Fig. 166–168. Miridae 166A–F: *Bryocoris pteridis;* A: egg, lateral; B: normal to anterior pole; C: micropyle; D: opercular edge of cephalic pole (seen in the direction of the arrow in B); E, F: front edge of cephalic pole; E: vacated shell. 167. *Monalocoris filicis*, cephalic pole of shell, artificially opened, anterior view. 168A–H: *Bryocoris pteridis*, embryogenesis, lateral view; A′: fore side of egg; G: part of front pole of serosal cuticle with eclosion line; H: operculum of serosal cuticle.


166
mp
cop
0.5
A
B
mp
0.1
C
mpi
crc
cop
D
167
apo
cop
mp
mpi
ail
cer
mp
E
scop
H
G
F
mpi
crc
0.05
sp
168
sc
c
A'
A
B
C
D
E
F
sc

GROSS EMBRYOGENESIS AND ECLOSION The germ band in most eggs is lateral from invagination until blastokinesis (fig. 168A–C). The band, except the head lobes, is immersed and occupies nearly the total length of the egg. The serosal cuticle undergoes an intensive darkening, which spreads from the anterior pole posteriad over a broad zone. The egg elongates to nearly twice its original length to reach the outer surface of the oviposition plant (fig. 168A, F). The lengthening is brought about by the stretching serosal cuticle, which opens the eclosion rent of the shell while the embryo is condensed. The serosal plug discharges all the yolk and persists until eclosion. The serosal cuticle breaks along an elliptical cap (fig. 168H), which may indicate that the chorionic cap was of the same size in the past. The boundary of the serosal cuticular cap is zig-zag, suggesting chance fracturing. However, the zig-zag is present in the intact cuticle as a line of weakness forming part of the hexagonal intercellular print of the serosal cells (fig. 168G). The cephalic structures of the embryonic cuticle and the flexing of the legs and antennae is as in other mirids.

Sahlbergella singularis

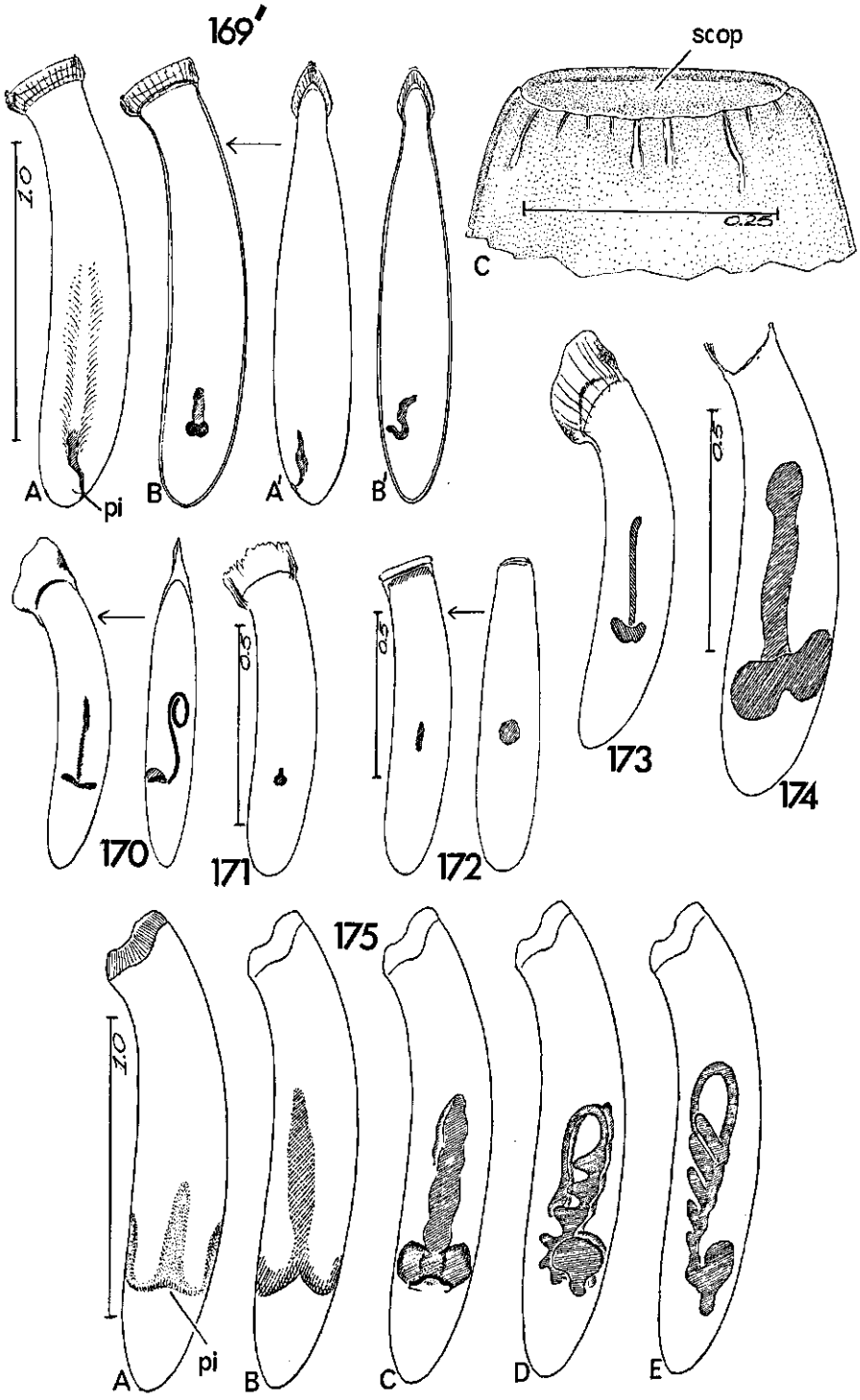
AERO-MICROPYLAR REGION The elliptical dome-shaped operculum and the two long horns on the rim are the only exposed parts of the egg which is inserted in the compact bark of the food plant (fig. 169H). The horns contain bundles of aeropyles, which thus are confined only to the fore and aft edge of the egg's neck. The aeropyles open individually to the outside in the apical part of the horn. The aeropylar tubes run inward close together but do not communicate with each other before opening into the thick aerostatic inner layer of the actual shell. There is no collar on the rim and the two micropyles are long and slender, and terminate in a club (similar in *Helopeltis*, fig. 187A).

EMBRYOGENESIS (fig. 169A–Q) The following data reveal complete picture of embryogeny, which is deduced only from material fixed in Bouin's medium in the Ivory Coast and stained with borax carmine after some weeks.

The germ band invaginates just latero-sinistral of the basal pole, and the blastodermal thickenings start, in relation to this lateral position, in the fore and aft side of the egg (fig. 169H, I). The blastopore moves upwards along the lateral side with progressing invagination. At the maximum extent of the germ band, its tail still remains far remote from the anterior pole. The total length of the band and the embryo until after revolution is half of the egg's length. With curling of the tail and the lengthening of the protocormic outgrowths, the embryo rotates gradually 90° to face venter aft

---

Fig. 169′–175. Miridae 169′. *Pantilius tunicatus*, invagination of germ band (A, A′), diapausing embryo (B, B′); C: serosal cuticle, cephalic pole of diapausing egg. 170. *Leptopterna dolobrata*, diapausing embryo. 171. *Megalocoleus molliculus*, diapausing embryo. 172. *Plagiognathus arbustorum*, diapausing embryo. 173. *Leptoterna ferrugata*, diapausing embryo. 174. *Macrolophus nubilus*, lateral position of young embryo. 175A–E: *Notostira elongata*, early embryogenesis.


169
scop
1.0
0.25
C
A
pi
B
A'
B'
0.5
170
171
172
173
174
175
1.0
A
pi
B
C
D
E

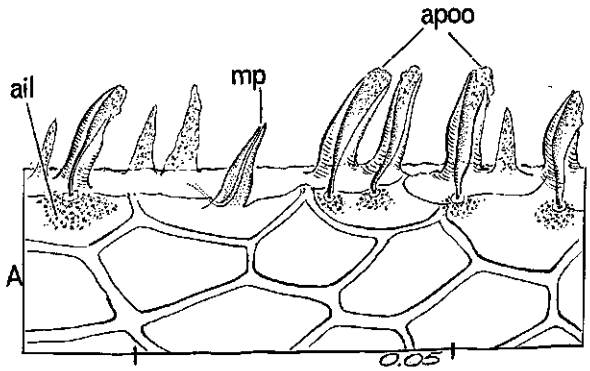
(fig. 169L–O); some eggs drop behind in this rotation. The serosal cuticle has meanwhile darkened under the operculum, which has dislodged from the actual shell. The stretching of the serosal cuticle until actual eclosion does not extend far and the operculum is held fast between the two respiratory horns (fig. 169P, Q). Besides the short cylindrical extrusion from the egg, there is a distinct increase in egg volume in the basal half, where the plant tissue is softer. More than in other mirids it is here almost certain that the subopercular part of the serosa is of hydropic nature. Swelling of the egg coincides with the development of a voluminous serosal proliferation which contacts the whole inner surface of the serosa-cuticular cap. Since the embryo remains proportionally small even after revolution, there is a long serosal plug. The fixed material shows two contractile zones in the plug. In the eggs P and Q (fig. 169), the respective plugs have been fixed in a state of actual contraction and relief. A distinct zonal flow of the nuclei is suggested during these phases. The plug remains all the time extra-embryonic; its proximal part, inserted behind the head of the embryo, ultimately becomes vacated of yolk and shrinks to form a thin stalk connecting the funnelled subopercular part (fig. 169B). The embryonic head bulges out after revolution, forming a wedge-shaped structure with normal hatching ridges (fig. 169B, P, Q).

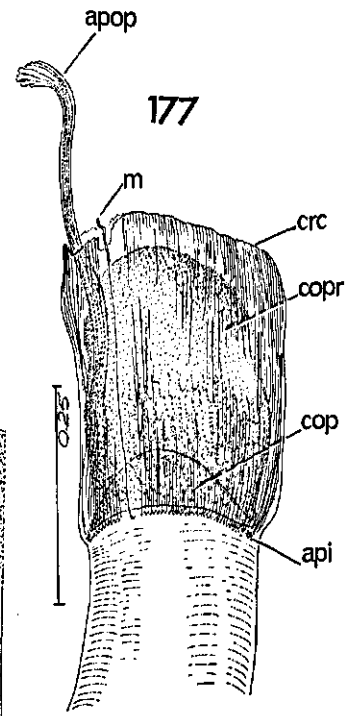
Comparing the data presented on *Bryocoris* and *Sahlbergella* it seems impossible that both genera should belong in the same subfamily, as is current. The sum of the diverse dissimilarities between the two, both chorionic and embryogenic, is not equalled in any two pairs of mirids, even of different subfamilies.

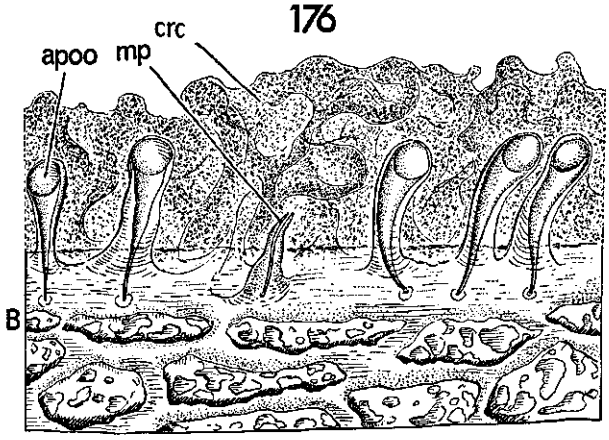
The early embryogenesis of other species

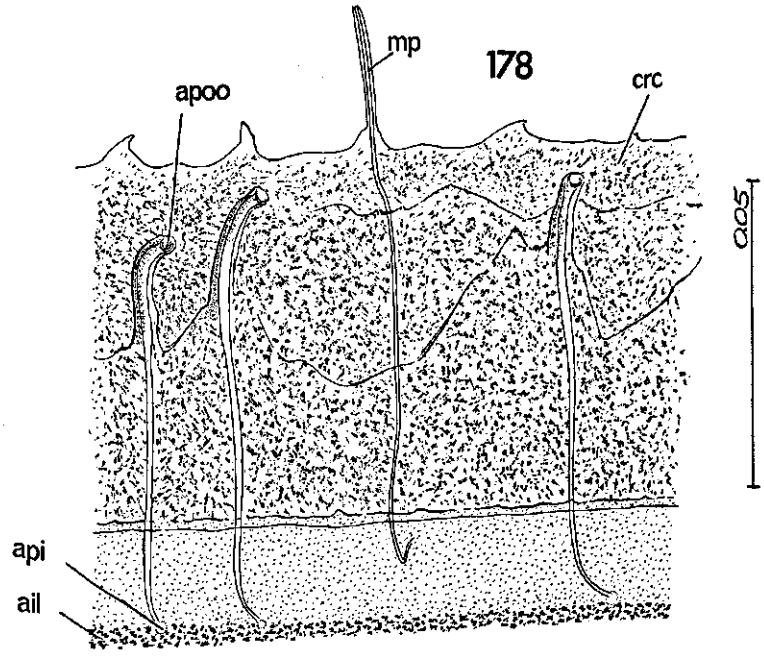
The early germ band of 12 other species (enumerated on p. 141) is usually found with the head lobes on the left (fig. 169B, 170, 173, 174, 175), as in previous species. Except *Notostira* and *Macrolophus*, these species overwinter as eggs. Diapause is passed in the early band stage, before formation of protocormic buds. The length of the overwintering embryo is quite different for each species and, in general, the embryonic dimensions are much smaller, particularly in *Pantilius tunicatus* (fig. 169), than in non-diapausing species at a seemingly equal stage of organization (compare fig. 160, 174 with fig. 170, 174). The overwintering germ band usually remains lateral; the contact between head lobes and serosa is sometimes broken but in *Plagiognathus arbustorum* and *Megalocoleus molliculus* the band rudiments are exceedingly minute and condensed as an undifferentiated disc, which migrates to the centre of the yolk (fig. 172). The serosa continues to secrete its cuticle, although embryonic growth has stopped.

Fig. 176–178. Miridae 176. *Exolygus rugulipennis*, lateral part of egg mouth; A: unripe; B: ripe ovarian egg. 177. *Deraeocoris olivaceus*, anterior pole, lateral. 178. *Strongylocoris luridus*, lateral part of chorionic rim.


apoo
ail
mp
A
0.05


apop
177
m
crc
copr
cop
api
0.05


176
crc
apoo
mp
B

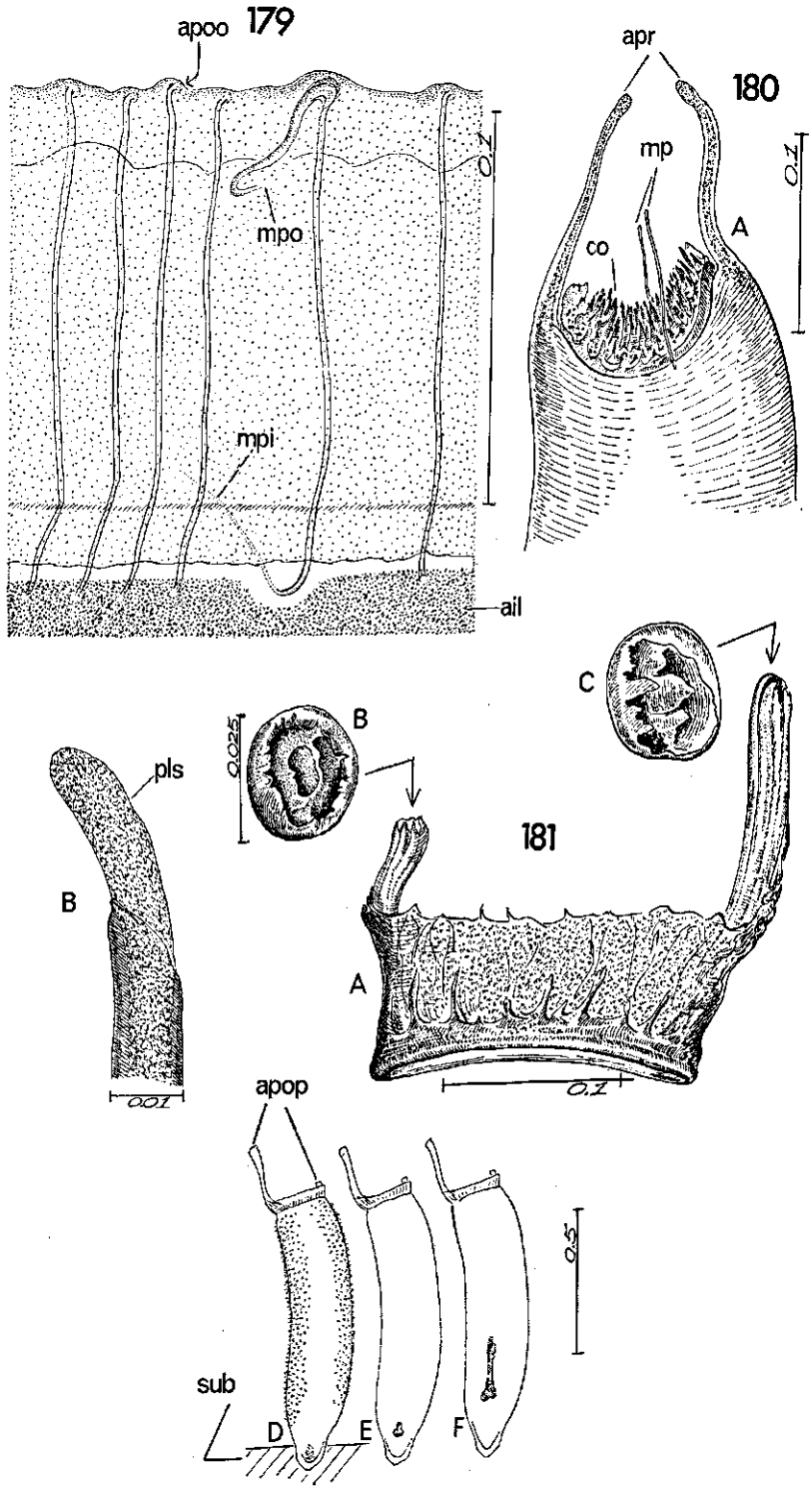

mp
178
apoo
crc
0.05
api
ail

The anterior pole of mirid eggs is of an overwhelming variety and our intention was to find whether pole types corresponded with the taxonomic divisions of the family. All eggs studied have two micropyles, usually lateral on the circumopercular ring; the varying shape and extent is revealed by fig. 176–190.

In *Deraeocoris olivaceus*, the micropyles have shifted towards the fore side, in *Orthotylus ericetorum* towards the aft side of the anterior pole. *Campyloneura virgula* has micropyles, although males of this species are extremely rare, so that the possibility of parthenogenesis has been proposed in literature.

A distinction must be made between the aeropyles of the anterior of the actual shell and those on the operculum. The number on the actual shell ranges from about 20 in *Orthotylus diaphanus*, through 30 in *Oncotylus* and *Pithanus*, 40 in *Polymerus*, *Capsus*, *Capsodes*, *Hoplomachus*, *Fieberocapsus*, *Alloetomus*, 50–80 in most species, 140 in *Harpocera*, *Halticus*, *Heterotoma*, 180 in *Deraeocoris cordiger*, to a maximum of about 400 in *D. olivaceus* and *D. ruber*, where the internal openings are in two alternating rows below each other. Generally the aeropyles are regularly distributed around the egg's neck. But in *Isometopus*, all *Dicyphus* species, *Campyloneura*, *Termatophylidea*, *Helopeltis* and related genera, *Megalocoleus*, *Oncotylus* and *Pithanus* they are confined only to the fore and aft edges. *Orthocephalus mutabilis* is intermediate. The corner aeropyles reach to the upper margin of the high rim but along the lateral sides of the egg they become shortest alongside the micropyles. The distribution of these differences do not closely correspond with the subfamily groupings. Even between related spp. or genera there is sometimes a great discrepancy. For instance *Cyllecoris histrionicus* has the aeropyles in a circle but in the related *Dryophilocoris flavoquadrimaculatus* they are concentrated on the edges of the neck. A similar divergence is noticed in *Orthotylus* spp.; in *O. ericetorum* we could not find a spur of aeropyles. On the other hand all seven European Dicyphinae checked reveal a rather constant pattern (fig. 159). In most *Dicyphus* spp. and in *Macrolophus* (fig. 186) the migration of aeropyles results in two cup-shaped hollow projections fore and aft on the neck. In *Campyloneura*,the projections are long and branched (fig. 188). The *Hyaliodes* species studied, which according to specialists should also be classed with the Dicyphinae, is in contrast with its circumpolar arrangement of aeropyles (fig. 189). For the major classification of mirids, these new data on the eggs must be considered seriously, as they may lead to reassessment of the taxa. Another striking divergence is the egg of *Termatophylidea opaca* (fig. 180). The basic arrangement of the aeropyles is dicyphine-like but this species has been considered to belong to the Deraeocorinae. The five typical deraeocorines nevertheless revealed the densest and most regular arrangement

Fig. 179–181. Miridae 179. *Pantilius tunicatus*, lateral part of chorionic rim, outer aspect. 180. *Termatophylidea opaca;* A: anterior egg-pole, lateral; B: top of respiratory horn. 181. *Strongylocoris luridus;* A: operculum, lateral; B, C: inlet of respiratory horn; D–F: early embryogenesis; F: diapausing germ band (Hte Loire, France).


apoo
179
mpo
mpi
ail
0,2
apr
180
mp
co
A
0,1
C
B
0,025
pls
B
181
A
0,1
0,01
apop
sub
D
E
F
0,5

of aeropyles around the pole. A further discrepancy is provided by the *Helopeltis* group, the eggs of which also have the two respiratory horns (fig. 187) derivable from the *Dicyphus*-type. *Helopeltis* is usually placed in the same subfamily as *Bryocoris* and *Monalocoris* but conditions in these latter genera are abnormal (p. 150–156).

The respiratory horns of *Termatophylidea* differ in structure and function from those of other mirids. A typical horn in Miridae has one or more circular apical openings (fig. 186, 188B) and sometimes others up the sides as in *Helopeltis*. Each opening communicates through a canal with the inner meshwork layer. The apex of the horn of *Termatophylidea*, on the contrary, forms a porosity, whereas the sides are of compact chorionin (fig. 180B). This provision suggests a plastron function of the horn. Plastron-like protuberances are found also in the egg of the unidentified cylapine from the Philippines. The arrangement of these flat triangular excrescences is, however, circumpolar (fig. 190A) as in Microphysidae. The pointed filaments seem to be very finely porous all over the surface, which also bears a hair-like cover (fig. 190B). Outgrowths like integumental microtrichia have never been found on shells of other insect eggs. This fine hair coat improves the air-holding system. Long hair-like extensions also occur on the operculum along the edges of the polygons (fig. 190C). The second cylapine studied, *Teratodella brevicornis*, has the pitted chorion as in *Termatophylidea* and the collar probably acts as a plastron. However, the collar in *Teratodella* forms a continuous network which makes a triangular incision left and right, leaving the long micropylar process free (fig. 190D). The aeropyles are confined to the anterior and posterior edge. The network consists of two layers, connected to each other by septa (fig. 190E). The outer layer seems to be finely porous and during submersion provides the egg with an extensive interface between external water and internal air, contained in the spaces of the collar.

The micropyles in mirid eggs are usually dissociated from the aeropylar system but in *Pseudoloxops coccineus* and *Malacocoris chlorizans* seemingly a combination of both occurs. The eggs of these species are strikingly alike, with an abnormal shape, indented posterior pole (fig. 158A) and rough sculpture adapted to semi-exposed deposition. In the many eggs studied of both spp., the micropyle arises from one of the aeropylar projections (fig. 158B). We are not sure whether it still functions in air exchange.

The structure of the mirid operculum is as variable, simple or highly ornamented, as the egg's neck just discussed. In the genera *Strongylocoris* (fig. 181). *Megacoelum* (fig. 182), *Deraeocoris* (fig. 177), *Alloetomus*, *Capsodes*, *Hyaliodes* (fig. 189) the operculum has developed its own system for air transport into the egg. These horns are of the same plan as the rim horns but the mass of aeropyles do not seem to communicate with a porous inner layer of the operculum. Optical sections and views of the inner surface of the operculum strongly suggest that the aeropyles traverse the inside of the lid separately (fig. 182D). In *Megacoelum*, the aeropylar outer openings are found all the way up the horn (fig. 182 A, C); the top of the horn of *M. infusum* (fig. 182B) differs in structure from that of the sibling species of *M. beckeri* (fig. 183). In all other species only the apex of the horn is open. Species of the genus *Strongylocoris* hardly insert their eggs. Only the extreme wedge-shaped base of the egg is pressed into the

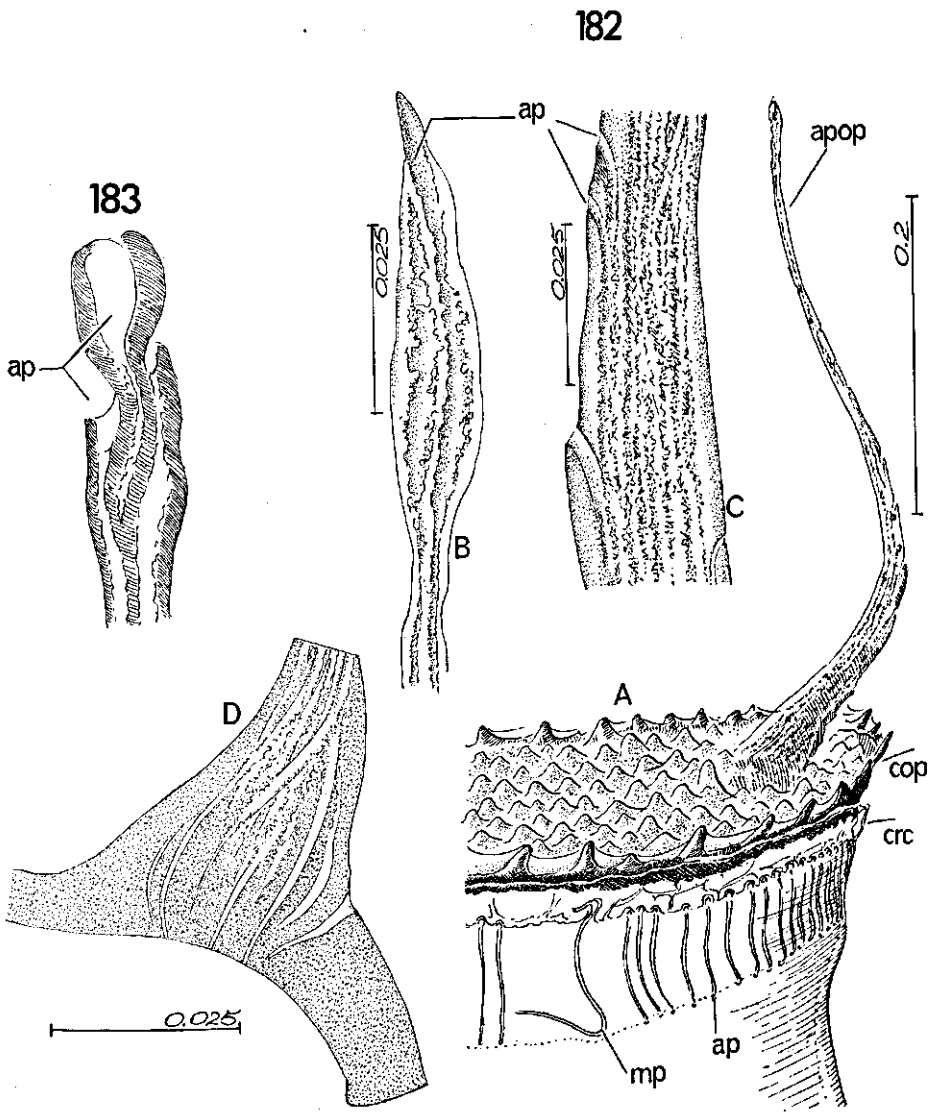


Fig. 182–183. Miridae 182. *Megacoelum infusum;* A: fore edge of anterior pole, obliquely from the side; B, C: top and base of respiratory horn; D: opercular aeropyles in base of horn, optical section of unripe egg. 183. *M. beckeri,* top of respiratory horn.

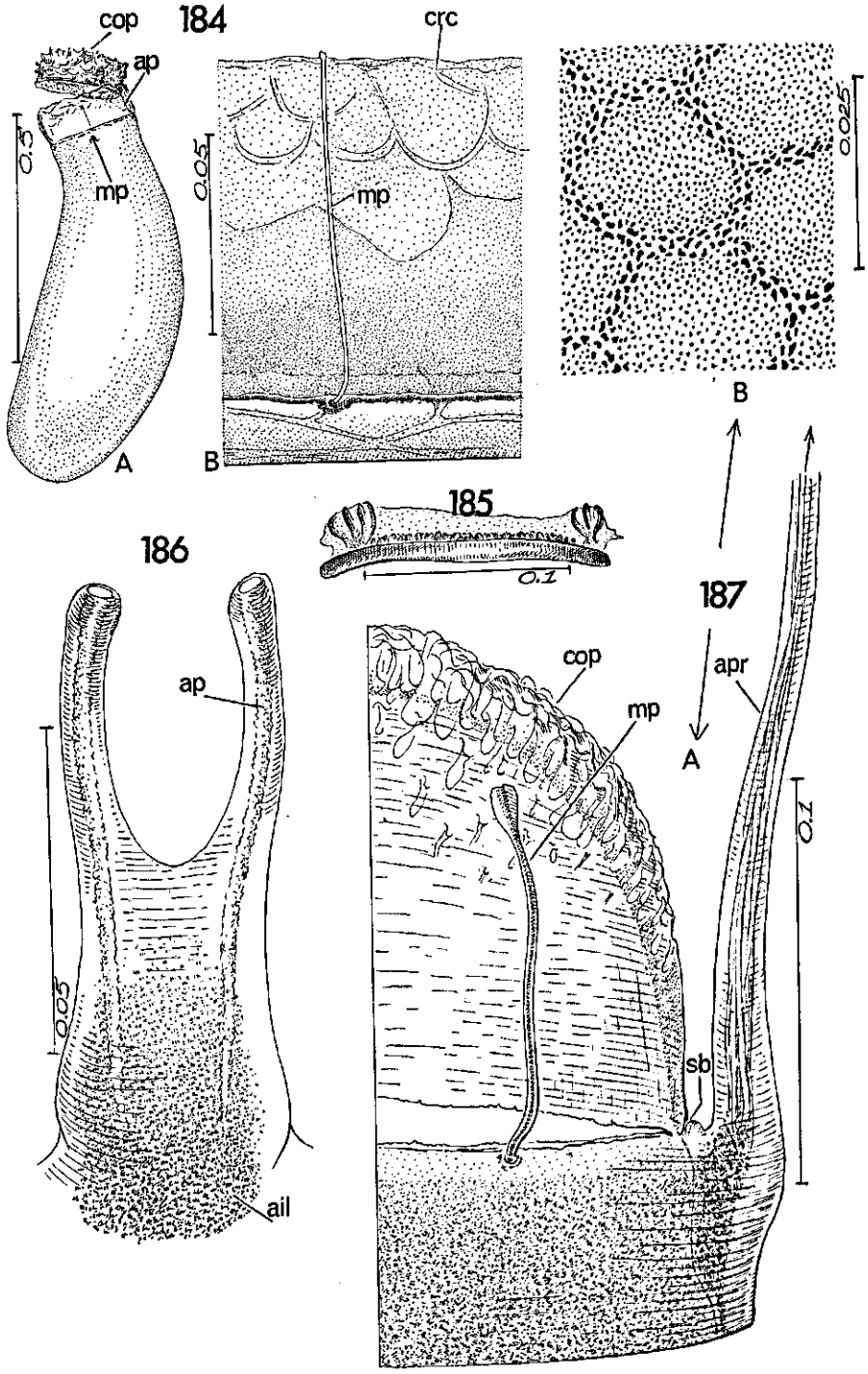
substrate (fig. 181D). *Strongylocoris luridus* and *S. leucocephalus* have distinct opercular horns (fig. 181A) but in *S. obscurus* the horns are rudimentary and do not project beyond the opercular collar. In those species with distinct opercular air channels, rim aeropyles are arranged centrically round the pole. The normal number of opercular horns is two, that on the fore edge being larger; *Megacoelum* has only latter one. The question arises whether the bilocal opercular perforation is a general character of mirid eggs. Whole mounts of the operculum of *Dicyphus* and other spp. with an elliptical flat lid *(Megalocoleus, Orthonotus, Orthotylus ericetorum, Fieberocapsus)* did not reveal any pores. However, additional sectioning is needed to clarify this point, since we got the impression that the egg cap of *Chlamydatus saltitans* has an inner porous layer. In all other spp. studied by us there are indeed differentiations, mostly rosette-like, on one or both edges of the cap perhaps for respiration. The upgrowths are more obvious on the flat caps of many Orthotylinae, Phylinae (fig. 185) and Mirinae, whereas they may be present, but obscured in the ornamented lids of other species.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) mentioned 43 papers dealing with mirid eggs and in the same year PUCHKOV and PUCHKOVA published data on the eggs of about 20 spp. The work done has been almost restricted to shell structure. KULLENBERG (1942, 1943) described and illustrated in colour the eggs of 103 species. Generally eggs are rather constant with the neck constricted laterally, a rim of variable height and a true operculum. With few exceptions, eggs are embedded with the operculum or a part of it exposed. KULLENBERG (1946, p. 387–442) elaborated on the structure of the aeropylar region. Yet he did not discover the micropyles and his interpretation of the egg of *Bryocoris pteridis* differs in many respects from our account given above. From text and figures in KULLENBERG (p. 393, 395, fig. 94, 124) we conclude that some erroneous statements were made: 1. he believed the edge of the operculum covered the whole truncate anterior; 2. he thought the aeropyles were present in the unpaired projection of the egg's edge and in the upstanding 'Wulst' running sagitally over the anterior pole. The 'Wulst' of KULLENBERG has been homologized by us with the two chorionic rims lying adjacent to each other, only separated by a single straight eclosion fracture. The aeropyle indicated in KULLENBERG's fig. 94 seems to represent this eclosion line on cross section; 3. he overlooked the small circular pseudoperculum and the two micropylar processes. KULLENBERG showed the deposited egg of *Bryocoris in situ*, laid obliquely and pointing out of the plant surface. In our rearings, such a position was rare. The eggs are normally inserted perpendicularly far below the surface. The slit made by the ovipositor remains open to air by necrosis of the fern tissue.

The sum of present knowledge on anterior egg structures suggests a mosaic type of

---

Fig. 184–187. Miridae 184. *Isometopus intrusus;* A: ovarian egg, operculum slightly lifted, lateral; B: micropyle. 185. *Plagiognathus arbustorum,* operculum, lateral. 186. *Macrolophus nubilus,* fore edge of anterior pole with aeropylar process, seen from front. 187. *Helopeltis antonii;* A: lateral half of anterior pole, ovarian egg, operculum partly loosened; B: plane view of the aerostatic inner layer, posterior part of egg, hexagonal arrangement of the vertical struts.


184
cop
ap
mp
0.5
A
crc
0.05
mp
B
0.025
B
185
0.1
186
ap
0.05
ail
187
cop
mp
apr
A
sb
0.1

evolution. The combination of characters seems to vary in a haphazard fashion within the family. The *Isometopus* egg (fig. 184) conforms to what we could call the *Miris*-type; other main groups in the family are at least a *Dicyphus*-type and a *Bryocoris*-type. Yet the lack of any subfamily characteristics is not surprising, since the eggs of most cimicoid families exhibit no decisive cladogenetic differences in structure.

HINTON and HARTLEY were the first to discover two micropyles in the family (HINTON, 1962). Their general occurrence, now shown, supports the observation of CARAYON (1954) that fertilization occurs after ovulation. This contradicts the statement of KULLENBERG (1946, p. 432, 433) that in four species sperm penetrated the basal pole of the egg before deposition of the chorion. The micropyles in some Bryocorinae of the *Helopeltis* group is stressed by HINTON as: "quite unlike that of any other known Heteroptera". We found, contrary to HINTON, that the distal end of each micropyle is not attached to the surface of the operculum. The micropyles open free (fig. 187A) and, indeed, could hardly be otherwise for normal sperm penetration. As mentioned on p. 158, the complete aero-micropylar system in *Helopeltis*, *Sahlbergella* and related genera recalls the conditions in Dicyphinae and, apart from the plastron structure, also in *Termatophylidea opaca* whose egg was first illustrated by VAN DOESBURG (1964). However, the discrepancies between shell structure and embryogenesis of the *Helopeltis* group and those of *Bryocoris* and *Monalocoris* have already been stressed (p.156) and suggest that the two groups may belong to different higher taxa. Dr. CARAYON comes to the same conclusion on the basis of other characters (pers. comm.).

KULLENBERG (1946, p. 389, 435) confused the endochorion with the serosal cuticle, but in the cross sections described on p. 394, 397, he found no endochorion in the opercular region. These sections are obviously taken from ovarian eggs, in which the serosal cuticle has not yet formed. In *Helopeltis*, the inner part of the shell (about 6 μ thick) has a porous air-filled layer with vertical columns; this layer separates a thin continuous sheet of chorionin from the main mass of shell (HINTON, 1962). As HINTON indicated, the vertical columns are arranged in hexagons, corresponding to the areas occupied by the follicular cells. This arrangement in the eggs of *Helopeltis antonii*, *Sahlbergella* sp. and many other species is clearly seen in surface view (our fig. 139, 187B). On the margin of the hexagons the struts are thicker, rod-shaped in cross-section, apparently higher and more widely spaced than within the hexagons.

Na data on early mirid embryogeny are available from the literature. JOHNSON (1934) studied the period before hatching in *Notostira elongata*. He paid special attention to what he called the 'yolk-plug', consisting of an extra-embryonic mass of yolk surrounded by a thick wall. We have pointed out that this wall represents the serosal cuticle, which is thickened anteriorly in many mirids and becomes extruded from the chorionic neck long before eclosion. The cell layer within which the yolk is enclosed (the epithelium of JOHNSON) represents the modified serosa after revolution of the embryo. For this system: yolk-body with serosa, but without serosal cuticle we proposed the term: 'serosal plug'. It is usually the normal result of the blastokinetic processes. In the eggs of most, if not all other families, the plug is rapidly engulfed by

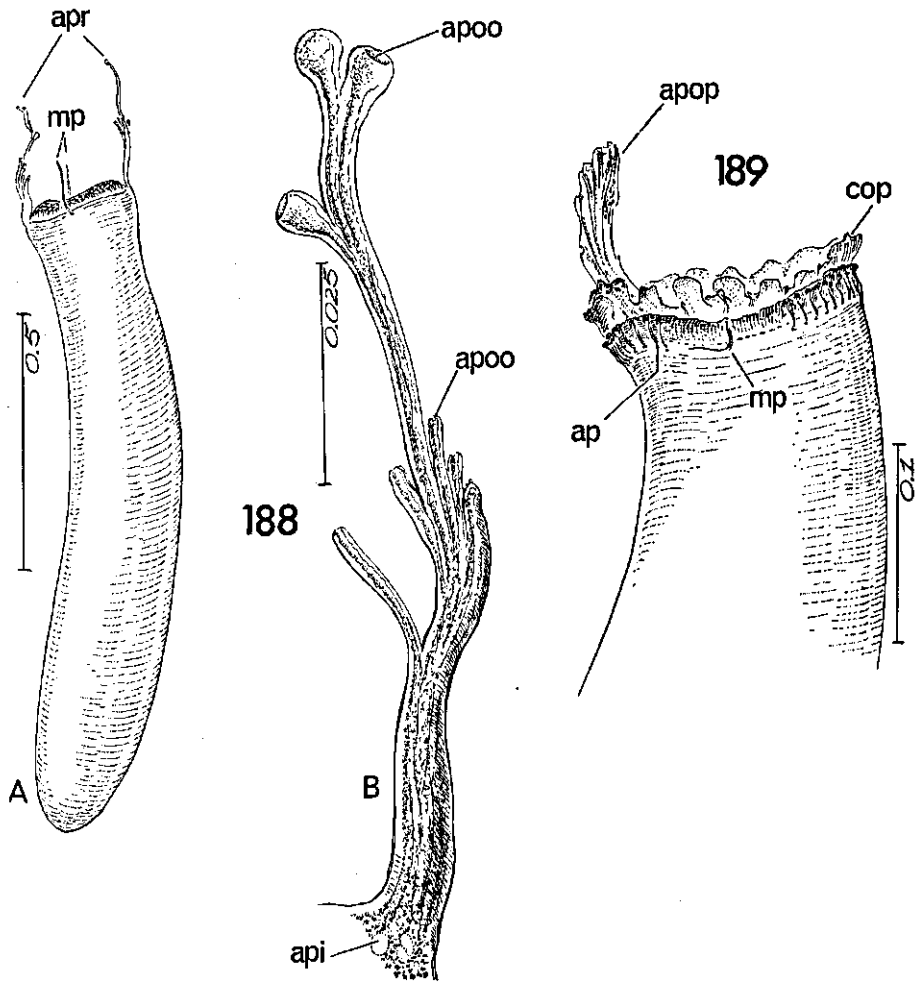


Fig. 188–189. Miridae, ovarian eggs 188. *Campyloneura virgula;* A: lateral aspect of egg; B: respiratory horn. 189. *Hyaliodes* sp., anterior pole, lateral.

the embryo to form the dorsal organ. In most Miridae, however, the plug remains as a conspicuous extra-embryonic organ until shortly before hatching. The yolk is sometimes entirely dissipated from this persistent serosal plug. JOHNSON reported details of the embryonic movements in *Notostira*, leading to hatching, but he missed the autonomous convulsions of the serosal plug. His very careful description of the hatching process conforms with our findings in *Dicyphus*, *Chlamydatus* and *Liocoris*. KULLENBERG (*op. cit.* p. 434–442) studied the same processes in *Notostira*, apparently unaware of the comprehensive work of JOHNSON on the same species. We doubt the statement of KULLENBERG that air is swallowed before the serosal cuticle (his endochorion) opens and that the embryonic cuticle of antennae and legs bears bristles to prevent the larva slipping back. The serosal plug (his: 'suboperculare Eigelbkissen') might, according to him, shelter the larval head and, when it bursts, provide a lubricant for hatching. In the light of our observations, a hydropic function seems more reasonable. The physical properties of the serosal cuticular stenopyle in this respect remains to be solved (Note the thinner grooves along the stenopyle of *Pantilius*, fig. 169C and *Bryocoris*, fig. 168G, see also p. 325).

2.3.5 Thaumastocoridae

MATERIAL: Thaumastocorinae: *Baclozygum depressum* Bergr. (origin Australia); *Thaumastocoris australicus* Kirk. (origin Australia), *Onymocoris hackeri* Dr. & Sl. (origin Australia).

Xylastodorinae: *Discocoris vianai* Korm. (origin Argentina); *Xylastodoris luteolus* Barb. (origin Florida). Of the five species, only ripe and unripe ovarian eggs were available.

The eggs have a clear operculum (fig. 191A, 192A). The eggs of the Thaumastocorinae are dark-coloured (in unripe eggs the darkening starts at the posterior pole) and have a fine but distinct sculpturing of many small hexagons. The eggs of *Discocoris* and *Xylastodoris* are pale, smooth and weakly lined with spherical cell-boundaries. The aero-micropylar system, distinct in each subfamily, is of great phylogenetic interest, as later discussions will show.

In *Baclozygum* and *Onymocoris*, the operculum is a flat plate of the same consistency as the rest of the chorion. In *Thaumastocoris* the operculum is fringed by porous knobs and the whole lid has a distinct porous inner layer. There is an inconspicuous low rim round the operculum of the three Thaumastocorinae; it bears cup-shaped projections (fig. 192A–C) which are not directly connected to the rim. The outer diameter of the cups is 4–5 μ but their circular inner wall tapers to a 0.5 μ wide channel into the porous inner layer of the shell. The number of projections varies between 20 and 35; they seem to be aero-micropyles. The morphological distinction between the micropylar and aeriferous systems is, however, not as clear as in typical pentatomomorphous processes; the next two species show that in this aberrant family the two systems are indeed combined. Separate micropyles could not be traced. None of the

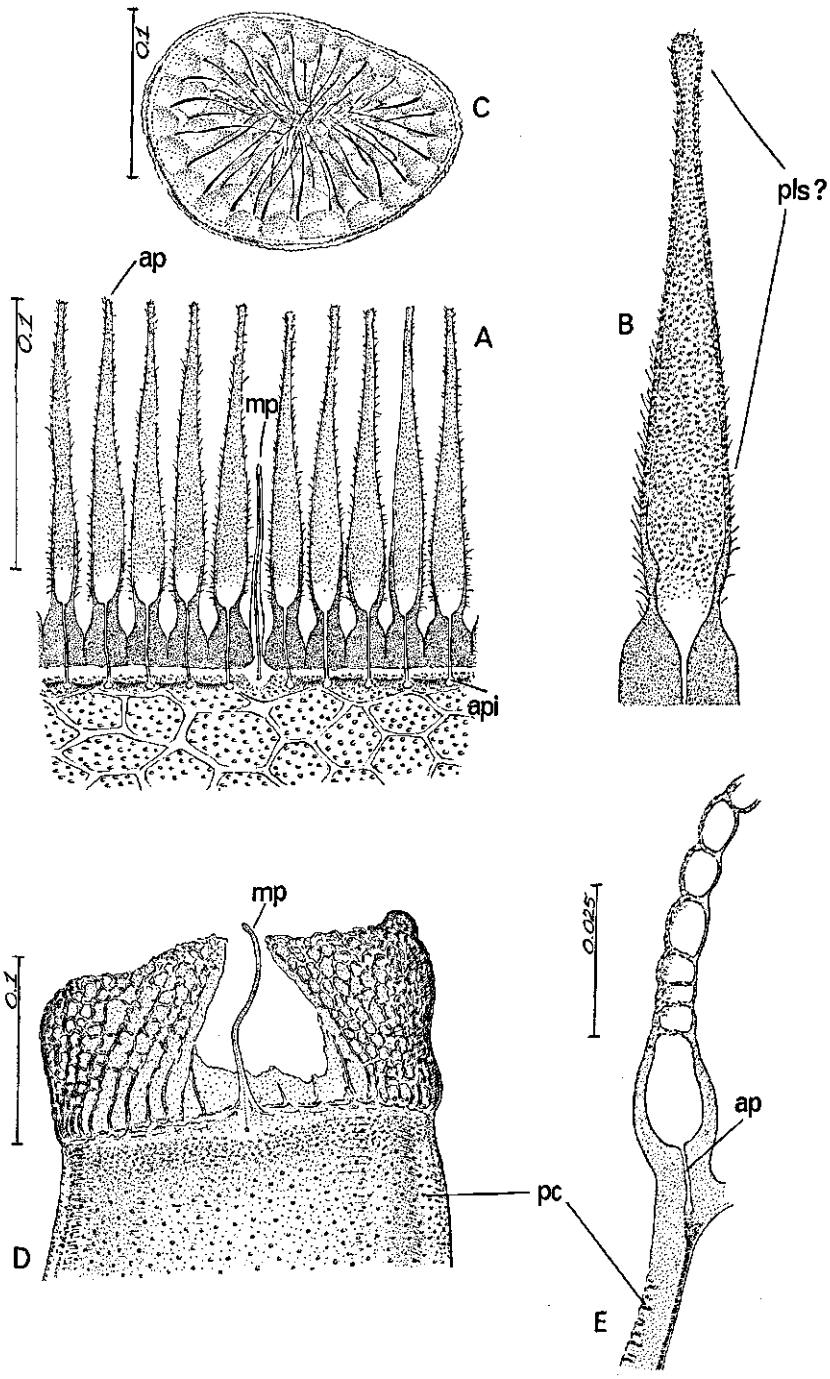


Fig. 190. Miridae A–C *Cylapofulvius?* A: lateral part of rim of neck; B: one aeropyle with supposed plastron structure; C: operculum, from above; D, E: *Teratodella brevicornis;* D: anterior part of egg, lateral; E: fore edge of neck-region and collar, optical section.

Emesinae: *Metapterus banksii* Bak. (origin Curaçao, Neth. Ant.).
Reduviinae: *Acanthaspis* sp. (origin Ivory Coast), *Reduvius personatus* L.
Triatominae: *Triatoma maculata* Erichs. (origin Curaçao, Neth. Ant.).
Ectrichodiinae: *Ectrichodea antennalis* Stål (origin S. Leone).
Phymatinae: *Phymata crassipes* F. (origin Portugal), *Syrtis pennsylvanica* M. (origin California), *Macrocephalus cimicoides* Swed. (origin Canada).

Empicoris culiciformis

Eggs are laid single, loosely or only very weakly affixed with their convex aft side to the substrate. The egg surface is covered with longitudinal lamelliform strips of cement (not indicated in our figures), which help in attachment to rough surfaces or to cobwebs. In addition the eggs are prevented from becoming submerged in water because of the large amount of air held by the ribs.

AERO-MICROPYLAR SYSTEM There are three micropyles and about 10 aeropyles in the few eggs investigated. There is some variability in the number of micropyles but their fewness is important. The canals, as in typical Cimicomorpha, traverse the chorionic rim, which in *Empicoris* is low and without reticulation (fig. 194J). The aeropyles suddenly widen before they meet the porous inner layer of the chorion. The micropyles extend higher up in the rim's collar; their openings are sharply defined and dilated. Inwards they bend sharply and run a distance parallel and close to the anterior margin of the chorion. The bend of each micropyle points clockwise as seen from the anterior.

EMBRYOGENESIS (fig. 194A–I) Complete incubation at 30 °C lasts 7–8 days. Invagination of the germ band starts slightly aft of the posterior pole. The excedingly elongating band is immersed but its long axis is closer to the convex side of the egg. The positional relations contrast with other cimicomorphous families when protocorm starts to bud. The ventral side of the band faces aft. The head remains superficial and initially does not move from the original point of invagination. The germ band never becomes S-shaped. Its trunk remains straight and gradually moves aftwards. The tail end reaches the anterior pole and doubles over ventrad. The appendages arise dorso-laterally and later flex down ventrad. The antennae are continuously directed caudad. No hydropic cells nor isolated germ cells have been observed. A thin serosal cuticle is present but its time of deposition was not ascertained.

During the phases just before blastokinesis the embryo becomes almost completely superficial, only the abdomen suspended within the yolk. Revolution starts directly from this position without any rotation. The activities during blastokinesis and the exact behaviour of the serosal plug could not be adequately studied, since the chorion is not sufficiently transparent. The ommatidia turn red only after the head has approached the anterior pole.

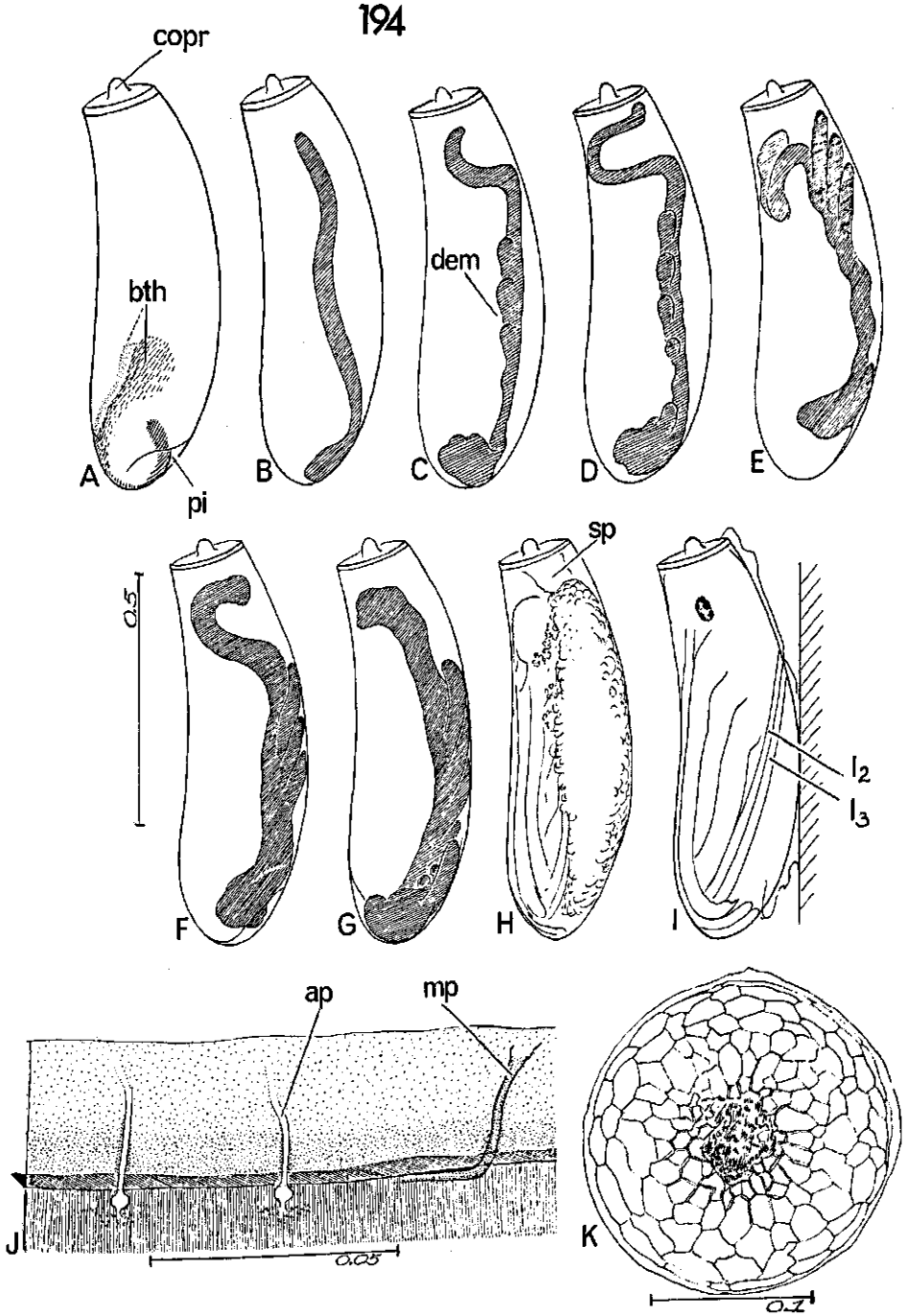


Fig. 194. Reduviidae, *Empicoris culiciformis;* A–I: embryogenesis; J: part of rim region, outer view; K: operculum, from above.

ECLOSION The attitude of the mature embryo is characteristic in that the ends of legs two and three of both sides remain parallel and turn back in an oblique course up to the mesonotum (fig. 194I). Thus, there is no bilateral asymmetry in contrast to most other groups. In the six eggs studied the posture of the prolarva was as shown in fig. 280N. The serosal cuticle does not protrude out of the chorionic neck. This cuticle breaks simultaneously with the operculum. There is no distinct sealing bar and the flat operculum is disrupted more or less irregularly (fig. 194K). The embryonic cuticle closely envelopes the head and bears two indistinct longitudinal spiny ridges on the frontal region.

Schidium callipygum

In captivity, the species glued all eggs firmly on filter paper in the orientation as figured (fig. 196). As in *Empicoris*, only three or four micropyles are present. Embryogenesis is as in *Empicoris*.

Lisarda vandenplasi

Most of the numerous eggs were deposited loosely in a specimen tube (the female was collected on a termitarium and MILLER (1956) suggests a relation of the bug with termites). The eggs are orientated, when leaving the female as in fig. 197H. The operculum slopes slightly, and distinguishes the fore and aft side of the nearly spherical egg. Micropyles are probably few and difficult to trace in the thick dark-brown chorion.

Embryogenesis differs in some aspects from the emesine pattern (fig. 197A–G). Invagination starts in the centre of the posterior pole, but it seems that the blastopore moves slightly fore-wards instead of aft-wards. It may also be that the anterior part of the band does not invaginate. Although accurate observations are here lacking, our findings in Harpactorinae suggest that invagination is not complete. The course of the band as it grows anteriad is initially at some distance from the egg-wall but later it lies adjacent to it. The thoracic appendages are folded towards each other ventrad and, as in other reduviids, never are spread out lateralwards (contrast Hydrocorisae). A serosal cuticle is formed as the protocormic buds appear. The squatness of the egg causes an extraordinary posture in the mature embryo. The whole thoracic ganglion-complex lies immediately beneath the operculum, whereas the head occupies only a marginal area at the fore end of the cap. The egg-burster presses this anterior point in contrast with pentatomoids. The burster is similar in form and function to that of other Reduviidae. Its relation to the larval epicranial sutures is shown in fig. 209. Also the opening of the serosal cuticle by a regular round cap suggests that eclosion is by pressure on the whole cap. The front legs in the prolarva are arranged in a loop on one side with the long antennal bundle. This loop, in all ten eggs checked, runs along the right side of the larva (diagram, fig. 280P). The second and third legs cross each other beneath this bundle.

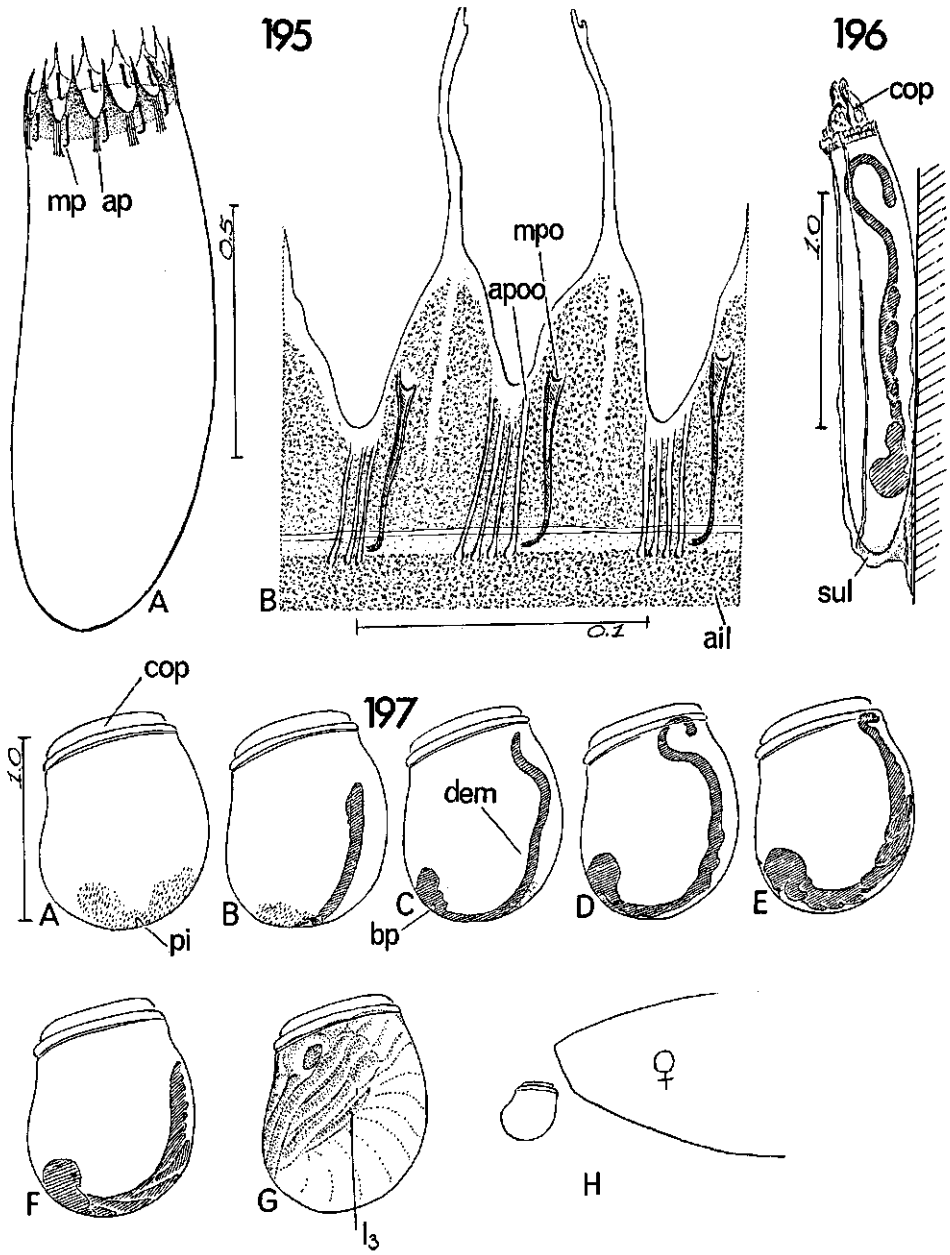


Fig. 195–197. Reduviidae 195. *Metapterus banksii;* A: ovarian egg, lateral, operculum removed; B: part of rim collar. 196. *Schidium callipygum*, egg *in situ*, with germ band. 197. *Lisarda vandenplasi;* A–G: embryogenesis; H: orientation of egg when leaving the mother.

Cethera musiva

Eggs of this bark species are dropped free. Incubation takes about 30 days at a temperature fluctuating between 25° and 30 °C. The main aspects such as type of egg (fig. 198A), embryogeny, and eclosion structures and posture, are similar to *Lisarda.* The paler chorion facilitates analysis of the anterior system of canals. There are 5–8 micropyles among the many aeropyles. The semi-diagrammatic fig. 198B shows the differences between each type of canal. The aeropyles do not reach up into the rim; they first cross the chorion vertically and then bend downwards to join the cavities of the inner layer of the shell. The micropyle starts in the rim itself and tapers downwards to a much smaller diameter than the aeropyles. After traversing the middle layer of the shell below the top of the air-filled inner layer, it turns back upwards and opens in front of that layer.

Edocla? sp.

Egg shape and oviposition site are shown by fig. 200. The number of micropyles is 4–5. The two embryonic stages seen and depicted, suggest a development as in *Lisarda.*

Sphedanovarus camerunensis

This subcorticular species in captivity glued its eggs on filterpaper (fig. 199). The chorion is ornamented with thickened and finely spined hexagonal ribs. The chorionic and the opercular porous collar is indented. About eight micropyles alternate with many more aeropyles; they are like each other except that the micropyles are slightly narrower. They all open externally at the same level below the collar indentations. The micropyles bend just above the aerostatic inner layer. Only a few stages of internal development were seen. The position of the invaginated band is analogous to that of the emesines studied but more superficial. Blastokinesis follows directly upwards from this position.

Rhinocoris, 6 spp. (listed on p. 168)

Eggs are laid erect in large batches. Copious tough brownish cement surrounds the individual eggs and particularly the circumference of the batch. Despite their compact erect arrangement, the elongate eggs have a slightly concave and a convex side (fig. 206). We saw that the greater convexity of the egg faces anteriad to the site of the laying female. The convex side thus would adhere to the substrate, if the egg were attached lengthwise (fig. 206E, supposed substrate at right). The opercular region has a rich ornamentation derived from the highly elevated network region of the operculum and the single veil which projects from the rim-collar. Both the lateral and central elevations are continuous with each other.

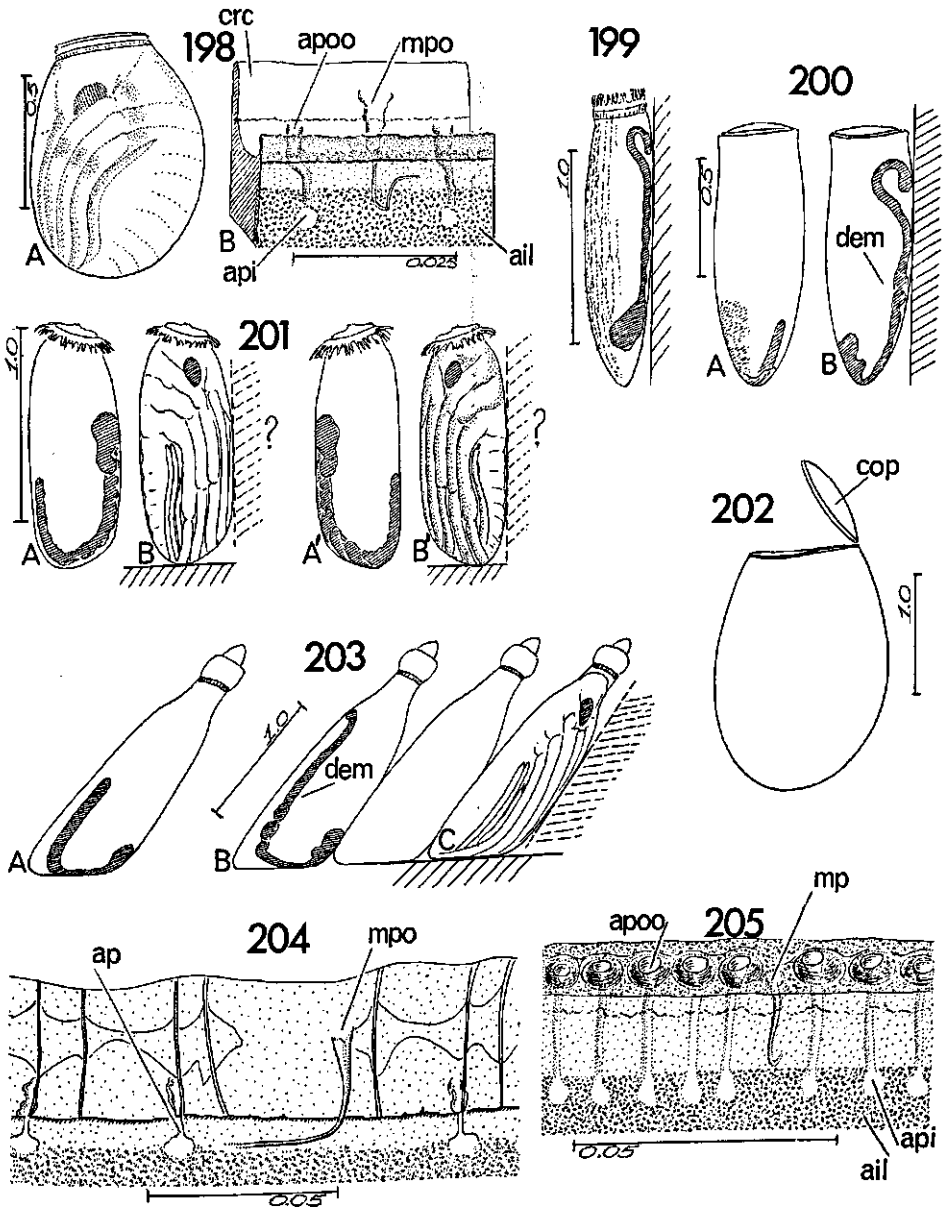


Fig. 198–205. Reduviidae 198. *Cethera musiva;* A: posture of prolarva; B: section of rim region, inner view. 199. *Sphedanovarus camerunensis*, egg *in situ*, with germ band. 200. *Edocla?* sp.; A: during invagination; B: position of germ band. 201. *Nagusta punctaticollis;* A: germ band; B: prolarva; A′, B′: rotated position (see text). 202. *Ectrichodea antennalis*, ovarian egg. 203. *Vestula lineaticeps*, part of batch, embryo in different stages (A, B), prolarva (C). 204. *Ectrichodea antennalis*, part of anterior rim structures. 205. *Acanthaspis* sp., part of anterior rim structures, outer view.

At eclosion this meshwork unit ruptures where the veil is attached to a remarkable white scaly structure on top of the opercular outgrowth (fig. 208B). This structure reveals with the scanning electron microscope as a crown of mushroomlike bodies (fig. 311). In the species with a moderate opercular outgrowth, the crown forms a circle within the uniform honeycomb of the opercular surface. The honeycomb outside the crown has solid walls (fig. 312B, D, F), but in the centre of the crown they are severely porous (fig. 312A, C, E). This latter is the area which is in direct contact with the atmosphere and thus an innate respiratory device is strongly evidenced for the centre of the operculum.

It is not clear from the scanning-electronmicrographs whether the mushroom structure is porous, but fine pores of about 0.3 μ may be present. There might thus be a functional relation between this structure and the central comb for respiration through the cap. As will be shown with the transmission electron microscope (p.446), the operculum of *Coranus* indeed contains aeropyles. *Rhinocoris iracundus* has the outgrowth on the operculum very pronounced so that the upper honeycomb cells are elongated. Compare the scanning-electronmicrograph (fig. 313A) and some details (fig. 313B–D) with fig. 208. The hexagons of the external veil suggest also to be finely perforated.

There are only 4–5 micropyles, regularly distributed between the many aeropyles in the rim collar.

Fig. 206A–E indicates the general outline of embryogenesis. The extent of invagination is intermediate between the emesine- and the *Coranus*-type (to be considered below). Only the posterior half of the band moves upwards inside the yolk; the fold of invagination remains at the basal pole. The serosal plug, filling the whole subopercular area, is entirely absorbed within the pronotal region (fig. 208A, B) long before eclosion. The lifting of the operculum during eclosion must involve considerable force as the apical line of fusion between the lateral and central network also must be broken. There is no egg-burster present. Only two longitudinal areas with very fine teeth run over the vertex, frons and clypeal region of the embryonic cuticle (fig. 208C, ecf). These strips terminate anteriorly at the base of the labrum. The spiny areas clearly have no function in bursting the egg-cap. Moreover, there is no cephalic vesicle as in *Mesovelia* or *Nabis*, nor is the operculum loosened simply by widening of the egg neck as in Miridae. The Reduviidae apparently do not absorb water from the environment for accomplishing eclosion and thus differ from the Hydrocorisae. The very beginning of eclosion has not been observed in *Rhinocoris* but the process was noticed after the operculum was loosened a distance (fig. 208C). No remnants of the serosal cuticle are left round the chorionic neck. This cuticle is broken in a circle just beneath a hyaline ring-like thickening. Thus the serosal cuticle has an operculum which remains attached to the cavity of the chorionic operculum after eclosion. When the egg cap is removed from the intact egg, this serosal operculum is seen to cover the embryonic cuticle and the larval head like a helmet (fig. 208D). We suggest that this strengthened and rigid ring of the subchorionic membrane helps to lift the chorionic operculum. Its ridge seems to wedge into the groove of the sealing bar of the shell.

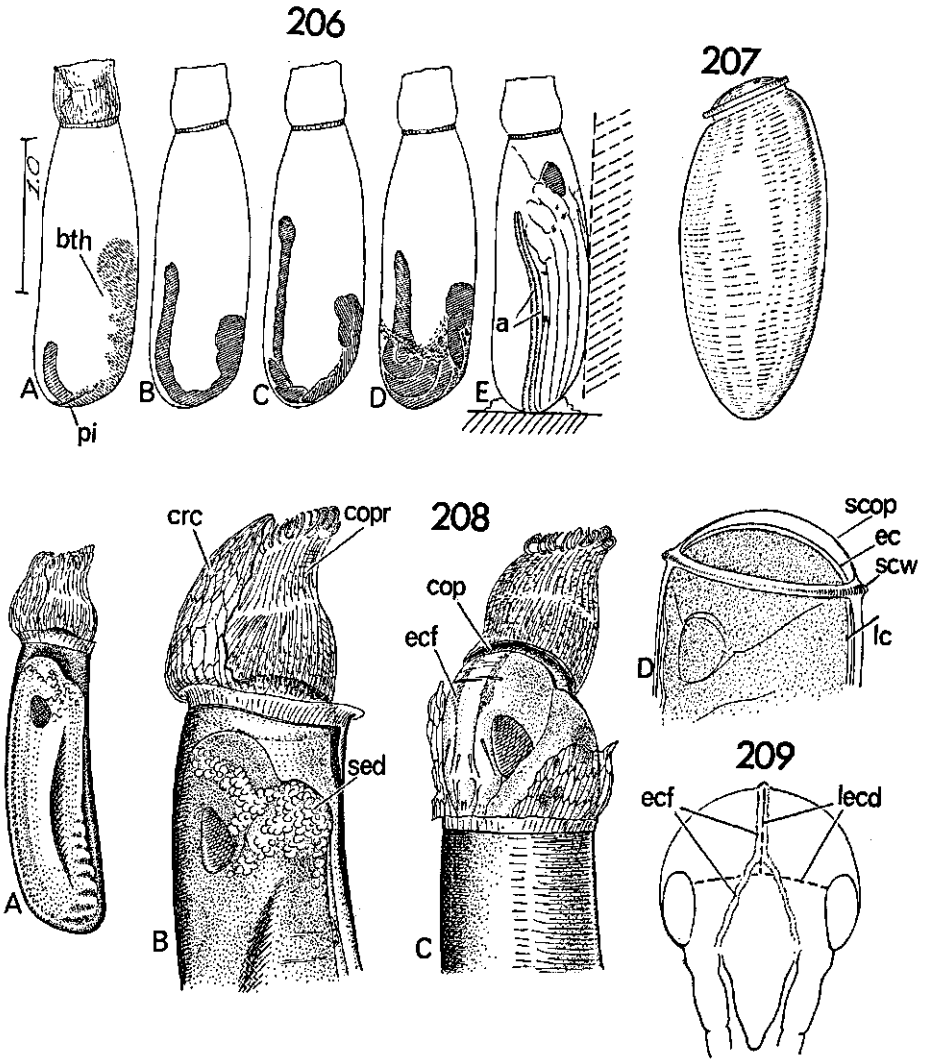


Fig. 206–209. Reduviidae 206A–E: *Rhinocoris obtusus*, embryogenesis. 207. *Rhodnius prolixus*, egg, lateral (modified from MELLANBY, 1936). 208. *Rhinocoris iracundus;* A, B: embryo after revolution, part of rim collar removed; C: hatching; D: prolarval head enveloped by the serosal cuticle (chorion removed). 209: *Lisarda vandenplasi*, prolarval head.

The attitude of the fully grown embryo is basically the same as described in previous reduviids. The antennal bundle usually runs along the right side of the larva. This right dominance is often significant but there is great variability between batches, even in the same species.

The eggs of the harpactorines *Vestula lineaticeps* and *Nagusta punctaticollis* each have features aberrant from the previous members of the subfamily.

Vestula has bottle-shaped eggs, triangular in cross section, which are deposited in separate rows of 2–5 eggs. Their bases are obliquely flattened, causing the longitudinal axis of the egg to lean over (fig. 203). The micropylar region was not studied. Invagination of the germ band is slightly more complete than in *Rhinocoris.*

The eggs of *Nagusta* are deposited in a vertical position, always in two adjacent rows. A search has been made for the micropyles but we failed to detect them. Embryogenesis approaches the *Coranus*-type. The difficulty of ascertaining the orientation of the egg is noteworthy (see the exposition of the subject in the discussion sub 3.4). Oviposition has not been observed but the prolarval orientation suggests the egg orientation in fig. 201B, like other harpactorines. But in that case the slope of the operculum in *Nagusta* would be towards the substrate (contrast *Rhinocoris*). Therefore it is not certain which of the two possibilities of egg orientation (fig. 201B or fig. 201B') is found in *Nagusta.*

Coranus subapterus and C. aegyptius

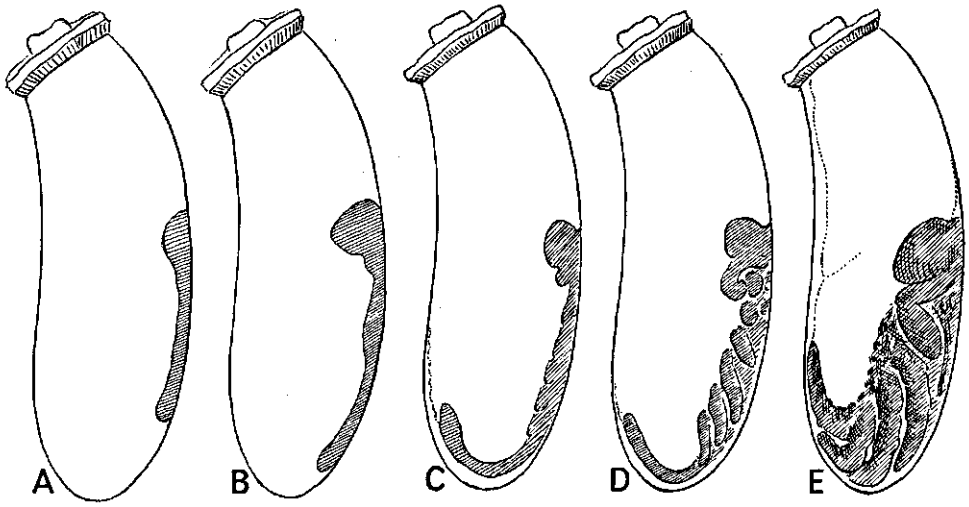
The following account applies for both species; *C. subapterus* has an embryonic diapause.

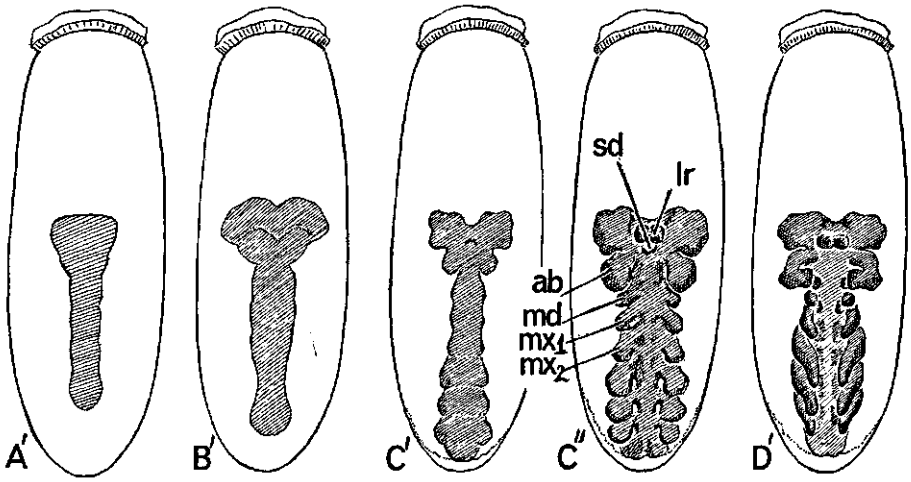
The singly laid eggs are attached to the substrate by their more convex side (fig. 210F). Although the point of attachment is small, the greatest part of the egg is enveloped by a gelatinous sheath.

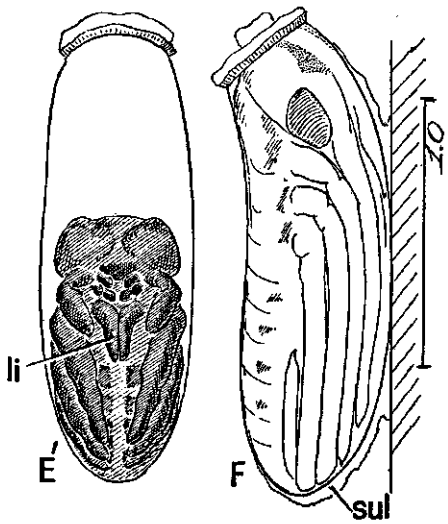
AERO-MICROPYLAR SYSTEM The rim-collar is low and with the radial outgrowth of the central opercular plug forms a continuous veil over the apex of the egg. The marginal veil-structure is all porous and consists, in micrographs of *C. aegyptius*, of a fine, outer film supported by extensions of the outer opercular wall (fig. 300C, D; fig. 301D). Towards the centre of the cap, the veil is lower and thicker (fig. 301B). This widely vacuolar structure of the cap most likely is involved in air capture. It is significant that, unlike *Reduvius*, the solid shell of the cap contains canals (about 0.25 μ wide). These might also function as aeropyles when the egg is submerged, because they are in contact with the air-store trapped in the veil. There are about 10 micropyles and about 110 aeropyles arranged in a rather regular alternation round the rim. The

Fig. 210–211. Reduviidae 210A–F: *Coranus aegyptius*, embryogenesis, lateral view; A'–E': aft side; C'': intermediate stage between C' and D'. 211. *C. subapterus*, cephalic pole from above, operculum lifted, diapausing egg.

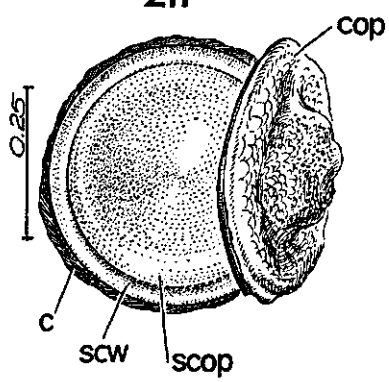
210







211



micropyles are bent internally so that the continuation of all bends together form a clockwise circle around the rim. The aerostatic inner layer of the shell is much thinner than in *Reduvius*. Anteriorly it starts below the operculum and its further course downwards is shown in the micrographs (fig. 301A and fig. 300A, respectively). The latter photograph shows further that the outer chorion is only slightly darker than inwards. In sections stained with KMnO4, the contrast is clearly visible (fig. 300B).

EMBRYOGENESIS The earliest stage of development we could trace appears from fig. 210A and A'. The still short and undifferentiated germ band is entirely superficial half way up the aft side. There is no yolk between the ventral side of the band and the serosa along the shell. The head lobes are remarkable in pointing towards the anterior region of the egg. It looks as though the band in these species has never invaginated. Theoretically, the position shown could result from a very early shift round the surface of the yolk from a similar position on the fore side. Such displacements sometimes occur in Hydrocorisae. The data on reduviid eggs, already described, make the assumption of such a rotation in *Coranus* very unlikely. Nevertheless, further development reveals the striking fact that the *Coranus*-embryo does not shift and that blastokinesis is wholly absent. The band is liable to only a small degree of elongation. The metameres of the head are already visible when the part which later gives rise to thorax and abdomen, is still very short and compact. After that, the head region narrows, the remaining part of the band elongates round the posterior pole and the thoracic buds start forming. The subsequent steps in growth of the embryo are shown in fig. 210A–F. The winter-diapause of eggs of *C. subapterus*, which are laid in late summer, is spent at a stage between A and B (fig. 210), apparently shortly after the serosal cuticle has been secreted.

The embryo, shown in fig. 210E, has not yet moved upwards. The amnion has already fused with the serosa and is curved upwards. The opacity of the chorion prevented close study of the process in life. The eye starts to pigment only when the embryo is approaching the anterior pole, despite the large size and numerous ommatidia of the first larval instar. Five to six elements in the centre of the eye disc colour first and the process of pigmentation spreads outwards. The attitude of the fully grown embryo is depicted in fig. 210F. The hind legs are crossed and the mid legs with their crossed tips lie hidden below the remaining appendages. There is a slight asymmetry but whether this is preferentially to one side has not been examined. The embryonic cuticle on the head bears no distinct cranial framework. Two elongated triangular areas, densely clothed in minute teeth, cross the frontal region. The egg has an indistinct sealing-bar. The serosal cuticle under the operculum is solid and shows a ringed marginal vaulting (fig. 211 scw). In the micrographs (fig. 301A, D), the serosal cuticular ring is seen to fit as a wedge in a weak recess of the chorion. The future chorionic eclosion line can be traced from this recess upwards to the top only as a slight contrast in electron density (fig. 301D, cel), as the operculum is slightly darker than the adjacent shell region. The subopercular part of the serosal cuticle remains

considerably thicker than elsewhere where it thins out (fig. 301D), when the eclosion time approaches. The serosal cuticular operculum is lensiform with many fine superposed lamellae in its inner zone and a dark inclusion along the margin (fig. 301A).

One *Coranus* sp. from Ivory Coast conforms in all essentials to the description above.

The aero-micropylar area of some additional species

Metapterus banksii

The opercular region shows more advanced differentiations than in the two Emesinae, already described. The rim is broken up into 12–15 stiff filaments (fig. 195A, B), which assumedly are not hygroscopic in contrast to Microphysidae. It is, however, supposed that the tips of the filaments originally were directed concentrically towards the elevation in the centre of the operculum and that they became erect after oviposition (we studied deposited eggs). In many reduviid eggs with a high cuff-like rim, similar terminal slips of the rim become visible only after eclosion, when the protruding operculum has pushed them upwards. In other species the rim is a continuous sheet completely fused with the raised opercular centre. In *Metapterus*, this raised crown is higher than in *Empicoris* and it consists of porous material as well as the thick follicular ribs on the rest of the operculum. The functional morphology of this central region needs further detailed study, since a secondary aeropylar system might be involved as was suggested for *Coranus* and *Rhinocoris*.

In *Metapterus*, there are 12–15 micropyles according the corresponding number of filaments. The number of aeropyles is three to four times higher. Both aeropyles and micropyles are confined entirely to the incisions of the rim. The micropyles, which open at the outside of the rim, lie consistently at one side of each incision. The outline of both types of canals and the remarkable constant internal deviation of the micropyles appears from fig. 195.

Acanthaspis sp.

The many aeropyles open to the outside of a low strip of the egg-mouth (fig. 205). Openings lie close together, each opening being fitted in a cup-shaped elevation, suggestive of the pentatomoid processes. The 2 μ wide aeropylar canals discharge direct into the aerostatic inner layer of the shell. The four or five micropyles are narrower and shorter, opening externally on the inner side of the strip and bending in front of the air-space inner layer before discharging into the lumen.

Reduvius personatus

Number of micropyles about 12, of aeropyles 40–50. Micropyles are to be recognized as such by their dilated external opening. Thickness of chorion about 8 μ. The

shells of eclosed eggs have been sectioned for analysis with the electron-microscope. The micrographs reveal a distinct air-space inner layer of a spongy nature (fig. 299D, E). This porous sheet covers a fifth of the shell diameter in the subopercular region, but its thickness decreases up to a seventh posteriad. The otherwise entirely solid shell has a thin outer zone of slightly lower electron density (fig. 299D, col). The same contrast occurs in the operculum, which otherwise lacks the spongy inner layer entirely (fig. 299A). The junction of the opercular margin to the neck of the shell body can be deduced from fig. 299B and E. There is no sealing bar and, thus, the eclosion structure is much simpler than in *Rhodnius*. The eclosion line (cel) divides a thin inner connective strip between the main shell and the operculum. Since the micrograph B (fig. 299) is 1.4 times more magnified than E, it follows that the opercular margin falls within the rim collar (crc) in the unhatched egg.

Triatoma maculata

Number of micropyles 7–12, of aeropyles 80–100. Between both types of canals one can easily discriminate without applying special techniques. They are of the same length, but the micropyles are narrower and are on the whole found on a slightly higher level than the aeropyles.

Ectrichodia antennalis

The alternating arrangement of the 10–14 micropyles and the 85–100 aeropyles is regular. Each aeropyle is flanked at one side by two upstanding ribs in the low rim, the micropyle only by one. The long transverse deviation of the micropyle further distinguishes it at once from the short aerostatic canals (fig. 204).

Phymata crassipes and the other two Phymatinae.

Eggs are outwardly very close to those of, for instance, *Lisarda*, *Cethera* and *Ectrichodia*. Three or four micropyles and around 110 aeropyles were observed in *Phymata* and *Syrtis*. In *Macrocephalus*, about 170 aeropyles are present, but we could not trace the micropyles, because of the dark colouration of the chorion.

PREVIOUS DESCRIPTIONS SOUTHWOOD (1956) included 48 references in his survey of reduvioid eggs. Besides the eggs of Phymatidae (considered by other authors and in our account above as a reduviid subfamily), he summarized the egg-characters of 11 of the nearly 30 subfamilies described in literature but treated by him and most recent students with great reserve. The eggs we have described represent some widely diverse types within which can be grouped nearly all other known reduviid eggs, at least as suggested by their exterior. However the data available from literature are confined mainly to what might be proved to be superficial characters. The survey of SOUTHWOOD is based predominantly on the data given by READIO and MILLER (cited in

SOUTHWOOD, 1956) and he concluded (p. 200) that: "it has been shown that, contrary to the statements of some workers, it is possible to allot egg characters to the Reduviid subfamilies (the only aberrant genus is *Leptoderma*). The egg types of the Emesinae, Stenopodinae, Piratinae and Salyavatinae are all unique. The Harpactorinae, Apiomerinae, Physoderinae and Phonolibinae share a common egg type characterised by the presence of the network region (not fragmented) and the operculum thickened, at least in part. The eggs of the Reduviinae, Triatominae and Ectrichodiinae are similar in shape; the network region is very small or absent and the operculum thin and almost flat". A comparison of the illustrated eggs of 94 spp. in MILLER (1956) invalidates SOUTHWOOD's conclusions considerably. We only need to refer to the diversity of the eggs of Stenopodinae and Salyavatinae (MILLER's fig. 5–14, p. 77) and to the filamentous rim which recurs in at least five of MILLER's subfamilies.

Other than the detailed knowledge of the *Rhodnius* shell (BEAMENT, 1946–1951; number of micropyles about 15) and the embryology of the same species (MELLANBY, 1935, 1936), the information on the occurrence, number and arrangement of aeropyles and micropyles and on embryogenesis in other eggs is almost nil. In addition, the orientation of the mature embryo in relation to egg shape and oviposition site (compare our fig. 194 I of *Empicoris* with that of *Coranus*, fig. 210F) should be considered along with other characters.

Besides the three common methods of oviposition described in our examples (exposed horizontal, vertical and simply dropping), some species of Stenopodinae and Piratinae lay their eggs in the soil with only the opercular end exposed. The inclusion with cement of whole batches, as in many Harpactorinae, tends towards the formation of oothecae and this is particularly the case in *Isyndus heros* (MILLER, 1956). The incubation period is rather short in *Empicoris, Coranus, Rhinocoris* (7–10 days at 30 °C), but distinctly longer in *Rhodnius* and *Cethera. Platymeris rhadamanthus* needs 28–30 days (28 °C) for complete development (EDWARDS, 1962).

The exterior chorionic pattern of haematophagous species proved to be highly specific per species (BARTH and MUTH, 1958; RYCKMAN, 1962). On the basis of chorionic ornamentation RYCKMAN distinguished three divergent egg types in the *Triatoma protracta* complex. Within *T. protracta protracta* two geographically separate populations occur, of which one lays rough and the other smooth eggs.

The thickened ring of the serosal cuticle, mentioned under *Coranus* and *Rhinocoris* is also formed in *Rhodnius* and referred to as the 'epembryonic ring' by BEAMENT (1949). This author thought that "this ring might give considerable protection to the embryo against invasion from the micropyles". On p. 176 we suggested that the ring dislodges the operculum from the sealing bar. The chemical constitution and the permeability of the ring and its bearing membrane have been thoroughly investigated by BEAMENT. The envelope in question is termed by him the 'epembryonic membrane' and not the serosal cuticle, because its initial formation should commence before the serosa differentiates. The maximum secretion of the cuticle and its ring, however, occurs in the second quarter of the incubation period. In most other heteropterous eggs the serosal cuticle becomes visible at this time. Since BEAMENT himself stated, on

p. 474: "One can assume that the epembryonic membrane is chiefly a product of the serosal cells", the name 'serosal cuticle' also for reduviid eggs seems correct within the taxonomic frame-work of our relatively rough comparisons.

The embryogenesis of *Rhodnius*, studied by MELLANBY (1935, 1936) is intermediate between *Empicoris* and *Rhinocoris*. As in *Empicoris* the *Rhodnius* embryo invaginates backwards at the basal pole, moves upwards close to the aft side of the egg but shows no caudal flexure. Before involution starts, the embryonic rudiment of *Empicoris* and *Rhodnius* occupies a central position at one side of the egg. This actual situation is maintained in at least some Harpactorinae throughout embryonic life.

MELLANBY reports the early existence of germ cells, which according to BUTT (1949) develop in the same way as in *Oncopeltus*. The clump of germ cells comes to lie at the extreme tail end of the invaginating embryo of *Rhodnius*. It is not certain whether this group of cells can be traced as such in whole mounts. In *Empicoris* and in the other reduviids, we have not noticed them, whereas in other groups, where they are more or less isolated from the band, we easily observed them in gross view by the same techniques.

The egg shape of *Rhodnius* reflects a similar intermediate position as the embryogenesis (fig. 207, note that the convexity of the fore and aft side of the egg is the reverse of the *Coranus* egg, but that the sloping of the cap is similar). The concise account on *Pristhesancus papuensis* by MUIR and KERSHAW (1911) suggests a similar embryonic behaviour as in *Coranus*.

In conclusion it could be argued that the three reduviid types of embryogenesis discussed here represent only test samples taken from one and the same anagenetic line. We will, however, discuss later how the picture implies that cladogenesis has occurred at least once in Reduviidae.

2.4 Hydrocorisae

Eggs of the true waterbugs have attracted the attention of many naturalists for a long time. The chorionic structures and functions of the Nepidae have been recently investigated in great detail by HINTON (1961).

In the following survey we will give additional descriptions of shell structures of other waterbugs only where it is needed to compare the complex of characters adequately for each family. Many problems concerning the physics of respiration and thus the interpretation of some structures remain unsolved since their solution falls outside the scope of this study.

In analysing our next figures it may be thought that shape and embryogenesis present no difficulties in distinguishing dorsum and venter of eggs. However, we have just cited in Reduviidae a remarkable reversion of conditions in the egg (compare fig. 194I with fig. 210F). Hydrocorisae eggs, moreover, show the most displacements of the embryo and at quite different stages of development. Therefore, we will continue to call the dorsal and ventral side topographically: the 'aft side' facing the substrate, or, in case of vertical deposition, facing to the site of the ovipositing female; the 'fore

side' opposing the aft side. The final choice of a morphologically justified determination will be discussed later (section 3.4.5).

2.4.1 Corixidae

MATERIAL: Micronectinae: *Micronecta browni* Hutch. (origin Ivory Coast), *M. meridionalis Cost.* (origin Poland), *M. poweri* Dgl. & Sc., *M. scutellaris* Stål (origin Israel), *M. sp.* (a few fixed stages of deposited eggs, hatched eggs; origin Ivory Coast); *Tenagobia incerta* Lundbl. (origin Brasil).

Diaprepocorinae: *Diaprepocoris zealandiae* Hale (fixed stages of deposited eggs; origin New Zealand).

Cymatiinae: *Cymatia coleoptrata* Fabr. (living deposited eggs), *C. bonsdorffi* Sahlb.

Corixinae: *Agraptocorixa hyalinipennis* F. (hatched eggs; origin Malaya), *Corixa punctata* Ill. (living deposited eggs), *C. panzeri* Fieb., *Hesperocorixa linnei* Fieb. (living deposited eggs), *Sigara fossarum* Lch, *Glaenocorisa propinqua* Fieb. Unless otherwise stated ovarian eggs were studied.

Micronecta, 6 spp. (enumerated above)

The elongated egg has one flat side, which is glued to bare objects (fig. 213), and has for Corixidae an atypical shape. A closer investigation of its chorion reveals more very peculiar properties, which separates it from the Corixinae eggs.

CHORION The micropylar area is at first sight suggestive of the nipple structure of Corixinae. However, the projection in *Micronecta* is formed by a single solid cylinder, padded inside with porous substance (fig. 212B, 214). The single micropyle is difficult to detect, masked as it is in the plug of the cylinder. It consists of a simple, oblique penetration of the chorion in the bottom of the cup. Mostly it is situated excentric in the crater and it extends backwards into the lumen (fig. 214). The whole structure forms a remarkable parallel with the single aero-micropylar structure of some fulgoromorphous leafhopper eggs. From the micropylar cup originates a straight band, which stretches a third of the length of the convex side. The band represents a deep fissure in the chorion, varying in width between 2 and 8 μ. The fissure is filled with a gritty material, which apparently goes down into the thin chorionic inner sheet. Ovarian eggs from dried females of *M. scutellaris* were softened in a mixture of alcohol, acetic-acid and water. When covered in euparal, the cleft shone as a silverwire (fig. 212B) suggesting that air had been retained in the gritty substance. This structure, which unlocks the chorion (the eclosion rent occurs along this line), is entirely separate from the pore system which covers the whole egg. Such an eclosion band has been met with in all eggs but in *M. browni* it seems to be more solid and not distinctly porous. We collected this species in the Ivory Coast in small pools on black rocks along a large river; the temperature of the shallow rock pools rises so high that waterbugs would not have been expected.

The structure of the chorion in all species studied have common features but species differ in structural details. It consists of a regular system of pores, which is often covered locally by chorionic warts. The rugosity thus formed is a specific characteristic. The chorion of *M. scutellaris* has dome-like structures as well, which are scattered on the egg's fore side (fig. 212B, cd). The domes have wide openings and the underlaying layer bears the same pores as elsewhere. The chorion of *M. meridionalis* is uniformly porous without any elevation or hexagonal reticulation. In *M. browni*, the closely packed pores have stellate branches inwards but the side branches of adjacent pores are not confluent.

Contrary to the situation in Cymatiinae, to be described below, there seems to be no continuous porous inner layer in *Micronecta*, when observed light-optically, unless it be extremely thin. Micrographs confirm that there is indeed a very thin (about 0.1 μ) open inner layer, which is supported by irregularly spaced struts (fig. 302A, B). The sections were made of the deposited eggs of an African species close to *M. scutellaris* as judged on adult characters but quite different in chorionic texture. The chorion bears a distinct regular pattern of circular pits and lacks the domes. From the border of each pit fine canals run obliquely to the inside of the shell. The micrographs reveal a double-layered chorion: a solid inner layer of about 0.1 μ and an outer layer 25 or 50 times thicker (dependent on the egg-side), which consists of the struts and a pored mid-zone, which extends outwards to form solid ridges surrounding the circular pits. The pore-canals communicate with the continuous, open inner layer.

EMBRYOGENESIS Embryonic stages are available only from the time of thoracic bud formation (fig. 213). The course of events afterwards and presumably also before is as in Corixinae. Possibly through unsufficient staining at too late a date after fixation of the eggs in Africa, we could not trace hydropic cells. The whole band is superficial with its ventral side against the fore side (fig. 213; the legs are flexed dorsad following the slope of the shell; therefore one can readily confuse this picture with the condition in, for instance, fig. 125D; in fig. 213 the venter of the band faces to the left but in fig. 125D it is the dorsum of the band which is oriented to the left!). Although eclosion has not been observed, it is likely that the mechanism of breakage is the same as employed by *Corixa*, *Cymatia* and in fact all other waterbugs studied.

Tenagobia incerta

The egg is, in several respects, intermediate between the *Micronecta* and the Corixinae egg. Although essentially outlined as in *Micronecta*, it has a short basal stalk and thus it is not glued lengthwise but placed upright (fig. 215A). The basal pad is composed of a central, inversed dish-like outgrowth of the inner part of the shell, which connects basally with a pored cylinder arising from the external chorionic layer at a higher level of the shell. There is no porous longitudinal groove running back from the micropylar process. The latter is like the *Micronecta*-nipple, but it is surrounded by a thinner, slightly lamellated zone, which is not perforated (fig. 215B).

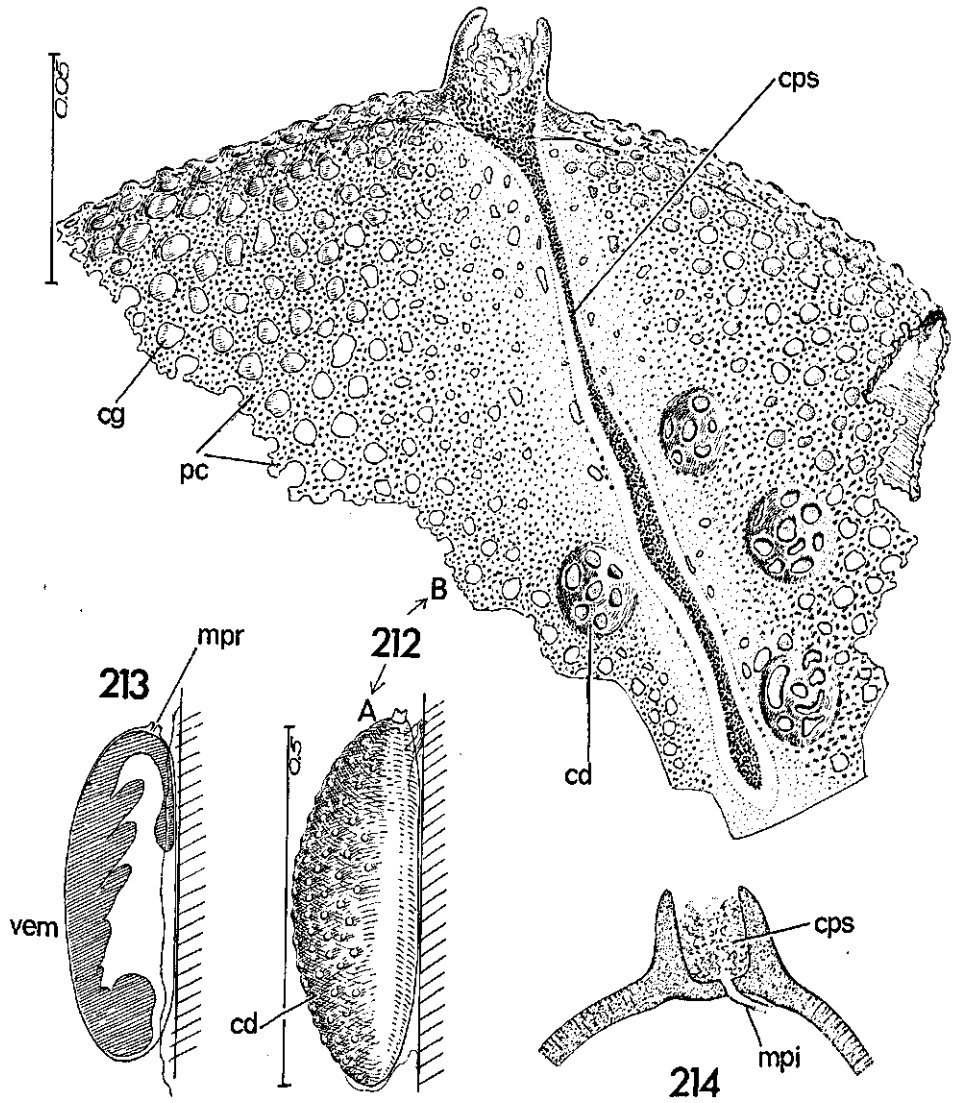


Fig. 212–214. Corixidae 212. *Micronecta scutellaris;* A: egg *in situ;* B: anterior pole, fore side. 213. *Micronecta* sp. (Ivory Coast), position of embryo. 214. *M. browni,* optical section of micropyle, longitudinal.

Thus, the eclosion fracture most probably will be a rosette, instead of a longitudinal line. The relatively thick shell (about 7.5 μ in diameter) looks striated in sections; this is due to closely packed canals of roughly one μ diameter. What may be the follicular lining, is a very irregular design which is, peculiarly, made up of one series of sheer pore-canals, which are a little wider than the common pores.

Diaprepocoris zealandiae

Oviposition and egg-shape (fig. 216C) is much as in *Micronecta*. The anterior pole is flatter and bears a circular transparent area with two, rarely three micropyles.

CHORION The micropyles pass through vaguely defined outer projections, which are stuffed, both inside and outside, with flocculent chorionic substance (fig. 217A). The central canal, when traversing the shell, measures about 2 μ. The perimicropylar area has a faint circular design (fig. 217C) and some maceration-breaks suggest that this area opens like rays at eclosion as in Corixinae and Cymatiinae. The straight porous band, occurring in *Micronecta*, is here lacking altogether. The shell is regularly covered with large (8–10 μ) pits, from the arrangement of which no hexagonal pattern is apparent. Each ring of 5–7 of these large holes, however, has one single minute pore in its centre, suggesting this pore represents the print of the middle of one follicle cell (fig. 217B). If so, the shell must be the product of many small follicle cells. The entire thickness of the chorion measures about 20 μ along the fore side of the egg. A continuous porous inner layer seems to be lacking. From the bottom of the wide pits, fine canals branch interiad, but the branches of one pit remain separated from the others (fig. 217B, cbe).

EMBRYOGENESIS Some gross embryonic stages do not show more primitive conditions than in other Corixidae studied. From the beginning of invagination, the germ band moves along the surface of the yolk forwards, and the superficial position is retained throughout (fig. 216A–C). Although our observations are not quite conclusive due to inadequate fixing and staining of the sample, we gained the firm impression that the posterior pole possesses a serosal hydropyle. At the anterior pole, no trace of cell clusters could be detected but the micropylar spot leaves a print behind on the underlying serosal cuticle. In all eggs with revolved embryos, fully grown or not, the embryo's ventral side faced the convex fore side of the egg. It is therefore concluded that revolution takes place simultaneously with a 180° rotation, as occurring in other Corixidae.

Cymatia coleoptrata

The dorsal and ventral sides of the balloon-shaped egg are readily recognized by their differences in convexity, the most convex side being the fore side. The micropylar area is flat without a nipple. The egg is attached to the substrate by a long transparent

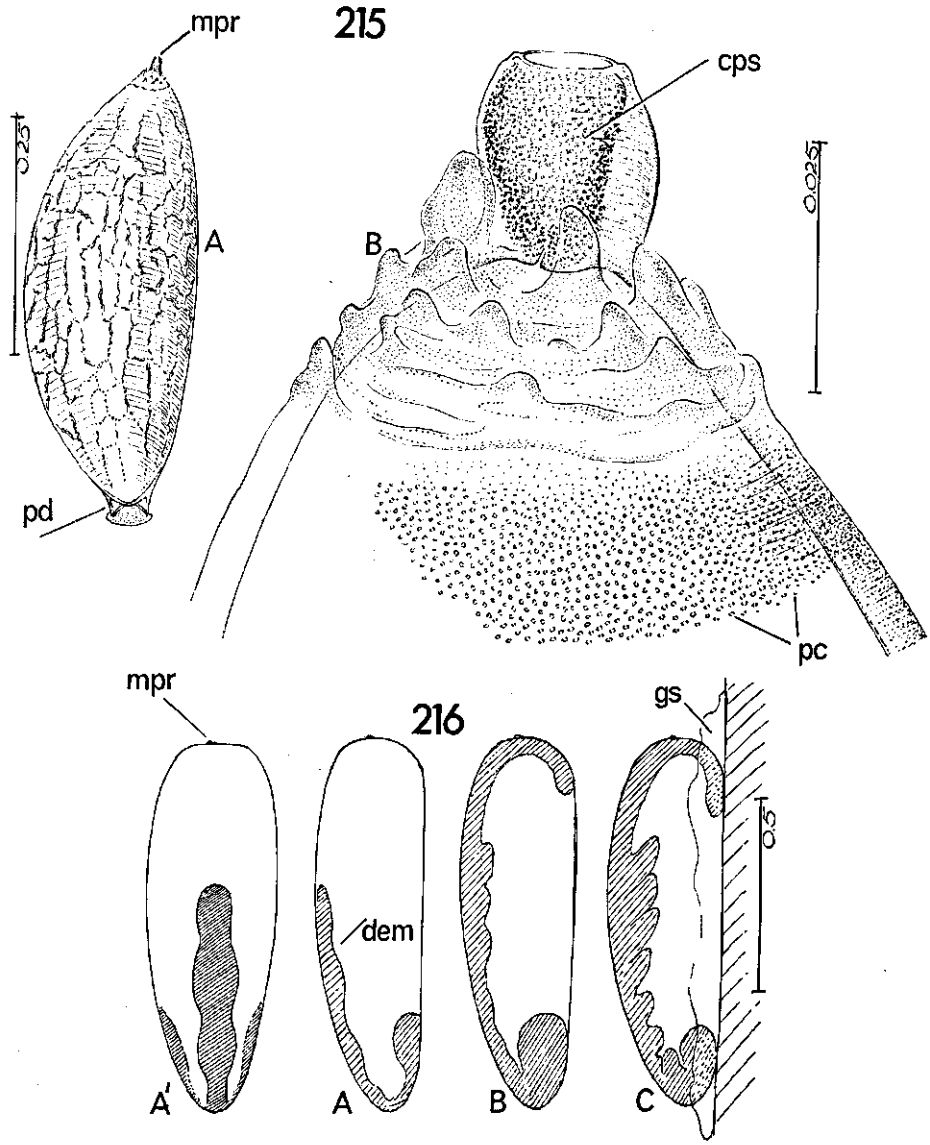


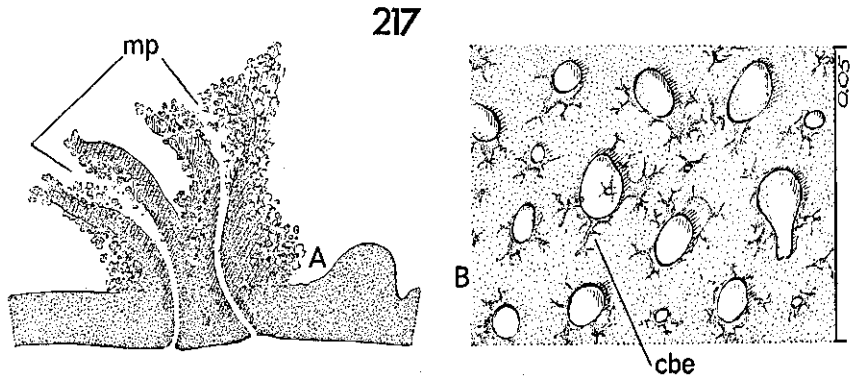
Fig. 215–216. Corixidae 215. *Tenagobia incerta;* A: ovarian egg, lateral; B: anterior pole. 216. *Diaprepocoris zealandiae;* A–C: early embryogenesis, lateral; A′: fore side.

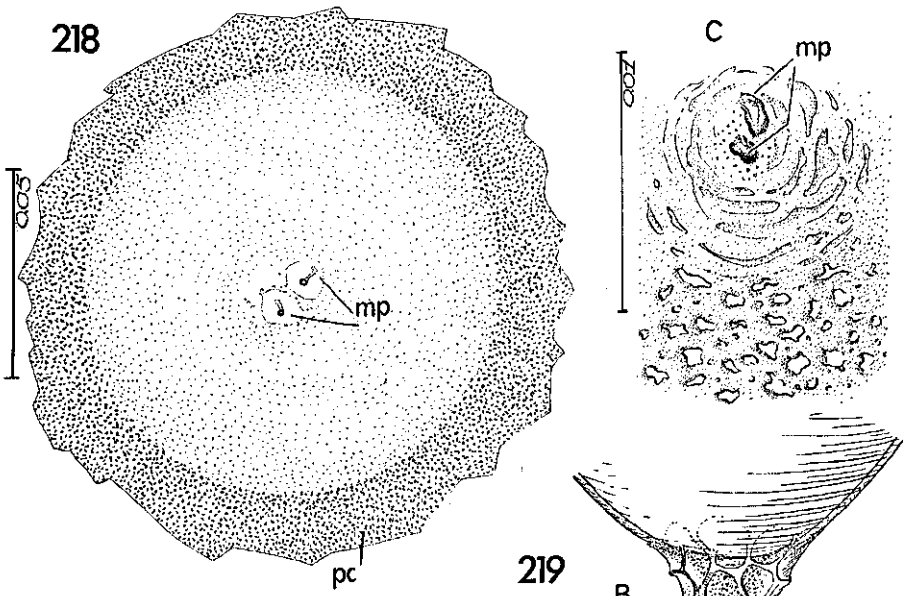
stalk, which is as long as the body of the egg (fig. 220). The incubation time of *C. coleoptrata* is distinctly longer than that of the Corixinae studied.

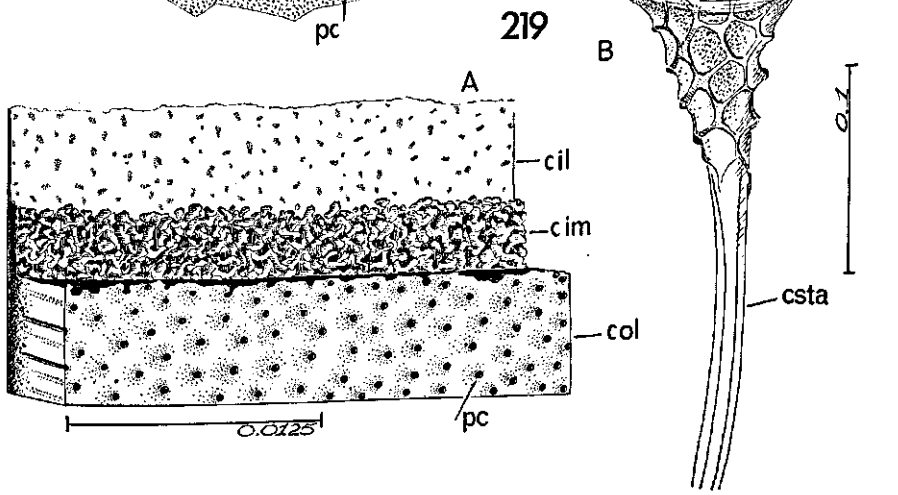
CHORION No trace of hexagonal reticulation is present except at the extreme posterior pole in the transitional zone to the stalk (fig. 219B). The egg shell is uniform in structure throughout and coarsely porous in the inner layer, giving it a felty appearance visible even with low magnification. The total thickness of the shell amounts to 11 μ. The outer surface is regularly and densely pored; the openings, about 0.5 μ wide, give entrance to perpendicular canals (fig. 219A, col). These canals communicate with the open spaces of a thick inner meshwork (fig. 219A, cim). The meshwork has an inner lining of a very thin sheet, in which irregular patches are seen with the optical microscope (fig. 219A, cil). Perhaps these patches are merely thinner than the rest of the sheet. Two micropyles seem to be constant in both *Cymatia* spp. studied. In *C. bonsdorffi*, the outer opening hardly measures 1 μ and from this projects a short canal obliquely interiad (fig. 218). Each micropyle is found within a small confined area, probably derived from a single follicular cell. The neatly circular field, in the flat centre of which lie the micropyles consists only of the inner part of the chorion, which is here more finely porous than elsewhere. The stalked, hyaline pedestal seems hollow. It consists entirely of chorionin; the egg contents do not extend into it. The inner porous layer of the shell extends some distance into the upper widened part of the stalk (fig. 219B). The surface here bears distinct ribs and faint pores. Further downwards the stalk represents a smooth thick-walled pipe with a discoid base, attached to the substrate by an adhesive. There was no evidence that the pedestal should function as a chorionic hydropyle.

EMBRYOGENESIS AND ECLOSION Development, arrangement of the appendages and the mechanism of hatching are similar to those in the Corixinae (see next species for a fuller account). A distinct hydropyle could not be detected. As nearly all hairs of the prolarva remain pale, its pose is difficult to unravel. The two orange dorsal glands, the black hind claws and some very long black hairs at the abdominal apex serve as landmarks (fig. 220). These black hairs cross over alongside the lateral border of the abdomen on the same manner as the hind legs. The shell splays open under the pressure of the water-filled serosal cuticle (fig. 220B). Each of the chorionic flaps bears a part of the thin circular polar region. The small central piece with the micropyles remains attached to the aft flap (fig. 220D, E, ps).

Fig. 217–219. Corixidae 217. *Diaprepocoris zealandiae;* A: longitudinal section of the micropylar plug; B: outer aspect of chorion; C: micropylar area from above. 218: *Cymatia bonsdorffi*, micropylar area from above, ovarian egg. 219: *C. coleoptrata;* A: diagram of the shell stratification; B: transitional zone of the egg into the basal stalk.


217
mp
A
B
cbe
0.05


218
0.05
mp
pc
C
mp
0.02


219
A
cil
cim
col
pc
0.0125
B
0.1
csta

Corixa punctata

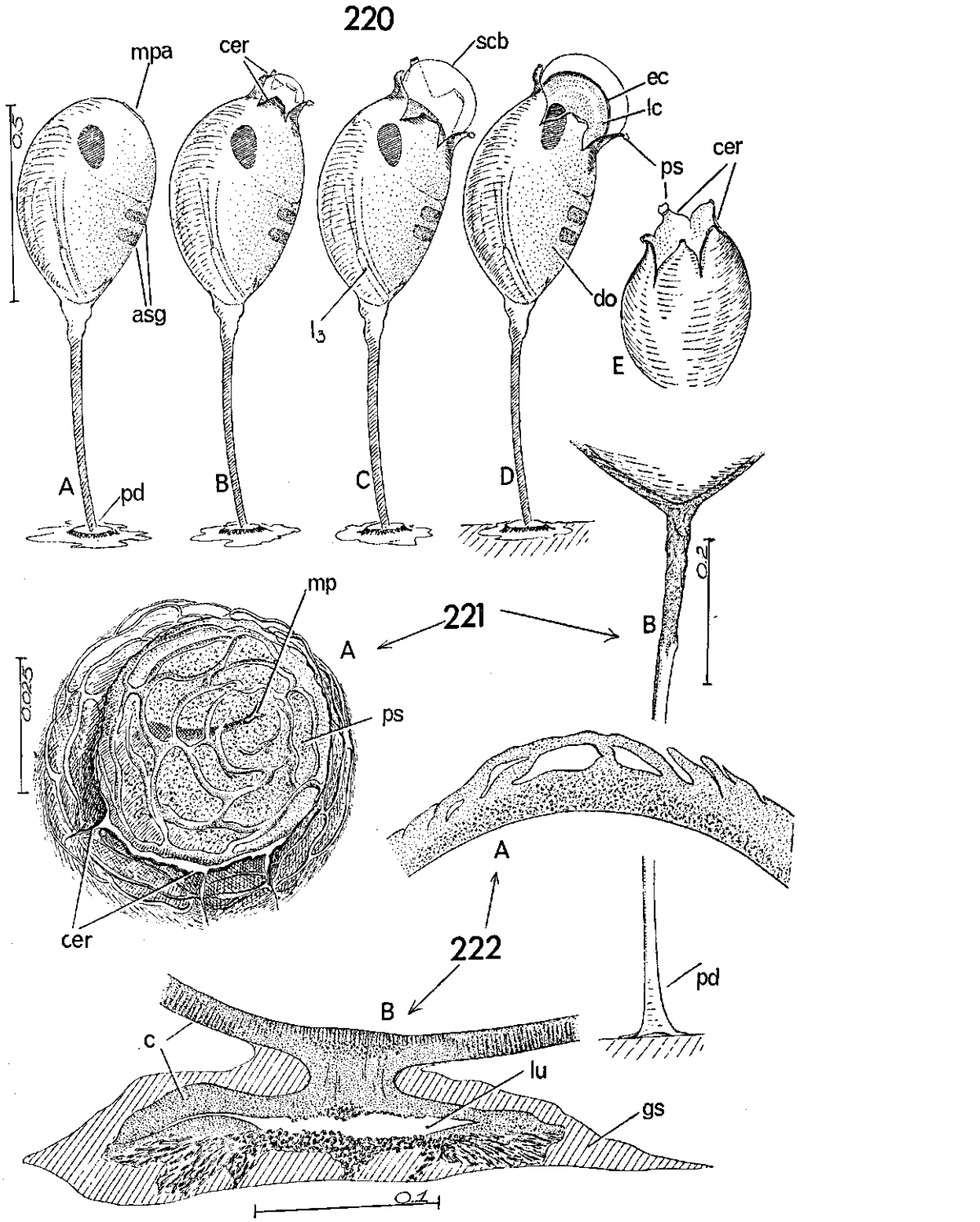
Eggs are pyriform and affixed with their long axis nearly normal to the substrate by a small, sessile pedestal (fig. 226D). The slightly pointed anterior pole is marked by an apical white plug. A transverse section from this plug towards the basal disc would divide the egg into two unequal halves. This inequality is not markedly changed during incubation. The half which has the most convex profile is distinguished as the fore side of the egg. The embryo's venter fills it after revolution.

CHORION The shell is about 15 μ thick basally and apically and reaches a thickness of about 22 μ at the greatest width of the egg. The shell is smooth but the egg being just laid often bears transverse wrinkles around its waist and longitudinal grooves towards the top. Surface-views exhibit a faint but densely punctured facies. A faint hexagonal pattern results from variation in density of the punctures but some eggs have a clearer hexagonal lining. The optical microscope shows little differentiation in the cross-section of compact chorion. In one 10 μ thickly sectioned egg it looks distinctly two-layered along the middle of the egg. The outer layer, 5 μ thick, seems more or less porous through a dense faint cross-striation. These lines communicate with a narrow irregular space between the outer layer and the compact inner layer which is more than three times thicker (fig. 223B). In another egg cut into slices of 4 μ thick, we cannot distinguish between two layers and the striation seems to run nearly across the whole section. This condition seems to be normal, as is indicated by the transmission electron microscope. The punctures are real pore-canals which vertically penetrate the whole dimension of the shell (fig. 302C). Along the inner wall of the shell they join a thin porous layer, lined by a fine chorionic sheet. The interspaces are probably all filled with water under natural conditions. This architecture strongly resembles that of the *Gerris* shell.

The micropyles are obscured within the white plug at the top. Unripe ovarian eggs show their number and arrangement clearly. There are only two to four, usually three tiny pores (1.5 μ wide) in the centre of a rosette-like railing structure (fig. 224). In unripe ovarian eggs of the closely related *C. panzeri*, each micropyle forms the central axis of a thick-walled chorionic 'cell' (fig. 225). In this incomplete state of shell formation, the micropyles represent only pores without an inner projection. The exact course of their outer canal, which is formed later, becomes completely hidden in the surrounding chorionic structure of a remarkable constellation (fig. 223A). To understand the latter structure in deposited eggs, see again fig. 224 with the basic plan in young ovarian eggs. The normal hexagons are flattened out transversely towards the micropylar region, as is normal in eggs with a true operculum (*e.g. Miridae*). In Corixidae we have to suppose that the follicular cells at the base of the dome-shaped

---

Fig. 220–222. Corixidae 220. *Cymatia coleoptrata;* A–D: initiation of hatching; E: vacated shell. 221. *Agraptocorixa hyalinipennis;* A: micropylar area from above; B: stalk. 222. *Corixa punctata;* A: transverse section close to micropylar plug; B: longitudinal section of pedestal.


220
mpa
cer
scb
ec
lc
ps
cer
0.5
asg
l_3
do
E
A
pd
B
C
D
0.2
mp
221
A
B
0.025
ps
A
cer
222
pd
B
c
lu
gs
0.1

top region of the eggs are transversely dilated. The common boundaries of these cells secrete much more chorionic material which on cross-section is revealed by thickly packed vertical scales (fig. 222A, 223A). Higher up at the dome the cells are not so flattened but they are irregular in outline. These cells seem to produce compact chorionic material only along their boundaries. In young ovarian eggs, not treated with any chemical agents, the areas between the ribs seem to be completely open. At the inner side these frames are assumed to be lined by a transparent very thin chorionic sheet. Upon the solid ridges, equally thick branches are later deposited exteriad which ramify to the sides to meet each other. The resulting open grating soon, if not already, becomes filled with porous material. This substance is white and as it protrudes from the supporting solid framework it exhibits altogether as a white nipple. Longitudinal sections through the plug indeed reveal that the porosity between the solid ribs goes down to the inner limit of the shell (fig. 223A). The inner porosity of the nipple approaches or just touches the spaces in the rest of the shell. Just beyond the outer scales of the apparatus in question (fig. 223A, crw), a thin zone of the chorion seems rather spongy throughout its diameter. The actual texture is not readily resolved with the optical microscope. When eggs are softened in potash, the circular micropylar area completely separates from the shell along this weak ring without affecting the nipple proper. This artificial fracture partly coincides with the normal eclosion fracture (see under eclosion).

The section (fig. 222B) shows the structure of the pedestal. Its base consists of granular and fibrous material and it is attached to the substrate by adhesive. The stem connecting the disc with the actual egg seems massive. Corixid eggs absorb much fluid water. This water plays a decisive role in breaking the chorion and subchorionic membrane during eclosion. A basal stalk in some other Hemiptera is known to act as a hydropyle and hydropyles so far detected in Heteroptera are at or near the posterior pole. The shell around the pedestal attachment is in *Corixa* striated from the outside as far as the inner layer. But, just above the attachment the striation is seen only in the inner layer of the shell. The inner striation joins a zone of greater porosity in the centre of the region where the stem fuses with the actual shell. Although a direct passage of water cannot be resolved optically, it might be present. In the much thicker chorionic hydropyle of *Nepa*, HINTON (1961) could not detect spaces or canals in the inner zone. He showed, however, that water does traverse this zone. In *Corixa*, embryogenesis strongly suggests that the water-absorbing organ is located beneath the micropylar area; a serosal hydropyle in the basal region of the egg was not found. In *Ilyocoris* (p. 214) it is near the anterior pole.

GROSS EMBRYOGENESIS The germ band appears first along the aft side of the egg and involutes at the posterior pole; the blastopore faces the pedestal (fig. 226A). From there, the band, which is rather vaulted longitudinally (fig. 226A'), elongates obliquely to the fore side across the yolk. Soon it rests entirely against the fore side (fig. 226B–C) and lengthening continues around the anterior pole. In gross view no germ cells were traced at the distal end of the band. The tail curves back far along the aft side. At

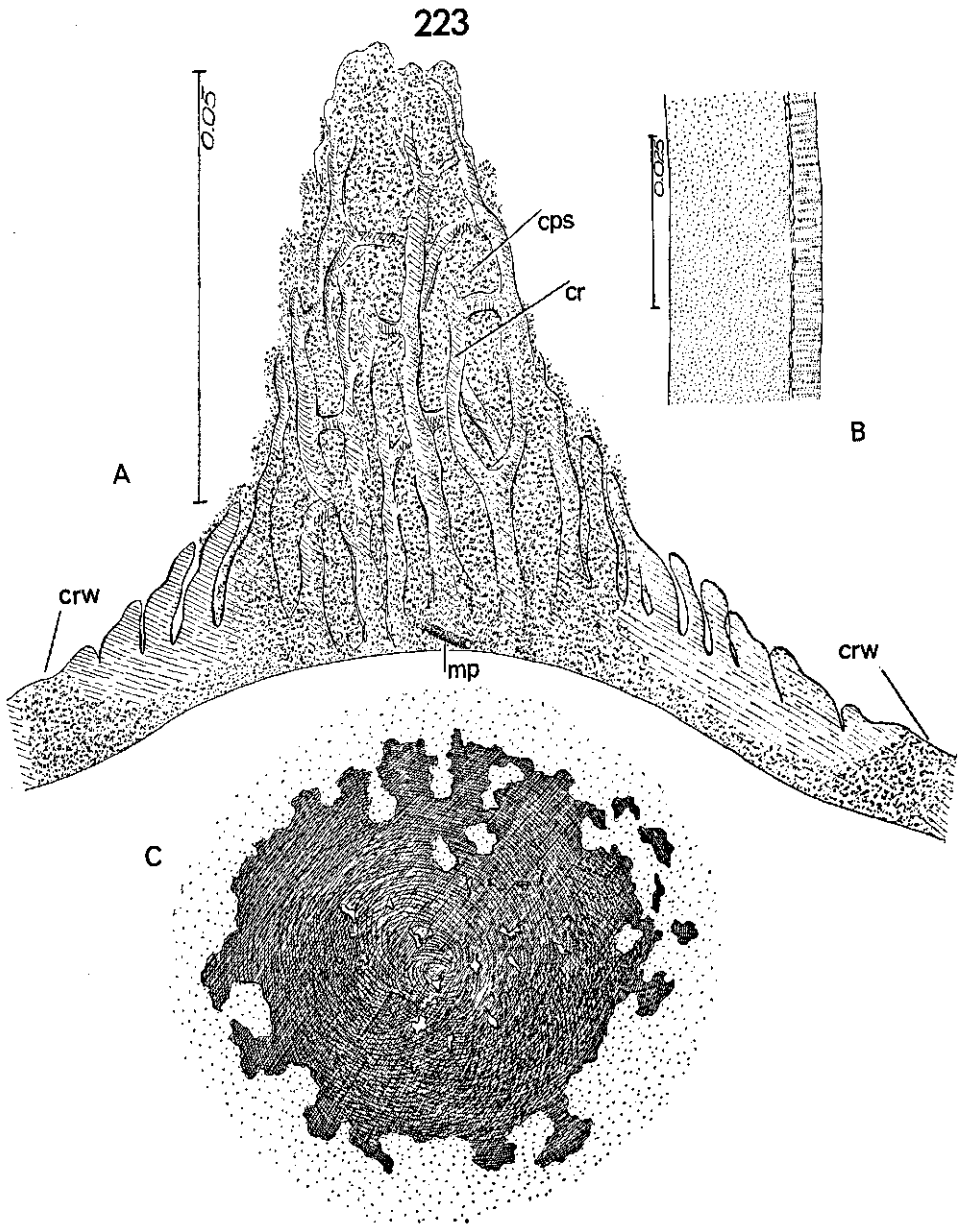


Fig. 223. Corixidae, *Corixa punctata;* A: longitudinal section of micropylar plug; B: longitudinal section, mid region of shell abnormal stratification (see micrograph fig. 302C); C: submicropylar part of serosal cuticle, plane view.

maximum elongation, the tail is near the head of the germ band (fig. 226D). Meanwhile the thoracic appendages have begun to bud. They initially point laterally round the convexity of the shell. This gives the impression that the ventral side of the band faces the yolk (fig. 226E). In fact it is the ventral side which borders the shell without any yolk between. At this stage, the serosal cuticle, which is secreted earlier, commences to darken under the chorionic nipple. When this part of the serosal cuticle is removed, the outline of a circular frayed black area becomes readily visible (fig. 223C). No pores or prints of micropyles on this membrane could be detected. The germ band now shortens and the first four legs become folded along the venter. The metathoracic legs still bend sharply to each side but eventually come to lie side by side under the micropylar region, where thick serosal cells have appeared (fig. 226D, E″, sh?). In other eggs, we termed such a cluster of enlarged cells in the same place: the serosal plug. But, in nearly all other eggs we have already described, this plug results from serosal contraction during revolution of the embryo. In *Corixa*, the plug exists long before this process, suggesting a special function with the chorionic nipple, which may be hydropylar. Hydropic cells near the posterior pole have not been detected. MECZNIKOW (1866) reported thickened cells in this region but BRANDT (1869) did not find them.

Revolution of the embryo is by a spiral movement as indicated by the arrow in fig. 226F. The embryo moves upwards first along one lateral side of the egg and soon finishes with its venter along the fore side but now in the reversed position. The eyes turn red after blastokinesis.

The posture of the mature embryo is peculiar because the head is pressed aft with the clypeal region underneath the nipple-structure (fig. 226G). The first two pairs of legs lie side by side in a straight line; the long mid legs follow the curve of the posterior pole and approach the head from the other side (fig. 226G, 1_2). The hind legs are bent distally and cross each other under the preceding legs (fig. 226G, 1_3 and fig. 280R). In the eight eggs studied, it was always the left hind leg which remained entirely latero-distal. The right hind leg has an inner course and its end passes beneath the base of the left middle leg. Thus only one of the two asymmetric positions seems to be realized. In other families of water bugs we will find a similar significant dominance in larger samples.

ECLOSION Rupture of the chorion is explosive. It bursts open under the pressure of the serosal cuticle, which suddenly bulges out of the aperture as a tough bladder (fig. 226I). The tapered top of the shell is now broken up usually into six flaps which are forced to stand out like sepals. The spherical region with the nipple remains attached to the top of one of the flaps. In fact, this very small nipple should be considered as the actual pseudoperculum. Because of its weak circular boundary it loosens first from the shell. The aperture is too small to let the prolarva through. The chorionic cone is simply widened by the swelling serosal cuticle and it eventually splays open. The cracks were not existing lines of weakness. Maceration of the eggs never yielded a petaloid fracture. Once the voluminous serosal cuticular bubble has appeared, the

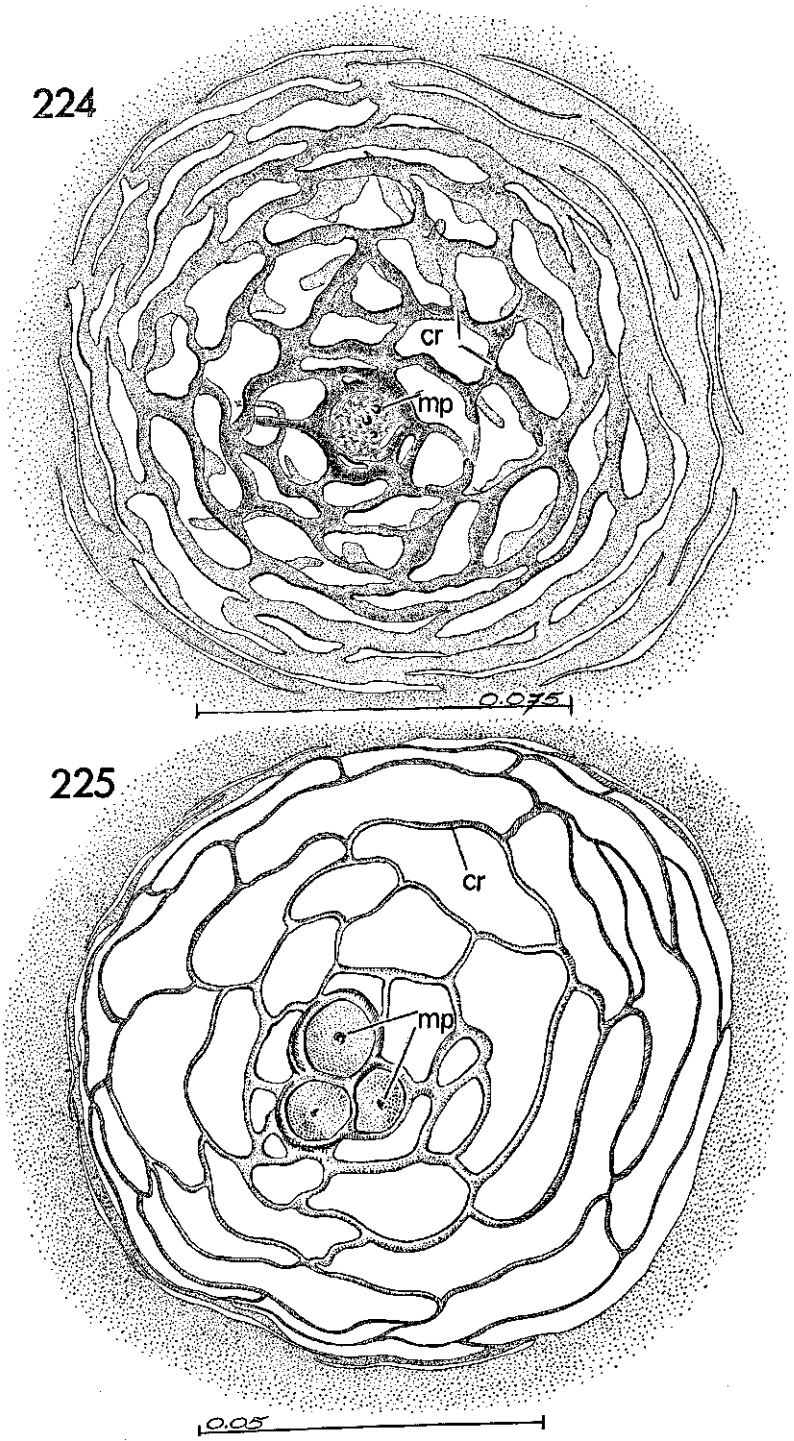


Fig. 224–225. Corixidae 224. *Corixa punctata*, inner view of micropylar area (nearly ripe ovarian egg). 225. *C. panzeri*, outer view of micropylar area (unripe egg).

prolarva does not move. The bubble is filled with liquid, probably mainly water. The prolarva now starts to absorb this liquid and its size steadily increases at a visible rate. Still within the embryonic cuticle, the head rises through the chorionic calyx, until it fills the vesicle. This situation is through expansion by liquid uptake rather than by active movement of the prolarva itself. The whole lumen of the egg, even the posterior pole, remains occupied by the prolarva. When the serosal cuticle is entirely filled, some minutes may elapse before the final exit ensues. The tension in the head region rises and both membranes, the serosal and the embryonic cuticle, burst longitudinally and consecutively. During the whole hatching manoeuvre the front pulsates steadily. No reinforcement could be detected on the embryonic cuticle. A peculiar property of the hatching larva of Corixidae is the fact that its hairs and spines initially are pale. Even the darkening of the skin precedes that of the setae. In most other Heteroptera and in other water-bug families the hairs darken when the larva is still within the egg.

With one exception described below, the other Corixinae studied do not differ in essence from above.

Agraptocorixa hyalinipennis

The adhesive disc is a long stalk of the same structure as in *Cymatia* (fig. 221B). The chorion of the actual egg seems solid, but very faint points might represent a canal system. The micropylar area is distinguished from other Corixinae eggs we have seen by its single micropyle, which is well marked and bears a dark projection inside the egg (fig. 221A).

PREVIOUS DESCRIPTIONS The outline of corixid eggs has been described by several early authors, *e.g.* DUFOUR (1833), RATHKE (1861, erroneously under *Naucoris cimicoides*), MECZNIKOW (1866), BRANDT (1869), BUTLER (1923), TEYROVSKÝ (1924). LEUCKART (1855) found only one micropyle in *S. striata* and *S. nigrolineata;* this error was corrected by POISSON (1933). In the egg of *Micronecta meridionalis* POISSON overlooked the longitudinal porous cleft, which starts from the micropylar plug. He stressed the presence of long filaments on the exposed side (his fig. 31), which according to him are porous and probably serve for respiration. This spikiness of the egg is copied by SOUTHWOOD and LESTON (1959). WRÓBLEWSKI (1958), on the other hand, illustrated the egg of the same species without projections. Our own observations, mentioned above, confirm this view. The shell has no differentiation whatsoever, which could eventually grow out as spikes. It seems therefore doubtful whether the filaments, described by POISSON, were constituents of the shell. Possibly they represented fungal growth, as is suggested too by WRÓBLEWSKI *(in litt.)*, or POISSON had another species. The egg of *M. quadristrigata* Bredd. has indeed short tubular projections each arising from the centre of a polygonal area (FERNANDO and LEONG, 1963). BANKS (1939) described the egg of *Arctocorisa germari* and HUNGERFORD (1948) devoted a paper to corixid eggs and decribed 30 species. The eggs of *Tenagobia selecta* and

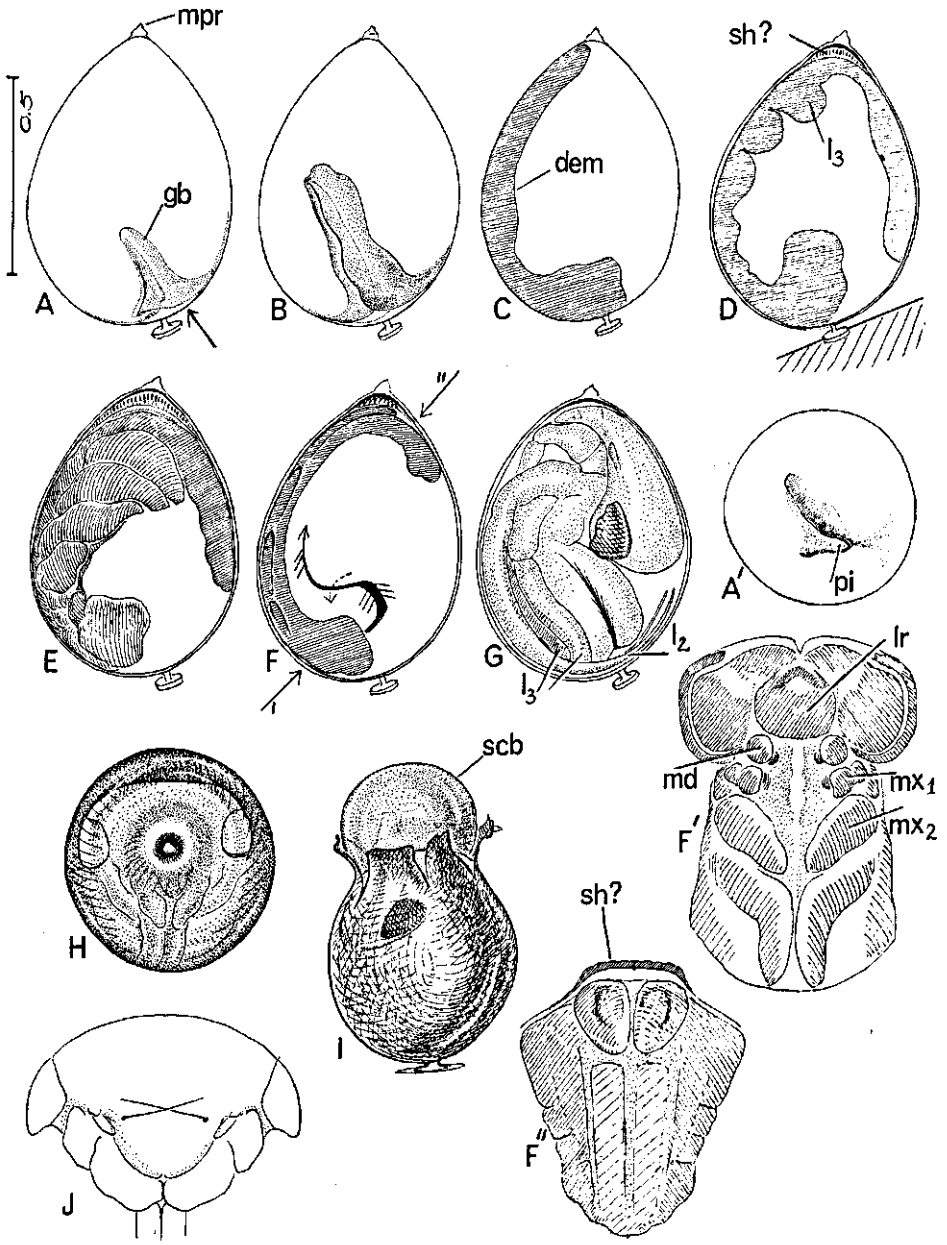


Fig. 226. Corixidae, *Hesperocorixa linnei;* A–F: embryogenesis; A′, F′, F″: represent views according to the respective arrows in stage A and F; G: prolarva, lateral; H: from above; I: break of the chorion; J: prolarval head.

Cymatia americana are long-stalked as are those of two *Heterocorixa* spp., which belong to a separate subfamily. Unlike our European *Cymatia*, *C. americana* bears a micropylar plug. The egg of *Stenocorixa protrusa* Horv. is shaped like that of *T. incerta* (described above). HUNGERFORD erected a new subfamily for the single species of *Stenocorixa*, which combines several primitive features. The chorion of this species is minutely pitted, a property otherwise found in only two *Krizousacorixa* spp. among the 30 species studied by HUNGERFORD. From our examination above, we conclude that the most primitive species generally have the greatest shell-porosity. The long-stalked condition appears to be characteristic for other *Agraptocorixa*-eggs: *A. hyalinipennis* (FERNANDO and LEONG, 1963), *A. eurynome* Kirk, and *A. hirtifrons* Hale (HALE, 1924), and *A. gestroi* Kirk. (WALTON, 1962). Thus the literature seems to have quite a bit of information on Corixinae eggs. However to straighten out phyletic lines, more detailed information is needed on the shell and micropylar structures.

The gross embryonic development of an unidentified species (probably *Sigara* sp.) has been studied by MECZNIKOW (1866) and BRANDT (1869). The quality of these contributions and the excellent illustrations compel the greatest respect. Our account of the gross embryogeny upholds in large measure the findings of these pioneers, except in one major point. Both authors thought that the embryo revolved upwards along the shell-side, opposite to where it was before blastokinesis. MECZNIKOW thought that the convexity of the shell becomes modified under pressure of the revolving embryo. BRANDT resolved the supposed absence of rotation by the fact that the corixid embryo had already assumed a superficial position before blastokinesis. In the eggs of other insects he studied, he thought rotation was necessary for the embryo to escape from the immersed position. In our presentation above it is clearly shown that the outline of the most convex side remains constant. The embryo actually does undergo rotation, which results in a spiral course, since it interferes with the upward movement.

The eclosion fracture of the chorion in some Corixinae has been described by HUNGERFORD (1919, 1923), WEBER (1930), POISSON (1933), JORDAN (1937), GRIFFITH (1945), LEBRUN (1960), and DAVIS (1965). The two first authors and the last one noticed the appearance of the transparent bladder just after the chorion broke. HUNGERFORD mistook this membrane for the embryonic cuticle.

2.4.2 Nepidae

MATERIAL: *Nepa rubra* L., *Laccotrephes calcaratus* Mont. and *L. fabricii* Stål (origin Ivory Coast); *Ranatra linearis* L., *R.* sp. group *capensis* Germ., *R. parvipes vicina* Sign. (the last two from Ivory Coast).

Of *N. rubra* live deposited eggs; of all other species preserved deposited eggs.

The following survey applies to all species, since there were no essential differences except in the mode of oviposition in the *Ranatra* spp. from Africa (see p. 204).

CHORION HINTON (1961) made a comprehensive study on the structure and function

of the nepid egg-shell. This excellent work compares the eggs (mostly ovarian) of 16 species belonging to half of the known genera. Relevant points from HINTON's survey will be discussed only where they accord with our more fragmentary data on the eggs of other families.

The eggs of the familiar *N. rubra* (fig. 229D) and all other nepids studied are characterized by some long respiratory horns, 2 in Ranatrinae and 4 to 26 in Nepinae. The central core of each horn consists of a fine meshwork surrounded by a coarser meshwork. This porosity opens to the atmosphere through a peripheral plastron, mostly confined to the top of the horn (fig. 229D, pla). Basally, the meshwork of each horn joins the meshwork of the inner layer of the shell. This open system, surrounding nearly all the egg, is filled with air and remains so, even when the egg is entirely under water, due to the plastron of the horns. The inner meshwork of the shell which is about 25 μ thick is not 'unicellular' but represents a porous layer nearly 10 μ thick with more coarse interstices outwards than in the inner zone. The meshwork is absent in the central area between the horns, around the micropyles and at the hydropyle. Many thousands of aeropyles, mostly branched, are dispersed over most of the shell and extend from the surface to the inner meshwork. HINTON thinks that they are of only minor importance in transporting oxygen but that they provide a short cut for the escape of carbon dioxide. Their disadvantage is the possibility of rapid desiccation and this could be significant. The egg fills with air after it has left the common oviduct. HINTON forced females to lay below water level and their eggs remained waterlogged. Normally the respiratory horns project above water and the plastron is functional only when it is raining heavily or when the air-filled horns submerge.

Just aft of the posterior pole, an oval parchment-like area is found (fig. 229D, ch), which is slightly raised above the general surface of the egg and which represents a complex chorionic hydropyle. In the middle of its cross-section, this structure consists of a coarse meshwork and conducts fluid to the inner chorion. HINTON found that the inner surface of the hydropyle has openings large enough to permit the passage of water, although these ducts could not be distinguished optically.

The two micropyles are in a small transparent spot medially just behind the ring of horns in *N. rubra* (fig. 229D, mpa). In other Nepinae, HINTON found two to five, in the Ranatrinae three to six micropyles. The funnelled canals are relatively minute and they penetrate the chorion obliquely posteriad. The canals have a diverging course entad and, if there are four micropyles, their outer openings lie in a semicircle (fig. 228, 229A).

A viscous substance, produced in the ovarioles and deposited on the outside of the shell and also between the horn bases, functions as a cement coat. As it is hygroscopic, it could also serve to regulate humidity.

GROSS EMBRYOGENESIS The following account on early development is based on many hundreds of eggs of *Ranatra linearis*, deposited in a single 4-inch long stem of a waterplant and stored for more than 30 years in alcohol. Staining with borax carmine proved not satisfactory but two days treatment of the eggs in cold 10% potash and

their subsequent transfer into lactic acid made details of the germ band visible (fig. 230A–F). We also studied the preserved eggs of other Nepidae and they revealed an identical course of events.

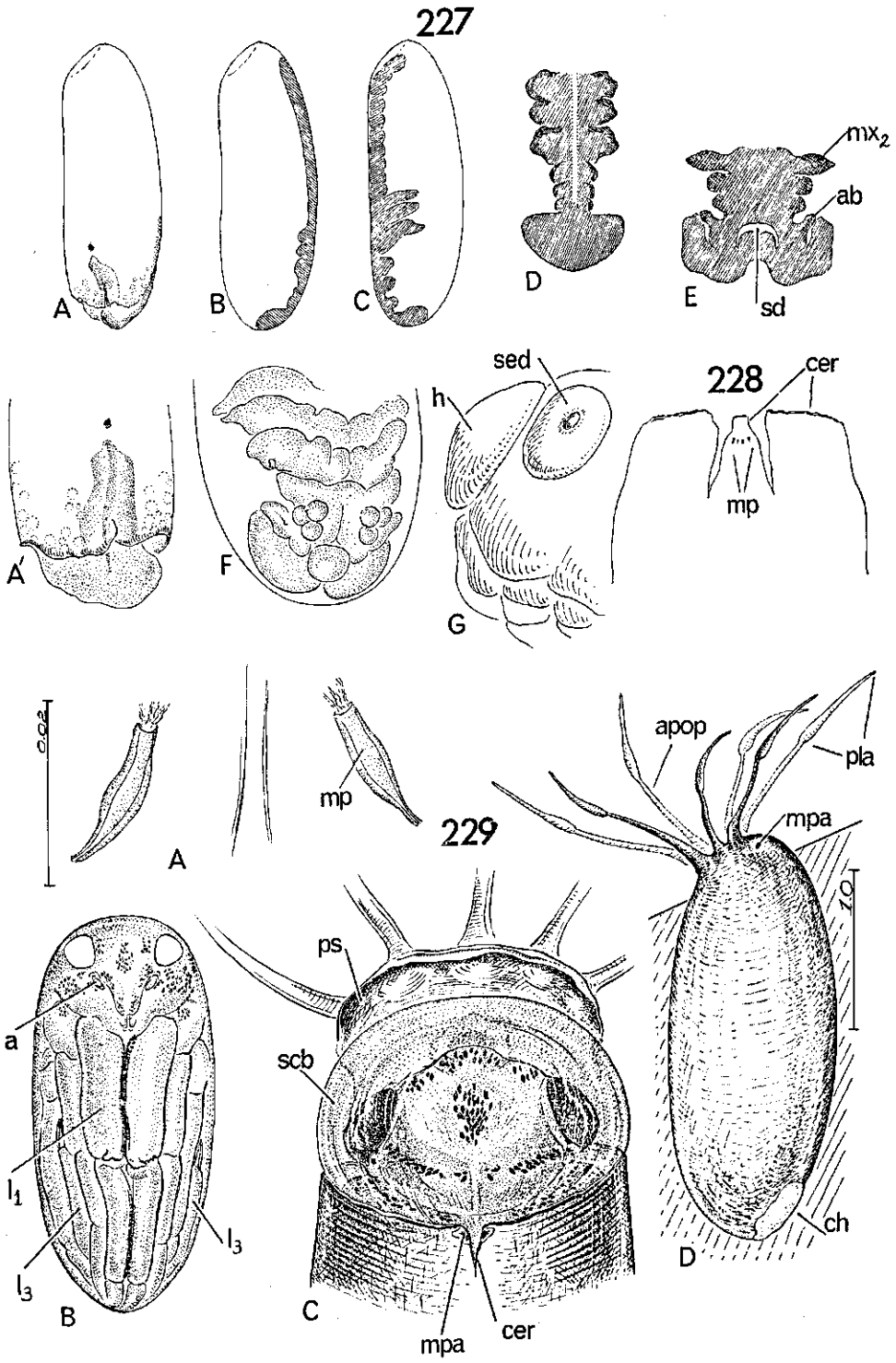
Invagination of the germ band of *Ranatra* occurs posteriorly along the fore side of the egg (fig. 230A, pi). In *Ranatra* this side is more convex than the aft, but in *Nepa* and *Laccotrephes* the differences in convexity are reversed. In the first stage of involution, the embryonic rudiments in the blastoderm on the opposite side already reflect the basic embryonic pattern, complete with protocormic outgrowths (fig. 230A, B and A″). This is in great contrast with nearly all previously treated groups, in which at most vague cephalic plates can be recognized as blastodermal thickenings. However the early differentiation in Nepidae and further features in the embryogeny offer some striking points of contact with certain groups of Reduviidae. Because of the differentiation the involuting band of *Ranatra* is provided from the onset with thoracic buds (fig. 230C). The prothoracic ones, giving rise to the grasping legs, are larger than the other pairs (fig. 230D, D′). This initial allometry is entirely confined to a much wider base of the first limb than of the others. The band grows upwards and at maximum length reaches nearly the anterior pole, meanwhile the blastopore shifts posteriad. It is difficult to conclude that the ventral side of the band faces outwards; in fact the general picture seems the opposite. Despite some isolated drops of yolk between the abdomen of the band and the exterior envelopes, the embryo as a whole is superficial. Dorsally on the extreme top of the tail a definite group of cells, most probably the germ cells, could be traced in stages A–E (fig. 230). In stages D–F moreover a much smaller group of unknown origin is found going in front of the band's tail and entirely isolated from it. In *Nepa*, such isolated cells are already present at the beginning of involution (fig. 227A), which process takes place more posteriorly than in *Ranatra*. Further embryogenesis of both species is identical. A batch of *Nepa* eggs was incubated at 30 °C. Development at such a high temperature was anomalous (fig. 227B) and none of the eggs developed further.

A serosal cuticle is present in the stage, when the fore leg makes a characteristic bend forwards (fig. 230F) and thus it is secreted about the previous stage E. Unlike the eggs of other hydrocorisous families, the serosal cuticle remains pale in Nepidae.

Blastokinesis comprises a half rotation and an upward movement. The embryo glides along the posterior pole and crosses obliquely round the left side to reach the fore side of the egg, which it faces now in a reversed direction. This position is unchanged until eclosion. The eyes turn red after blastokinesis. The serosal plug occupies the whole anterior division of the egg and prevents the head from reaching the anterior pole for some time. The uptake of the serosal plug to form the dorsal organ (fig. 227G,

---

Fig. 227–229. Nepidae 227. *Nepa rubra;* A–F: some stages before blastokinesis; B: abnormal position of germ band; G: anterior part of embryo after revolution. 228. *Ranatra linearis*, rupture of shell, aft side. 229. *Nepa rubra;* A: micropylar area; B: prolarva, enveloped by the serosal cuticle; C: hatching, the contents of the serosal cuticular bladder is swallowed by the prolarva, aft side; D: egg, lateral view.


227
A
B
C
D
E
mx2
ab
sd
A'
F
sed
h
G
228
cer
mp
0.02
A
mp
229
apop
pla
mpa
0.1
a
l1
l3
l3
B
ps
scb
C
mpa
cer
D
ch

sed) is rather rapid. The similar process in *Notonecta* will be described in more detail (p. 224).

ECLOSION The basic arrangement of the appendages of the prolarva of *Nepa* is as in Corixidae. Fig. 229B shows the arrangement, which has been encountered only in 16% of the 74 eggs checked on this subject. The other 84% showed the mirror-image (fig. 280Q), in which the right hind leg finishes between the bases of the left middle and hind leg. The rudimentary conical siphon is bent double against the posterior pole. Noteworthy are the dark scale-hairs, which are visible through the chorion. The primary hairs are very fine and long, but are not seen in this situation through lack of dark pigment. The mechanics of eclosion is apparently as in the Corixidae. First, an enlarging transparent and fluid-filled bladder breaks the anterior region of the shell. An irregular circular area bearing the respiratory horns is lifted and the first break occurs at the aft side. There is no chorionic sealing bar or a thickened ring on the serosal cuticle. The rest of the actual shell always splits a short distance across the micropylar area (fig. 229C, cer). In *Ranatra*, there are two splits, one on each side of the micropylar field (fig. 228). Once the empty serosal cuticular bladder reaches the extent depicted (fig. 229C), its interior slowly fills with the prolarva as it swallows fluid. Later rise in pressure in the anterior region of the prolarva helps to burst the serosal and embryonic cuticles longitudinally. Whereas on all segments of the latter membrane a very fine transverse sculpture occurs, the head is completely devoid of any burster-like differentiation.

The four African species studied added nothing, since the chorionic structure and the gross embryogeny conform to the general plan of the family. One striking observation on the two *Ranatra* spp. must be stressed as it reveals another serious problem about egg respiration. Whereas the European species and also the two African *Laccotrephes* do not develop when they are completely submerged from the beginning, the eggs of the two *Ranatra* species actually did. Moreover, in aquaria all the many females, hanging head down, inserted the eggs consistently far below water level. Even when bugs had ample opportunity to deposit eggs in wet soil or floating material, they never did. Incubation and hatching passed in a normal way (about 8 days at 25°–30°C). The extremely long respiratory horns, which point downwards into the water (fig. 231) never came in contact with atmospheric air. Still, they seem normally constructed, bearing a plastron over the whole surface except the most proximal 0.2 mm. Scanning-electronmicrographs show the fine porosity in the middle of the horn (fig. 308) and one ring of wide pores round its apex (fig. 307). Unfortunately, we had no opportunity to check on the spot whether the inner layer of the shell has been filled with air. We doubt it, since in the European species the air enters the egg after delivery from the female. The pools, from which the species were collected in the Ivory Coast, were completely covered with a dense carpet of *Pistia* (see p. 281).

PREVIOUS DESCRIPTIONS SWAMMERDAM (1737) illustrated the eggs of *Nepa rubra*

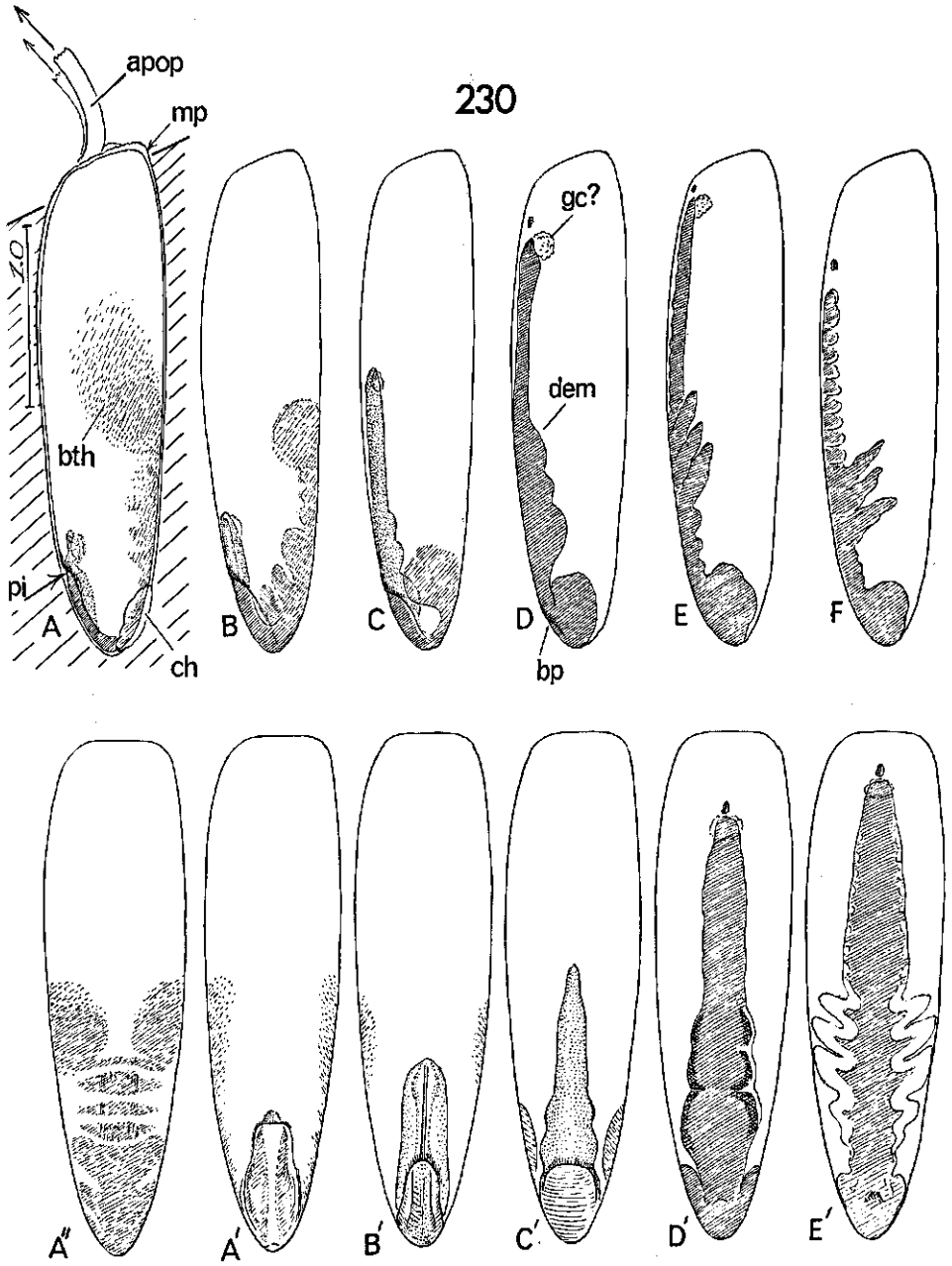


Fig. 230. Nepidae, *Ranatra linearis;* A–F: early embryogenesis, lateral; A″: aft side of egg; A′–E′: fore side.

(tab. 3, fig. 8). HINTON (1961) says (p. 225): "The eggs of *R. linearis* and *N. cinerea* have for long attracted attention, but the only serious attempts to discuss the structure and function of the shell were made by LEUCKART (1855), KORSCHELT (1887, a, b) and KÖHLER (1907)". To these authors POISSON (1924) should be added. From the key to the eggs of 14 spp. from 6 genera (HINTON, 1962b) it is evident that taxonomically only the subfamily characteristics are clearly marked (egg shape and number of horns). When more species are studied, the genera may not be so well differentiated on egg characters, at least not on the present generic concepts.

For nepid embryology there are early studies of the pleuropodia of *Nepa* sp. and *Ranatra fusca* (WHEELER, 1889; HUSSEY, 1926, respectively) and of the external morphology of the *N. rubra* embryo (HEYMONS, 1899). HEYMONS overlooked the spiral movement of the revolving embryo and so he wrongly interpreted the side along which the embryo invaginates as the aft side. HUSSEY (1926) made the same error, if is assumed that *Ranatra fusca* behaves as the European *Ranatra*.

Whereas hatching has been described by several authors, *e.g.* BUENO (1906), BROCHER (1913), HUNGERFORD (1919) and LEBRUN (1960), none of them discovered the important role of the serosal cuticle in breaking the shell unless this membrane was wrongly interpreted as the embryonic cuticle. BROCHER (1913, p. 262) mentioned that the lid of the shell lifts under pressure from the head of the larva but his fig. 98 clearly shows that the serosal cuticle does it. DAVIS (1961, 1964) recognized the role of this cuticle (his 'blister membrane') during the eclosion process in *Ranatra fusca* and *absona*.

2.4.3 Belostomatidae

MATERIAL: *Sphaerodema* sp. (some preserved stages of deposited eggs, origin Ivory Coast); empty shells of the following species: *Lethocerus indicus* Lep. & Serv. (origin Indonesia), *Poissonia longifemorata* Brown (origin S. Africa), *Sphaerodema ampliatum* Bergr. (origin unknown), *S. annulatum* Fabr. (origin Australia), *S. rusticum* Fabr. (origin Australia), *Belostoma anura* H. S. (origin Brazil), *B. micantula* Stål (origin unknown), *Abedus ovatus* Stål (origin N. America), *A. signoreti* Mayr (origin Guatemala).

Sphaerodema sp.

Eggs are laid in batches on the back of the male. As each day some eggs had to be taken for fixing and staining, we dislodged the only batch available from the male. However, these eggs were attacked by the few adults kept in the same container. As a result only a few undamaged eggs could be conserved for the study of their contents. Eggs are fastened upright in a cushion of mucilaginous adhesive (fig. 232B').

CHORION The shell (about 12.5 μ thick) appears porous towards the inner half. About ten aeropyles (1.5 μ diameter) are spread over each hexagon but they are absent

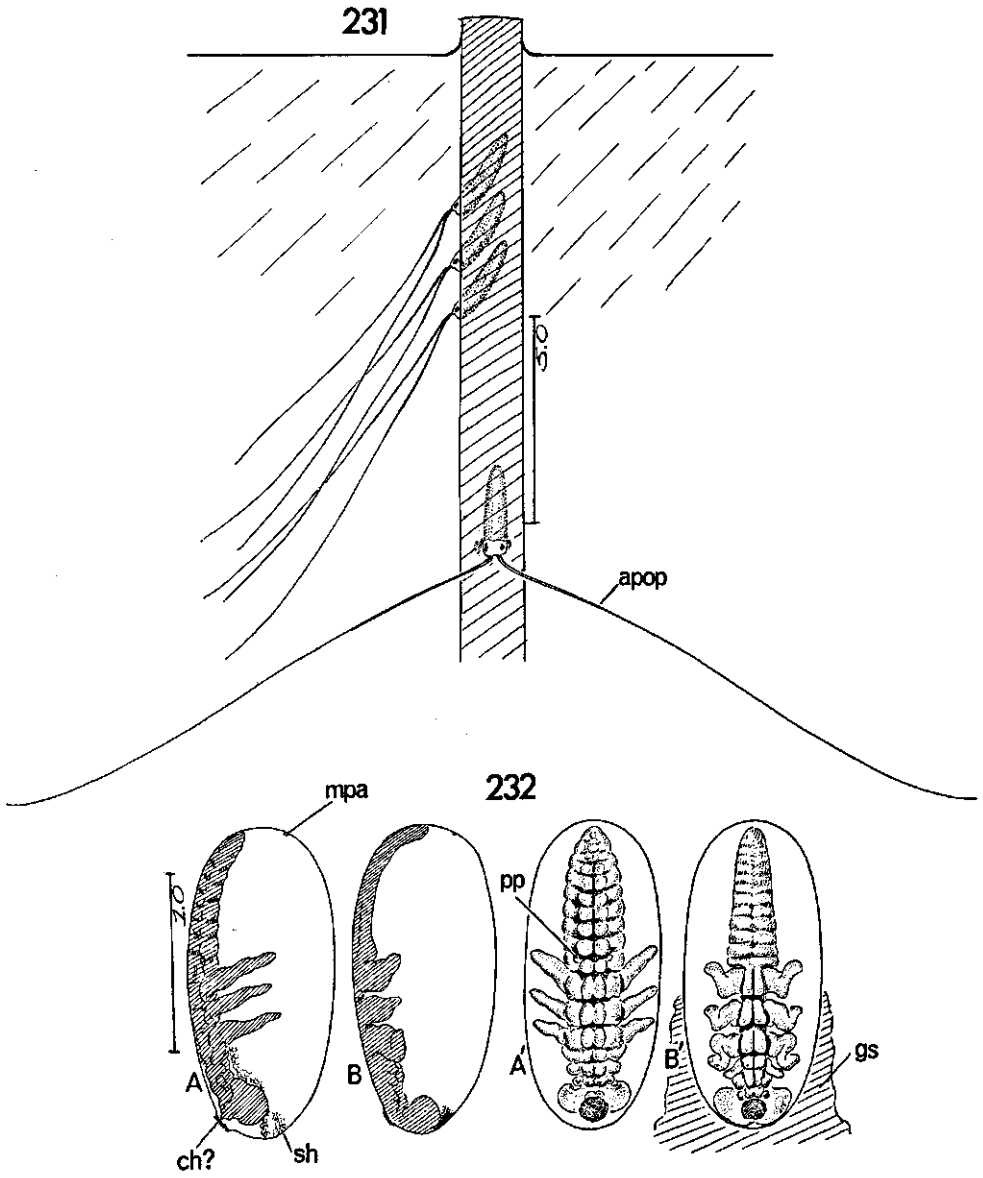


Fig. 231–232. Nepidae, Belostomatidae 231. *Ranatra* sp. (Ivory Coast), deposition of eggs in polystyrene foam below water. 232. *Sphaerodema* sp., some embryonic stages; A, B: lateral; A′, B′: fore side.

on the bottom of the egg. There are 4–5 micropyles, in a transverse row as in Nepidae and rather excentric of the cephalic pole, to the aft side as in Nepidae. This analogy seems correct, when the orientation of the embryo and the serosal hydropyle is taken into account (fig. 232A). The hydropyle is indicated as a dark area on the serosal cuticle, but is not recognizable on the shell. On the other side of the basal pole lies a strange structure, a flattened sphere densely clothed with filaments. This brush certainly serves to anchor the egg in the mucous disc but whether this is its sole function remains to be seen (see next species).

GROSS EMBRYOGENESIS We can present only the two stages shown (fig. 232A–B), which are suggestive of Nepidae. There is only a slight darkening of the serosal cuticle in the anterior half of the egg.

Lethocerus indicus

Eggs are laid in upright clusters on branches and other subjects. The chorion has an inner porous layer and a number of aeropyles on the polygonal planes. There is a nepid-like chorionic hydropyle (fig. 233A). On the fore side of the shell below the mid line, a white circular pattern is surrounded by a dark area. On this area the number of aeropyles is considerably reduced. As it is present on all eggs, it might be a secondary hydropyle. It is possibly homologous with the brush structure in the *Sphaerodema* egg above. The 7–11 micropyles are funnel-shaped and have an inner diameter of about 1–2 μ. They do not form a transverse row but are arranged in a longitudinal narrow ellipse. The micropyles on the extremes of the ellipse have a more oblique course through the shell than those on the middle. Each micropyle points to the centre of the ellipse (fig. 233B). The bursting of the shell is effected through a transverse rent just below the micropylar area; but as the fracture does not reach the fore side, the cap remains hinged to the egg shell after hatching.

ADDITIONAL MATERIAL The remaining eight species studied provide a general picture of the belostomatid egg. The location of the micropyles and the eclosion fracture as described above are constant. The number of micropyles amounts mostly to 3–5 (5–7 in *S. rusticum;* 11–16 in *Poissonia*). They are grouped in a transverse row or on a semicircle. The aeropyles, normally 10–20 per hexagon, are vertical canals without any branching at the top (contrast Nepidae). The external openings are somewhat sunk in a meandering sculpturing of the outer shell. The porosity of the shell is very complex and differs between species. The outer half of the shell of *S. ampliatum*, for instance, is solid and traversed only by the aeropyles; the inner half, separated from the outer layer by a thin open sheet consists of an outer thick layer of fine holes, a thin layer of wider porosity and a thin inner lining. The solid outer layer in *S. rusticum* comprises more than two third of the total shell thickness and its upper lamina is vacuolate. The inner shell layer is throughout spongy and is widely spaced from the outer layer. The brush-like chorionic extensions at the basal pole, mentioned

above (p. 208), seem to be restricted to the genus *Sphaerodema*. A distinct chorionic nepid-like hydropyle has been found so far only in *Lethocerus*.

PREVIOUS DESCRIPTIONS Fragmentary data on belostomatid eggs have been gathered by HUNGERFORD (1919), POISSON (1933) and USINGER (1956). Generally eggs are deposited at night. The peculiar habit of carrying the eggs on the male's back, had been mentioned already in the last century for several species (see POISSON). HUNGERFORD reported that during the period of incubation the male *Abedus* spends much of his time 'aerating' the eggs. As such he considered the raising and lowering of the wings, which should accomplish a displacement of the air-store from below the wings towards its dorsal side where it should be taken up by the eggs. Observations must be carefully repeated to analyse whether or not these actions serve only for adult respiration. The male's habit of aerating the eggs with its back partly out of the water is probably effective in storing gas. Those species which deposit their eggs on immobile substrates (such as waterplants and margin of ponds) always do so above the water line. HINTON (1961) briefly commented on the similarity in chorion structure with nepid shells, except for absence of horns and thus of plastron.

POISSON (1933) reported 10–14 micropyles in *Hydrocyrius columbiae* Spin., which are arranged in a true circle (!). The embryo shift in *Belostoma flumineum* is presented by HUSSEY (1926) as though there were no spiral revolution. Since she probably overlooked such a spiral course in *Ranatra fusca* too, this information seems rather suspect.

2.4.4 Naucoridae

MATERIAL: Potamocorinae: *Coleopterocoris kleerekoperi* Hungf. (ovarian eggs, origin Brazil).
Ambrysinae: *Ambrysus* sp. (ovarian eggs, origin Aruba, Neth. Ant.).
Naucorinae: *Ilyocoris cimicoides* L. (living, deposited eggs).
Cryphocricinae: *Cryphocricos barozzi* Sign. (ovarian eggs, origin Brazil).

Coleopterocoris kleerekoperi

The egg is large relative to the small female; its shape suggests a superficial mode of oviposition (fig. 234A). The polygonal sculpturing is distinct and spacious, and contains flat areas with many pores. The chorion is distinctly double.

The outer layer is about 10 μ, somewhat thicker on the ribs; the inner layer is 6–7 μ. The aft of the egg bears no extending ribs. A pseudoperculum is lacking but a smooth longitudinal eclosion line crosses the anterior pole (fig. 234B). The single micropyle is beside the eclosion line. The micropylar tube, 3 μ wide, lies within one hexagon, which lacks the pores. The micropyle bears some external mucous projections (fig. 234C).

Ambrysus sp.

To judge from the suboval egg, this species probably glues the eggs lengthwise to the substrate. There is no outline of a pseudoperculum and the micropylar plug is situated in the centre of the anterior pole (fig. 237A). The prominence consists of a tangle of micropylar tubes (fig. 237B); their number is difficult to ascertain but they usually seem to exceed five. The plug is surrounded by a ring of chorion more transparent than elsewhere and it bears a fine hexagonal pattern.

The shell structure otherwise resembles *Ilyocoris* except that the pored outer layer is distinctly thicker than the inner layer.

Ilyocoris cimicoides

Eggs are embedded in plant tissue under water.

Adults, brought indoors during the winter, deposit after one week at room temperature.

CHORION The egg (fig. 239H, I) has an elliptical pseudoperculum of a solid single layer. It is irregular in thickness (25–40 μ), because of its sculpture which resembles a cobbled surface (fig. 235). The elongated follicular pits are filled with more material in their central areas than at their boundaries with adjacent pits. Near the aft edge of the lid, a whitish plug indicates the micropylar area (fig. 239G). It is an irregular raised crater of seemingly loosely-packed chorionic material. Three, sometimes four, micropylar canals twist through the plug (fig. 235). Their outer openings, about 5 μ wide, are situated on rod-like projections (fig. 236A). The plug dissolves in potash but the micropyles are resistant as dark ducts. In unripe eggs the exact origin of each micropyle is easily seen in the inner edge of one large follicular pit (fig. 236B). From there they run a distance transversely in the lumen. Their diverging direction and mutual arrangement seems initially rather regular but obviously becomes secondarily changed during the final modelling of the follicular ribs to which the outstanding rods are joined (fig. 236A).

The narrow frill on the margin of the pseudoperculum extends slightly beyond the neck of the egg. A layer of cement is accumulated in this anterior niche and is found to be precipitated in serial sections in a distinct way (fig. 236E). To start from the lid, the chorion becomes clearly two-layered. The inner layer is solid and measures about 6 μ. The outer layer being of the same thickness has regular pores (fig. 236C). The pores give access to perpendicular canals, which at first narrow inwards and then widen towards the inner layer. Inward the lumina of the canals are partly filled by tubercular prominences of the inner layer (fig. 236D) and the outer layer joins the inner layer only at the central point between four canals. Between both layers there is a nearly continuous, though thin, interspace which seems full of water. How gaseous exchange occurs through such a thick solid inner layer remains obscure. The chorionic structure makes the shell surface seem as a fine sieve; it is uniform over the whole egg. There is

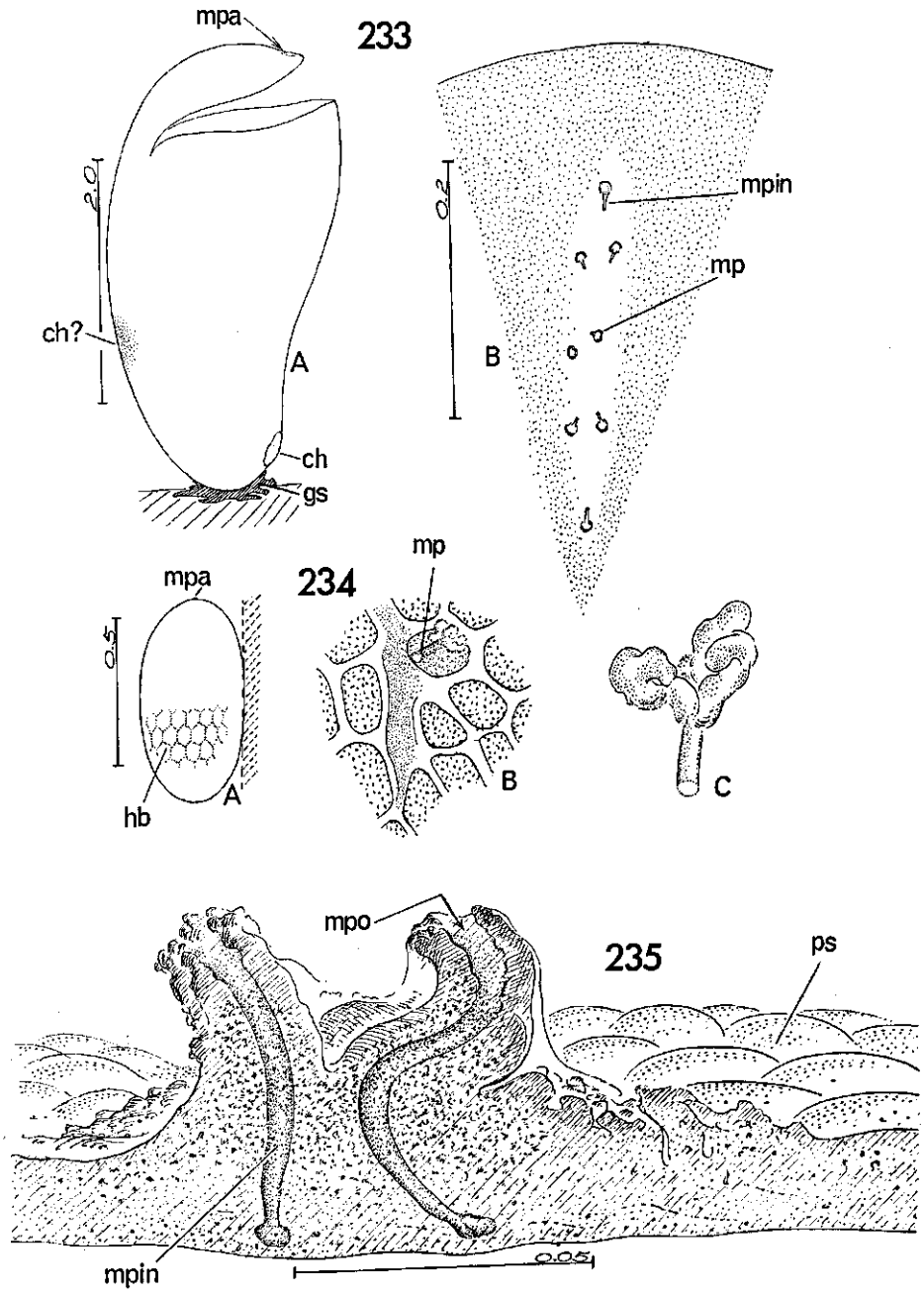


Fig. 233–235. Belostomatidae, Naucoridae 233. *Lethocerus indicus;* A: vacated shell, lateral; B: micropylar area, inner surface. 234. *Coleopterocoris kleerekoperi;* A: ovarian egg, side view; B: micropylar area, surface view; C: micropyle. 235. *Ilyocoris cimicoides,* hand section traversing micropylar plug.

not even any irregularity of the pattern beneath the lowest edge of the lid, where there is a serosal hydropyle.

EARLY EMBRYOGENESIS Incubation takes about 14 days at 25 °C. A temperature of 30° does not interfere with development (contrast *Nepa, Notonecta*), which then takes about 8.5 days altogether.

Invagination occurs just fore of the posterior pole and this takes place after one and a half days at 20 °C. The germ band elongates in a straight, almost entirely superficial course along the fore side (fig. 238A–C). No cluster of isolated cells on top of the band's tail has been observed. The three pairs of thoracic buds are already weakly outlined in the blastoderm thickenings before involution (fig. 238A, 239A). In fact, just after invagination the thorax forms the greater part of the band, the abdominal part being only a short flap (fig. 239C). In the same figure a slight bilateral asymmetry of the band is recognizable and its greater part lies right of the sagittal plane. This is the condition in all eggs observed at this stage. Just before the band reaches the lower border of the pseudoperculum, a drastic shift in its position occurs. The embryo, persisting in its superficial situation and longitudinal orientation, moves round the right half of the egg (clockwise, seen from the front pole) to assume a position on the aft side. The rate of this rotation and the question, whether or not the whole yolk system is involved, has not been ascertained.

Indirect indications do suggest that the rate must be slow, since some growth and differentiation of the band takes place between the fore and aft position (fig. 238C and E). There is also indirect proof that it is solely the embryo which rotates, although the exact mechanism is not known. The earlier bilateral asymmetry of the band is very distinct in the transitional position (fig. 239D). The side of the embryo, which faces the direction of movement, is much broader than the other, right half. This is not caused by an oblique position of the band, because it remains superficial throughout. The longitudinal axis of the band makes a wide bow, following the direction of the rotation and this bow is maintained to a lesser degree long after the rotation is complete. These deformations in shape could be explained by having arisen under the influence of direct forces beyond the embryo. However it seems quite certain that the serosa has nothing to do with the displacement as its anterior area of thickened cells (fig. 239D, sh), becoming visible half-way through the rotation, is not involved in any shift. It does not seem likely that the whole yolk system participates in the turning process, at least not the anterior part. The yolk completely occupies the anterior region at the time of rotation, also the marginal edges beneath the pseudoperculum. A rotation of this system in this region is difficult to imagine without a preceding retraction from the shell boundary, because the egg space here is far from cylindrical.

The abdomen now grows up to almost the extreme anterior top of the egg without flexing. The gnathal elements elongate and separate into segments simultaneously with the metameric division of the abdomen. At this time, the legs are spread considerably to the sides and, because of the rounding of the egg, they seem to point to the middle of the egg in side view (fig. 239F). However the outer plane of the embryo,

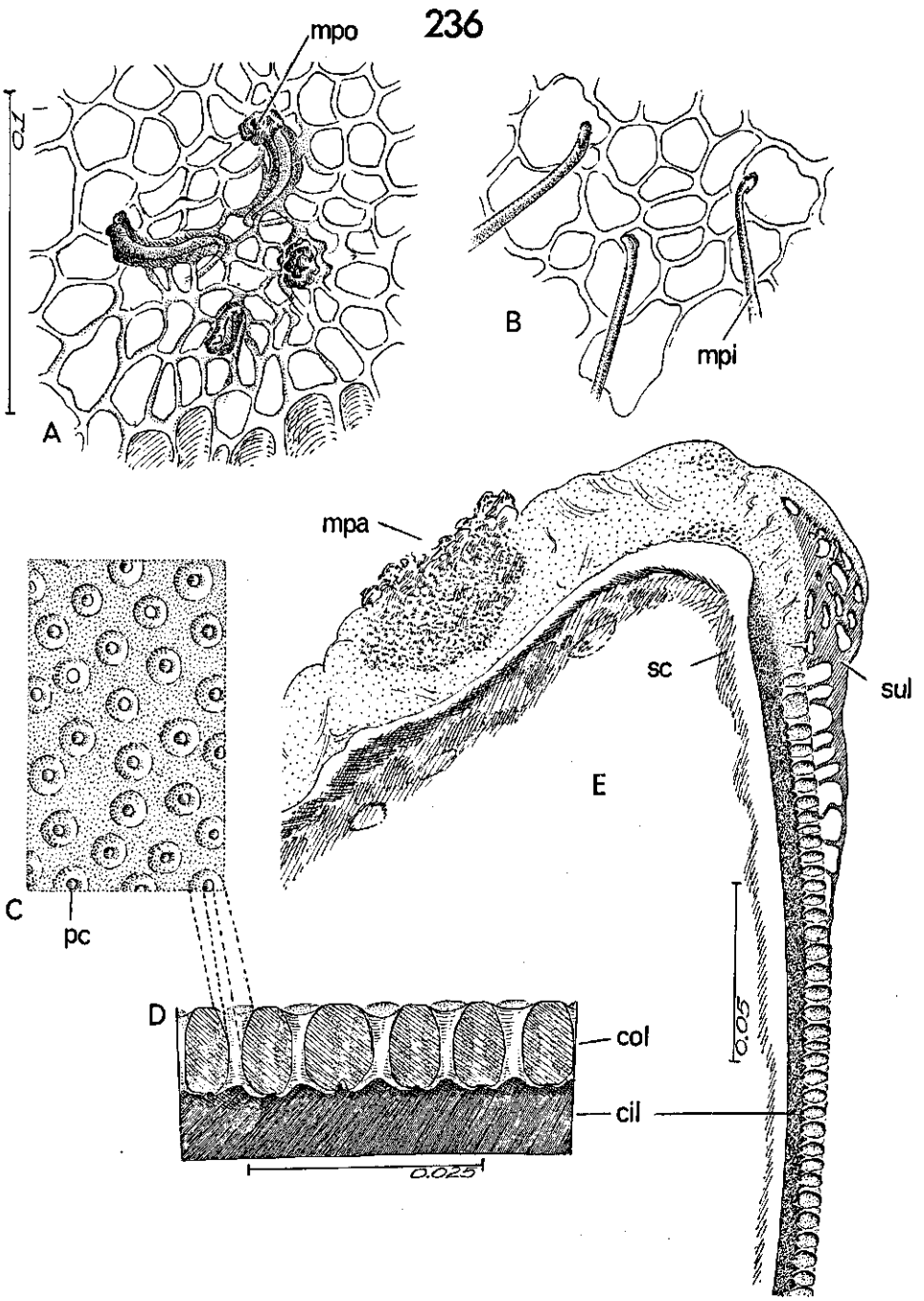


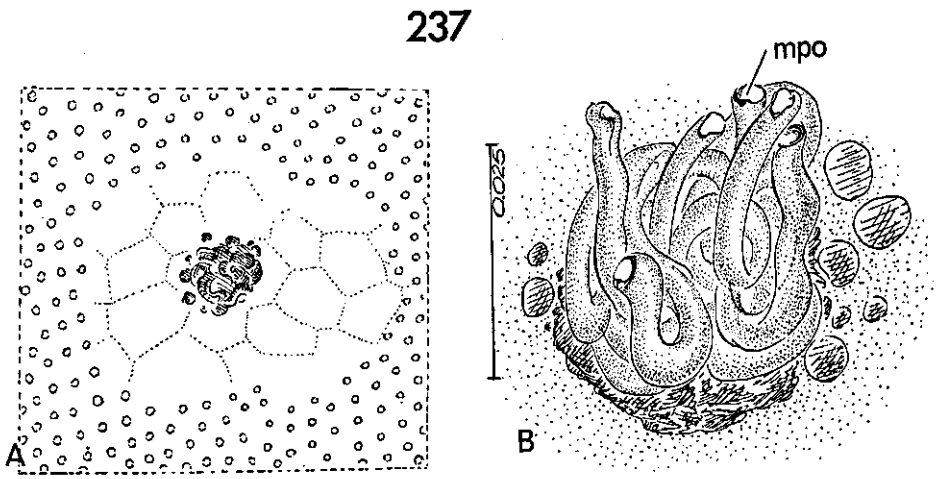
Fig. 236. Naucoridae, *Ilyocoris cimicoides;* A: micropylar area, outer surface view; B: inner surface view, unripe egg; C: chorion structure, surface view; D: section of chorion; E: longitudinal section of upper edge of pseudoperculum.

facing the shell, is its ventral one. Again, some bilateral asymmetry can now be noticed. The legs on the left side of the egg touch the serosa with their tapering ends but the right legs are not wholly superficial, as a thin layer of yolk separates the serosa and amnion on that side. The serosal cuticle is formed in the period just before the stage drawn in fig. 238C. Soon after its origin, the outer film of this cuticle darkens into irregular blots under the pseudoperculum. Also the fore side darkens irregularly but its upper part remains clear. This area, which is posteriorly limited by a falcate zone (fig. 239F, scp) corresponds to the circular thickening of the underlying serosa. This is the hydropyle, which in *Ilyocoris* is characterized by a position, which for Heteroptera is very uncommon. The normal place for this structure, *i.e.* the caudal pole, is definitely devoid of hydropic cells in this egg. Water accumulation there could not be traced after removing the chorion but in the anterior pole it can. The strong tension of the shell bordering the serosal hydropyle in *Ilyocoris* forces the absorbed water to be transported along both sides to the aft side of the egg's neck. The day before the condensed stage of the embryo, all eggs bulged out at that spot as soon as the chorion was peeled off from the serosal cuticle. The water is seen to be stored temporarily between the serosa and the yolk (fig. 240A). The next day, some other eggs of the same batch again had filled the whole anterior chamber with yolk, in others the serosa had retracted from the cuticle and become contiguous with the shrunk outline of the yolk, the water now resting outside the serosa.

LATER EMBRYOGENESIS Revolution of the embryo is, as in other Hydrocorisae, a combined upward and rotatory movement of 180°. The spiral movement in all six eggs tested was clock-wise, when observed from the cephalic pole. Fig. 240B shows that the abdomen with the retracting amnion leaves a spur in the yolk, which marks the spiral course. The constriction of the yolk column (fig. 240B) must probably be a help for the amnion to turn inside out. In some eggs, a ligature already appeared at this early time which clearly marks off the amniotic from the serosal part. This ligature is formed almost abruptly (fig. 240C, D), but it has not been determined how far one or both of the embryonic envelopes contribute to its formation. The circle of hydropic cells initially retains its original position but later retracts to a position just lateral under the pseudoperculum; there it remains unchanged for a long time discernible as a transparent circle on the condensed yolk.

Once the serosal plug has been swallowed in the prothorax, the embryo can be found in steady rotation around its long axis. Its orientation is readily ascertained by the notch which divides the eye into a small and a large part. The notched margin of the eye points to the ventral side of the embryo.

The eye never darkens until after revolution. The prolarval turnings, which sometimes result in 360° rotations in succession, is accomplished by a series of short jerks. This remarkable phenomenon will be mentioned in more detail under *Notonecta*. Another feature was many dark, rod-like bodies of about $5 \times 1\ \mu$ (fig. 240E) in the extra-embryonic fluid. Initially we thought they were micro-organisms, but closer observation shows that the bodies are most probably crystals. What is seen as rods are



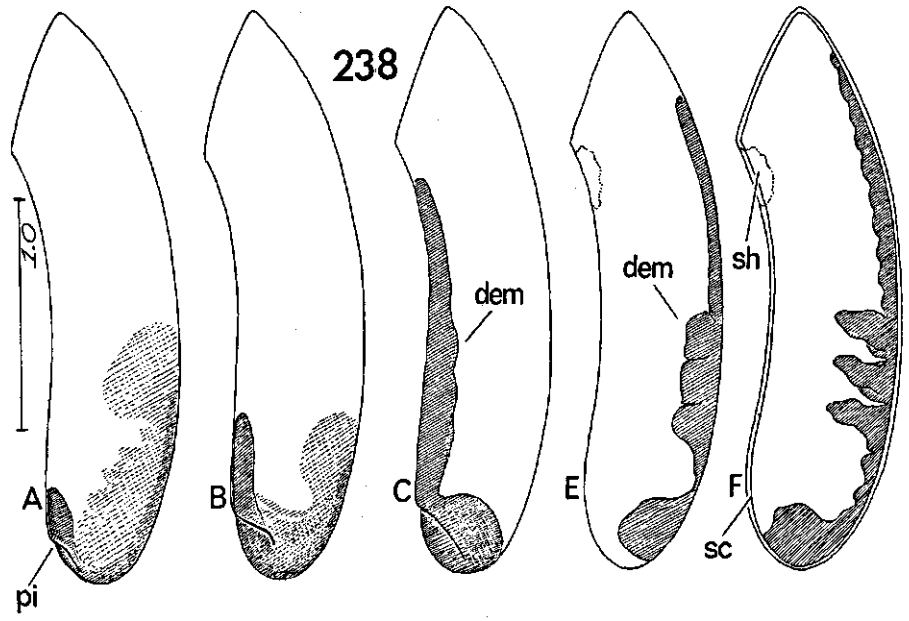


Fig. 237–238. Naucoridae 237. *Ambrysus* sp.; A: micropylar area, surface view; B: micropylar plug, external view. 238A–E: *Ilyocoris cimicoides*, early embryogenesis, lateral.

the smallest optical sections of tiny square plates. In surface view they disappear, as they do not refract light. Since the bodies roll around in the fluid, they are visible in dechorionated eggs in a ray of light even with magnification 30 × as flashes of light. The crystals appear first during the condensed phase of the embryo, where they are found in the lumen between the serosal cuticle and the serosa. It is thus possible that they represent dissolved products of the inner layer of the serosal cuticle.

During blastokinesis the crystals are close to the serosal cuticle but after yolk uptake they concentrate mainly in the layer of viscous liquid, closely surrounding the embryo. The bodies also occur in the nepid egg but in less density. Yet they have not been observed in *Notonecta*. In Corixidae we made no intensive search to trace whether they occurred.

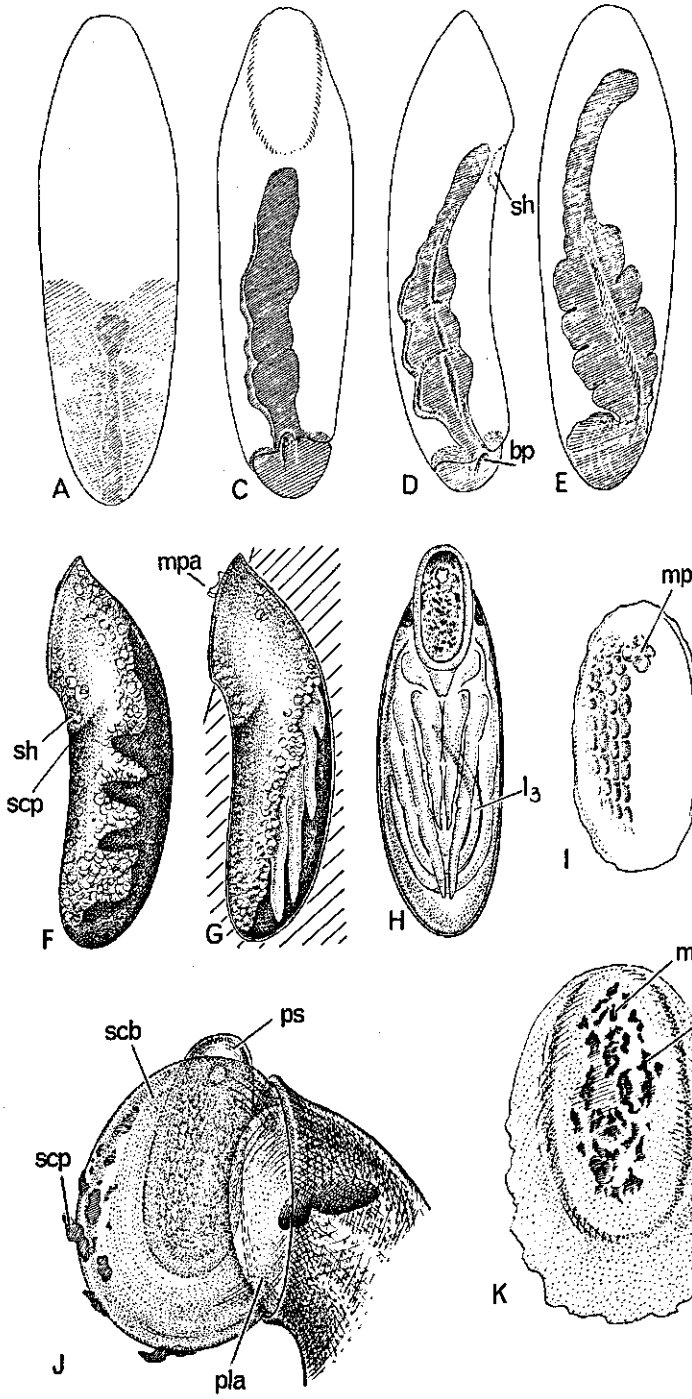
ECLOSION The prolarva has the same asymmetrical arrangement of the legs as in Corixidae and Nepidae and this asymmetry in the majority of eggs is likewise directed to the same side. Of the 89 eggs checked, 79 (88.6%) had the arrangement as illustrated (fig. 239H), the remaining 10 eggs showed the mirror-image. The prolarva ready for eclosion, now lies with its legs against the concave side of the egg, as a result of more or less numerous rotations. Hatching is essentially as in the Hydrocorisae already mentioned and still to be treated. Fig. 239J shows that the dark outer layer of the bulging serosal cuticle very soon breaks. Its fragments remain attached to the vesicle of the stretching layer below. The serosal cuticle breaks along a median slit, despite its protruding from the chorion along a circular line, coinciding with the boundary of the chorionic cap. The embryonic cuticle bears a band of fine tubercles on the thorax and abdomen but its head is free from such differentiation.

Cryphocricos barozzi

The fact that the egg is strongly dorso-ventrally flattened, suggests that it is glued to the substrate. The number of micropyles cannot be determined externally, because the openings are masked by a small protuberance in the centre of the anterior pole. The inner view shows four canals radiating out in opposite direction. A crescent-shaped part of the future eclosion fracture exists in the unhatched egg. It is a transverse suture in front of the micropyles, recognizable by lack of chorionic sculpture along its sides.

PREVIOUS DESCRIPTIONS POISSON (1933) investigated the micropylar apparatus of *Ilyocoris cimicoides* and *Naucoris maculatus F.* and found four micropyles in both species. Outwardly the egg of *N. maculatus* resembles the egg of the western *Pelocoris*

Fig. 239. Naucoridae, *Ilyocoris cimicoides;* A–E: early embryogenesis; A, C and E: similar stages to the correspondingly labelled drawings of fig. 238; A, E: aft side; C: fore side; D: half way through the germ- band rotation; G: revolution; H: attitude of prolarva; I: pseudoperculum, outer surface view; J: explosive chorionic break; K: subopercular part of the serosal cuticle.


A
C
D
sh
bp
E
mpa
sh
scp
F
G
H
l_3
mpa
I
scb
ps
scp
J
pla
mpp
scp
K

femoratus P. B. (BUENO in HUNGERFORD, 1919), the *Ambrysus* sp., described above, and *Ambrysus mormon* Montd (USINGER, 1946).

LEBRUN (1960) showed that in *N. maculatus* the egg opens by an almost circular lid, and this is the case also in *Aphelocheirus* (LARSÉN, 1927). The last author has given an adequate description of the egg of *A. aestivalis* F., a member of another naucorid subfamily with both generalized and specialized features. Of great interest is the single micropyle, a simple canal projecting slightly from the centre of the anterior pole. The zone around this canal is without sculpture but the shell otherwise bears distinct hexagonal ribs. Pores in the hexagons penetrate obliquely into the ribs. The eggs are attached superficially to the substrate as were those of *Naucoris*, *Pelocoris* and *Ambrysus*. HEYMONS (1899), in his classical work, misinterpreted the dorso-ventral orientation of the embryo of *I. cimicoides*, since he overlooked the early and the later rotation, as well as the spiral manner of the revolution. The action of a membrane, which breaks the chorion and which, in our opinion, represents the serosal cuticle has been noticed by RAWAT (1939, *I. cimicoides*, p. 122: "... membrane continues to expand like a soap bubble" and by USINGER (1956, *A. mormon*, p. 201: "...the nymph emerging through a crescent-shaped tear". This striking phenomenon was overlooked by LEBRUN (1960), who described the eclosion in *I. cimicoides* and *N. maculatus* (p. 181: "Lors de l'éclosion, sous la poussé de la larve, l'opercule se détache").

The last author states that in *I. cimicoides* a ruptor ovi is present. He found on the head region of the cast embryonic cuticle two spines and continues: "Grâce au movement de rotation de l'embryon à l'intérieur de l'oeuf, le ruptor ovi incise la zone périoperculaire, permettant ainsi à l'opercule de se détacher sous la poussée de la larve". The incorrectness of this is selfevident. The embryonic cuticle in none of the hydrocorisous eggs studied bears cephalic differentiations which could act as egg-burster. But, even when the presence of a powerful opener is supposed, its use as stated by LEBRUN would make an incision across the cap rather than round it.

2.4.5 Notonectidae

MATERIAL: *Notonecta glauca* L., *N. viridis* Delc., *N. maculata* F., *N. obliqua* Gl., *N. lutea* Ml., *N. reuteri* Hung. (living deposited eggs of all species); *Enisthares maculata* Dist. (ovarian eggs, origin Madagascar); *Anisops*, two species (some fixed deposited eggs, origin Ivory Coast); *Buenoa* sp. (ovarian eggs, origin Curaçao, Neth. Ant.).

Notonecta 6 spp. (enumerated above)

Eggs of all species, except *N. maculata*, are superficially inserted in plant tissues under water, for which purpose shallow slits are bored. All species apparently have only one generation and *N. glauca*, *N. viridis* and *N. obliqua* hibernate as imagines. Adults lay no eggs in autumn but if brought straight indoors after a short cold period, they immediately start depositing eggs on the same day. This suggests oogenesis at low temperatures. *N. lutea* and *N. reuteri* overwinter as eggs; the embryonic stage of

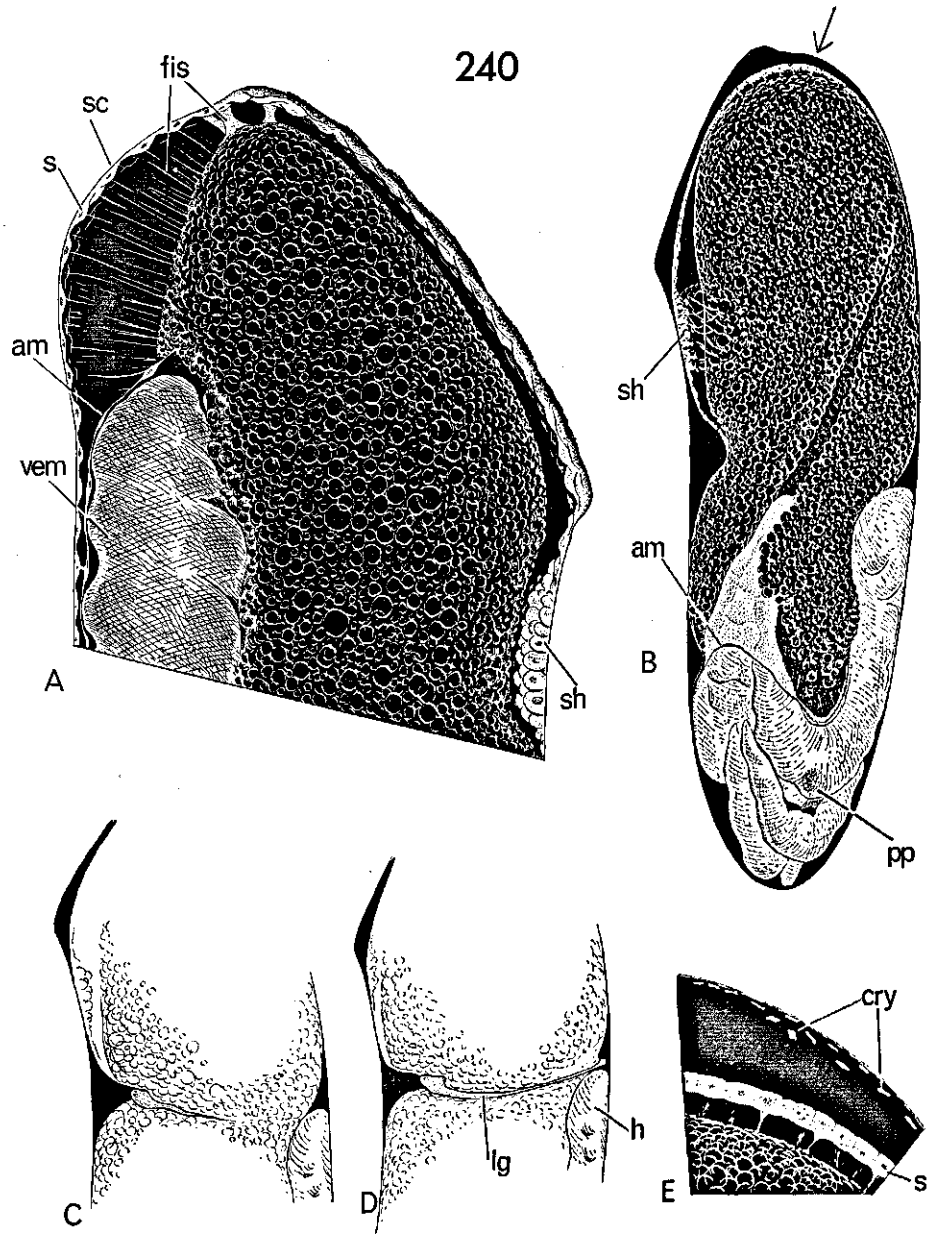


Fig. 240. Naucoridae, *Ilyocoris cimicoides;* A: anterior part of egg, lateral, phase before revolution (fore side of egg at right); B: total egg system during revolution; C, D: stages slightly later as in B, formation of serosal plug; E: fragment of figure B (region of arrow).

diapause is for 100% fixed but completely differs between species (see below). Eggs of *N. maculata* are glued entirely exposed, preferably on solid material (stones, glass). The diapause of *N. maculata* in the Netherlands seems not to be balanced. Eggs are laid predominantly in autumn but also later when temperature is again suitable and surviving adults have been found late in spring. Eggs of this species, deposited in autumn, spend the winter in diapause (see below). However when females were first exposed to cold, eggs deposited on the day when temperature rose, have no diapause. In diapausing eggs, the young embryo needs cold to break the resting stage. In eggs without diapause, cold has influenced the ripe but still unlaid and unfertilized eggs.

CHORION The shell is distinctly double. In *N. glauca*, *N. viridis* and *N. obliqua*, the solid inner layer is almost equal to the thickness of the outer layer, apart from the extending ribs of the polygons (fig. 244B). The inner layer is much thinner near the micropylar region (fig. 245D). In the other species with overwintering eggs, the outer layer is distinctly thicker throughout (fig. 244A, C). Each species is distinguishable by the sculpturing of the chorion but they all have a uniform basic pattern. The specific differences are a different cover of knobs or more uniform deposits on the variably high polygonal ribs. The plain polygons are covered with fine pores leading to oblique canals reaching the inner layer (fig. 245F). The broad zones bordering each adjacent polygon, are free of pores. There is no continuous open space between the outer and the inner layer of the shell. The hydropyle, which is slightly aft of the posterior pole (see below), is not recognizable by another chorionic design. The vertical canals in the shell are a bit more densily packed at the posterior pole and some canals seem to traverse the inner layer (fig. 244B).

The notonectid egg bears only one micropyle, situated centrally in the anterior pole *(N. maculata, Enisthares)* or in front of the centre (other species). The micropyle runs obliquely and extends to the outside as the widening lumen of a white chorionic horn. The horn is short and solid in *N. maculata* (fig. 249A, B), longer and porous in the other species (fig. 245A–D and 303, cross-sections under optical and electron microscope, respectively). With dyeing according to MASSON, the exterior horn stains light brown, whereas the outer shell and inner layer stain yellowish and violet, respectively. The micropylar wall within the shell contrasts sharply with the surrounding chorion (fig. 245C). The black solid quiver, through which the narrow micropyle (diameter around 2 μ) runs, projects just into the interior of the *N. maculata* egg (fig. 249B) but extends far in *N. glauca* (in the empty shell discernable as a long isolated black thread, fig. 243C, mpi). The pictures (fig. 245A–D) show further that the micropylar area of the shell is not penetrated by the numerous canals elsewhere and that the inner layer is absent just around the micropyle.

EARLY EMBRYOGENESIS Incubation in *N. glauca* takes about 14 days at 18–20°C and 9.5 days at 25°. A continuous temperature of 30°C kills the eggs during the first days.

The positional shifts of the germ band in nearly all species studied are about the

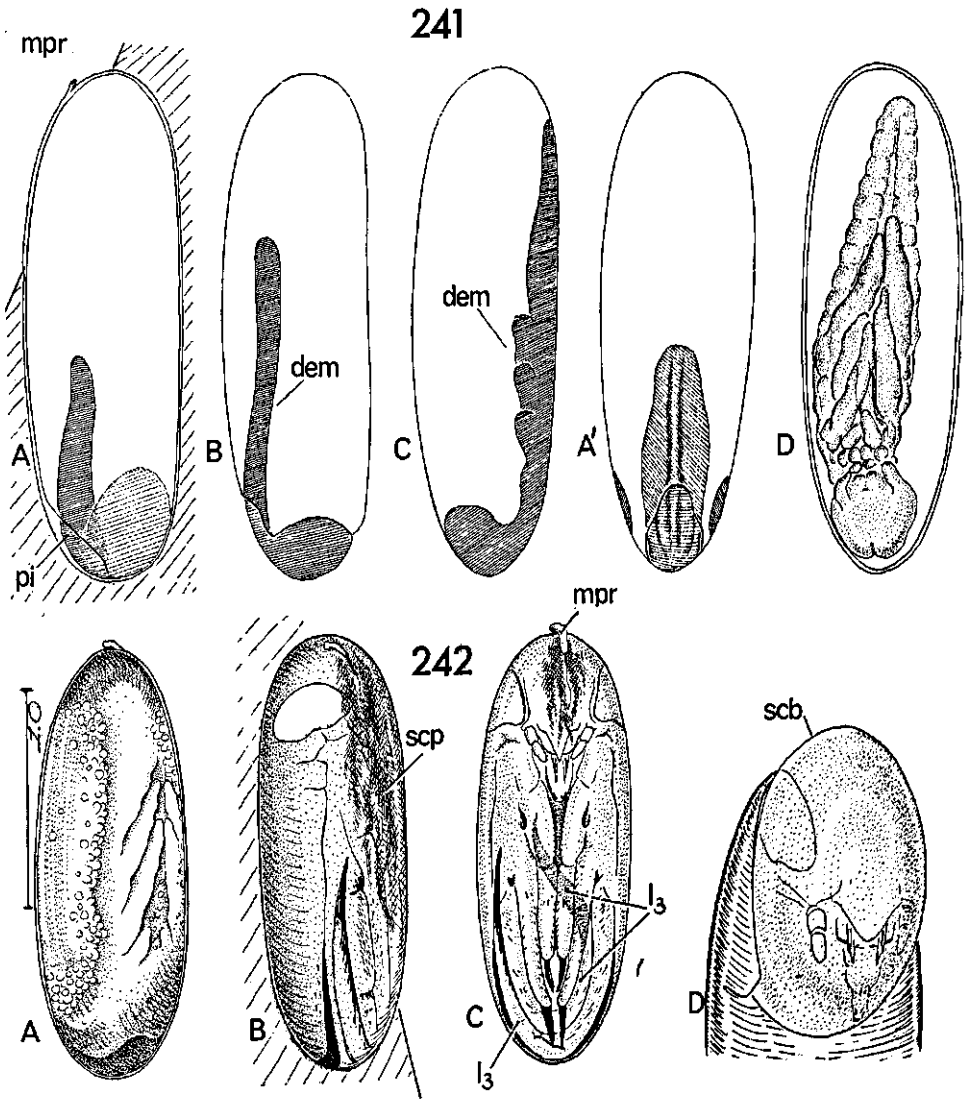


Fig. 241–242. Notonectidae 241A–D: *Notonecta obliqua*, early embryogenesis; A′: fore side; D: aft side of egg. 242. *N. glauca;* A: before revolution; B, C: prolarva (A and B: egg shown from the opposite lateral side as compared with fig. 241A); D: eclosion, fore side, the bladder of the serosal cuticle is filled by the prolarva.

same as in *Ilyocoris*, *N. maculata* behaving, however, more as the Corixidae and Nepidae embryos. Thus: as a rule an early rotation of the band from the fore towards the aft occurs (fig. 241B, C) and this shift is round the right half of the egg and at the same stage as in *Ilyocoris*. In contrast to *Ilyocoris* and the Nepidae, the *Notonecta* band, initially remains away from the serosa during involution (after 1.5 day, 20 °C). It moves wholly to the yolk surface only when the thoracic buds differentiate (fig. 241C) and these latter outgrowths appear a bit later than in *Ilyocoris* and Nepidae. The metathoracic buds, later giving rise to the rowing legs, are larger than the preceding two pairs of buds. The serosal cuticle appears when the thoracic buds lengthen and the process of blastokinesis is passed as in *Ilyocoris*. Except in *N. maculata*, revolution is along the aft side.

Eggs of *N. reuteri*, *lutea* and *maculata* enter diapause in summer or autumn. The eggs of *N. reuteri* spend the winter in the condensed phase of the embryo, comparable with stage D in fig. 241. In *N. lutea* and *maculata*, development stops when the thoracic divisions show just slight ventral outgrowths. The germ band then lies along the convex side in *N. maculata* but along the opposite side in *N. lutea*. In the meanwhile the serosal cuticle is secreted in the resting eggs of *N. lutea*. In the diapausing egg of *N. reuteri* and in the active eggs of the other species, this cuticle appeared at a later morphological stage of the embryo. If we assume that the serosal cuticle appears at the same time in *N. lutea* and *maculata*, we have to conclude that the outer embryonic system remains active some time after the actual diapause of the embryo has set in. The serosal cells may be activated to secrete by a stimulus outside the embryo.

The serosal cuticle gives the fore side of the egg a dark appearance, since the extra outer coat on that side is dark and shows through the thick shell. In *N. reuteri*, the aft is also darkened. The black coat bears a clear print of the internal part of the micropylar canal in *N. glauca* (fig. 245E). Especially in species with diapausing eggs, an even more intense circular darkening marks the micropylar area of the shell.

After removal of the chorion, a circular area of the serosal cuticle shows indistinctly as a convex lens aft of the basal pole. This is the area corresponding to the hydropic cells of the serosa. No differentiation can be resolved in the chorion or in the serosal cuticle at the posterior pole which can be distinguished with the optical microscope from the structure of adjacent regions. The serosal cuticular hydropyle in most dechorionated but intact living eggs shows minute black dots when seen under water. It was not certain whether these dots are structural or whether they are only specks of dust on it. Similar specks are seen also in mounts of that part of the serosal cuticle directly after excision, thus suggesting that they form part of it. This area of the serosal cuticle is more easily assessed after revolution of the embryo, when the hydropic cells have retracted, so that the cuticular area is pressed outwards (fig. 246D, sch). The area is also the first to be affected by external growth of micro-organisms in peeled eggs.

The fate of the serosal hydropyle is depicted in fig. 246. In the phase before blastokinesis, the serosa retracts from the cuticle at the basal pole. This process takes several hours in *Notonecta* and cytoplasmic filaments remain attached for a long time to the

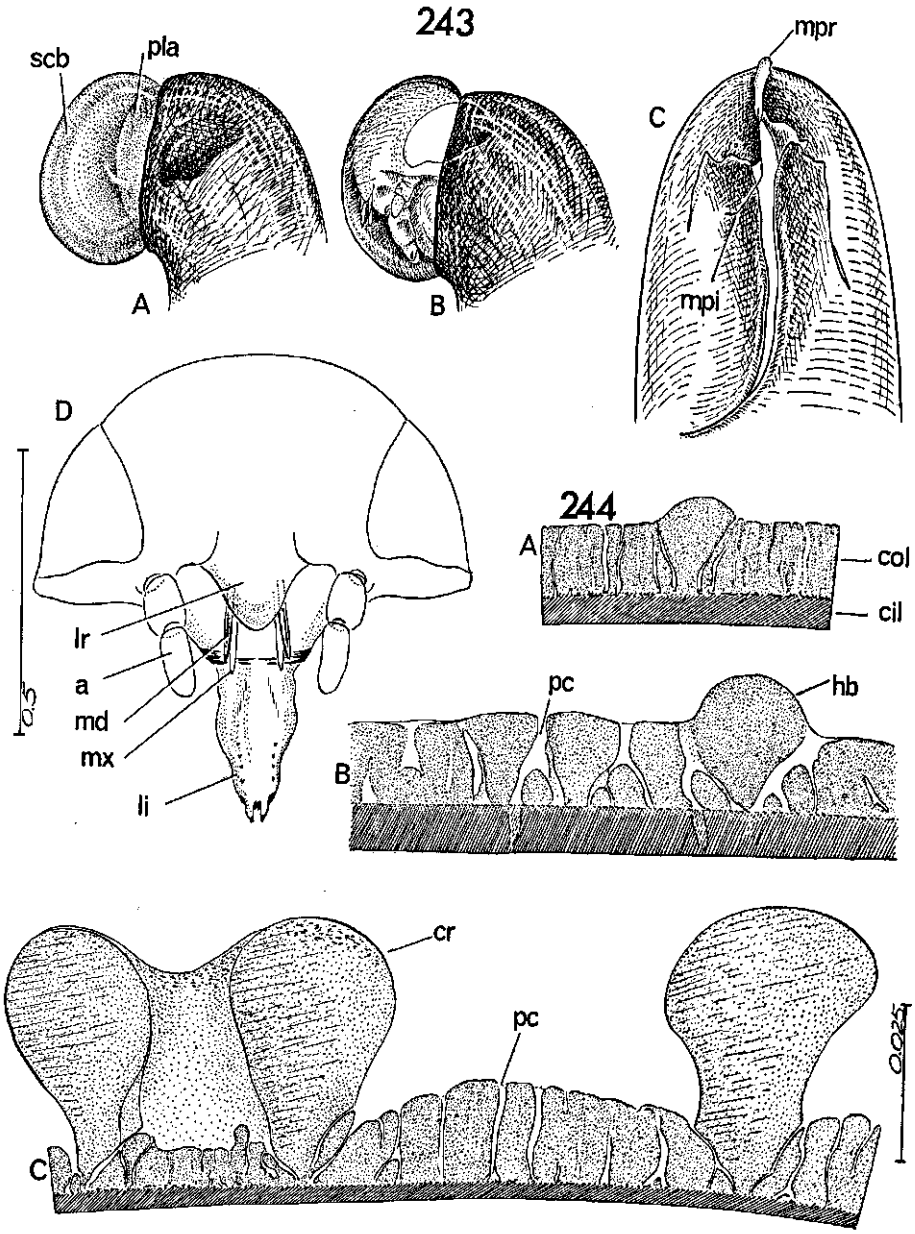


Fig. 243–244. Notonectidae 243. *Notonecta glauca;* A, B: eclosion; C: eclosion rupture of vacated shell, fore side; D: larval head enveloped by the embryonic cuticle. 244. *Notonecta,* transverse section of chorion; A, C: *N. maculata;* B: *N. glauca;* A: lateral side; B: near posterior pole; C: fore side.

outer envelope (fig. 246C). The mass of hydropic cells are released as a whole from the serosal cuticle and the retraction compresses them and pushes the central cells out of the mass (fig. 246B). The surrounding cells flatten out as a normal part of the serosa but the cells expelled swell up and their nuclei disintigrate (fig. 246D, E) and eventually disperse.

LATER EMBRYOGENESIS Blastokinesis follows the pattern for *Ilyocoris* but the embryo of *N. maculata* rises along the fore side of the egg. Crystalline particles in the amniotic liquid (see *Ilyocoris*, p. 214) have not been observed in *Notonecta*. The legs grow a great deal during the retarded revolution. Just before this process, the slightly asymmetric arrangement of the legs is as depicted (fig. 241D). The embryo has moved half way up the egg; the hind legs are still stretched side by side, though much longer. The embryo, during completion of two thirds of the revolution, flexes the legs in the final arrangement. The eye then starts to redden in *N. maculata;* in *N. glauca* and *obliqua* this occurs later, when the dorsal organ is formed.

The dorsal organ has been studied in some detail in live dechorionated eggs of *N. maculata*. For a day or more the serosal plug coincides with the anterior outline of the egg and the serosal layer is moderately thick. A constriction in the yolk column behind the embryonic head (fig. 247A) suggests the junction between amnion and serosa. But this junction, in fact, lies slightly further anterior as a thin line visible under high magnification (fig. 248C, bas). The early rhythm involved in the retreat of the serosal plug has not been timed, since only a few slight changes occur over long periods. The actual invagination of the plug takes about 1.5 h (21 °C) and comprises only two bursts of heavy contraction, drawn in fig. 247A–H. Fig. 247A shows the penultimate relaxing stage after a contraction. The serosal plug remains in an intermediate shape for 10 minutes (fig. 247B). The subapical constriction in the amnion remains and the thick-walled serosal plug is, partly, tucked into the mouth of the amnion. The plug is typically dome-shaped with a concave front above the head. It is this latter shallow hole which is suddenly sucked in through intrinsic cell-modifications, immediately changing the plug's appearance (fig. 247C). This position remains for 10 minutes during which the initial zone of invagination is again folded out. The next stages, D and E, show transition (after 20 min.) and the final moment, respectively, of the fading away of the convulsion, which occurs after another 35 min. The result of this slow relaxation is a flow of yolk into the amniotic sac and a slight rise of the embryo's head. The position of the brain, as a landmark (fig. 247, b), shows that the progression is caused mainly by swelling of the anterior of the head. Probably this is passively achieved by rising tension in the yolk column which presses against the dorsum of the head. We have the impression that the whole process of the serosal plug uptake involves no intrinsic motion by the embryo. It could be that the stimulus for cell contractions near the amnio-serosal junction results from a secretion of the pleuropodia. Before the next and last contraction, the fluid-filled cavity around the plug suddenly turns milky-white. The fluid-filled space at the posterior pole remains clear all the time. Within five minutes, the spherical remnant of the plug sinks into the amnion

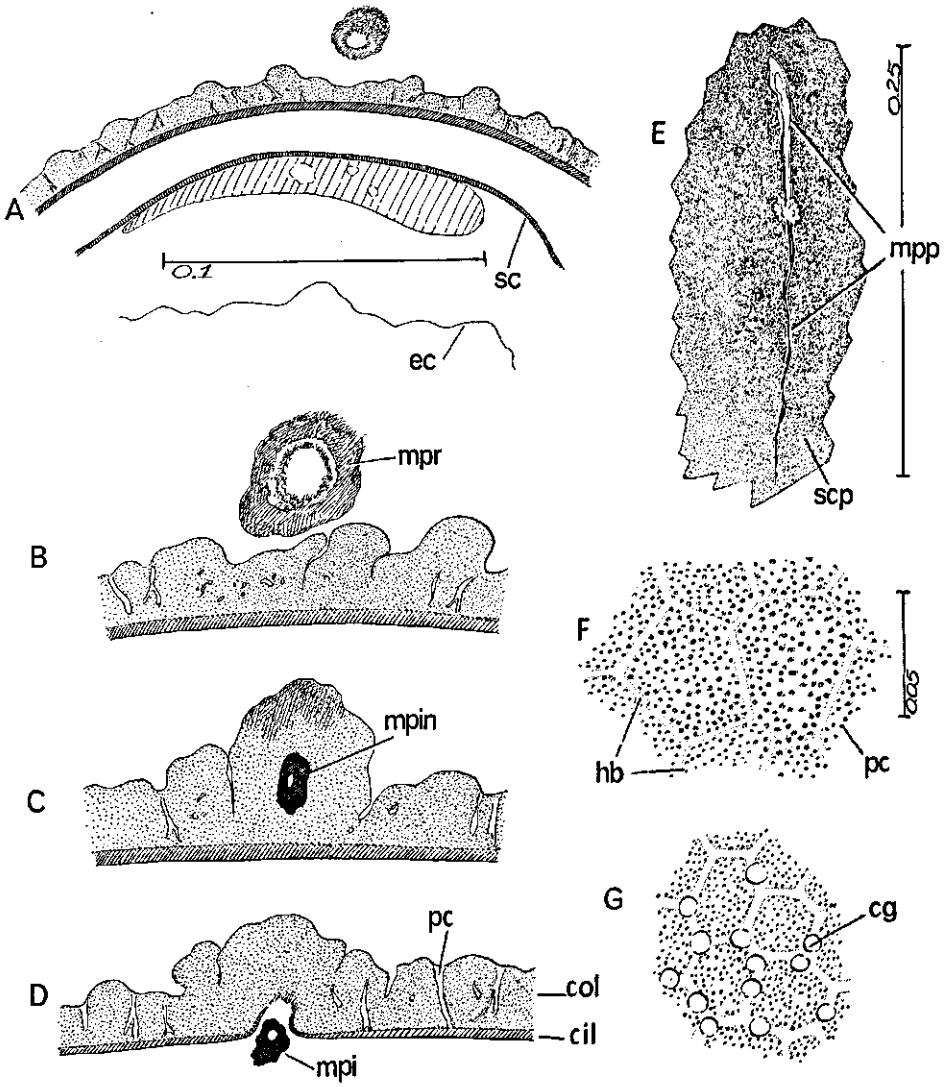


Fig. 245. Notonectidae, *Notonecta glauca;* A–D: transverse section of chorion through micropyle, the sequence of sections is from anterior to posterior; E: submicropylar part of serosal cuticle, imprint of the chorionic micropyle; F, G: surface view of chorion; F: lateral part of egg; G: exposed area, fore side.

(fig. 247F, G) and after 10 more min. the secondary dorsal organ is evident (fig. 247H).

In several peeled eggs, studied for the process, a membrance was found in the posterior edge of the egg at stage H. This pellicle, about 0.5 μ thick, follows the curve of the pole; it is separate from the embryo in the lumen between the embryo and the serosal cuticle. As the embryo and the yolk more anteriad are contiguous with the serosal cuticle, the outline of the membrane becomes obscured further upwards. In the anterior pole, the membrane is then absent at the same time. Half a day later, when the dorsal closure is complete, it is likewise free in the lumen. At the posterior pole, the membrane is now adjacent to the larval skin, although not entirely as it is stiff and stretched and consequently does not follow the many folds of the larval integument. These observations are too fragmentary to conclude unequivocally that this membrane might be an early embryonic cuticle (see discussion, p. 315).

ECLOSION As in *Ilyocoris*, the notonectid eggs (checked in four species) show the remarkable phenomenon of the prolarva in continuous motion around its polar axis, sometime after the dorsal closure is formed. Also *N. maculata* has this habit, although it is from the revolution onwards in the final orientation which is needed for eclosion. Thus, this type of rotation is not primarily concerned with bringing the prolarva into the final position for eclosion. In those species in which the prolarva faces backwards after revolution, only a half turn would bring it in the correct position but rotations continue beyond this limit. Moreover, the rotations have nothing to do with reaction to light, as was once suggested in the literature. Rotatory motion also starts and proceeds continuously in those eggs kept in darkness and, more significantly, the final orientation of the prolarva is just as in eggs held in light. The function of the prolarval rotations might be connected with a possibly dissolving process of the inner surface of the serosal cuticle, or with the uptake and pushing forward of water. But the question remains why these motions are absent in Nepidae and Corixidae, which have the same type of eclosion.

The following scanty observations of the notonectid embryo during this phase provide a basis for experiments. The rotation of the prolarva occurs after yolk uptake is complete and eyes have reddened, but before the larval hairs darken. The rotation is the result of regular short jerks. The rate varies but one jerk every 10–20 seconds is normal. The turning effect of a jerk is almost imperceptible but a continuous series of them makes the embryo rotate 135° in about three quarters of an hour. Both left and right rotations were observed but we did not analyse possible predominance in one direction. The latter possibility would not be improbable, considering the unidirectional asymmetrical folding of the legs (see below). The nature of the jerks was studied in a series of eggs from which the chorion was peeled off. The centre of motion seems to be the left part of the abdominal base, which intermittently contracts abruptly dorsoventrally, causing a vigorous flow of the viscous ambient fluid. The legs quiver convulsively at an independent rate; the head jerks slightly backwards and forewards. The abdomen seems to turn first, then the fore parts. These actions may not be a direct cause; yet when rotations stop, the pleuropodia become inactive. This is shown by the

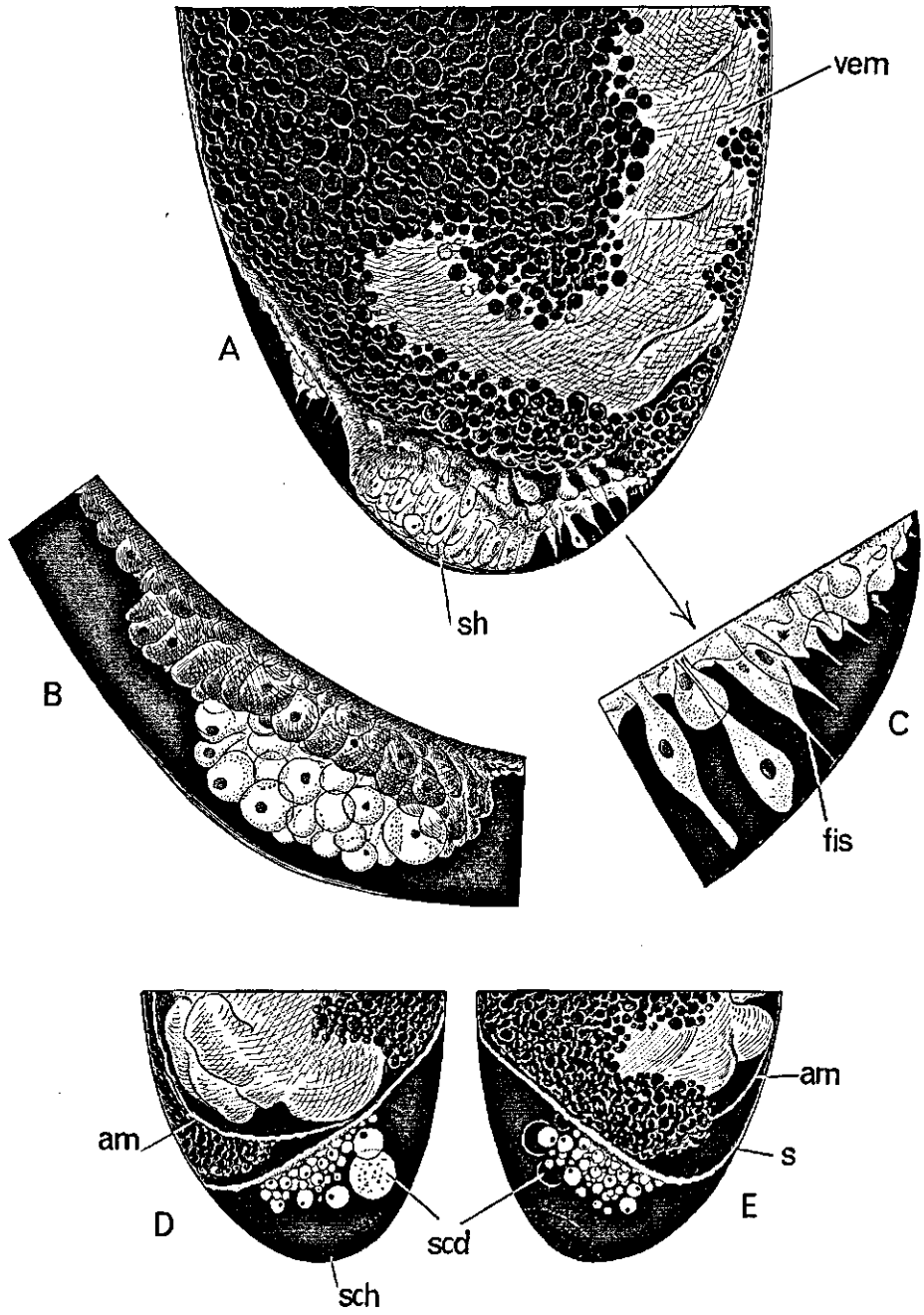


Fig. 246. Notonectidae, *Notonecta glauca*, basal pole, chorion removed, retraction of serosal hydropyle (A), expulsion (B) and degeneration (D, E) of central cells; D and E: opposite lateral sides of the egg.

sudden appearance of a black plug over the outlet of the pleuropodial gland.

Before rotation the head and thorax is entirely surrounded by fluid. Later on, the swollen body fills up the whole lumen and the friction of the turning prolarva causes wrinkles in the serosal cuticle. The absorption of water through the serosal cuticular hydropyle is meanwhile clear from the expansion of the whole egg. In eggs dechorionated just after dorsal closure, the lumen under the hydropyle enlarges and over the next days the egg lengthens considerably and widens at its anterior pole. This second swelling occurs now in absence of the serosal hydropyle. Some watery substance remains outside the prolarva in the cephalic pole until the hairs are turning black (fig. 242B). At the same time the basal pole is full of fluid too but half an hour later the prolarva occupies the whole inner face of the serosal cuticle. In all eggs, dechorionated some days before, the black outer coat of the serosal cuticle along the fore side of the larval head disintigrates through a slight bulging of the serosal membrane itself. Fig. 243A, B and 248A show an eclosion identical with Hydrocorisae already described; it becomes now clear from the foregoing observations that the bubble which protrudes from the chorion is the weakest ring of the serosal cuticle. By a sudden disgorging of watery substance from the prolarva, it is only this area which inflates and breaks the chorion (fig. 241D). That the prolarva plays a momentarily active role in inflating the serosal membrane, is revealed by the lack of bladder formation, when the egg is deprived of the chorion just before eclosion. The prolarva gradually fills the protruding membrane by swallowing the fluid from the serosal cuticular bladder.

Vibrations of the larval skin, two circular areas on the frons and one area on the vertex show the muscular activities concerned with drinking. The two pairs of stylets too are in steady vibration. Although they are short stiff bristles, they have no part in breaking the serosal cuticle. The latter pushed out to its maximum extent splits longitudinally. The chorion always breaks into rays (fig. 243C). The lateral deviation of the longitudinal ray of this scar shows no significant preference for one direction. The folding of the legs in the prolarva is as in *Ilyocoris*. Only two eggs of the 32 of *N. glauca* showed the mirror-image of fig. 242C. In *N. obliqua* the unilateral dominancy was less pronounced, namely 3:1 (number of eggs 27).

Anisops sp., Buenoa sp.

The micropylar outer projection is fitted in a flat seemingly porous scale, which is part of the pseudopercular rim (fig. 250). The chorion of the embedded eggs is finely and densely perforate on the polygonal areas. It seems that the cap is formed before it functions as a pseudoperculum. At least in the *Buenoa* egg, a longitudinal line over the lid is split, when the egg is heated in lactic acid. Such a line can be traced in intact eggs, which suggests lengthwise eclosion despite the distinct pseudoperculum. In one of the two Anisopinae from Africa, the same condition occurs; yet empty shells show a longitudinal split.

The available fixed eggs of *Anisops* contain the embryo in the condensed and some earlier stages lying along the aft side of the egg. This suggests an early rotation of the

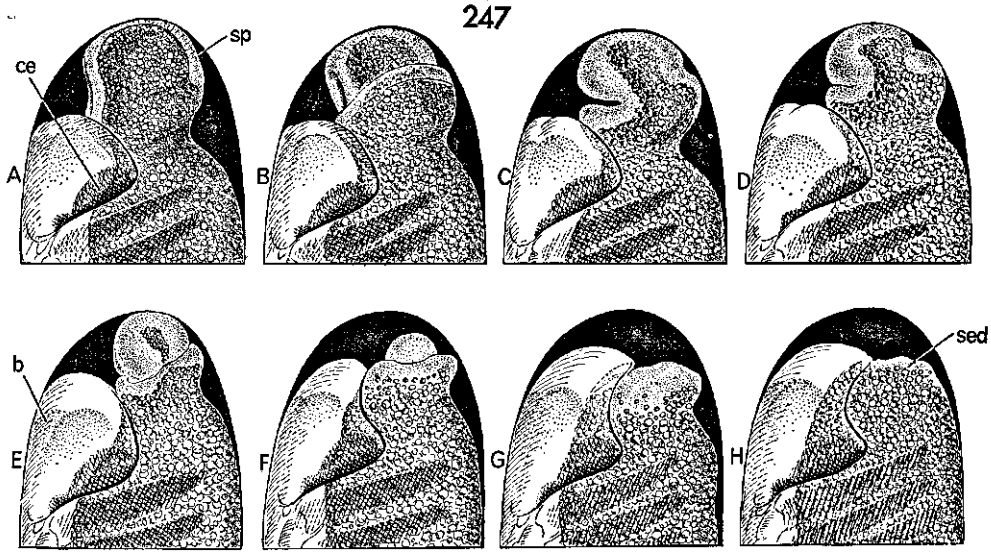


Fig. 247. Notonectidae, *Notonecta glauca;* A–H: anterior pole, chorion removed, formation of secondary dorsal organ by beat-like involution of the serosal plug (see text, p. 224).

band, as is normal in most typical Notonectidae.

PREVIOUS DESCRIPTIONS The external patterns of the chorion have been described as specific differences in several European (LARSÉN, 1930) and American notonectids (HUNGERFORD, 1919; KORSCHELT, 1884; RICE, 1954).

The Anisopinae eggs, studied thus far, are embedded and look operculated: *Anisops producta* Fb. (POISSON, 1926; micropyle erroneously located by him at the lower edge of the pseudoperculum), *A. breddini* Kirk. (LEONG, 1962), *Buenoa margaritacea* Bueno (HUNGERFORD, 1919).

Rotations after blastokinesis, described above, have been reported by HUNGERFORD (1919), LARSÉN (1930), LESTON (1955b), LEONG (1962) and DAVIS (1964). LEONG mentions that in *A. breddini:* "...the insect rotates almost continuously on its longitudinal axis, first in one direction, then in the opposite direction. Each rotation takes 2 to 3 minutes and it changes direction every 2½ to 3 turns. Rotation is accompanied by pulsation of the abdomen". The opinion that the rotations are provoked by light (LESTON, 1955) has already been disproved on p. 226. LARSÉN (1930, his p. 228–229) gives another unlikely explanation of the phenomenon, based on the wrong assumption that the eggs are inserted *(N. glauca)* in a variably turned position. According to him, the prolarva has to rotate in order to find the split in the substrate from which it can freely leave the egg. This would imply that the split would be found in morphologically different sites on the shell. However, as shown above, the split follows a constant pattern below the micropyle. For that matter, one need only compare the identical situation in opercular eggs: *Ilyocoris, Anisops,* to refute LARSÉN's theory. LEONG (1962)

mentions the appearance of haemoglobin in the egg of *A. breddini*. Without any discussion or elaboration he reports in his time-table on the gross embryogeny that irregularly scattered haemoglobin masses appear on the fourth day (beginning of segmentation of the germ band), which accumulate mainly ventrally. The haemoglobin is said to be found as four round masses in the mid-ventral abdominal region some days before eclosion. Haemoglobin is known to occur in the pelagic Anisopinae, so its occurence in the first larval instar is not surprising. There are, however, several inaccuracies of observation in LEONG's paper, so that any formation of haemoglobin at such an early stage in the egg needs careful confirmation.

DAVIS (1964) observed hatching of *Notonecta melaena* Kirk. and he ascribed the swelling of the serosal cuticle (his 'blister membrane') entirely to osmosis. Our observations (p.228) suggests that inflation of the cuticle is at least partly due to disgorging of water by the prolarva.

2.4.6 Pleidae, Helotrephidae

MATERIAL: Pleidae: *Plea atomaria* Pal. (living deposited eggs), *Plea puella* Barb. (ovarian eggs, origin Curaçao, Neth. Ant.).

Helotrephidae: *Tiphotrephes indicus* Dist., *Helotrephes* sp. (for both species ovarian eggs, origin Malaya), *Esakiella hutchinsoni* China (ovarian eggs, origin Uganda).

Pleidae

Plea atomaria

The eggs are large in relation to the insect, and are embedded in submerged plants. Whereas *Ranatra*, *Ilyocoris* and *Notonecta* sp. readily embedded their eggs in polystyrene foam, *Plea* did not. The aft of the egg is convex, the fore side slightly concave in profile and only a narrow, elliptical strip is exposed from the oviposition slit.

Many females, collected in mid April, failed to deposit eggs, despite the fact that they preyed voraciously on morbid drosophilid flies. Twenty or thirty of these females were dissected in June and they all had atrophied ovarioles but fully developed wing muscles. Nevertheless, we saw no attempted flight to escape from the containers. Females, collected one month later from the same pond, started laying within a few days. Both males and females of this latter sample had degenerated wing muscles, whereas the reproduction organs occupied a great deal of the thoracic lumen. Laying extended over a long period under the same indoor conditions as the first sample. Although we had not checked the wing musculature of the latter specimens on the day they were caught in April, it seems that under unfavourable conditions the species can switch to a flying state at the cost of the oogenesis.

CHORION The shell bears distinct, large and thickly ribbed hexagons. Marginal knobs occur within each hexagonal plane (fig. 251H). The 5 μ-thick shell is further

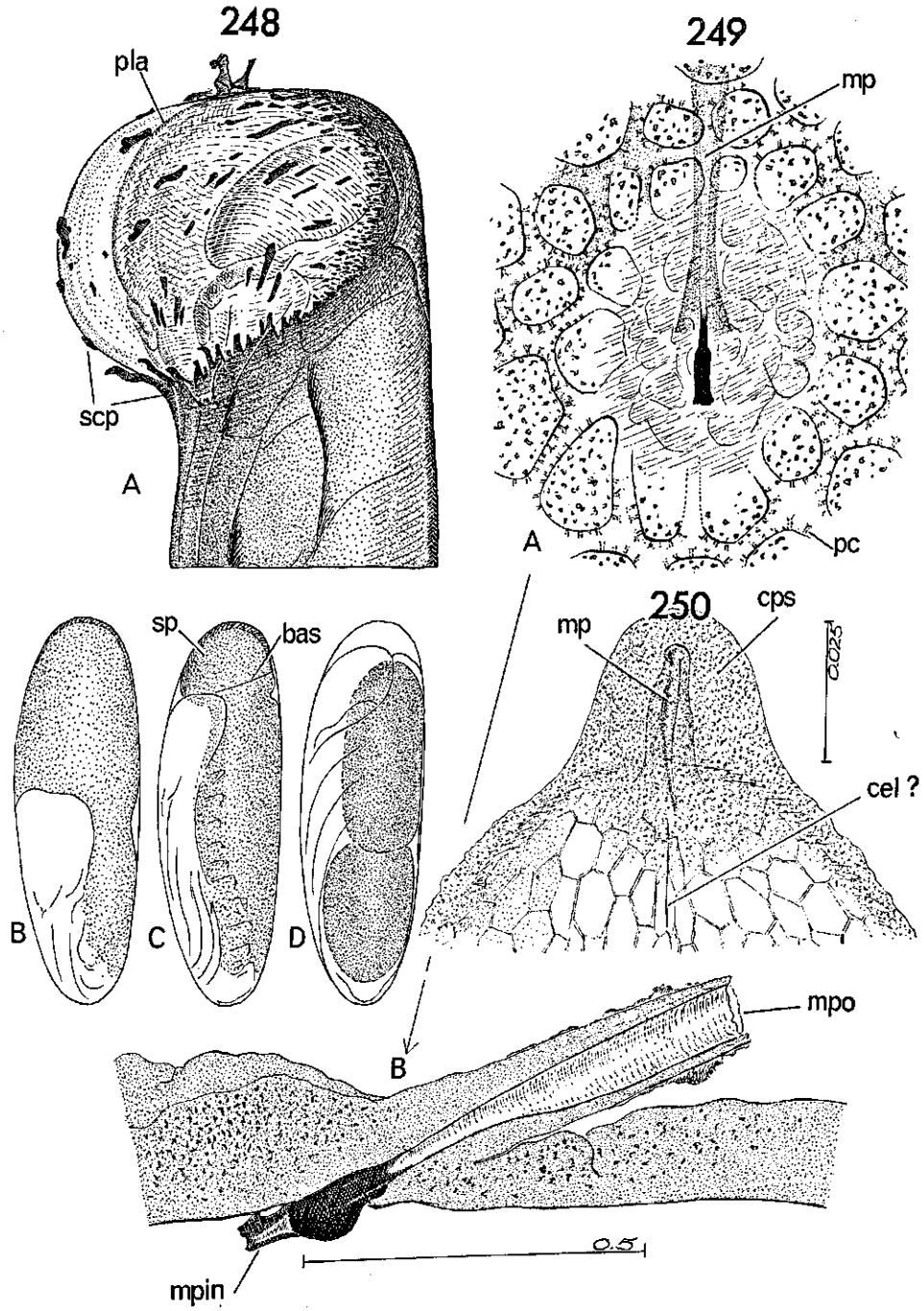


Fig. 248–250. Notonectidae 248. *Notonecta glauca;* A: the bladder formation of the serosal cuticle in a dechorionated egg; B–D: diagram of the yolk column during and after revolution. 249. *N. maculata,* micropylar area; A: inner surface of shell; B: longitudinal section. 250. *Buenoa* sp. (Neth. Ant.), anterior edge of shell, fore side, ovarian egg.

traversed by fine tubules (fig. 251G, pc). The internal structure has not been analysed but surface views and optical sections suggest there is no inner porous layer. The single subapical micropyle has an external diameter of about 10 μ and an internal one of 1 μ. The micropyle does not project into the lumen of the egg (fig. 251G). The oval exposed area of the shell along the fore side (fig. 251A′) suggests that it forms the boundary of a pseudoperculum. As will be demonstrated below this is not the case.

GROSS EMBRYOGENESIS A constant temperature of 30 °C is not lethal to the egg; complete incubation lasts about 10 days. At room temperature, development takes about 22 days. Invagination starts in the centre of the basal pole and the band rises along the fore side, entirely superficial (fig. 251A, A′). From the beginning, the band elongates along a line which makes a small angle to the mid line of the egg.

Soon this deviation becomes marked and the band flexes obliquely along the right side of the egg to reach first with its tail the aft side (fig. 251B, B′). The embryo assumes a remarkable torsion. With further elongation it occupies the whole length of the aft side of the egg but initially still in a slightly oblique orientation (fig. 251C, C′). Apart from the asymmetrical position of the whole band within the egg, the band itself shows a distinct bilateral asymmetry until blastokinesis (C′–E′). The two flanks of the band are differently crenate even after the outbudding of the appendages when both the embryo's and the egg's polar axis coincide (D′). In addition, the long and narrow abdominal part with an inward kink at its base leans over to the left of the egg (D, D′). This lateral deflection is constant and is maintained in the condensed stage (E, E′).

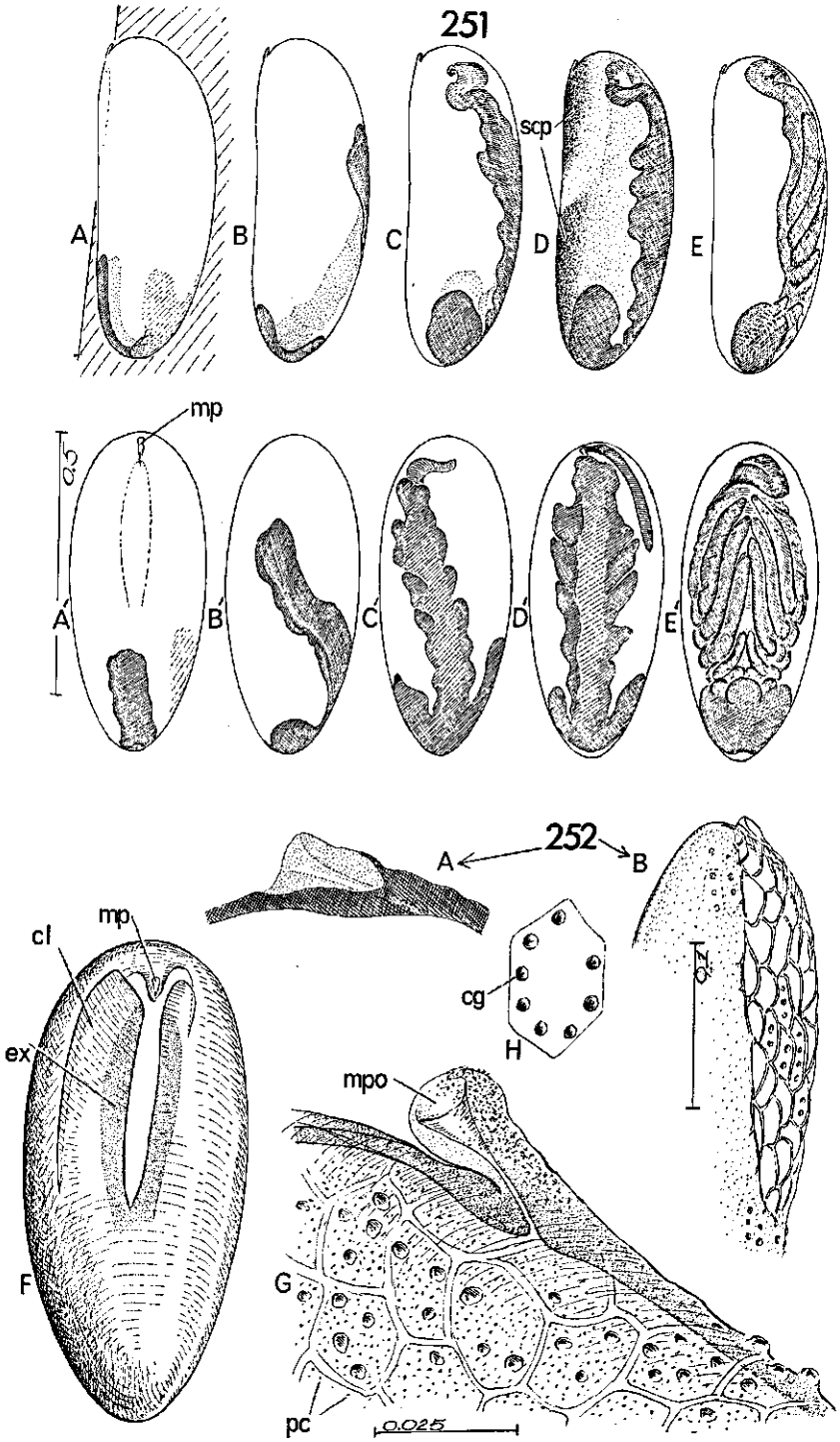
The serosal cuticle is discernible as such in stage C and has darkened by stage D (fig. 251). The darkening is intense black along the fore side and light grey elsewhere. A spot at the basal pole and a broad ring obliquely over the anterior pole remain whitish. It may be that these exclusions relate to water uptake, although we could not detect a distinct serosal hydropyle, either in living or stained eggs. The eye spots are pale red before the embryo turns.

Blastokinesis comprises a simultaneous 180° rotation and revolution of the embryo. The resultant spiral causes the reversed embryo to face ventrally to the aft side. Contrary to *Ilyocoris* and *Notonecta*, this orientation is maintained until about one day before eclosion (room temp.). Only on the last day did all the many eggs studied show the prolarva in the right position for emergence, facing the eclosion slit. Continuous rotations, however, have not been observed.

ECLOSION The posture of the mature embryo is as in all other Hydrocorisae but the asymmetric folding of the legs in all 35 eggs studied showed the mirror-image of the arrangement usually predominant in other waterbugs (fig. 280U). The mechanics of eclosion is by water pressure as usual in Hydrocorisae; the pressure expands the fore

---

Fig. 251–252. Pleidae 251. *Plea atomaria;* A–E: early embryogenesis, lateral view; A′: fore side; B′–E′: aft side; F: vacated shell; G: micropylar area, optical section; H: chorionic hexagon. 252. *Plea puella;* A: micropyle, longitudinal section; B: anterior pole, lateral.


251
A
B
C
D
E
scp
mp
as
Á
B́
Ć
D́
É
252
A
B
cg
H
as
cl
mp
ex
F
mpo
G
pc
0.025

and anterior of the serosal cuticle. The protruding serosal cuticular bladder lifts up a flap of chorion, which may almost be considered as a pseudoperculum. It appears, however, against expectation that its boundary does not concur with the oval flat area, the only part of the shell which is exposed (stippled area in fig. 251F). From the same figure it can be seen that the design of the fracture resembles the pattern in *Notonecta* eggs (fig. 243C). The development of the lateral eclosion flap as one mode of operculum-formation will be discussed on p. 276).

The shell structures of *Plea puella* (fig. 252A, B) agree in the main with the *P. atomaria* egg. The exposed area seems somewhat more evolved. This area differs in texture from the rest of the shell and is structurally more sharply defined. It is not certain whether its boundary indicates a similar later fracture.

Helotrephidae

Tiphotrephes indicus, Helotrephes sp., Esakiella hutchinsoni

Eggs are large and fill the thorax as far as the middle of the pronotum. The egg shape of *Tiphotrephes* (fig. 253A, B) suggests an entirely exposed deposition (analogous to *Notonecta maculata*) and a non-circular eclosion rent. The egg of *Helotrephes* and *Esakiella* may also be attached lengthwise to judge from its similar shape (dorsoventrally compressed, flat aft side thinner and without extending ribs). The anterior pole in these latter two genera, however, bears an irregular annular porosity which most probably represents the boundary of an eclosion cap (fig. 254A). The undulating line of porosity follows the upper rib of the adjacent polygons (fig. 254B) which are arranged in a circle. The polygonal lining on the cap is much less pronounced but otherwise has the same wide tubules on the polygons as elsewhere over the shell. The tubules ramify inward, but these do not form a continuous open system with connecting canals. In *Tiphotrephes* the polygonal ribs are thick and pitted along their margins by pores (fig. 253C). The three species have only one micropyle with only a very short inner projection. The exterior horn is short in *Tiphotrephes* and longer in *Helotrephes* and *Esakiella* where it is found on the cap.

PREVIOUS DESCRIPTIONS The only data from literature are the descriptions of the exterior of the *Plea atomaria* egg by WEFELSCHEID (1912) and of the *P. striola* Fb. egg by HUNGERFORD (1920). The former concluded that the flat side covers the dorsum of the late embryo. His figure D, however, demonstrates that there is an ultimate rotation of the prolarva. The helotrephid eggs have not been described before, as far as we know.

2.4.7 Ochteridae

MATERIAL: *Ochterus marginatus* Latr. (living, deposited eggs, origin Ivory Coast), *O. perbosci* Guer. (ovarian eggs, origin Curaçao, Neth. Ant.); *Megochterus nasutus* Mont. (ovarian eggs, origin Australia).

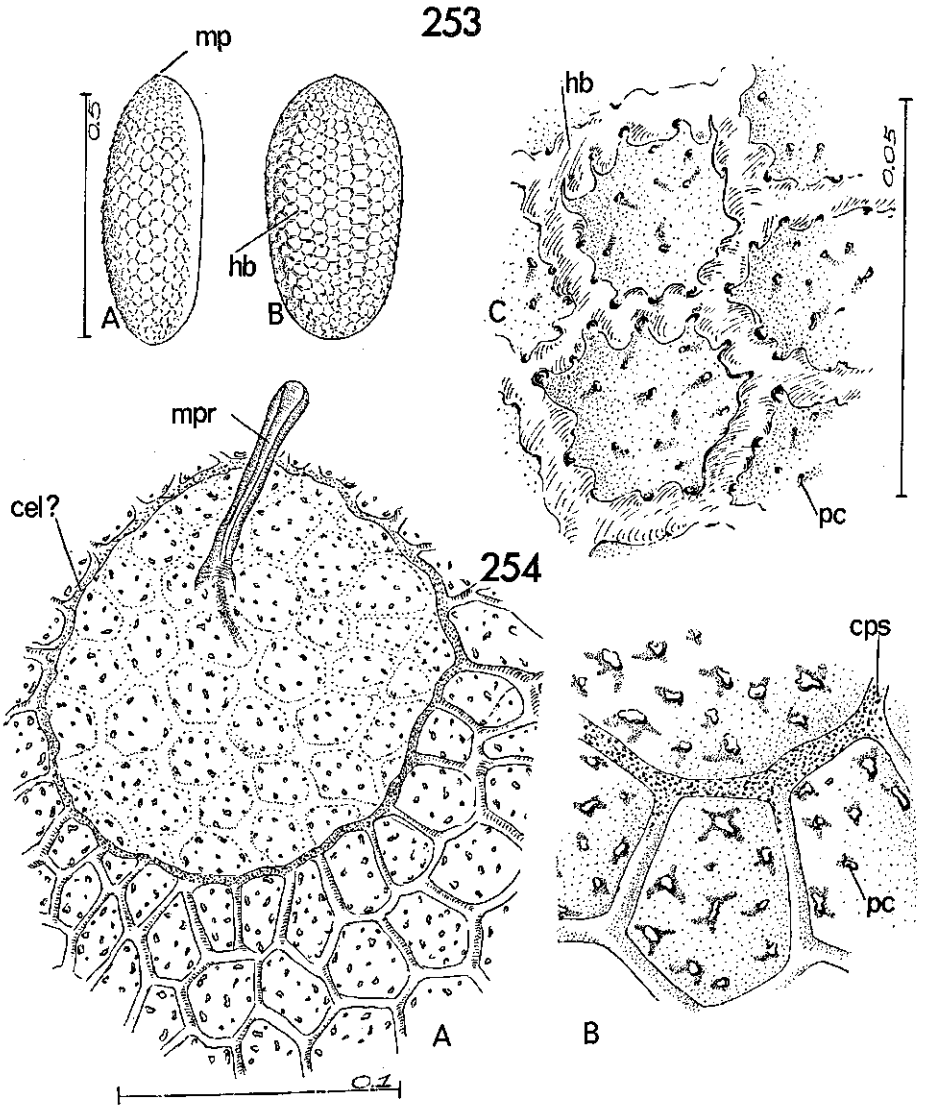


Fig. 253–254. Helotrephidae. 253. *Tiphotrephes indicus*, egg; A: lateral; B: fore side; C: surface view of chorion. 254. *Helotrephes* sp.; A: anterior pole, fore side; B: fragment of supposed pseudoperculum.

Ochterus marginatus

Captive bugs lay eggs horizontal on moist filter paper. The less convex side faces the substrate. When only wet soil was offered, eggs could not be traced, although larvae appeared later. It may be that eggs are normally buried or covered with soil particles, as are the larvae.

CHORION The entire circumference of the shell has circular pores (1–2 μ), leading to tubules down to the inner chorion. These canals are referred to as aeropyles, although they may be filled with water, considering the wet habitat in which the eggs are laid. The pores border both sides of the indistinct follicular ribs. The oblique tubules from each side point towards each other and branch half way through the shell (fig. 255H). As a result, an internal reticulate pattern is seen following the polygonal design, observed in surface view (fig. 255G). It seems that a continuous porous layer separates the inner layer and outer layer which is about 7.5 times thicker. The egg has a round anterior cap. Its boundary is lined but a sealing bar is not developed. The single micropyle, in the centre of the cap, is a simple hole of about 7 μ and is bordered by a raised rosette. A distinct chorionic hydropyle is lacking.

GROSS EMBRYOGENESIS Invagination starts at the apical pole (fig. 255A). The elongating germ band loops through the yolk and shows a cluster of what could be germ cells dorsal to its tail (fig. 255B). The band flexes back apically over the dorsum at the time the protocormic outgrowths appear. Without touching the serosa, the extreme top folds again fore-wards (fig. 255D). Up to blastokinesis, the embryo assumes a position close to, but still distinctly separated from, the fore side of the egg (fig. 255E). Blastokinesis has not been followed in life but, to judge from the later position of the embryo (fig. 255F), it comprises a rotatory or spiral displacement. The serosal cuticle colours the fore half of the egg brownish, whereas the submicropylar area always possesses a black spot. In the eggs which have been fixed and after three months stained, no serosal hydropyle could be distinguished.

ECLOSION Eggs have not been observed steadily so that it remains unknown the embryo rotates after blastokinesis. The folding of the legs is as in other Hydrocorisae but any unilateral dominance of the folding has not been checked. The pseudoperculum is lifted by a serosal cuticular bladder and the embryonic cuticle is entirely devoid of egg-burster.

O. perbosci

The egg surface bears small tubercles, each penetrated by a vertical tubule of varying shape ramifying interiorly (fig. 256A). The tubercles are regularly spaced anteriorly but laterally they are grouped on the indistinct follicular ribs, thus revealing a polygonal pattern. The hexagons each bear a small group of canals in the centre. That there

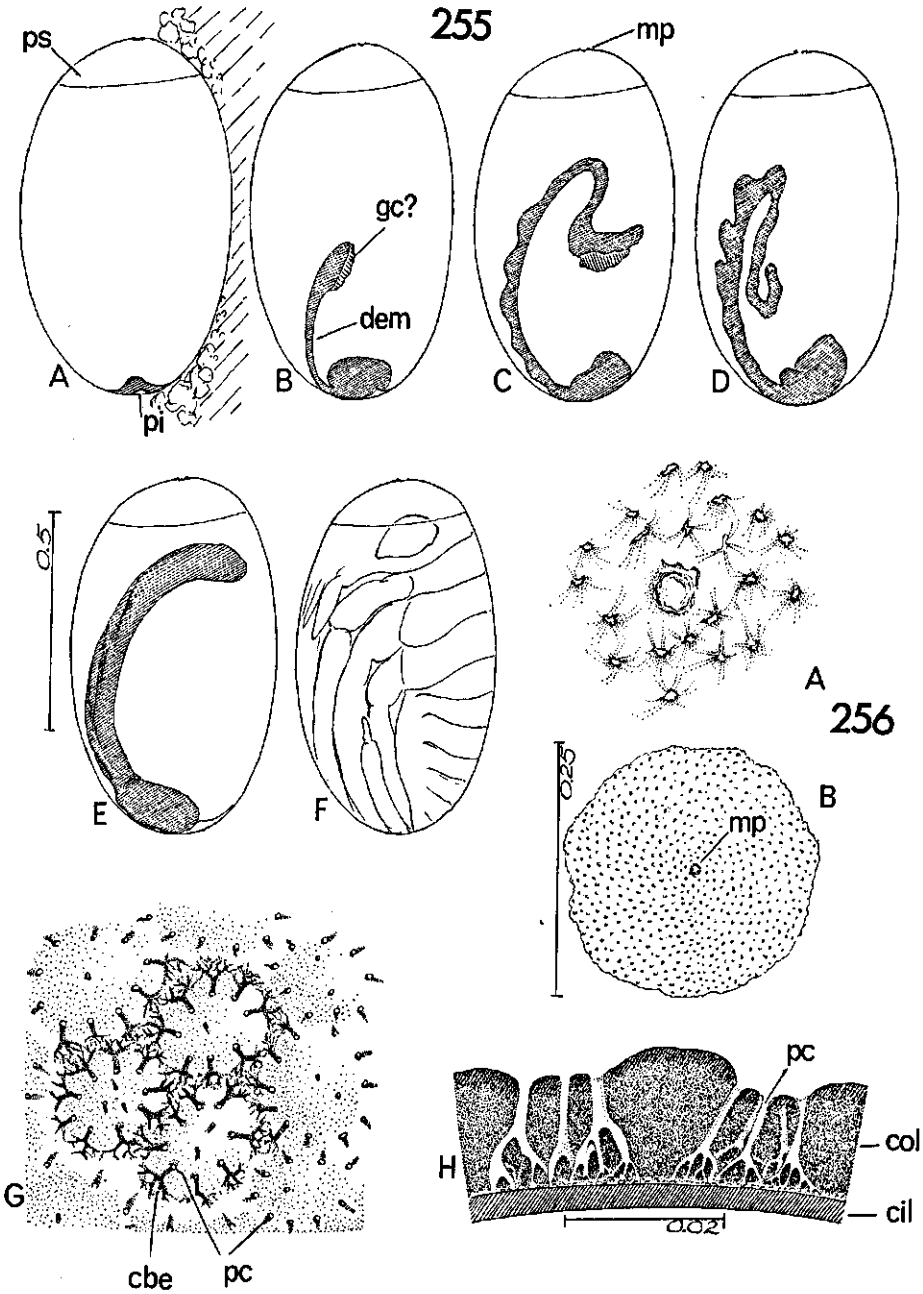


Fig. 255–256. Ochteridae 255. *Ochterus marginatus;* A–E: first half of embryogenesis; F: prolarva; G: surface view of the shell showing the internal branching of the pore canals with lower focusing; H: transverse section of shell. 256: *O. perbosci;* A: micropylar area; B: pseudoperculum.

is a continuous open layer between the inner and outer layer, as seen by optical microscope in *O. marginatus*, is confirmed by electron micrographs (fig. 304A–D). The sections were transversely through the waist of an ovarian egg. Notice that the outer surface of the inner layer is delimited by a sharp black meandering lining. The open interspace is lacking in the anterior cap (fig. 304E). The latter breaks very irregularly during maceration (fig. 256B). The micropyle is as in the foregoing species.

Megochterus nasutus

It differs in several important respects from the foregoing two species. First, there are two micropyles and, second, the inner chorionic meshwork extends uninterrupted up to the micropylar area. It is furthermore most likely that natural eclosion follows a longitudinal course.

PREVIOUS DESCRIPTIONS BOBB (1951) has given an outline of the egg of *Ochterus banksi* Barb., which is deposited singly on plant debris and on grains of sand.

2.4.8 Gelastocoridae

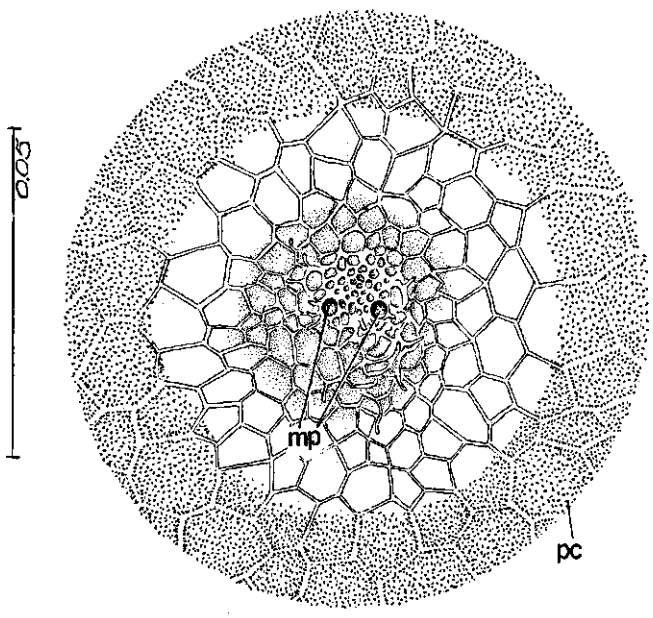
MATERIAL: *Nerthra* species (origin Surinam), *N. terrestris* Kev. (origin Trinidad); *N. laticollis* Guer.-Men., *N. colaticollis* Todd (origin of both, New Guinea); *Gelastocoris nebulosus* Guer.-Men. (origin Argentina). Only ovarian eggs were studied of all species.

Nerthra sp. and N. terrestris

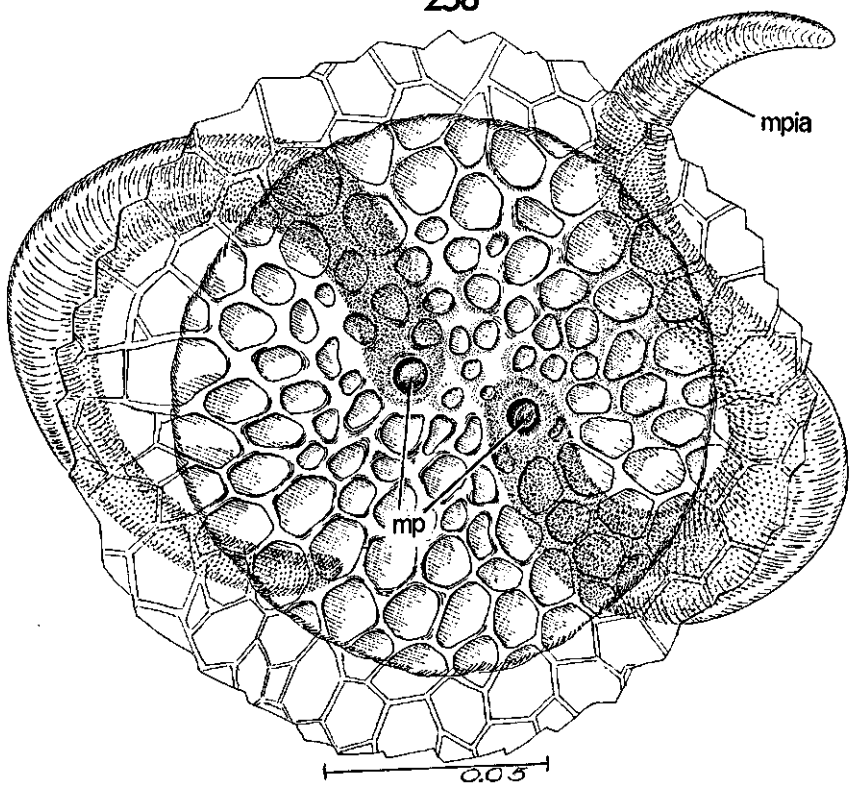
The nearly isoradial broadly oval eggs have rough hexagonal sculpture and are densely perforated with aeropyles within the hexagons only. The blunt cephalic pole is marked off by a circle from the rest of the egg but maceration of ovarian eggs with lactic acid never loosened a round lid. Therefore it has not been determined whether the eclosion is by a longitudinal or a circular crack. A ring of transversely widened hexagons, surrounding the micropylar area at a distance, suggest the latter alternative for the first species. If so, an eclosion rent of the *Corixa* type may be expected. In both species there are two simple micropyles in the centre of the anterior pole (fig. 257, 258). These are obviously formed each by one rounded follicular cell (diameter, 5 μ in *N. sp.* and 2 μ in *N. terrestris*). In the former species, the pore is in contact with a long thick inner projection shaped like a cow's horn (fig. 258). This consists of a testaceous stiff gelatinous substance, in which no canal could be traced. The horns resemble identical structures in some naucorid eggs. A wide circle around the micro-

Fig. 257–258. Gelastocoridae 257. *Nerthra terrestris*, anterior pole, surface view, ovarian egg. 258. *Nerthra* sp. (Surinam), micropylar area, surface view, ovarian egg.

257



258



pylar area is entirely devoid of aeropyles. No chorionic differentiation of possible hydropic nature was traced.

N. laticollis and N. colaticollis

The micropylar area is much smaller and contains only one micropyle in the 10 eggs studied. The pore lies in a slight depression at the pole and projects obliquely inward towards the fore side. The ring surrounding the micropyle and devoid of aeropyles, is small. Heating in lactic acid splits the eggs down the middle through the micropylar region. The many aeropyles ramify in the inner half of the shell, thus forming a continuous porous layer. This open inner layer is shown in the electron-micrographs (fig. 305A–D). It is slightly thicker than in *Ochterus*, with which the shell agrees in general stratification.

Gelastocoris nebulosus

The eggs are longer than of *Nerthra* and have fewer and large hexagons. The hexagonal areas are penetrated by spacious canals (fig. 259), dividing inwards and ending in a porous layer. The latter is adjacent to a thin chorionic inner layer. There are one to three micropyles, difficult to see as they are hidden in the rim of a complex crater at the cephalic pole (fig. 259). The micropyles are only recognizable by their inner projections which point away from the pole. There is no circular area around the crater, which could suggest a cap eclosion and all eggs split lengthwise in macerating fluid.

PREVIOUS DESCRIPTIONS HUNGERFORD (1919, 1922) showed the outline of the egg of *Gelastocoris oculatus* Fabr. Eggs are completely or partly buried in sand, anterior end up. The shell splits lengthwise at eclosion. HUNGERFORD (1922) noticed a white bulge through this rent, which he compared with the bubble found above the head of *Corixa*. Thus it is certain that eclosion is effected in *Gelastocoris* by the serosal cuticle and that it happens as in other Hydrocorisae. *Nerthra martini* Todd lays eggs in small holes in mud beneath stones several feet from the water's edge (USINGER, 1956). In both instances where USINGER found eggs, the female was sitting over the egg cluster in the hole, indicating a possible guarding of the eggs.

2.5 Dipsocoroidea, Enicocephaloidea

2.5.1 Dipsocoridae

MATERIAL: *Pachycoleus rufescens* Shlb. (living deposited eggs), *Cryptostemma japonica* Miyam. (ovarian eggs, origin Japan), *Ceratocombus coleoptratus* Zett. (living deposited eggs).

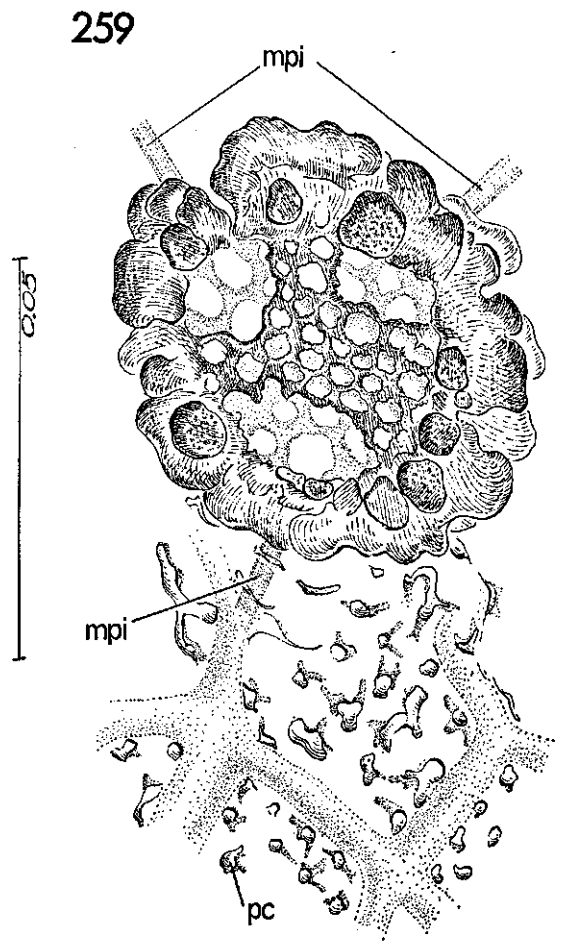


Fig. 259. Gelastocoridae, *Gelastocoris nebulosus*, micropylar plug with three micropyles, ovarian egg.

Pachycoleus rufescens

In rearing boxes eggs were preferably deposited in debris, particularly in sheltered places such as within dead blackened peaces of *Equisetum* stalk. The very typical egg, resembling the shell of the molluscs of the genus *Cypraea* (fig. 260C) is laid flat with the convex side pressed in the muddy substrate.

CHORION The shell of the large eggs is thin (2 μ), but of very hard consistency. It is one of the most difficult eggs for sectioning. The shell's surface is glossy, smooth, with a spacious but indistinct polygonal reticulation and without any sign of porosity. Electron-micrographs of a section through the side of the egg reveal one solid layer, distinguished only by colour into a dark inner zone and a lighter outer zone four times as thick (fig. 291A). In the whole cross-section not one opening is to be traced. It is

only the straight fore side of the egg, which seems to be adapted particularly to trap atmospheric air. Two parallel rims, with their upper margins nearly touching each other, run from one pole to the other. The rims contain aeropyles which have a remarkable course, which is not easily traced in three dimensions. Close to the poles the aeropyles are seen as a continuous fine grating, starting below the apex in the rim and emptying into a straight line of pores within the chorion at the base of the rim (fig. 260D). At a greater distance from the poles the aeropyles are grouped in bundles, especially in the upper half of the rim. Perforations in the rim are concentrated particularly in the region in front of each aeropylar bundle, thus suggesting respiratory relation between them. Although we are not quite sure, the air channels seem to run along within the rim, where they contact the air column contained in the rim tunnel during flooding. The rim from the innerside appears as drawn in fig. 260E. It looks as if the aeropyles are centred through the openings of a balustrade-like thickening of the rim's base. Whereas more canals emerge from each portal than went in, a regular series of pores marks the zone where the aeropyles end in the inner layer of the chorion. It seems that the porosity serving for gas exchange is confined solely to the two lines of interstices, corresponding with the implantation of the two rims.

There are three to four micropyles aft of the anterior pole (fig. 260D, mp). Being very narrow (scarcely 1 μ) and inconspicuous they are traceable with difficulty. They are prolonged interiad as a slender tube curving posteriad.

GROSS EMBRYOGENESIS Invagination of the band occurs along the fore side of the egg at a quarter of the egg's length from the posterior pole. The band remains entirely submerged. The early orientation of the embryo is illustrated (fig. 260B, incipient legs facing the convex side of the egg). The orientation before eclosion is such that the venter of the prolarva faces the rims of the egg. This implies blastokinesis without any rotation of the embryo, if it is assumed that prolarval rotations are absent.

ECLOSION Hatching has not been followed in life. One fully grown embryo dissected from the egg, revealed no special cephalic structures on the embryonic cuticle. The split is longitudinal between the two parallel rims. It has not been verified whether this line occurs along both rims, thus lifting the whole strip as a highly constricted pseudoperculum from the chorion but it seems probable.

The egg-shape and shell-structures of *Cryptostemma japonica* closely resemble *Pachycoleus*. There are four slit-like micropyles, which run obliquely through the chorion so that an opening is not discernible (fig. 261). The large delicately lined hexagons along the fore half of the egg have fine internal pores, suggesting a more widespread porosity than in *Pachycoleus*.

Ceratocombus coleoptratus

A population (both sexes, some old larvae) was collected early in August 1967. In the laboratory about a hundred eggs were laid some weeks later but all these went in

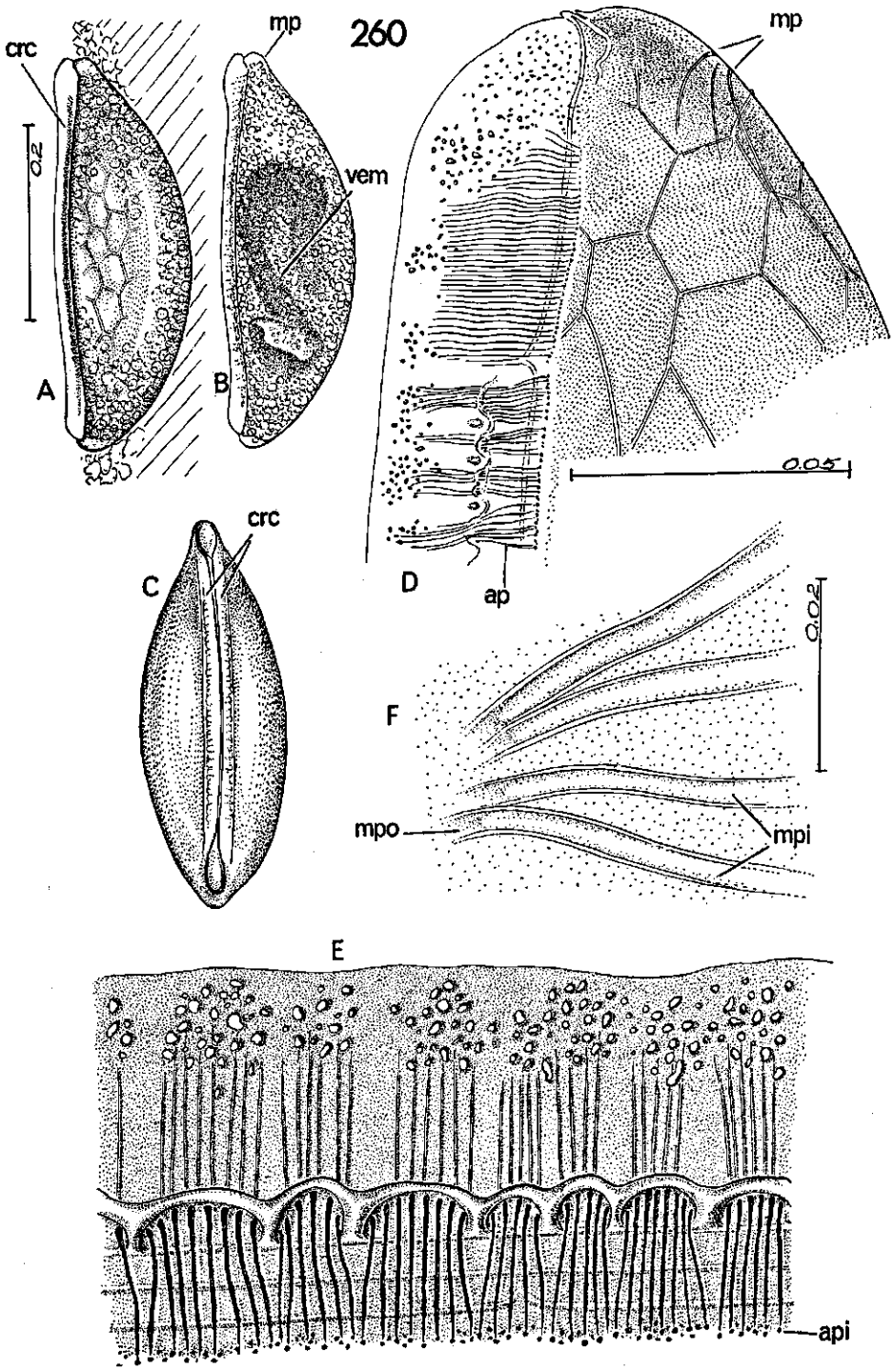


Fig. 260. Dipsocoridae; A–E: *Pachycoleus rufescens;* A, B: egg, lateral view; C: fore side; D: anterior pole, lateral; E: part of the rim collar. F: *Cryptostemma japonica*, micropyles, surface view.

diapause in an early stage of the germ band (both males and females died during August). Some eggs were laid entirely exposed, the majority however were inserted into filter paper up to the anterior pole.

CHORION The egg is quite unlike *Pachycoleus* and *Cryptostemma*, and is of a more normal shape. It resembles a cimicomorphous egg in outline and shape of the anterior pole (fig. 261D), but there are obvious distinctions. The foam-like crown around the truncate pole (fig. 261A) is soon thoroughly impregnated with air when the egg is allowed to dry out, but there are no defined aeropylar canals. The crown leaves the central area of the pole free, where there is a fine, smooth reticulation over the thin chorion. The shell cylinder just posterior to the crown is over a distance of 70 μ very thin, smooth and with a spacious hexagonal lining. It seems that this lining represents an intrachorionic tunnelling, which could lead air from the crown through the thin cylinder posteriad. The shell below the thin neck region is considerably thicker, everywhere traversed by a dense system of tubules. In the transitional zone on the aft side are a few micropyles, mostly three. Thus the position is almost as in *Pachycoleus* and *Cryptostemma*, but the course of the micropyles is the reverse. In *Ceratocombus* the internal canals run longitudinally towards the anterior of the egg (fig. 261A). Laid eggs were heated in lactic acid and in all these the chorion split in a similar way; therefore the break may conform to the natural eclosion rupture. It was irregular round the crown along the fore and lateral sides; on the aft side the chorion remains intact (fig. 261A). The split extends far downwards over the fore side along the median line.

EMBRYOGENESIS The eggs were still in diapause as the manuscript went to press (November 1967), so data remain incomplete. Some 20 eggs were stored for two weeks at –20 °C but all these died. Only a few of the eggs placed for two or four weeks at –2° or +3° developed after return to room temperature, though development was slow and irregular. The picture series (fig. 261D–J) seems to represent the normal course of embryogeny. Invagination invariably occurs aft from the basal pole and eggs diapause in stage E (fig. 261), when the germ band is still very short. The contact between head and serosa remained, except in one egg (fig. 261F). Further embryogeny after diapause is characterized by the immersed ♀ -stage with asymmetric head lobes, by the antennae flexed against the head and by absence of a distinct serosal hydropyle. Nevertheless, there must be absorption of water, since there is distinct swelling of the egg during incubation. A serosal thickening remains present just beneath the blastopore and this might be a hydropyle. Although stages right after revolution were not then available, one egg died during blastokinesis, half way through a 180° rotation of the embryo. The ultimate position of the prolarva is with its venter towards the concave fore side of the egg, and this position fits with the curvature of the egg. Actual eclosion has not been observed, but absence of any egg burster suggests hatching through fluid pressure within the serosal cuticle. The embryonic cuticle bears transverse ridges with minute pegs (fig. 261C), preventing the prolarva from slipping backwards into the

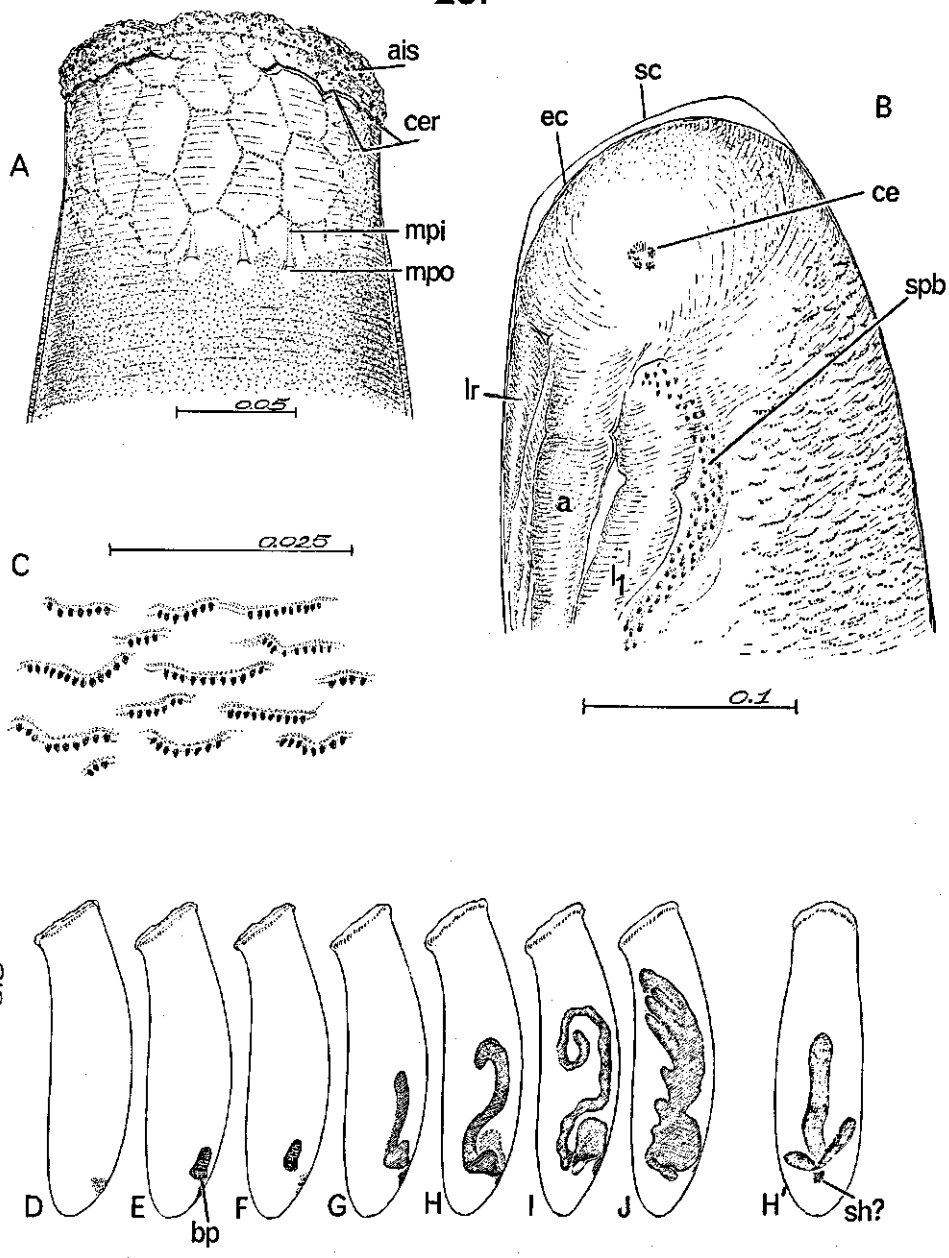


Fig. 261. Dipsocoridae, *Ceratocombus coleoptratus;* A: aft side of anterior pole, deposited egg heated in lactic acid; B: anterior part of egg before eclosion, chorion removed; C: rugose sculpture of embryonic cuticle; D–J: early embryogenesis, lateral view; E: normal position of germ band during diapause; F: exceptional position; H′: aft view of stage H.

shell. The same purpose serves a longitudinal, spiny band almost covering the base of the first leg.

If the patterns of embryogeny sketched for *Pachycoleus* and *Ceratocombus* are indeed representative for both taxa, they reveal an important dissimilarity, because *Pachycoleus* performs no embryonic rotation.

PREVIOUS DESCRIPTIONS The egg of an African species (*Trichotanannus dundo* Wyg.) is briefly described by WYGODZINSKY (1953). The long egg bears hexagonal ribs, most pronounced on the egg cap, which sits obliquely on the anterior pole. SOUTHWOOD (1956) interpreted the figure of WYGODZINSKY as though some form of chorionic rim was present, which would not seem to coincide with the margins of the cap; and further that the hexagonal sculpturing is less easily visible upon the top. Yet WYGODZINSKY claimed that the hexagonal ribs are most distinct on the egg cap "were they are well perceptible in lateral view". He refers to his figure, in which this elevation is shown in optical section, which could be mistaken for a rim.

2.5.2 Schizopteridae

MATERIAL: *Hypselosoma* sp. (ovarian eggs, origin Japan), *Nannocoris* sp. (ovarian eggs, origin Costa Rica).

Hypselosoma sp.

The large egg is covered throughout with small polygons with meandering borders (fig. 263). At the anterior pole, the polygons are regular and bear extending ribs, enclosing deep pits. No pores could be observed but they may be present, judging from the greyish appearance of the polygonal planes. Although no visible fracture line exists, the shell opens most probably by a circumpolar cap. This is concluded from the constant break in three eggs macerated in lactic acid. The micropyles are three or four, diameter 2 μ. They are along the convex side just above the eclosion fracture. They lie on one transverse hypothetical line, each in the plane of one polygon and are contained in a loop from one of the polygonal sides (fig. 263B). These loops and the internal micropylar tubes run clock-wise, when seen from the anterior pole.

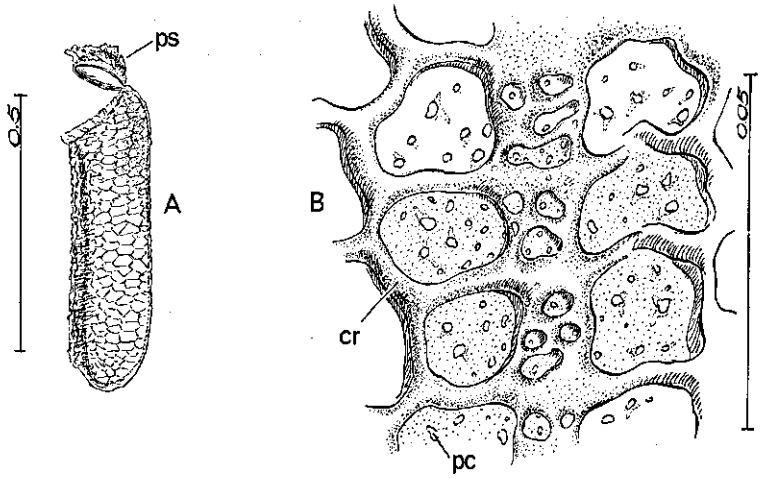
Nannocoris sp.

The long roughly sculptured egg (fig. 262A) is very large (occupying almost the whole length of the female's abdomen). The shape suggests that eggs are deposited

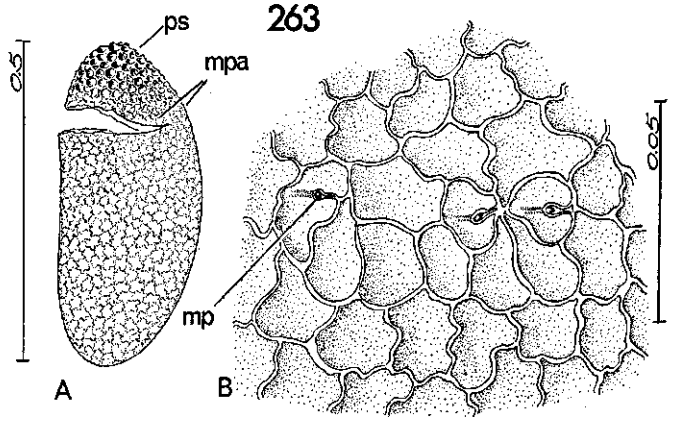
---

Fig. 262–263'. Schizopteridae, Enicocephalidae 262. *Nannocoris* sp.; A: ovarian egg, lateral view; B: surface view of chorion, fore side. 263. *Hypselosoma* sp.; A: ovarian egg, lateral view; B: surface view of the micropylar region (arrow in A). 263'. *Oncylocotis curculio*, external view of micropylar area.

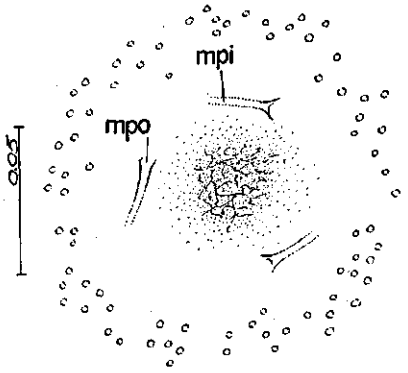
262



263



263'



exposed or almost entirely so. The shell has a diameter of about 27 μ on the fore side and about 12 μ aft. The polygons form an irregular pattern, because of a thick upgrowth on the ribs (fig. 262B). There is a distinct round cap, surrounded by a low rim on the egg's mouth. The whole surface is traversed by pore-canals of varying diameter and a porous inner layer seems to be present everywhere, even in the cap. Careful inspection of the single egg did not reveal any inner or outer spur of micropyle(s).

PREVIOUS DESCRIPTIONS ESAKI and MIYAMOTO (1959) give a detailed figure of the outer aspect of the egg of *Hypselosoma hirashimai* Es. & Miyam. The distinct reticulation consists of small cells with undulating edges and this sculpturing is much higher at the anterior pole. An anterior pseudoperculum separates from the loose deposited eggs. The presence of aeropyles and micropyles are not recorded, also not in the eggs of four species from Angola, described by WYGODZINSKY (1950). The latter belong to four genera and are strikingly divergent in shape but have all a well defined cap in common. The egg of *Machadonannus ocellatus* seems to be the most generalized with a simple anterior isoradial lid. In the other species the cap is slightly excentric, bearing filaments or a lacy hood-like elevation. In *Vilhenannus angolensis*, WYGODZINSKY noted that the shell bears numerous small perforations within the hexagons, which might suggest the presence of an inner meshwork-layer.

2.5.3 Enicocephalidae

MATERIAL: *Oncylocotis curculio* Karsh (ovarian eggs, origin Cameroon); *O. occipitalis* Jeann. (ovarian eggs, origin Nigeria).

In relation to the female, the eggs are large and subspherical; both species are essentially the same. The chorion is about 8 μ thick and seems entirely solid without any porosity or meshwork. Globules of chorionin extend slightly from the external surface of the smooth shell. The position of the globules is irregular, not forming hexagons. They are absent from the extreme anterior pole which bears 2–4 micropyles. The micropyles (2.5–3 μ wide) traverse obliquely through the shell and extend a short distance into the lumen. The micropyles are arranged in a circle and their inner extensions point anticlockwise when the anterior pole is observed from above (fig. 263'). It is extremely important to recognize that this course of the canals is just the reverse of what we have seen in all other heteropterous eggs with transverse micropylar canals. The centre of the micropylar area bears irregular cracks. Their presence in all eggs studied suggests a primitive respiratory function.

PREVIOUS DESCRIPTIONS Only superficial information on the enicocephalid egg is available (MYERS, 1926; JEANNEL, 1942; CARAYON, 1950). Eggs are simply affixed to the substrate. CARAYON studied the same species as we did; he noted the absence of any chorionic differentiation, even micropyles. The chorion splits transversely over the anterior pole and an egg-breaker seems absent. These data are too few to conclude that

enicocephalid eggs show similarities to hydrocorisous eggs as suggested by SOUTHWOOD (1956). From this, KUMAR (1964) inadmissibly generalized: "SOUTHWOOD showed that the eggs of Enicocephalidae are similar to those of aquatic Heteroptera".

3 Comparative evaluation of data. Appraisal of anagenesis and cladogenesis

With information from literature and acquired here we tried to trace separately the evolution of each egg-character.

3.1 Chorion

There is much confusion over what is chorion and what layers exist inside and outside the true chorion. According to the techniques used this has led recently to controversies of opinions (see HINTON, 1963). Interpretations of the sites within the shell, where the air is stored, vary. HINTON (1959, 1960) found that in air-filled eggs this air fills spaces between the vertical columns of the porous inner layer (in Diptera and also in some Heteroptera (1961, 1962a)). WIGGLESWORTH and BEAMENT (1950, 1960) thought that there is no free air in the shell of *Rhodnius* and that air merely permeated the 'solid protein layer', found earlier by BEAMENT. In 1962 WIGGLESWORTH and SALPETER concurred with HINTON over the position of air in the shell. The early incorrect conclusions must be due mainly to the injection of the shell with cobalt sulphide (HINTON, 1960). SOUTHWOOD (1956) gained little from the same technique in comparing eggs of land-bugs; often he could not trace micropyles and confused micropyles with aeropyles in some groups. Too great a value may have been given to the claim that in *Rhodnius* the micropyles are occluded with cement in the deposited egg and the aeropyles are left open. Another method used by SOUTHWOOD (1956), and based on BEAMENT (1947), is to soften the shell with dilute potassium hydroxide before cutting sections. It can not be recommanded as the effect of this medium on certain important structures is so drastic in Corixidae (see p. 194) and in Naucoridae (p. 210), that minor structural alterations must be frequently expected.

Our optical appraisal without injection confirms the experience of HINTON (1963) that the chief structures of the lumen-holding systems seen with the electron-microscope, can almost always be distinguished optically. The finding and recognition of micropyles in eggs, in which they have been claimed to be absent, also proves the superiority of simply careful examination of the whole shell or fragments. In some eggs, however, such as *Microvelia*, *Gerris* and *Corixa*, an inner mesh-work layer could not certainly be traced optically, whereas electron micrographs show a more porous inner layer of the shell. We could also not detect the aerostatic layer in whole mounts in some large Pentatomomorpha. The oversight of this layer, which was revealed in micrographs as a very thin open inner layer, is due to the extremely thick dark brown chorion.

The primary purpose of this paper is to identify those chorionic characters that have true phylogenetic value. Such fundamental characters must be separated from those characters that represent temporary adaptations to a specific environment. The chorionic layers are referred to here only in a topographical sense, since the data available from micrographs are still too scanty and variable to permit a homology with the terms endochorion, exochorion and extrachorion. The name extrachorion was introduced by HARTLEY (1961) to indicate the outer coating secreted in the common oviduct of Acrididae. In *Rhodnius* such an outer coating has been termed cement layer. Since the origin of this outer deposit(s) can be different, we prefer to call them 'suprachorionic layers' in analogy with the term subchorionic layers, already in use. The layers not derived from chorion will not be discussed here, although some notes on them have been given in the previous survey.

3.1.1 Architecture and aeropylar system

Leptopodoidea (fig. 1–40)

The shell of all the 39 saldid species (except *Aepophilus*) we studied conforms to the same basic plan: a solid relatively thick inner layer, an outer layer several times thicker and a hollow sheet between, held open by short props extending from the outer layer. The continuous porous layer opens along almost the whole circumference of the egg to the exterior with vertical canals in the areas enclosed by the hexagons, which are mostly indistinct. The same porous layer opens also along wider channels on the anterior fore side of the egg, mostly leading to the formation of what we termed the air clefts and sometimes to a basket-work. The sculptures of these structures are taxonomic distinctions, only at the specific level. As their types often do not bear a fixed relation with genera or subfamilies, which are otherwise morphologically well defined, we suggested that they originated recently, after the main phylogenesis of the family was already settled. For instance, the respiratory area of the two *Chiloxanthus* spp. (Chiloxanthinae) studied resemble typical Saldinae. *Pentacora* spp. (also Chiloxanthinae) are more like the Saldinae of the genus *Calacanthia* and *Saldula, scotica* group. Of this latter group *S. madonica* is completely distinct in shell porousness. Since Saldidae deposit the eggs above water level, the anterior shell openings probably serve for respiration and for trapping atmospheric air during flooding. Yet the significance of the widespread perforations is not understood, as it increases the danger of desiccation. Even in embedded eggs, this method of deposition is not as perfect as for instance in Miroidea. Much of the shell often remains exposed and the risk of water loss before formation of the serosal cuticle seems considerable, especially in the many species found in unstable moist habitats. On the other hand, the risk in such habitats is diminished by the brief incubation. Saldid eggs are covered outside with a thin sheet of material secreted in the ovarioles. This suprachorionic coat runs likewise over the pores and often over the air clefts. Besides serving as an adhesive, it may therefore also limit changes in humidity. Its physical properties cannot be predicted without ex-

periments. Such an outer layer is stated to be impermeable to water in the grass hopper *Chorthippus parallelus* but not in other species of the same genus (HARTLEY, 1961). During embryogenesis of Saldidae, water is absorbed through the posterior pole, where the spongy inner layer of the shell is less open. The chorionic hydropyle is not markedly differentiated. The respiratory physiology of saldid eggs is amphibian. Incubation time and successful hatching were not affected by continuous submersion or damp atmosphere. Embryogenesis is complete under water even when there is no reserve air in the shell, if the female is forced to deposit the eggs just under the water surface. The only exception in the Dutch species tested is *S. orthochila*, which prefers drier habitats. The egg larvae of this species, when hatched under water, did not succeed in reaching the water surface, since they cannot entirely free themselves from the embryonic cuticle.

The egg of *Leptopus marmoratus* shares the essential features of saldid eggs. It is densely pored and has the air clefts. Thus there is evidence that the chorionic pattern is a threedimensional reflection of the close relation between both families, despite the quite dissimilar physical demands it must meet in *Leptopus*. The shell of *Leptopus*, as far as its consistency is concerned, is different from the saldid egg. It remains flexible throughout incubation and water is certainly not taken up. Electron micrographs will most probably reveal a special protection of the shell, *e.g.* impregnation with a wax to protect the egg against desiccation. The respiratory system in Leptopodidae seems more variable than in Saldidae. *Leptopus marmoratus* has air clefts, *L. hispanus* some hexagons of greater porousness, and *Valleriola moesta* possesses special hexagons, which presumably serve as plastrons.

The shell of the marine *Aepophilus* differs morphologically from all other saldid eggs studied. Even under the electron microscope there was no trace of porosity. The two chorionic layers are of almost equal thickness and merge completely into each other. Optical investigation of whole mounts suggests that this structure is uniform round the entire circumference. No micrographs of the marine *Omania* egg are available but its structure as seen with magnification 750 × could suggest a similar compactness of the shell. Both *Omania* and *Aepophilus* live below high-tide level but the postembryonic stages have a normal respiratory system adjusted to free air. The egg structures mentioned may represent a special adaptation to prolonged contact with seawater, but the method of gas exchange through the shell remains obscure. The only perforation of the shell is the single micropyle. Other more typical Saldidae, pertaining to different genera and living along the sea-shore have normal perforated eggs, although they are temporarily flooded with water of high salinity. *P. signoreti*, occurring in largely salty habitats, possesses the most open shell. The eggs of *Ch. pilosus*, which bear pores and air clefts, incubate quite normally, when placed from the beginning in 30‰ saline.

Amphibicorisae (fig. 41–64)

Members of this group preferably deposit at or slightly above water level but some

gerrid species submerge completely to place their eggs below water. We have seen that the gerrid and veliid eggs studied are evenly porous. This porousness is much finer than in saldid eggs and the innermost chorionic layer is particularly thin and is about a hundred- and - twentieth or a thirtieth of the thickness in *Gerris* and *Microvelia*, respectively. The meshwork which lines the inner layer looks spongy due to a tangled system of fine anastomosing canals. There are no special aeropylar differentiations at the anterior pole. We have no micrographs of sections taken through the micropylar region, but such photographs of *Gerris* taken just below that region show no greater porousness. The thicker region over the micropyle in Microvelia seems no more porous than the rest of the chorion. The general spongy architecture of the shell and the habitat in water or damp places suggest the ability to soak up water as well as air. A serosal hydropyle has been found at the posterior pole. It is an open question whether only a restricted part of the chorion at that pole transports water or whether the porous inner layer of the entire shell is a reservoir for this uptake.

The *Hebrus*, *Mesovelia* and probably also the *Speovelia* and *Mesoveloidea* eggs on the contrary, have an entirely solid shell without any cavities except the traversing single micropyle. Micrographs show the sections to be uniform without stratification. *Hebrus* deposits eggs free or partly exposed on wet substrate. *Mesovelia* deposits close to, but always above, water level. The released gerrid, veliid and hebrid eggs are embedded in a gelatinous substance which swells in water. Moreover there is, in the *Gerris* and *Microvelia* species which were sectioned, a fine sheet close to the outer surface of the shell and below the gelatinous layer. The fine sheet may be homologous with the suprachorionic coat of Saldidae. Both the thin sheet and the jelly matrix are present in the ripest ovarian eggs. The substances apparently are secreted by the ovarian follicles and not, as was assumed by BRINKHURST (1960), by the accessory gland of the spermatheca. From the electron micrographs and the optical studies, it is apparent that the gelatinous coat is supported by processes like marbles, pillars or rivets. Although these projections are definitely chorionic, their bases are distinct from the underlying chorion. The knobs correspond in position to the angles of the hexagons and one or a few projections are within the enclosed areas. HARTLEY (1961) described the suprachorionic layer (his extrachorion) of *Locusta* as though this layer contained granules. The layer in question with the granules resembles, in its shrunken state, very much the condition in the Amphibicorisae eggs under discussion. Since in *Locusta* also the arrangement of the granules is hexagonal, they are unlikely to be added to the chorion later in the common oviduct as is claimed by HARTLEY, and not by the follicle cells.

The eggs of all the Amphibicorisae considered can develop fully and hatch normally either in water or a damp atmosphere. The embryonic development of *Gerris* is slightly retarded above water. The eggs of some Amphibicorisae do not conform to the gerrid-veliid type. Similar deviations of genital structures were observed also in these same forms (to be described in Part II). The remarkable shell of *Hydrometra*, which we analysed in some detail, renders it and that of *Limnobatodes* approximately terrestrial. The chorion contains an open air-filled inner layer. The extensive lace-like area of the

outer chorion covering the whole egg stores air during flooding. Micrographs show that the transverse partitions in the external layer bear openings. This thick, outer film communicates with the porous inner layer probably only round the top of the micropylar tube. Water uptake by the egg does not seem necessary for development. Yet the air store is not necessary for normal development and hatching when the egg is kept under water. It is surprising that eggs kept submerged develop normally even without an air supply, if free air is prevented from penetrating the shell cavities from the release of the eggs onwards.

The egg shape of both *Hebrovelia* and *Macrovelia* and the more terrestrial ecology of these bugs suggest that the eggs are attached lengthwise, partly or completely exposed and more remote from the water. The 7.5 μ-thick shell of *Hebrovelia* is densely and distinctly porous, as seen by optical microscope. The shell of *Macrovelia* shows an inner meshwork more clearly than other Amphibicorisae. Although no distinct outer pores could be traced, micrographs might reveal their presence, since anterior wider aeropyles are absent without doubt. The inner meshwork seems to be absent or at least very much reduced at the anterior end of the egg, which is enclosed by the ring of micropyles. The shells of the aberrant genera *Oravelia* and *Chepuvelia* are more vaguely porous.

Pentatomomorpha (fig. 65–132)

Those eggs tested, did not develop when placed under water although they can resist flooding when in diapause. The thickness of the shell in this terrestrial group ranges from a few microns to 0.1 mm *(Mictis)*. There is no close relationship between chorion thickness and egg size. Nor is the thickness readily affected by changing environmental conditions. Among the thin-walled eggs are those of Idiostolidae, Lygaeidae, Pyrrhocoridae, Thaumastellidae, Cydnidae and Acanthosomatidae. Most of them are laid protected in or close to the ground. But many species of Lygaeidae, the Corimelaeinae among Cydnidae and of Acanthosomatidae deposit higher up, those of acanthosomatids often being completely exposed (*Elasmostethus* without egg-guarding). Other egg-characters in these groups are rather plesiomorphous; the thinness of the shell probably reflects a generalized feature too. With a few exceptions, the shell is entirely solid and the inner meshwork is connected with the atmosphere only by the porous shafts surrounding the micropyles. They occur mostly close to the anterior end (most Lygaeidae) or at some distance from it but in one tessaratomid egg described they are below the waist of the egg. The position and number of the aeropylar shafts correspond to that of the micropyles and will be discussed under the next heading. The inner meshwork also runs along the pseudoperculum, if any, but whether it always extends towards the posterior pole could not be verified. In those species of the lygaeoid complex having radial cleavage of the anterior pole, the aerostatic inner layer seems to be reduced or perhaps absent towards the polar polygon. The still scanty information on shell stratification as in electron micrographs shows besides the thin air-filled inner layer, a single solid and uniform wall in the phyllocephaline

Macrina juvenca. In others *(Oncopeltus, Elasmucha)* the wall consists of two adjacent layers of which the outer layer has a higher electron-density. Somewhat similar is the condition in *Neuroctenus*, but the outer layer here has a coarse flaky porosity, which lays loosely upon the inner layer. It may be that the air-containing flaky outer layer contacts the air sponge round the micropyles.

To what extent the outer chorionic spaces in the eggs of some Plataspidae play an important role in gas exchange, is not certain. SOUTHWOOD (1956) claimed the presence of tubules from the bottom of each follicular pit. His fig. 2C shows these canals extending only half way through the solid layer. If indeed canals throughout the chorion empty into the inner meshwork, the air store in the outer chorionic spaces, whose outer openings we found along a median strip of the egg, could be used when the egg becomes flooded.

The isolated position of *Idiostolus* sp. (Idiostolidae) in the Pentatomomorpha must be stressed. The shell of this species lacks the sponge around the micropyle and the chorion seems entirely solid without an inner meshwork layer. The egg of *Thaumastella aradoides*, recently considered as belonging to a separate family, likewise deviates from the pentatomomorphous type. There is an aerostatic inner layer, but air-sponge around the micropylar canals is apparently lacking.

Cimicomorpha (fig. 133–211)

Eggs of the cimicoid groups can survive submersion throughout development, but eclosion is hampered. The general plan in this group is a continuous inner chorionic meshwork around the egg, but except apparently often the plane of the operculum. A very thin open inner layer shows the operculum of Microphysidae *(Myrmedobia)* and such an opercular inner porous layer is in Nabidae *(Nabis)* continuous with the aerostatic layer of the actual shell. Several species belonging to different subfamilies of Miridae, have developed an opercular structure for gas exchange, separated from that of the main shell mass (a similar trend is present in the Reduviidae: Harpactorinae). The meshwork of the shell body is generally one open layer supported by pillar-like struts. The lines where these struts are thicker and higher, follow a hexagonal arrangement, especially in Miridae and Anthocoridae. The internal air space opens only at the anterior pole, generally around the egg's mouth outside the operculum. The normal situation is a system of aeropyles distributed regularly in a collar of the chorionic rim and bearing no relation to the micropyles (except to some extent in *Malacocoris* and *Pseudoloxops*).

There are from about 10 in *Empicoris, Discocoris* up to about 100 in many Reduviidae. In Miridae, the range is from 20 to 400 according to the species. In *Isometopus*, the aeropyles are more clustered towards the fore and hind edge of the rim collar. In *Dicyphus* spp. they are completely limited to these edges; the voluminous spongy inner layer of the shell opens outwards and bears several wide aeropylar rings on top. This arrangement has led to long respiratory horns, one on each median edge in *Helopeltis* and related genera and in some species of other subfamilies. All these projections are

to be considered as bundles of isolated aeropyles but in genera such as *Termatophylidea* each appendage ends in a plastron. Other mirids of various subfamilies have aeropyles on the operculum combined in two groups and sometimes fitted in a long projection. The perfection of all these divergent systems has occurred randomly within the family. We only partly agree with SOUTHWOOD (1956, p. 173, 200) who believed that absence or the presence of only a small network region on the chorionic rim is secondary. Such might be the case in Miridae which have evolved long opercular aeropyles, or in those which reveal distinct clustering and extension of the rim-aeropyles into two bundles and whose long micropylar processes probably reflect the height of a former network region. The excessive enlargement of the network in others might well be recent (some Miridae, the tingid *Sakuntula* and typical Harpactorinae). Besides these examples deviating from the normal group type, there are some striking exceptions in just those taxa which are in other respects aberrant.

First: the fernicolous Bryocorinae *Bryocoris pteridis* and *Monalocoris filicis*. Respiratory exchange in the latter species is through a single anterior horn, whose enclosed air perhaps functions as a plastron. The two micropylar cornicles are surrounded by a porous sheath resembling the aero-micropylar projections as in pentatomoids, but whether the porousness connects with the inner meshwork could not be decided. The condition in *Bryocoris* seems much the same, although no porosity in the shell and in the cone-shaped median projection could be detected. A porous cylinder around the micropyle is present here too. Other egg characters (embryogenesis, eclosion rent) mark off these bryocorines from all other mirids, whose eggs are so far known, even from the *Helopeltis* group, which generally is considered to be in the same subfamily. The *Bryocoris* egg type is so distinct from the typical cimicomorphous egg that it is difficult to imagine how the *Bryocoris* type could have evolved from it. However, on the basis of other egg characters, we are inclined to consider it as rather apomorphic. Because the porous sheath around the micropyle is not connected with the rudiments of the rim collar we think this porosity is of recent origin.

Second: *Embiophila myersi*. Unlike members of the related Microphysidae and the Anthocoridae (the latter normally incubate also half-way within the ovarioles), *Embiophila* shows no trace of chorionic differentiation. Although a careful examination with the electron microscope as yet is necessary, the thin chorion seems to lack any porosity or pore canals.

The third atypical case refers to the Thaumastocoridae, a small family with lygaeid-like species, but since 1957 being considered on some grounds as cimicomorphan (DRAKE and SLATER, 1957). Although the examination of the chorionic canal system was not adequate, we had a strong suggestion that pentatomomorphous features prevail. In the three species of Thaumastocorinae studied, there are 25–35 aeropylar cups, not standing in relation to the rim. In the Xylastodorinae, there are 6 to 10 aeropyles within the rim collar and each of them seems to surround a micropyle. The important question whether or not the inner meshwork is continuous under the operculum has not always been verified but it is present in *Thaumastocoris australicus*.

Hydrocorisae (fig. 212–259)

The unifying character of all the many hydrocorisous eggs studied is the dense perforation of the outer chorion layer. The pore canals are distributed over most of the shell. Frequently they are simple vertical canals, circular and measuring 0.5–1.5 μ in diameter. In Nepidae they branch towards the outer surface of the shell, in *Ochterus* they divide inward. If a distinct polygonal pattern is present, the pores lie within the areas of the polygons. In *Tenagobia*, however, the ribs lining the cell boundaries of the follicle are likewise pored, whereas in *Diaprepocoris* the pores are wide pits confined mainly to the common edges of the polygons. In the more primitive groups of Corixidae *(Diaprepocoris, Tenagobia, Micronecta, Cymatia)* the sheer canals are obvious but in most Corixinae they are scarcely visible with the optical microscope, despite the often large egg. The canal system and the varying outer sculpturing of hydrocorisous eggs causes specific patterns which are valuable for taxonomy.

The Corixidae share the characteristics of the Nepidae and typical Amphibicorisae, whose innermost layer is very thin and which have a thicker spongy layer (very distinct in *Cymatia)* bordering this sheet and the thick outer layer. *Micronecta* is an exception because the spongy layer is very thin, although forming a continuous space held open by widely dispersed minute struts. In *Ochterus*, a thin spongy layer is present throughout except the lid and the innermost shell layer is relatively thick. The inner porous layer in Nepidae opens more effectively through the anterior respiratory horns and HINTON (1961) showed that the open shell system becomes air-filled after the release of the egg. We have shown that the plastrons of the eggs of some African Ranatrinae do not communicate with the free air; yet a normal development of the egg occurs. Assumedly the belostomatid eggs are normally air-filled. *Lethocerus* eggs are deposited above water level. There are records mentioning that egg-carrying *Belostoma* males float at intervals with their backs above the water surface. This behaviour may allow aeration of the eggs. Both families Nepidae and Belostomatidae are closely related, but no vestigia have been found in the belostomatid egg to suggest that they ever had repiratory horns. The inner meshwork which is absent between the bases of the horns in Nepidae, continues without interruption along the anterior pole in Belostomatidae. As in all other heteropterous eggs lacking a combined aeromicropylar system, the meshwork is absent in the area of the micropyles.

Gelastocoridae as well as the Ochteridae have a thin inner meshwork and they probably behave physiologically like the eggs of typical Amphibicorisae and Saldidae.

Apart from the inner porosity in most Corixidae, it is also strange that some of its taxa possess porous structures reminiscent of the terrestrial eggs in other hemipterous groups. The *Micronecta* and *Tenagobia* micropylar cup is exactly paralleled in many generalized Homoptera Fulgoromorpha (COBBEN, 1965c). It really remains a puzzle how to interprete these porous sheaths, the porous longitudinal band in *Micronecta* and the porous circular band in *Helotrephes*, since these latter two structures are unlikely to have arisen to function only in the eclosion split. Their function may now be water absorbtion, especially since we found in *Corixa* a serosal structure below the

micropylar nipple suggestive of a hydropylar function. The eggs of Corixidae and all other families of water-bugs, except Nepidae and Belostomatidae (in part), Gelastocoridae and Ochteridae, are deposited under water and normally never come in contact with free atmospheric air. We could not demonstrate the presence of air in the shell of *Cymatia*, *Corixa*, *Ilyocoris*, or *Notonecta*. Presumably the eggs of all aquatic bugs are not provided with air in the oviduct of the mother. Evidence indicates that all those porous cylindrical outgrowths are vestigia of air-containers in terrestrial eggs. The less porous micropylar nozzle and the porous squama in notonectoid eggs might also be considered as vestigia, a condition which is also found in aphid eggs (COBBEN, 1965c). This should enhance the taxonomic value of such chorionic structures, as they are retained after their original function has gone.

All hydrocorisous eggs have relatively thick shells, the thickness in the small species *(Tenagobia, Plea, Helotrephes)* exceeding 5 μ. The shell of the very tiny *Coleopterocoris* even exceeds 15 μ. Except in the eggs with an inner chorionic meshwork the shell is distinctly two-layered and the inner layer represents a half to a seventh of the total cros section.

A chorionic hydropyle occurs, visible as such, only in the Nepidae close to the posterior pole at the aft side, and in some Belostomatidae *(Lethocerus)*. In *Belostoma* and *Notonecta*, a serosal hydropyle occurs under the same area, but there is no chorionic differentiation at the spot when studied with the optical microscope. There is no external indication of a hydropyle in *Ilyocoris*, whereas the serosal organ is visible anteriorly below the fore edge of the lid. In the Corixinae, the area around the anterior plug, containing the micropyles, probably functions as a chorionic hydropyle. A special sphere on the fore side of the egg of *Belostoma* and *Lethocerus* possibly represents a secondary hydropyle.

A chorionic or serosal hydropyle could not be detected in *Diaprepocoris*, *Micronecta*, *Cymatia* and *Plea*.

Dipsocoridae, Schizopteridae, Enicocephalidae (fig. 260–263′)

The eggs of two Dipsocoridae we studied are so at variance with what we now know about shape and aeropylar system of heteropterous eggs that there is doubt whether their species belong to the same Suborder. Other characters (micropylar system and genital structures) give reason to consider this question more closely later. The egg shape of *Pachycoleus* and *Cryptostemma*, and in particular the two parallel rims, running from pole to pole, has striking resemblances to that of the psocopteran *Cerobasis guestfalicus* K. (illustrated by JENTSCH, 1939). The lateral displacement and excessive constriction of the lid, together with the confinement of the aeropyles to this narrow region, is shared by the eggs of some Flatidae (COBBEN, 1965c). As in these Homoptera, the aberrant features of the dipsocorid eggs must be derived from the more normal condition with an apical cap as found in *Ceratocombus*, *Trichotanannus* and in *Nannocoris* and several other Schizopteridae, mentioned in literature. Most of the shell of *Pachycoleus* is compact. This compactness is probably secondary since the

whole shell of other species described seems to be punctured by aeropyles. The two species of Enicocephalidae studied apparently have an entirely solid shell.

Main types of shell structure

The previous survey demonstrated the high systematic value of the shell, particularly at the species and the superfamily level, when all its local differentiations are considered together. The stratification of the chorion, where it is not specialized for a particular function, may indicate the evolution of the general shell structure through the major groups of Heteroptera. The best guarantee for an evaluation of the morphology is given by the electron micrographs. These are diagrammatically presented in fig. 264–267A–U, supplemented with a few optical micrographs. Our experience with the many other eggs studied, allows some scope for generalizations, although only we have seen plane views and optical sections of these other shells. Only the actual chorionic material is considered. Suprachorionic layers are not considered, though evidence strongly suggests that they are also generally secreted in the ovariole.

There are four main types of shell structure:

A. Entirely solid shells without cavities or open layers have been found in the saldid *Aepophilus bonnairei* (fig. 264A), the amphibicorisal genera *Hebrus* (fig. 264D) and *Mesovelia* (fig. 265H) and for the greater part of the shell in the dipsocorid genus *Pachycoleus* (fig. 266P). Optically a compact structure of the shell is indicated also in *Embiophila*, *Oncylocotis* and *Idiostolus*.

B. The eggs of the remaining Saldidae (fig. 264B), and of *Nerthra*, *Ochterus* (fig. 266Q), *Ilyocoris* (fig. 236D) and *Notonecta* (fig. 267U) share a thick, solid inner layer and an outer layer one to four times as thick which is traversed by a canal system up to the inner layer. Only in Saldidae, Gelastocoridae and in Ochteridae (except in the cap) the canals intercommunicate on the outer surface of the inner layer, thus forming an open sheet.

C. In other Hydrocorisae, Nepidae (fig. 267T), probably Belostomatidae and in Corixidae (fig. 267R, S), and in the Veliidae (fig. 264E) and Gerridae (fig. 264F), the inner layer is extremely thin (about 0.05–0.2 μ). The thick outer layer is traversed by radial canals which discharge in a fine open meshwork layer, interfacing the outer layer to which it belongs, and the inner layer. In Corixidae, there is much variation in the thickness of the inner meshwork layer. It is extremely thin in the typical Corixinae but distinct in *Cymatia* (fig. 219A). In *Micronecta* (fig. 267R) conditions more nearly approach those of group B.

The differences in the structure of each group A, B and C are apparently not related to the environmental differences to which the released eggs are exposed. Eggs of group A are deposited normally just above water level; they develop also when continuously flooded. The same, however, is true for the eggs of shore bugs of group B and the water-striders of group C. On the other hand, eggs of the water bugs of group B and some of group C are entirely independent of free air and do not develop in moist atmosphere. Whatever the physics of respiration in the eggs of group

A, B and C, it probably takes place through the general surface of the chorion (except in *Pachycoleus* and *Cryptostemma*, where one side of the egg bears aeropyles). The diffusion path for oxygen through the chorion is very variable. The solid layer in *Notonecta*, for instance, is almost 20 μ, whereas in *Aepophilus* and *Hebrus* it is 4 μ and 2.5 μ, respectively; in Corixidae it is far less than 1 μ. One might argue that the high porousness of the shell is related to a greater expansion capacity of eggs which absorb water. However such a relation does not seem to exist and there is no interrelation between shell type and egg size.

D. Eggs with an air-filled layer towards the inside of the otherwise almost solid shell. The aerostatic layer communicates with free air mostly at the anterior pole. This condition occurs in the eggs of nearly al Geocorisae (fig. 265, 266L–O); probable exceptions in *Embiophila*, *Idiostolus* and Enicocephalidae. We have seen that the egg of *Hydrometra* belongs also to this type. Comparing the micrograph of *Hydrometra* (fig. 265G) with some representatives of the real terrestrial families, it is significant that the inner lining of the shell facing the aerostatic layer is still thick. The *Hydrometra* egg is an intermediate towards the perfected respiratory mechanism of terrestrial eggs.

Group D allows comparison of the stratification of the heteropterous chorion. The contrast of black and the varying greyish tints in the diagrams (fig. 264–267) are presented as revealed by electron densities in the micrograms. Most sections were not stained but if stained, stratification did not change. Only the contrast becomes sharper (compare fig. 300A with fig. 300B). Thus, the pictures seem to reflect the morphology of the shell reasonable well for comparison (fig. 266M and 267T are from HINTON and are based on sections for the optical microscope; the density of the stippling may not be compared with our own figures).

In most eggs the outer layer is darker than the inner layer but in *Pachycoleus* (fig. 266P) it is the reverse. Each layer is usually separated from the other by a straight or undulating lining of the inner layer and, where a vacuolar lamina between them is present, the outer layer seems to be distinct from the inner one. The most significant conclusion is that this interstitial, vacuolar layer, for example in Saldidae, Ochteridae, Gerridae, Corixidae, seems not to be homologous with the inner aerostatic layer of the geocorisous eggs. This is best illustrated by the lamination of the *Neuroctenus* shell which is unusual in having both the interstitial and the inner aerostatic layers (fig. 265K). The most inner porous layer conducting air from the anterior aeropyles thus forms a part of the layer which in many aquatic and semi-aquatic eggs represents in fact the solid inner lamina of the shell. This homology seems also valid in the lygaeid and acanthosomatid eggs (fig. 265I, J). In other thick-shelled terrestrial eggs, the division between outer and inner chorionic layer is obscured or lacking (fig. 266L, N, O) but the aerostatic inner layer most probably has the same origin also in these eggs. The section of the *Hydrometra* shell (fig. 265G) unfortunately has not enough contrast to distinguish between layers. It is, however, significant that there the aerostatic layer is irregular along the inner side, thus differing from the open layers as in Saldidae and some Amphibicorisae. Evidence is thus strongly in favour of the conception that

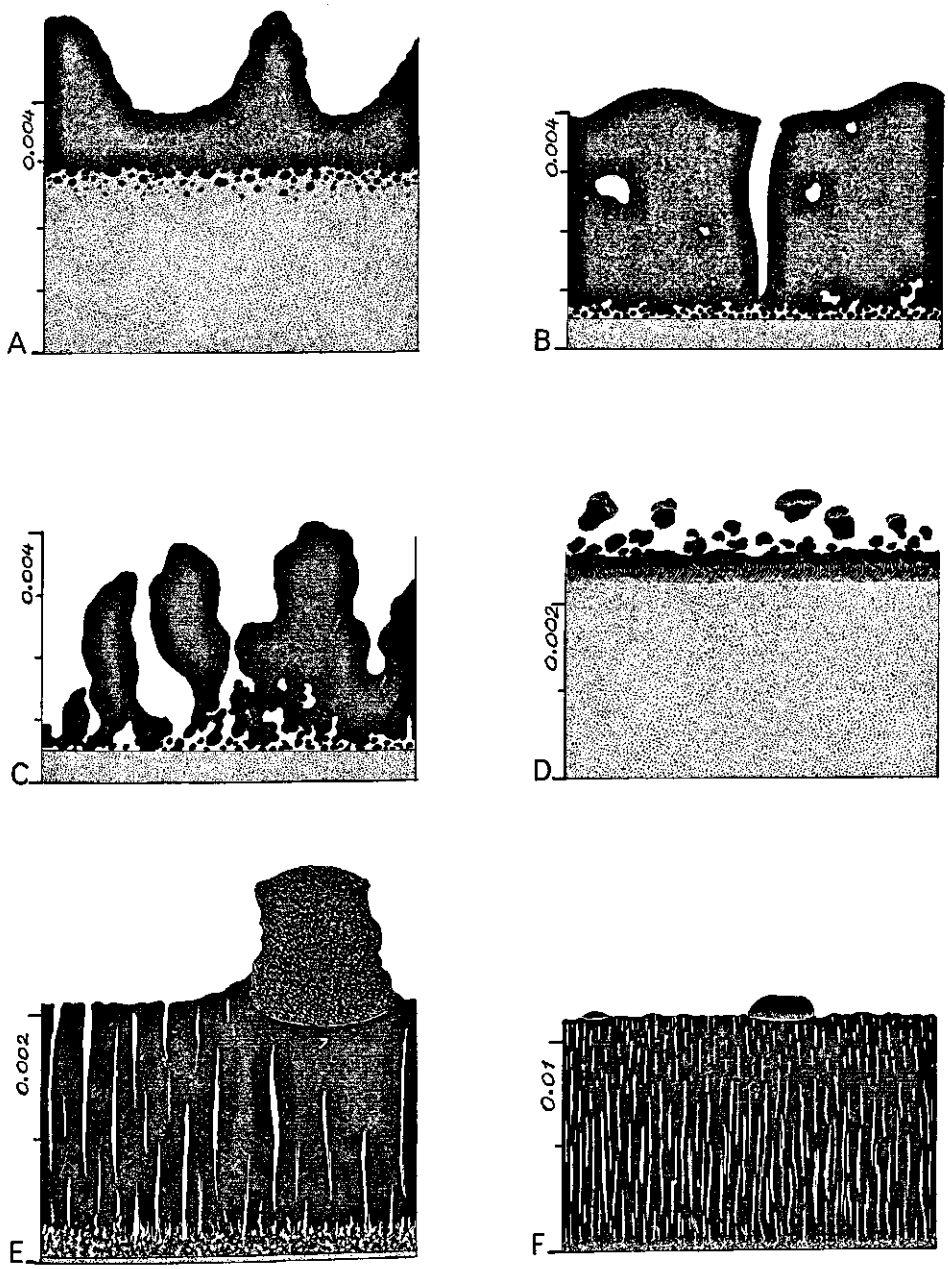


Fig. 264. Transverse section of the unspecialized area of the shell; schematic, based on electron-micrographs. A: *Aepophilus bonnairei;* B: *Saldula palustris, Orthophrys pygmaeum;* C: *Pentacora signoreti;* D: *Hebrus elimatus;* E: *Microvelia reticulata;* F: *Gerris thoracicus.*

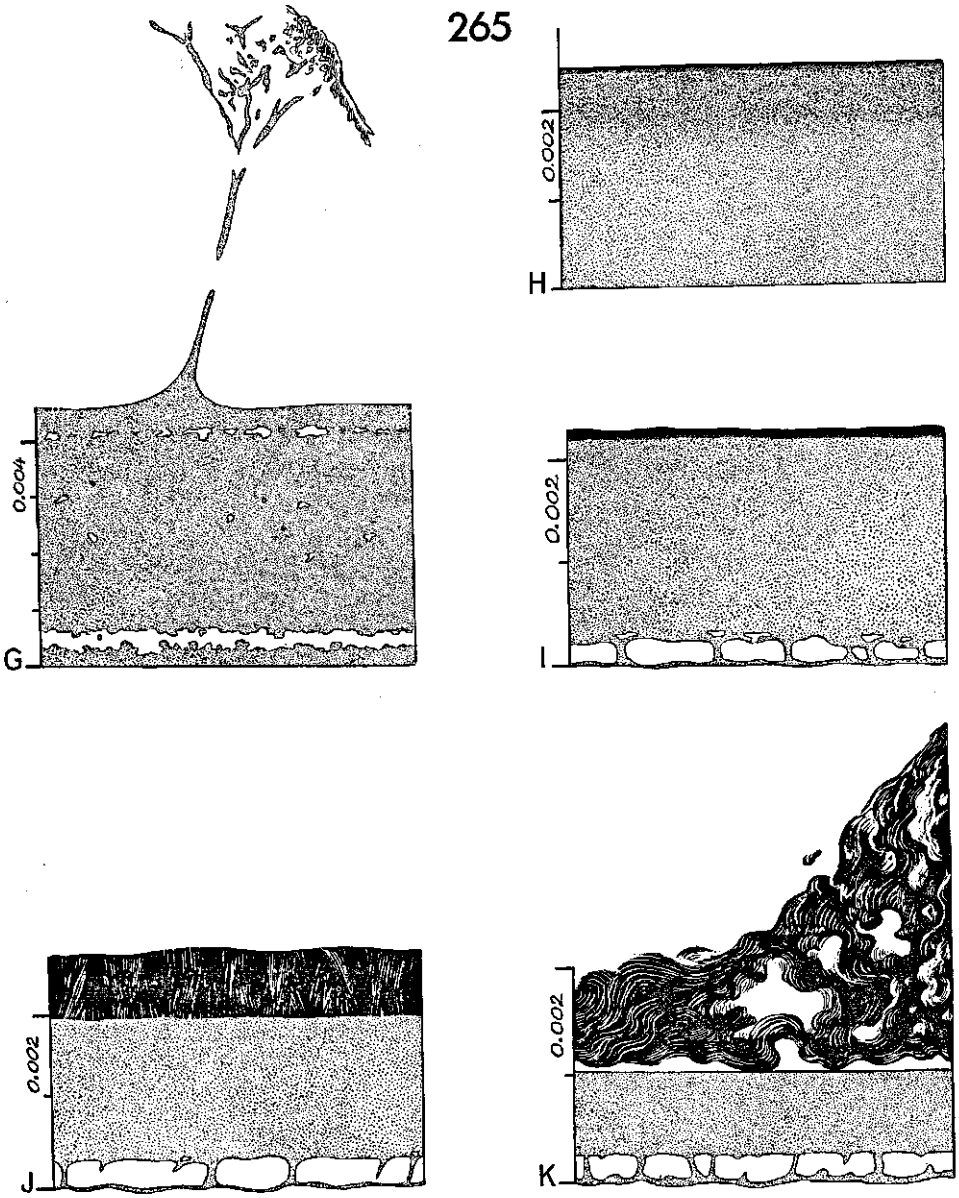


Fig. 265. The same as fig. 264. G: *Hydrometra stagnorum;* H: *Mesovelia furcata;* I: *Elasmucha grisea;* J: *Oncopeltus fasciatus;* K: *Neuroctenus* sp.

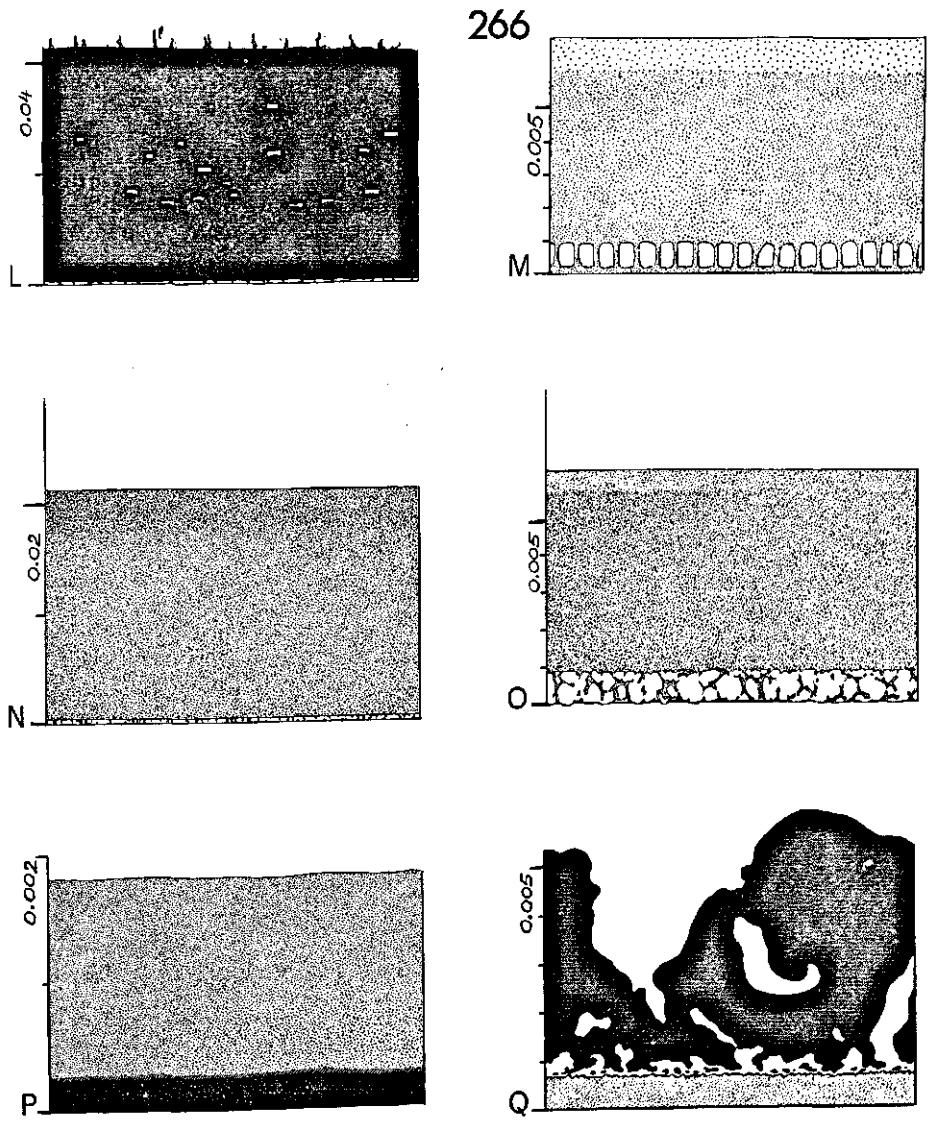


Fig. 266. The same as fig. 264. L: *Macrina juvenca;* M: *Helopeltis schoutedeni* (redrawn from HINTON (1962), optical); N: *Coranus aegyptius;* O: *Reduvius personatus;* P: *Pachycoleus rufescens;* Q: *Ochterus marginatus.*

the aerostatic inner layer in *Hydrometra* originated in the same way as in true terrestrial eggs.

Although in most heteropterous eggs the shell is two-layered, the use of the terms endochorion and exochorion has been abandoned throughout this study. The stratification must be described in detail provisionally before homologies can be safely made between different layers. The innermost layer of the corixid or gerrid shell, for instance, is likely to be overlooked, whereas in the pentatomid *Macrina* there is no visible subdivision of the shell. There are, moreover, shells with a very vague transition from one layer to the other.

It is speculative to argue which of the modern shell types is the most plesiomorphic. Prejudging our general conclusions on the phylogeny of the Heteroptera, the shell of the Amphibicorisae should be most seriously taken into account. Then we have to consider the largely porous shells of the gerrid-veliid complex in contrast to the entirely compact shell of Hebridae and Mesoveliidae. Some reasons seem to favour the last alternative as the most primitive shell condition (see further discussion, p. 282).

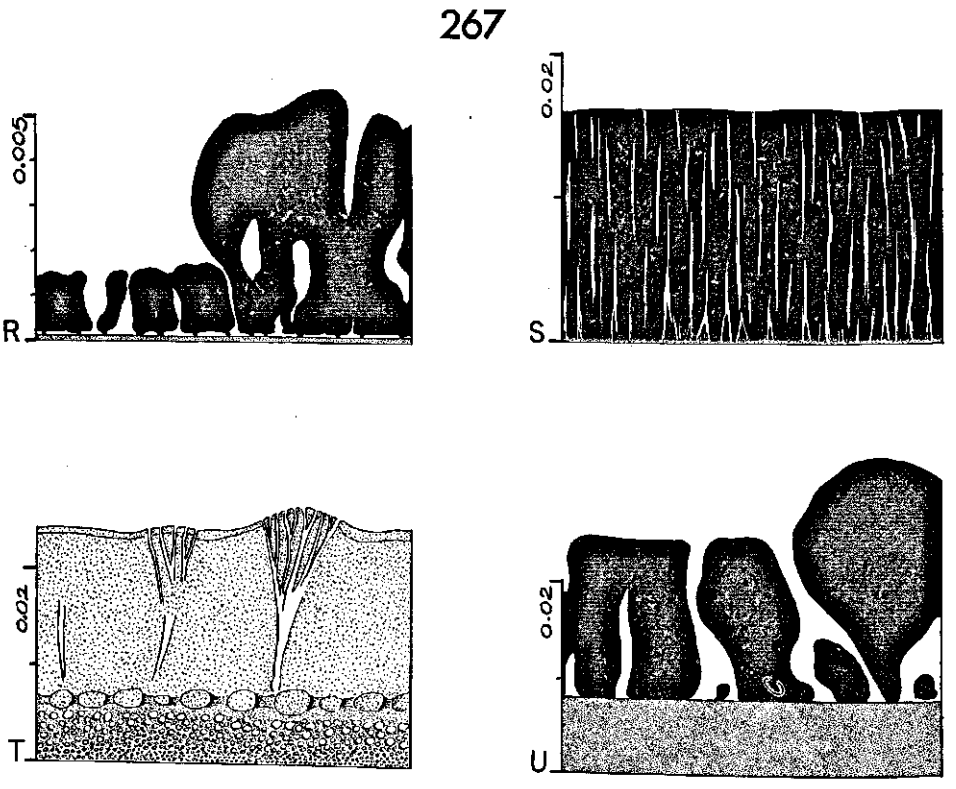


Fig. 267. The same as fig. 264. R: *Micronecta* sp.; S: *Corixa punctata;* T: *Nepa rubra* (redrawn from HINTON (1961), optical); U: *Notonecta glauca* (optical microscope).

3.1.2 Micropylar system

Number

The number of micropyles in Heteroptera varies from 0 to 70. The distribution of numbers over the families is shown in fig. 268. The number is almost constant for each species when it is low. The variation is greater when the number is larger and the number may decrease with ageing of the females as BEAMENT (1947) showed for *Rhodnius*. Within the Pentatomomorpha, the high number seems more evolved than the low number. The families listed with a micropyle number below ten, are generally considered as more primitive in comparison with the other families, e.g. the Pentatomidae and Coreidae. We believe, as will be shown by the further discussion of other egg characters, that basically there is in Heteroptera and also Homoptera (see COBBEN, 1965c) only one micropyle at the cephalic pole.

A single micropyle at the anterior pole is shared by all Saldidae, *Leptopus*, *Omania* and supposedly all remaining Leptopodoidea, all Amphibicorisae except most veliid-like bugs and a few Gerridae, among the Hydrocorisae by the Micronectinae and a few Corixinae, the naucorids *Coleopterocoris*, *Aphelocheirus*, all Notonectoidea, most Ochteridae and some Gelastocoridae. It thus seems that only aquatic and semi-aquatic eggs have retained the original number. It is significant that the greatest increase of micropyles in these groups is found in more terrestrial eggs (*Hebrovelia*, *Macrovelia*, Nepoidea). But also strict water eggs as those of Corixidae and Naucoridae show some parallel increase. In the typical terrestrial bugs, the single micropyle occurs only in Nabidae and in *Scotomedes minor* (Velocipedidae). Since in other cimicoid families with normal fertilization the modal number seems to be two, paired laterally in the chorionic rim, this condition most probably applies also for typical nabids. Here, sometimes the left and sometimes the right micropyle has been lost; these left and right types occur together in the progeny of one female. Traumatic insemination made the last micropyle superfluous too (Nabidae in part, Anthocoridae, Cimicidae). The absence of micropyles in *Pachynomus brunneus* (Pachynomidae) perhaps reflects the same phenomenon. The modal number two in the Cimicoidea distinguishes this group from the Reduviidae in which a progressive increase from 3 up to 15 has so far been found. In Miridae three micropyles were sometimes encountered as an intraspecific variation, but in such cases two of them are very close to each other. This does not suggest that the modal number of two has arisen from secondary loss of more micropyles, but rather an accidental duplication of one of the present pair. The three canals in the reduviid *Empicoris* are equidistant, forming the pattern for further increase in higher Reduviidae. The position of the two micropyles in Rhopalidae is normal for coreoid eggs; two is the modal number in this family. They are arranged on a hypothetical circle around the anterior pole. If Rhopalidae ever had more micropyles, it could only be a few more, since the circle of micropyles is still small. In *Serinetha*, each of the two micropyles has apparently given rise subsequently to a ring of more than ten micropyles.

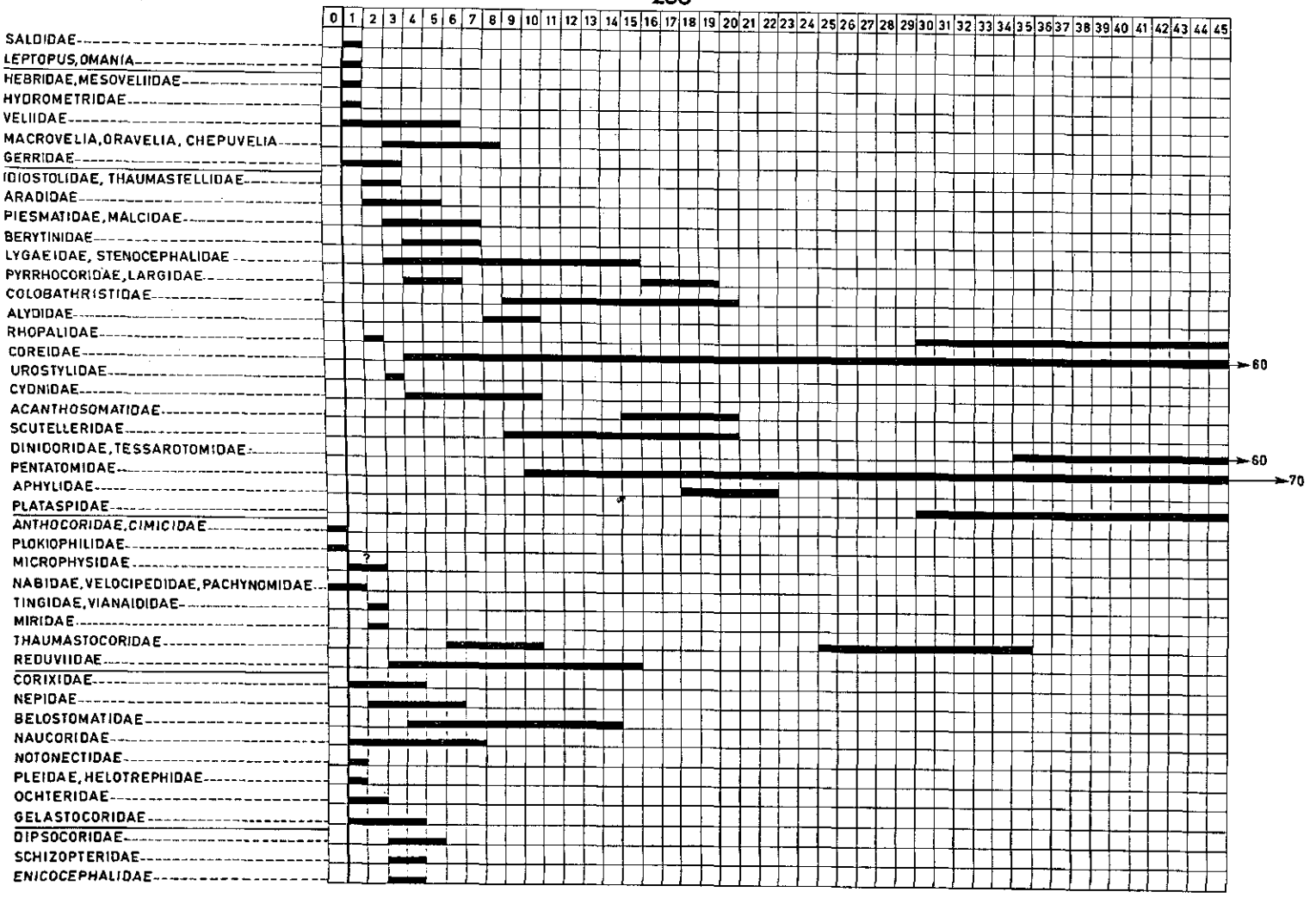
The diameter of the heteropterous micropyle, measured at its narrowest point through the chorion, is about two microns (1–3, rarely 4). Thus, there is no relation with the large variation in volume of the egg (the *Tessarotoma* egg is seven times longer than the *Microvelia* egg and proportionally much wider). This implies a constant size of the spermatozoids of small and large species, if it is assumed that the micropylar diameter is only just sufficient. Nor is a general correlation evident between the micropyle number and the size of the eggs. In the Pentatomomorpha, there may be some tendency towards increase in number in larger eggs. It should be remembered that in this group each micropyle has a sheathing fine meshwork, which communicates with the inner meshwork of the shell. Surface enlargement of the egg and therefore increased need for aeration, *i.e.* enlarged contact with free air, could have encouraged the rate of micropyle multiplication.

Displacement of the micropyles

As mentioned before, the original site of the single micropyle is in the anterior centre. This condition is retained in *Omania*, Gerridae, Hebridae, Hydrometridae, Micronectinae, *Agraptocorixa*, *Aphelocheirus*, most Notonectoidea and Ochteridae. In those Saldidae with the respiratory area developed up to the anterior pole, the micropyle is shifted slightly towards the aft side of the egg. In *Aepophilus*, the shift from the egg summit is pronounced, whereas the chorion lacks pores. The egg is found near seawater. Perhaps an anterior respiratory system has existed in the past (see also p. 16 regarding supposed loss of the inner meshwork layer). In Nepidae and Belostomatidae, a shift towards the same side is achieved. This could mean that the nepid type with respiratory horns has been the precursor of the actual belostomatid type, which lacks any trace of them. Similarly directed shifts of the micropyle(s) seem to have evolved also in other groups as in Dipsocoridae and, when egg rotation is taken into account (see COBBEN, 1965c), also in Homoptera (Delphacidae, most Cicadomorpha, Psylloidea). However, a causal relation between such a shift and a respiratory differentiation is questionable in the Homoptera mentioned. In several notonectoid species, the micropyle has moved slightly towards the fore side of the egg apparently through the tendency to insert the eggs, and the same seems to have occurred in opercular eggs such as *Ilyocoris* and *Mesovelia*. Since the eggs are bent to conform to the embedded mode, it may be that the geometrical centre of the anterior pole in these eggs still concurs with the micropylar area.

The arrangement of the micropyles in a circle most often starts concentrically around the anterior pole. The micropyle is formed by one follicular cell and about three of them are adjacent to each other in some Corixinae. In *Ambrysus*, a cluster of micropyles is formed. If a few micropyles are present, however, these are generally separated from each other by polygons, originating from individual follicle cells. In

Fig. 268. Number of micropyles by family


0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
SALDIDAE
LEPTOPUS, OMANIA
HEBRIDAE, MESOVELIIDAE
HYDROMETRIDAE
VELIIDAE
MACROVELIA, ORAVELIA, CHEPUVELIA
GERRIDAE
IDIOSTOLIDAE, THAUMASTELLIDAE
ARADIDAE
PIESMATIDAE, MALCIDAE
BERYTINIDAE
LYGAEIDAE, STENOCEPHALIDAE
PYRRHOCORIDAE, LARGIDAE
COLOBATHRISTIDAE
ALYDIDAE
RHOPALIDAE
COREIDAE
UROSTYLIDAE
CYDNIDAE
ACANTHOSOMATIDAE
SCUTELLERIDAE
DINIDORIDAE, TESSAROTOMIDAE
PENTATOMIDAE
APHYLIDAE
PLATASPIDAE
ANTHOCORIDAE, CIMICIDAE
PLOKIOPHILIDAE
MICROPHYSIDAE
NABIDAE, VELOCIPEDIDAE, PACHYNOMIDAE
TINGIDAE, VIANAIDIDAE
MIRIDAE
THAUMASTOCORIDAE
REDUVIIDAE
CORIXIDAE
NEPIDAE
BELOSTOMATIDAE
NAUCORIDAE
NOTONECTIDAE
PLEIDAE, HELOTREPHIDAE
OCHTERIDAE
GELASTOCORIDAE
DIPSOCORIDAE
SCHIZOPTERIDAE
ENICOCEPHALIDAE
60
60
70

Piesmatidae each micropyle is in the middle of one polygon. The micropylar 'cells' touch each other and they all together enclose one free 'cell' at the pole (fig. 69). In Malcidae, this central 'cell' is displaced later (fig. 67), but in the other lygaeoid groups micropyles multiply, while the normal shell polygons increase in number and decrease in size (fig. 68). Continuous centrifugal displacement of the micropyles is not initiated by need for space. The only case in which they remain adjacent in an already widened ring has been met with in some Plataspidae, where displacement is caused by strong flattening of the aerostatic cup surrounding the micropyle. The widening of the circumpolar ring of micropyles is independent of cap formation. But once a closed circular eclosion rent was formed and the micropylar ring approached it, the ring did not migrate further downwards. The fixed combination of micropyles around the cap is then evolving in a stable ring (most Pentatomidae). In one tessarotomid egg (fig. 115B), the micropylar ring has broken out far below the cap. Since the cap in this egg is simple without a ring suture, we suggest that its circular form was not yet balanced when the micropyles passed it. It may also be that the long axis of this cap sloped already too obliquely for making concurrence of its boundary with the trajectory of the micropyles possible. Concurrence would be impossible in the coreoid families where the micropyles intersect the oblique or entirely lateral pseudoperculum (fig. 97–100). The sole pentatomid parallel we found was the coreid *Catorhintha* (fig. 96), which is therefore of particular phylogenetic interest and the phyletic line of this taxon needs further attention. It is unlikely to have evolved along the *Coreus-Dalader* line (fig. 97, 98), if we consider egg shape.

The path of micropylar multiplication is vaguer in the Cimicomorpha, since an operculum is present in nearly all species (the only exceptions are the Ploikiophilidae and the Enicocephalidae). The micropyles in this group are arranged round the operculum, except in *Bryocoris* and *Monalocoris*, where the lid must have been reduced and displaced backwards (fig. 166B, 167), if our explanation on the origin of the eclosion fracture (p. 275) is right. The presence of the respiratory sheath round the micropyles and the transverse canals of the two micropyles running parallel in *Bryocoris* and *Monalocoris* contrasts with what is seen in all other opercular Cimicomorpha, including other Miridae, studied so far. This brings us to consider the structure of the micropyles and the polarized route which is shown by them.

The structure and orientation of the micropyles

The varying types are shown diagrammatically in fig. 269. The micropyle forms a simple tubule through the chorion, radial (Gerridae, Ochteridae) or oblique *(e.g.* Saldidae, Nepidae). The oblique course apparently is connected with the shift of the micropyle from the pole. A second trend is that the micropyle tends to project from the innerside of the shell, this projection becoming longer in the following sequence (not proposing a phyletic line!): *Plea, Hebrus, Mesovelia, Notonecta,* Acanthosomatidae, Cydnidae, Scutelleridae. The inner projection of the single micropyle in the former four taxa points towards the fore side of the egg (in *Micronecta* towards the aft side).

In the pentatomoid families just mentioned, all micropyles, arranged in a ring, project inside the egg centripetally (N′ in fig. 269), but in the Cydnidae (M′) and the Stenocephalidae the canals all bend slightly to one side. On the other hand, *Macrovelia, Ilyocoris* and *Gelastocoris* reveal a more centrifugal pattern. In *Nerthra, Hebrovelia, Chepuvelia,* Urostylidae, Thaumastellidae, Piesmatidae, Malcidae, Idiostolidae, nearly all Lygaeidae, Emesinae, most Miridae and in the schizopterid *Hypselosoma,* however, the inner projections deviate in cross direction and these extensions all point to the same side, clockwise when observed from the cephalic pole (fig. 269N, O, S, Z, B′–F′). From the data a general trend in directional shift of the inner micropylar tube can be deduced, which is particularly apparent in the Pentatomomorpha. The inner canals turned form a centrifugal direction clockwise (egg seen from above) towards a centripetal direction. The exactly intermediate circular stage is found in several families. In a few families (most Cydnidae, Stenocephalidae) the turning of the micropyles has covered 3/4 of the semicircle. A full turning has been accomplished in the Acanthosomatidae and Scutelleridae to reach an exact centripetal arrangement of the internal canals. A circular course of the micropyles is also seen in the two species of Enicocephalidae studied. However, the direction of these is the reverse, anti-clockwise. Apparently there is an annular polarity in the anterior structure of the shell, which is demonstrated also in the mode of cap formation. In *Lethocerus,* the micropyles are placed on a constricted ellipse; the axis of the short intrachorionic canals run centripetally. The 10–14 canals of the *Hydrocyrius* eggs extend, apparently inside the egg lumen, and approach the centre of the ring. The same polarization exists in Nepidae, although the canals, two to six in number, are confined to a semicircle at most. It is in line with other characters to consider the nepid condition and that of some belostomatids (fig. 269I, K) as approaching the circular arrangement. For completion of the circle a number of micropyles approaching ten is needed, whereas in pentatomomorphous eggs the elementary circular arrangement is already fixed with a few micropyles. From this and from the diagrams in fig. 269 it may be concluded that the splitting and the circular grouping of the micropyles in Heteroptera occurred independently at different times by different methods. It seems that multiplication of the micropyles right at the pole results directly in a circular grouping of them. If the single micropyle has first migrated from the polar's centre, a later multiplication starts initially on a cross-line (apart of the Nepoidea mentioned, also in Dipsocoroidea (fig. 269M, N) and in *Microvelia signata* (fig. 269X)). For the same reason it is expected that the intermediates between the typical rhopalids, bearing two micropyles, and the *Serinetha* egg with two circles have or had eggs on which the micropyles are arranged in two isolated semicircles.

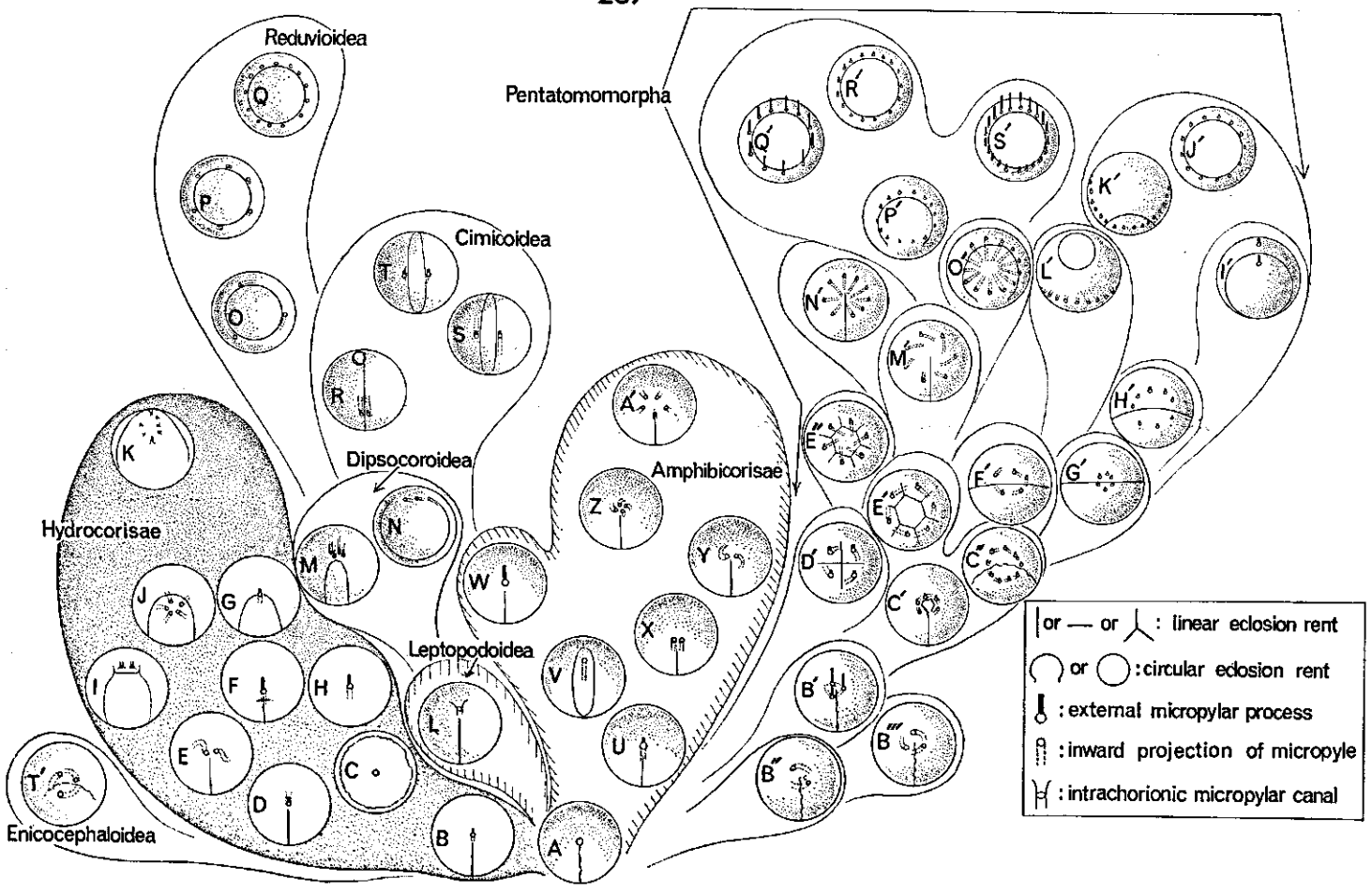
The inward projection always consists of compact chorionic material, sometimes of greater density than the rest of the shell *(Mesovelia, Notonecta).* In some *Nerthra* and *Ilyocoris* eggs, however, there project inward thick horns of a tough mucilage in which no canal could be traced (fig. 258); the origin of these tubes is obscure and probably not chorionic. Perhaps they are like the fertilization cone reported from *Drosophila* eggs (COUNCE, 1959) and which remain during the maturation divisions and synagamy.

Identical directional types of the inward projections do not always indicate interrelationships of families or family groups, but a given type usually remains constant within its family or higher levelled taxon. The discrepancy in this between *Bryocoris*, *Monalocoris* on the one hand (fig. 269R) and all other Miridae on the other hand (fig. 269S, T) seems therefore significant. The difference represents a cladogenetic divergence, since it is not seen how the one type could be derived from the other. The same is true for the enicocephalid egg (fig. 269T′, transverse canal running anti-clockwise), in contrast to all other taxa with transverse canals *(e.g.* fig. 269 E, N, O, Z, B′, B″, B‴–F′).

Considerable lengthening of the micropylar canal to the outside occurs in combination with its aerostatic sheath in Asopinae, *Ceraleptus*, *Hydrometra*. In these eggs the micropyles do not project inward and the egg of the plataspid *Ceratocoris* demonstrates a possible antagonism between proximal and distal lengthening. The short micropyles along the fore side have a transverse inner projection, those highly elongated micropyles along the aft side have not (fig.269R′). The micropyles are not prolonged inward in Aradidae, most Berytinidae, Pentatomidae and only a little in Alydidae, whereas the outer cups are rather short. The long, freely extending micropyles in some Miridae (*Helopeltis* group, *Termatophylidea*, Dicyphinae) certainly have resulted from loss of the rim collar, because of the confinement and bundling of aeropyles onto the anterior edges.

When the basal deviation of the micropyle is only short, it is difficult to decide by a routine examination whether it runs horizontally within the shell or whether it extends beyond it for some distance in the lumen along its inner side. According to SOUTHWOOD (1956), extension within the shell occurs in *Oncopeltus*, where the transverse canal must run close to and parallel to the inner porous layer of the shell. It must terminate on the inner surface of the chorion without extending into the lumen, but we pointed out (p. 94) that this is very unlikely. SOUTHWOOD named the proximal deviations also in *Sehirus* and some Scutelleridae as transverse canals, and here they are in our opinion tubes, which actually project within the lumen of the egg. It may be that the transverse canal proper, thus intra-chorionic, occurs as intermediate stage between complete absence and a real inner projection.

Fig. 269. Diagrammatic representation of the eggs as seen normal to the cephalic pole; structure and arrangement of micropyles and eclosion fracture. A: *Gerris;* B: *Coleopterocoris kleerekoperi;* C: *Ochterus;* D: *Micronecta;* E: *Nerthra;* F: *Notonecta;* G: Anisopinae (in part); H: *Helotrephes;* I: *Ranatra;* J: *Ilyocoris;* K: *Lethocerus;* L: Leptopodoidea; M: Dipsocoridae; N: *Hypselosoma;* O: *Empicoris;* P, Q: Reduviidae (in part); R: *Bryocoris, Monalocoris;* S, T: Miridae (in part), Tingidae; U: *Hebrus;* V: *Mesovelia;* W: *Hydrometra;* X: *Microvelia signata;* Y: *Hebrovelia;* Z: *Velia;* A′: *Macrovelia;* B′: Urostylidae; B″: Idiostolidae; B‴: Thaumastellidae; C′, C″: Lygaeidae; D′: Malcidae; E′: Piesmatidae; E″: Stenocephalidae; F′: Aradidae; G′: Pyrrhocoridae; H′: Alydidae; I′: Rhopalidae; J′: Coreidae (in part); K′: Coreidae (in part); L′: Tessarotomidae; M′: Cydnidae; N′: Acanthosomatidae; O′: Scutelleridae; P′: Pentatomidae (in part); Q′: Asopinae; R′: Pentatomidae (in part), Plataspidae (in part); S′: Plataspidae (in part); T′: Enicocephalidae.


Reduvioidea
Pentatomomorpha
Cimicoidea
Dipsocoroidea
Amphibicorisae
Hydrocorisae
Leptopodoidea
Enicocephaloidea
or — or : linear eclosion rent
or : circular eclosion rent
: external micropylar process
: inward projection of micropyle
: intrachorionic micropylar canal

3.1.3 Eclosion rupture

There is little doubt that the simplest way of shell eclosion is a longitudinal split running from the anterior pole downwards along the median line of the egg. This condition, simultaneously considered as the most primitive in Heteroptera (and in Homoptera Cicadina, *cf.* COBBEN, 1965c), is still retained in representatives of all main groups: Amphibicorisae, Hydrocorisae, Leptopodoidea, Pentatomomorpha and very rarely in Cimicomorpha *(Embiophila?)*. We assume that originally this split was not along a line of weakness and suggest that an anterior median egg-burster on the embryonic cuticle started the break. It depends from the shape of the egg along which side or sides the split proceeds downwards. In ovoid, almost isoradial eggs, probably the archetypical shape, the split runs along the median line of the fore side of the egg. Presumably the longitudinal birefringence of the shell keeps the split sharply lengthwise in eggs of most Amphibicorisae. We affirm the statement of SATTLER (1957) that in *Aquarius* there is not a line of weakness and the shell elements of all Gerridae, Veliidae, Hebridae studied have a longitudinal polarity.

In all the Saldidae studied eclosion is likewise longitudinal but is here assisted by a weakness along the rupture-line except possibly in *Aepophilus*. This line is forked anteriad around the micropylar region (fig. 4). In the related family Leptopodidae *(Leptopus)*, the opening made in the shell is, however, small and irregular (fig. 37C, D). The sharp egg-burster has to operate here throughout as an active opener, since water has not been absorbed and thus there is not enough internal pressure to make the flabby shell split further after initial puncture by the burster.

The non-opercular eggs of terrestrial bugs are said to split irregularly, except in Acanthosomatidae (SOUTHWOOD, 1956; PENDERGRAST, 1958). Still, there is more order in these supposed irregularities, which can throw light on the formation of the egg-cap. We start with the vacated shell of *Oncopeltus*, of which several chorionic breaks have been drawn and discussed (fig. 74A–E, p. 88). The burster lies just below the anterior pole and the split is median along both the fore and aft sides. The ends of this line bend variably to one or both lateral sides. In most cases, however, a flap is lifted on one lateral side. In a few cases the initial break is transverse through the micropylar ring but in *Pyrrhocoris* this transverse break is quite common. In the likewise soft and, in addition, dorsoventrally flattened egg of *Neuroctenus*, a transverse break over the anterior pole is the rule (fig. 65C). This manner of eclosion is further perfected in the Alydidae and Pseudophloeinae (fig. 88B). Here, the split forms a crescent in the thicker shell and marks off a bilaterally symmetrical flap on the fore side of the egg. It seems that at least the upper part is adapted for the rupture. This type of eclosion is clearly the precursor of the oblique pseudoperculum of most other Coreoidea (fig. 97–99).

Fig. 270. Anagenesis of eclosion rent and of multiplication (rarely reduction) and displacement of micropyles; the site and number of micropyles is indicated above each egg; note that progressive changes are parallel in different lines of descent.

270
geocorisae
hydrocorisae
amphibicarisae
leptopodoidea
Thaumastocoridae
Pentatomidae
Scutelleridae
Plataspidae
Dinidoridae
Tessaratomidae
Acanthosomatidae
Cydnidae
Cercopidae
Aradidae
Colobathristidae
Rhyparochromidae
Rhopalidae
Alydidae
Coreidae
Pyrrhocoridae
Berytinidae
Lygaeidae
Miridae
Tingidae
Nabidae
Thaumastocoridae
Leptopodidae
Saldidae
Omaniidae
Gelastocoridae
Ochteridae
Nepidae
Naucoridae
Belostomatidae
Notonectidae
Helotrephidae
Corixidae
Gerridae
Hydrometridae
Hebridae
Veliidae
Reduviidae
Dipsocoridae
Schizopteridae
Tingidae
Miridae
Vianaidae
Enicocephalidae

The heteropterous eggs, known so far, never have a dextral or sinistral cap (except in *Bryocoris*, *Monalocoris* and *Plea*), although the tendency towards it is seen. The change towards a median flap is probably induced by change in egg shape (dorso-ventral asymmetry, flattening of the anterior pole), changing of the longitudinal into a transverse lamination of the finer shell elements and lastly the development of transverse components in the egg-burster. Transverse components have not markedly developed in the Coreoidea but started early in the Pentatomoidea. A further characteristic in Pentatomoidea is the shortening and broadening of the egg and thus enlargement of its cap, and a shift of the primary eclosion puncture from the anterior pole towards the edge on the aft side. This latter shift went hand in hand with morphological displacement of the ruptor ovi (see next paragraph, p. 319). As a consequence, the circumpolar pseudoperculum arose, typical in Pentatomidae and occurring in at least one coreid (*Catorhintha*, p. 100). The polar caps in *Catorhintha* and in Pentatomidae are only seemingly alike. The burster breaks the chorion on the same side of the pole (compare fig. 96 with fig. 124C). The morphological position of the burster in relation to the larva is however different and the same effect is achieved by a different posture of the prolarva in the egg.

The phylogenesis in pentatomoids of eclosion in association with egg shape and the micropylar ring is shown in the dendogram (fig. 270, extreme right branch with shaded border). A transitional stage between the straight line hatching of the basic families and the circular eclosion of all other families is not represented. The two eclosion types given in the same dendogram for the Aradidae (left of the pentatomoid branch) could well be inserted here as hypothetical intermediates. The successive types cannot all be arranged in a straight line evolution. In particular, for *Aspongopus*, *Eumenotes* and the tessarotomid sp. cladogenetic deviation has to be assumed. All the many scutellerid eggs known are almost spherical; this shape is derived from the originally ovoid and never proceeds further towards flattening of the anterior pole. The slightly oblique lid with a constant course across the micropylar ring (fig. 108) is equally conservative. The pentatomids have evolved furthest with the cap concentric with the flattened pole and the ring of micropyles, as a consequence of the economic and dense packing of the erect eggs; these eggs have become cylindrical. Some genera, *e.g.* *Edessa* and *Dalpada* have slightly surpassed the scutellerid type (fig. 119). The horizontal arrangement of the eggs by *Sciocoris* is probably secondary as an adaptation to its terricolous habit. The tessarotomid eggs studied resemble the scutellerid eggs in shape and eclosion rent but the micropyles are much more evolved. Eggs of *Aspongopus* (Dinidoridae) are placed in chains (p. 112) and this manner of deposition must have already occurred before the pentatomoids had evolved a distinct pseudoperculum and before the backward shift of the egg-burster was complete (fig. 114). Through the pole-to-pole arrangement of the eggs, the prolarva had to bend forward to break the chorion with its burster at the free edge of the egg. A lid completely displaced to the fore side of the egg is the result. It would not be surprising to find in this group of the Pentatomoidea an egg showing exactly the same aspect as in chain-laying Coreinae (fig. 100); we found such a parallel in *Eumenotes*. In the cylindrical very thick-shelled

eggs of the Coreinae, eclosion cannot otherwise be effected by the activity of the hatching larva than with a well defined subapical pseudoperculum. There is a special point of weakness in the cap margin for receiving the ruptor.

A quite different means of eclosion in the Pentatomomorpha is revealed by *Piesma* (fig. 69). Such radial fracture needs only a few large follicular hexagons, which is in our opinion a primitive condition. We have seen that the *Piesma* type is not as isolated as first thought, since several lygaeids and the Stenocephalidae have a nearly identical configuration of follicular cells (fig. 68B, 269E″). In other lygaeoids (fig. 68A) the region of the shell between the micropyles is 'multicellular'; the 'cell' boundaries do not fix the course of the split. It seems thus that a generalized lygaeid egg would have radial eclosion but that this method is retained and used in practice in Piesmatidae and probably in Stenocephalidae. It is perfected in Malcidae by the disappearance of the central cell, resulting in a + or a λ eclosion rent (fig. 67).

The information regarding the eclosion of the many cimicid, reduviid and thaumastocorid eggs studied gives little evidence how the true operculum has evolved. With few exceptions all have a perfect ring-closure, elliptical or circular. Among the Reduviidae studied only the emesine *Empicoris culiciformis* is less evolved with a rather irregular opercular margin and apparently no sealing bar. Among the cimicoid groups, the typical Bryocorinae and the *Embiophila* eggs reveal an important difference from the *Cimex* or mirid type. The simple egg of *Embiophila* breaks presumably along a longitudinal line as does also, but partly, the *Bryocoris* egg. In *Bryocoris* a small circular part of the chorion is distinct. This is the pseudoperculum proper which is lateral of the median straight eclosion line (fig. 166B). Since *Bryocoris* and *Monalocoris*, judging from adult characters, certainly belong to the mirid group, we first tried to relate their eclosion to the normal annular suture found in Miridae and related families. The lineage along which the *Bryocoris* type could have arisen from the mirid type is given in the diagram, fig. 271. The cladogenesis shown must have begun before the existence of a sealing bar and the opercular rudiment in *Bryocoris* and *Monalocoris* still lacks a neat annular suture.

The structure of the pseudoperculum and the circular striation of the surrounding part of the chorion in *Bryocoris* seems to be paralleled in *Corixa, Cymatia* and *Agraptocorixa* (compare fig. 167 with fig. 221A). The micropylar area is surrounded by an annular weakness in these corixids which forms a pseudoperculum too small for the larva to emerge and the shell neck cracks further radially. Superficially this configuration is like the *Piesma* type but the transverse lines in Corixidae do not correspond with cell boundaries. It is still doubtful how far the archetypal longitudinal eclosion has led to the evolution of the modern *Corixa* type. Longitudinal splitting still occurs in *Micronecta* (probably not in *Diaprepocoris* and *Tenagobia*), but it is unlikely that the porous cleft in the *Micronecta* egg (fig. 212B) is a precursor of all other corixid eggs. Since we know nothing about the function of the porosity of the cleft, this structure is for the moment better to be considered as a cladogenesis from other corixid eggs.

The eclosion of the remaining hydrocorisal eggs is diverse. Gelastocorid eggs split

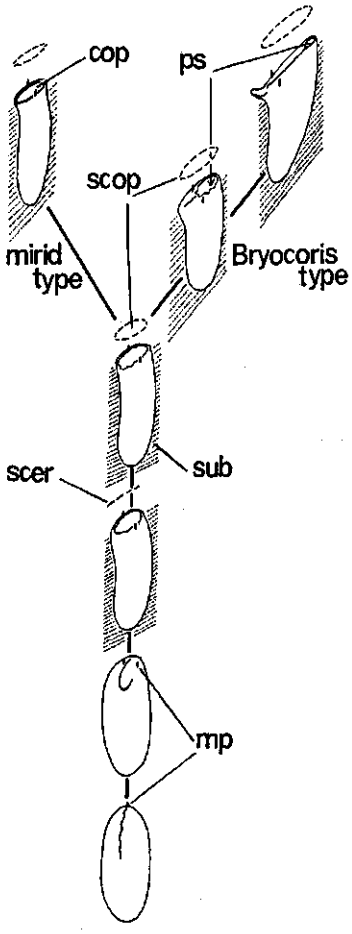
lengthwise but some eggs show a tendency towards circular lids by the cell zonation around the micropylar area reminiscent of corixines. The round cap in *Ochterus* is only vague and shows no sign of derivation from a longitudinal split. The incomplete cap of belostomatid and nepid eggs, which is lifted initially at the aft side (fig. 229C, 233A), similarly cannot be derived straight from a longitudinal precursor. In Nepidae, the egg's neck is too narrow for the escaping larva. An additional longitudinal rupture of constant form widens the neck, one line passing through the micropyles in *Nepa* and two lines enclosing the micropylar area in *Ranatra*. Naucoridae have a circular suture, without a frame in the exposed eggs of *N. maculatus* and *Aphelocheirus*, and with a frame in the embedded egg of *I. cimicoides*. The *Coleopterocoris* egg, however, has probably retained the longitudinal rent and its shape suggests exposed deposition. It thus seems that in Naucoridae the cap appeared before the embedding method of oviposition. In Notonectidae, on the contrary, information suggests a slower adaptation towards a complete ring. The many *Notonecta* eggs of several species seen, whether or not they embed their eggs, have a characteristic †-shaped split (fig. 243C). The longest, longitudinal component of this rent always curves towards one of the lateral sides. In the pentatomomorphs, we showed that such a bend is a first stage towards a pseudoperculum, initially lateral of the median plane. The notonectids, however, show a quite different pathway along which the lid is evolving (shown diagrammatically in fig. 272). A flap-like structure, almost a pseudoperculum, is found in the vacated shells of *Plea atomaria* on the right fore side (fig. 251F). The complete fracture is derivable from the † rent in *Notonecta*. The *Plea* egg is entirely embedded and only a narrow elliptical strip remains exposed. The chorionic differentiation of this area suggests that it functions as the operculum but this strip is halved at eclosion. The adaptation of the egg to insertion has proceeded further in the Anisopinae. Eggs are clearly opercular and the boundary of the cap seems to have originated from the left and right transverse suture, as in *Notonecta*, meeting at the lower end. In the *Buenoa* eggs studied, the cap still reveals a longitudinal band of elongated cells, which probably still serves as the main eclosion line (fig. 250). The notonectid branch clearly shows that exposed deposition preceded embedded. The eggs of the two Helotrephidae studied suggest that this family is more remote from the Notonectidae since the operculum of *Helotrephes* sp. (fig. 254A) implies a distinct origin. The shape of the *Helotrephes* and *Tiphotrephes* eggs studied indicates exposed deposition and the eclosion line of *Tiphotrephes* is probably longitudinal or transverse, but not forming a cap.

The nine species of Dipsocoridae and Schizopteridae studied so far, have a pseudoperculum, although not all species seem to insert their eggs in solid material. In *Hypselosoma* it is circumpolar and vague but in the others the ring is more distinctly closed. Nevertheless, the circular rupture in *Ceratocombus* extends also far longitu-

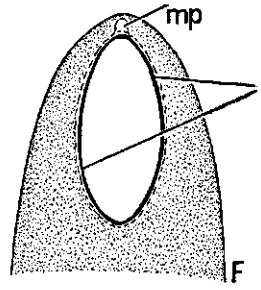
---

Fig. 271–272. 271. Anagenesis of the eclosion rupture of serosal cuticle and chorion in Miridae, showing the pattern of divergence near the top of the branch. 272A–F: Anagenesis of the chorionic eclosion rupture in the Notonectoidea; the stippled areas mark the embedded parts of the shell.

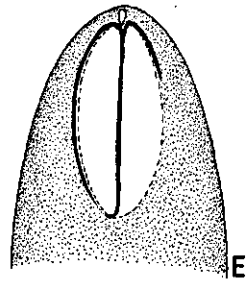
271



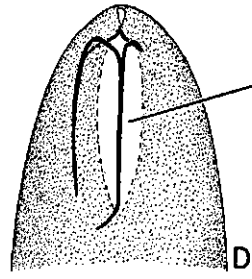
272



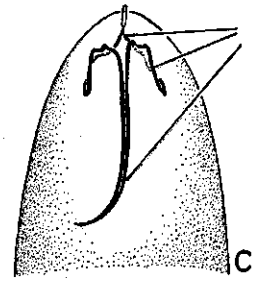
most Anisopinae?



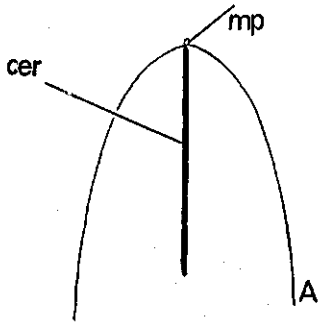
Buenoa spec.



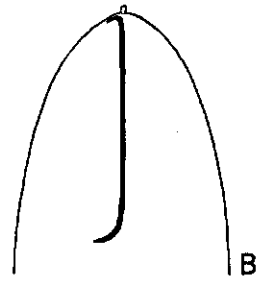
Plea atomaria



Notonecta glauca



ancestral type



Notonecta maculata

dinally along the fore side. The cap tends to shift to the fore side of the egg; extreme examples are the unusual eggs in *Pachycoleus* (fig. 260) and *Cryptostemma*.

A survey of eclosion lines in heteropterous eggs and their common derivations is shown in the cladogram (fig. 270). Some lineages with hypothetical interrelations are indicated in fig. 271 and 272.

3.1.4 Discussion

Chorion and aeropylar system

On the basis of our findings in heteropterous eggs, we decided, as a precautionary measure, not to use the terms endochorion and exochorion. The same policy has been followed by PANTEL (1913) and HINTON (1963) in their evaluation of the egg shells of Diptera. In many places of the descriptive part of the present work, earlier confusions and misinterpretations of shell structures have been brought to light. On p.250, we referred to rapidly changing ideas on the morphology and physiology of the egg shell in modern literature. There is still a great confusion in interpreting the superimposed egg coverings. Only a few examples are: BOCK (1939) most probably confounded the innermost chorion with a subchorionic layer in *Chrysopa*. SALT (1953; see SLIFER and SEKHON, 1963) confused the endochorion in *Melanoplus* with the vitelline membrane. In the papers on the eggs of Culicidae (TELFORD, 1957; ROSAY, 1959; IDRIS, 1960), the endochorion is said to become darker and thicker during development. The latter characteristic certainly must be attributed to a subchorionic layer. The term endochorion in culicid eggs seems to be misused in the paper of HARWOOD and HORSFALL (1959).

It seems premature to try to co-ordinate all the many published data on the subject known from other insect Orders. As a consequence of the extremely great diversity found in heteropterous egg shells, summarized and considered together under 3.1.1., we confine the discussion here to some general impressions and remarks. The classical and well known work on the shell of the insect egg by BEAMENT (1946), fortunately, is based on a heteropteran, the reduviid *Rhodnius prolixus*. The chemical approach of BEAMENT revealed: "some seven layers of proteinaceous material modified in various ways by tanning, by association with lipids and perhaps by the formation of sulphur linkages" (summary from WIGGLESWORTH, 1965). It is noteworthy that electron density in our micrographs, even the stained one, reveals only one obscure division of the shell. We did not study *Rhodnius* but the *Reduvius* and *Coranus* egg. Especially the egg of *Reduvius* conforms in principle to the *Rhodnius* type, as might also be expected from a similar ecology of the egg and the rather close relationship of the adult taxa. If the outer shell layer of *Reduvius* (fig. 299D, 266O) conforms to the exochorion of BEAMENT in *Rhodnius*, then no one division between the resistant and the soft endochorion is seen in *Reduvius*. The resistant endochorion layers of BEAMENT would comprise the inner air-conducting meshwork with its inner and outer boundary. The substance of the

meshwork proper (fig. 299D, ail) would be resistant protein, and the upper and lower limitation of this layer must represent the outer and inner polyphenol layer. The whole thick mid part of the *Reduvius* shell would correspond with the *Rhodnius* soft endochorion. The morphological picture, as revealed from microsections, is of a rather simple nature. The innermost boundary of the chorion is formed by a fine sheet, which apparently escaped detection in the chemical analysis. BEAMENT described the inner polyphenol layer as consisting of irregular droplets over the vitelline and later secured by the primary wax layer. Micrographs demonstrate that the outer struts of the meshwork form one entity with the solid mid region of the shell. It may be that the drops which constitute BEAMENT's outer polyphenol layer just refer to these strut basements. The next superimposed lamina, counting outward, is indentified by BEAMENT as the amber layer, which is the only layer of the *Rhodnius* shell with a marked colour. Nothing of the kind is seen in the micrographs of the reduviids we studied, nor in other shells with a distinct air-holding layer. The morphological picture of the operculum in *Reduvius* (fig. 299A–C) deviates from that of the shell body in the complete absence of the vacuolar inner layer, and in the greater thickness of the darker shell layer. The inner meshwork is also entirely absent in the cap of the *Coranus* egg, although a new porosity of aeropylar canals is developing. All the seven layers recognized by BEAMENT, would also be present in the cap of the *Rhodnius* egg, but in changed dimensional ratios. The amber layer and the soft exochorion are much thicker. The soft endochorion and the resistant protein layer are reduced. Yet, the air-holding meshwork also is lacking in the *Rhodnius* cap (HINTON, 1962d). The aerostatic meshwork was not then recognized as such by BEAMENT (1946). TUFT (1950) in his experimental work on the respiration of the *Rhodnius* shell, wrongly postulated the presence of a continuous gas space beneath the chorion (HINTON, 1961b).

These comparisons may indicate the difficulties of harmonizing the chemical and the morphological stratification. The morphological approximation, as conveyed over a longer series of species in the present work, seems to give appropriate results, particularly in understanding the open conducting systems. As shown in our descriptive review, the chief characteristics of the heteropterous shells can, with some experience, be resolved optically. The interpretation of the micrographs of heropterous shells did not offer obvious difficulties, because of the solidity of the greater part of the shell. In dipterous eggs, where often extensive areas of the shell and sometimes the whole shell is compartmented, likely chorionic and outer-chorionic layers are confounded. According to the technique of treatment of the shell for optical study and the often incomplete sections for electron-microscopy with the further risk of creating artefacts, examinations have caused misinterpretations of structures and mislabelling of layers (see discussion in HINTON, 1963). The same author (1962d) showed that the innermost wall of the *Rhodnius* shell appears as a continuous solid sheet in micrographs with a resolution af about 100 Å. The inner layer of the shell of a fly is composed of fibrils about 10 to 15 Å wide, when examined with a resolution of about 8 to 10 Å. These fibrils form a meshwork, the interstices of which are usually 20 to 50 Å wide. Solid shell parts therefore may have meshworks at a level that permits impeded passage of

respiratory gases. HINTON (1962d) refers to TUFT (1950) who found after covering the anterior aeropyles of the *Rhodnius* egg, still a little oxygen uptake presumably entering through the apparently solid outer layers of the chorion.

There are no indications that the structure of the heteropterous egg shell changes markedly during incubation. The inner sheet of chorionin of the *Cymatia* egg shows a finely mottled pattern (fig. 219A) which presumably is brought about by small islands where the sheet is thinner. It was known that the shell of Acrididae becomes disrupted into fragments during embryonic development. It has now been shown by MCFARLANE (1960) that in the cricket *Acheta domesticus* the inner chorion layer, about 0.4 μ thick, breaks up into many small, rectangular fragments. This structural change, due to phenolic tanning, would permit water to be absorbed by the egg. Water absorption appears to cease with the phenolic tanning of the lipid layer of the serosal cuticle.

The chorion of heteropterous eggs is translucent in aquatic, semi-aquatic (except *Hydrometra*) and in many terrestrial forms, the latter especially when they are embedded or laid in sheltered places. As has been shown in the descriptive sections, dark colouring of aquatic and semi-aquatic eggs during the first third of incubation is due to darkening of the serosal cuticle. The occurrence of this process has some taxonomic significance. Darkening of the serosal cuticle apparently excludes the possibility of a coloured chorion, and vice versa. Darkening of the outer coverings of the egg can develop by various means. The usual procedure is darkening of the chorion itself beginning in the proximal part of the ovarioles; this occurs in many Geocorisae (Reduviidae, Lygaeidae, Coreidae, and others). The chorionic browning starts first at the basal pole and proceeds up the circumference. A similar forward spread is noticed in *Hydrometra*, which colours the chorion thoroughly from white to jet black. Here, however, the colouration starts outside the female. If the eggs are submerged as soon as they are released by the female, the shells do not darken, even when subsequently exposed to the atmosphere. The oxidase or the substrate for it is probably washed off from the shell. Such a water treatment also prevents blackening of the eggs of the Asopinae, where the cement blackens only under dry conditions, the actual chorion remaining pale. Later, there is local darkening of the egg by coloration of the enclosed larva. There is no general rule for this process; the integument and hairs of the egg larvae of some species of Corixidae and Saldidae start to pigment only after hatching. In contrast to what we have seen in some heteropterous eggs, the inner layer of mosquito shells which darken rapidly in new laid eggs, retain their pale colour when they are removed from contact with water immediately after being laid (MARSHALL, 1938).

Although knowledge of the structure and physiology of the shells has increased considerably (data and discussions in the papers of HINTON, see bibliography), our findings leave a number of open questions. These questions (among others, the physiology of the amphibicorisal and saldid eggs which behave simultaneously as strict water and strict terrestrial eggs) have been enumerated briefly sub 3.1.1 and we have given fuller accounts of the structures on the respective pages in the descriptive sections. It seems that originally the shell had a wide safety margin allowing it to meet the risks

of fluctuating physical conditions. Some features suggest that whenever special adaptations to particular conditions have been acquired, these new structures may be retained long after loss of their function. The horns in the two African species of *Ranatra* studied were probably forced to elongate so much through a dense uninterrupted floating cover of plants (see p. 204). When oviposition at the water surface was no longer possible, the behaviour of the species could have changed in depositing far below the water surface. The horns being from then onwards most probably not air-filled, nevertheless retained their original plastronic structure. The porous micropylar quiver in Notonectidae, Pleidae, Helotrephidae, and some Corixidae contains no free air but the structure strongly recalls the outgrowth in some fulgoromorphous and aphidoid eggs, where it functions mostly for trapping and transference of air. It was shown that in the shell of some leafhopper species, the connection of the inner meshwork with the anterior aero-micropyle was broken, but this has not yet affected the outgrowth of the latter structure (COBBEN, 1965c).

Insect eggs have no regulatory apparatus for circulating the air in the respiratory system of the shell, the exchange of gases depending entirely on diffusion. Some progress has been made to overcome this inertness of the egg stage in those adult Heteroptera which carry their deposited eggs (ventilation in Belostomatidae (p. 209), escape from too strong insolation and evaporation in *Phyllomorpha*). Perhaps the first example of motility of chorionic parts during incubation has been demonstrated in Microphysidae (p. 138). The aeropylar filaments alternately radiate out and close again with humidity changes, undoubtedly affecting the rate of gas exchange.

A coarse vacuolar system over nearly the whole outer surface of the thick inner chorionic layer occurs in most Saldidae, Ochteridae and Gelastocoridae. A much finer porous system up to the very thin chorionic inner layer is present in Gerridae and Veliidae. In all these families (biological observations on gelastocorid eggs are still lacking), the spaces in the chorion communicate with the outside by radial canals over the whole shell but need not be filled even temporarily with atmospheric air for optimal and continuous development of the embryo. Saldidae have developed air clefts on the fore side of the anterior pole as another simple adaptation to trap air. The highly elaborate shell structure of *Hydrometra* proved to be of interest for two reasons. First, the spacious encircling lattice-work of the egg probably functions as a plastron (p. 56, 58). Secondly, the inner chorionic layer has been subjected to a horizontal shearing which established an open air connection with the anterior pole (fig. 265G). This shell opening can be considered as the preliminary stage of the more evolved inner aerostatic meshwork of the shells of the Geocorisae. The opening has presumably occurred independently in different groups. It occurs in the fulgoromorphous Homoptera, except in delphacids (COBBEN, 1965c). The various ways by which the inner aerostatic chorion communicates with the free atmosphere are reviewed for Heteroptera sub 3.1.1. Analogous features have evolved independently in fulgoromorphous leafhopper eggs in which usually a single anterior aero-micropylar projection communicates with the inner meshwork. In Flatidae, the meshwork around the micropyle and the generally distributed aeropyles gradually disappeared and a new aeropylar opening of

the inner chorionic meshwork evolved elsewhere in the cap (COBBEN, *op. cit*).

On p. 264 we considered whether a solid or a vacuolar shell represented the primitive condition in Heteroptera. The generally porous shell of the *Gerris* type or the thin solid shell of the *Hebrus* type merited consideration. It is assumed that protoheteropterans were small and occupied moist habitats. A fine but solid chorion would not there hamper the extraction of sufficient oxygen through the whole shell from the ambient air of water. A solid, little differentiated chorion is probably primitive in Hemiptera. A careful examination of the shell of Psocoptera which seems solid, should provide more evidence for our suggestion.

Respiratory horns evolved several times in the Heteroptera. Short respiratory cups are typical for most Pentatomomorpha. In a few groups (Urostylidae, Plataspidae) they are long because of a thick coat which covers the egg. Especially in the Miridae, there is a strong tendency for bundling and extreme lengthening of the aeropyles after their displacement towards the dorsal and ventral edge of the rim. In other mirids, the operculum developed one or two horns. All such horns have separate aeropyles within the bundle; each opens to the outside separately by one pore (fig. 188B). The horns of the *Termatophylidea* egg, however, terminate in what is thought to be a plastron (fig. 180B). According to HINTON (1962) the term plastron has been restricted in entomology to "describe a gas layer of constant volume and an extensive water-air interface. Such layers are held in position by a system of hydrofuge structures that resist the entry of water under pressure. In well aerated water a plastron enables an insect to remain immersed indefinitely, when it obtains the oxygen it requires from the ambient water". The morphology and the physiological advantage of the plastron-bearing horns in Heteroptera (Nepidae), many Diptera of various families and the Encyrtidae amongst the Hymenoptera, thus of predominantly terrestrial eggs, has been discussed recently in a series of papers (HINTON, 1960b; 1961a, b; 1962d). Plastral horns are structures adapted both for extraction of oxygen dissolved in water and for atmospheric respiration. HINTON has provided evidence for the view that these horns have evolved independently at least 15 times. To these examples, the variable types of plastral horns in several leafhopper families can now be added (Tettigometridae, plastron coarse foamy-like; Acanaloniidae, horn very long, curled like watch-spring, with fine pores). The other horns, sometimes branched (Tropiduchidae), in species studied of other fulgoromorphous families bear no plastron (COBBEN, 1965c). Plastrons may also be confined to special areas or the whole surface of the dipterous shell (HINTON, 1961). Widely porous strips on some hemipterous eggs *(Saldula madonica*, fig. 7; *Wagneripteryx germari)* or special hexagons (*Valleriola*, fig. 39C) may have the same function. It may even be that the network in the rim of the shell's neck and the opercular margin, often elaborated into veil-like structures (Cimicoid groups, Reduviidae), have a plastral function. The mobile anterior filaments of the microphysid eggs and the outgrowths in the leafhopper families Dictyopharidae and Derbidae should be considered as a plastron. Whereas the aero-micropylar cups of the pentatomomorphous eggs have one narrow opening to the outside, those cups in fulgoromorphous Homoptera are wider, with a larger porous interface with the air. It

is not known how far water can penetrate into the central lumen of the cups during flooding. If this penetration does occur, then a simple plastron function is suggested here too. Strong tendencies for enlargement of the air sponge round the outer micropylar canal occur in the Orsillinae (Lygaeidae). In *Ortholomus* these elaborate structures probably achieved plastral function. HINTON (1962d) considered the porous band of the shell of the staphylinid *Ocypus olens* as a rudimentary plastron on account of its effect on respiration (LINCOLN, 1961). The surface area of this plastron is not sufficient for normal development under water. The eggs of *Calliphora erythrocephala* die when the interstices of the real plastron at the waist of the egg are blocked (ANDERSON, 1960). All arguments about the efficiency of the various type of plastrons considered in literature are based on the opinion that an air-store in the shell is necessary for a successful incubation. Yet we observed that those amphibicorisal and saldid eggs which possess a vacuolar shell can develop either with or without an air-store. Eggs, deprived of the internal air incubate normally even when continuously flooded in non-aerated water. This applies also to the remarkable egg of *Hydrometra*, although the striking features of the chorion must be terrestrial adaptations. It has been suggested on p. 58 that the principal function of the outer network in this egg may be to limit fluctuation in humidity.

The follicular hexagonal lining produces a pattern on the shell surface of many species. Sometimes, the struts of the aerostatic inner layer reflect this hexagonal pattern (fig. 139, 187B). Small species seem to produce eggs which are large in relation to body size often with a distinct and spacious hexagonal reticulation. But the eggs of large species bear numerous hexagons which appear smaller. The discrepancy arises partly from optical illusion because the eggs of large species are larger and bear more hexagons and are therefore usually studied at lower magnification. The stretched follicular cells seem to fluctuate in size around a mean when the hexagons of eggs of species of all sizes are compared (black dots in the graphs, fig. 273, 274; some data for homopterous eggs are added). The hexagon's width usually varies from 15 to 50 μ, but exceptions are up to 90 μ among eggs of the small species. The graphs further show the relation between egg size and body size of the adult female. The examples are arbitrary, except that species with greatly elongated eggs were limited. Comparisons, of course, are rough since the relative dimensions of the species and their eggs are not equal (length of female is exclusive of extended wing).

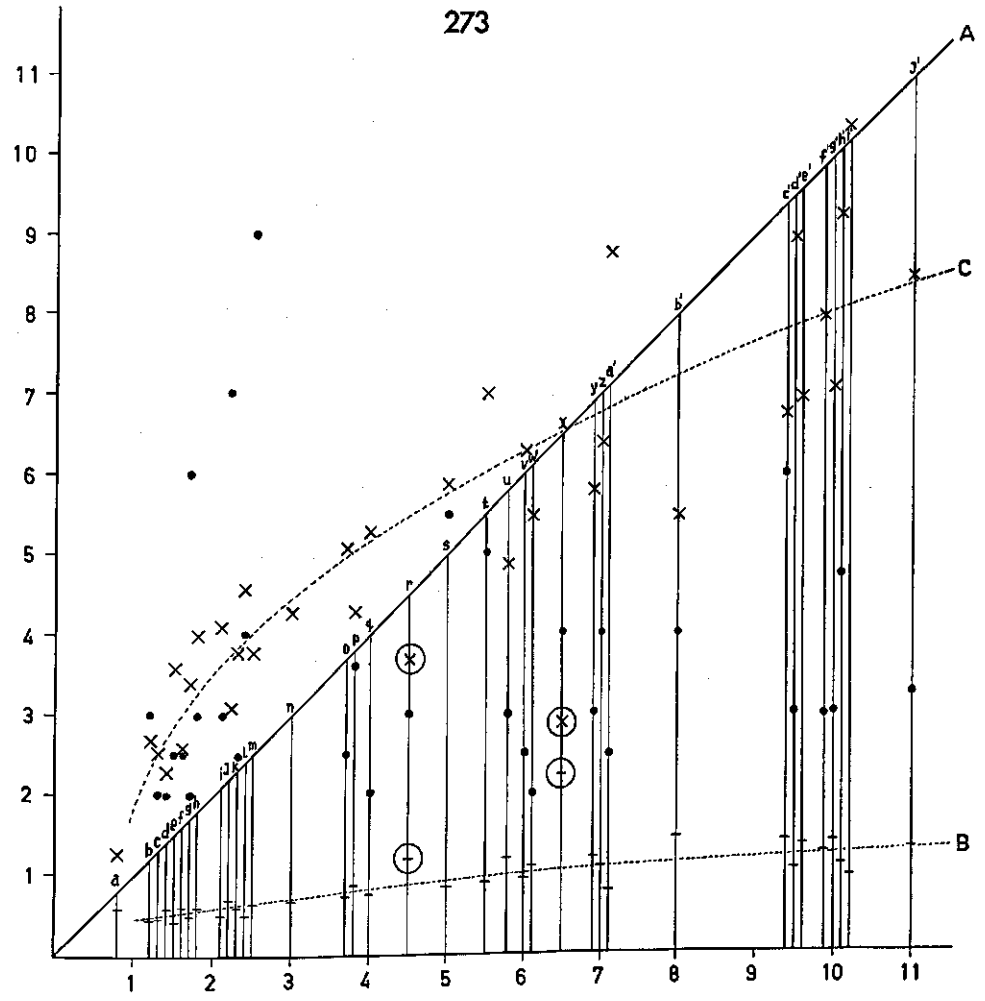
In relation to the body size of the females (line A, fig. 273), the eggs of small species are only slightly longer (line B) than in large species. Species r and x show how bugs with narrow eggs (more than four times longer than wide) deviate from the regular pattern. The regression line of the ratio female length: egg length (line C) slopes steeply downward among the smallest species. Thus in relation to body size, the small species have large eggs and the largest hexagons. We considered species from diverse families. The same correlations may be more apparent in each phyletic line, when species are arranged by body size. The phenomenon of anagenesis, expressed as a decrease in relative egg size, progresses parallelly during the evolution of different phyletic branches, and could more readily be analysed in a larger series of species.

Larger eggs usually mean that fewer of them ripen at once. Indeed, species of the highest evolved taxa produce many eggs simultaneously. These are deposited in batches or series at short intervals. In general the small species have a longer oviposition period, during which series of a few eggs ripen in sequence. The data on the ovarioles in Heteroptera (CARAYON, 1950c; WOODWARD, 1950; MIYAMOTO, 1957, 1959, and our observations) show a range per ovarium from two (only *Hesperoctenes* and *Halovelia*) to eight (some Reduviidae and Miridae), with the remarkable exception of 17-29 in five species of *Elasmucha*. The commonest number is seven. Each of the four major groups repeat the shift of ovariole number. We believe that anagenesis is towards multiplication of the ovarioles, a trend matching the decrease in egg volume.

The change in egg volume has a fixed evolutionary pattern in Heteroptera but fluctuates and is controlled by season in Homoptera Aphidoidea. The most striking example is Phylloxeridae. Generations with females, delivering many small eggs per female (eggs of gallicolous forms differ from those of the radicicolous forms), alternate with long-winged sexuparous individuals producing only a few large eggs and the apterous female producing only one large winter egg. The winter egg is on a stalk which is lacking in all other eggs of the same species. The sexuparous egg containing a female embryo is one and a half times the size of the male egg. Thus six different types of eggs occur in one and the same species. The large eggs bear distinct hexagons, all almost equal in size, averaging 0.03 mm (fig. 1422 in PESSON, 1951). Consequently, the male eggs are produced by far fewer follicular cells than the female eggs. The same polymorphism is expressed also in the ovarioles, both in their number and histology (BALBIANI, fig. 1309, 1310 in PESSON, 1951). In Phylloxeridae, there seems to be no causal relation between ovariole number and body size of the mother. In *Leptoconops becquaerti* (Ceratopogonidae), a positive correlation exists. The number of ovarioles in this species ranges from 48 in small females up to 159 in large ones (LINLEY, 1965).

Micropyles

The original number of micropyles in Heteroptera is argued in 3.1.2 to be only one, in the centre of the anterior pole. This number occurs in many recent aquatic and amphibious species and has increased in most phyletic lines of all major groups of Heteroptera. The displacement of the micropyles, the variety of micropylar types and their frequent directional circular polarisation has also been reviewed. Some striking parallels have been noted in Homoptera Auchenorrhyncha in our paper of 1965. In this series of Hemiptera, one major group of families retained the anterior single micropyle (as in Aphidoidea), in one family the single micropyle moved posteriad and in the other families the micropyles have multiplied and have moved posteriad. In Psyllidae, the group of micropyles (hitherto overlooked) approach the basal pole and in the Aleyrodidae, the micropyle became incorporated in the basal stalk, which has four functions. By incomplete knowledge of the literature and, in particular, of the work of WEBER (1931), POINAR (1965) suggested that the stalk of aleyrodid eggs does not function as a micropyle.



leg. 273. Relation between length of female (line A) and length of egg (line B), scale in millimetres; ine C represents the ratio A/B (note the steep slope in the smaller species); black dots are rough istimates of the mean length of the chorionic hexagons, reflecting the dimension of the follicular cells (scale 100 times that of A and B); further explanation in the text.
a: *Eriosoma lanigerum;* b: *Myrmedobia coleoptrata;* c: *Hypselosoma* sp.; d: *Nannocoris* sp.; e: *Pachy-*
coleus rufescens; f: *Omania marksae;* g: *Tenagobia incerta;* h: *Discocoris vianai;* i: *Microvelia signata;*
j: *Coleopterocoris kleerekoperi;* k: *Plea atomaria;* l: *Xylastodoris luteolus;* m: *Proutista fritillaris;*
n: *Dictyla symphyti;* o: *Pseudoloxops coccineus;* p: *Leptopus marmoratus;* q: *Ochterus marginatus;*
r: *Helopeltis antonii;* s: *Zoraida* sp.; t: a cydnid; u: *Chiloxanthus pilosus;* v: *Diaprepocoris zealandiae;*
w: *Anisops* sp.; x: *Nabis rugosus;* y: *Ricanula* sp.; z: *Dermatinus* sp.; a′: *Hesperocorixa linnei;* b′:
Flatoidinus sp.; c′: *Nerthra laticollis;* d′: *Elasmostethus interstinctus;* e′: *Lawana conspersa;* f′: *Eury-*
gaster integriceps; g′: *Odontotarsus* sp.; h′: *Mezira* sp.; i′: *Cethera musiva;* j′: *Hotea subfasciata.*

It would be interesting to investigate whether other Orders of insects show parallel trends in the micropylar system. For convenience, some characters may be listed, without implications, as revealed by a survey of the literature:

Apterygota As far as we know, the only record refers to *Lepisma*, where one micropyle occurs at the anterior pole (DENIS, 1949). The *Campodea* egg is said to lack micropyles.

Ephemeroptera 1–7 (53 species), four types, at the middle or in the basal half (DEGRANGE, 1956).

Odonata 4–14 (12 species), annularly arranged around the anterior pole; minimum number in *Calopteryx atrata*. *Sieboldius* must have about 9 micropyles anterior but others are at the posterior pole (ANDO, 1962).

Plecoptera 3–12 (5 species), in a circle, in anterior half or at the egg's waist (DEGRANGE, 1957).

Dictyoptera Blattidae. 1 (1 species), anterior (LEUCKART, 1855).

Isoptera 4–12, according the species, in a half-circle on the convex egg side (GRASSÉ, 1949); 12–14, posterior in *Kalotermes flavicollis* (TRUCKENBRODT, 1964).

Phasmida 1 (2 species), posterior (LEUCKART, 1855).

Orthoptera Tettigoniidae. 1–23, mostly lateral about one fifth of the way from the posterior end (LEUCKART, 1855; HARTLEY, 1964); 1–3 micropyles occur in Gryllacrididae and 4–9 in Stenopelmatidae, in both cases in the middle of the egg; although CAPPE DE BAILLON (1920) talks about a reduction and migration of the micropyles anteriad, RICHARDS and DAVIES (1957) refer to these grasshoppers as two rather primitive families; two or three micropyles occur also in *Saga* and the maximum number is found in Pseudophyllidae.

Gryllidae Usually 2 (1 species), on the convex egg side, somewhat below the middle (SAUER, 1966).

Acrididae 30–45 (several species), posterior (LEUCKART, 1855, and others).

Psocoptera Micropyles have not been found in any of the species studied (GOSS, 1954).

Mallophaga, Siphunculata 5–70, anterior (WEBER, 1939; RICHARDS and DAVIES, 1957).

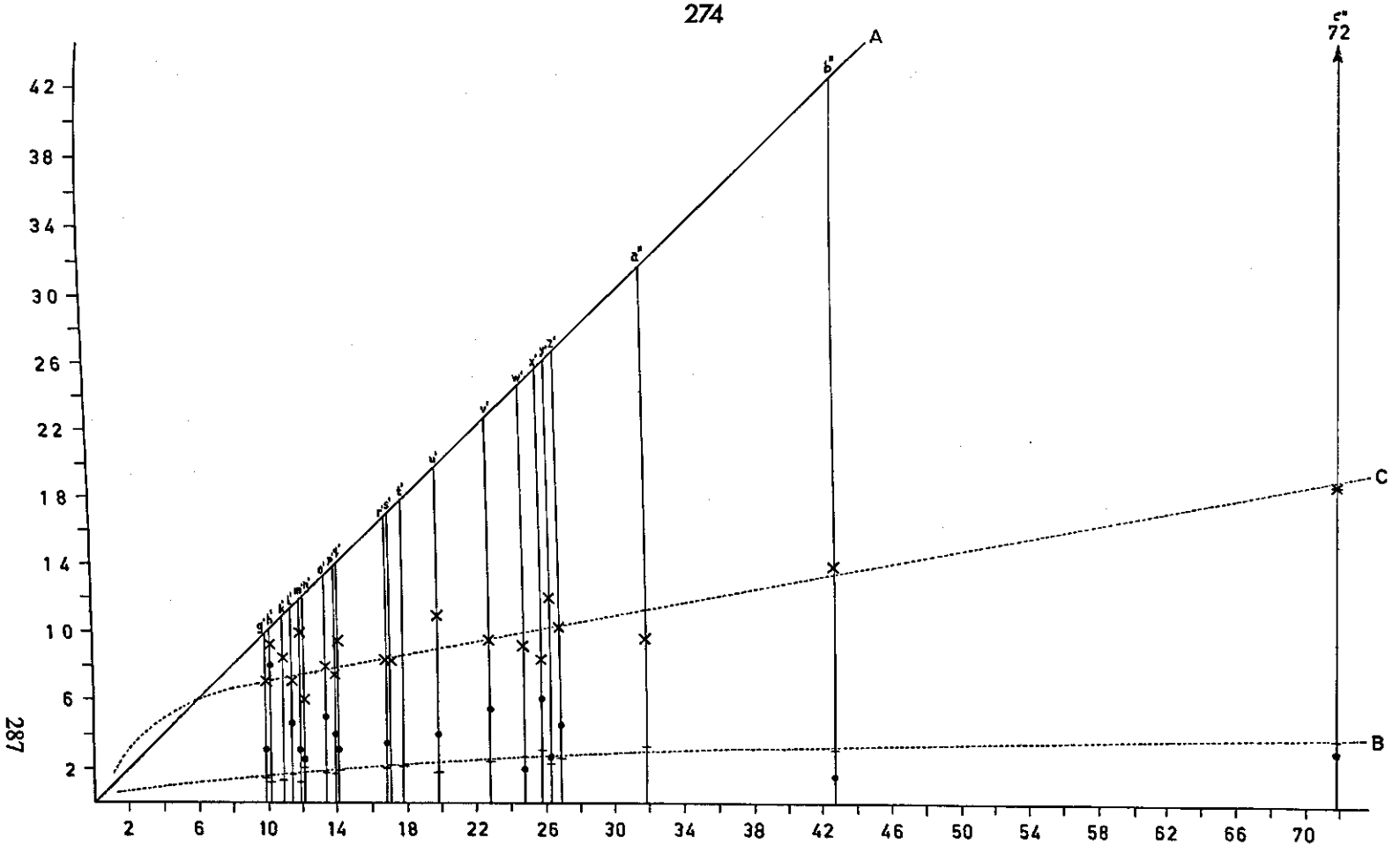
Neuroptera 1 micropylar process (LEUCKART, 1855).

Lepidoptera Mostly 4–6, anterior (LEUCKART, 1855).

Diptera 1 (species of several families) (LEUCKART, 1855; HINTON, 1960a).

Hymenoptera 2–30 (in a number of ichneumonoid genera), anterior; no micropyles were found in Tenthredinoidea (LEUCKART, 1855).

Fig. 274. Continuation of fig. 273 on a lower scale.
g′: *Odontotarsus* sp.; h′: *Mezira* sp.; k′: *Hotea subfasciata;* l′; *Scotomedes minor;* m′: *Picromerus bidens;* n′: *Coranus aegyptius;* o′: *Coreus marginatus;* p′: *Notonecta glauca;* q′: *Rhinocoris* sp.; r′: *Rhinocoris* sp.; s′: *Agapophyta viridula;* u′: *Leptoglossus* sp.; v′: *Nepa rubra;* w′: *Rhinocoris nitidulus;* x′: *Mictis metallica;* y′: *Ectrichodia antennalis;* z′: *Anoplocnemis* sp.; a″: *Siphnus alcides;* b″: *Platymerus* sp.; c″: *Lethocerus indicus.*


A
B
C
72
42
38
34
30
26
22
18
14
10
6
2
2
6
10
14
18
22
26
30
34
38
42
46
50
54
58
62
66
70

287

Coleoptera A number in irregular association or in an anterior circle; 1 in the cerambycid *Acanthocinus;* besides the anterior micropyles a few are said to occur at the basal pole in *Lytta* (Meloidae) (LEUCKART, 1855; REMPEL and CHURCH, 1965).

Siphonaptera A circular group of equivalent pores both at the anterior and posterior pole (1 species, own observation).

Absence of micropyles can be explained where the eggs are fertilized early in the ovarioles before the chorion is deposited (*e.g. Metatetranychus*, BEAMENT, 1951). This is found also in Heteroptera with traumatic insemination where the number of micropyles is reduced from two, through one, to zero in several Cimicoidea. When the micropyle is considered to serve only for the passage of the sperm, their multiplication must be associated with the appearance or advancement of polyspermy. In *Drosophila* species with only one micropyle, polyspermy is general. Considerable specific difference in the degree of polyspermy has been shown in nine species, among which the sperm appeared in the embryo and elsewhere (COUNCE, 1959). The remarkable arrangement of the micropyles in the dragonfly *Agrion puella* must be combined with a hydropylar function (DEGRANGE, 1961). The existence of a serosal hydropyle beneath the micropylar chorionic nipple is suggested in *Corixa*.

Finally there is the question whether the micropyles contribute to the exchange of respiratory gases. From the work of BEAMENT, other workers have generalized that the micropyles are sealed after fertilization of the egg. Our findings show that blackening of the serosal cuticle as in Saldidae occurs just below the micropyle, suggesting free passage of air there. Micropyles in Heteroptera, despite their various locations, are almost always exposed, whether the eggs are embedded or not.

Whatever other functions the micropyle may have, its formation and structure has been investigated to some detail in the Diptera (PANTEL, 1913; CHRISTOPHERS, 1945; KING and KOCH, 1963). There it is often complex and consists of an ectomicropyle in the shell proper and an entomicropyle penetrating the vitelline membrane. The egg spike in *Culex*, a distinct structure set in the endochorion, seems to be a plug formed after fertilization. Nipples superficially resembling structures found in some amphibious and aquatic eggs of Heteroptera, occur in *Drosophila*. The vitelline membrane which has recently been shown to be a product of the follicle cells too (KING, 1964), protrudes into the micropylar cone. In the new laid egg of the meloid *Lytta viridana*, the vitelline membrane is porous. The pores may be associated with sperm penetration since they are completely closed some hours later (REMPEL and CHURCH, 1965).

Eclosion split

Throughout this work we have used the terms: pseudoperculum and operculum *sensu* SOUTHWOOD (1956), although their limits have been rather blurred during the present treatment. SOUTHWOOD defined the operculum as follows (his p. 173, 174): 1. Separated from the rest of the chorion by a distinct sealing bar. 2. Differing from the rest of the chorion in structure, usually with much deeper follicular pits and with

thicker amber and soft endochorion layers. 3. Surrounded by the micropylar apparatus, which is situated in the rim of the chorion.

This definition which he generalized as applying to all Cimicomorpha, is largely based on the conditions found by BEAMENT in *Rhodnius*. The shell structures of *Bryocoris* and *Monalocoris* do not conform to any of the three prepositions listed. *Empicoris*, among Reduviidae and probably most typical cimicoid groups have no distinct sealing bar. It seems that the typical operculum with its perfect sealing system has arisen independently in the cimicoid and the reduvioid groups, while the eclosion mechanism by pressure of the serosal cuticle was developing. The serosal cuticle functions as such also in the Hydrocorisae and its function is taken over by the embryonic cuticle in the Mesoveliidae. Where in these latter groups a round cap has evolved, this possesses no sealing bar but its existence may be once incipient. According to the terminology of SOUTHWOOD (*op. cit.* p. 174), such a lid without sealing bar must be called a pseudoperculum. Additional characters of a pseudoperculum are: "having the same structure as the rest of the chorion; not bearing any fixed relationship to the micropylar apparatus, this may surround it or occur both on and off it". It has been shown in 3.1.2 and 3.1.3, how the cap arose along different lines from a longitudinal split and that the aero-micropylar system has evolved independently by multiplication and migration of canals. The structure of the cap often differs markedly from that of the shell body, and some of our observations suggested that the aerostatic inner layer may diminish or even be absent in the centre of the cap. The pentatomomorphous pseudoperculum is lifted by a firm egg-burster. It seems that this burster is still evolving towards perfection. The margin of the lifted pseudoperculum is not smooth but has irregularities. Where this lifting system is best adapted we may expect a sharply defined boundary of the cap but not a sealing bar which is adapted to receive, in its recess, the ring of the serosal cuticle so characteristic of many cimicomorphs. The cap of some eggs of the aquatic and amphibious groups could also be termed a pseudoperculum, although it may reach a true operculum, because of eclosion by fluid pressure. Thus the usage of the term pseudoperculum involves two inconsistent ideas. In order to give the terms operculum and pseudoperculum a wider application throughout eggs of the whole Class of insects, we recommend restricting the operculum to the typical reduvioid structure with a sealing bar, implying the particular mode of eclosion concerned with fluid pressure. Among the Homoptera Auchenorrhyncha, the higher Delphacidae then have a true operculum, but in other homopterous families, the cap should probably be termed a pseudoperculum. The micropylar system and the differences in chorionic structure are better omitted from the definition, because they are subject to independent processes and functions and play no part in the actual method of eclosion. We have seen how longitudinal eclosion fractures in one Suborder (Heteroptera) evolved along so many different lines with equal diversity in cap construction; parallel phenomena may be expected in other insect groups. For example, a longitudinal eclosion occurs in the Apterygota, Ephemeroptera, Odonata-Anisoptera, a group of Plecoptera, Psocoptera and most Homoptera. A cap occurs in Odonata-Zygoptera, a group of Plecoptera and in all Mallophaga and Siphunculata, studied so far.

3.2 Gross embryology

3.2.1 Incubation time, diapause

Incubation time

At a constant temperature of 30 °C, the shortest complete development, through hatching, occurred in the *saltatoria-pallipes* group of the genus *Saldula*, namely four days. No variation in this time was observed whether or not the eggs were continually submerged. The survival of eggs did not decrease with this high temperature and there was no abnormal hatching. The average developmental time, in days, also at constant 30 °C in some other Saldidae and in representatives of other families is indicated between brackets:

Chartoscirta cincta (6), *Saldula orthochila, S. marginalis, Chiloxanthus pilosus*(7–8) and *Salda littoralis* (9, excluding time of diapause); *Gerris lacustris* (6–7 in water, 8–9 in saturated atmosphere), *Microvelia reticulata, Hydrometra stagnorum* (6–7), *Mesovelia furcata* (10.5); *Oncopeltus fasciatus, Dysdercus cingulatus* (5), *Ischnodemus sabuleti* (9), *Carpocoris pudicus* (5), *Graphosoma lineatum* (4.5), *Bagrada cruciferarum* (4; ATWAL, 1959); *Nabis rugosus, Liocoris tripustulatus, Notostira elongata, Empicoris culiciformis* (7–8); *Dicyphus pallicornis* (9); *Ilyocoris cimicoides* (8.5), *Plea atomaria* (10). At 30°C all the eggs of *Nepa rubra* and *Notonecta glauca* and *obliqua* die. The high rate of development of *Sehirus biguttatus* and the Acanthosomatidae studied at room temperature suggests a very rapid incubation at 30 °C.

Some species were reared in the Ivory Coast at a fluctuating temperature of 25°–29 °C: the scutellerids *Sphaerocoris* and *Hotea* (7–8); five Pentatomidae (7–8); the Coreidae *Hydara* sp. (6–7), *Acanthomia, Homeocerus, Leptoglossus, Anoplocnemus* (8–10); seven sp. of Harpactorinae (8–12); the reduviid *Cethera* sp. (30); the Hydrocorisae *Ranatra* sp. (8) and *Ochterus* sp. (16–17).

EDWARDS (1962) mentions about 29 days at 28 °C for *Platymeris rhadamanthus* Gerst, and IMMEL (1955) 11–18 days (26°–32°) for *Reduvius personatus*.

Development of *Notonecta* was as long in complete darkness as with the natural photoperiod (April–May). OHM (1956) found, however, that it took twice as long for eggs of *Aphelocheirus* to develop in complete darkness, 45–47 days (24°–26 °C).

It is, of course, an oversimplification to consider all these data as comparable, if the complete temperature-velocity graph of the embryonic development is not known for each species. The curve for *Oncopeltus fasciatus* resembles a hyperbola between 15° and 35 °C but at these extreme temperatures many hatchings are unsuccessful (LIN *et al.*, 1954). In *Oncopeltus*, no hatching at all occurs at constant 38 °C, whereas the upperthreshold for the Indian *Bagrada cruciferarum* is about 45 °C (ATWAL, 1959). Initial subthreshold temperatures of 5–10° are tolerated by *Oncopeltus* eggs for only a few days, but do not entirely prevent embryonic growth. The same is mentioned for *Cimex lectularius* (JOHNSON, 1940). Fluctuating temperatures usually accelerate incubation rate in *Oncopeltus* and *Cimex*. JOHNSON and ATWAL both showed that pre-

conditioning of the eggs may have a very complex effect and may change the constant-temperature thresholds.

If the data of incubation times are therefore compared reservedly, there seems to be a correlation between the stability of the habitat and the duration of the egg stage in Saldidae. The four *Saldula* sp. of the *saltatoria-pallipes* group inhabit places with erratic moisture conditions and these species have the shortest egg span. They hibernate, often far from their breeding places, as adults with atrophied ovaries. The other Saldidae listed incubate in 6–9 days and among them is *S. orthochila* which also inhabits soils unstable in humidity. However it is better adapted to dry conditions. The progression towards terrestrial life is also reflected by the inability of the egg larvae to emerge through the water film if incubated under water. All other Saldidae, like all typical Amphibicorisae, can reach the water surface without difficulty after eclosion.

As expected, major differences in incubation times cannot be closely related to taxonomy. However, provisionally the development in Reduviidae and Hydrocorisae seems slowest. These two groups are taxonomically more compact, as indicated by embryonic characters. The shorter developmental time in pentatomoids than in higher Coreidae might become more widely significant if comparisons extend over long series of species. The effect of humidity changes on the egg would be highest in those hygrophilous species which deposit in temporarily moist sites and is closely dependent on whether water is taken up for development. Most Amphibicorisae and probably all Saldidae need saturated conditions for normal egg development. They take in free water but *Hydrometra* and *Leptopus* do not. Free water must also be absorbed by those Hydrocorisae laying at the water surface, because of the characteristic eclosion as in submerged eggs of other waterbugs. The embedded eggs of many Miridae and to a lesser degree of Nabidae need water to force out the serosal plug and the embryonic cuticular vesicle, respectively. Incubation of these bugs may be hampered if moisture supply is not adequate. For example, the egg stage of *Gerris* lasts some more days if they are kept in humid air instead of below water. In terrestrial eggs the contrary may occur. In *Blissus* eggs the increase in incubation period is fairly directly proportional to the duration of submergence (JANES and HAGER, 1936).

Erratic air humidity does not markedly affect the duration in some Cimicomorpha (*e.g. Cimex*, JOHSON, 1940), Reduviidae and probably most Pentatomomorpha. In *Oncopeltus*, relative humidity below 50 at optimum temperature significantly diminishes hatching percentage. LIN *et al.* (1954) pointed out that low humidities raise the upper limiting temperature for *Oncopeltus* a few degrees. In Pentatomidae, wide ranges of humidity (in *Bagrada* from 20–80%) have no influence on rate of development or viability of the eggs (ATWAL, 1959; POLIVANOVA, 1965).

Diapause

Egg diapause intervenes at various stages of embryonic development but never at or before the blastoderm stage. Development usually ceases before the embryonic revolution. The only exception we found was *Nysius thymi*, whose eggs in diapause con-

tained the prolarva, nearly ready to hatch (laid in August, room temperature). A similar hibernation is reported for some other Lygaeidae in North America (two *Stygnocoris* spp.; *Drymus unus*, SWEET, 1964).

The data from our work are diagrammatically arranged in fig. 275, according to stage of development at hibernation. All these diapausing embryos have a serosal cuticle, even if the germ band does not yet bear protocormic outgrouwths. The serosa remains active for a time after morphogenesis of the embryo is inhibited.

Except in Miridae, egg diapause is unusual for hibernation in Heteroptera. Of 200 species of Miridae in the Netherlands, 85.5% hibernate in the egg and 13.5% in the adult stage. One species, *Dicyphus pallicornis*, hibernates in the Netherlands normally in all instars (larvae, adults, occasionally eggs), but none of these seem to exhibit a real diapause. Only one mirid, *Macrolophus nubilus*, was found to have a constant diapause in the fifth larval instar. Under normal conditions it has an annual cycle of two generations. The synchronization of diapause to winter in the fifth instar seems extremely well-fixed. In two extraordinary years with a cold spring and summer (1962, 1965), there was only one generation. The larval development of this generation was so prolonged that again only the last instar hibernated. In the eight years of observation a partial generation never arose.

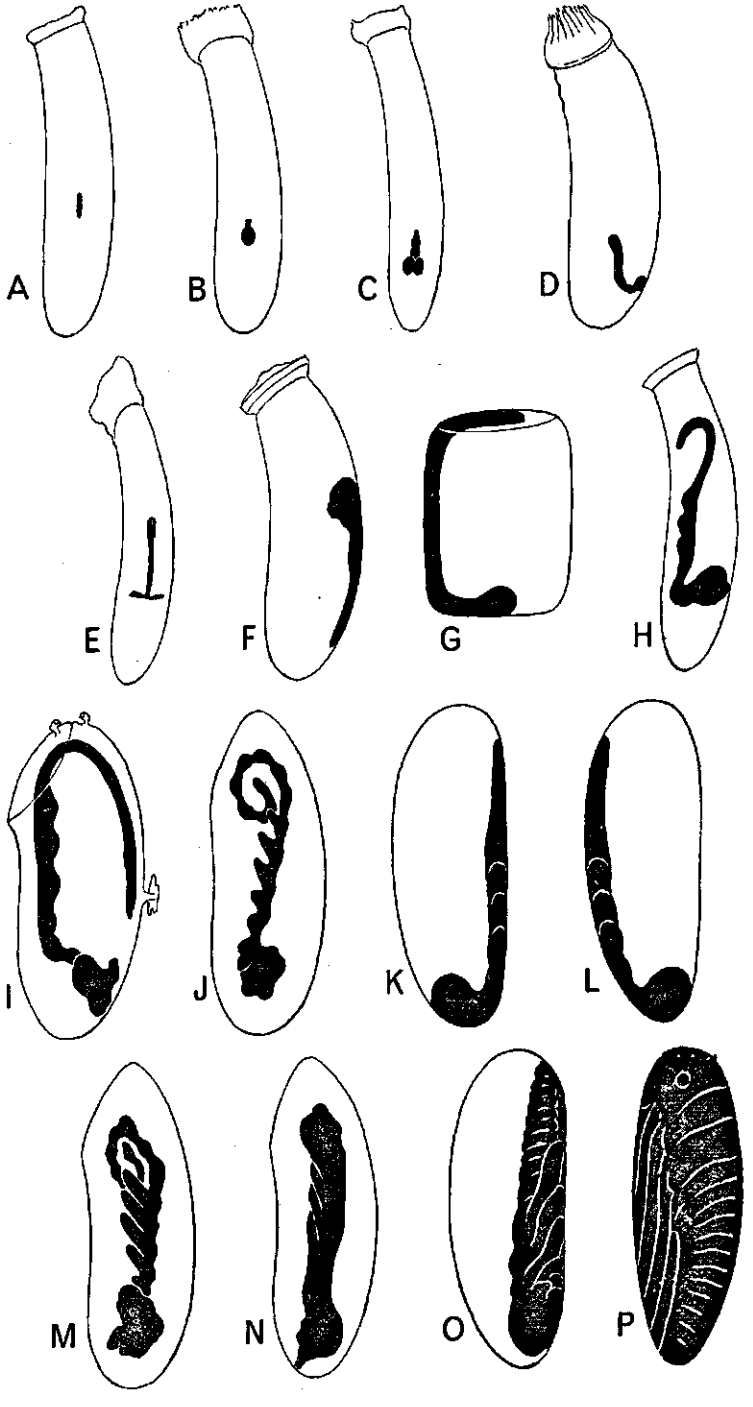
The larvae are active in winter, if temperature is not too low. The diapausing larvae of the second instar of the saldid *Chiloxanthus pilosus*, collected in October, behaved and preyed actively at 30 °C for months without performing any further moult. Hibernating larvae of Heteroptera have been encountered in *Aradus*, *Aethus*, *Odontoscelis*, *Pentatoma*, several Lygaeidae, *Acalypta*, *Reduvius*, some Xylocorinae, Micronectinae (YOUNG, 1965), *Ochterus banksi* (BOBB, 1951). These larval hibernations are probably photoperiodically induced and of true diapause nature in many cases but this has been proved experimentally only for the semivoltine *Ischnodemus sabuleti* (TISCHLER, 1960). The occasional occurrence of larvae in winter after cool summers (Lygaeidae, Saldidae, Hydrocorisae) suggests the possibility of quiescence after a retarded developmental cycle.

Other than Miridae, most Heteroptera hibernate as adults. Like diapausing larvae, those adults are not at all in a stage of general immobility (discharging of scent gland reservoirs if disturbed, even below o °C; lively movement; escaping by jumping away). Reproduction starts early in most Hydrocorisae, but *Plea atomaria* is a late species. The observations described on p. 230, suggest that in *Plea* a switching mechanism regulating the formation of wing musculature at the cost of oocytes operates even in April, when environmental conditions are suboptimal. Fig. 275 shows that the devel-

---

Fig. 275. Strong diapause in heteropterous eggs; dextral lateral side, except for G, I and P which show the morphological left side of the egg (see sub 3.4.5). A: *Plagiognathus arbustorum;* B: *Megalocoleus molliculus;* C: *Pantilius tunicatus;* D: *Loricula elegantula* (almost similar in *Ceratocombus coleoptratus);* E: *Leptoterna ferrugata* (most other Miridae); F: *Coranus subapterus;* G: *Picromerus bidens;* H: *Himacerus apterus;* I: *Myrmus miriformis, Chorosoma shillingi;* J: *Chiloxanthus pilosus* (30 °C), *Halosalda lateralis (Stygnocoris pedestris* almost the same); K: *Notonecta lutea;* L: *Notonecta maculata;* M: *Chiloxanthus pilosus* (20 °C), *Saldula marginalis;* N: *Salda littoralis* (20 °C); O: *Notonecta reuteri;* P: *Nysius thymi.*

275



opmental stage at which egg-diapause occurs is independent of the relationship between different taxa. Diapause in *Notonecta lutea* is much earlier than in the closely related *N. reuteri*, at the same incubation temperature (fig. 275K, O). But a difference in temperature may cause diapause at different embryonic stage in one species (*Chiloxanthus pilosus*, fig. 275J, M). The egg of *Stygnocoris pedestris* diapauses in the Netherlands at a stage before revolution but in New England, according to SWEET (1965), this occurs much later after completion of blastokinesis. *Myrmus miriformis*, however, diapaused in Upper Loire, France (1000 metres elevation) in exactly the same embryonic stage as in the Netherlands. On the other hand, all hibernating eggs of Miridae we studied (13 species) diapaused in the germ-band stage. Thus it seems that the strong-diapause stage may have some taxonomic meaning.

The incomplete data on hibernation of heteropterous eggs reveal a wide range of types of quiescence and diapause of many different grades and, possibly, intensities. As compiled here, they form a challenging framework for future experimental research on the evolution of diapause phenomena in Heteroptera. The categories listed below are considered apart, without suggesting mutual relationships or progressions.

1. Ovarian growth at low winter temperatures.

This occurs in many Corixidae; in some of them maturation of eggs and oviposition takes place at temperatures from 0°–4 °C (YOUNG, 1965). The eggs do not go into diapause and something similar happens in some *Notonecta* spp. *Notonecta* has an univoltine cycle but many Corixidae can have two or more generations. Under experimental conditions of a 16-h photoperiod and temperatures of 12°–32 °C, corixid imagines mature and deposit at all times of the year.

Initiation and continuation of ovarian growth during chilling is also suggested in the terrestrial *Chlamydatus evanescens*. It may be that *Velia caprai* also must be grouped in this category. The data we gathered in the Netherlands deviate from the cycle suggested in literature. SOUTHWOOD and LESTON (1959) conclude that in England eggs are laid in May and June. In different years, we collected males and females containing mature eggs in April and earlier. They behaved actively in the laboratory, copulating and feeding on dead flies, but not laying eggs. They were kept for months under apparently suitable conditions (moving water-film, floating material, natural photoperiod). After death, dissection still revealed the presence of ripe eggs. Other females, kept for one month at 3° and 10 °C, did not change their behaviour after restoration at a temperature fluctuating between 10° and 25°; they did not release their eggs. Our experience from the field is that in winter and the beginning of spring, young larvae normally occur. We must therefore assume ovarian maturation and egg deposition in the late autumn or in relatively mild periods in winter. Perhaps some of the old adults miss the critical point for oviposition and wait until the next autumn. Dr. J. LATTIN has told us that a similar maturation period during the cold season seems to occur in *Macrovelia horni* in Oregon.

2. Eggs laid in September, but without diapause (*Mesovelia furcata*, bivoltine).

Some eggs hatch in the autumn (the Netherlands), when temperatures remain higher. The species is distributed through whole Europe, but its northern limit is in the

extreme south of Scandinavia.

3. Retention of ripe eggs within the female during autumn and winter.

Field observations over several winters show that ripe eggs are normally retained within the female of the bivoltine *Saldula orthochila*. Perhaps females reaching adulthood earlier than the rest of the population lay in autumn. One female, collected in mid September 1963, laied immediately when kept at 30 °C, and normal hatching soon followed. In 1965, however, the eggs laid by some mature females, collected on 3 and 23 October, did not continue development. Eggs died at different embryonic stages and 30° was obviously injurious. As eggs laid in the spring and summer readily endure such high temperatures there may be a preconditioning of the eggs in the female. Most of the pregnant females collected in autumn, died after some time at room temperature without releasing their eggs. The cycle in England could suggest a similar type of hibernation as in the Netherlands (*oppos.* WOODROFFE, 1963). Mr. P. LINDSKOG wrote us that in Sweden (near Stockholm) the species definitely hibernates in the egg stage. Retention of ripe ovarian eggs in autumn and winter is also substantiated in the leafhopper *Mocydiopsis longicauda* (REMANE, 1961), whose males, unlike *S. orthochila*, die in autumn.

4. Retention of eggs with embryo within the female during late summer, autumn and winter.

Many females of *Temnostethus gracilis* collected at the end of July and in August 1967, in the Netherlands and southern France (upper Loire, elevation 1000 metres) were dissected and contained one ripe egg in each ovariole. As is usual in Anthocoridae such ovarian eggs had already completed the early phases of embryogeny. It was however strange that all eggs of the females dissected were exactly in the same embryonic stage, with ♀ -shape but still without protocormic buds. No eggs were deposited in the laboratory during August and September (20° and 30 °C, natural and long-day photoperiod). Some females were exposed to outdoor conditions, because normal temperature fluctuations or cooler temperatures would perhaps evoke egg deposition. No free eggs were found, however, when the tubes were inspected in November and there was no change in the reproductive organs of the still living females. All published data say that both *T. gracilis* and *T. pusillus* hibernate as adults, so that the remarkable type of reproductive diapause in *T. gracilis* must be a regular phenomenon. Thus in one individual there are two forms of diapause in autumn: 1. The females do not oviposit the eggs which are ready to be deposited; 2. These undeposited eggs in turn are in embryonic diapause.

The cycle of *T. pusillus* may be slightly different. Three of five females (collected late in September 1967) were dissected and these revealed as many ripe eggs as there were ovarioles. Most of them had an embryo in the ♀ -stage but some were developed abnormally. The remaining two females were kept alive at room temperature, and these soon laid eggs which diapaused but a large proportion of these died rapidly.

As said before, there was in the *T. gracilis* females from August only one egg in each ovariole, that is 14 eggs together. It may be that in spring renewed oogenesis will yield additional non-diapause eggs after delivery of the original 14 eggs which have

hibernated within the ovarioles. If so, some parallels can be drawn with the reproductive category 5 to be discussed next.

5. Release of diapause eggs before and of non-diapause eggs directly after the winter.

This phenomenon occurs in *Notonecta maculata*, a species which lays most eggs in autumn. Such eggs need chilling to break the embryonic dormancy. However, if females are chilled during laying, they deposit retained ripe eggs as soon as the temperature rises and such eggs develop at once. Cold thus seems effective in preventing diapause in the ripe, but not yet deposited and fertilized eggs. If this chilling effect operates directly on the ripe ovarian eggs, the sensitivity of such eggs to chilling is expressed much earlier than in eggs, released before the winter.

The cycle of the univoltine *Stygnocoris pedestris* shows a parallel. Oviposition starts in September and proceeds through November. Diapause eggs are laid in blasted flowers of *Calluna* (first days of November in the laboratory) and the risk that the females are caught by a period of frost is great. Females with distended abdomen, taken outdoors at the beginning of November, were kept at 3 °C for one month. Non-diapausing eggs were laid as soon as these females were returned to room temperature. SWEET (1965) mentioned that two females of the bivoltine *Ligyrocoris diffusus*, collected late in November, laid non-diapause eggs. The eggs of earlier collected specimens had a diapause of varying intensity. SWEET concluded (p. 112): "This indicates that the exposure to cold had broken the diapause initiating phenomenon in the female before the eggs were formed". From his account, however, it is not clear whether the two females could have had ripe eggs in the ovaries.

6. Exceptional seasonal types of strong diapause of eggs in univoltine species.

Most species of this group lay in the summer and early autumn. Some species with an unusual cycle, ovipositing either early or late, show that the duration of the egg stage remains about the same, roughly 10 months. *Harpocera thoracica* lays eggs in May and June, which hatch as soon as the oak buds burst the next year, and larval development is very fast. The phenological counterpart is another mirid, *Pantilius tunicatus*, living on alder and hazel. It lays in late autumn and the eggs hatch probably not before August of the next year. In both species, the cycle results in a striking adaptation to a short feeding period on buds, particularly those giving male flowers. In the first cycle, the eggs are exposed to warm conditions for a long time before the winter; in the second cycle, the eggs are first subjected to cold and need subsequently several months with moderate and warm periods to complete incubation. Some less extreme early maturing and late maturing univoltine Rhyparochrominae are listed by SWEET (1965).

7. Release of the eggs in response to lowering or fluctuating temperatures.

Whereas most species can readily be stimulated to deposit their eggs by raising the temperature, it causes an inverted effect in *Himacerus apterus* to withhold them. Many specimens, containing fully ripe eggs, lived for many weeks at 30 °C and died without laying one egg. In a container, placed outside at a fluctuating temperature of 1°–15 °C, many eggs were obtained. A similar reaction is probably evoked in other

autumn species *(Pantilius, St. pedestris)*, although any direct photoperiodic response must still be analysed. SWEET (1965) mentions five species of Rhyparochrominae belonging in this category, all of them with one annual generation like the species we mentioned.

8. Unstabilized cycles in Saldidae.

Some aspects of the cycle of *S. orthochila* are discussed under 3. The dependence of the occurrence of diapause on changing environmental conditions appears from field populations of other Saldidae. The coastal *Chiloxanthus pilosus* was found during two years to pass the winter in a diapause at the second larval instar. At the beginning of September after a cool summer in 1965, we found only adults of both sexes. Reared in the laboratory at 20° and 30 °C these bugs started directly to lay eggs which all hibernated. Only one female laid eggs which did not diapause. It has not been checked whether in the subsequent young larvae of this batch diapause was induced. *Ch. pilosus* normally has two generations. The growth of the larvae and the maturation of the adults seemed so retarded in 1965 that abnormally diapause was initiated in the egg. *Halosalda lateralis*, collected at the same date, also laid diapause eggs, whereas we have the impression from other years of hibernation mainly as adults. One female of another bivoltine, *Saldula (Micracanthia) marginalis* (collected 20 August 1958), produced one batch of eggs, of which half developed at once, and the rest hibernated. In the Netherlands, Germany (JORDAN and WENDT, 1938) and most probably at all higher latitudes, *Salda littoralis* eggs have an obligatory diapause lasting nine months. In our rearings of material from the North Sea coast, none of several hundred eggs developed during six months storage at room temperature. A temperature of –20 °C is survived for six months. Temperature shocks from +20° to –20° and from –20° directly to + 30 °C during diapause have no deleterious effect. Our data suggest that the rate of development of the embryo after diapause increases with intensity and duration of chilling. In England, the same species is said to have two distinct types of life cycle (SOUTHWOOD and LESTON, 1959), one cycle involving overwintering as adults. The description of the diapausing eggs by BRINDLEY (1934) suggests that the embryo might hibernate in England at a later stage than in the Netherlands.

The phenomena traced show a wider adaptability in development than expressed in the six seasonal reproductive types of Heteroptera classified by WOODWARD (1952).

To what extent photoperiod and temperature independently or together, have a direct effect, must still be tested. In other Hemiptera, especially the Cicadina, several interesting analyses have been made. These reveal wide plasticity in diapause and might provide explanations of some of the phenomena mentioned above if more phenological and ecological data are collected. For example, see the papers of MÜLLER (1961a, quiescent larvae and eggs; an increasing percentage of diapausing eggs with later deposition, in *Euscelis;* 1961b, different photoperiodic effects on oogenesis in *Stenocranus*) and STRÜBING (1960, diapause in Delphacidae). MÜLLER (1965) proposed to use the term dormancy for all deviations from the normal speed of development. He proposed further to discriminate between the following main types of dormancy:

quiescence, oligopause, parapause and diapause. These types and their further subdivisions are the manifold results of physiological, ecological and genetic adaptation.

3.2.2 The main features of embryogenesis and their supposed phylogeny

Rotation of the egg during passage through the genital tract has indirectly been proved to occur sometimes (p. 334).

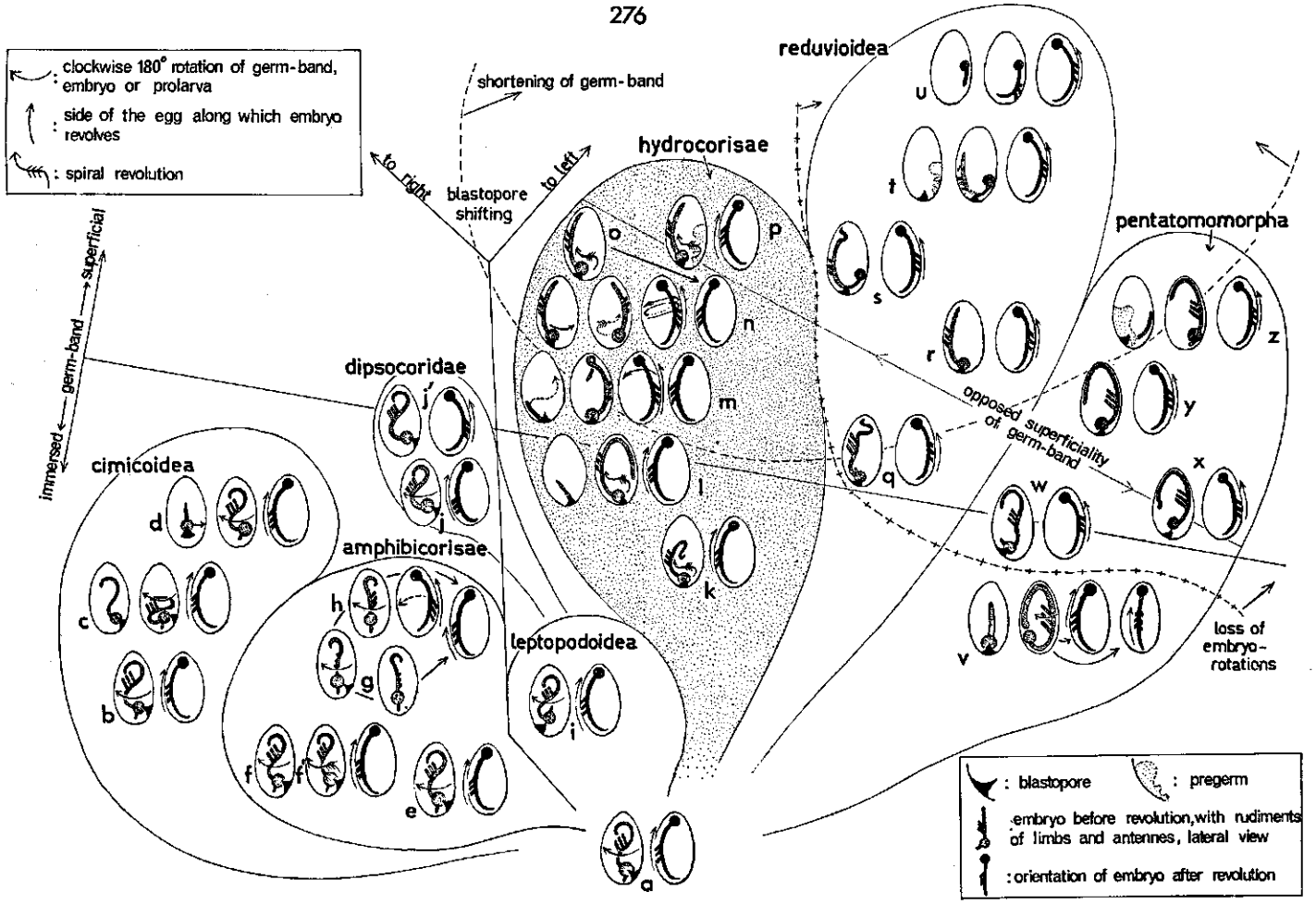
Embryonic development is often characterized by one or more rotations of the embryo. These changes in orientation and the variation in egg shape and oviposition site hinders classification of embryonic types. The surrounding egg system and oviposition site are better ignored initially on the assumption that the early germ band gives the best guarantee for purposeful first comparison; a diagrammatic survey is given of the different types found in this study (fig. 276). The newly invaginated germ bands are all shown in the same position, the ventral side facing to the left. If there is no invagination, the position of the early embryo as drawn (fig. 276u) is justified in homology with others of the same group showing partial invagination (s, t). The site and orientation of the band in *Coranus* (u) corresponds with that of the germ-band 'anlage' in the other series illustrated (p, t). Several Cimicoidea initially have a lateral invagination. The position of the band in these species after a 90° rotation (d) is chosen as comparable with that of other series. Blastokinesis is considered here as the process restricted to the embryonic shift in the middle of the developmental period and thus is concerned with the revolution of the embryo, often directly preceded or accompanied by a rotation of 180° or less.

Rotations

For convenience, the rotation of the embryo around the polar axis is termed here according to the stage of development when it occurs:
band rotation, during the first third of development
embryonic rotation or spiral, during the second third of development
prolarval rotation, during the last third of development.

Fig. 276. The main features of embryogenesis in Heteroptera, reconstructed in diagrammatic form from the author's data; the major groups are arranged more or less phylogenetically, but the position of the area furthest right (Pentatomomorpha) would be more realistic if it was branched in a plane normal to the median line of this page. Each horizontal pair or trio of eggs normally represents the developmental type of a family or family-group.

a: archetype; b: Nabidae, Miridae (in part); c: Anthocoridae, Cimicidae; d: most Miridae, Tingidae?; e: Hebridae; f: Mesoveliidae; f': *Microvelia;* g: Hydrometridae; *Gerris* (in part); h: *Gerris* (in part); i: Saldidae; j: *Ceratocombus;* j': *Pachycoleus;* k: Ochteridae; l: Corixidae; m: Pleidae; n: *Ilyocoris*, most *Notonecta* spp.; o: *Notonecta maculata;* p: Nepidae; q: Emesinae; r–t: Reduviidae (in part); u: *Coranus;* v: Acanthosomatidae, probably also Cydnidae; w: Aradidae (in part), Piesmatidae, Lygaeidae (in part); x, y: *Oncopeltus*, Pyrrhocoridae, most coreoid and pentatomoid families: z: *Anoplocnemis.*


: clockwise 180° rotation of germ-band, embryo or prolarva
: side of the egg along which embryo revolves
: spiral revolution
shortening of germ-band
to right
blastopore shifting
to left
immersed
germ-band
superficial
reduvioidea
hydrocorisae
pentatomomorpha
dipsocoridae
cimicoidea
amphibicorisae
leptopodoidea
opposed superficiality of germ-band
loss of embryo-rotations
: blastopore
: pregerm
: embryo before revolution, with rudiments of limbs and antennes, lateral view
: orientation of embryo after revolution

Whereas embryonic rotation is brought about principally by intrinsic action of the serosal amniotic complex, the other rotations must be of a quite different nature. Some speculations on how they are displaced have been given on p. 212, 226.

Most of the rotations are through 180° but the band rotation in Cimicoidea is limited to 90° and the irregular prolarval rotations in some Notonectidae and Naucoridae are through several circles (fig. 276n). These complete rotations are described on p. 30, 142, 214. *Plea* and sometimes *Gerris* too rotate as prolarva, but only half a turn. These prolarval rotations probably compensate for band rotation, which occurs in the same species. This band rotation takes place very early in several Hydrocorisae, when the trunk is just starting to segment, and in *Gerris* and *Hydrometra* later, when the thoracic buds have appeared. The direction of rotation in these Hydrocorisae is clockwise, when the egg is viewed from the anterior pole; the rotation is a sort of displacement of the germ band around the egg's surface. A similar direction is followed in all embryo rotations. In *Hydrometra* and occasionally in *Gerris* there is a band rotation but no prolarval rotation (fig. 276g). This seems to be related to the loss of the intermittent embryonic rotation. The 180° embryonic rotation occurs in other Amphibicorisae, Saldidae, cimicoid families and in Hydrocorisae. It is lacking in Reduviidae, in one of the two dipsocorids studied and in Pentatomomorpha with the possible exception of Cydnidae and Acanthosomatidae (see fragmentary observations on p. 106 and 108). In the Hydrocorisae and in *Microvelia*, the embryonic rotation is simultaneous with upward movement and results in a spiral twist.

Figure 276 shows that the great variety of embryonic shifts has the final result that the fully grown embryo faces either to the left, or to the right. The relation of this diversity to egg-laying behaviour and evolutionary adjustment of egg shape is considered under 3.4.

Positional embryonic types

The Heteroptera have the invaginated type of embryogenesis, characteristic of most hemimetabolous insects as yet studied. However Harpactorinae among Reduviidae show various stages of abandonment of this type and invagination and blastokinetic displacement are entirely lacking in the three *Coranus* species studied (fig. 210, 276u). The most complete immersion within the yolk occurs in Saldidae, some diapausing Miridae, in *Gerris* and in *Hesperoctenes*, where the germ band, including the head, becomes completely sunk within the yolk system. In other Amphibicorisae, the cimicoid families and in the dipsocorids, the band penetrates the yolk system, but the head apparently does not loosen from the serosa. In *Nabis rugosus*, only one head lobe remains attached to the serosa, the other lobe pointing obliquely into the yolk. In Pentatomomorpha, Reduviidae and Hydrocorisae there is a marked trend towards the superficial position. In the first group, the germ band tends to adjoin the right wall of the egg (directions as in the profiles, fig. 276!) and the ventral side of the embryo faces the yolk. In species with bands closest to the wall, a thin film of yolk still separates the germ band from the serosa. The head seems to touch the serosa in gross pictures

but in sections of the lygaeids *Oncopeltus* (BUTT, 1949) and *Ischnodemus* (SCHNEIDER, 1940) there is a temporary slight loosening from the serosa, thus approaching the immersed condition.

The band in reduviid and hydrocorisous eggs flexes in the opposite direction and, if flexing is extreme, it rests with the amnion close to the serosa without yolk inclusion. In both these different lineages intermediate developmental types bridge the gap between the immersed and the superficial forms (*Neuroctenus*, *Mezira*, *Berytinus*, several Lygaeidae, *Hydara*, *Empicoris* and *Ochterus*). In some Reduviidae embryogenesis proceeds without invagination.

An indication of the start of loss of invagination is differentiation of cephalon and protocorm already in the germ-anlage as in Nepidae and Naucoridae (fig. 230A, 238A, 276p). The distinct blastodermal thickening in higher Coreidae (fig. 97A, 276z) and the progressive shortening of the band in the three main groups Pentatomomorpha, Reduvioidea and Hydrocorisae perhaps indicate the start of a similar trend.

Shape of the embryo, shift of the blastopore

Saldidae, Amphibicorisae and the cimicoid groups, including *Hesperoctenes* (HAGAN, 1931) have a ʔ -shape embryo, because the anterior and posterior halves are coiled in opposite directions. The caudal flexure is directed to the ventral side and the cephalic flexure to the dorsal side of the band. The opposite directions of convolution disappear with superficial development. The ventral caudal flexure, still present in some Reduviidae, disappears phylogenetically through an intermediate double-folded stage *(Empicoris, Ochterus)*. Especially in *Ochterus* (fig. 276k) the primary caudal flexure is now dorsal; this reversion is not evoked by a superficial position of the trunk. The retention of the cephalic flexure round the posterior pole as a mechanical result of superficial position, gives the typical reduviid-hydrocorisous embryo an L-shape. Corixidae are the only group in which the tail is bent much dorsally, round past the anterior pole. But the ventral caudal flexure is always retained in Pentatomomorpha. The cephalic flexure in this group, however, tends to bend from a dorsal to a ventral direction, thus changing the form into a ⊐-figure. The budding out of the protocormic appendages generally proceeds in the sagittal plane of the embryo. In most Reduviidae and Hydrocorisae, the embryo's ventral side moves up against the serosa. Only in Hydrocorisae (except *Ochterus*) the legs are splayed out laterally, whereas in Reduviidae they remain folded parallel to the median plane (compare fig. 210 and 232).

The point of invagination is in the centre of the basal pole (some Reduviidae, *Plea*, *Ochterus*, *Elasmucha*, *Coptosoma*) or, as topographically indicated in fig. 276, to the left of it (Saldidae, most Reduviidae, Pentatomomorpha), or to the right (Amphibicorisae, cimicoid groups (lateral in some Cimicoidea)). The blastopore shifts slightly and gradually during embryonic development. This shift is generally to the right round the curvature of the pole, but in *Elasmucha* and *Coptosoma* it is to the left.

The entire collection of embryonic types and their supposed phylogeny are shown in

fig. 276, stressing the diversity of patterns and the consistency of the pattern within the major groups. In the Hydrocorisae, Reduvioidea and Pentatomomorpha, anagenesis (shortening of germ band and trend towards superficial position in all three, loss of rotation in two of the groups) has a long progression, in which the first steps bridging the gap with other main branches are still lacking. Future embryonic studies of the most primitive members of these groups should yield information on early phylogeny. The archetype in embryonic development seems to have had a germ band immersed with an anterior and posterior flexure. The germ band rotated 180° just before revolution. It is uncertain whether invagination originally occurred centrally at the pole or to the right and whether the head was immersed or not. The alternatives chosen (fig. 276a) seem the most logical, according to the projected scheme and information on other Orders of insects (discussion, p. 308). The archetype would thus be most like the *Hebrus* and *Mesovelia* type (fig. 276e). Amphibicorisae and some Cimicoidea would thus have the most generalized type, and particularly for Amphibicorisae this confirms our findings on the male genitalia (COBBEN, 1965a). The saldid type (fig. 276i) diverges from the archetype in two ways: shift of the blastopore to the left of the pole, causing a twisting of the head (note different direction of antennae in fig. 276i and e) and temporarily a distinct detachment of the head from the serosa.

3.2.3 Other embryonic features varying between taxa

Blastoderm

The embryonic anlage of *Oncopeltus* and *Pyrrhocoris* differs considerably from that in *Rhodnius*. The blastoderm thickens on one side of the egg to give the embryonic rudiment; from the thinner blastoderm area on the opposite side arises the serosa. The initial lateral thickenings fuse together towards the posterior pole, forming a rudiment delimited enough in *Rhodnius* to be seen in whole mounts (MELLANBY, 1935). In *Oncopeltus* and *Pyrrhocoris* the rudiment is faintly defined with the right and left halves sometimes irregular in shape and unequal in size (BUTT, 1949; SEIDEL, 1924). Our analyses reveal that this divergence is more general, each line showing more differentiation. Thus, in Reduviidae (except *Empicoris*) and in Hydrocorisae (except *Ochterus*, *Plea*, *Notonecta* and Corixidae) the embryonic rudiment is clear. The outline, the thoracic metameres and evaginations are already visible in *Ilyocoris* and Nepidae, and in Reduviidae with decreasing invagination whereas the rudiment is still primordial. In all others, Saldidae, Amphibicorisae, Pentatomomorpha and the cimicoid groups, only faint lateral areas are indicated in the blastoderm, converging towards the blastopore. Higher pentatomomorphs have a distinct rudiment. This differs from the reduviid type, however, in position (*cf.* fig. 97, 100 and 210, 230), bilateral asymmetry and the absence of metamerism.

Germ cells

The germ cells are initially at the posterior pole of the egg and their transport forward at the tail end of the invaginating embryo is similar to that in *Rhodnius* and *Oncopeltus* (MELLANBY, *op. cit;* BUTT, *op. cit.*). Since the clump of cells in these bugs is very close to the band tissue, the germ cells could hardly be distinguished in whole mounts. Most Heteroptera may be like *Rhodnius* and *Oncopeltus* but in others the cluster of the supposed germ cells is temporarily separated from the band and distinct enough to be seen in whole stained mounts, as in Saldidae, *Gerris* (distinctly isolated) and in *Nabis*, *Anthocoris*, *Cimex*, *Ochterus* and Nepidae (distinct but adjacent). The meaning of these differences cannot be assessed until more information is available. As was argued on p. 136, the germ cells in *Cimex* may form one unit with symbiont-bearing cells.

Pigmentation of the eye

The time of eye pigmentation varies much. Development is earliest in Saldidae. The whole larval compound eye is well developed before revolution. The grooved eye disk is then mostly darkish red. But in *Oncopeltus*, the cells of the eye disk begin to differentiate after at least 130 hours of development, that is some 30 hours after blastokinesis; pigmentation is first visible about 10 hours later (BUTT, 1949). Perhaps the lesser number of ommatidia in the compound eye of *Oncopeltus*, which is not adapted for preying, causes a later development. Yet the eye of the first larval stage of *Nabis* and the water bugs is large and specialized, but pigments after blastokinesis; only a few faintly coloured ommatidia if any, are discernable before revolution, and this is also the case in the Amphibicorisae. In the eggs of the terrestrial bugs, the coloration occurs in the second half of embryogeny. The edge of the eye disk begins to pigment early in *Rhodnius* but MELLANBY (1936) did not clarify when the eye actually starts darkening. Probably it is after the embryo revolves, as in the reduviids we studied, which have small or large eyes. The statement that *Reduvius personatus* shows eye spots at the posterior pole of the egg (IMMEL, 1955) needs checking to confirm darkening of the optical elements. The existence of the compound eye in Saldidae so early seems exceptional for Heteroptera. The pigmentation of the eye usually proceeds centrifugally. In Miridae, *Nabis*, *Gerris* and *Mesovelia*, some five to eight ommatidia in the centre of the eye-plate appear first. The huge finely faceted eye of *Coranus* has initially only five or six elements deeply pigmented.

Hydropyle

A serosal hydropyle at the posterior end of the egg occurs in Saldidae and Amphibicorisae except *Hydrometra*. The fate of the hydropyle during retraction of the serosa before blastokinesis has been described in detail. In Saldidae and *Gerris*, it becomes detached from the serosa, in *Gerris* with rapid rupture (fig. 64). The cluster of hydropic

cells of *Mesovelia* is pushed forward into the serosal plug. Observations on larger numbers of eggs should clarify how constant these processes are in differentiating species or genus. A conglomeration of serosal cells at the posterior pole, which would suggest hydropic function, could not be found in cimicoid eggs. Yet water is believed to be absorbed in those eggs, from which a serosal cuticular plug extrudes at hatching and absorption is probably through the anterior pole. Among Hydrocorisae, the six *Notonecta* species have a serosal hydropyle excentric to the basal pole and adjoining a circular differentiation in the serosal cuticle. In the few eggs examined closely, the central cells of the hydropyle are extruded before the serosa retracts anteriad (fig. 246). A restricted hydropyle could not be detected in the related *Plea*. The hydropyle of *Ilyocoris* needs to shift only a short distance during blastokinesis, as it is initially anterior beneath the fore edge of the cap (fig. 240). In Corixinae, the hydropyle seems to be represented by the thickened cells beneath the anterior pole, which thus already form the serosal plug before revolution. The serosal hydropyle in Nepidae is indicated by a distinct chorionic hydropyle away from the apical pole. Conditions in the related Belostomatidae are similar but they may also have a secondary water-absorbing organ mid way up the fore side of the egg. Lack of adequately preserved material prevented comparison of Gelastocoridae or Ochteridae. Chorionic hydropyles in the eggs of these families are not differentiated.

Water-uptake may be the function of the strange cephalic organ found only in Saldidae (p.28–30). It is a long cylindrical extension of the embryonic head tissue, which traverses the primary hydropyle and the serosal cuticle. The organ forms a sheet between the serosa and the chorion mainly along the fore side of the egg, almost to the anterior pole (fig. 18K). The subchorionic part of the organ is left behind during blastokinesis. This cephalic structure is reminiscent of the 'dorsal organ' of Collembola and Diplura. In Saldidae it is behind the primordial head and sends out filaments, which in Collembola radiate out over most of the egg. The filaments in Apterygota remain beneath a cuticular membrane which might be a serosal cuticle. This dorsal organ may be concerned in absorption of water (TIEGS, 1942a, b).

Blastokinesis and formation of dorsal organ

The process of revolution has been described in some detail in several species of Saldidae, Gerridae, Mesoveliidae, Miridae, Naucoridae. In all instances the process seems to be triggered by the amniotic and serosal envelopes and not by activity of the embryo itself. Intrinsic contractions of the endoplasma and yolk system may also play an important role. Revolution has not been watched in living terrestrial eggs with a superficial germ band. The absence of embryonic rotation in most of these and the different position of the embryo in pentatomomorphs and reduviids may indicate modifications in the detailed mechanics of revolution. In Saldidae and *Mesovelia*, the first break by the embryo through the fused amniotic and serosal membrane occurs just before the 180° rotation is complete. It is the 'knee' of the folded antennae which apparently forces open the area of fusion of the two membranes. In *Gerris* and *Chlamy-*

datus, however, the tips of the antennae push through the slit. The retracted serosa, above and behind the upward gliding embryo, now forms a thick sheet around the yolk column, for which we introduced the term serosal plug (p. 33). In *Nabis* the thickening of the anterior serosal cells starts before blastokinesis begins. A thickened serosal area is present early also in *Corixa* beneath the anterior pole. The precociously contracted serosal cells may function in these situations as a separate hydropyle. Except in Miridae (next paragraph), the serosal plug is gradually engulfed behind the head to form the secondary dorsal organ. This uptake appears to be accomplished by increasingly vigorous pulsation outside the embryo. Rhythmic contractions and relaxations of a cell band near the junction of amnion and serosa are responsible for this spectacular process, described in detail in *Saldula* (p. 34, fig. 28) and *Notonecta* (p. 224, fig. 247).

More detailed differences in embryogeny may prove to be of taxonomic or phylogenic significance, when studied in larger series. There were the variations in the changes in external appearance of the embryo, shown in the developmental series illustrated in chapters 1 and 2; the flexure of the gnathal region and the position of the antennae. Coelomic sacs have been found in *Rhodnius* (MELLANBY, 1935) but not in *Oncopeltus* (BUTT, 1949). In *Ilyocoris* and the nepid eggs, but not in *Notonecta*, crystalline products occur in the ambient fluid of the embryo after revolution (p. 214, 216). The composition of the yolk is another variable. Its translucency varies during growth. Size and density of the globules may be quite diverse in different taxa. In Saldidae the yolk column is opaque, so that the early development cannot be studied in live eggs. In most Amphibicorisae, some Hydrocorisae, Dipsocoridae, Anthocoridae and some of the lower Pentatomomorpha, the yolk is translucent and loosely packed.

Extended explorations in the subject of symbiont transmission will add new scopes to taxonomy and phylogeny. The discovery of symbionts and their peculiar transfer into the egg in the carnivorous *Mesovelia* (p. 50) will be of extreme importance in later discussions. Symbionts were found in the submicropylar area of ripe ovarian eggs of the 5 species of Orsillinae studied (p. 90), but in some other Lygaeidae they are initially in the basal pole of the egg.

3.2.4 Discussion

Incubation time, diapause

The longer time needed for embryonic development in hemimetabolous insects has been suggested to be a critical difference from holometabolous insects (WEBER, 1954, p. 33–35). Our information, four-day development in some bugs (three days at 25 °C in some Adelgidae, EICHHORN, 1961), and the wide diversity of incubation time in other members of the same Order, cast doubt on such a critical difference. A scan over the literature shows that incubation periods below one day at higher temperatures are exceptional among holometabolous insects, most of which need at least a few days. The embryonic data compiled by JOHANNSEN and BUTT (1941) give a longer period for

various Holometabola than the mean for our examples of Heteroptera. The concurrence in Reduviidae between extension of egg development and the trend towards the embryogenic type found in Holometabola also conflicts with the supposed discrepancy between Hemimetabola and Holometabola. The parallelism may be valid too, when development is compared at the same temperatures.

Firm egg diapause has evolved independently in most main groups of Heteroptera and bears only a weak relation to systematic affinities of the bearers. When good correlations exist, they must be considered in relation to distribution and ecology. The stages at which embryonic growth ceases for diapause have evolved haphazardly in the smaller taxonomic units of the Suborder and preconditioning may influence this stage. Diapause after revolution occurred in only one species of Heteroptera. Hibernation in the differentiated but not yet revolved embryo seems common in other diapausing Hemiptera (Cicadina, MÜLLER, 1951; Aphididae, BAKER 1921 and personal observations). Embryonic diapause occurs both before and after revolution in Odonata (ANDO, 1962). The widest range of diapause from the blastoderm till prolarva is in Orthoptera (ANDREWARTHA and BIRCH, 1951; RAKSHPAL, 1962a). Egg development never ceases as far as is known, before blastoderm formation. The stage passed in hibernation or aestivation is usually characteristic for each species. But some variation would be expected with laboratory treatments of the eggs and in different geographical regions. For one species incubation at two different constant temperatures causes the embryo to stop development at unequal morphogenetic levels (p. 294).

Intensity of egg diapause can vary widely. RAKSHPAL (1962b) confirmed results by workers on Orthoptera that *Acheta pennsylvanicus* eggs do not diapause after exposure to cold in the pre-diapause phase. This is reminiscent of the observations on *Notonecta* and *Stygnocoris* (p. 296), that chilling prevented diapause of ripe but not yet fertilized eggs within the female. But when cricket eggs are exposed to cold (6°–7 °C) one day after laying, thus before distinct embryos form, the eggs are killed. The eggs can only withstand cold after the embryos have taken shape. Then, the pre-diapause eggs continue developing at 6–7 °C until they reach the true diapause stage. The physiological effect of chilling eggs before diapause should, according to RAKSHPAL, be similar to that on diapause eggs, that the yolk becomes assimilable. The egg diapause of *Aphis fabae* is highly complex (BEHRENDT, 1963). The diapause intensities in eggs of the same age and treated the same are very variable. BEHRENDT distinguishes three phases in diapause, which react differently to temperature with diapause intensity.

SOUTHWOOD (1956, p. 205) suggested a relation between thicker chorion and longer aeropyles in diapausing eggs. We could not find any positive correlation and it is likely that in particular the structure of the serosal cuticle and the impregnation of the chorion and subchorionic membranes with wax provide prolonged protection of the diapausing egg against desiccation. HINTON and COLE (1965) showed that the dipteran *Leptohylemyia coarctata*, which diapauses as a first-instar larva within the egg shell, has a waxy membrane between the shell and the subchorionic membranes. This is unlike *Erioischia brassicae*, whose egg does not diapause. Since all diapausing heteropterous eggs possess a serosal cuticle, even if embryonic growth ceases early, this

membrane might be a safeguard against extended exposure.

Embryogenesis

The evolutionary diagram (fig. 276) assumes that primitively emergence of the embryo from the yolk is combined with a 180° rotation round the embryo's long axis. This assumption is based on the absence of embryonic rotation in nearly all pentatomomorphous and reduviid eggs. These are just the groups, which are considered apomorphic on the basis of most other characters. Absence of rotation parallels superficiality of the germ band, which is generally considered in insects as derived from the immersed type (RICHARDS and DAVIES, 1957; WEBER, 1954; but contrast JOHANNSEN and BUTT, 1944, p. 55–56). Embryo rotation (not to be confused with band and prolarval rotation, see p. 298) has been demonstrated in many Homoptera, Cicadina and Psyllina (discussion in COBBEN, 1965c; MAO-HUA, 1963, must be added), in Odonata (*Platycnemis*, KRAUSE, 1939) and in Orthoptera (*Melanoplus*, SLIFER, 1932; *Austroicetes*, STEELE, 1941; *Locusta*, *Locustana*, JONES, 1956a). But the same groups Cicadina (MÜLLER, 1951) and Orthoptera (MAHR, 1960b) contain taxa without any rotation or only a very weak one. Nor has it been reported in the Siphunculata and Mallophaga (SCHÖLZEL, 1937; BAUDISCH, 1958). Comparison of the orientation of the aphid embryo before and after its revolution in a few species suggests that rotation is failing. In his comprehensive work on Odonata embryology, ANDO (1962, p. 60) merely stated that generally the embryo rotates 90–180° but his accounts on embryogenesis are not entirely conclusive and do not allow generalization. To judge from the position in the egg of the fully grown psocid embryo with dorsum against the substrate (PEARMAN, 1928; WEBER, 1939; Goss, 1954), there has probably been a 180° embryonic rotation but a modified egg-laying behaviour may have caused egg rotation (see p. 334, 336). In fact, little attention has been paid to embryonic shifts of this kind in relation to egg coverings. A search through the voluminous literature on embryogeny of other groups of insects (*e.g.* Thysanoptera) yielded little evidence on presence or absence of intermittent rotations. The main reason is that eggs are often completely equal in cross-sectional radius, so that rotation is readily overlooked, particularly when research is focused on other subjects such as symbiont transmission or organ development. Early 180° rotation in holometabolous insects was probably first demonstrated by ROSAY (1959). She found such a rotation in five Culicidae and IDRIS (1960) noticed it in *Culex pipiens*, a fact which had eluded former investigators. In this connection it is important that YAJIMA (1960) found the *Chironomus* egg to be more of the indeterminate type contrasting higher members of the Diptera.

When rotation occurs in Heteroptera, it is nearly always 180° and in the many eggs examined the rotation was clockwise, as seen from the upper egg-top. The evolutionary loss of rotation must have evolved by degrees through gradually lessening turns. The varying rotation in *Elasmucha* is presumably the stage before normal pentatomomorphous development without rotation. Another example is the leafhopper *Pyrilla* (SANDER, 1956). Embryo rotation is here only 90° and clockwise in little more

than 50% of the eggs. The embryo turns another 90° much later than revolution, to reach the right position for eclosion. The plecopteran *Pteronarcys* performs also a 90° rotation but this phenomenon cannot be fully explained by economy of the space for growth as was done by MILLER (1940).

Little is known of the mechanics of embryo rotation. A possible factor, suggested on p. 32, could be the bilaterally asymmetric fusion of amnion and serosa along the embryo's ventral side or twisted diaphragm fusion near the head region. The restricted contracting serosa anteriorly and the contracted yolk body, which presses on the twisted fusion of amnion and serosa, should force the twist to unroll. The association of the rotation with revolution and the resulting asymmetric shape of the serosal plug (fig. 25) after revolution favours this view.

The positional embryonic types in Heteroptera form three main branches from the immersed type with cephalic and caudal flexure (fig. 276). There is as yet little phylogenic evidence whether the most primitive is entire immersion or immersion with the head lobes not detached from the serosa. In our diagram, we have arbitrarily chosen the latter. The former condition is common in Homoptera and other hemipteroid Orders. Orthopteroid Orders usually have the cephalic connection. Complete immersion is not necessarily related to subsequent rotation (Siphunculata and Mallophaga, SCHÖLZEL, 1937). In the cimicoid group, there is a conservative retention of the immersed invagination but in Reduviidae and Hydrocorisae, and the Pentatomomorpha progression to superficiality is marked. Pentatomomorpha has the least drastic change. The embryo's dorsum lies against the serosa and thus no implications for the amniotic site are involved. Before revolution, the embryo must again take a central position in the yolk column. In most Reduviidae and Hydrocorisae, the actual amnion approaches the serosa. Embryo rotation occurs only in the latter group and this is accomplished by a half-turn corkscrew roll during revolution. Superficial position and spiral movement occur also in some Orthoptera (STEELE, 1941). The simultaneous occurrence of these two phenomena seems, however, not to be essential. For instance the immersed embryo of *Microvelia* and *Platycnemis* (KRAUSE, 1939) have likewise a spiral turn.

The most conspicuous evolutionary event in the superficial type of heteropterous embryogeny is the progression of superficiality so far that it becomes dissociated from invaginating. Such progress is furthest in the three *Coranus* species studied (p. 130) and intermediate stages occur in other genera of Harpactorinae. *Coranus* shows embryogeny without blastokinesis, even when this concept is taken in its broadest sense. These species need thorough histological investigation by embryologists. Outwardly they match the developmental type which before was only known in holometabolous groups (KRAUSE, 1958; WEBER, 1954). Points needing checking are: whether in *Coranus* the embryonic envelopes are formed as overfolds of the germ band; whether the plasma-contents are higher than in other hemipterous eggs; and whether there is any gradual decrease in the regulative capacity of reduviid eggs. The fully outlined germinal primordia in the blastoderm in other Reduviidae and in Hydrocorisae (*Ilyocoris*, Nepidae) presumably foreshadows the progressed developmental type of

Coranus. Compared with all other types in Heteroptera, which represent a typical 'Kurzkeim' (short-germed) condition, we see in the reduviid branch a distinct trend towards the 'Langkeim' (long-germed) condition. With the broad overlap in incubation periods as shown on p. 305, this may be a second argument for the idea that Holometabola, according their developmental type, are not simply to be superimposed on the hemimetabolous type. The alternative idea which considers both types as being evolved one from the other (WEBER, 1954, p. 35), in our opinion, is based on too scanty evidence, reflecting less diversity than might be expected to occur in each subdivision. A polyphyletic origin since the very beginning of insect evolution with much parallelism in the separate cladogeneses cannot yet be rejected.

The sequence of embryogenic patterns in Heteroptera explained in our evolutionary diagram, does not correspond with the view of JOHANNSEN and BUTT (1941, p. 55–56). They considered the immersed type to be derived from the superficial one. All our data on eggs of Heteroptera makes this latter interpretation most unlikely. So far as we know all Homoptera studied have immersed embryos. Besides, the eggs of the viviparous bug *Hesperoctenes* (HAGAN, 1931), despite its small content of nutrients, has normal ♀ -invagination and normal revolution. The relationship of Psocoptera, Mallophaga, Siphunculata and Thysanoptera to other hemipteroid Orders, makes it significant that as yet only the invaginated ♀ -condition has been established, except in the viviparous *Archipsocus fernandi* (SCHÖLZEL, 1937; GOSS, 1954; BOURNIER, 1961).

The most comprehensive survey of embryology to elucidate phylogeny with a wide range of species within a single Order of insects was by ANDO (1962) in Odonata. He studied 30 species from the families of the three Suborders. Briefly his conclusions on the embryogenic affinities of Odonata to other Orders of insects were (p. 179):

Thysanurous type → invaginated and partially invaginated type (Odonata, Ephemeroptera) ↗ superficial type (4 orthopteroid Orders)
↘ immersed type (Plecoptera and the 5 hemipteroid Orders)

Heteroptera possess all these types, except the first but some have, moreover, embryogenesis without blastokinesis. Thus one Suborder, Heteroptera, shows a wide range in embryonic types. This discovery suggests that gross embryogenesis is largely governed by parallelism and that similarities or differences in types do not necessarily elucidate relationships between Orders. The scanty embryological data from other Orders makes it almost pointless trying relate our data to other major groups. The range of anagenesis in each Order or Superorder must be examined first, especially for position and shape of the embryo. Besides the immersed invaginated type, Heteroptera have two different kinds of superficial germ band. The one type seems to be retaining the invagination procedure (higher Pentatomomorpha). The other type is gradually abandoning this involution, ultimately resulting in an unreversed developing germ band (some Reduviidae). Thus three types of superficial position are present: reversed with ventral side of embryo against the egg coverings; reversed with dorsum of embryo outward; unreversed with venter of embryo outward. Such characteristics of the superficial type must be recognized. Yet a clear discrimination between them is lacking in the extensive discussion of embryonic evolution given by SHAROV (1966,

p. 140–149). He reduces the definite arrangement of the embryonic membranes in insects to four steps in succession: *Machilis*, *Lepisma*, Hemimetabola, Holometabola. He recognizes two distinct manners of formation of the membranes in the Pterygota, having developed independently from the *Thysanura* type (his p. 146–148). He does not agree with ANDO (1962) who believed that one manner is a derivative of the other. ANDO based his idea on the fact that the band invaginates for only half its length in a few families of Odonata and that in the same families there is a different manner of formation of the amnion. As partial invagination and even loss of invagination occurs in Heteroptera and transitions occur in some other Orders of insects, doubt is cast on SHAROV's dichotomy of insect evolution (his fig. 60). All ancestors of the various pterygote Orders may have had invagination with minor differences in the formation of the embryonic membranes. Especially in holometabolous Orders, these types may have developed from the reversed superficial to the unreversed superficial position in slightly different ways, but in parallel fashion within different Orders.

The development physiology of the holometabolous egg system *(Dermestes)* and the hemimetabolous egg system *(Ischnura, Acheta)* has been recently analysed by various modern methods. The striking differences found between the activation dynamics of both systems have been summarized by SEIDEL (1966). It is hoped that the techniques used by experimental embryologists will be applied in future to evolutionary taxonomy.

Almost all known morphological and orientational types of insect embryos occur in Heteroptera but are restricted to one or a few types in other Orders. Still, within the Order or Suborder the embryonic shape is almost constant in smaller taxa and our study clearly shows that the type is not influenced by volume or shape of egg (compare for instance fig. 88 and 97; eggs of related families are inverted in shape). The extent of the embryo before revolution does not reflect the length-width ratio of the future larva *(Hesperocorixa*, fig. 226, and *Ranatra*, fig. 230, demonstrate this; the first larval stage of *Ranatra* is about five times as slender as that of *Hesperocorixa)*. The more striking is the fact that allometric growth of legs appears even during bud formation (rowing leg in *Gerris*, fig. 63; preying leg in *Ilyocoris*, fig. 238).

Hydropyle

Of the subjects dealt with in 3.2.3, only the hydropyle and the revolution will be discussed here. As shown, a serosal hydropyle in Heteroptera occurs mostly at the posterior pole but in Hydrocorisae its position varies between families. A chorionic hydropyle is rarely visible, so that comparisons between ovarian eggs could not be so thorough. In those eggs of aquatic and semi-aquatic bugs without a differentiated chorionic hydropyle, water probably enters through the whole chorion as in *Phyllopertha* (LAUGHLIN, 1957), *Acheta* (MCFARLANE and KENNARD, 1960) and in some *Chorthippus* species (HARTLEY, 1961). The period or periods when water is absorbed, presumably differs largely between groups. Thus in *Notostira* JOHNSON (1937) recorded a regular increase in moist weight during the whole of incubation and ascribed this

increase predominantly to water absorption. The way water enters has not been determined. The mirid species studied had no posterior conglomeration of serosal cells to indicate a distinct hydropyle. BANKS (1949) found in *Corixa* a pronounced absorption only before revolution. It is conceivable (p. 196, 198) that in this taxon as in other Hydrocorisae water is also absorbed before hatching. This uptake would be connected with the manner of eclosion. A posterior hydropyle occurs also in other hemipterous insects (Psyllidae, WILCKE, 1941; Aleyrodidae, WEBER, 1931; Aphididae, WEBSTER and PHILLIPS, 1912; probably many Cicadomorpha, MÜLLER, 1951). The posterior pole of Mallophaga and Siphunculata eggs contains canals in the chorion ('Eistigma') but these are said to provide the egg with a better attachment through the substance which glues the egg to the host (WEBER, 1939). The well known hydropyle of acridid Orthoptera, whose chorionic and subchorionic structure has been thoroughly studied (MATTHÉE, 1951, and SLIFER, 1964), is also situated at the basal pole. The detachment of the serosal hydropyle just before revolution in Acrididae (MATTHÉE, *op. cit.*; LE BERRE, 1952 and others) strikingly resemble the process described in *Gerris* (p. 70). The serosa constricts to form a narrow trabeculum before becoming disrupted from the cluster of hydropic cells. A review of supposed hydropic organs in insects is given by MILLER (1940), who introduced the neutral term 'grumulus' (cluster of serosal cells) and 'grumorium' (corresponding thickening of the serosal cuticle) to avoid the functional implications conveyed by the term hydropyle. The often identical location of hydropyle in species of different Orders renders it an unimportant taxonomic character. Its occurrence seems to depend of the environment of the egg stage. Thus Saldidae have a hydropyle; the related *Leptopus marmoratus* does not. *Gerris* and other Amphibicorisae checked have a hydropyle; it seems to be absent in *Hydrometra.* When, however, the taxon has members needing similar environmental conditions, the position and structure of the hydropyles certainly would follow the same taxonomic trends as other characters (some examples: identical chorionic hydropyle in Nepidae and Belostomatidae and a supposed additional organ in the latter; the cephalic organ with probably hydropic function, characteristic for Saldidae).

Revolution, formation of dorsal organ

Our observations of live revolving embryos of some species indicate that movement is promoted not by the embryo but by forces outside the embryo. The rate of the upward movement excludes the likelihood of promotion by growth of the embryo. The whole process including the rotation if any, takes less than an hour at room temperature in many Heteroptera. Even long after revolution, when the embryo fills the anterior lumen during uptake of the serosal plug, its stretching seems to be largely caused by pulsation outside the embryo by the serosa and amnion, Although not always explained, there is evidence that contractions confined to the embryonic membranes invert the long axis of the embryo in other related groups (Psocoptera, Goss, 1954; Siphunculata & Mallophaga, SCHÖLZEL, 1937, BAUDISCH, 1958; Homoptera Cicadina, MÜLLER, 1951, SANDER, 1956), and in Odonata, where an anterior serosal

strand occasionally draws the embryo out of the yolk (ANDO, 1962). The strand in *Tanypteryx* remains against the anterior pole; perhaps it represents a hydropyle as well. The actual embryo of the orthopteran *Melanoplus*, however, is said to move by vigorous waves of contraction along the sides of the abdomen (SLIFER, 1932). LE BERRE (1952) stated that in *Locusta*, growth and serosal activity were moreover responsible for the shift of the embryo. The serosal mechanics have been examined in *Acheta* (= *Gryllus*) *domesticus* by MAHR (1960). Embryonic contractions did not occur until after revolution when the embryo's sides undulated to embrace the yolk column. The eye disc in this species starts pigmenting after revolution, whereas in the acridids studied it pigmented before. Acrididae may thus have progressed further in physiology at this embryonic stage.

The serosal behaviour, described by MAHR for *Acheta*, agrees in many respects with our observations in Hemiptera, for example the retraction from the basal pole, the formation of the slightly lateral serosal window and the anterior constriction of the yolk column. This constriction of the yolk was in *Acheta* eggs studied below water. A similar constriction in *Ilyocoris* (p. 214) may be due to water uptake.

The dramatic engulfing after revolution of the serosal plug from above the head by Heteroptera (see pp. 34 and 224) is nowhere mentioned in embryological literature on insects we have seen. This is remarkable since other processes within the egg have been recorded in detail by a number of authors. The peculiar way of engulfing the plug and the abrupt changes of shape are probably a general embryonic feature in insects. It might be that in other Orders the actual uptake occurs within a short period after a longer period of constancy of the plug. The spectacular inpocketing process due to sudden cell contractions of the embryonic envelopes may therefore have escaped attention. SCHANZ (1965) put down the swallowing of the anterior yolk body in the egg of *Ischnura* entirely to a contraction within the actual yolk. She concluded this from pictures by time-lapse microphotography. If superficial contractions as we observed in Heteroptera occur also in the Odonata eggs, these could be missed by her filming at the slow speed of one exposure per minute.

3.3 Dynamics of eclosion

3.3.1 The persistent serosal plug

The structure is put under this heading because it remains until eclosion. It occurs in Miridae but its extent and fate varies between species. In *Chlamydatus*, the plug empties of yolk and is engulfed within the embryo earlier, but in *Dicyphus* the vacated plug persists until just before hatching. Whereas in *Chlamydatus* the operculum does not loosen until larval emergence, it becomes detached much earlier in *Dicyphus*, and also *Sahlbergella*, because of a slight prolongation of the serosal cuticle beyond the shell collar. Conditions are more striking in *Liocoris tripustulatus*, where the serosal cuticle starts stretching before revolution. The serosal plug remains against a wide inner surface area of the protruded part of the serosal cuticle and in this condition in

Notostira JOHNSON (1934b, p. 10) called it the 'yolk plug'. He defined the yolk plug as the structure which "consists of a mass of yolk surrounded by a non-cellular wall which is apparently secreted by the epithelium of cells lying between it and the yolk". It is now clear that this epithelium is the serosa and that the wall of the plug, whose outer layer is blackish, represents the serosal cuticle. As stated on p. 33, a differently defined term is used throughout the present work: 'serosal plug', indicating only the serosal remnant which exists after revolution and before it is engulfed within the thorax. The formation of the serosal plug is a normal consequence of serosal contraction and thus a general feature of insect embryology. Its persistence is a specialization in many Miridae. It is rather a feature of a number of Miridae that the serosal plug is emptied of yolk, although the serosal squamous cells remain adjacent to the anterior pole. The term 'yolk plug', certainly if defined as walled by serosal cuticle, seems therefore inappropriate.

A stretch of serosal cuticle considerably beyond the egg's mouth occurs in *Notostira elongata* (JOHNSON, 1934; KULLENBERG, 1946), *Capsus ater*, *Leptoterna dolobrata* (SOUTHWOOD, 1956), *Liocoris tripustulatus*, *Bryocoris pteridis* (the present work) and in *Neoborus illitus* (USINGER, 1945). These are all Mirinae, except one bryocorine. There is a short extrusion in the dicyphine *Dicyphus pallicornis* (this paper) and the orthotyline *Orthotylus flavosparsus* (KULLENBERG, *op. cit.*). In the phyline *Chlamydatus evanescens* (this paper) and the orthotyline *Malacocoris chlorizans* (KULLENBERG), there is no stretch at all. SOUTHWOOD (1956, p. 177) claims the presence of a suboperecular 'yolk plug' in *Dolichonabis limbatus* but the structure in Nabidae is not homologous with the persistent serosal plug of Miridae. No direct evidence of the function of the mirid plug can be presented, but its possible significance is discussed on p. 322. We have seen on p. 150 that the persistent serosal plug can pulsate as in other families where it does not persist. But, since the top of the plug in some Miridae is firmly attached under the operculum, the pulsations merely transport the yolk downwards. The serosal plug is finally modified as a funnel, whose stem fits into the pit of the presumptive dorsal organ. Continuous contractions compress the funnel and secondary peristaltic waves run down the stem. In the most persistent serosal plugs, as in *Notostira* and *Liocoris*, these strong pulsations do not extract all the yolk from below the operculum and no dorsal organ is formed, because the whole serosa disrupts or disintegrates outside the embryo.

3.3.2 Embryonic envelopes

Serosal cuticle

In nearly all heteropterous eggs studied, a cuticular membrane could be traced as a product of the serosa (and not of the pleuropodia as is wrongly interpreted by MELLANBY (1936) and copied by SOUTHWOOD (1956, p. 177)). The first sign of depo-sition in diapause-less eggs in gross dissections is about the time that the protocormic evaginations become visible. This cuticle is a stiff transparent membrane, which gradu-

ally takes over the structural support of the egg. In diapausing pentatomomorphous eggs as *Myrmus*, *Chorosoma* and *Picromerus*, it is an elastic translucent layer. Although in all eggs studied the cuticle is present at the protocormic stage of the germ band, there does not seem to be a strict relation to developmental stage. In eggs which diapause just after the band has involuted and before protocormic outgrowths develop (*e.g. Notonecta lutea, N. maculata; Ceratocombus, Loricula*, several Miridae), the serosal cuticle is stil fully formed. Thus the system outside the embryo remains active for some time after embryonic diapause has begun.

The serosal cuticle is colourless but its surface, mostly lining the exposed areas of the chorion, darkens in many species of Amphibicorisae and Hydrocorisae. This character varies between families and differences do not correspond to habitat. Thus, *Gerris, Microvelia, Notonecta, Plea* and Naucoridae become largely and intensely pigmented, while there is no marked general darkening of the serosal cuticle in Nepidae, Belostomatidae, Corixidae, *Hebrus, Mesovelia, Hydrometra* or Saldidae. Except for *Hydrometra*, the chorion in all these groups is colourless. Since there is no distinction in pigmentation between fully exposed and inserted eggs, the occurrence of melanin seems to be of systematic significance. The dark pigment is confined to the outside of the outermost transparent membrane of the serosal cuticle. The amorphous pigment can easily be scraped off and the layer fragments when the underlying membrane is suddenly stretched (fig. 239J). As the pigmentation arises gradually after most of cuticle has been secreted, it is probably the result of a slow oxidation. The blackish pattern is variable and the hexagonal pattern of the chorion is often repeated in it. This could be through a local variation in oxygen absorption rather than a restricted distribution of tyrosine. The most intense stain is in *Notonecta* around the micropyle (fig. 245E) and darkening in the clear or only vaguely pigmented serosal cuticle of Saldidae, Corixidae and *Ochterus* occurs juist below the micropylar inlet. Black spots also arise as wound repairs when the chorion is finely punctured. There is no correlative evidence whether the pigmented layer protects against sunlight and it is not formed in response to light. Similar pigmentation develops in eggs kept in darkness. The oxidation of the outer layer of the serosal cuticle is clearly shown in those mirid eggs where the anterior part of the serosal cuticle protrudes from the chorion. This exposed cylinder (fig. 168) is the only area of the cuticle which blackens. Darkening of the serosal cuticle has not been observed in any other eggs of terrestrial families. Whatever the protection provided by the cuticular pigment in terrestrial eggs, it may be replaced by darkening of the chorion itself or the suprachorionic layer, when the eggs are completely exposed to wheather. One of the functions of the pigment layer of the serosal cuticle may be regulation of water absorption (see discussion, p. 325).

Envelopes of uncertain origin

In *Gerris* an additional membrane surrounds the embryo before and after revolution (p. 70). This membrane initially is not complete but is open at the posterior pole of the egg. As it is outside the serosal system it has presumably originated from

the serosa. It might represent the inner layer of the serosal cuticle; the part along the posterior pole could already be resorbed by the serosa just before blastokinesis. This explanation seems however unlikely, because resorption of the thick inner layer of the serosal cuticle, which actually occurs just before eclosion, would gradually diminish the thickness of the serosal cuticle and not loosen the laminae. The membrane therefore could be a new serosal product with a gap around the hydropyle (fig. 64).

Another membrane of doubtful origin (p. 226) was traced soon after revolution of the *Notonecta* embryo. We had slight evidence that this membrane could be an embryonic cuticle but its shedding so early is counterevidence. However SHARAN and SAHNI (1960) claim the deposition of two embryonic cuticles in *Dysdercus cingulatus* before the definitive larval cuticle forms. According to them, the production of these provisional cuticles is due to development. Shedding of the cuticles should provide a proper attachment of the muscles to the larval cuticle. The production of the first and second provisional cuticle occurs after 60 and 89 hours, respectively, and their shedding coincides with activity of the thoracic glands after 89 and 102 hours, respectively. Since the whole incubation lasts 120 hours (30 °C), the first cuticle must originate during blastokinesis and must moult some 30 hours later. The membrane in *Notonecta*, secreted about the same time, might thus be the first embryonic cuticle. Yet it seemed to cover the embryo as a sac, and not to envelop each limb separately, as would an epidermal derivative. Unfortunately, the paper of SHARAN and SAHNI on *Dysdercus* gives no decisive anser. It remains difficult to imagine how an embryonic cuticle could be secreted when the embryonic dorsum is provisionally covered by the amnion.

The sac-like membrane in the pentatomid *Carpocoris* (p. 120) bears a well differentiated egg-burster besides the normal sublaying burster of the true embryonic cuticle (fig. 127C). That the former membrane represents a serosal cuticle is dubious because of the burster-like cephalic structure. Since the design of the embryo's limbs and the segmentation is seen on the pellicle but no indentations whatsoever, it may have been deposited at revolution. If so, the ventral components of the membrane may be of different histological origin from those of the dorsal side. Anyhow, it is hoped that these fragmentary observations may be an incentive for close comparison of the subject.

Embryonic cuticle

Excluding the species with the membranes of uncertain origin mentioned above, none of the prolarvae of the many species dissected out of the chorion had two membranes enveloping the individual legs; they only had one. All following examples refer to the membrane which is shed during the first moult after the serosal cuticle breaks. Besides the typical cephalic egg-opener, the embryonic cuticle bears fine outgrowths and sculpturation in many species. Where these differentations were of special interest, they were mentioned in the descriptive part. A thorough study of this moulted skin (exuvia) will provide a new set of important taxonomic characters. The common sculpturing is of small transverse rows of very fine spines, pointing back-

wards and arranged in metameric bands to give the pellicle a scaly appearance (fig. 46G; 261B, C). Where it has been checked, this feature was found in Hydrocorisae, Saldidae, Amphibicorisae and Dipsocoridae. In waterbugs the embryonic cuticle does not break before the prolarva has entirely escaped from the egg; only the abdominal tip of the cuticle remains attached to the chorion. In terrestrial eggs the cuticle splits much earlier through desiccation and the anal part of the exuviae is stuck to the serosal cuticle half way the egg. This general rule can be proved when eclosion of amphibicorisous and saldid eggs under water is compared with that of the same species above water. All rough parts of the embryonic cuticle will provide friction to help the prolarva to push out from the smooth inner surface of the serosal cuticle. Special structures (*e.g.* lateral spined bands in *Mesovelia* (fig. 46A), *Ceratocombus* (fig. 261B) and pronotal areas with a set of varying outgrowths in *Myrmus* (fig. 90)) will be more efficient for this function. *Hebrus* has two long stout bristles on the vertex of the embryonic cuticle; they may be the precursors of the extremely long trichobothria of the free larva.

3.3.3 Tools for breaking membranes and chorion

Four mechanical methods for breaking open the egg were described in the descriptive section: cutting, puncture and lifting, pressure from the embryonic cuticle, and pressure from the serosal cuticle. These different functional types run almost parallel with the major taxonomic units. Since some annectent types and hints of anagenesis are available, it is worth trying to analyse the phylogenesis of the various structures.

The original type in Heteroptera before the main branching of the group, is difficult to reconstruct. But, the types in related insect groups (see discussion, p. 326), the other egg characters already reviewed and information on the genitalia (to be dealt with in the forthcoming Part II of this series) suggest that the sclerotic egg-burster and its position in Amphibicorisae is the most generalized situation.

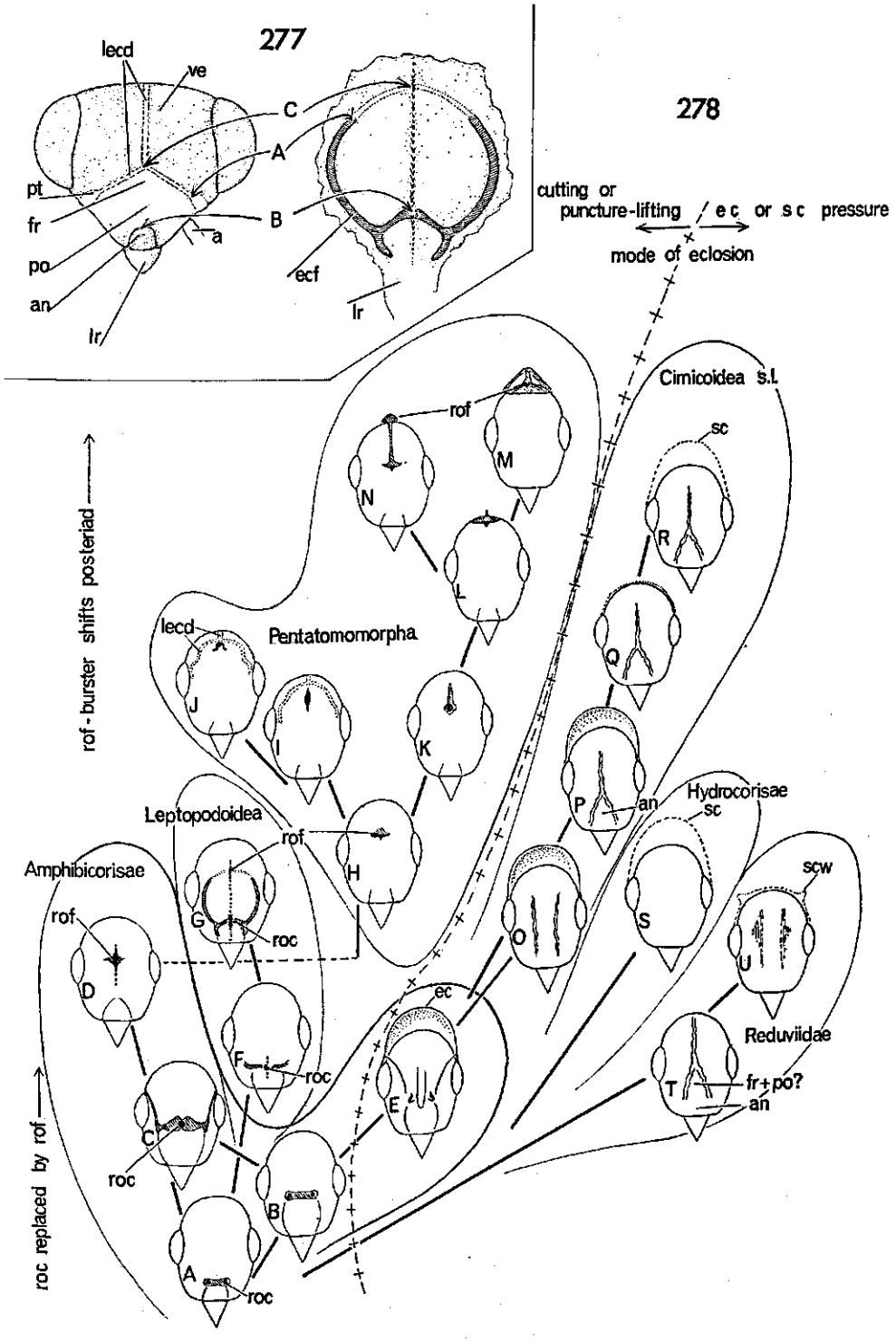
Cutting or puncture and lifting

When *Hebrus*, *Mesovelia*, *Microvelia*, *Gerris* and *Hydrometra* are considered in sequence, evidence from other features suggests the series indeed reflects true anagenesis in Amphibicorisae. The series then shows a transition of the burster from a transverse

---

Fig. 277–278. 277. Saldidae, comparison of cephalic structures of first larval instar (left) and embryonic cuticle (right). 278. Evolutionary scheme of the structures concerned with eclosion; only the prolarval heads are compared, but also the serosal cuticle is drawn when it functions as burster.

A: archetype; B: Hebridae; C: Veliidae; D: Hydrometridae, Gerridae; E: Mesoveliidae; F: *Leptopus;* G: Saldidae; H: Piesmatidae, Berytinidae, Lygaeidae, Aradidae; I: *Oncopeltus;* J: Coreoid families; K: Cydnidae, Acanthosomatidae; L, M: Scutelleridae, Pentatomidae, Plataspidae; N: Dinidoridae; O: Nabidae; P: Tingidae?; Q: Anthocoridae, Cimicidae, Miridae (in part); R: Miridae (in part); S: all hydrocorisous families; T: Emesinae and other Reduviidae (in part); U: Reduviidae (in part)


277
lecd
ve
C
A
pt
fr
B
a
po
an
lr
ecf
lr
278
cutting or
puncture-lifting / e c or s c pressure
mode of eclosion
Cimicoidea s.l.
rof
sc
M
N
R
L
lecd
Pentatomomorpha
Q
J
I
K
P
an
Hydrocorisae
sc
Leptopodoidea
rof
H
scw
Amphibicorisae
rof
G
roc
S
O
U
D
ec
Reduviidae
F
roc
T
fr+po?
an
E
C
roc
B
A
roc
rof-burster shifts posteriad
roc replaced by rof

into a longitudinal structure (fig. 278). In fact, the structures should not be directly compared, because the median transverse part of the burster as in *Microvelia* (fig. 55) is not homologous with one as in *Hydrometra* (fig. 50G) or *Gerris* (fig. 62B).

The cephalic armature in Saldidae (fig. 33) helps to solve the homology. For convenience, a schematic figure is given of the embryonic cuticle of the head and the head of the first free instar (fig. 277). To relate the armature of the embryonic cuticle with the underlying parts of the larval cuticle is not easy, because the ecdysial sutures, the best landmarks, are not visible while the larva is still enclosed within the embryonic envelope. This embryonic cuticle must be compared with the morphology of the free larva very cautiously, as the topography of the parts of both skins is not easily homologized because of the slightly condensed and flexed state of the prolarva within the egg. Contrasting the left and right drawing in fig. 277, the point A of the frame of the embryonic cuticle in Saldidae seems to coincide with the pits of the larval internal apodemes, characteristic for Leptopodoidea. The further, more weakly defined continuation of the frame from this point over the dorsum caudad follows the arm of the ecdysial line and meets the same from the other side to empty in the median ecdysial stem. The region enclosed by the ecdysial fork would represent the *frons*, according to PARSONS (1962) who studied the last larval instar. Towards the labral side the embryonic cuticular frame forms a cross-bridge marking off the anteclypeus from the postclypeus. The actual egg-burster, which is a median ridge with fine teeth, starts on the vertex and runs over the fronto-clypeal area to the base of the labrum. The part of the burster effecting the first break of the serosal cuticle and chorion, lies at point B, just between ante- and postclypeus. The ruptor ovi of *Leptopus* is more knife-shaped and restricted entirely to this join (fig. 38).

In Amphibicorisae ruptors are of two types of different morphological origin. The first type corresponds with point B in Saldidae, which we shall name the *clypeal ruptor*. It occurs in *Hebrus*, *Mesovelia* and *Microvelia*. It is confusing that these ruptors are further posterior on the head (fig. 42A, 55) than in Saldidae. This is due to enlargement of the anteclypeal region in these amphibicorisans and simultaneous shortening of the vertex, a tendency which has progressed furthest in pentatomoids. The second type of burster is found in *Gerris* and *Hydrometra*, and corresponds with point C in the saldid situation (fig. 277). This we shall call the *frontal ruptor*, since its central component lies on the division between frons and vertex. In *Hebrus* the clypeal burster is a double structure consisting of two projections, one on each side of the median line. These knobs do not cut the egg walls, as there is only one median eclosion split. Their function is to stretch the chorion so that it bursts open into two halves with increasing pressure helped by the birefringence of the shell. In none of the amphibicorisous species studied is there already a line of weakness in the chorion. If the chorion became thicker, a more direct opener would be more effective. The paired projections thus fused together into a single median pointed cone in *Microvelia* and *Leptopus*. The sharp medio-longitudinal blade of *Gerris* and *Hydrometra* has arisen morphologically further back at the upper margin of the frons, while the clypeal burster and clypeal frame-work are completely lost. The paired egg burster of *Hebrus* is still visible in

Mesovelia, although the method of action has markedly changed and is considered under the heading: Pressure from the embryonic cuticle. The cephalic strengthening in *Microvelia* and *Mesovelia* consists moreover of a strip running from the clypeal bridge along the inner margin of the eyes to terminate behind the eyes. These lines are not related to any existing morphological sutures of the head capsule.

We will now try to relate the sclerotic bursters of pentatomomorphous bugs with those of amphibicorisans. In Piesmatidae, Berytinidae, Aradidae, Lygaeidae, Cydnidae and Acanthosomatidae, there is a single sharp projection pointing directly at the centre of the anterior pole of the egg. These eggs break longitudinally, transversely or radially. Because of the weak differentiation of the embryonic and larval cuticles it is difficult to say exactly what part of the head the burster belongs to. In the free larvae the point where the ecdysial stem starts forking, has shifted near to the hind margin of the head and the vertex has almost completely disappeared. The burster lies some way in front of the fork but in *Sehirus* and *Elasmucha* a longitudinal strip trails back from the actual burster to the supposed origin of the ecdysial stem (fig. 105). The egg-tooth in these groups therefore lies within the frons, and not on the anteclypeo-postclypeal junction, nor on the frons-vertex junction. The condition in coreoid members supports this view (compare fig. 92A). Here, the small burster: transverse, longitudinal or horseshoe-shaped, is situated within the triangle, enclosed by the ecdysial fork. A transverse ridge occurs in these eggs, running along the posterior edges of the eyes of the larva when enclosed still within the embryonic cuticle (fig. 92). This ridge coinciding with the front of the basal triangle of the burster may represent the junction between postclypeus and frons. This division is generally not visible in postembryonic stages of Heteroptera. In pentatomoid families other than Cydnidae and Acanthosomatidae the burster has eventually shifted further back into the junction of head and pronotum mainly over the cervical region (fig. 111). Here too, it is the small triangular area of the frons which is covered by the tooth of the burster. The ecdysial stem and much of the lateral parts of the vertex have disappeared. This becomes noticeable in the first free larva where only the ends of the epicranial arms remained, diverging towards the eyes (fig. 127E). SOUTHWOOD (1956) thought that the pentatomid burster belonged to the vertex but VAN EMDEN (1925) already expressed the view confirmed by our observations. The structure of the pentatomoid burster is rather constant for each family or subfamily, but divergence is not yet enough for ti to be used in practice as group distinctions. Its function is puncturing the serosal cuticle and chorion with the anterio-median tooth. Thickening of the chorion would demand considerable forces for the prolarva to come out. On the one hand, this resulted in re-inforcing of the whole burster plaque which coincides exactly with the underlying brains and might therefore also have a protective function. Electron micrographs of the pentatomoid shell did not reveal any pre-existing suture along the pseudopercular margin. The resulting sharply notched line of rupture of the shell could cause damage to the larval head without the shield-like cover of the ruptor. But in very thick-walled coreid eggs, there is medio-anteriorly in the pseudopercular ring a weak point, which is adapted to receive the egg-opener (fig. 100I).

The egg-burster in *Aspongopus* (fig. 114B) deviates from the bulk of pentatomoid bugs, and the tessarotomid burster (fig. 115A) is intermediate. An explanation is found in the habit of *Aspongopus*, exceptional for the superfamily, of placing the eggs in chains. One part of the burster lies on the interconnecting membrane behind the head capsule; the other part bearing the perforator is between the eyes. Both parts are connected by a thin sclerotized bar. Since the loss of vertex has progressed as far as in other pentatomoids, it is likely that the anterior component of the burster has made a secondary shift anteriad. This must have passed through while the habit to arrange the eggs 'head to bottom' was evolving. This change in oviposition compelled initial eclosion through the fore side of the egg, otherwise the prolarva could not leave the egg. Thus the tooth in *Aspongopus* points just to the opposite edge of the anterior pole from pentatomid eggs (compare fig. 114A with fig. 124C).

In all instances discussed under this heading, it is clear that the serosal cuticle is penetrated first by the burster, before the break of the chorion. As both covers are in complete contact, they are broken in one action by the egg-burster.

Pressure from the embryonic cuticle

This method is employed by *Mesovelia* and *Nabis* and less spectacularly by most other Cimicomorpha. Some structures of the embryonic cuticle in *Mesovelia* could be derived from the normal amphibicorisous burster. The burster of *Mesovelia* operates by pressure within the remarkable ampulla, whose origin and function have been described fully on p. 52. The serosal cuticle has developed an adaptation, a central inward projection to take the whole force of the ampulla. The *Mesovelia* structure probably is developed in relation to the rapidly evolving operculum, and provides a link with the Cimicomorpha. This link is assumed to be parallelism, but may indicate phylogeny as will later appear in the general discussion. A cephalic ampulla is present in *Nabis* too, but its function is a bit different as it remains more plastic and pulsates. This type has been described in detail on p. 126. The effect of the fluid-filled ampulla in *Mesovelia* and *Nabis* is that the operculum and the underlying lid of the serosal cuticle bursts explosively. Fixed eggs of the tingid *Urentius* sp. showed a widened cuticle at the head end (fig. 150C) suggesting the presence of a cephalic ampulla and the same conclusion can be derived from the general drawings by KOGAN (1960) of another tingid. The Anthocoridae and Miridae studied (without persistent serosal plug) do not have a distinct ampulla. But a layer of fluid within the embryonic cuticle still provides the pressure. In all these cimicoid families except Nabidae, a spiny ⅄-shaped ridge runs along the cephalic part of the cuticle (fig. 278P–R). This ridge forks along the edge of the clypeus. In *Nabis*, however, the two strips start from the outer margins of the labrum and remain parallel without joining posterior (fig. 287O). They may follow the sutures of the clypeus and frons. The rows of teeth on the strips have no direct burster function but obviously prevent the prolarva from slipping back during the upward movement.

Pressure from the serosal cuticle

In some Miridae the chorionic operculum is lifted some time before eclosion. This loosening is evoked by the serosal cuticle, which remains intact as it distends beyond the egg's mouth. The degree of distension is related to the persistence of the serosal plug. The eclosion has been described for *Dicyphus*, *Liocoris*, *Bryocoris*, *Sahlbergella*, and from earlier published information on *Notostira*. The opercular region of the serosal cuticle bears a structure which has been termed by JOHNSON (1934b) the 'stenopyle', defining it as the pigmented split of the thick 'yolk-plug wall' through which the embryo emerges. The condition in *Dicyphus* (fig. 161) suggests homology with the adapted inward projection of the cuticle in *Mesovelia*. The stem of the spiny ⅄-structure of the embryonic cuticle, in these mirids too, could assist in opening the stenopyle. The stenopyle needs a thorough morphological reconsideration throughout the Miridae. The term is somewhat misleading since the serosal cuticle does not open by a slit but along a narrow cap. This serosal cuticular operculum is distinct in *Bryocoris* (fig. 168H), *Sahlbergella* (fig. 169A) and *Pantilius* (fig. 169C) because of lack of further differentiation. A circular eclosion rent of the serosal cuticle occurs in all cimicoids (except perhaps in *Embiophila*), *Mesovelia*, reduviids but not in Hydrocorisae.

The serosal cuticular method in Miridae seems to have evolved from the embryonic cuticular pressure method already considered. Eclosion is by serosal cuticular pressure also in reduviids and water bugs but the method seems to have developed independently of that of cimicoids. The reduviid type may originally have worked simply by embryonic cuticular pressure. In the two Emesinae studied, the operculum and serosal cuticle are torn off together and the break of both is irregular. In the other reduviids studied, the serosal cuticle has a thickened ring (fig. 208D) which during its formation has occupied the circular space of the sealing bar. As internal pressure rises, the ring ('epembryonic ring' of BEAMENT, 1949, p. 474) wedges in the recess between the main shell and the cap, thus dislodging the chorionic operculum. That the operculum loosens first is hardly noticeable, since the serosal cuticle breaks at almost the same time. The wedging effect is clearly demonstrated by the fracture of the serosal cuticle just beneath the thickened ring. How far fluid beneath the serosal cuticle or direct outward pressure of the embryonic cuticle and the larval head is responsible could not be decided. There is no burster on the embryonic cuticle, but cephalic bands with fine teeth may provide friction as in Cimicoidea. Detailed investigations are needed to find out the taxonomic significance, if any, of these spiny bands. Reduviidae have the same two types: ⅄ (*e.g. Lisarda)* and ‖ (Harpactorinae), as the cimicoid groups. In *Lisarda* the fork of the crenulate strip is between the clypeus and the frons of the larva, whereas the unpaired stem coincides with the ecdysial line of the larva (fig. 209). Thus, there is no relation between the structures of the embryonic cuticle and the lateral ecdysial lines of the larva. The ⅄ structure of the embryo and of the first free larva may have paralleled each other in the past. This hypothesis is supported by the greater overlap in Saldidae and by the general trend in other families, where the ecdysial fork shifted posteriad.

This trend progresses distinctly in Amphibicorisae and Pentatomomorpha. The function of the embryonic structures in eclosion have delayed the backward shift of dermal structures compared with the free larva.

Although the embryonic cuticle represents a first larval cuticle discarded to release the free larva, it splits only a short way back along on the head. None of the varied cephalic structures on heteropterous prolarvae assists in fracture of its own cuticle. In some Pentatomidae, such as *Dalpada* (SOUTHWOOD, 1956), *Antestia* (PENDERGRAST, 1963) and *Carpocoris*, two rows of teeth are found as in Nabidae and Harpactorinae, as well as the normal burster.

The hatching prolarvae of Hydrocorisae, including littoral Ochteridae and Gelastocoridae, are eminent examples of the use of fluid pressure within the serosal cuticle (see descriptive part, p. 196, 204, 216, 228). Eclosion is by sudden anterior swelling of the serosal cuticle, which breaks the thick chorion. The prolarva remains immobile within the main shell (fig. 220, 239J, 243A) during this act. It moves upwards soon afterwards, swallowing the ambient fluid and filling the serosal cuticular bladder. Only after further pumping of fluid into the head does the cuticle break. None of the waterbugs studied had structures on the head of the embryonic cuticle. The serosal cuticle breaks lengthwise in all hydrocorisous eggs, whether operculated or not.

Once the serosal cuticle has been broken, eclosion proceeds according to a general plan in Heteroptera. The prolarva swallows air or water, according to environment, to distend the body and break the embryonic cuticle. The process has been described by many authors, notably SIKES and WIGGLESWORTH (1931) in *Cimex*.

The data on eclosion types assembled in this chapter are incorporated in a tentative phylogenic scheme (fig. 278).

3.3.4 Discussion

Serosal cuticle and the persistent serosal plug

The stretching of the serosal cuticle in *Notostira* is suggested by JOHNSON (1937) to be directly associated with uptake of water. This is indeed likely, since the serosa in the anterior part of the egg of some other groups obviously acts as a temporary hydropyle, but usually before blastokinesis *(Corixa, Ilyocoris, Nabis)*. KULLENBERG (1946, p. 438–439) being unaware of the detailed paper by JOHNSON (1934), likewise studied *Notostira*. He thought that the persistent serosal strand assisted in eclosion. The contents of the burst plug would function as a lubricant. Whatever the secondary effects, the egg distension in *Notostira*, according to KULLENBERG, is an adaptation to oviposition site. Eggs are placed sideways between grass sheaths and the distending plug brings the prolarva closer to the free surface of the substrate. The scanty evidence from mirids on this point does not yet clearly correlate serosal extrusion and depth of the embedded egg. In *Bryocoris*, however, the positive relation is convincing (fig. 168). A thorough study may reveal a parallel anagenesis in different subfamilies, as is suggested by the ornate opercular region of the chorion. A closer association

has been established in leafhopper eggs by MÜLLER (1951). A long serosal hatching cylinder occurs in some Delphacidae, whereas in several jassoid species, there is only a slight stretching to widen the oviposition slit. Among delphacoids *Cixius* has no extra stretch of the serosal cuticle, in *Kelisia* only a small amount; the serosal cuticular bladder is small in *Stenocranus*, and in other Delphacidae it can reach considerable length. The same sequence of genera reflects an increasing anagenesis for many other characters (W. WAGNER, 1963; COBBEN, 1965c).

MÜLLER's view of why the serosal cuticular bladder occurred in Delphacidae some time before eclosion is that after revolution the serosa forms a secretion by autolysis which would raise the osmotic uptake of water. He considered that the turbidity of the extra-embryonic fluid indicated the disintegration of the serosal cells. Text and figures of MÜLLER's work suggest that the remnant of the serosa after blastokinesis, which we termed the serosal plug, disappears very early in Delphacidae. Precisely when and how disintegration occurs is, unfortunately, not given for adequate comparisons with our findings in Heteroptera. It seems, that the serosal plug in the higher delphacids is completely absent when the serosal cuticle starts protruding from the egg's mouth. MÜLLER related his findings to KULLENBERG's data on *Notostira* and traced a striking similarity. He was unaware of the more detailed presentiaton of JOHNSON's paper of 1934. It is however one of the characteristic features in the embryogenesis of *Notostira* and several other Miridae that the serosal plug persists until hatching. Thus, if the serosa disintigrates in Miridae (fig. 164D), it is after the maximum prolongation of the serosal cuticle and the disintigration cannot be directly responsible for water-uptake. The serosal plug in some jassoids *(Cicadella, Idiocerus)*, studied by MÜLLER, remains for longer. The yolk shifts into the dorsum of the embryo; then the base of the plug separates and the serosal cells completely dissolve (compare the analogy just before eclosion in *Liocoris*, p. 150). The finely granular 'secretion' which results, must be identical with the 'Schlüpfsekret' of the delphacoids. MÜLLER concluded from the voluminous cylindrical transformation of the serosal cells after the revolution that these cells must have a secretory function. The data now available shows that the epithelial thickening of the serosa is entirely a direct result of the sharp contraction of this layer during revolution. Typically the whole plug remains intact, unmodified for a period after revolution and is then completely engulfed in the presumptive pronotum. This process is common for insects, but no holocrine activity of the serosa has been shown, although a milkiness of the ambient fluid occurs in all groups, whose live eggs were studied. The eggs of Hydrocorisae accumulate much water during the second half of incubation for the later explosive swelling of the serosal cuticle. But the whole serosal plug is soon swallowed in these eggs to form the dorsal organ without earlier extrusion or dissolving of individual cells. Part of the water passes through the serosal cuticle by osmosis after break of the chorion.

Although MÜLLER's concept of the serosal plug's function in leafhopper eggs may be true, the force of his arguments are weakened by new facts. Our observations on the eggs of Miridae rather suggest that the persistent serosal plug directly transmit water. The serosa intimitely contacts the opercular area of the serosal cuticle. Such a close

contact is also observed in the normal, mostly posterior, serosal hydropyles of most aquatic and amphibious species. The milky substance just mentioned could be the product of the pleuropodial glands (fig. 21), which hitherto have been found in most hemimetabolous insect embryos. Their function, demonstrated experimentally by SLIFER (1937) on *Melanoplus*, seems to be to secrete a substance dissolving the inner layer of the serosal cuticle. JONES (1956b) showed that in *Locusta* and *Locustana* the pleuropodia are activated to secrete by the growth and differentiation hormone from the ventral head gland. This gland (= thoracic gland) is also responsible for inducing embryonic moult, which occurs within a day after revolution (JONES, 1956a). In *Dysdercus*, where two embryonic cuticles are said to occur (see p. 315), their moults are accompanied by significant histological changes in the cerebral neurosecretory cells and subsequently in the thoracic glands (SHARAN and SAHNI, 1960). The pleuropodia would usually have a digestive function helping the prolarva's escape from the serosal cuticle after it has thinned out and eroded. The continuous prolarval rotations in *Notonecta* and *Ilyocoris* may assist this digestion. As soon as the rotations stop, the pleuropodial tuft disappears and its pore in the embryonic cuticle is occluded by a black pellet (p. 226, 228). A dissolving function is ascribed to the pleuropodia also in viviparous Heteroptera (CARAYON, 1960; contrast HAGAN, 1931, 1951). Other, possibly secondary, effects have been suggested: lubrication during revolution (SEIDEL, 1924); digestive enzyme to dissolve the yolk within the gut (BAUDISCH, 1958); assisting in uptake of water by the eggs (ROTH and WILLIS, 1958). ANDO (1962) found pleuropodia in all Odonata studied but doubted their enzymic function, since he could not detect reduction in thickness of the serosal cuticle. The pleuropodial products may even be capable of digesting the serosal plug in several of the leafhoppers studied by MÜLLER (1951) and the persistent serosal plug in some Miridae. RAKSHPAL's suggestion (1962a) that the pleuropodia in *Acheta assimilis* regulate embryonic growth is very unlikely.

Swelling of the egg and lengthening of the serosal cuticle do break the chorion before hatching in some Miridae, all Hydrocorisae and in many homopterous Auchenorrhyncha. A chorionic break some time before hatching has been reported also for other insect groups, including Aphididae (the black serosal cuticle in some species has been taken for the chorion by many authors in the past, as has been signalized by MÜLLER, 1951, and confusion occurs in the present, *e.g.* PETERSON, 1962); Thysanoptera (ULJANIN, 1874, break before revolution); Orthoptera (*e.g.* HARTLEY, 1961, 1962); Odonata Zygoptera (DEGRANGE, 1961; ANDO, 1962); in some holometabolous insects (*Dytiscus*, JACKSON, 1959) and in Collembola (MILLER, 1940, 1942; TIEGS, 1942). We found a similar early chorionic rupture, evoked by a distending underlying tough membrane, in an oribatid egg. In all these ruptures, the origin of the stretching membrane must be ascertained before it is concluded that the serosal cuticle is a general primitive arthropodous feature. Water uptake must be responsible for the early chorionic break and in some of these eggs the occurrence of a restricted hydropyle has been demonstrated. A special expansion chamber in the orthopteran *Tetrix* allows the serosal cuticle to swell within the chorion without rupturing the latter (HARTLEY, 1962).

The early chorionic break is not causally related to or evoked by endophytic oviposition. In Delphacidae and Miridae, the progressive stretching of the serosal cuticle may be governed by the selective advantage of sinking the eggs deeper into plant tissue.

The evidence from the data on Heteroptera, that the blackening of the serosal cuticle is not a direct protection against ultraviolet light applies also to other groups of insects. Yet SCHERF (1960) attributes the intense and general darkening in eggs of many Curculionidae to such an influence, as it occurs in those eggs which are laid freely at soil level. However, camouflaging, transpiratory and strengthening effects cannot be eliminated. Strengthening occurs in the shield-like and reticulate structures of the black outer layer of the serosal cuticle in some cicadomorphous leafhopper eggs (MÜLLER, 1951). MCFARLANE (1960) showed that the eggs of the house cricket stop absorbing water with the phenolic tanning of the lipid layer of the serosal cuticle. It is remembered that the black pattern on the serosal cuticle of heteropterous eggs is discontinuous. A light area on the serosal cuticle covers the posterior hydropyle in *Notonecta* and the anterior hydropyle in *Ilyocoris* (fig. 239); there are light furrows and a light circular band on the subopercular membrane, presumably for passage of water, in *Pantilius* (fig. 169C) and *Bryocoris* (fig. 168G), respectively.

The great confusion in literature between serosal cuticle, other subchorionic membranes and embryonic cuticle(s) prevent their discussion here, because important deductions for phylogeny cannot yet be made. For example, TELFORD (1957) speaks of a vitelline membrane in *Aedes*, which according to his own account must be serosal. The same is suggested by the membrane in *Culex*, which thickens and darkens later but is considered by ROSAY (1959) and IDRIS (1960) to represent the endochorion. DEGRANGE (1961) reports that in zygopterous Odonata a vesicle forms which pushes off the cap of the chorion. He claimed it to be the vitelline membrane. Undoubtedly it is again the serosal cuticle, since ANDO (1962) showed that in Odonata generally the serosa secretes a cuticle. BEAMENT (1949) hesitated to homologize the epembryonic membrane in *Rhodnius* with the serosal cuticle of *Melanoplus*, since he considered it to be only partly serosal. Its time of secretion and the resorption of its inner layer before eclosion indicates that the *Rhodnius* membrane represents the layer here called the serosal cuticle. Further discussion is in MILLER (1940), HINTON (1963), and KING (1964).

The important points for more comment and future study from the present work on Heteroptera have been stressed on several occasions (*e.g.* p. 315) and are the number, extent and time of secretion of the embryonic cuticle(s). The discrepancy in deposition time of the embryonic cuticle in Orthoptera, Plecoptera and Odonata is noteworthy. In Orthoptera and Plecoptera, this occurs during the upward revolving growth of the embryo (JONES, 1956; MILLER, 1940). In Odonata it happens at a much later date, about the time of definite dorsal closure (ANDO, 1962). An embryonic cuticle occurs also in certain Holometabola. In Coleoptera, its occurrence is more widespread than earlier records suggested (JACKSON, 1957). The third embryonic membrane, reported in *Rhodnius* by MELLANBY (1936), most probably refers not to the serosal cuticle, because it is said to be formed during embryonic revolution. Perhaps some parallel

can be traced between this membrane in *Rhodnius* and the membrane we observed in *Notonecta* (p. 226) and *Gerris* (p. 70).

Egg burster

Heteroptera have evolved several perforating and pressure methods of eclosion, depending on structure of the chorion and serosal cuticle and on the orientation of the prolarva within the egg. Originally a paired egg-burster occurred on the transverse ante-postclypeal division (p. 318) as in many Homoptera Auchenorrhyncha. Some anagenetic and cladogenetic parallels with Heteroptera are obvious in leafhopper eggs. In the delphacoid branch, the primitive genera *Cixius* and *Kelisia* (WAGNER, 1963; COBBEN, 1965c) have a paired burster (two small teeth left and right). Higher delphacids possess an operculum and use pressure within the serosal cuticle. They have developed two crenulate bands along the postclypeal sutures (MÜLLER, 1951). In other Fulgoromorpha, the paired burster (*Oliarius* and *Pyrilla;* SANDER, 1956) gave way to a median longitudinal knife in *Siphanta* (MUIR and KERSHAW, 1912). In the aphid *Lachnus roboris* a heavily sclerotized saw-tooth burster runs along the centre of the back of the head to the pronotum. Such a structure seems common in other aphids and in coccids (WEBER, 1930). From what part of the head this burster originates must be checked, but the shift back is probably provoked by the attitude of the prolarva with its venter to the substrate.

In the opercular eggs of Mallophaga and Siphunculata (SIKES and WIGGLESWORTH, 1931; SCHÖLZEL, 1937), and in the not opercular Aleurodidae (WEBER, 1931) and Psyllidae (WILCKE, 1941), a variable group of paired teeth burst the egg. A median egg-burster predominated in the few psocids studied (WEBER, 1954). MILLER (1940) surveyed egg-bursters in other Orders and included earlier compilations by VAN EMDEN (1925) and HEYMONS (1926). Recently, DEGRANGE (1960) added much information on egg-bursters in Ephemeroptera, Plecoptera, Odonata and Trichoptera.

The divergence of these structures is great in the one Suborder Heteroptera. More speculation on the phylogeny of eclosive structures and methods in related insect groups is unwarranted until more is known about the evolution of such structures within each group. Study of egg-bursters when they still surround the larva and are not broken is a first requirement. Too much confusion has arisen by interpreting homology from the cast pellicles. Any sculpturing of the embryonic cuticle of thorax and abdomen may also be of value. These structures can be analysed by allowing the prolarva to hatch in a small dish of warm water. If eclosion is successful the discarded embryonic cuticle is evident, spread out on the water film. MÜLLER (1951) found transverse rows of fine pegs on the embryonic cuticle of the leafhopper *Eupelix cuspidata*. He correlated this sculpturing with the exceptional absence of air swallowing when ecloding. However similar roughness of the embryonic cuticle occurs in many Heteroptera, which certainly inhale air or water, thus suggesting a general occurrence and function.

3.4 Bilateral asymmetries. Problems arising from the determination of the polarity of the egg system

3.4.1 Asymmetries, in particular the folding of the embryo's appendages

Besides the normal dorsoventral asymmetries, an unexpected amount of bilateral asymmetry occurs in the developing embryonic system. Dorsoventral asymmetry is not merely restricted to internal events as a logical consequence of the organization of the prospective insect. True isoradial eggs probably do not occur in Heteroptera; those claimed to be isoradial appear to have one side always slightly more convex than the opposite side. The shell usually has dorsoventral asymmetry especially through structures such as cap, aero-micropylar system, hydropyle, anchoring devices and differences in chorionic texture.

A fixed bilateral disparity in the shell is rare. Besides a general asymmetry in some Plataspidae (fig. 132A), bilateral disparity is caused by the micropylar system in lower Pentatomomorpha and in many Cimicomorpha. The transverse internal micropylar canals in those eggs all point clockwise (egg observed from the cephalic pole, *e.g.* fig. 67–69); thus the canals of the right and the left side are not mirror images. In Enicocephalidae *(Oncylocotis)*, the internal canals run anti-clockwise, the reverse direction. If the eclosion line is evolving from longitudinal to circular, ruptures are often bilaterally asymmetrical (fig. 74). The most remarkable aberrations are the spherical pseudoperculum in the mirids *Bryocoris* and *Monalocoris* (fig. 166, 167), and the chorionic flap in the *Plea* egg (fig. 251F), which lie entirely and invariably right of the median plane.

Internal bilateral asymmetries include asymmetries in the blastodermal thickening (*e.g. Coreus*), in the cephalic lobes (fig. 66C′), the position of the blastopore (fig. 100A′; 162B–D) and the shape of the early germ band (fig. 100B; 230D′; 239C–E; 251). All the different types of rotation and the surrounding events intimately concerned with them can be reduced to asymmetries. Many such facts can be derived from the observations described in chapters 1 and 2. Examples are the unilateral displacement of the serosal hydropyle in *Mesovelia* (p. 50) and *Ilyocoris* (p. 214), the left-right differences in the whole embryonic system before blastokinesis reflected in the dispersion of the yolk, and the frequent asymmetry of the retracted serosal plug (fig. 25K′). An astonishing degree of asymmetry in embryonic shape and displacements is shown by *Plea atomaria* (fig. 251). The rotations and particularly the embryonic dextral one, indicate a lower anagenetic level.

Special attention is devoted to the characteristic folding of antennae and legs. These are most economically tucked away against the embryo's venter but there are many ways of achieving the arrangement. Theoretically it should be possible to stretch out the appendages of the left and the right side straight downwards and past the posterior pole into a symmetrical pattern. In practice this never seems to be simultaneously so for all limbs. The appendages of both sides flex together transversely, thus providing a bilateral asymmetry. Flexing can be either by the limbs crossing each other so that

the asymmetry is less obvious (*e.g.* fig. 279L) or more often, the legs form a jigsaw, ranged behind each other in the same plane so that the asymmetry is more obvious (*e.g.* fig. 279H). Many variations in the folding arrangement exist and the main types are drawn (fig. 279, 280). These figures represent individual types and there may occur some variation within one batch. But there are many examples where one of the two mirror images occurs more often than could be explained by chance. According to LUDWIG's (1936) terminology the appendage arrangement is always true asymmetry, since the left and right form are distinct, without intermediates. LUDWIG discriminated between racemic, monostrophous and amphidromous asymmetry indicating a 50%, an at least 90% and a 50–90% occurrence of the left or right asymmetric forms.

One of the most striking general results from our descriptive data is the large dominance of one of the two mirror images. In all hydrocorisous eggs studied (fig. 280Q–U; each figure representing a member of a different family), the percentage of eggs showing the arrangement drawn, is significantly higher than their mirror image. The percentages (*Nepa* 84%, *Ilyocoris* 88,6%, *Notonecta glauca* 94%, *N. obliqua* 75%, *Plea atomaria* 100%) closely approach monostrophy or belong entirely in that category; the numbers of eggs checked were 74, 89, 32, 27 and 35, respectively. The monostrophous forms of all Hydrocorisae studied are entirely similar, except for *Plea*, in which the dominant posture is the mirror image. In the eggs of other groups, individual fluctuations occur. For instance, the species of Harpactorinae studied showed a marked predominance of the form with the long antennal bundle along the right side of the egg (fig. 280P). In *Rhinocoris iracundus*, however, batches were found with about 70% of this dextral form but other batches had both the right and left form each almost 50%.

The allometric growth of the mid legs causes the asymmetric aspect of the fully grown embryo of *Gerris* (fig. 62B). Among 82 eggs there was a racemic ratio but SATTLER (1957) detected in 160 eggs of the gerrid *Aquarius najas* 77.5% with the dextral form. The characteristic looping course in *Hydrometra* has been found to be directed as illustrated in all 25 eggs studied (fig. 279E). The eggs of other amphibicorisous families reveal less obvious asymmetry. Of 33 eggs of *Microvelia* 85%, and of 34 eggs of *Mesovelia* 74% showed the picture drawn in fig. 279D and C, respectively. Here the regular asymmetry is brought about by the hind legs, which show predominantly a folding inverse to that of hydrocorisous prolarvae. If all legs flex to the opposite lateral side, several combinations are possible, depending on the course each individual leg takes. In a saldid species, it has been shown on p. 38 that there is a coupling of the asymmetries of the mid and the hind legs. Other couplings between different pairs of appendages occur in Reduviidae and *Hydrometra*, where the antennae and fore legs are intimitely associated in their deviation from the median axis.

Only rarely is the arrangement of appendages obviously related to the egg shape. The antennae spread far apart in the flattened egg of Alydidae (fig. 87B) and *Leptopus* (fig. 39). The constricted fore side of the rhopalid egg might have brought about the unique pattern shown in fig. 280M. Dextral and sinistral forms of the prolarval posture are almost equally represented. The data available also suggest, irrespective of these spacial adaptations, some taxonomical significance. The pattern in hydrocorisous eggs

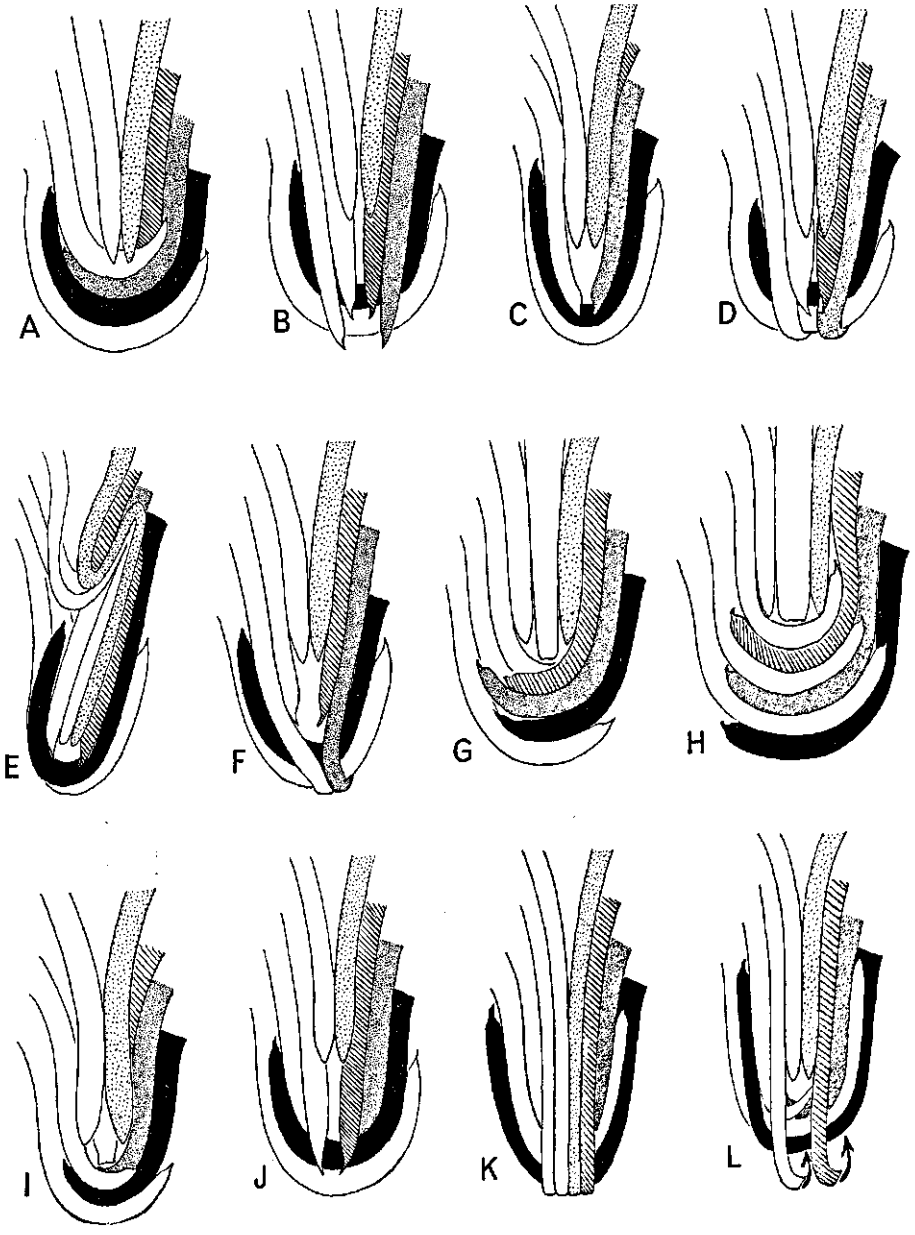


Fig. 279. Flexing pattern of antennae and legs of the prolarva within the egg; for the occurrence of mirror-images see text. A: Saldidae; B: *Hebrus;* C: *Mesovelia;* D: *Microvelia;* E: *Hydrometra;* F: *Gerris;* G: *Sehirus;* H: *Pyrrhocoris, Elasmucha, Coreus, Anoplocnemis, Eurygaster, Carpocoris;* I: *Oncopeltus;* J: *Acompocoris, Cimex;* K: *Nabis;* L: *Dicyphus, Chlamydatus, Berytinus* almost identical.

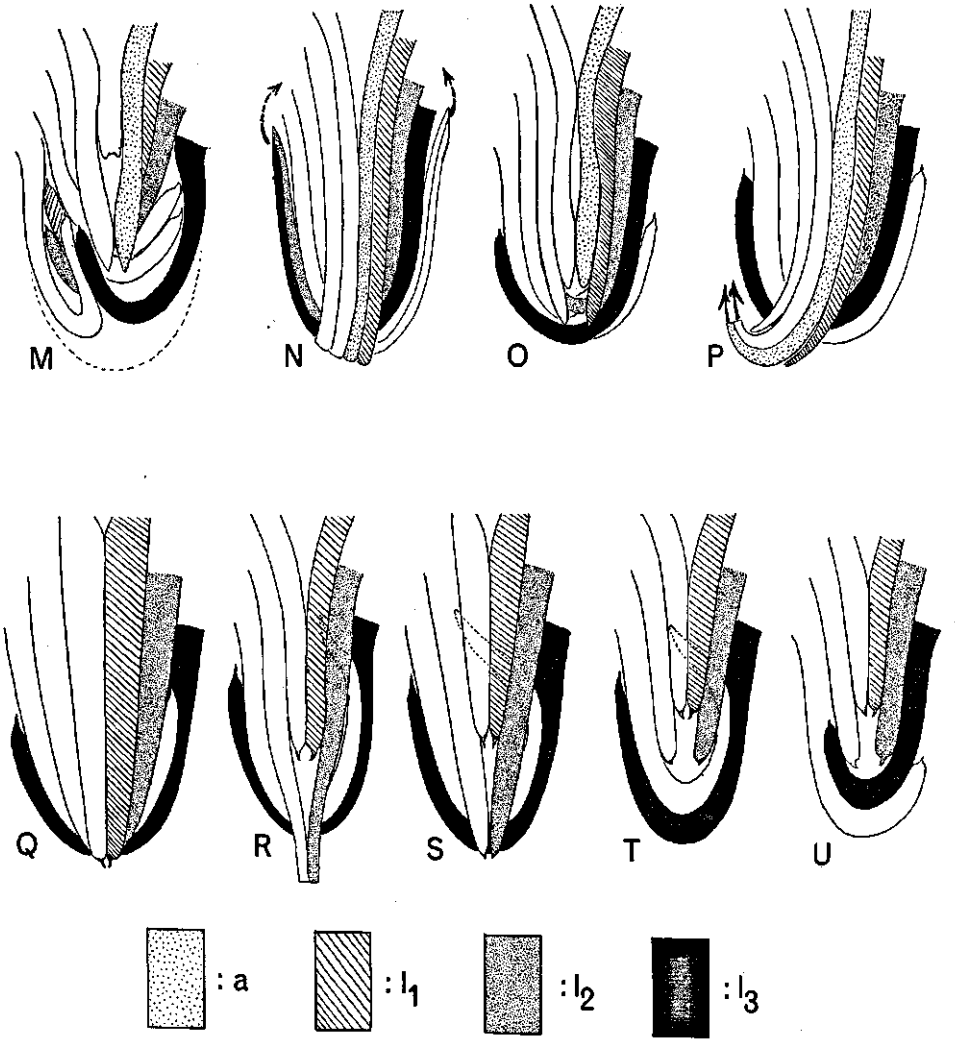


Fig. 280. Continuation of fig. 279. M: *Chorosoma;* N: *Empicoris;* O: *Coranus;* P: *Lisarda, Rhinocoris;* Q: *Nepa, Ochterus;* R: *Hesperocorixa;* S: *Ilyocoris;* T: *Notonecta;* U: *Plea.*

is very consistent, despite family differences in larval habits and egg shape. Since the antennae are minute, they have no influence on the pattern assumed by the legs. Further conformity is noted in reduviid eggs where the mid legs as well as the hind legs cross each other. A similar attitude occurs in the few mirids studied and in berytinid eggs. The types found in the terrestrial eggs vary and more species must be checked to detect any regularities and to distinguish parallelisms. Of the Amphibicorisae, only the *Hebrus*, *Microvelia* and *Gerris* types are equal (fig. 279B, D, F). *Hydrometra* (fig. 279E) and *Mesovelia* (fig. 279C) both deviate from this pattern, particularly in that the front legs dive under the posterior legs as in Saldidae (fig. 279A) and *Oncopeltus* (fig. 279I).

3.4.2 Position of released eggs

The deposited egg will be discussed here without yet considering the orientation of the female during oviposition. For clarity only three major stances of the released eggs will be distinguished: 1. the lateral superficial position, sometimes sheltered; 2. the upright position; 3. the embedded position. Of course intermediates occur. These have been catalogued in too artificial a scheme (ten categories) by MICHALK (1935). SOUTHWOOD (1956) recognized four types: exposed, semi-exposed, embedded in dead and embedded in living plant tissue. We feel that our ternary division more correctly reflects the major adaptive tendencies of egg-laying behaviour. We will only refer to intermediate forms, when a trend appears for transition from one main to another main type. The lygaeoid method of inserting the eggs with a tube-like ovipositor into existing holes is considered in principal to belong to the first type, to allow distinction from the drilling insertion by the cimicoid ovipositor. Between the first and second type are the unorganized egg batch deposited in soil and litter by some Lygaeidae, Cydnidae, Pyrrhocoridae and those eggs which are dropped (some Coreidae, Reduviidae). The inserted type is restricted to species which actually saw or drill.

A survey of data available is given in table 2. Type I is the most general method of oviposition by Heteroptera. If type II is reduced to the related type I, nearly all families are seen to possess type I exclusively or predominantly. Families, whose members seem to use only the insertion method, are Mesoveliidae and Microphysidae, both few in species. Mesoveliidae is an aberrant group of the Amphibicorisae. Microphysidae is a basic family of the cimicoid groups, which are characterized by an ovipositor of the drilling type for insertion. Cimicidae and some Anthocoridae affix their eggs by one lateral side and this is explained as a secondary change, away of the embedded method with ovipositor reduction. This certainly is the case in *Arachnocoris*, the eggs of which are especially adapted (fig. 140) to be attached, probably to spider-webs. Other evidence of a recent change from insertion is shown in a few Miridae (*Strongylocoris* (fig. 181D), *Pseudoloxops* (fig. 158A), *Malacocoris* and in some Saldidae (*Saldula scotica*-group; presumably *Calacanthia*, *Aepophilus*). These bugs lay their eggs exposed. It is peculiar that the shape of the eggs is already adapted to the new site but that the solid ovipositor shows no traces of reduction. In all other main groups,

however, including the Reduviidae, the superficial position seems to be primary, according to harmonies found in our comparisons of genital structures and of features of the egg proper.

The typical amphibicorisous eggs are the most generalized according to chorionic structures and embryogenesis and recent knowledge on the phallus leads to the same conclusion (COBBEN, 1965a). Other than Mesoveliidae, only the gerrid *Rhagadotarsus* (egg-shape, fig. 61) has presumably developed the insertion method. Hydrocorisous

Table 2. Position of released eggs (+, *as a rule*; •, *exceptional; further explanations in the text*).

	II upright	I superficial, horizontal		III embedded
Saldidae		•		+
Leptopus, Omania		+		
Hebridae		+		
Mesoveliidae				+
Hydrometridae	+			
Veliidae		+		
Gerridae		+		•
Aradidae, Piesmatidae		+		
Malcidae, Berytinidae	•	+		
Lygaeidae, Colobathristidae	•	+	•	
Pyrrhocoridae, Largidae	+			
Alydidae, Rhopalidae, Coreidae	•	+		
Cydnidae	+	+		
Acanthosomatidae	+	•		
Scutelleridae	+			
Dinidoridae		+		
Tessarotomidae	+			
Pentatomidae	+	•		
Plataspidae		+		
Plokiophilidae		+		
Microphysidae				+
Anthocoridae, Cimicidae		+		+
Nabidae	•			+
Tingidae		•		+
Miridae		•		+
Thaumastocoridae		+		
Reduviidae	•	•	+	
Corixidae	+	+		
Nepidae			+	+
Belostomatidae	+			
Naucoridae		+		+
Notonectidae		+		+
Pleidae, Helotrephidae		+		+
Ochteridae		+		
Gelastocoridae	+	+		
Dipsocoridae		+	+	•

eggs show generalized and more evolved traces in egg structures and embryogenesis, and the embedding of eggs into plant tissues occurs in members of some families. Retention of exposed oviposition is frequent in Pentatomomorpha; in present members of nearly all families, lateral attachment of the eggs is predominant. Since egg characters in some families (Cydnidae, Acanthosomatidae, Lygaeidae) are even more generalized than those of the Cimicomorpha, the superficial position here suggests an original condition, not derived from a past insertion. The lygaeoid ovipositor is not like that of cimicoids but can direct the egg into a more sheltered, but not truly inserted site. The data available suggest that this sheltering of eggs is recently acquired only in Lygaeidae, and must be here more evolved than exposed placing of eggs. The long ovipositor in Lygaeidae may not solely have developed for egg laying. It acts also as a copulatory tube, as in Amphibicorisae, but in contrast to Saldidae and Cimicoidea, where we have seen that the phallus penetrates the base of the ovipositor. Much information on oviposition in lygaeids is now available (SWEET, 1964). Generally eggs are placed in crevices, surface roughnesses, soil and rarely into rather tight substance. A few rhyparochromine species are able to oviposit into soft parenchyma and could therefore be placed in our third type. This represents a new advance in behaviour for this group, to judge from the still untoothed hairy ovipositor.

The upright arrangement may have appeared by selection of various advantageous working mechanisms, on which discussion can be only largely speculative. In pentatomoids and some reduviid groups, that arrange the upright eggs in tight formations, this habit is the most economical spatial usage of egg substrate and could have led to parental guarding behaviour of the egg batch. Parental care is known from different families of Pentatomoidea: Acanthosomatidae, Scutelleridae, Phloeidae and some Pentatomidae: Podopini. Guarding of the eggs in these groups may have arisen early, as lower evolved pentatomoidans are represented among these and as maternal care is related to a special method of symbiont transmission in the more primitive terricolous Cydnidae (SCHORR, 1957). Among Reduviidae, maternal and even paternal behaviour occurs in some Harpactorinae. This may well be recently evolved in view of the advanced type of the harpactorine embryogenesis. PARKER (1965) showed that, if a *Pisilus* female was separated from its egg batch, it could find its own eggs amongst those of other females. But his conclusion that recognition is based on grouping of the individual eggs within the batch needs experimental confirmation with models. Olfactory and other influences were not entirely eliminated in PARKER's procedure. Whatever the initial stimulus keeping the female or male close to the egg mass, the momentary effectiveness of guarding behaviour is difficult to deny, although MILLER (1956, p. 47, 48) has done so. Besides the well known defensive behaviour of the guarding insect, there are a few direct observations of repulsion of parasites (PARKER, 1965). The supreme example of batch formation in Heteroptera is the ootheca of some Plataspidae, in which the eggs lie horizontal, and in Urostylidae. Some Harpactorinae show an approach to formation of an ootheca in that standing eggs are covered with a sticky substance.

The selective pressure to restrict the eggs to a limited space appears also in those

species which attach their eggs to their own bodies. Gerridae and Nepidae can readily be stimulated to do this, if no suitable substrate is provided for oviposition. Females of *Halobates*, dwelling far from land, have been collected with eggs clinging to the abdomen (HUNGERFORD, 1919). Egg carrying in *Phyllomorpha* and in Belostomatidae may have developed through lack of substrate and also through ecological needs: *Phyllomorpha* moves eggs out from the zone just above the soil which overheats and Belostomatidae aerate eggs (p. 209). Belostomatidae oviposit on the male's back; this may have been a favoured characteristic in selection because of the risk that eggs on the female may be punctured by the copulating male. The reduviid *Stenolemus arachniphagus* Mald. & Doesb. places the eggs upright in two rows underneath the wings in the dorsal concavity of the abdomen (van DOESBURG, personal communication). This habit might have evolved during the adaptation of the bug to life in spider webs. The shift from horizontal to vertical of the hydrometrid egg could allow for its greater dependence on atmospheric air and might be favoured as an escape from predators. The strong tendency in Corixidae towards upright eggs, and then to evolve a lengthening stalk is probably protective against 'grazing' predators. The frequency of mixed and dense populations of Corixidae and of cannibalism on each others eggs in captivity suggests that such selection may have been elicited by competition within the family.

Another selective pressure inducing vertical attachment of eggs is of a different nature. Lateral attachment of eggs may create an unfavourable position for the prolarva to escape from the shell, if by loss of embryo rotation the ventral side of the embryo comes to face the substrate. This is a special impediment, if the attached side is flat and if the egg-burster is on the topographical ventral side of the prolarva. Although other ways of eluding the blocked exit can be evolved such as change in egg shape, shift of the egg-burster, rotation of the whole egg (see next section), raising of the egg would theoretically be possible.

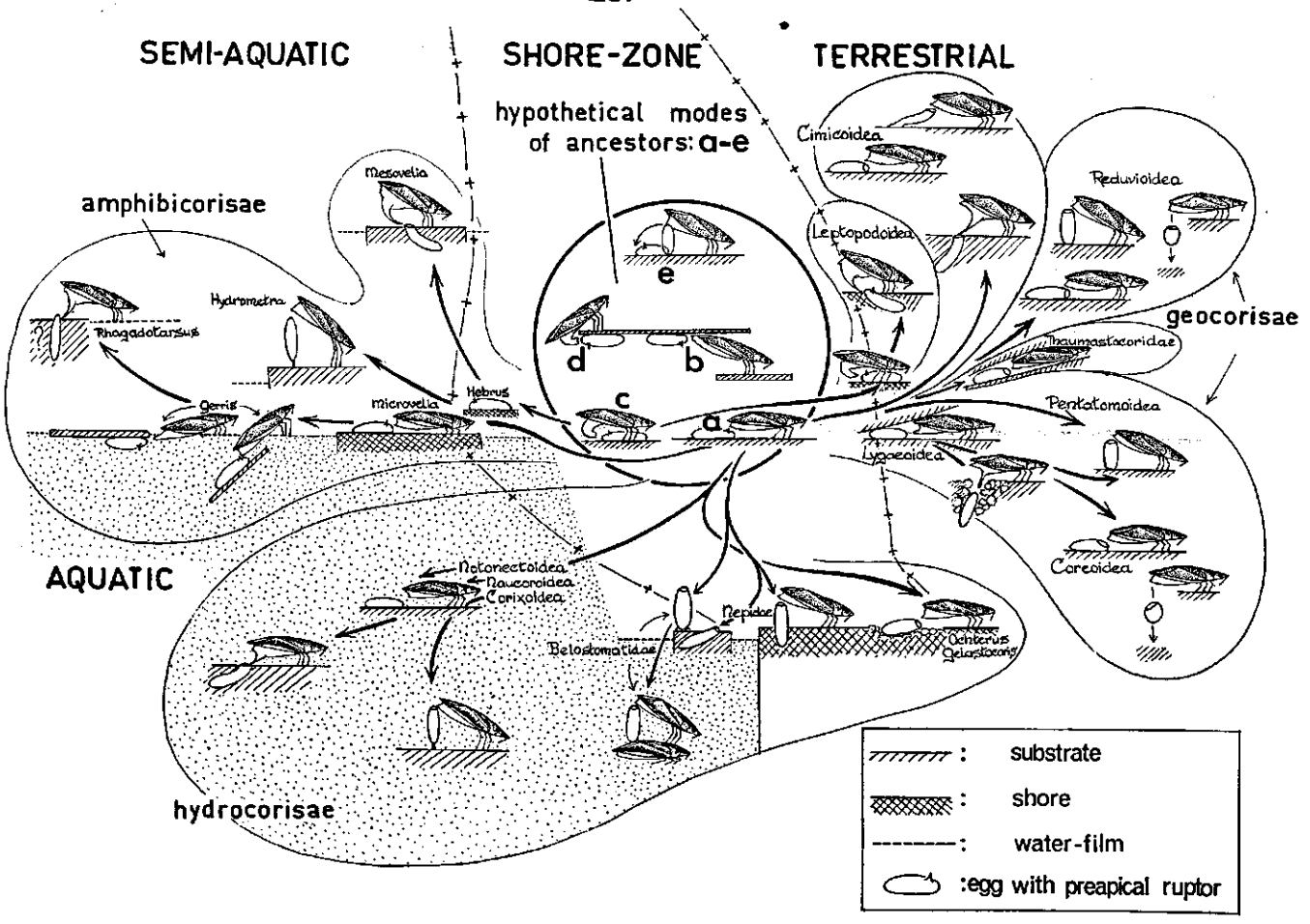
A compilation of the relation of eggs to the substrate is given in the scheme (fig. 281). The orientation of the ovipositing female, also drawn in this scheme, will be discussed next.

3.4.3 The first evidence of egg rotation

The observations on oviposition by Saldidae (p. 10) and Mesoveliidae (p. 48) have shown that their eggs are always deposited such that egg rotation through 180° of its polar axis within the female must be postulated. The behaviour of *Gerris* in response to two possible oviposition sites (p. 66) shows that a single female can regulate the delivery of rotated or unrotated eggs depending whether the eggs are glued upwards or downwards. The ovipositing female of *Gerris* (fig. 282D) has the posture typical

---

Fig. 281. Evolution of ovipositional stances (Dipsocoroidea omitted); any rotation of the egg can be deduced from the position of the subapical ruptor ovi.


SEMI-AQUATIC
SHORE-ZONE
TERRESTRIAL
hypothetical modes of ancestors: a-e
amphibicorisae
Mesovelia
Hydrometra
Rhagadotarsus
Gerris
Microvelia
Hebrus
e
d
b
c
a
Cimicoidea
Leptopodoidea
Reduvioidea
geocorisae
Saumastacoridae
Pentatomoidea
Lygaeoidea
Coreoidea
AQUATIC
Nepidae
Ochterus
Belostomatidae
hydrocorisae
: substrate
: shore
: water-film
:egg with preapical ruptor

of those Heteroptera which glue their eggs exposed and horizontal to the substrate. Bugs ovipositing in dense litter, moss, clumps of grass could also use the inverted method of *Gerris* (compare fig. 281 type b (within circle) with the *Gerris* type furthest left in the scheme). Lygaeidae, Berytinidae and Aradidae are particularly likely to do this but evidence must come from direct observation. In Saldidae and Mesoveliidae, the characteristic inversion of the egg depends on the morphology of the ovipositor. If extruded this organ points with its apex forwards (fig. 282C) so that the egg comes to lie in the reverse position from the normal backwardly delivered egg of Heteroptera. This corresponds with type c in fig. 281; type c must be rotated longitudinally, to correspond with type a in morphological position of the egg-burster. To find out whether saldid-type oviposition occurs in other groups than Saldidae and Mesoveliidae, the concave curvature of the ovipositor can be choosen as an indication of parallel use or, if the ovipositor is straight, the turn of its extreme tip ventrad. Weak concavity of the rudimentary or well developed ovipositor occurs in some Amphibicorisae *(Hebrus, Ocellovelia, Chepuvelia, Speovelia, Mesoveloidea)*, in Leptopodidae (very striking in *Martiniola madagascariensis)* and in the dipsocorid *Ceratocombus*. All these groups very likely place the eggs inversely, free or embedded. In Leotichiidae, the situation may be similar to judge from the ovipositor curve, but not in *Omania*.

Another remarkable type of egg rotation in some pentatomoids, which place their eggs in vertical position, has been mentioned on p. 118. Without alterating its body axis, the female produces two rows of eggs, whose aft sides touch each other (fig. 120). Thus, the eggs are rotated 90°, those of one row clockwise, those of the other row anticlockwise. The other possibility, that the direction of the rotation in both rows is the same but in the eggs of one row is through 270°, seems unlikely. This method of oviposition is performed by the pentatomine *Aeliomorpha* sp. and the phyllocephaline *Macrina juvenca*. In the two-rowed batches of other pentatomoid species and the more common multirowed batches there is no such rotation. Slight left-right deviations are caused by small turnings of the female on its long axis. A secondary feature of the eggs of *Aeliomorpha* and *Macrina* is their flattened fore side (fig. 120, 121) and this character may assist in tracing more such examples of 90° egg turning. The eggs of the coreid *Catorhintha* sp. are stuck to the substrate almost on one lateral side (fig. 95). The egg projects from the female terminalia probably in a normal way and the mother turns it over after complete delivery.

Attachment horizontal to the substrate is the original practice in Heteroptera. This condition can be achieved by two distinct methods of oviposition (a and c in the circled centre of diagram fig. 281). Both are used by some of the most generalized Heteroptera, the Amphibicorisae. Comparing the embryonic type at this basic evolutionary stage, egg-rotation must be involved in one of the two sites illustrated. This early use of both methods of oviposition makes it impossible to decide which type, a or c, was original in the Suborder. Because of the simpler action involved for the female, type a seems more likely as the archetype. But perhaps the archetypical bug had a flexible abdomen and bore only short terminalia. According to environmental conditions, progeny could easily specialize to one or the other method of

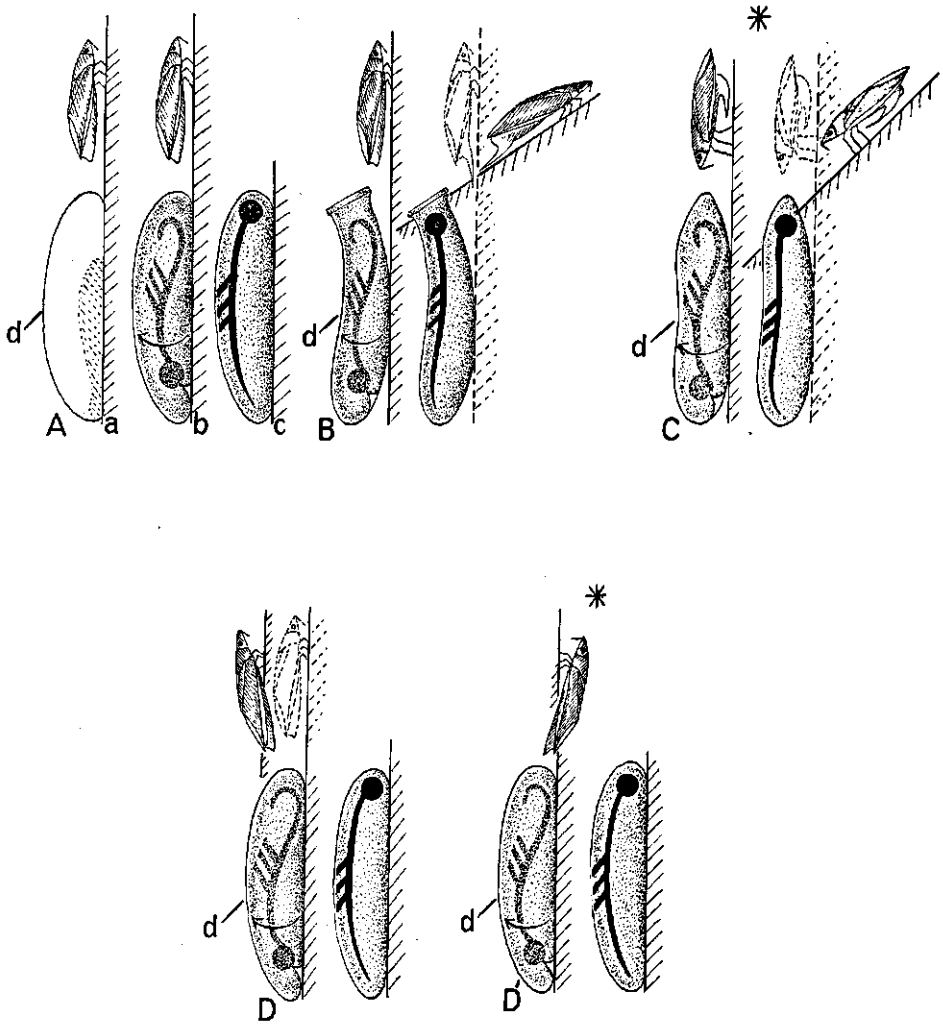


Fig. 282. Determining polarity of the egg system (see text, p. 338–343); an asterisk indicates that rotation of the egg is involved; broken lines are imaginary substrates to show the stance of the female (also broken lines) if the egg were glued superficially along its long axis as in A. A: *Microvelia;* B: cimicoid groups; C: Saldidae, Mesoveliidae, Hebridae? D, D′: Gerridae.

oviposition. Method c could have arisen through shortness of substrate. Or it may arise through the advantage of having oviposition under better control, because the female is standing over the egg during release and thus improves its range of vision in selecting the site for oviposition. On p. 363, preliminary arguments are presented to show that the heteropterous archetype had poor vision. This would favour placing type c chronologically after type a. It may be of significance that Mesoveliidae and Saldidae using the most perfected form of method c have well developed compound eyes. However Miridae and Tingidae using method a, first probe the site where the egg will be inserted, with their stylets (KULLENBERG, 1946; THONTADARYA and BASAVANNA, 1959; our own observations). Some other theoretical possibilities for oviposition are presented within a circle in fig. 281. Method d is behaviorally similar to c. The egg is inverted as compared with a, but need not be rotated. Such an oviposition would be effective when a terrestrial dweller suspends eggs from floating material. Method b in the diagram might be employed by bugs, which oviposit in dense litter or in narrowly spaced vegetation. Type e, lastly, signifies a tipping over of the egg into a similar orientation as in c. KERSHAW and KIRKALDY (1910) described this method in the leafhopper *Pyrops candelaria* and it could be detected occasionally in Heteroptera.

Whether procedure a or c existed first is an important question for determination of the dorsoventral polarity of the egg within the female. This aspect will now be discussed.

3.4.4 Comparison of embryonic types in standardized eggs in position as laid

The section on embryology has shown the variation in internal shifts and rotations of germ band, embryo or prolarva. As it has now been demonstrated in several species that turning of the whole egg may take place, a new problem is added to the determination of dorsoventral polarity of the egg.

The first problem is whether egg rotation occurs also in other heteropterous groups where secondary evidence of the kind mentioned in 3.4.3 (shape of ovipositor, shape of egg and batch) do not indicate such a rotation. The drawings of the eggs in position, presented in the sections 1 and 2 and indicating embryogeny, if known, must be compared with fig. 276. In this scheme the embryonic types are reduced to a comparable basis, whereas our earlier figures of eggs are all standardized with substrate on right and head end up. The main representatives of earlier figures are redrawn diagrammatically in fig. 282–285 to allow comparisons with fig. 276. The position of the ovipositing female is indicated. If the eggs are deposited upright, they are drawn as though they are released horizontal to the substrate. The imaginary line of the substrate and the imaginary position of the female belonging to such an horizontal deposition are indicated with interrupted lines (*e.g.* fig. 283J). The true manner of oviposition is shown in solid lines, to show that the egg is released at an angle differing by 90° from that of an egg laid horizontal to the substrate. Harmonizing these two

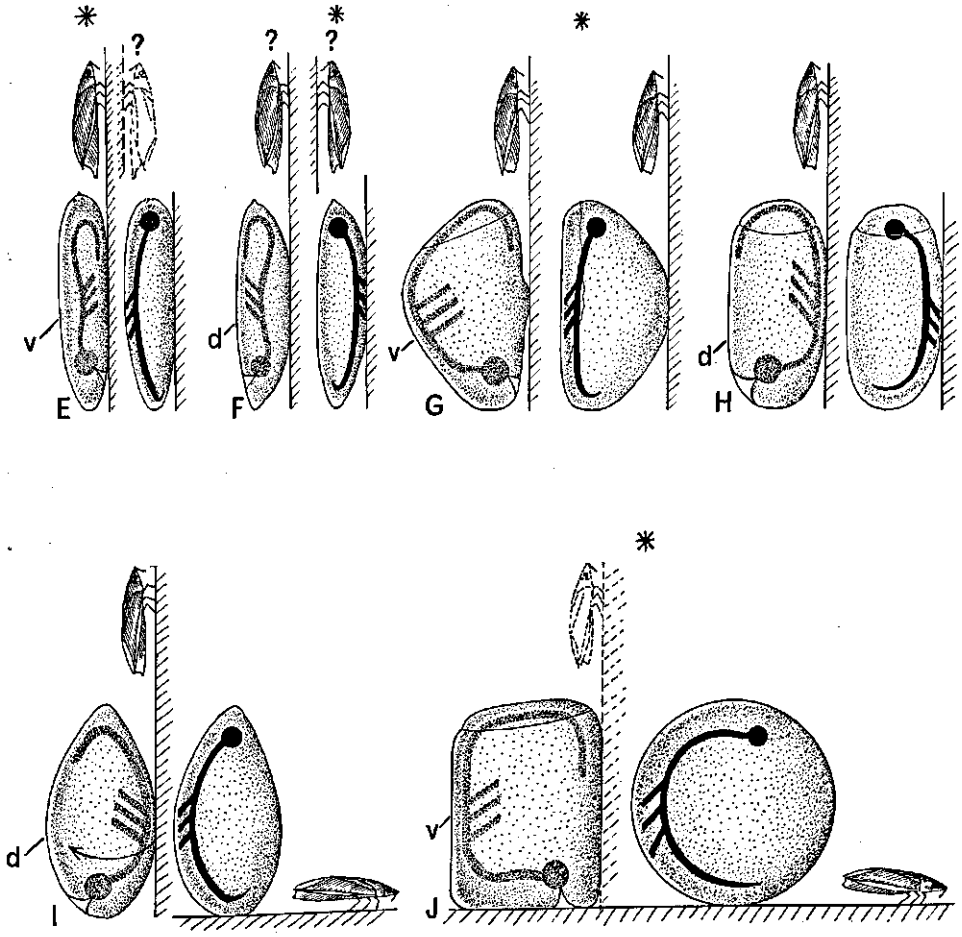


Fig. 283. Continuation of fig. 282. E: Piesmatidae, Lygaeidae, Berytinidae; F: *Neuroctenus;* G: Alydidae, Rhopalidae, Coreidae; H: *Sciocoris;* I: Acanthosomatidae; J: Scutelleridae, Plataspidae, Pentatomidae.

different methods in the diagram seems justified as no confusion over possible rotation of the egg around its polar axis can be involved. In some of the pairs, trios or fours of the diagrams (fig. 282–285), quite different egg types of two genera have been illustrated within one set (*e.g. Coreus* and *Alydus*, fig. 283G; *Notonecta* and *Ilyocoris*, fig. 285U). This is done to emphasize that embryogeny and oviposition are not drastically affected by alteration of egg shape. Fig. 285U shows thus that both *Notonecta* and *Ilyocoris* species follow all the stages a–d.

To detect egg rotation first comparisons are of those figures in which the female has a similar position: head facing upwards, legs to the right. Figure 282A, B is thus the starting point. This type (*Hebrus*, *Microvelia*, most Cimicoidea) represents the archetype without egg rotation (p. 302). The legs of the embryo before revolution point to the left. This situation is repeated in all Hydrocorisae, in most Harpactorinae, the pentatomid *Sciocoris* and possibly in Cydnidae and Acanthosomatidae. In other Reduviidae (the harpactorine? *Sphedanovarus*, the emesinans *Empicoris* and *Schidium*, the reduviinous genus near *Edocla* and the salyavatinans *Lisarda* and *Cethera*), and the Pentatomomorpha *Berytinus*, all Coreoidea studied and the remaining pentatomoid families, the early embryo faces ventrally to the right side. In all these examples (asterisked in fig. 283, 284) 180° rotation of the egg's length axis must have occurred. Egg turning thus appears not to be exceptional in the Suborder and is not confined to the types discussed in Saldidae, Mesoveliidae and occasionally Gerridae (note the aberrative female orientation in the standardized manner of presentation in fig. 282C, D'). In some families the relation of the released egg to the ovipositing female has not been seen. Thus the position of the *Neuroctenus* egg could theoretically be either the right or the left specimen in fig. 283F, since Aradidae live under bark. Only in the situation on the right can egg turning be assumed. The embryo of *Pachycoleus* (fig. 284O) at first sight indicates egg turning. But since in other Dipsocoridae with a better developed ovipositor, it is flexed as in Saldidae, the right alternative of the depositing female is possible and this should mean no rotation of the egg.

3.4.5 Dorsoventral polarity of the egg system

In trying to determine which side of the egg system is the dorsal one, there are various difficulties. This section covers only situations in Heteroptera. In the discussion (3.4.6), the problem will be considered in a broader context.

A fixed orientation of the eggs in the ovarioles could not be found. In specimens from different families, the eggs were found in various orientations, as soon as chorionic structure distinguished a dorsal and ventral side (see fig. 142, 143, 154). This is due to the irregular contorsion of the ovarioles. The morphological sites of the future egg must be determined very early during oogenesis and the polarity of these sites in relation to the mother must be alike for all oocytes. Because our information starts only from the eggs as they are being released from the female's terminalia, a hypothesis on their orientation in the female can only be provisional. There is little doubt that the archetype of embryogenesis in Heteroptera behaves as is in fig. 276a,

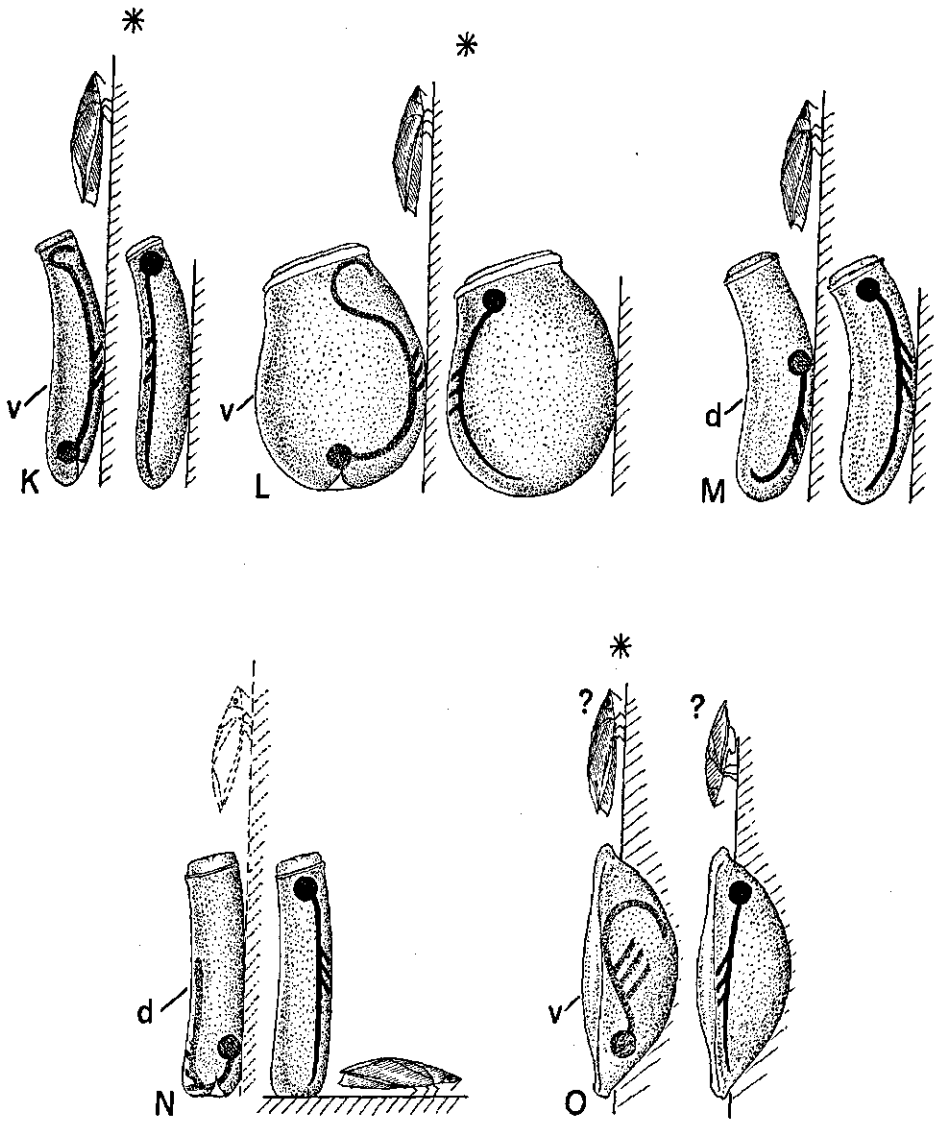


Fig. 284. Continuation of fig. 282. K, L: Reduviidae (in part); M: *Coranus;* N: *Rhinocoris;* O: *Pachycoleus.*

that is: embryo immersed and performing a 180° rotation. Evidence suggested that originally the egg was released backwards (most Amphibicorisae) and not forwards as in some recent Amphibicorisae and in Saldidae. If this concept is maintained here, implying no egg turning during delivery, the egg polarity in relation to the female can be explained most plausibly with the site of the 'Vorkeim' as the venter of the egg. For convenience, Vorkeim is here translated as 'pregerm'. It is the first distinct position of the prospective germ band, before involution and bodily organization starts. The site of the pregerm can readily be ascertained as the side of the egg which faces the dorsum of the invaginated germ band (fig. 282A, b). The ventral side of the pregerm is contiguous with the subchorionic and chorionic covers (fig. 282A, a). All morphological axes of the pregerm and the egg as a whole should correspond in this stage to the axes of the female.

When our procedure for determining polarity is continued, some important consequences can be drawn. For the first time it is now possible to identify positively the dorsum and venter of the egg (shown with d and v, respectively, in fig. 282–285). The following appears:

1. All superficially laid eggs with a 180° embryo rotation (Amphibicorisae, Saldidae, Cimicoidea, Hydrocorisae) are attached with their ventral side to the substrate, irrespective of whether they are deposited backwards or suspended *(Gerris)*, or whether they are deposited forwards (*Saldula scotica)*. The prolarva faces with its venter towards the dorsum of the egg (fig. 282). In practical usage of entomological literature this dorsum is, on the contrary, called the ventral side in correspondance with the orientation of the prolarva. The effects of band rotation and prolarva rotation(s) in some Hydrocorisae (fig. 285U) cancel each other out and do not influence the statement.

2. Those eggs whose embryos do not rotate, are attached ventrally to the substrate (fig. 283H, I; 284M) but, when the deposited egg is turned 180° by the female, conditions are reversed (fig. 283G; 284K, L). Either way, the morphological sites of the prolarva coincide with those of the whole egg.

The same rules apply also to embedded or vertical eggs, when these eggs are illustrated as though they be deposited superficially and horizontally (broken lines of substituted substrate in fig. 283J; 284N).

Thus one can only ascertain the egg's polarity if the major embryogenic history and the manner of oviposition is known. The data gathered here on Heteroptera allows almost certain determination of the polarity of any species of the better known families without knowing the embryogeny. The analysis shows further that the dorsoventral orientation of the prolarva is the best criterion. In the eggs without embryo rotation, this prolarval orientation corresponds to the main axes of the egg; the prolarva is ultimately inverted in eggs with embryo rotation. Turning of the whole egg does not influence these phenomena.

Polarity determination is difficult by extrapolation from the outward appearance of the egg and the site where it is deposited. This is due to the variety of turnings, the evolutionary ability of the bugs to adapt egg shape to the modified position and the

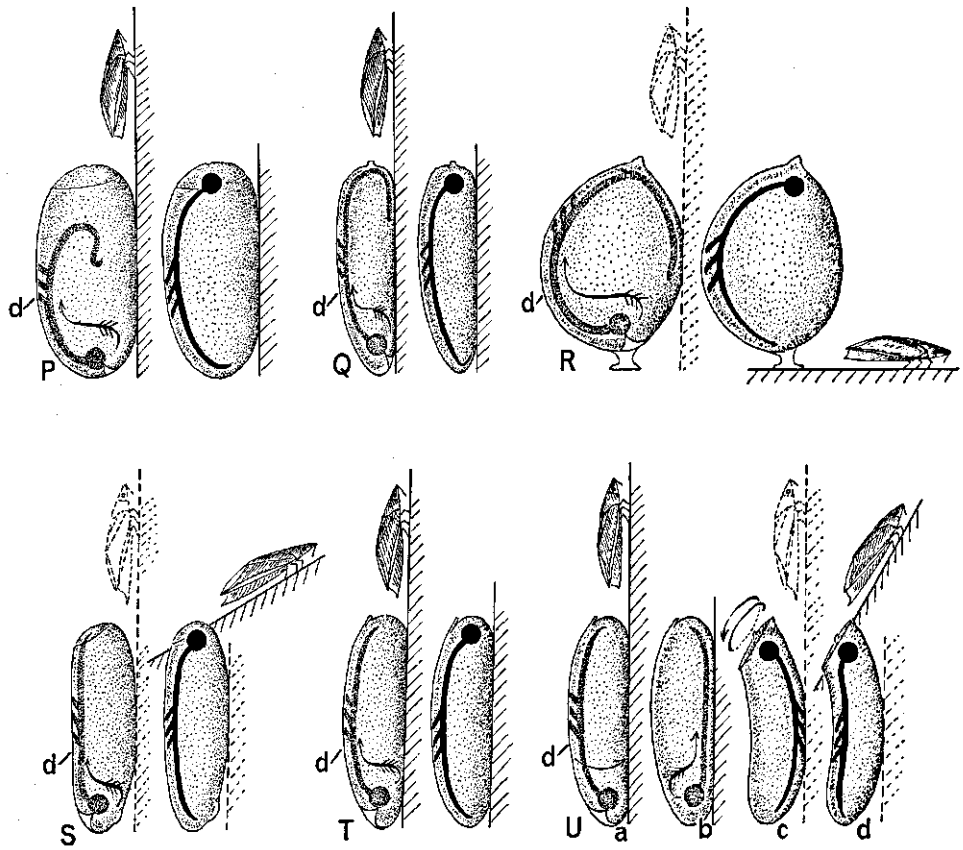


Fig. 285. Continuation of fig. 282. P: *Ochterus;* Q: *Diaprepocoris, Micronecta;* R: Corixinae; S: Nepidae; T: *Notonecta maculata;* U: *Notonecta, Ilyocoris.*

general variation in egg shape. A good illustration of this is given by the two reduviid types. Fig. 284K en fig. 284M have similar curved eggs and oviposition sites. However, the emesinous egg is turned 180°, the harpactorinous egg is not. This means that adaptation of the egg to the substrate has evoked a curvature towards two morphologically opposite sides but an ultimately similar outer aspect in the two types. If there is a lateral egg cap, it may be on the dorsal side as in *Ilyocoris* (fig. 285U, c) or on the ventral side as in *Leptoglossus* or *Anoplocnemus* (fig. 283G; 100I''). The complete ventral displacement of the cap in *Anoplocnemus* and others must have occurred after the acquisition of egg rotation. Otherwise the exit for the hatching larva would be completely blocked.

In the complex life of the egg system, many interacting evolutionary factors are involved inviting speculation about the role they have played in the past or will play in the future. So one might speculate about what would happen if progressing

embryonic evolution should lead to loss of embryo rotation in an egg which has already developed a lateral egg cap and which is glued flatly to the substrate. The result would be that the prolarva should face the enclosed substrate. In a hydrocorisous egg the question could be solved by a readily performed prolarval rotation backwards. In other groups the solution depends entirely on the curvature of the prolarval head and how far and where egg bursters are developed to break the chorion close to the most anterior part of the cap. If such eclosion could be effected, there would be a selective pressure for a return shift of the cap. A modified flexure or shape of the egg or a turning or upright arrangement of the egg could theoretically be more efficacious. Mechanical barriers could already be such that the hypothetical situation could not be overcome. Progressive embryonic evolution would then be largely suppressed. The example given is admittedly extreme, since it seems not applicable to any of the actual data. However less extreme situations could be chosen and from the reasoning above it is likely that, if many more species, especially of annectant groups, are studied, a clearer picture may form of the rate and method of egg evolution in Heteroptera. Our data suggest that egg turning has acquired some taxonomic significance. But the absence of it in the pentatomid *Sciocoris* could mean that the phenomenon is labile. The mechanics of such turning needs further investigation.

3.4.6 Discussion

Asymmetries

Asymmetry, in particular the enigmatic unidirectional dominance in bilateral asymmetry in quite unrelated systems of the egg (p. 327–331), is a feature not confined to the egg but occurs in large degree in adult heteropterans. The origin of adults asymmetries are more understandable. Although it is still too far-fetched to assume a causal relation, it is striking that Hydrocorisae have the most amphidromous asymmetries in both the eggs and adults (six monostrophous asymmetries in corixid adult, KEILBACH, 1935). In snails, a direct correlation has been found between the direction of the adult shell coiling and spiral cleavage (RAVEN, 1961). It would be of interest to analyse whether the dextrally asymmetric *Corixa* spp. behave embryonically in the reverse way to the left-asymmetric remaining genera of the same family. The *Plea* egg has many asymmetries, whereas the adult seems to lack cuticular bilateral asymmetries. Yet in all 14 copulating pairs observed, the male mounted the right side of the female. The remarkable jigsaw flexing of the prolarval legs and antennae and the sometimes striking regularity in this seems to reflect genetically fixed asymmetries in many species (p. 328). No comparable data from other insect groups are available from the literature, but a jigsaw pattern seems to be a general feature in the hemipterous Orders. This is in contrast to palaeopterous and orthopterous Orders, where the sharply 'kneed' legs bend forwards without overlapping across the median line and thus give no occasion to asymmetric configurations. In Ephemeroptera, all prolarval limbs are flexed forwards (DEGRANGE, 1960); in Odonata only the hind legs, whereas the other

pairs point straight caudad (ANDO, 1962). The legs in Orthoptera are all folded, slightly touching each other medially (LE BERRE, 1959; MATTHEE, 1951).

Situation of released eggs

The data suggest that the heteropterous egg was originally deposited in a superficial horizontal position. We concluded the same while studying the evolution of egg structures of Homoptera, especially of Auchenorrhyncha (COBBEN, 1965c). Superficial laying occurs predominantly in Homoptera Psyllina, Aleurodina and Aphidina. In exposed eggs of Psyllina and Aleurodina a subapical egg stalk with hydropylar function is implanted in the substrate. Eggs stalked near the apex are preferably laid hidden between bud scales and the stalkless egg of *Livia juncorum* is entirely embedded in plant tissue (HESLOP-HARRISON, 1949). Significantly Psocoptera, so far as is known, lay eggs only superficially (PEARMAN, 1928; BADONNEL, 1943) and the two Suborders of Thysanoptera are based on laying of eggs exposed or in plant tissue. A check on the direction of anagenesis of the ovipositor in each of these Suborders and Orders should be considered with embryogenic and chorionic differentiations.

Egg polarity

The rotation of the egg before or during oviposition, as demonstrated above in Heteroptera, might be general in insects. The most significant hint of this is the two types of ovipositor in different Orders. To remain first in the hemipteroid groups, most families of Thysanoptera Terebrantia have the ovipositor curved downwards, but in Aeolothripidae it curves upwards (PRIESNER, 1964). This division thus parallels the concave type of Mesoveliidae and Saldidae and the convex type of Miridae. In Hymenoptera, the two types, apart from the perpendicular ovipositing act, are found in different major groups: many sawflies (*e.g. Dolerus* spp.) of Symphyta, and many Cynipidae and Bethylidae of Apocrita have the ovipositor concave. Certainly thorough study of the literature will show more examples. Illustrations in textbooks show that two behavioral types of oviposition exist in parasitic Hymenoptera with a straight ovipositor. *Lysiphlebus* (Aphidiidae) lays eggs in aphids by bending its abdomen forward, so that the ovipositor reaches forward under and past the wasp's head. The same posture holds for species of the ichneumonid genera *Banchus* and *Perithous*. *Platygaster dryomiae* (Platygastridae) exhibits a similar but less pronounced habit. The analogous behaviour in some Heteroptera might be related to a decision, based on visual information, where to lay the egg (p. 338). In the parasitic insects, reviewed here, visual selection seems likely. Gasteruptiidae flex the long abdomen normal to the substrate but the fore body remains borne by the hovering wings so that the eyes of the insect are focused on the abdominal tip (illustrated by RAYMENT, 1955). But *Aphelinus* heads away from the host aphid. The forwards or backwards syringing act employed by ants is probably derived from an analogous duality of abdominal behaviour. A similar division may be made in Diptera, which primarily lack an ovipositor. *Mydas*

(Mydaidae) releases the eggs just in front of its head (GIBSON, 1965) and the most extreme example known of projecting the egg forwards is the parasitic fly *Rondania dimidiata* Mg. (DE FLUITER and BLIJDORP, 1935).

The majority of those exponents are parasites, for which egg orientation may make no difference. Egg turning in one of the alternatives of deposition would therefore not be necessary. In sawflies and thrips, however, a 180° degrees turning of the egg might be necessary to allow the larva to escape easily from the shell. The shape of the released egg of the sawfly *Pristiphora conjugata*, in relation to the orientation of the depositing female, as illustrated by DELMAS (1926), indeed suggests 180° rotation of the egg.

Egg rotation in general can be detected from gross embryogeny and the position of the mother in relation to the egg just laid. This has been shown in Heteroptera on p. 338–340. Comparisons were based on our postulate that the blastodermal thickening or ventral plate is on the morphological venter of the egg (p. 342 and fig. 282A, a). This stage marks the first detectable polarity of the incipient embryo. Since other criteria such as position and migration of germinal vesicle and cleavage cells are not available, these must be excluded from consideration of egg polarity. We have tried to determine the polarity of the whole egg in relation to that of the female, thus comparing two already organized structures. Therefore the choice of the ventral plate as a basis seems most convenient and reliable. At an earlier stage, a serious complication would be that the precursor elements of the pregerm seem to originate more from the opposite side of the egg. The blastoderm cells flow from that side along the left and the right surface (fig. 194A) to meet at the fore side of the egg. This flow is governed by contraction of the yolk-endoplasm system in the central yolk column, as was shown experimentally in *Acheta* (MAHR, 1960).

The polar bodies occupy a position on the dorsal side of the egg in *Blatta*, *Eutermis*, *Liposcelis*, *Melophagus*, *Drosophila* but on the ventral side in *Coccidae* and *Pteronarcys* (GOSS, 1954). In *Tachycines* and *Acanthoscelides*, the site of the germinal vesicle is said to become the dorsal, but in *Platycnemis*, *Apis* and *Tenebrio* the ventral side of the egg (RAVEN, 1961). Such findings need confirmation after a thorough study of all positional relationships in the history of the egg. The complexity of positional relationships found in Heteroptera makes one wonder how far ventral and dorsal are here trustworthy.

The relation of the position of the ventral plate in laid eggs to the position of the depositing female suggests that the main axes of unripe eggs in Heteroptera have the same orientation as those of the mother, if it is assumed that the orientation of the egg-cell anlage is constant for all eggs. If the eggs are rotated during delivery, polarity is no longer the same. The frequency of germ band, embryo or prolarva rotations make the final position of the fully grown embryo misleading as an indicator of dorsoventral polarity of the egg. Only where the egg has lost internal rotation, does the ultimate orientation of the embryo conform to that of the ventral plate. The venter of the encased prolarva is then against the ventral side of the shell. If further there is no preceding longitudinal or transverse turning of the egg, orientation of longitudinal,

dorsoventral and dextrosinistral axes of mother, fully grown embryo and egg are identical. Only this situation is in agreement with what HALLEZ (1886), intended to stress in his 'law of orientation', or at least, with what he was justified in deducing from his own findings. This law has often been discussed in the literature. Textbooks and reviews on reproduction and embryology refer repeatedly to this supposed regularity of egg orientation and comment that there are exceptions. A steadily greater content has been attributed to HALLEZ's statement by later authors. HALLEZ based his generalization on orientation of the depositing female, the deposited egg and its fully grown embryo. He studied those conditions in *Tettigonia viridissima* and *Hydrophilus piceus*, and said he had investigated insects of other Orders but without enumerating them. He concluded that his observations gave "...exactement les relations qui existent, d'une part, entre l'axe principal de la mère et l'axe organique de l'oeuf, et, d'autre part, entre l'axe organique de l'oeuf et l'axe principal de l'embryon". Later he stated: "La cellule-oeuf possède la même orientation que l'organisme maternal qui l'a produite: elle a un pôle céphalique et un pôle caudal, un côté droit et un côté gauche, une face dorsale et une face ventrale; et ces différentes faces de la cellule-oeuf coïncident aux faces correspondants de l'embryon". By 'cellule-oeuf' HALLEZ probably meant simply the ripe egg body, since he had apparently no data on the earliest egg formation. The only relation traced by him within the female, was one ripe ovarian egg and one egg passing through the ovipositor, and these two eggs had the same orientation as the *Tettigonia* female. Nor is there any indication that he studied early embryogenesis, so that his term 'embryon' could probably be replaced by 'prolarva'. After studying his paper, we can only conclude that HALLEZ compared the orientation of the female, the new laid egg and the later orientation of the egg larva. Thus if the law of HALLEZ is applied in this restricted original sense to Heteroptera, only a small proportion of species conform: the unrotated eggs of higher Geocorisae. The validity of the law in its wider interpretation depends entirely on when the orientations are compared. Beginning with the egg orientation in the common oviduct and assuming that egg rotation may have occurred earlier, rotated eggs of Amphibicorisae and Saldidae would also affirm the law, if any forward releasing of the egg and reversal of its longitudinal axis is ignored.

This account on Heteroptera makes it possible to take an earlier point in time where orientation is still regular, namely the ventral plate stage. The reasonableness of the evolutionary picture suggested for the many varying embryonic types in Heteroptera (fig. 276), if based on orientation at the ventral-plate or germ-disk stage, strengthens our premise that during oogenesis and egg ripening congruence of the main axes of egg-system and mother do indeed correspond, despite the often irregular, tortuous arrangement of the eggs in the ovarioles. The law of HALLEZ, applied to Heteroptera, could therefore be modified for a more logical and wider application: *The orientation of the longitudinal and transverse axes of the released egg shell and the enclosed embryonic rudiment correspond with those of the depositing mother, unless eggs are rotated during delivery or the longitudinal axis is reversed in relation to that of the female by tumbling.* The regularity indicated can be extended to the final orientation of the

prolarva if there are no positional shifts of the embryo during egg life. This restatement of the law is based on the assumption that the early egg system in the ovariole has the same orientation as the mother, both longitudinal and dorso-ventrally. If this assumption can once be proved, the statement could be treated as the most general law of orientation.

As far as we know, only one account in literature suggests egg rotation, in the psocid *Liposcelis divergens* (Goss, 1954). In trying to accord HALLEZ's law with the relations found in *Liposcelis*, Goss supposed 180° turning of the egg when passing through the genital tract. As an indirect proof for such rotation he used the position of the germinal vesicle in the ovarian egg. He found that this vesicle *usually* occurs on the dorsal or dorso-lateral side in relation to the mother's body. The incipient germ disk would then be on the opposite side. Goss's reasonings may be valid but an embryo rotation could explain the final orientation of the prolarva without egg turning. Such a rotation has not been eliminated; in bugs it is mostly during revolution. Goss (1953) found only three *Liposcelis* eggs in revolution "out of well over 1000 which were examined in sections or as whole mounts". Unfortunately Goss's paper on early embryogeny (1952) does not show whether the germ disk faces the substrate side of the egg. If so, the embryo certainly must have rotated and this, with other data on psocid embryogeny, would be invaluable as Psocoptera-like insects are often considered the precursors of Hemiptera. The ultimate position of the psocid prolarva, lying with its aft to the substrate seems common in the Order (WEBER, 1939) and the vague possibility that the egg is tumbled during deposition must still be checked by direct observations of laying. Such a tumbling, in which the polar axis of the egg is reversed in relation to the axis of the depositing female, occurs in the homopteran *Pyrops candelaria*, which likewise lacks an extended ovipositor (KERSHAW and KIRKALDY, 1910). This method is nearly similar to the forward depositing of the egg by a concave ovipositor of the *Mesovelia* type. In the egg rafts of *Culex* and other genera, the anterior pole of the eggs points downwards. Remarkably the 180° tumbling of the egg along the transverse axis must occur in the oviduct (IDRIS, 1960)! A tumbling is performed by the prolarva of Phasiinae (Diptera). In species with thick-shelled eggs, the fully grown embryo turns and leaves the egg at the basal pole (DUPUIS, 1963).

Confining ourselves to the hemipteroid Orders, 180° egg rotation is unavoidable in several families of the Cicadina and Psyllina (COBBEN, 1965c). Embryo rotation has ceased to occur in part of the Delphacidae. In the literature on embryogeny in Aphididae there is no exclusive mention of embryo rotation. Identical orientation of female and prolarva, both in viviparous and oviparous forms, seems to be the rule. Our comparisons of embryonic positions before and after revolution in winter eggs of *Aphis*, *Myzus* and *Lachnus* did not reveal embryo rotation, and the position of the eggs suggests absence of egg turning. Dr. D. HILLE RIS LAMBERS told us of an interesting observation on the aphid *Cerataphis orchidearum* (Westw.). Females on the underside of leaves of *Vanda* sp. bore larvae whose legs could make contact with the substrate. When, however, a leaf with aphids was placed upside down in a petri dish, larvae were born with their venter away from the leaf. This change during parturition

is, in contrast to *Gerris*, difficult to explain but shows how easily larval rotation may be induced.

In the remaining hemipteroid Orders, Mallophaga and Siphunculata, no obvious egg rotation occurs according to figures in SCHÖLZEL (1937) of three and seven species, respectively. Since there is no embryonic rotation in these groups, the main axes of the germ disk, prolarva and shell correspond with those of the female during laying.

A seeming reversal of the long axis of the egg is effected if the embryo completes its development without revolution. We never saw this in Heteroptera but in other Orders this absence of blastokinesis has been sometimes shown. Normally such prolarvae die, partly because they cannot break the shell. This phenomenon seems more regular in Ephemeroptera. The embryos of fertilized eggs develop normally but the prolarvae of the same species point to the caudal pole of the egg in parthenogenetic batches (DEGRANGE, 1961). Dr. D. HILLE RIS LAMBERS informed us that the larvae of Aphididae occasionally leave the female gonopore head first. Absence of revolution may be the cause but, as in *Culex*, it could also be tumbling of the egg or prolarva within the genital tract.

4 A preliminary discussion of the phylogeny of the suborder

4.1 The data and their bearing on classification above generic level

Leptopodoidea

This superfamily shares the presence of only one anterior, median micropyle (only Leotichiidae could not be studied) with many representatives of the Amphibicorisae and the Hydrocorisae. The structure of this single micropyle distinguishes the Leptopodoidea from all other groups. It is only intrachorionic, as an oblique canal which tapers interiad. The general chorionic architecture is not exclusive and relates part of the group to some Amphibicorisae and another part to some Hydrocorisae. The specialized respiratory area of the shell with the typical air clefts have evolved in most members of the Leptopodoidea but are not paralleled elsewhere in Heteroptera. The embryonic pattern shares most features with Amphibicorisae and the cimicoid groups. However, a divergence from these groups is the opposite shift in position of the blastopore which is a link of Saldidae with Hydrocorisae, Reduviidae and Pentatomomorpha. The peculiar cephalic organ discovered in Saldidae, was not encountered in any other heteropterous family. The egg burster and its bearing framework, though related to the amphibicorisous burster, is typical for the leptopodoid families.

From the association of these egg characters, Leptopodoidea seems to form a natural group, distinct from other Heteroptera. Within the Saldidae, at least, egg structures are only discriminatory between species and cannot yet be used to distinguish genera or subfamilies (except for the isolated *Aepophilus*). The shell of *Omania* yields no conclusion about its status. On the basis of adult characters to be dealt with elsewhere, it deserves a separate family.

Amphibicorisae

The egg systems in this major group are diverse. The shell (without any pores in *Hebrus* and *Mesovelia*) and eclosion structures distinguish the small families Hebridae (the position of *Hyrcanus* needs revision), Mesoveliidae, Hydrometridae. The discrepancies between them have been stressed in the observational sections. Shell structure shows that the South American *Mesoveloidea* belongs to or is close to Mesoveliidae. In Part II, some features of the male genitalia of *Mesoveloidea* will supply some more arguments relevant to its status. *Mesovelia* is aberrant among sur-

face dwellers by its exceptional manner of eclosion (embryonic cuticular vesicle, chorionic cap), its flexing pattern of the prolarval extremities and its possession of symbionts. Its extraordinary shell places Hydrometridae apart from other Amphibicorisae (remarkable plastron structure, incipient features of land bugs in interior of chorion, no hydropyle).

The gerrid-veliid complex differs from the amphibicorisous groups just mentioned by a finely and densely porous shell and an inner meshwork layer bordering an extremely thin inner sheet of chorionin. There has been growing doubt that the Gerridae and the Veliidae are separable at all on the basis of adult characters (CHINA and USINGER, 1949). In 1957, CHINA added some disparities in the phallic structures to diagnose the two families. The eggs of the two groups show divergence in several respects. The gerrid eggs studied demonstrated with a few exceptions a strong retention of the single micropyle. The veliid eggs (incl. of *Hebrovelia*, *Ocellovelia*) have rarely one er two micropyles, but usually more. The embryogenic pattern of *Gerris* was slightly different. The positional shifts of the embryo are more complex than in *Microvelia* but more species must be checked on this point. *Gerris* spp. have a frontal burster, whereas *Microvelia* has the clypeal type. Of interest are the isolated genera *Chepuvelia*, *Macrovelia* and *Oravelia*. The egg shell (general structure and micropyles; absence of cap) suggests strongly an affiliation with the Veliidae and certainly not with Mesoveliidae, where it is placed by CHINA and MILLER (1959). The more widely separated and circular arrangement of the micropyles and the spacious inner meshwork of the *Macrovelia* chorion are of great interest as a link with Geocorisae, especially Pentatomomorpha. A considered judgement about the family status of *Macrovelia*, *Oravelia* and *Chepuvelia* will be given later after the decisive evaluation of larval and adult structures. The most significant characteristic of the Amphibicorisae is the type of embryogeny which resembles the hypothetical archetype. *Hebrus* most closely resembles it, whereas the type in *Gerris* and *Hydrometra* is slightly progressed with some variation in the embryo rotation. It is common practice to recognize only one superfamily, the Gerroidea. The diversity shown and the overall conservatism will make a splitting into at least two superfamilies desirable.

Pentatomomorpha

There is no question that the Leptopodoidea, which recently were placed in the Pentatomomorpha (WAGNER, 1961, 1966), should not be incorporated in this group. All properties of the egg system contradict such a grouping. The eggs of representatives of most pentatomomorphous families were studied (we missed only the Lestoniidae, Phloeidae*, Hyocephalidae**, which are small families of

* The eggs of Phloeidae have been described recently by LENT and JURBERG (1966). They noticed absence of a cap and presence of a crown of black spines (aero-micropyles?) and a simple egg burster. More exact data are necessary to place the phloeid egg in one of our phylogenic schemes.

** The hyocephalid egg is now known (see p. 354).

restricted distribution (Australia, South America)). They form a natural group except for the atypical Idiostolidae, and the less atypical Thaumastellidae. The dendograms of each separate set of egg characters (fig. 269, 270, 276, 277) are strikingly similar in anagenetic levelling. The lygaeoid branch stops at a low level, whereas the pentatomoid branch represented by modern members, follows the entire vertical distance of the schemes. In this latter lineage, the Urostylidae, Cydnidae, Acanthosomatidae and Scutelleridae are the more generalized ones. Some diversity of opinion has been expressed recently on the status of these groups (DUPUIS, 1948; LESTON, 1953a; SOUTHWOOD, 1956; PENDERGRAST, 1957; KUMAR, 1962). Primitive and evolved characters in the reproductive and intromittant organs occur simultaneously and it is a problem to weight these characters. Since other authors have overlooked some of the most important characters in the male organ, the problem will be discussed more fully in Part. II.

In all members of the entire dendogram of the Pentatomomorpha, there is only one type of embryogeny. This has progressed from the inversed immersed type (initially with embryo rotation) to the inversed superficial type. The families are characterized by the different levels reached in this anagenesis. Some degree of parallel evolutionary progression and different levelling in each family is shown also in the structures of the chorion and embryonic cuticle (thickening of chorion, perfection of eclosion system, disappearance of internal micropylar canal, increase in micropyle number). A cladogenesis of the families is, because of these parallels, more apparent in advanced families than in the more generalized ones. The familial differences are in less obvious features and often features of less importance (egg shape, structure and number of micropyles). There can be little doubt that the taxa considered here as separate families from egg characters, indeed deserve this status. This conclusion accords with all major revisionary work by other authors after 1950. CHINA and MILLER (1959), however, prefer to speak of the pentatomid subfamilies Tessarotominae, Dinidorinae, Scutellerinae and Acanthosomatinae. SOUTHWOOD (1956), in dealing with the eggs of the Pentatomoidea, treated the Scutelleridae as a subfamily. Scutellerid eggs, however can be distinguished from pentatomid eggs by the persistence of a long internal micropylar canal. Clear familial dichotomy is suggested since some pentatomid species have the same low anagenetic level for their egg structures (arrangement of micropyles and incomplete pseudoperculum) as Scutelleridae but lack the internal canal. Within the Pentatomidae, the Asopinae are separated as a group more distinct than the other subfamilies (long micropylar extensions, smooth chorion and blackening of the coat of the chorion). The egg makes it doubtful whether the Eumenotinae belong to Pentatomidae. Some authors (PENDERGRAST 1957; KUMAR 1962) stressed that Urostylidae Acanthosomatidae and Dinidoridae have several genital features in common with Pyrrhocoridae. Our dendograms strongly suggest that such overlap means no mutual relation but parallelism.

It is generally accepted today that the Pentatomoidea form a natural group distinct from other pentatomomorphous families which constitute another group. Such a divergence is not clearly reflected by chorionic differentiation but may be portrayedin

embryogeny when representatives of the basic families are better known. Embryo rotation is presumed in the cydnid and acanthosomatid species studied. The chorionic structures of the urostylid eggs are the most primitive of the pentatomoid line. The still unknown embryogeny of this family may reveal also rotation. Some basic families (Piesmatidae, Lygaeidae, Aradidae) of the other superfamily or superfamilies have no embryonic rotation whereas their chorionic devices are even more generalized than those of Cydnidae and Acanthosomatidae. If embryonic processes are weighted higher, it means that the Pentatomoidea have a longer ancestry. More arguments for this supposition will be presented later in the discussion of newly discovered genital and other characters. The most primitive chorionic structures in the Pentatomoidea are revealed by the egg of *Thaumastella aradoides*. In fact, it links close with some amphibicorisous eggs. On account of the exceptional position of this species ŠTYS (1964b) created a new family for it. His conclusion that Thaumastellidae must be regarded as an early offshoot of the pentatomoid stock is confirmed by our findings.

The second pentatomomorphous branch is discussed now briefly. The phylogeny of the lygaeid-coreid complex of families has been repeatedly studied and was heatedly debated by SCHAEFER, SCUDDER and ŠTYS. ŠTYS (1961) proposed one superfamily, the Coreoidea, to include the Lygaeoidea, Berytinoidea, Pyrrhocoroidea and Coreoidea. He created a new superfamily for the Piesmatidae. SCUDDER (1963) recognized the Coreoidea (incl. Stenocephalidae) and the Lygaeoidea (incl. Piesmatidae and Pyrrhocoridae), using a quantitative analysis of the phenetic affinities. His method has been criticized by SCHAEFER (1963) who on his turn, concluded (1964) with a grouping into Lygaeoidea (incl. with probability Piesmatidae, Berytinidae, Colobathristidae), Coreoidea (incl. Stenocephalidae) and Pyrrhocoroidea. SCHAEFER objected in several respects to the phyletic weighting of characters by ŠTYS (1961). In supplying detailed information on the morphology of the Hyocephalidae (only ♀) (1964a) and of the Thaumastellidae (1964b), ŠTYS upheld his classification of 1962 and, with his 1965 paper, he classified the trichophorous families into four superfamilies: Idiostoloidea, Piesmatoidea, Coreoidea and Pentatomoidea. The first group is erected as new and contains only two species which SCUDDER (1962) placed in the lygaeid subfamily Idiostolinae. In his procedure, ŠTYS used SCUDDER's descriptions without having seen the original material. Meanwhile, SCHAEFER (1966) re-examined the morphology of *Idiostolus insularis* Berg. He gave family status also to this taxon, but incorporated it in the Lygaeoidea.

We were very lucky to be able to study the *Idiostolus* egg and showed its extremely generalized condition (p. 78). Our data and supplementary new findings concerning adult structures reveal that ŠTYS (1965) was right in erecting a superfamily for the Idiostolidae. ŠTYS erected his Coreoidea *sensu lato*, because he thought that the higher evolved families arose from different subfamilial origins of the lygaeid stock. The three authors mentioned exclude, by implication, the Aradoidea from their discussions; ŠTYS (1964b) omits it in his list of all the other trichophorous (more or less synonymous with Pentatomomorphous) families (from egg system, Aradoidea certainly belongs in here). All these discussions use diverse characters, including

cytology. The problem arising here will be considered later, augmented by our own data.

For the eggs, the three authors had to rely upon the facts gathered by SOUTHWOOD (1956). We have reasoned that the hexagonal eclosion break of the Piesmatidae forms the original state (p. 275) which is shared by some Lygaeidae and the Stenocephalidae. The latter family has progressed further in that the deviation of the internal micropylar canals shifted half way from the original circular to the centripetal arrangement. This directional shift is only seen in pentatomoid eggs (Urostylidae on the one hand and Acanthosomatidae, Scutelleridae on the other hand as the extremes, with Cydnidae in the transitional stage). The higher pentatomoid families lack an internal micropylar canal as do the typical coreoid families. It is therefore possible that these latter families passed through the same paths in their early history. The micropylar structure and hexagonal eclosion in Stenocephalidae is essentially lygaeoid-like and strongly suggests it is a very early offshoot of this stock. SCUDDER (1963) and SCHAEFER (1964) included the family in the Coreoidea *sensu stricto*. The Hyocephalidae (only one species known) is very close to the Stenocephalidae as has been shown by ŠTYS (1964a) from the accurate counting of the female structures. It is hoped that eggs and males may become available to define this rare taxon further*. Since the remarkable chorionic structure of the four species of Malcidae studied seems typical for this small family, it is suggested to be remote. The few micropyles, their internal canals and their circular course are generalized conditions. The fixed cruciform or ⅄-shaped eclosion rent is distinctly cladogenetic, though derivable from the hexagonal eclosion (p. 275). Our re-evaluation of lygaeid eggs with emphasis on the aero-micropylar complex, eclosion sutures and symbionts (see p. 90–93) brought to light some new aspects. Extension of such studies over a larger series of species certainly would help to clarify subfamilial relations. STICHEL (1957) classed the Orsillinae *Nysius* and *Orsillus* in the Lygaeinae, but *Kleidocerys* in the Ischnorrhynchinae. This is clearly wrong because all orsilline genera studied by us have egg symbionts anterior initially and there is a distinct tendency for proliferation of the air sponge round the micropyles. The colobathristid egg proved to be coreoid *(sensu stricto)*, apart from its somewhat abnormal shape (pseudoperculum crossed by ring of many micropyles without internal canal). SCUDDER (1963) and SCHAEFER (1963) grouped the family in the Lygaeoidea and also ŠTYS (1965) considered it an ancient taxon. The eggs of the Pseudophloeinae, considered thus far as a subfamily (a primitive one, SCHAEFER, 1964) of the Coreidae, in all respects resemble those of the Alydidae. Recently, KUMAR (1965) concluded from genital structures that the Pseudophloeinae

* More species of the Hyocephalidae have been gathered recently by Mr. J. A. GRANT who is engaged in a revision of the group. He kindly informed us about the ovarian eggs of several species. There are 2–3 or 4–5 micropyles according to species and these have a short internal canal pointing towards the polar axis. There is a thin polygonal lining between the ring of micropyles. The hyocephalid egg thus resembles the stenocephalid egg but is slightly more evolved as revealed by the turning of the internal micropylar canals.

should be transferred to the Alydidae, which are generally accorded family rank but ŠTYS (1965) casually relegated it again to a subfamily without giving reason. It is true that the just gradual dissimilarities between this taxon and the typical Coreidae could be considered as a simple ancestor-descendant relation. In Alydidae and Pseudophloeinae, the eclosion rent is a transverse slit, in *Leptocorisa* becoming almost circular (parallel anagenesis in Aradidae). Yet, there remains a gap between this and the pseudopercular differentiation in true Coreidae. Some pseudophloeinous genera seem more evolved by having more micropyles than the Alydidae studied so far. On the contrary, the pseudophloeine genus *Ceraleptus* shows a firm retention of the transverse slit eclosion; the slit extends along the whole fore side of the egg and is related to the peculiar batch formation (fig. 86'). This is distinct from the general coreid trend of egg evolution. The *Hydara* egg (Coreidae, tribe Hydarini, "quite generalized" according to SCHAEFER, 1964), however, has the alydid-type of eclosion. If this taxon is indeed coreid, the inclusion of the Alydidae in the Coreidae can be no longer objected to from the eggs. Whereas all eggs of the coreoid members studied can be placed on one anagenetical line, the egg of *Catorhintha* cannot (p. 100). Egg characters, particularly of the Coreoidea *(sensu lato)* show trends which are traceable step by step and whose direction of phylogeny is unequivocally known. The study of ovarian eggs from dried specimens should be added to the routine methods of museum entomologists and will prove valuable for study of phylogeny.

Cimicomorpha, Reduviidae et familiae incertae sedis

LESTON *et al.* (1954) classed within the Cimicomorpha the: "Reduvioidea, Tingidae, Cimicoidea and Joppeicidae". "Dipsocoroidea are probably allied to the Cimicomorpha". DRAKE and SLATER (1957) added to these the Thaumastocoridae.

The most salient conclusion from our study is that in embryology (position of blastopore, superficial germ band, loss of embryonic rotation) the Reduviidae widely diverge from the cimicoid families ('cimicoid' is used here, for convenience only, in the broadest sense comprising Nabidae, Velocipedidae, Microphysidae, Anthocoridae, Cimicidae, Tingidae, Vianaididae, Miridae). Significantly this divergence is already apparent in the most archaic reduviidans and the dissimilarity is about as great as between typical Cimicomorpha and Pentatomomorpha.

There is thus strong evidence that the Reduvioidea should be removed from the Cimicomorpha. But the system of isolated micropyles and aeropyles, their arrangement around a distinct operculum and the pressure method of eclosion still links the groups together. The circular arrangement of the aero-micropylar system, just outside the opercular rim, is eventually reached also in one group of the Pentatomomorpha. As discussed earlier (p. 289), the well developed cap with a sealing bar deserves the name operculum whether or not the micropyles are arranged concentric with it. The evolution of such an operculum is associated with evolution of eclosion by fluid pressure all over the margin of the lid. The less differentiated pseudoperculum of the higher Pentatomomorpha evolved with a sclerotic lifter acting on a limited area of the

suture. The remaining similarities between the cimicoid groups and the Reduviidae would thus be confined to two characteristics: aeropyles in no direct relation to the micropyles, eclosion by fluid pressure. These two points of similarity need not indicate a close relation. The amphibicorisous stock already shows divergences from which the conditions in land bugs have evolved. Only four combinations of these characters are possible of which three have been realized in opercular eggs of land bugs: aeropyles distinct from micropyles, pressure eclosion; combined aero-micropyles, pressure eclosion; combined aero-micropyles, puncture-lifting eclosion. The modal number and the derived condition of the micropyles contrast Cimicoidea *sensu lato* from Reduviidae: two micropyles in the cimicoid groups, often reduced to none, if insemination is traumatic; three micropyles, progressively augmented to more than 15 in Reduviidae. There are still some other discrepancies between both groups. A thickened subopercular ring of the serosal cuticle functioning as a wedge in the opercular recess, has developed only in the Reduviidae. The secondary respiratory apparatus, if present, is situated in the centre of the reduviid operculum, but evolved in the fore and aft edge of the mirid operculum.

In addition to the convincing data from embryogeny, evidence from other organ systems, to be presented later, justify our concept of Cimicomorpha with only the cimicoid families. The eggs of this group: Cimicomorpha *sensu stricto* appear in various critical respects more variable than is defined by SOUTHWOOD (1956, p. 198). The operculum is absent in *Embiophila* (Plokiophilidae). It is only weakly developed and displaced away from the micropylar system in the Bryocorinae *Monalocoris* and *Bryocoris*. Mirid eggs seem to have evolved explosively in morphological types but exploratory studies of more species may throw new light on subfamilial limits and interrelations. The *Helopeltis* and *Sahlbergella* group most probably should be removed from the Bryocorinae, their eggs resembling more those of the Dicyphinae. The genera *Hyaliodes* and *Termatophylidea* may be classified in incorrect subfamilies.

Lateral invagination characterizes embryogeny of many Miridae, the single tingid species examined, and in some Microphysidae and Nabidae. A frontal vesicle of the embryonic cuticle, demonstrated in a few Nabidae, may be characteristic for this family and perhaps for Tingidae. Such features may be important in superfamily grouping and more species must be investigated in future.

Velocepid and *Arachnocoris* eggs are nabid-like, which confirms the position currently alloted to these taxa. Since micropyles are lacking, fertilization may occur in the vitellarium as in some cimicoid groups only and never in Reduvioidea (CARAYON, 1961). Surprisingly exactly the same condition (nabiform, no micropyles) occurred in *Pachynomus*. Pachynomidae were placed close to Nabidae, until CARAYON (1950b) proposed that it be relegated to a subfamily of Reduviidae. He reinstated this taxon as a valid family, side by side with the Reduviidae in 1954. This latter opinion is shared also by DAVIS (1957). However, egg characters are strikingly cimicoid, but from adult anatomy, Pachynomidae can neither be placed in Cimicomorpha *sensu stricto* or in the Reduvioidea, unless the definitions of these taxa be drastically revised. It is absolutely wrong to incorporate *Pachynomus* in the Reduviidae as done by

DISPONS and STICHEL (1959) and WAGNER (1963).

The new information on chorionic structures of the Thaumastocoridae excludes this family from the Cimicomorpha as now defined. This despite the fact that SLATER and DRAKE (1958) placed it close to the Anthocoridae and KUMAR (1964b), on very inadequate grounds, close to the Cimicidae. ŠTYS (1962) preferred a reduvioid relationship. The phytophagous Thaumastocoridae almost certainly possess aeromicropyles as Pentatomomorpha, but other characters (probably pressure eclosion) are definitely quite remote from this group.

In recognizing the Pentatomomorpha, the Cimicomorpha and the Reduvioidea as major taxa of somewhat comparable contents, the Dipsocoroidea falls beyond the limits of any in many respects. The same applies for Enicocephalidae of which only the significantly aberrant chorionic structures are known. Dipsocoroidea and Enicocephalidae have been combined into one new group: the Dipsocorimorpha by MIYAMOTO (1961). Combining the two is incorrect although these taxa certainly deserve a more isolated status than has been practised up to now (*e.g.* STICHEL (1956) classed the Dipsocoridae within the Cimicomorpha). Data on the eggs of Joppeicidae are still lacking. CHINA (1955b) treated the morphology of *Joppeicus paradoxus* in detail, the only representative of the family known at present. He concluded of its taxonomy: "It is a relict genus representing an ancestral form of the Reduviidae living at a time when the latter family was diverging from the ancestral Cimicoidea, as represented by the generalized Nabidae". The type of fertilization relates *Joppeicus* more to cimicoid groups (CARAYON, 1954, 1961).

A full re-appraisal of all these odd groups is urgently required.

Hydrocorisae

It is now generally believed that Ochteridae and Gelastocoridae belong in this series. Chorionic structures support this conclusion. The transfer of the Corixidae to a special group, the Sandaliorrhyncha (BÖRNER, 1904), was adopted among others by REUTER (1912). POISSON (1957) recognized Corixidae as equivalent to the Hydrocorisae and the Amphibicorisae. In spite of the various aberrant features mostly of the alimentary system, the Corixidae is rightly retained in the Hydrocorisae on other characters (CHINA, 1955a; PENDERGRAST, 1957). SCUDDER (1959) again advocated separating Corixidae from other Heteroptera from the structure of the female genitalia but KUMAR (1961) criticized his findings. Of this diverse family, SCUDDER studied only two Corixinae. MIYAMOTO (1961) followed the concept of BÖRNER because of the aberrant salivary glands.

The pattern of embryogeny definitely brings Corixidae (representatives of four subfamilies were studied) within the Hydrocorisae. This latter major group as treated here comprises the families given in our observational sections.

The arrangement of the families in superfamilies and their relationships remains a vexing problem. Many combinations of families have been made illustrating the lack of a clear understanding of the phyletic relations and the frequency of convergences.

For example, POISSON (1951) following older workers, used the following groups: Corixoidea (Corixidae), Notonectoidea (Notonectidae), Pleoidea (Pleidae, Helotrephidae), Nepoidea (Nepidae, Belostomatidae, Naucoridae), Telmatobioidea (= Telmatobia ESAKI and CHINA, 1927) (Gelastocoridae, Ochteridae, Saldidae!). A general lumping is followed by STICHEL (1955) and WAGNER (1961) in including in Notonectoidea all families except Corixidae and Ochteridae; Gelastocoridae are not dealt with. PENDERGRAST (1957) suggested from the reproductive organs the following division: Notonectoidea (Notonectidae, Pleidae, Helotrephidae, Gelastocoridae), Nepoidea (Nepidae, Belostomatidae), Naucoridae and their allies (Naucoridae, Aphelocheiridae, Corixidae, Ochteridae). SCUDDER (1959) using the female genitalia came to a slightly different arrangement: Corixoidea (Corixidae), Notonectoidea (Notonectidae, Pleidae), Nepoidea (Nepidae, Belostomatidae), Naucoroidea, (Naucoridae, Aphelocheiridae), Ochteroidea (Ochteridae). The Helotrephidae and Gelastocoridae could not be placed appropriately in any of these groups. When the Helotrephidae are included in the Notonectoidea, SCUDDER's division conforms with the grouping of CHINA's diagram (1955a, fig. 1) and with our data on the eggs.

The embryogenic pattern has common features for all Hydrocorisae and isolates the group from all other Heteroptera studied so far. The ventral side of the germ band is near the surface of the egg; there is always spiral revolution; eclosion is effected by a serosal cuticular bladder. Additional early and late rotations of the germ band and prolarva, respectively, occur in *Ilyocoris*, *Plea* and most species of *Notonecta*. *Ochterus* is the most primitive among the species studied (the gelastocorid embryology is still unknown) and this supports CHINA's view (1955a) that Hydrocorisae arose from an ochterid-like archetype, However, the grade of embryonic primitiveness in *Ochterus* (slightly more immersed germ band) needs only a slight evolutionary advance to achieve the condition of other aquatic families. Other families, in particular Naucoridae, may show even more generalized conditions in their lower members, when more data are available on their embryogeny. Chorionic structures (micropyles, eclosion split) vary widely in anagenetic refinement in the naucorid species studied (contrast *Coleopterocoris* with *Ilyocoris*). Some Ochteridae have the primitive number of micropyles, one, but this also occurs in some Naucoridae, Gelastocoridae, Corixidae and in all Notonectoidea. The *Ochterus* egg is more advanced in possessing a pseudoperculum. The main reason why CHINA considered the Ochteridae the most generalized aquatic bugs (the ochterid line in his diagram originates and remains at the lowest level) is the littoral habitat and the sequence from siphon and air-bubble respiration into plastron respiration in the remaining Hydrocorisae. Such a pattern, however, reflects only the adaptive transition from land to water. The phylogeny of respiration need not parallel the diversity of the whole organism with which CHINA was concerned. For example, his Aphelocheirinae, more properly to be considered as a family, is illustrated as the most evolved group. It should however be placed low in phylogeny, despite some specialized features. CHINA has presented little morphological evidence for his concept of the Proto-Ochteridae, unless it be his opinion, (1955b), that the *Ochterus* male genitalia are very primitive. Our Part II will take just the opposite view.

Summarizing the data on hydrocorisous shell structures the following are some major taxonomic problems. Because of the multiplicity of parallelisms in all aquatic groups, here more than elsewhere definite conclusions should only be drawn later after incorporation of the data from other structures. Nepidae and Belostomatidae have in common a very thin inner sheet of the highly vacuolar shell, a similar type and position of micropyles (always more than one), annular dehiscence and similar position of the hydropyle). This combination distinguish the Nepoidea from other Hydrocorisae and the distinction is more than between other superfamilies. Each family has its own distinctions (different type of aeropyle, respiratory horns in Nepidae, a supposed additional hydropyle in Belostomatidae). The embryogenic pattern of the superfamily shows advanced features (visibility of the embryo's limits even at the blastoderm stage) over other hydrocorisous families (fig. 276). This fact, besides other evolved egg structures (micropyles, eclosion rent), seems crucial and contradicts the conclusion of CHINA (1955a) and others who place recent Nepoidea at a low evolutionary level.

The second group to be distinguished is the Corixoidea. The unspecialized parts of the shell of this group are, apart from the greater porosity of the outer layer, similar to the Nepoidea with a thin inner sheet bordering a thick or thin *(Micronecta)* spongy layer but *Diaprepocoris* seems to lack such a porous inner layer. The micropylar system is perhaps associated with a serosal hydropyle and is typical but shows a wide range of progression from a generalized to an evolved condition within the superfamily. With differences in oviposition site and egg shape (stalks acquired several times independently within the group) and eclosion fractures, ramifications appear which suggest familial rank for some taxa considered until now as subfamilies (Micronectinae, Diaprepocorinae).

All members studied of other families (Ochteridae, Gelastocoridae, Naucoroidea and the notonectoid families) share a thick inner layer of the chorion. The notonectoid branch is characterized by stasigenesis of the single micropyle. The embryology has been studied only of some Notonectidae and one species of Pleidae. With chorionic structures, a rather uniform pattern unites the two families which have a strong tendency for embedding the eggs. A greater contrast apparently exists between the groups Notonectidae and Pleidae, and the Helotrephidae (the development of the pseudoperculum is different in the contrasted groups). Knowledge is needed of helotrephid embryogeny.

The eggs of Ochteridae and Gelastocoridae can be placed provisionally in one group until embryonic data is available for the latter family (similar chorion stratification, almost equal number and structure of micropyles (1–3), simple shell eclosion). Much more work is needed in the eight subfamilies of the Naucoridae. The eggs of the few species examined are so diverse in some principal characters (micropyles, eclosion split) that some of the subfamilies probably deserve familial rank. This surmise is based too on new evidence from structures other than the egg and of the greatest interest in this respect is the South American taxon Potamocorinae.

4.2 The relation between the major subdivisions of Heteroptera

Reflections on this subject can only yet be preliminary. In his classic anatomical work of 1833, DUFOUR divided Heteroptera into three families: Geocorises, Amphibicorises and Hydrocorises. These groups, elevated to series, are still in general use, however with varying familial constitution. Historical accounts of the various classifications are given by KIRITSHENKO (1951, presentation of earlier published phylogenic schemes), LESTON, PENDERGRAST and SOUTHWOOD (1954) and SCUDDER (1959).

The concise paper of LESTON *et al.* introduced the '-morpha' era also in heteropterology but with confusing results. It is unfortunate that LESTON *et al.* proposed Cimicomorpha and Pentatomomorpha so prematurely and without reconsidering the relation of these groups to the surface and the water bugs. Authors of textbooks and faunistic works are thus faced with a bewildering array of 'higher classification' and proper selection is extremely difficult. Confusion and error is bound to occur.

STICHEL (1955) extended the procedure of LESTON *et al.* over all Heteroptera and created the following new divisions: Hydrocoriomorpha; Amphibicoriomorpha, Henicocephalomorpha of equal rank to the Cimicomorpha and the Pentatomomorpha*. Whether or not these divisions are equal in value (this will be discussed later), this procedure was unfortunate for two reasons. First, families whose position had been uncertain for LESTON *et al.* were placed in one definite division without new supporting evidence (*e.g.* Dipsocoridae, Saldidae). Second, as SCUDDER (1955) has already pointed out, the new -morpha divisions of STICHEL should be formed on the names *Nepa* and *Gerris* in place of Hydrocorisae and Amphibicorisae, respectively. The same inconsistency ensued with MIYAMOTO (1961) when erecting the Dipsocorimorpha to contain both Dipsocoridae and Enicocephalidae. Entirely unsuitable and against current practice of nomenclaturists is the major classification of WAGNER (1961, 1966). He reduced the Geocorisae and Amphibicorisae to superfamilies and attached to these taxa the authors LESTON, PENDERGRAST and SOUTHWOOD, instead of DUFOUR.

Since a proposal for a modified major classification of the Heteroptera will be settled at the end of this series, our findings are interpreted here without nomenclatural implications. The study of egg system splits the Suborder up into the following more or less equivalent groups: Amphibicorisae, Leptopodoidea, Cimicomorpha (*sensu stricto:* only the cimicoid-like families), Dipsocoroidea, Enicocephalidae, Joppeicidae?, Reduviidae, Thaumastocoridae, Pentatomomorpha (with the Idiostolidae very remote) and Hydrocorisae. Perhaps it will be necessary later to give all these categories -morpha endings for consistency. All these groups, except the first and the last one, are currently assigned to the Geocorisae. The diversity demonstrated in this study renders it inappropriate to retain Geocorisae as a group equivalent to Amphibi-

* wrongly spelled as Pentatomorpha by STICHEL, many other workers and even in the original paper of LESTON *et al.*

corisae and Hydrocorisae. As a working hypothesis, these terrestrial groups can best be conceived as originated independently; for each group an archetype could be constructed based on modern features and species. Thus the terrestrial Heteroptera must have a strongly polyphyletic origin and the name Geocorisae as a taxonomic unit should be abandoned. To the eight or nine isolated branches of the terrestrial groups (inclusive of the Leptopodoidea), the Hydrocorisae must be added as an equivalent group close to or even with Reduvioidea.

A phylogenic scheme should give a picture of radiating lines each arising from the surface of the black sector in fig.316, p.459. The lines represent the elements of the defunct Geocorisae and one line refers to the Hydrocorisae. The body of the black sector (A) represents the heteropterous stock from which the lines diverged. Evidence here suggests that this stock was of Amphibicorisae-like bugs and more reasons for this concept will be presented in Parts II and III of this series. The typical amphibicorisous egg has the primitive type of embryogeny, a simple micropylar and eclosive system and a simple chorionic structure. Yet the group is diverse and this diversity is best visualized in the diagram as the irregularity of the upper margin of the ancestral stock (stippled area). The crenations round the ellipse refer to aberrant Amphibicorisae with some striking trends ultimately expressed in terrestrial Heteroptera.

For example: *Mesovelia* has method of eclosion in common with Nabidae (embryonic cuticular bladder, chorionic lid) and, though carnivorous, it has symbionts. *Macrovelia* and relatives show initial trends towards multiplication and centrifugal displacement of the micropyles and of loosening of chorion structure to trap air, trends perfected in most terrestrial branches. Hydrometridae have developed through an extensive circumferential plastron, the basic plan of the aero-micropylar cup characteristic of Pentatomomorpha (except Idiostolidae). These atypical Amphibicorisae form only small families or subgroups, whereas the main stem of Amphibicorisae consists of the large families Gerridae and Veliidae. It is true that the evolved structures of the aberrant Amphibicorisae would be correlated with changing conditions during the evolutionary transition from life on the water surface or at the water's edge towards terrestrial habitats and habits. This might cause convergence with truly terrestrial Heteroptera. This is only partly so. Quite other structural changes of adult Heteroptera, dealt with later, clearly separate the Amphibicorisae from the 'Geocorisae'. Some aberrant Amphibicorisae partly bridge this gap too. This, of course, does not imply that modern atypical Amphibicorisae are direct ancestors of land bugs. The origin must be traced further back and the recent aberrant and relict forms help to show how the evolutionary changes could have taken place.

Though the author has a particular group in mind for each radiating branch in fig. 316, they are not labelled. This illustrates the temporary nature of such a scheme and prevents the thoughts expressed here from being settled in literature as a definite classification. The unequal distance between the rays figured could suggest a dichotomy in the upper half of the diagram. This is, however, without evolutionary meaning. The median gap is created to show the more generalized main line of ascent in the Amphibicorisae (stippled). The problem of the clustering of the origins of the lines

is shifted to the black area (A) and remains obscure. The arrangement projected also reflects the consequent evolution of ecological adaptation: Originally, water-loving bugs, probably littoral, the main line of modern Amphibicorisae (Gerridae, typical Veliidae) becoming well adapted for life in the water film. Atypical Amphibicorisae show a strong tendency towards land habitats *(Heterocleptes, Ocellovelia, Hebrovelia, Macrovelia* (CHINA, 1955a); *Chepuvelia, Oravelia,* some *Mesoveliidae* (PENDERGRAST, 1959), *Paraphrynovelia* (POISSON, 1957), *Madeovelia* (POISSON, 1959*)). This shift is paralleled in the Saldidae (contrast the opinion of BROWN, 1948), whereas the other rays in the diagram refer mainly to the explosion of terrestrial groups and only one branch reverting to submerged aquatic life.

The concept of all Heteroptera deriving from Amphibicorisae-like ancestors is new. There has been little speculation about the relationships of the major divisions. SCUDDER (1959) suggested including the Amphibicorisae and Hydrocorisae (excluding Corixoidea) within the Cimicomorpha. Thus, according to SCUDDER, the Heteroptera should be made up by three main groups: Pentatomomorpha, Cimicomorpha and, with some hesitation, the Corixoidea. His information was based predominantly on a study of the female genitalia upon which several comments must be made in Part II of this series. CHINA (1955b) criticized the "rather hasty and very much over-simplified" classification of the Geocorisae by LESTON, PENDERGRAST and SOUTHWOOD (1954): "..., the wholesale lumping of the numerous families of Geocorisae into two main groups, the Cimicomorpha and the Pentatomomorpha on a fragmentary study of their characters is in my opinion doubtfully correct". We concluded that this lumping indeed was wrong. However, CHINA expressed in his new phylogenic tree (his fig. 5) exactly the same idea as LESTON *et al.*, a bifurcation. The only exceptions refer to the regularly contested groups such as Leptopodoidea and Dipsocoroidea. CHINA wrongly placed Leptopodoidea at the base of Amphibicorisae but correctly isolated the branch Dipsocoroidea from its origin. CHINA (1955a) speculated on the evolution of water bugs. He concluded, as did CARAYON (1962), that Amphibicorisae derived from a saldid-like ancestor. But we have pointed out (COBBEN, 1965a) that phallic structures are much more complex in Leptopodoidea than in Amphibicorisae, and, more significantly, that leptopodoid structures are derivable directly from amphibicorisal structures. More evidence compiled here suggests the reverse of CHINA's version.

GUPTA (1963a) considered the systematic position of Saldidae and Mesoveliidae and became indirectly involved in the relations of the major groups. He derived the Heteroptera from a cimicomorphous stock ancestral to modern Cimicomorpha and Hydrocorisae. The first branching from this main stock starts low and represents the Pentatomomorpha; the second branch much higher leads to Amphibicorisae in which he included Ochteridae *(sic)*. GUPTA's paper is based on oversimplified and

* POISSON erected a new family for *Madeovelia guineensis,* of which one male has been captured in Guinea, Africa. Although not particularly stressed by this author, the species seems to have some affinity with the Tropical American *Mesoveloidea.*

limited evidence and on wrong observations and interpretations. Where opportune, comments on these will be given in this volume and later.

4.3 A preview of other investigations

As it may be some time before the remaining Parts are published, major points are indicated here to show some new aspects of phylogeny of interest to Heteropterists. Supply of further information and of critical material would be highly appreciated.

a. The eye of the first larval instar

The basic type consists of only five ommatidia (lenses large, circular, scattered). This condition had been noted in the Tingidae (SOUTHWOOD and SCUDDER, 1956; KOGAN, 1960; LIVINGSTONE, 1962; ŠTUSÁK, 1962). The important fact that in this original state, two trichobothria are inserted on the surface between ommatidia, eluded earlier workers. The combination of the two characteristics: five ommatidia and two trichobothria (abbreviated hereafter as 5 + 2 tr) occurs in the Anthocoridae, Cimicidae, Tingidae and Dipsocoridae. Whereas the five-faceted condition seems to be the original modal number, some bugs living in unusually sheltered conditions have a lower number (*Aneurus*, only two and loss of trichobothria; contrast *Aradus cinnamomeus*, 19 + 2 tr; *Xylastodoris luteolus*, Thaumastocoridae, 3 + 2 tr). The number of ommatidia in other larvae living under similar conditions, is not markedly affected, although the eye elements are only weakly defined and pigmented, *e.g.* in the terricolous *Sehirus biguttatus* (9 + 1 tr), in *Pyrrhocoris* and *Dysdercus* (about 22 + 1 tr). The general trend in heteropterous egg larvae is a multiplication of the facets and in some instances stasigenesis of the two trichobothria, in other instances loss of them in the anagenetically higher taxa. Progressive increase in ommatidial number is shown in the Amphibicorisae by the following series: *Hebrus* (10), *Microvelia* (28), *Hydrometra* (38), *Mesovelia* (55), *Hebrovelia* (about 70), *Gerris* (about 130). In Lygaeidae, the number ranges from 15 *(Plinthisus)* to innumerable *(Geocoris)*; in Pentatomoidea from 28 *(Podops)*, 40–70 (most Pentatomidae) to 90 *(Eurygaster)*; in Rhopalidae, Alydidae and Coreidae the number is very high. *Leptopus* has 37 ommatidia but in Saldidae (except *Aepophilus)*, *Nabis* and most Hydrocorisae, they are innumerable, whereas Miridae have a countable number (15–40). Results from studies on general biology and sensory behaviour must be considered with these data. A preliminary judgement suggests that the eye characters are of taxonomic significance, particularly in association with the fate of sensory hairs. The two ocular trichobothria are present, whether the eye has many lenses or not, in the Lygaeidae (except some Lygaeinae), Amphibicorisae (except *Hydrometra*), Leptopodoidea, Thaumastocoridae, Anthocoridae, Cimicidae, Tingidae, Nabidae, most Miridae, probably most Dipsocoroidea. They are reduced, displaced or partly lost in Pyrrhocoridae, Pentatomoid groups, Aradidae, and completely absent in the Coreoid families. Whereas the disappearance

of the trichobothria generally indicates an anagenetic trend, complete loss in *Hydrometra* shows a separate line of evolution. The discrepancies in the embryogeny have shown that Reduviidae should be removed from Cimicomorpha. The reduviid eye pattern is also distinct. The first instar of the three species of Emesinae studied have six ommatidia, *Reduvius* eight, *Triatoma* about 30 and the eye of the Harpactorinae has a multitude of facets (this trend of ommatidial multiplication runs parallel with the progression in embryogeny). But in all these Reduviidae and in the many-lensed eyes of the Hydrocorisae there is no trace of trichobothria. There is probably at least one exception in Hydrocorisae, in the Potamocorinae. The *Coleopterocoris* adult has a 40-lensed eye on which two distinct sense-hairs are inserted. The ontogeny of trichobothria in other bugs has shown that, if these setae are present in the adult, they are present in the first instar too. This fact demonstrates with other characters the peculiar position of *Coleopterocoris*.

Surveying this data, one is struck by the fact that multiplication of ommatidial facets in general coincides with anagenesis as shown from study of the egg system. The anagenetically lower taxa of each major group have fewer lenses than higher taxa. The behavioral outcome seems to be governed by the same evolutionary trends. Preliminary studies in Homoptera Auchenorrhyncha revealed analogous trends in the development of the larval eye. In other groups of insects, the evolutionary significance of the eye character has been recognized. The many-lensed stage in larvae of Aphididae is considered advanced over the primitive three-lensed eye (HILLE RIS LAMBERS, Higher categories of the Aphididae, Seminar on the current status of research on Aphids, Berkeley, Calif., March, 1964); this opinion is diametrically opposite to that of BÖRNER (1930). The eye of the first instar larva of the generalized species of Odonata has consistently 7 ommatidia (ANDO, 1962).

b. Trichobothria

TULLGREN (1918) has shown the great taxonomic value of the abdominal trichobothria in those families which he grouped as the 'Heteroptera trichophora'. His findings have been recognized in publications since 1950 and LESTON *et al.* (1954) used the general presence or absence of these sensory hairs, with other characters, to establish a dichotomy of terrestrial bugs. Cimicomorphous families *(sensu* LESTON *et al.)* should not have abdominal trichobothria. However, Dr ŠTYS told us in 1964 that he has indeed seen them in Pachynomidae. With the major groupings of Heteroptera in a vertical system with Amphibicorisae at the base, it is of interest to trace whether trichobothria occur in Amphibicorisae. TULLGREN stated their absence in amphibicorisous families. However many Amphibicorisae in fact do have trichobothria, though of a special kind and arrangement. They will be fully analysed later. CHINA (1950a) directed attention to the cephalic trichobothria of Amphibicorisae. The similar condition in Saldidae (not eight to ten pairs as is stated by GUPTA, 1963b) was one of his arguments to affiliate the two groups. Yet many other groups have members with cephalic sensory hairs, probably homologous, and thus derivable from the

amphibicorisous condition. Since the trichobothrial pattern is often reduced during ontogeny, it can be studied more effectively in the young larval instars.

c. Pretarsal structures

DASHMAN (1953b) described the unguitractor plate of 39 species from 20 families of Heteroptera. His study does not pretend to test the structures for their taxonomic value but he presented the characters as an implement for identification. His figures are too schematic. Also, the unguitractor plate, although complex on its own, is so intimately associated with other, often more important, pretarsal structures that the entire pretarsus should be scrutinized. Where DASHMAN is dealing with some of these other structures, his terminology is not in accordance with his own glossary of purified terms presented in the same year (1953a). Our findings revealed a perplexing plasticity in pretarsal organization, a variation which would not have been expected from the numerous data available from literature. The problem of naming the various structures has not been finally solved.

Without drawings, which will be presented later, a preliminary naming of the most influential outgrowths is made here. To the appendages currently called the 'pseudoarolia' (*e.g.* most Pentatomomorpha, Miridae *in part*) in the literature on Heteroptera, we will refer to as the pulvilli because they are primarily attached to the ungues. The 'arolia' (some mirid subfamilies) are extensions of the unguitractor plate and should be termed the parempodia. The arolium proper is reserved for the structure originating dorsal to the unguitractor and between but isolated from the bases of the ungues. Most Amphibicorisae have two arolia, flattened and inserted in a vertical plane, one curved upwards, the other downwards. This remarkable structure is possibly an adaptation enabling the bugs to deform the meniscus to be drawn up the slope at the margin of a water mass. The arolic bristles were recognized as such by REUTER (1910, stated only in *Hebrus*, absent in other Amphibicorisae), EKBLOM (1930, *Mesovelia*) and MCKINSTRY (1942, members of all families of water striders). GUPTA (1963, *Mesovelia*) interpreted them incorrectly as pseudoarolia, whereas other workers confused them with claws (COOKER, MILLSAPS and RICE, 1936; DRAKE and CAPRILES, 1952; DRAKE and ROZE, 1955; POISSON, 1957). The most complex pretarsus is in the deeply cleft median tarsus of the Rhagoveliinae. Besides the two arolia, there is the well known fan of feathery hairs. The stem of this latter structure arises laterally from the parempodia, one of which is strongly reduced. Since the fan originates from the unguitractor it is considered as a secondary parempodium. Some atypical Amphibicorisae show modifications of the arolic pattern. The dorsal arolium is reduced to half the size in *Macrovelia* and is entirely absent in a moss-inhabiting *Mesovelia*-like species from New Zealand and in *Chepuvelia*. This condition links up with that found in the larvae of *Aepophilus* in which one parempodium is also strongly reduced. In the adult of *Aepophilus* and in all stages of other Saldidae, no spur of the single arolium remains. Saldidae other than *Aepophilus* show a further ontogenic reduction of the parempodia.

Of great interest is the pretarsal organization in the anomalous amphibicorisan

Heterocleptes. Here, both arolia have disappeared and the parempodia grow out as a weak pad, widening distally, thus paralleling some Miridae. Like other modifications in aberrant Amphibicorisae, the pretarsal changes suggest more than simple modifications to terrestrial habitat. Hebridae, living on wet soil and not on the open water-film, have exactly the same pretarsal elements as true water-dwellers.

None of the other heteropterous major groups have revealed arolia, exept for one median arolium in some Dipsocoroidea (often only in male) and in a few Hydrocorisae. It is challenging that it are just those hydrocorisans in which egg structures and other important aspects are more generalized: *Aphelocheirus*, Potamocorinae, Helotrephidae. Homology of this single arolium with one of the arolia of Amphibicorisae is thus not excluded. A small arolium occurs also on the fore leg of the first larval instar of *Ochterus* but disappears in later instars.

d. Scent apparatus

Voluminous literature exists on the dorso-abdominal and the metathoracic glands. GUPTA (1961), under the title: "A critical review of the studies on the so-called stink or repugnatorial glands of Heteroptera with further comments", omits many important references such as GULDE, 1902; HENRICI, 1938; KULLENBERG, 1946). The purported critical sifting of the data leaves much to be desired.

The larval dorso-abdominal glands, often still present in the adult (function during flight?), occur in various metameric combinations. They are unpaired or secondarily paired, originally intersegmental and there may be up to four. The theory of the originally unpaired condition of the gland per segment (DUPUIS, 1947; PUCHKOVA and PUCHKOV, 1958; DRAKE and DAVIS, 1960; CARAYON, 1962) corroborates our findings. Although the gland formula has been used successfully for relationships within families, the main lines of evolution of the complex apparatus through the Suborder is far from clear. The Amphibicorisae possess only the first gland in a rudimentary state and the ostiole has shifted posteriad to assume a position on the fourth tergite. It is present in this condition in *Hebrus*, *Mesovelia*, *Macrovelia*, *Oravelia*, *Chepuvelia* and in *Hermatobates* (the last considered as gerrid by CHINA, 1957 but not by MATSUDA, 1960); in others it is completely lost. The same gland, the only one present, is liable to both ontogenic and phylogenic reduction in the Leptopodoidea. It is well developed in *Aepophilus* (contrast REUTER, 1910) and in most Chiloxanthinae, but the reduction in other members of the superfamily is not complete. With the exception of the Corixidae which have three glands, some families of the Hydrocorisae (Naucoridae, Pleidae, Helotrephidae) have only the first gland (paired in *Aphelocheirus*, *Ilyocoris;* unpaired but strongly bilobed and with two ostioles in *Coleopterocoris*). No gland is present in other Hydrocorisae; the disadvantage of the loss is apparently compensated in Ochteridae and Gelastocoridae by the larva camouflaging its dorsum with debris.

It is still premature to do more than speculate on the general evolution of the abdominal glandular system. The most obvious explanation would be that at least four glands were originally present. However, to accord the data with our belief that

Amphibicorisae are the most generalized bugs, another hypothesis should be considered. Perhaps only the first gland originated in the amphibicorisal archetype, later to persist or be lost secondarily. The usual condition of four glands in the Dipsocoroidea makes this hypothesis less likely but the possibility should still be considered. With the explosion of the terrestrial groups other glands evolved as necessary adaptations to the new environment.

Among Amphibicorisae, the adult metathoracic gland is absent in *Hydrometra* and in some Gerridae. The ostiole still exists in *Mesovelia* but the scent apparatus proper is very minute. A single reservoir with one median outlet occurs in *Hebrus*, *Oravelia*, *Macrovelia* and in most Veliidae and Gerridae. From the aperture an external groove leads laterad, left and right, into the metacetabular region in several genera of Gerrinae (MATSUDA, 1960) and in most Veliidae.

The most known heteropterous metathoracic gland apparatus is as in *Oncopeltus* (JOHANSSON, 1957). It consists of a transverse, medially slightly constricted, reservoir in which two patches of glandular tissue are incorporated in the wall, the accessory glands. On both sides of the reservoir there is a tubular gland and a secondary reservoir. The whole apparatus opens out through two lateral ostioles. This condition is intermediate between the *Hebrus*-type and the other extreme as in Tingidae and many Reduviidae, in which two symmetric halves, each of one gland, one reservoir and one ostiole, are widely separate. DAVIS in DRAKE and DAVIS (1960) suggested that the paired condition is a specialization after reduction of the median part of the reservoir. CARAYON (1962) agreed and extended the theory assuming that the gland formed primarily as a medio-ventral unpaired invagination of the intersegmental membrane between thorax and abdomen. This assumption concurs also with our findings. But CHINA (1955a) reasoned the opposite in his paper on the evolution of water bugs. He argued that the general trend in Amphibicorisae is reduction and disappearance of the external lateral channels, then fusion of the two glands and their openings into one single structure, and ultimately loss of the entire apparatus. It is certainly true that absence of the scent gland in *Hydrometra* is secondary. Progressive, arresting and regressive evolution of this glandular system in the Amphibicorisae obliterates what would have been a clear anagenesis if the gland had evolved progressively.

The type in Heteroptera closest to the primitive type, has a singular sac wholly or mainly lined with glandular cells (Schizopteridae and some Dipsocoridae, CARAYON, 1962). *Hebrus* perhaps displays a similar state. Preliminary examination of macerated specimens, did not reveal a cuticular lining of efferent ducts which would have demonstrated a gland on both sides of the median reservoir. Such glands, representing the next step in evolution, are in fact present in some Gerridae *(Gerris, Aquarius)* and in typical Veliidae (BRINDLEY, 1930; BRINKHURST, 1960; myself). One accessory gland is recognizable as a small patch in the dorsal wall of the reservoir. Reduction and loss of the scent apparatus seems to have occurred at this stage in Gerridae. Scrutiny is needed to trace exactly how this reduction was achieved. Since it is unlikely that regression is by precise reversal steps of the progressive development of the apparatus, it should be possible to deduce from the anatomy of the organ, the muscular control-

ling mechanism and the external channels whether it is regressing or not. In *Halobates princeps*, the large transversely shaped reservoir is slightly bilobed (accessory dorsal gland undivided) and the four apodemes controlling the single outlet are arranged differently from species with a simple reservoir.

The first step towards the formation of lateral evaporative channels is revealed by the aberrant amphibicorisous *Oravelia*. The single spacious reservoir with a wide accessory ring gland discharges through one median aperture controlled by four apodemes for the dilator muscles. The external orifice is broadly overgrown by integument, so that the secretion has to flow left and right through two short channels. Similar conditions prevail in *Macrovelia*. This arrangement may ultimately evolve into long channels reaching the pleural region of the thorax. We could trace, in the one specimen of *Oravelia* studied, the cuticular lining of only one median gland, inserted ventral to the ostiole. If so, this situation would be very unusual. CHINA reported the primitive stage with two distinct ostioles in *Ocellovelia* and of a single opening in *Heterocleptes*. But we found also paired ostioles and, of more importance even, paired reservoirs in *Heterocleptes* (probably the same species as studied by CHINA). Conforming with our earlier reasonings, this expresses a progressed phase in the evolution of the apparatus, paralleled in terrestrial groups and in some Leptopodoidea.

Saldidae (except *Aepophilus*) have one reservoir and one ostiole (not two as stated by BRINDLEY, 1930, and GUPTA, 1963, despite CARAYON (1950) having already stressed the occurrence of one orifice). The glands do not open near the ostiole, but laterally in the apical half of the reservoir. In *Aepophilus bonnairei* the scent apparatus is entirely double (CARAYON, 1962; myself). The reservoirs are extremely voluminous and the glands have crossed the top of the reservoirs so that their outlets are more median. CARAYON (1962) mentioned an unpaired condition in Leptopodidae but we found that *Leptopus marmoratus*, *Erianotus lanosus* and *Valleriola* sp. have two distinct reservoirs and two orifices. Yet the cave-dwelling *Leotichius speluncarum* has one reservoir with two efferent ducts and ostioles. *Omania* possesses two reservoirs, but only one ostiole. To the various aberrant features of this taxon must be added a sac-like organ flanking each reservoir. These paired organs seem to form part of the scent-apparatus but because of the minuteness of the object (adult insect hardly 1.5 mm long), the observations on a few specimens are not yet conclusive. The paired and thus more evolved condition in Leptopodidae and Aepophilinae, and the unpaired state in other Saldidae conflicts with general morphology as a basis for deciding evolutionary level. In contrast to *Aepophilus* and Leptopodidae, Saldinae and Chiloxanthinae have acquired on the seventh abdominal sternite extra glands (COBBEN, 1961) which might have arrested evolution of the metathoracic apparatus. These protrusible abdominal glands are most likely repugnatory, although perhaps its secretion could push the bug along the water film by lowering surface tension (as in *Stenus*, LINSEMAIER and JANDER, 1963). Theoretically the metathoracic glands could have such a function. The association of both distinct types of glandular systems in Saldidae is reminiscent of similar mutual relationships in Reduviidae and Tingidae. The distinctly paired metathoracic system in

these families tends strongly towards reduction and, in some species, even loss. But both families carry other sets of glands including paired glands in the base of the abdomen. In Reduviidae, they are called the glands of Brindley. CARAYON (1962) considered the similarly placed glands in Tingidae as homologues. According to him, both families should be more closely related than is now recognized. In view of experience with embryology this might be convergence. It is of great interest that we found a gland also in the abdominal base at the lateral edges in the primitive pentatomomorphous Thaumastellidae (not to be confounded with the likewise present strigil!). Reduviidae have acquired a multitude of glands, probably all for defense. There are four different types simultaneously in *Themonocoris* (CARAYON, USINGER and WYGODZINSKY, 1958). *Arilus* has a unique type communicating with the rectal sac (BARTH, 1961). *Platymeris* spits toxic saliva at vertebrate predators (EDWARDS, 1960).

The evolution of the metathoracic scent apparatus of all the phyletic lines of Heteroptera have features in common. Real taxonomic differences are not easy to assess by routine dissections. CARAYON (1962) found gross structure similar in Tingidae and Piesmatidae but histologically quite different.

An admirable attempt to analyse the function of the secretions was by REMOLD (1962). He found five distinct manners, all defensive, in which larvae and adults use the secretion or its volatile substance as poison or repellent against predators or parasites disturbing. These manners bear no relation to systematic groupings (only Pentatomomorpha and some Cimicomorpha were studied). REMOLD dismissed the problem that the secretions might act also as pheromones, and he explained the presence of secondary reservoirs in the males of some Lygaeidae as accumulations of secretion when little is discharged. Accurate behavioral studies on this subject are lacking but some patterns in courtship suggest an intraspecific action of these glands. Indirect proof for pheromonal properties is provided in those species with glands restricted to the male only (some Anthocoridae (CARAYON, 1954), Enicocephalidae (CARAYON, 1948), *Lethocerus indicus* (BUTTENANDT, 1955)). Other functions of heteropterous glands have been suggested, *e.g.* fungicidal action by *Scaptocoris* (ROTH, 1961; TIMONIN, 1961), producing an oil film on the ventral pile to waterproof dwellers on the water surface (BRINKHURST, 1960; provided only weak evidence based on questionable experiments).

e. Reproductive organs and ectodermal structures

MALE Literary and observational evidence will be put forward in Part II that follicle numbers of testis have increased progressively in all main groups of Heteroptera, after these groups had already diverged from one another. A single follicle in each testis is considered as the basic number (also in Miridae, contrast LESTON, 1961). The Amphibicorisae have retained the most primitive genitalia and reproductive organs (low number of testis follicles, absence of ejaculatory bulb and usually of mesadenia, simple organization of phallus). SINGH-PRUTHI (1925) concluded from the male genitalia that Heteroptera may be arranged in only two basic types: a pentatomid

and a reduviid type. To the reduviid type he attached the Amphibicorisae. The subsequent voluminous literature usually assumes this concept.

Our re-appraisal demonstrates at least seven main types. The cladogenesis of these types conform with the phylogenic scheme proposed in fig. 306 on the basis of egg systems. A new theory on the origin and evolution of the basal articulatory apparatus has been given earlier (COBBEN, 1965a). All authors since SINGH-PRUTHI considered the basal apparatus of Amphibicorisae evolved in that the basal plates are fused together medio-ventrally. But we think that the basal plates originated later as sclerite insertions lateral to the membranous U-profile of Amphibicorisae. A definition of the fundamental type of genitalia is given here as the model from which to try and derive all other modern types.

The amphibicorisan-type: Parameres always directly and firmly attached to basal apparatus. Articulatory apparatus very simple, to be considered as the U-shaped frontispiece of the incomplete basal aula. No apodemes for insertion of protactors and retractors. Retractor muscles grouped in a single broad bundle inserted on mid-ventral part of articulatory apparatus. Basal foramen of aula opens very wide anteriorly (not covered by septum) and also more or less dorsally. Duct very thin, membranous, running entirely free through basal apparatus, aula and endosoma. Phallotheca distinct, partly weakly sclerotized. Endosoma divided into conjunctiva and vesica. Two lateral endosomal sclerites usually present as principal armature. No ligamentary process. No hyaline band. No fluid pump and no conducting chamber. Anagenetic trends: Reduction and total loss of parameres in the main gerroid stem. Increasing hardening of phallotheca and complexity of endosomal sclerites. Initial development of phallic pivot by doubling of ventro-posterior wall of capsule. Initial weak tendency for asymmetrical transformation of pygophore.

Anagenetic trends in atypical Amphibicorisae point in another direction. Several features reflect incipient development towards the geocorisan types of genitalia. The ductus seminis severely shortened, flattened and, consequently, became highly distensible in *Mesoveloidea*, *Heterocleptes* and the *Macrovelia* group. This structural modification proceeds further in Leptopodoidea. An important advance is in *Macrovelia*, *Oravelia* and *Chepuvelia*, in which the duct has been attached to a medio-ventral extension of the base of the phallotheca. The dorsal diaphragm in *Ocellovelia* is stretched tight as a roof of the basal aula and fused completely with the lateral walls of the aula to form a firm cylinder. A well developed inflatible endosoma is primitively present in Amphibicorisae but is severely reduced in *Hydrometra*. An unpaired sclerotic peg is inserted at one side of the secondary gonopore in *Mesovelia*, and this structure adds another significant character to those in common between Mesoveliidae and Nabidae. Whereas none of the Amphibicorisae studied have an ejaculatory bulb, a moss-inhabiting *Mesovelia*-like species (New Zealand) seems to have one.

Of groups other than Amphibicorisae, only a few indicative notes on new discoveries and re-appraisals may be made here. The heteropterous phallus is composed of numerous parts many of which have evolved independently or at different rates. The phallic pattern of the Dipsocoridae is partly archetypal (basal apparatus) and partly

highly modified and in no way homologous with that of other Heteroptera. Its ejaculatory bulb is topographically and structurally quite unusual for Heteroptera. Leptopodoidea have an evolved type of genitalia unique among Heteroptera (COBBEN, 1965a). This type is definitely not pentatomomorphous or amphibicorisous. SINGH-PRUTHI (1925) wrongly considered the saldid phallus as of normal pentatomid type resembling in all respects the Aradidae: he did not notice the unique constellation of the complex of endosome, duct and filum gonopori, the ligamentary process and the lateral sclerites. Several authors since SINGH-PRUTHI tried to resolve the structure of the saldid phallus, the most recent ones (KUMAR, 1961; GUPTA, 1963) with distressingly inadequate results. Whereas conjunctival appendages are absent, KUMAR counted 8 pairs of them (utilizing for this assessment haphazardly the heavily sclerotized parts of the organ). GUPTA misinterpreted nearly all internal phallic structures, the purported ejaculatory reservoir being in fact the secondary gonopore. In appraising the structures of Saldidae and Mesoveliidae he stated: "On comparing the structure of the female genitalia, the aedeagus, the presence of ejaculatory reservoir, paratergites, and the seven pairs of abdominal spiracles, the two families are found to be very similar". This conclusion contradicts for the most part GUPTA's own, though wrongly interpreted, observations earlier in the same paper!

The Pentatomomorpha exhibit an almost uniform genital type. Important deviations are found in some taxa which are of phylogenic interest in other respects too. Such deviations suggest primitiveness and warrant the hope that still undiscovered facts may help bridge the gap between Pentatomomorpha and Amphibicorisae. *Hotea curculionides* has a completely open entrance to the basal aula and lacks the hyaline band. This band, discovered by BONHAG and WICK (1953) in *Oncopeltus*, has been overlooked or not recognized by all subsequent workers. It is usually an elaborate structure partly separated from the duct. But sometimes it is very tiny and may surround the sperm duct. Of all the pentatomomorphous families we have studied, it is absent only in Acanthosomatidae and often in Scutelleridae: *Hotea, Odontoscelis, Odontotarsus* and according to LATTIN, personal communication, *Phimodera. Idiostolus* sp. differs from all other Pentatomomorpha studied in the complete absence of the erection fluid pump.

The group Cimicomorpha (*sensu* LESTON *et al.* is more variable and represents several types of genitalia; it includes the hydrocorisous type occurring also among Reduvioidea. *Coleopterocoris* (Naucoridae, Potamocorinae), however, does not conform the reduviid type in several important respects. The 'undifferentiated' (CHINA, 1955b) phallus in some land bugs, in some Hydrocorisae and also in many Homoptera Auchenorrhyncha is, in our view, a secondary modification indicating specialization. As said above, the endosoma was originally a long membranous cylinder when inflated. Despite other drastic modifications, this condition is retained in the Tingidae. DRAKE and DAVIS (1960) stated that the endosoma in this family can be everted only little and surmised that the internal lateral diverticulae are reservoirs for semen. These diverticulae, however, belong to the extremely long swelling body and are cut off from the seminiferous duct. Reduction of the endosoma and concomitant widening of the

sperm duct have evolved in most major groups of Heteroptera. Only at this stage of the phallus is the condition convenient for the passage of possible spermatophores. Evidence obtained from our work renders it feasible that spermatophores or analogous structures have evolved in Heteroptera several times independently and recently. Absence of these structures, at least in this Suborder, must thus be primitive and not secondary (contrast HINTON, 1964; DAVEY, 1965).

FEMALE In the internal structures, primitive members of the Leptopodoidea appear to be more amphibicorisan-like and the evolved taxa more pentatomomorphan-like. The presence of an accessory canal leading from the gynatrial sac to the common oviduct seems to be primitive in most Amphibicorisae. There are more arguments favouring the idea that this condition has anticipated the recent type of internal genitalia of at least Leptopodoidea (accessory canal retained in *Leotichius* and *Omania*) and in Pentatomomorpha (canal retained in *Hotea*, rudiments in others). In Part II, stress will be laid on internal structures of relict species and generalized forms of the geocorisal and hydrocorisal branch to reconstruct the evolution of the diverse gynatrial and associated structures throughout the Suborder.

There is strong suggestion that the number of ovarioles gradually multiplied in the higher levelled taxa of most major groups parallel to the follicles of the testis. SCUDDER (1959) has made an extensive study of the genital structures and their bearing on classification of Heteroptera. The conclusions he drew regarding relationships are indefinite. From the same results, other combinations are certainly just as logical because of the close parallelism in the evolution of the female terminalia and because of his predominantly 'horizontal' analysis of the data and consequent neglect of anagenetic phenomena. It is generally believed that the presence of an ovipositor of the laciniate type is the primitive condition in Heteroptera. We believe, however, that this apparatus provided with gonoplacs is one of the most evolved types (*cf.* DUPUIS, 1955, p. 207). The development of the gonoplacs, which SCUDDER sometimes overlooked, has evolved independently in unrelated groups. Much more detailed work on these subjects must be done to resolve the finer structures of real cladogenetic significance. Later Parts will show that it is indeed possible to derive evolutionary trends almost parallel to those derived from other structures.

f. Cytotaxonomy

Caryotype patterns have been useful only in analysis of smaller taxonomic units of Heteroptera. The cytology of over 650 species is known (MANNA, 1962). Regular chromosomal complements have been found in some groups, *e.g.* the Triatominae, mostly 20 A + X + Y (USINGER, WYGODZINSKY and RYCKMAN, 1966); Corixidae, mostly 22 A + X + Y (SOUTHWOOD and LESTON, 1959); in others, the number of chromosomes varies widely, *e.g.* four species of *Lethocerus sensu lato* have a number of 4, 8, 26 and 30, respectively (MANNA, 1962). PFALER-COLLANDER (1941) studied 45 species of Lygaeidae and found a constant autosomal type within genera and tribes.

Some seventy Miridae revealed a diploid number of 22–48 (XY type) and LESTON (1957, 1961) concluded that 32 A + X + Y was the basic mirid caryotype from which all subfamilial numbers have arisen. In *Isometopus intrusus*, belonging to a mirid subfamily of which no cytogenetic data were previously known we found the highest complement, 50–52 autosomes, X, Y.

Ancestral diploid numbers have been suggested for many other groups of Heteroptera but these are of restricted value, unless they are deduced from a thorough phylogenetic knowledge of the groups. Understanding of mirid phylogeny is far from adequate (see our section on mirid eggs) and LESTON's interpretation of characters used for testing subfamily interrelationships is open to criticism. Much work has been done on the cytogenetics of Pentatomomorpha (review in MANNA, 1962; SCHAEFER, 1964) and Hydrocorisae (MANNA, 1958, 1962). As SCHAEFER said, this work is not easy to evaluate and the conclusions drawn by some authors discredit the accuracy of their work. First of all, detailed knowledge of cytology and ways of recognizing the different chromosomes and studies on their behaviour are needed (good examples are LEWIS and SCUDDER (1957, *Dicranocephalus*) and LEONARD (1966, *leucopterus* complex of *Blissus*)). The difficulties from evolutionary variation of the chromosomes, both numerical and structural, have been discussed by HUGHES-SCHRADER (1958), who successfully introduced the cytophotometric estimation of DNA as a tool for analysis of cytotaxonomic relations. However attempts to apply chromosome studies to the solution of problems of major relationships, are sheer guess work. Results are contradictory to current classification, especially when the cytologist is not a taxonomic specialist of the group in question. This is, for example, clearly demonstrated in the dendrogram of the caryotype changes in Heteroptera as presented by MANNA (1958), in which extremely remote groups are linked together.

LESTON (1958) concluded that in the evolution of the Pentatomomorpha the chromosome number was first reduced and later on increased again. He assumed a reduction also in other heteropterous groups, starting from an incorrect assumption "...such primitive families as Belostomatidae, Naucoridae, Nepidae, Notonectidae, Mesoveliidae and Reduviidae have high diploid numbers..." The problem of parallelisms and convergences in chromosomal evolution: small changes in diploid number, absence or presence of *m*-chromosomes, multiplication of X chromosomes, conversion of XY into XO mechanisms (and the reverse, see WHITE, 1954, p. 96) is highly likely. To remove doubt, many more species of each phyletic line must be studied for chromosomal anagenesis. In particular, those series of species must be selected whose morphological evolution is known in detail and in which the stage of anagenesis has been analysed numerically (*e.g.* the leafhopper family Delphacidae, W. WAGNER, 1963). Secondly, a start must be made on families about which little or nothing is known. Among such families are those which appeared of the utmost importance for heteropterous phylogeny in the present study.

Apart from Gerridae, the cytogenetics of only a few species of Amphibicorisae and Leptopodoidea have been investigated (only one species of Veliidae, Mesoveliidae, Saldidae, a few of Hydrometridae). Nothing is known of Hebridae, Leptopodidae,

Ochteridae and Dipsocoroidea. We made aceto-orcein testes squashes of several species from these groups. The plates have only been examined cursorily, so that the following data must be treated with reserve, especially on the genetic sex mechanism. The diploid number of autosomes in the Saldidae seems to vary greatly: 18 *(Chiloxanthus pilosus)*, 32 *(Salda littoralis)*, 34 *(Saldula saltatoria, S. c-album)*, 46 *(Saldula scotica,* Dutch population, see p. 18), all with XO-type. *Leptopus marmoratus* has about 26 and an XY-type mechanism is suggested. *Hebrus ruficeps* and *Hydrometra* have in common 18 autosomes, *Microvelia reticulata* and *Pachycoleus rufescens* 20, and a *Hebrovelia* sp. (origin *Ivory Coast*) had 20. All these have XO males. *Ochterus marginatus* (origin Ivory Coast) revealed a diploid number more than 50, sharing with *Ilyocoris cimicoides* and *Isometopus intrusus* the highest number so far found in Heteroptera.

The general occurrence of the XO sex mechanism in the Amphibicorisae contradicts our concept that this group is the most generalized. XO occurs scattered throughout the Suborder: Coreoid complex, Phymatidae, two species of Pleidae, (22 + XO, JANDE, 1959; however SOUTHWOOD and LESTON, 1959, mention 22 + X + Y for *Plea atomaria!*), Naucoridae, most Amphibicorisae, Saldidae, Dipsocoridae *(Pachycoleus)*. The XO condition is generally assumed advanced over the XY state. However translocations between sex chromosomes and autosomes may again convert an XO mechanism into XY, (WHITE, 1954, p. 97).

Perhaps amphibicorisal caryotypes may contain an overlooked Y, indistinguishable from the X, and thus represent a primitive stage. Anyhow, it seems of evolutionary significance that *Mesovelia* possesses 30 autosomes + 4X + Y (EKBLOM, 1941). This is a deviation from the normal amphibicorisal pattern as are also several characters of the egg system. It is hoped that more aberrant Amphibicorisae will soon become available for cytotaxonomic studies. There is indirect evidence that the caryotype of of Amphibicorisae may conform with our findings that this group deserves a fundamental place in Heteroptera. This evidence appears from two aspects of HALKKA's (1959) work on Homoptera Auchenorrhyncha. Only about twenty species of the 175 studied had the XY type. HALKKA made it conceivable that in certain species there is a recently evolved Y. Delphacidae have an XO type but three species of this family have XY; it seems significant that two of them are among the anagenetically highest species according to the quantitative analysis of the family by W. WAGNER (1963).

Although the size of the chromosomes depends on several factors, it is striking that *Hebrus* possesses unusually large chromosomes. HALKKA found that among leafhoppers, chromosomes are distinctly smaller in Delphacidae than in Cicadomorpha. However in Cixiidae they are almost the same seize as in certain Cercopidae and thus a parallel anagenesis is suggested as by egg structures (COBBEN, 1965c). HALKKA assessed that chromosome cytology of the Cicadellidae accords very closely to WAGNER's phylogenetic tree of the group and that all species at the base of the tree have abnormally large chromosomes. Especially in the Homoptera Cicadina it should be possible to analyse evolutionary taxonomy by harmonizing the results of cytogenetics, morphology of all stages, including the egg, and the endosymbiotic populations.

g. Salivary system

Gerris, *Notonecta* and *Reduvius* have a primitive salivary pump, Pentatomidae and Pyrrhocoridae *(Dysdercus)* a more evolved one. POPHAM (1962) conforms these differences with feeding habit. Other data from literature and our own preliminary work suggest that the pump also depends on taxonomic relationships of the groups as do the actual salivary glands. A voluminous literature continues to increase on the external morphology of the glands and the number of species where the action and composition of the saliva has been analysed. SOUTHWOOD (1955) showed that the accessory gland in the Pentatomomorpha is tubular but in the Cimicomorpha *(sensu lato)* vesicular.

MIYAMOTO (1961) collected facts from nearly all families of Heteroptera (except Thaumastocoridae and Leptopodidae, but data on these are now available) and considered the phylogenetic relationships. We have studied European representatives of some critical families (Amphibicorisae, Leptopodoidea, Dipsocoridae), and with data from recent literature have gained a reasonable picture of the evolution of the glandular system. In accord with MIYAMOTO, the earliest condition is where the principal gland is composed of a simple aggregation of few large cells with a narrow lumen; the duct is as thick as that of the accessory gland. This type occurs in Amphibicorisae (relict aberrant forms have not yet been examined), Enicocephalidae, Dipsocoroidea, Ochteridae, primitive Naucoridae, Pleidae and Helotrephidae. Already most have a clear distinction between the anterior and posterior lobe of the principal gland and both lobes usually each form an externally fused or rarely a distinct aciniform structure (Gerridae, Ochteridae). MIYAMOTO contradicts himself when he writes on p. 224 that the glands in Hebridae and Mesoveliidae are not aciniform, whereas it appears from his table on p. 245 that they should be aciniform. The aciniform condition is retained during subsequent multiplication of the cells throughout Hydrocorisae (except for Corixidae). MIYAMOTO considered the incomplete bilobed principal gland as primitive (Dipsocoroidea, Enicocephalidae). Many Amphibibicorisae, including *Hebrus*, have the anterior and posterior lobes clearly separate and our data on egg phylogeny supports such primitivity; a similar separation occurs in many Homoptera.

The accessory gland is vesicular in all major groups (including Thaumastocoridae, KUMAR, 1964b), except for the Pentatomomorpha and Enicocephalidae. MIYAMOTO grouped his Dipsocoridae (Dipsocoridae and Schizopteridae relegated to subfamilies) and Enicocephalidae together in a new division, the Dipsocorimorpha, because of similarities in salivary glands and alimentary canal. The erection of a new taxon should not be founded on such limited evidence. The characters noted are of anagenetic nature, and the families deviate in one important respect which appears from MIYAMOTO's own descriptions and figures (tubular accessory gland in Enicocephalidae, vesicular type in Dipsocoridae). The salivary system of Saldidae (many species studied by us; *Aepophilus* not yet known) and Leptopodidae (*Leptopus marmoratus*, personal observation; *Valleriola wilsonae*, KUMAR, 1964a) is distinctly more evolved than in Amphibicorisae.

h. Alimentary canal

From structural modifications of the food pump of the Hydrocorisae, PARSONS (1966) concluded that Ochteridae and Gelastocoridae are rather late offshoots from the ancestral hydrocorisal line (contrast CHINA, 1955a). Studies on the food pump of land bugs are few (see RASTOGI, 1965). The bulk of data on the actual digestive canal has been accumulated by MIYAMOTO (1961) in an admirable fashion. Generalized features of the alimentary organ are, according to him: entire system short; mid gut subdivided into two portions; pylorus small, sac-like; hind gut with a small ileum and rectum, lined with a thick layer of tall cells; malpighian tubules uniform, short and simply curved.* This set of characteristics occurs in the Dipsocoroidea, Enicocephalidae, and amongst Amphibicorisae in *Hebrus, Microvelia, Mesovelia.* In other Amphibicorisae, the malpighian tubules have elongated and characteristically contorted. *Hydrometra* is unusual in having an alimentary system in several respects like that of Hydrocorisae (this implies more than a coincidence!).

GOODCHILD (1966) has commented MIYAMOTO's interpretations of the pyloric and ileal structures. He gave a fascinating account of the evolution of the alimentary system in Hemiptera. Besides the well known filter chambers, he considered the various modifications and specializations, including the gastric caeca in Pentatomomorpha, as primarily for water excretion. For his scheme of evolutionary relations between Hemiptera, based on alimentary structure and function, GOODCHILD assumed that Hemiptera were originally mesophyll suckers. Ancestral hemipterans would have sucked surface cells of plants as do modern Thysanoptera. The heteropterous stock would have been omnivorous or carnivorous while some recent groups have reverted to plant eating and, a few have developed into real sap-suckers. Consequently in the scheme of GOODCHILD Heteroptera are superposed on Homoptera. Such a grouping does not ensue from the digestive system on which the scheme is purported to be based. Homoptera are phytophagous and the general view that they are fundamentally more primitive than Heteroptera may underlie Goodchild's scheme. This is doubtful. The egg system and the genital structures of Homoptera Auchenorrhyncha do not start lower anagenetically than do the Heteroptera. GOODCHILD laid emphasis on the Peloridiidae, a peculiar group of Hemiptera, placed separately as the Coleorrhyncha, and considered the most primitive member of the Order. Though certainly several structures of this group are generalized (PENDERGRAST, 1962), it is doubtful whether this whole taxon is more primitive than the most generalized Heteroptera (COBBEN, 1965c). Our theory is that the archetypical hemipteran was a predominantly carnivorous insect.

* MIYAMOTO considered three pairs as the primitive number. He found this number, however, only in the male of one species, a schizopterid. All other Heteroptera had two pairs as do most homopterous groups.

i. Spiracles

Much has been written on the number and structure of spiracles (sometimes in a controversial way, *e.g.* HANDLIRSCH, 1899), but still there is no uniformity of opinion. This applies particularly to the first abdominal spiracle which, if present, is often difficult to detect, because it is displaced and hidden. HESLOP-HARRISON (1952) pushes the idea that originally there were eleven pairs in Hemiptera. The first thoracic spiracle usually considered as the mesothoracic one, would belong to the prothorax. Most recent Heteroptera would consequently have three thoracic and seven abdominal pairs. But HESLOP-HARRISON's logic is not sound; the study of the ontogeny of the tracheal system shows that there are primitively two thoracic and eight abdominal spiracles. The first spiracle of the abdomen occurs, so far without exception, in both larvae and adult of Amphibicorisae (occluded in *Hebrus* by thickening of the integument), Leptopodoidea, Hydrocorisae and Reduviidae. This spiracle was overlooked in Saldidae and Mesoveliidae by GUPTA (1963b). POPHAM (1960) counted only seven abdominal pairs in *Ilyocoris* and *Notonecta* but to judge from his figures, he overlooked the second pair. HESLOP-HARRISON (1952) reports only one functional pair in *Nepa (sic)*.

The first spiracle in Heteroptera migrated dorsad in the adult. The first larval instar of the surface, water and shore bugs and the Reduviidae have all spiracles in the pleural membrane in one straight line with the two thoracic pairs. The one exception is *Mesovelia*, where the first abdominal stigma is already displaced onto the tergite in the egg larva. Thus, in this respect again, this taxon differs from typical Amphibicorisae. The thoracic tracheal openings in *Mesovelia* are distinctly larger than the abdominal series, as in the egg larvae of other bugs, but in the first instar of *Hebrus* all spiracles are of equal size.

The occurrence of the first abdominal spiracle in other land bugs is debatable. DRAKE and DAVIS (1960) and DAVIS (1966) stated its existence in Reduviidae, Pachynomidae, Thaumastocoridae, but its absence in Joppeicidae, Tingidae, Anthocoridae, Cimicidae and Miridae; absence is also recorded for the Microphysidae (ŠTYS, 1962). However HANDLIRSCH (1899) noted the first ostiole in some Nabidae and Miridae, and MAMMEN (1912) mentioned it for Cimicidae and Miridae. We found in *Anthocoris* a distinct scar of the first spiracle in the larva, hardly traceable in the adult, but could not find it in other members of the cimicoid families.

There is equal doubt about the first abdominal stigma in the Pentatomomorpha. It is claimed to be absent in Pentatomoidea by CHINA (1955c) but to be present in Pentatomidae by HANDLIRSCH (1899) and MAMMEN (1912). MAMMEN has also seen the spiracle in Coreidae, Pyrrhocoridae, Berytinidae, Piesmatidae (claimed to be absent in this family by DRAKE and DAVIS, 1958) but not in the Lygaeidae. We found a small first spiracle in the larvae of the lygaeids *Oncopeltus*, *Trapezonotus*, and in Acanthosomatidae. The same spiracle is distinct in the Alydidae but vague in the Coreidae studied. In the first larval instar of species of other families (*e.g.* Dinidoridae, Tessaratomidae, Scutelleridae) we could not detect it.

Thus a functional first abdominal spiracle and the primitive total of ten tracheospiracular metameres, exists in Amphibicorisae. The 1st abdominal spiracle has been retained in the Leptopodoidea, Hydrocorisae and Reduviidae; the 8th abdominal spiracle sometimes tends towards reduction in Hydrocorisae and Reduviidae. Other terrestrial families still often possess the 1st abdominal spiracle, but usually reduced and presumably not functional. This spiracular anagenesis does not conflict with the evolutionary picture of the egg system, and the difference between Reduviidae and the cimicoid families is once more confirmed.

In complete contrast with all these groups (and also with the Enicocephalidae) is the severe reduction of the spiracular system in Dipsocoroidea. Modern species have several anterior segments of the abdomen free of spiracles and in some species the reduction has proceeded to the complete disappearance of abdominal spiracles. The structure and closure mechanism of the spiracles, the tracheal system itself and additional quantitative data will give more evidence for a predominantly anagenetic evolution of the respiratory orginization.

This preview (a–i) of other investigations directed towards the problem of heteropterous evolution does not, of course, exhaust the possibilities. The morphology of the three adult tagmata, the wing articulation and wing coupling and venation, the nervous and circulatory system, and the sound production are subjects which will be considered later. The subjects previewed reveal cladogenetic splits, most of which are in concord with those in the egg system, whereas anagenetic trends often proceed at different rates for each feature.

There is, however, a discrepancy between the Dipsocoroidea and whole the rest of the Heteroptera which is greater than was concluded from the eggs. This fact will make it necessary later to modify fig. 306, which was based on egg evolution. The scheme will then show a clear dichotomy already starting in the basal black area. But this dichotomy has, of course, nothing to do with the supposed branching in Pentatomomorpha and Cimicomorpha (*sensu* LESTON *et al*, 1954). The data from wing venation seem at first sight contradictory to our main conclusion that Amphibicorisae are the most ancestral bugs. Venation patterns should now be re-examined to test whether Dipsocoroidea are the first offshoot from the amphibicorisous stock.

5 Summary and conclusions

1. This work, the first volume of a series dealing with evolutionary trends in Heteroptera, is concerned with the egg system of about 400 species. The data are presented systematically in chapters 1 and 2 with a critical review of the literature after each family.

2. Chapter 3 evaluates facts about each egg character. I have attempted to distinguish between anagenetic and cladogenetic processes of evolution.

3. The actual chorion reveals a wide range of types of architecture and of aeropylar systems (fig. 264–267). The aerostatic inner layer of the shell of most Geocorisae and of *Hydrometra* is not homologous with the porous inner layer of Saldidae, many Amphibicorisae and Hydrocorisae. A thin, entirely solid chorion is considered as a plesiomorphous condition *(Hebrus, Mesovelia, Idiostolus, Embiophila, Oncylocotis)*. Some of the specific features of shells are: air clefts; respiratory horns on the rim or on the operculum; porous structures in different stages of evolution, ultimately acting as a plastron; regulation of respiration by movable slips of the rim.

4. The general trend of evolution of the micropylar system (fig. 268–270) represents multiplication and displacement of the micropyles, starting from a single micropyle in the centre of the cephalic pole; in some groups reduction and complete loss of the micropyles is associated with traumatic insemination. The structure and orientation of the micropyle(s) and their changes during evolution have been discussed. *Monalocoris*, *Bryocoris* and *Oncylocotis* are divergent from the general pattern.

5. The primitive longitudinal dehiscence of the shell has evolved independently and along different pathways into a cap in most major groups (schemes in fig. 270–272), sometimes intermediately on one of the lateral sides. The lygaeid-coreid types of eclosion are derived from a transitional, radial structure which has consolidated in Piesmatidae, and also in Malcidae after loss of a central polygon. The terms operculum and pseudoperculum are redefined on a more functional basis. The cap of the serosal cuticle has evolved more slowly than the cap of the chorion.

6. The progressive evolution in size is usually accompanied by some regularities as shown graphically in fig. 273, 274: small eggs have a spacious hexagonal pattern from the follicle; plesiomorphous species are usually small, have a long period of oviposition and few ovarioles in which a few, relatively large, eggs ripen simultaneously; apomorphous species have a larger body, smaller egg and follicle cells, more ovarioles, and synchronous egg maturation and deposition.

7. A survey is given of incubation periods, diapause phenomena and reproductive cycles; the phylogenetic consequences are limited. With one exception, diapause of the

egg intervenes in embryonic development between the stages of the early germ band and revolution (fig. 275), but does not affect the formation of the serosal cuticle.

8. Family groups are distinguished by different types of embryogenesis. A wide range of progressive evolution of the embryonic development is apparent within most of the major phyletic lines. Altogether, the diversity of embryonic features and processes in Heteroptera is not equalled in any other Order of insects as far as is known.

9. The variable characteristics utilized in reconstructing the genealogy of embryogenic patterns (fig. 276) are: degree of visible development of the 'pregerm'; location of blastopore; growth, orientation, transformation in shape and displacement (mostly clockwise rotations) of the germ band, embryo and prolarva.

10. Since relations between the various ontogenies of the embryo appear to be independent of evolutionary adaptations, the phylogeny of the embryogenetic patterns gives a most reliable picture to contrast with quite different characters used for major classification.

11. The archetype of embryogenesis is distinguished by invagination of the embryo (morphologically at the caudo-ventral edge of the egg) along the longitudinal median axis of the yolk column without loss of contact between head lobes and serosa and by a 180° rotation of the embryo before revolution. *Hebrus* most closely conforms to this type, followed by most Amphibicorisae and by cimicoid groups which tend to invaginate at the left side of the egg. Temporary complete invagination occurs in Saldidae, *Gerris* and *Hesperoctenes*, and in diapausing mirid eggs.

12. The variability in the type of egg rotation and embryo rotation in Gerridae, Hydrometridae, Cydnidae and Acanthosomatidae suggests that the egg system is not yet in equilibrium.

13. Pentatomomorpha reveal gradual loss of embryo rotation, while Hydrocorisae retain such rotation, sometimes with germ-band and prolarval rotations. Both groups show a transition (anagenetic *intra se*, cladogenetic *inter se*) from the immersed towards the superficial type of embryogenesis.

14. The superficial condition of the hydrocorisous type prevails in Reduviidae after complete loss of rotations. The progression in embryonic evolution reached a high level in Harpactorinae; many perform semi-invagination, and species of *Coranus* entirely omit the invagination stage, and have no blastokinesis in the broadest sense. This deficiency is associated with early differentiation of the prospective germ band in the blastoderm stage. Similar early development occurs in some Hydrocorisae and, through cladistic divergence, also in evolved taxa of the Pentatomomorpha.

15. The standard of embryogenesis is not influenced by egg shape. The dimensions of the embryo do not foreshadow those of the future larva but allometry of the limbs appears already during bud formation.

16. In contrast to other Heteroptera, saldid embryos have the eyes differentiated before revolution. They possess a peculiar cephalic organ, possibly hydropic, extending through the serosal cuticle and underlying a great part of the chorion.

17. A survey is given of the various positions and fates of the serosal hydropyle.

The revolution of the embryo is predominantly brought about by local contractions of the fused amnion and serosa, and not by intrinsic action of the embryo itself.

18. The remains of the contracted serosa, the serosal plug, is rapidly engorged in course of time into the future pronotal region to form the secondary dorsal organ. The involution is the result of a spectacular peristalsis, in the first instance caused by sudden contraction of cells close to the line of fusion between amnion and serosa.

19. In many Miridae, the serosal plug, with or without yolk content, persists till eclosion of the egg, apparently absorbing water from the outside in order to stretch the serosal cuticle. The subsequent lengthening of the egg enables the prolarva to escape out of the sunken oviposition slit.

20. The blackening of the egg is reducible to different principles, depending on whether suprachorionic, chorionic or subchorionic layers are involved. The blackish exudate of the serosal cuticle, restricted to some families of Heteroptera, may play a role in water regulation. Extra-embryonic envelopes of uncertain origin have been noticed in a few species.

21. The embryological data are compared with the literature dealing with other insect Orders. Because the evolution of embryonic development of insects seems to be largely governed by parallelism, a clearer distinction between cladogenetic and anagenetic phenomena in other Orders must be made first before relationships between Orders can be settled. The differences between the holometabolic and the hemimetabolic type of development may not be as fundamental as has been suggested.

22. The evolution of structures involved in four different methods of eclosion is outlined in fig. 278. A transverse, paired ruptor ovi forming part of the embryonic cuticle and delimiting the anteclypeus from the postclypeus is considered as the archetypical condition (as in *Hebrus*).

23. Cladogenesis of the eclosion process evolved within the Amphibicorisae. In *Mesovelia*, eclosion is caused by fluid pressure within the embryonic cuticle. The situation in the Nabidae represents a link between this procedure and that in the Cimicoidea *sensu lato*, but the function of pressure transfer is gradually taken over by the fluid-filled serosal cuticle.

24. The main device in eclosion of Reduviidae and Hydrocorisae is part of the serosal cuticle. Sudden forcing of extra-embryonic fluid anteriad explosively breaks the chorion in Hydrocorisae. Prolarval rotations may accelerate solution of the inner layer of the serosal cuticle, and the function of the pleuropodia is discussed in relation to this behaviour.

25. In Amphibicorisae other than Mesoveliidae, and in the Leptopodoidea the transverse clypeal ruptor developed into a longitudinal frontal ruptor; Saldidae have both a frontal and a clypeal ruptor.

26. Pentatomomorpha reveal anagenesis of the ruptor system resulting in displacement of the cephalic armature up to the pronotum through loss of the vertex.

27. An account is given of the many sorts of bilateral, mostly monostrophous asymmetries found in the heteropterous egg system. The typical flexing pattern of limbs and antennae of the prolarva (a characteristic of the hemipteroid Orders) is

racemic. In Hydrocorisae this asymmetry is constant and either amphidromous or monostrophous (the reverse asymmetry occurs in *Plea*).

28. The different orientations of the laid egg are reduced to three main types (Table 2, p. 332) the evolution of which is outlined in fig. 281. Some speculations are made on the selection factors involved in switching from one type to the other.

29. The archetypal Heteroptera did not possess a well developed ovipositor, and they were able both to deposit the eggs 'backwards' or 'forwards'. The theoretical possibilities of oviposition in ancestors are shown within the central circle of fig. 281.

30. Saldidae and Mesoveliidae have a firm 'concave' ovipositor; oviposition is such that 180° rotation of the longitudinal axis of the egg within the genital tract must be supposed. *Gerris* regulates delivery of rotated or non-rotated eggs according to the oviposition site selected. Pentatomids of the genera *Aeliomorpha* and *Macrina* exhibit 90° rotation of the eggs and the alteration in egg shape conforms with this mode of laying.

31. Comparison of embryogenic types (fig. 276), the egg types drawn in a standardized way (fig. 282–285), and the stance of the depositing female demonstrated that 180° rotation of the eggs is more common in Heteroptera and most probably also in other insects.

32. The side of the egg where the embryonic anlage develops into the blastoderm is taken as the ventral side. The following rules have been drafted for the dorsoventral polarity of the egg-system: 1. All eggs laid exposed, whether rotated or not, and whose embryo rotates through 180°, are attached with the ventral side against the substrate; the venter of the fully grown embryo lies below the dorsal side of the egg. 2. Eggs without embryo rotation are likewise ventrally attached to the substrate, except when the egg is rotated before laying; the morphological sides of the fully grown embryo correspond with those of the egg.

The same rules hold for erect or embedded eggs, when these are figured as being laid horizontally.

33. The data obtained from the study of heteropterous eggs have been compared with relevant data from other Orders of insects. The 'HALLEZ law' is redefined on pages 347–348.

34. A preliminary discussion of the phylogeny of the Heteroptera is given. The group characters derived from the egg system are discussed on p. 350–363.

35. The Leptopodoidea forms a natural group sharply defined from others. It seems improbable that Amphibicorisae arose from a proto-saldid stock; the opposite direction of evolution, Saldidae from proto-amphibicorisae is more in accordance with our findings.

36. The Amphibicorisae appear more diverse than was assumed on the basis of other character complements, and comprise more than one superfamily. Mesoveliidae and Hydrometridae deviate considerably from the group type. Gerridae and Veliidae could be delimited more clearly from each other. *Macrovelia* and other aberrant genera show close affinity with Veliidae, not with Mesoveliidae.

37. Pentatomomorpha constitute a natural group of families but the Idiostolidae

are remote. The families are distinguished by the height reached on the anagenetic scale. The origin of the Pentatomoidea dated further back and the anagenesis advanced further than in the other superfamilies. Stenocephalidae appear more lygaeid-like and Colobathristidae more coreid-like. Malcidae are cladogenetically derivable from Piesmatidae. Eggs of Pseudophloeinae and *Hydara* resemble those of Alydidae.

38. Reduvioidea, Thaumastocoroidea and Dipsocoroidea ought to be excluded from the Cimicomorpha which should contain only the families of the Cimicoidea *sensu lato*. On the basis of the eggs, Bryocorinae, excluding the *Helopeltis* group, merit family status. Several mirid genera seem to be classed under wrong subfamilies. The eggs of Velocipedidae and Pachynomidae are essentially nabid-like.

39. Thaumastocoridae, Dipsocoroidea and Enicocephalidae are all isolated groups. There seems to be no justification for combining the two latter in one group.

40. Hydrocorisae, inclusive of Corixidae and Ochteridae, share similar types of embryogenesis and eclosion dynamics but are heterogeneous in chorionic architecture. The common predecessors of Hydrocorisae probably must be found in the naucorid, not in the ochterid branch. Several taxa, considered as subfamilies, perhaps merit family rank (Potamocorinae, Aphelocheirinae, Diaprepocorinae, Micronectinae).

41. The unintentional nomenclatoral consequences of the new major classification of terrestrial Heteroptera (LESTON *et al.* 1954) are discussed. Terrestrial Heteroptera are widely polyphyletic. Hence, the taxonomic use of the name Geocorisae should be avoided.

42. The results of our study lead to the recognition of the following, more or less equivalent, major groups; Amphibicorisae, Leptopodoidea, Cimicomorpha *sensu stricto*, Dipsocoroidea, Enicocephaloidea, Reduvioidea, Thaumastocoroidea, Pentatomomorpha and Hydrocorisae (eggs of Joppeicidae were not available).

43. Fig. 306 presents a provisional scheme of the phylogeny of the Suborder. The terrestrial groups and the Hydrocorisae are presented as radiations from an extinct amphibicorisous stock.

44. The book concludes with a concise account of some new aspects of evolutionary morphology, which will be elaborated later. The subjects refer, among others, to: eye of egg larva, trichobothria, pretarsus, scent glands, internal and external genitalia, caryotypes, salivary glands, alimentary system, stigmata. These and other characters will be evaluated and compared in Parts 2 and 3 of the series in search of a basis for phylogenetic weighting.

Acknowledgments

My thanks are due to the many who co-operated in the production of this book. Prof. Dr J. de Wilde carefully read the manuscript and suggested many improvements. Prof. J. D. Lattin (Oregon State University, Corvallis) and Mr J. C. Rigg (Pudoc, Wageningen) corrected the English. Jack Lattin was liberal with his help and encouragement during his stay in Wageningen. Miss J. M. Krythe, Biol. Drs (IPO, Wageningen) adapted the Dutch summary to the latest spelling.

Many colleagues supplied or loaned specimens of pinned female bugs from which ovarian eggs were dissected. They included: J. Carayon (Museum National d'Histoire Naturelle, Paris), P. H. van Doesburg Jr (Rijksmuseum van Natuurlijke Historie, Leiden), H. Eckerlein (Coburg), C. H. Fernando (Fisheries Research Station, Colombo), L. Hoberlandt (Národní Museum, Prague), I. Kerzhner (Zoological Museum, Leningrad), W. J. Knight (British Museum (Natural History), London), J. D. Lattin (Oregon State University, Corvallis), C. H. Lindroth (Entomologiska Institutionen, Lund), S. Miyamoto (Biological Laboratory, Fukuoka), J. T. Polhemus (Englewood, Colorado), R. Remane (Zoologisches Institut, Marburg/Lahn), A. Soós (Magyar Nemzeti Museum, Budapest), P. Štys (Department of Systematic Zoology, University of Prague), T. E. Woodward (University of Queensland, Brisbane), A. Wróblewski (Zoological Institute, Poznan), P. Wygodzinsky (American Museum of Natural History, New York).

Prof. R. L. Usinger (University of California, Berkeley) sent me living material of the Berkeley strain of *Cimex lectularius*. Dr A. von Peez (Brixen-Bressanone) twice provided me with living *Leptopus marmoratus*. Dr E. C. Young (University of Canterbury, Christchurch) and Mr J. P. van der Molen (as a Wageningen student seconded to the Ivory Coast) preserved embryonic stages of *Diaprepocoris zealandiae* and *Sahlbergella singularis* respectively. Dr J. A. Grant (British Museum (Natural History), London) allowed me to quote from his forthcoming work on the Hyocephalidae.

I was hospitably received by the directors and staff of the Rijksmuseum van Natuurlijke Historie, Leiden; the British Museum (Natural History), London; the Museum National d'Histoire Naturelle, Paris.

The Boards of WOTRO (formerly WOSUNA), The Hague, and the Agricultural University, Wageningen, respectively, financed expeditions in the Netherlands Antilles and in the Ivory Coast. I have incorporated some of the results of the explorations.

The following people took the photographs and have permitted me to publish them here. Mr S. Henstra of the Electron Microscopy Section of the Service Institute for Technical Physics in Agriculture, Wageningen, spent many days in making micro-

sections and photographs with the transmission electron-microscope (fig. 286–305). He and Mr Y. Makita made the photomicrographs (fig. 307, 311, 312, 315E) with the Jeol scanning electron-microscope in the demonstration centre of the Jeol Company in Paris. Prof. G. Pfefferkorn, Dr R. Blaschke and Dr R. Christenhuss of the Institut für Medizinische Physik of the University of Münster kindly made the photomicrographs (fig. 306, 308–310, 313–315A–D, F) with their Stereoscan apparatus.

The Netherlands Organization for the Advancement of Pure Research (ZWO) and the Centre for Agricultural Publishing and Documentation (Pudoc) financed the publishing of this book. Mr J. Vermeulen planned and supervised the typographical work.

Miss Riet Albers tediously typed and retyped most of the manuscript with patience, speed and precision. Mrs J. H. E. Barten-Roseboom and Miss G. v.d. Spek helped in preparing the indexes.

Samenvatting

Voorwoord

Dit boek vormt het eerste deel van een serie, handelende over evolutie 'trends' in wantsen (Hemiptera Heteroptera).

Het onderhavige deel behandelt het eisysteem. In het tweede deel zullen de reproduktie-organen en het genitale apparaat besproken worden. Onderwerpen van gevarieerde aard zullen in het derde deel verschijnen. Een inleidend overzicht van deze onderwerpen wordt gegeven op p. 363–378 van dit boek. Voor zover mogelijk wordt de evolutie van elke structuur of elk orgaan-systeem afzonderlijk nagegaan. Het derde deel zal besluiten met de synthese van al deze partiële evoluties tot een geheel om meer inzicht te krijgen in de waarschijnlijke evolutie van de suborde wantsen en de daaruit voortvloeiende fylogenie van de supra-generieke categorieën.

Materiaal en methoden

Het materiaal heeft betrekking op de eieren van ca. 400 soorten, behorend tot 55 families en afkomstig uit verschillende geografische gebieden. Het representatief karakter van dit betrekkelijk kleine monster wordt bepaald door de toegepaste selectie van typische en atypische soorten per familie. Aberrante relict soorten worden eveneens in het onderzoek betrokken. De methoden voor het verkrijgen van de eieren en hun behandeling worden beschreven.

1 Structuur en biologie van de eieren van de Leptopodoidea

Om bepaalde redenen vermeld op p. 1, wordt aan deze superfamilie en in het bijzonder de familie Saldidae, speciale aandacht besteed. De opbouw van de eischaal van 39 soorten Saldidae en de embryologie van 15 soorten worden beschreven.

2 Structuur en biologie van de eieren van leden van de overige families

In dit hoofdstuk worden de families systematisch behandeld. De uitwendige vorm van de eieren wordt niet beschreven, daar deze volgt uit de talrijke figuren. Om diverse redenen (p. 10) blijkt het vooreerst niet mogelijk met zekerheid één van de zijden van het ei als dorsaal of ventraal te bestempelen. In het beschrijvende deel wordt daarom

de neutrale benaming: voorzijde en achterzijde gebruikt (zie fig. 1C). In de discussie op p. 338–344 kan pas tot een definitieve morfologische determinatie van de ei-zijden besloten worden. Bij elke familie worden eerst de eigen waarnemingen vermeld, gevolgd door een kritisch overzicht van de literatuurgegevens.

3 Bewerking van de gegevens. Analyse van de anagenese en de cladogenese

Wij hebben getracht de evolutie van elk afzonderlijk ei-kenmerk na te gaan. Bovendien wordt gepoogd een onderscheid te maken tussen progressieve ontwikkeling van een bepaald kenmerk of structuur, welke zich parallel in verschillende phyletische lijnen heeft voorgedaan (anagenese) en het opsplitsen van de ontwikkeling van een bepaald kenmerk in twee of meer verschillende richtingen (cladogenese). Het herkennen van deze twee belangrijkste evolutie-gebeurtenissen vormt de basis voor onze gedachtegangen betreffende de fylogenese. Elk hoofdstuk (3.1–3.4) besluit met een discussie waarin het gevondene vergeleken wordt met overeenkomstige gegevens betreffende andere insektenorden.

3.1 Chorion

In het verleden werden de lagen welke binnen en buiten de eigenlijke eischaal (chorion) liggen dikwijls abusievelijk tot het chorion gerekend. Ook is er in recente tijd verschil van opvatting geweest over de plaats in het chorion waar atmosferische lucht wordt vastgehouden. Kanalen, die lucht doorlaten (aeropylen), werden in het verleden veelal verwisseld met kanalen voor passage van het sperma (micropylen) en omgekeerd. Chemische ingrepen, toegepast op de eischaal, hebben deze en andere vergissingen in de hand gewerkt. Dergelijke behandelingen werden daarom door ons vermeden.

3.1.1 Architectuur en aeropylair systeem

Leptopodoidea

Aepophilus bonnairei, levend langs de Atlantische kust in de tussengetij zone, heeft een geheel massieve eischaal. Dit geldt waarschijnlijk ook, hoewel dit door ons niet is gecontroleerd met het elektronenmicroscoop, voor de onder analoge condities levende *Omania* soorten in het Australische en oriëntaalse gebied. Alle overige onderzochte 41 soorten hebben een min of meer dunne binnenste eischaal, welke door een met lucht gevulde schede gescheiden is van de dikkere buitenlaag. De open tussenlaag communiceert met de buitenlucht via een systeem van kanaaltjes langs de hele eiomtrek. Aan de voorzijde van de voorpool bevindt zich bij de meeste soorten een grillig uitwendig patroon bestaande uit overlangs gespleten verdikkingslijsten. Deze spleten noemen wij 'air clefts', aangezien zij in contact staan met de open binnenlaag

van de eischaal. Soorten die dit respiratie-systeem missen, hebben een dichtere porositeit van de buitenste chorionlaag. Bij enkele soorten benadert de porositeit een plastron structuur die het risico van langdurige bevloeiing met water opvangt. De chorion-architectuur van Saldidae komt in zijn elementaire kenmerken overeen met die van typische landwantsen; de eieren worden boven de waterspiegel afgezet. Desondanks ontwikkelt het Saldiden-ei zich ook onder water geheel normaal, vanaf de eiafzetting tot en met het uitkomen, zelfs wanneer de schaal geen lucht bevat. In dit opzicht zijn Saldidae meer uitgesproken amfibisch dan de Amphibicorisae (wateroppervlakte-wantsen). De schaal van het Leptopodiden-ei vertoont morfologisch een sterke overeenkomst met de eischaal van de Saldidae. De consistentie van het chorion-materiaal is echter anders en beschermt het ei tegen uitdroging. Terwijl Saldidenеieren water opnemen, doen Leptopodidae dit hoogstwaarschijnlijk niet. De uitwendige chorion textuur is kenmerkend voor de soorten. De differentiaties van het chorion, verband houdend met het respiratie-systeem, lopen niet altijd parallel met de indeling in genera en subfamilies. Waarschijnlijk zijn zij pas ontstaan nadat de hoofdgroepenindeling van de superfamilie zich reeds gevormd had.

Amphibicorisae

Eieren worden afgezet boven, op, of onder de waterspiegel, afhankelijk van de soort, veelal constant per familie. Verschillende stratificaties van het chorion komen voor: compact, zonder holten (Hebridae, Mesoveliidae), fijn poreus met inwendige sponslaag (Gerridae, Veliidae), omvangrijke uitwendige en inwendige porositeit (Hydrometridae). Deze verschillen zijn van taxonomische betekenis, terwijl een duidelijke correlatie met oecologische verschillen ontbreekt. Zowel de gelei-laag, die de meeste Amphibicorisae eieren omgeeft, als de uiterst dunne suprachorale laag (ook in Saldidae aanwezig) worden in de ovariolen afgescheiden. De eischaal van *Macrovelia*, *Oravelia* en *Chepuvelia*, monotypische genera met een omstreden taxonomische positie, vertoont gelijkenis met die der Veliidae. De structuur van de eischaal van *Hydrometra* en *Limnobatodes* is uiterst ingewikkeld. Het uitwendige netwerk met een gedeeltelijke plastron-structuur staat via de micropylaire koker in verbinding met een open, normaliter met lucht gevulde, laag in de binnenste zone van de eigenlijke schaal. In tegenstelling tot andere Amphibicorisae is het *Hydrometra*-ei voor een normale incubatie niet aangewezen op wateropname. Ofschoon op grond van deze feiten het *Hydrometra*-ei overeenkomt met een typisch terrestrisch ei met speciale voorzieningen die het ei zowel tegen uitdroging als tegen de nadelen van langdurige bevloeiing beschermen, kan het zich normaal ontwikkelen bij een continu verblijf onder water, zelfs wanneer de schaal geheel beroofd wordt van de luchtvoorraad.

Pentatomomorpha

Eieren van deze groep zijn in het algemeen niet bestand tegen langdurige submersie. De schaal is gekarakteriseerd door een scherp begrensde inwendige laag met holten

welke via een gevarieerd aantal met poreus materiaal gevulde kokers (altijd meer dan één en meestal op de voorste helft van het ei) in contact staat met de buitenlucht; de kokers varieren in vorm en lengte en elk omgeeft een centraal micropylair kanaal (aeromicropyle). Overigens is het chorion massief, één- of meerlagig; de dikte varieert van enkele micra (de plesiomorfe conditie) tot 100 μ). Een uitwendige tralieachtige structuur met waarschijnlijk respiratorische functie tijdens langdurige regen komt voor bij vele tropische Plataspidae. De buitenste laag van de schaal van *Neuroctenus* sp. (Aradidae) bezit een merkwaardige vlokkige structuur welke los tegen de binnenste laag aanligt. *Idiostolus* sp. (Idiostolidae) uit Chili (*Nothofagus* bos) wijkt af van alle tot nu toe onderzochte Pentatomomorpha, doordat de schaal geheel massief is en geen spons-structuur rondom de micropyle vertoont.

Cimicomorpha

Eieren van de Cimicoidea *s.l.* overleven langdurige submersie, maar het proces van uitkomen wordt zeer bemoeilijkt. De eischaal bezit een inwendige aerostatische laag, welke terzijde van het eideksel in de aeropylen uitmondt zonder enige associatie met de micropylen. Alleen in *Pseudoloxops* en *Malacocoris* vormen de aeropylen een eenheid met de micropylen. Aantal, plaats en vorm van de luchtkanalen varieert van soort tot soort. De grootste variatie wordt gevonden binnen de Miridae; een vaste combinatie van eigenschappen is meestal niet gecorreleerd met de huidige indeling in genera en subfamilies. Alle overgangen komen voor tussen een regelmatige rangschikking der aeropylen rondom het eideksel en samenbundeling der aeropylen in de voorste en de achterste hoek van de voorpool. De laatste, apomorphe, toestand heeft vooral in de Dicyphinae en in *Helopeltis* en aanverwante genera geleid tot de vorming van lange ademhalingshorens. Hierin monden de aeropylen geïsoleerd uit, maar in *Termatophylidea opaca* en in *Monalocoris filicis* eindigt de hoorn in een soort plastron-structuur. Straalvormige uitstulpingen rondom de voorste eipool in enkele Cylapinae en in de Microphysidae functioneren waarschijnlijk ook als plastron. De aeropylaire kransslippen in soorten van de laatste familie zijn beweeglijk. De slippen sluiten zich bij hoge vochtigheid en vormen een gesloten kap boven het eideksel. Bij afnemende luchtvochtigheid wijken de slippen met zichtbare snelheid uit elkaar. In het algemeen heeft het eideksel geen pneumatische voorzieningen. In verschillende Miridae echter heeft zich hierop een nieuw poreus systeem ontwikkeld, met of zonder ademhalingshorens. Geheel afwijkend van het Cimicomorpha-type zijn de eieren van typische Bryocorinae, *Embiophila* (Plokiophilidae) en Thaumastocoridae.

Hydrocorisae

Het overgrote deel van de buitenste laag van de eischaal is geperforeerd door een systeem van kanalen, welke doorlopen tot op de dikke binnenste laag (Notonectidae, Pleidae, Helotrephidae, Naucoridae, Ochteridae, Gelastocoridae). Bij de Corixidae, Nepidae en Belostomatidae monden de kanalen uit in een sponslaag, welke aan de

binnenzijde door een zeer dun chorionlaagje wordt begrensd. Alleen in de Nepidae en Belostomatidae schijnt de aanwezigheid van atmosferische lucht in het chorion een vereiste te zijn voor een normale ontwikkeling van het embryo. Bij enkele *Ranatra*-soorten van de Ivoorkust bleek dit echter niet het geval te zijn, ofschoon hun chorionstructuur niet afwijkt van die der Europeesche Nepidae (ademhalingshorens met plastron). De sponsachtige micropylaire koker (Corixidae, Notonectoidea) en sterk poreuze strippen in de buitenste chorionlaag *(Micronecta, Helotrephus)* spelen mogelijk een rol in de waterabsorptie, vooral na de blastokinese. Hoewel in de meeste families een locale hydropyle in de serosa optreedt (plaats is verschillend per familiegroep), komt een duidelijke chorionische hydropyle alleen voor in de Nepidae en sommige Belostomatidae.

Dipsocoroidea, Enicocephaloidea

De eischaal van *Pachycoleus* en *Cryptostemma* vertoont een uniek stelsel aeropylen, beperkt tot een smalle longitudinale zone van het ei. *Ceratocombus* en de weinige soorten Schizopteridae die bestudeerd werden, hebben een geheel poreuze schaal. Enicocephalidae bezitten een dunne, naar het schijnt geheel massieve eischaal.

Aan de hand van diagrammen vervaardigd naar elektronenmicroscopische foto's (fig. 264–267) wordt nagegaan in hoeverre de stratificaties van de verschillende schaaltypen met elkaar te homologizeren zijn (p. 259–264). De aerostatische binnenzone van de schaal van de meeste Geocorisae en van *Hydrometra* is niet homoloog met de poreuze, al of niet met lucht gevulde, inwendige laag van bijv. Saldidae, vele Amphibicorisae en Hydrocorisae. Dit is een van de redenen waarom de gebruikelijke indeling van het chorion in exo-en endochorion niet door ons wordt gebezigd. Wij concluderen dat een dunne, solide eischaal op de primitieve toestand duidt *(Hebrus, Mesovelia, Idiostolus, Embiophila, Oncylocotis)*. Later opgetreden verschillen in de opbouw van de schaal zijn, wat de porositeit betreft, veelal niet rechtstreeks te herleiden tot actuele verschillen in de oecologische verhoudingen, waaraan de eieren zijn blootgesteld.

3.1.2 Micropylair systeem

Aantal

Een overzicht van het aantal micropylen per familie wordt gegeven in fig. 268. Onze conclusie is dat het wantsenei oorspronkelijk slechts één micropyle bezeten heeft, gelegen in het centrum van de voorpool. Deze conditie is nog behouden in de Amphibicorisae (behalve de meeste Veliidae en enkele Gerridae) en vele Hydrocorisae (Micronectinae, enkele Corixinae, de Naucoridae *Coleopterocoris, Aphelocheirus*, alle Notonectoidea en, gedeeltelijk, de Ochteridae en Gelastocoridae). De enkelvoudige micropyle aanwezig in een paar terrestrische taxa (gedeelte van Nabidae en in de enige onderzochte soort der Velocipedidae) is secundair ontstaan door het wegvallen van

een tweede. Twee micropylen is nl. het basisaantal voor de cimicoide-achtige families. Door de evolutie van traumatische inseminatie, waarbij micropylen overbodig werden, is het aantal van 2 gereduceerd tot 1, en tenslotte tot nul (deel van Nabidae, Anthocoridae, Cimicidae en zeer waarschijnlijk Pachynomidae). De Reduviidae vertonen in tegenstelling hiermee een progressieve toename der micropylen van 3 tot 15. Anagenetische vermeerdering vanaf 2 micropylen *(Idiostolus)* tot een maximum aantal van 70 heeft plaatsgevonden in de Pentatomomorpha. Enige correlatie tussen deze aantalstoename en volumetoename van het ei is in deze groep aanwijsbaar, hetgeen te verklaren is doordat de micropylen in het aeratiesysteem zijn geïncorporeerd.

Verandering van plaats

De centraal in de voorpool gelegen, enkelvoudige micropyle, is afhankelijk van de taxonomische groep, naar voren of naar achteren verschoven. Deze verschuiving is geschied onder invloed van een zich uitbreidend respiratorisch systeem of een wijziging in de manier van ei-afzetting. De vermeerdering van het aantal micropylen heeft op verschillende wijzen plaatsgevonden, afhankelijk van het al of niet verschoven zijn van de oorspronkelijke, enkelvoudige micropyle. Een indirecte aanwijzing werd verkregen dat, vooral bij de Pentatomomorpha, met de vermeerdering van de micropylen een toename in het aantal follikelcellen en een afname in hun afmetingen gepaard is gegaan. Toen de micropylen eenmaal in een kring gerangschikt waren, werd de mate van uitbreiding en verplaatsing van de kring geregeld door het tijdstip van ontstaan en de verplaatsing van het eideksel. Dergelijke wisselwerkingen tijdens de evolutie van het micropylaire apparaat worden uitvoerig besproken.

Bouw en oriëntatie

De verschillende typen micropylen (vorm; hoek waaronder de schaal wordt doorboord; inwendige en uitwendige verlenging) worden met elkaar vergeleken. De diameter van het kanaal (waarschijnlijk ook van de spermatozoiden) is vrij constant (1–3 μ), ongeacht de grootte van het ei. Oorspronkelijk bezat de ongepaarde micropyle een inwendig verlengstuk, dat binnen het ei naar de voorzijde omboog (o.a. *Hebrus*). Bij vermeerdering van het aantal micropylen en hun verplaatsing heeft de afbuiging van het inwendig verlengstuk een geleidelijke verandering van richting doorgemaakt. Bij de Pentatomomorpha kan dit proces als anagenese duidelijk in etappen achterhaald worden. De draaiing (maximaal 180°) vond hier, zowel als bij andere niet verwante groepen, plaats in de richting van de wijzers van de klok (voorpool naar waarnemer gericht). Een cladogenetische divergentie, wat deze eigenschap betreft, is opgetreden in *Monalocoris, Bryocoris* (in tegenstelling tot overige Miridae) enerzijds en in *Oncylocotis* (Enicocephalidae, in tegenstelling tot alle overige families) anderzijds.

De evolutie van het micropylaire apparaat wordt schematisch weergegeven in fig. 269.

3.1.3. Ontsluiting van eischaal

De plesiomorfe toestand welke bij vertegenwoordigers van alle hoofdgroepen der wantsen nog voorkomt, was ongetwijfeld een mediane lengtescheur vanaf de voorpool. De longitudinale ontsluiting heeft zich in de meeste hoofd-taxa tot een ringvormige ontsluiting ontwikkeld; dit geschiedde langs verschillende wegen in afhankelijkheid van de eivorm. Bij een van de mogelijkheden ontstond er tijdelijk een deksel in wording op één van de laterale eizijden; deze toestand is nog aanwezig in *Bryocoris*, *Monalocoris* en *Plea*. De uiteindelijke ligging van het deksel werd bepaald door veranderingen in eivorm, in ovipositie-modus, in gerichtheid van de micro-elementen van de schaal en in de vorm en plaats van de eitand.

Het ontstaan van de zeer gevarieerde verschijningsvormen van ei-ontsluiting wordt per hoofdgroep beredeneerd. Een overzicht der voornaamste typen en hun fylogenesen wordt schematisch weergegeven in fig. 270, 271 en 272. Piesmatidae hebben een stervormige ontsluiting. Een voorwaarde voor het ontstaan en behoud van deze structuur is het bezit van relatief weinig, grote follikelcellen. Uit andere gegevens wordt geconcludeerd dat een ovariool met dergelijke eigenschappen plesiomorf is. Het ontsluitingstype der Piesmatidae komt bovendien voor in de Stenocephalidae, een deel der Lygaeidae en, in cladogenetisch gewijzigde vorm, in de Malcidae. In de overige Lygaeidae zijn de follikelcellen kleiner en talrijker geworden, zoals uit hun opdruk op de schaal valt af te leiden. De radiale ontsluiting werd weer een medio-longitudinale. Zij ontwikkelde zich via een laterale longitudinale naad (Alydidae) tot een goed gedifferentieerd rond deksel in de hoger geëvolueerde taxa (Coreidae, Rhopalidae).

3.1.4 Discussie

Chorion en aeropylair systeem

De chemische samenstelling van het chorion van *Rhodnius* (BEAMENT, 1946) wordt besproken aan de hand van het morfologische beeld (onze elektronenmicroscopische foto's). De resistente proteïnelaag van BEAMENT is identiek met de van holten voorziene, inwendige schede welke met de buitenlucht communiceert via aeropylen. Van de meeste soorten kan het open geleidingssysteem lichtmicroscopisch geanaliseerd worden. In tegenstelling tot vroegere onderzoekers, konden wij volgens de optische methode en zonder toepassing van kleuring of injectie-methoden, duidelijk onderscheid maken tussen aeropylen en micropylen. Het melaninisatie-proces van wantseneieren wordt herleid tot verschillende principes. De eischaal heeft geen regelapparatuur voor gasuitwisseling. Alleen in de Microphysidae komen bewegende aeratieslippen voor. Bij enige andere soorten heeft het adulte dier de regelende functie overgenomen (Belostomatidae, ♂ draagt eieren op rug en aereert deze; *Phyllomorpha* (Coreidae) met eieren op de rug onttrekt zich aan brandzone). De bevindingen omtrent het respiratorische systeem van wantseneieren, i.h.b. de ademhalingshorens en plastronstructuren, worden vergeleken met literatuurgegevens. Enkele van onze gegevens (bijv. betreffende de ei-

ontwikkeling van *Hydrometra* en *Ranatra*) lijken vooralsnog niet in overeenstemming met de theorie van plastron-ademhaling. Van de onderzochte soorten wordt in grafieken (fig. 273, 274) zeer ruw het verband bepaald tussen de maximale grootte van de follikelcellen (indirect bepaald aan de hexagonale tekening op de eischaal), de eilengte en de lengte van het moederdier. Het gemiddelde van de absolute grootte van de cel verandert niet bij toenemende grootte-klassen der eieren; de absoluut grootste cellen worden bij de kleinste eieren aangetroffen. De kleinste soorten hebben bovendien in het algemeen de relatief grootste eieren. Met deze anagenese: kleiner worden der eieren en hun hexagonale bekleding bij grootte-toename der soorten, lopen andere verschijnselen parallel. Bij plesiomorfe soorten is het aantal ovariolen per ovarium zeer gering, rijpen weinig eieren tegelijk en is er een lange ovipositie-periode. Apomorfe soorten leveren als regel in korte tijd veel eieren uit een groter aantal ovariolen.

Micropylen

In aansluiting aan onze gegevens over zekere wetmatigheden tijdens de evolutie van het micropylair systeem bij wantsen, wordt een overzicht gegeven van aantal en ligging der micropylen bij andere insektenorden. Er zijn aanwijzingen dat bij nader onderzoek van meer soorten eenzelfde anagenese wat betreft vermeerdering en verplaatsing der micropylen vanaf de voorpool zal blijken. Eventuele bijkomstige functies van de micropylen worden besproken.

Ontsluitingsnaad

De taxonomische geldigheid van de begrippen 'pseudoperculum' en 'operculum' blijkt geringer te zijn dan door SOUTHWOOD (1956) werd gesteld. Een scherp onderscheid tussen beide typen en hun toepasbaarheid voor insekteneieren in het algemeen is alleen mogelijk wanneer de definitie wordt vernauwd. Een suboperculum heeft geen gegroefde ringsluiting en wordt afgeworpen door middel van een eitand. Een operculum wordt primair opgelicht met behulp van vloeistofdruk. In zijn perfecte vorm functioneert een verdikkingsring van de serosacuticula hierbij als wig en heeft het operculum een groefsluiting. In zijn nog niet perfecte vorm is het operculum niet van een pseudoperculum te onderscheiden, wanneer het mechanisme van de ontsluiting niet bekend is.

3.2 Schetsmatig overzicht van de embryonale ontwikkeling

3.2.1. Duur van de incubatie, diapauze

Incubatieperioden van een aantal soorten zonder eidiapauze worden onder enig voorbehoud met elkaar vergeleken. Saldidae-soorten levend in labiele habitats hebben een snellere ei-ontwikkeling dan soorten van meer stabiele vindplaatsen. De ontwik-

keling van Hydrocorisae en Reduviidae verloopt in het algemeen het traagst. Taxonomische affiniteit van beide groepen wordt op andere gronden aangetoond. Ruim 85% van de 200 soorten Nederlandse Miridae overwintert in het eistadium; in de overige families is het percentage laag. Diapauze treedt op in de eerste helft van de embryonale ontwikkeling (uitzondering: *Nysius thymi*), maar niet vóórdat het kop-romp stadium van de kiemband scherp is begrensd. Het stadium van diapauze is constant per soort (zie fig. 275). 'Preconditioning' van het ei van *Chiloxanthus pilosus* heeft een verschuiving in het stadium van de embryonale diapauze tot gevolg. Alle eieren in diapauze bezitten een serosacuticula, óók wanneer de ontwikkeling van het embryo tot stilstand is gekomen op een tijdstip waarop bij zich normaal ontwikkelende eieren de serosacuticula nog niet is afgescheiden. Deze beschermende laag is voor het overliggende ei van essentieel belang. Een overzicht van de overwinteringswijzen bij wantsen wordt gegeven. Zeer gevarieerde reproduktiecycli komen voor, welke onder de volgende secties worden besproken (p. 294–297):

1. eirijping bij lage temperatuur (0–4 °C, sommige Corixidae, Notonectidae, Veliidae, Miridae);
2. afzetting van eieren in de herfst, waarbij echte diapauze achterwege blijft *(Mesovelia)*;
3. overwintering van legrijpe wijfjes *(Saldula orthochila)*;
4. overwintering van legrijpe wijfjes *(Temnostethus gracilis)*; de ovariolen bevatten in de nazomer rijpe eieren met ontwikkelde kiemband in diapauze; deze eieren worden pas na de winter gelegd;
5. afzetting vóór de winter van eieren, die in diapauze gaan, en van eieren van hetzelfde wijfje en dezelfde oögenese-cyclus ná de winter, die géén diapauze doormaken (*Notonecta maculata*, enkele Lygaeidae);
6. uitzonderlijke seizoenstypen van strenge eidiapauze in univoltiene soorten *(Harpocera thoracica, Pantilius tunicatus)*;
7. ovipositie onder invloed van dalende temperatuur *(Himacerus apterus)*;
8. niet gestabiliseerde cycli (verschillende Saldidae).

Nauwkeurig experimenteel onderzoek is nodig om de evolutie van genoemde reproduktie- en diapauzeverschijnselen in een onderlinge samenhang te plaatsen.

3.2.2 De voornaamste karakteristieken van de embryogenese en hun waarschijnlijke evolutie

Bij het opstellen van het fylogenetisch systeem der embryogenesen worden de volgende verschijnselen met elkaar vergeleken: de plaats en mate van zichtbare ontwikkeling van het 'pro-embryo' (verdikking van blastoderm); plaats van blastopore; groei, oriëntatie, vormverandering en verplaatsing van de kiemband, van het embryo en van de prolarve (volgroeid embryo). Ten aanzien van al deze verschijnselen is er een duidelijke divergentie opgetreden, die parallel loopt met familiegroepen. De gegevens worden in diagrammen weergegeven en in een stamboom verwerkt (fig. 276). Een onderscheid wordt gemaakt tussen de verschillende vormen van rotaties rondom

de lengte-as, die door de kiemband, het embryo of de prolarve worden volbracht. De richting van de meeste rotaties is met de wijzers van de klok mee (voorpool van ei naar waarnemer toegekeerd). Betreffende het ontstaan van de rotaties worden verschillende mogelijkheden geopperd (p. 30, 142, 212, 214, 226).

Embryorotatie van 180° voorafgaande aan de omrolling beschouwen wij als een plesiomorfe eigenschap. Zij komt voor bij vertegenwoordigers van alle hoofdgroepen, behalve in de Reduviidae en het merendeel der Pentatomomorpha. Nog niet in balans zijnde overgangsfasen tussen embryogenesen met en zonder embryorotatie worden gevonden in Gerridae, Hydrometridae, Cydnidae en Acanthosomatidae. Een typering van de embryogenesen naar de vormingswijze van de kiemband en de positie van het embryo in het systeem van plasma en dooier wordt gegeven op p. 300–301. De oorspronkelijkste vorm van embryogenese in Heteroptera is invaginatie van de kiemband in het centrale gedeelte van de dooierkolom, waarbij het contact tussen kop en serosa niet verbroken wordt (meeste Amphibicorisae, Cimicoidea *s.l.*, Dipsocoridae). Tijdelijke totale immersie komt voor in Saldidae, *Gerris* en *Hesperoctenes*. De progressieve overgang van het immerse type naar het superficiële type is in etappes te vervolgen binnen de Pentatomomorpha en de Hydrocorisae. De progressie heeft echter een cladogenese gevolgd die beide groepen sterk doet divergeren; in de eerste ligt het embryo vóór de blastokinese met de rug tegen de eiwand, in de laatste daarentegen met de buikzijde. De embryogenese van de Reduviidae sluit aan bij die der Hydrocorisae, maar is verder geëvolueerd. Vele Harpactorinae vertonen het semi-invaginatie type. Soorten van het genus *Coranus* vertegenwoordigen, beoordeeld naar uitwendige aspecten, het holometabole type, d.w.z. zonder invaginatie en zonder blastokinese in de ruimste zin. De vormveranderingen van het embryo, ontogenetisch en evolutionistisch, en de verschuivingen van de blastoporus worden besproken op p. 301–302.

Het uitzonderlijk belang van de embryologische gegevens voor de hogere systematiek is duidelijk. Het embryogenesetype wordt niet beïnvloed door de eivorm; de lichaamsafmetingen van de kiemband weerspiegelen niet die van de toekomstige larve. Allometrie der poten echter komt reeds tijdens de knopformatie tot uiting.

3.2.3 Andere embryologische verschijnselen, welke variëren in verschillende taxa

Blastoderm

De voor-afbeelding van de kiemband in het blastoderm is in de meeste groepen zeer vaag. Een vervroeging van de differentiatie treedt echter op in Reduviidae (behalve *Empicoris*), Naucoridae *(Ilyocoris)* en Nepidae, en cladogenetisch verschillend in hoger ontwikkelde taxa der Pentatomomorpha.

Kiemcellen

Deze worden tijdens de invaginatie met het staartstuk van de kiemband naar boven gedrukt. Zij liggen vast tegen de kiemband, maar in Saldidae en *Gerris* raken zij er tijdelijk van geïsoleerd.

Verschijning van oog-pigment

In het algemeen treedt differentiatie en pigmentatie van het oog pas op na de blastokinese, ongeacht of het oog veel of weinig ommatidia bezit. De differentiatie geschiedt centrifugaal. In het embryo van Saldidae heeft het oog zijn uiteindelijke omvang en pigmentatie reeds bereikt vóór de blastokinese.

Hydropyle

Het vermogen van het ei om water op te nemen is niet altijd gecorreleerd met de aanwezigheid van een locale hydropyle. Een serosahydropyle in de basale en soms in de cephale helft van het ei komt voor in Saldidae, Amphibicorisae (behalve *Hydrometra*) en in de meeste Hydrocorisae. Het lot van deze hydropyle gedurende de blastokinese kan zeer verschillend zijn per taxon (waarnemingen beschreven op p. 50 *(Mesovelia)*, p. 70 *(Gerris)*, p. 224 *(Notonecta)*). Een mogelijk secundaire hydropyle komt voor in vertegenwoordigers van de Belostomatidae. Saldiden embryonen ontwikkelen een merkwaardig cephaal orgaan, dat zich door de serosacuticula heen onder een groot gedeelte van de eischaal uitspreidt (p. 28–30). Dit orgaan dient waarschijnlijk eveneens voor absorptie van water.

Blastokinese en vorming van dorsaal orgaan

De omrolling van het embryo werd *in vivo* bestudeerd bij een aantal soorten. Dit proces, alsmede de dikwijls eraan voorafgaande of gelijktijdig verlopende 180° rotatie wordt geheel geregeld door partiële contracties van het vergroeide amnion-serosavlies en mogelijk van het entoplasma-dooiersysteem, maar niet door intrinsieke bewegingen van het embryo zelf. Het restant van de samengetrokken serosa in de voorpool met de ingesloten dooier noemen wij de serosaprop (serosal plug). Deze prop wordt na verloop van tijd (behalve in enkele Miridae) opgenomen in het toekomstige pronotumgedeelte en vormt daar het secundaire dorsale orgaan. De opname geschiedt door een spectaculaire peristaltiek, in eerste instantie door een abrupte, sterke contractie van cellen dichtbij de vergroeiingsnaad van amnion en serosa (beschrijving van waarnemingen op p. 34, 224).

3.2.4 Discussie

Incubatie, diapauze

De geldigheid van de stelling dat er een principieel verschil zou bestaan tussen holo- en hemimetabole insekten ten aanzien van de duur van de incubatie, wordt door ons zeer betwijfeld. De waarnemingen over eidiapauze bij wantsen worden vergeleken met gegevens betreffende insekten uit andere Orden.

Embryogenesetypen

De enige Holometabola waarvan embryorotatie bekend is, zijn de Culicidae. De embryogenese der Culicidae is ten opzichte van de hogere Diptera meer van het ongedetermineerde type. Omgekeerd vinden wij bij wantsen enkele embryogenesen, die in de richting van het gedetermineerde type wijzen. De evolutionaire relatie tussen het hemimetabole en holometabole type wordt besproken. De diversiteit en de progressie in de evolutie van de embryogenesen bij wantsen is veel groter dan bekend is voor enige andere Orde der insekten. Ontwikkelingstypen die tot nu toe als karakteristiek golden voor bepaalde Orden, blijken als tussenschakels in de fylogenese van wantsen op te treden. De evolutie der insekten-embryogenesen wordt gekenmerkt door een hoge graad van parallelismen. Daarom heeft het voorlopig weinig zin om op gevonden overeenkomsten en verschillen tussen de Orden verwantschapsbetrekkingen te funderen. De cladogenese en de anagenetische progressies zullen eerst uitvoeriger binnen elke Orde vastgesteld moeten worden. Aan de hand van onze bevindingen, worden de opvattingen van SHAROV (1966) omtrent de ontwikkelingsevolutie van het insekten-embryo aan een discussie onderworpen.

Dorsaal orgaan

Het spectaculaire ontstaan van het dorsaal orgaan bij wantsen is vermoedelijk een algemeen entomologisch verschijnsel. Het ontbreken van nadere gegevens hierover bij andere groepen van insekten is waarschijnlijk te wijten aan te korte waarnemingstijden.

3.3 De ontsluiting van het ei

3.3.1 De persistente serosaprop

De serosaprop wordt normaliter in korte tijd geïnvagineerd tot het dorsaal orgaan. In sommige Miridae blijft de prop, met of zonder dooierinhoud, bestaan tot de eiontsluiting. Met de persistentie van de prop gaat een vroegtijdige zwelling van de serosacuticula gepaard.

3.3.2 Omhulsels van het embryo

Serosacuticula

In vele soorten Amphibicorisae, Hydrocorisae en Miridae van de Geocorisae verschijnt een zwart exudaat tegen de buitenkant van de serosacuticula. Het melaniniseringsproces is beperkt tot enkele families en heeft mogelijk een functie in de regeling van het watertransport.

Omhulsels van onzekere herkomst

In het ei van *Gerris*, *Notonecta* en *Carpocoris* wordt een extra omhulsel aangetroffen. In *Gerris* is het waarschijnlijk een additionele serosacuticula. Wat betreft het vlies in de twee overige genera en waarschijnlijk ook in *Dysdercus*, zijn argumenten aan te voeren, die er tegen pleiten dat het een produkt is van de serosa (bezit van eitand), of van de embryonale epidermis (tijdstip van afscheiding, geen poot-evaginaties).

Embryonale cuticula

De eigenschappen worden opgesomd voor zover ze niet betrekking hebben op de ruptor ovi.

3.3.3 Mechanismen voor het verbreken van membranen en chorion

Vier methoden om de ei-omhulsels te verbreken komen voor, nl. door snijden (A), door perforeren-optillen (B), door druk van de embryonale cuticula (C) en door druk van de serosacuticula (D). De evolutie van de structuren, die bij deze toepassingen gebruikt worden, is schematisch weergegeven in fig. 278. De conditie zoals die gevonden wordt in *Hebrus*, benadert het meest het archetype, d.w.z. het bezit van een dwarse ruptor ovi op de embryonale cuticula, en wel op de scheiding van ante- en postclypeus. De stam van de Amphibicorisae vertoont een cladogenese. Enerzijds heeft *Mesovelia* methode C ontwikkeld, alhoewel de cephale structuren nog direct zijn af te leiden van die van *Hebrus*. Op deze methode sluit die der Cimicoidea, *s.l.* aan, waarin het procédé C geleidelijk werd vervangen door D. Anderzijds werd in een aantal Amphibicorisae methode A geperfectioneerd. De gepaarde clypeale ruptor *(Hebrus)* werd ongepaard *(Microvelia)* en ontwikkelde zich tot een longitudinale frontale ruptor *(Gerris, Hydrometra)*. Deze anagenese heeft zich herhaald in de Leptopodoidea. De homologie van de cephale armatuur van de embryonale cuticula van Amphibicorisae wordt vastgesteld aan de hand van die van Saldidae; deze bezitten gelijkertijd een frontale en een clypeale ruptor (fig. 277). In de Pentatomomorpha werd de ontsluiting volgens principe B verder ontwikkeld; de anagenese startte vanaf het *Gerris*-type. De frontale ruptor verschoof door reductie van de vertex geleidelijk naar achteren tot aan de thorax. De ei-ontsluiting bij Hydrocorisae en Reduviidae volgt type D. De dynamiek

van het uitkomen van het ei wordt voor enkele soorten gedetailleerd beschreven, bijv. *Saldula*, *Mesovelia* en *Nabis* met cephale ampulle, *Carpocoris* met twee op elkaar liggende ruptors, *Dicyphus*, *Liocoris*, *Bryocoris* met vroegtijdige, langzame, cilindrische verlenging van de serosacuticula, Hydrocorisae met explosieve uitstulping van de serosacuticula.

3.3.4 Discussie

Serosacuticula en persistente serosaprop

Zwelling van de serosacuticula, voortijdige breuk van het chorion tot gevolg hebbend, is niet noodzakelijkerwijs gecorreleerd met endofytische afzetting van het ei; identieke verschijnselen bekend van andere Orden worden opgesomd. De cilindrische verlenging van de serosacuticula in Miridae en in vele cicaden is echter een aanpassing aan de ingezonken ligging van het afgezette ei. Onze gegevens duiden er op dat de persistente serosaprop voor directe overdracht van water van buiten het ei naar binnen zorgdraagt en niet indirect via holocriene activiteit van de serosa. De prolarvarotaties van Notonectidae en Naucoridae (voor waarnemingen zie p. 226, 228) dienen waarschijnlijk om het oplossen van de binnenlaag van de serosacuticula te versnellen. In verband hiermee wordt de functie van de pleuropodia besproken. Wij wijzen verder op de grote verwarring in de literatuur wat betreft de identificatie van subchorale lagen.

Ruptor ovi

In cicaden heeft zich een soortgelijke evolutie van ontsluitingsmechanismen voltrokken als in de wantsen. De gegevens over oviruptors in andere Orden worden gecompileerd.

3.4 Bilaterale asymmetrieën. De polariteit van het ei-systeem

3.4.1 Asymmetrieën

Een overzicht wordt gegeven van het onverwacht grote aantal gevallen van bilaterale asymmetrie. Deze worden veroorzaakt door: totaalvorm ei (Plataspidae), micropylaire systeem, ontsluitingsnaad, choriondeksel, verdikkingen van het blastoderm, cephale lobben, positie van de blastopore, vorm van de kiemband, dichtheid van de dooiermassa, rotaties, contractie van de serosa en verplaatsing van de serosahydropyle. Bijna al deze asymmetrieën zijn extreem monostroof. Het vouwpatroon van poten en antennen van de prolarva (diagrammen fig. 279, 280) vertoont racemische asymmetrie, d.w.z. linkstype en rechtstype zijn even talrijk vertegenwoordigd. Amfidrome en monostrophe asymmetrie komt vooral voor in de zeer uniforme en niet van de eivorm afhankelijke rangschikking van de poten in de Hydrocorisae; de asymmetrie is

gelijk gericht in alle onderzochte soorten (fig. 280Q–T), maar in *Plea atomaria* overheerst juist de inverse vorm.

3.4.2 De ligging van het afgezette ei

De standen worden gerubriceerd in drie groepen: I platliggend tegen substraat, II rechtopstaand, III ingezonken in substraat. De verdeling der standen per familie wordt aangegeven in tabel 2, p. 332. Wij beredeneren voor elke hoofdgroep hoe de evolutie van stand I naar II, of van stand I naar III (in sommige gevallen vice versa) heeft plaatsgevonden. Deze evolutietrends worden verwerkt in een schema (fig. 281). Selectiefactoren van geheel verschillende aard (tekort aan substraat, bewaking van het ei, pneumatisatie van het ei door de imago na afzetting, bescherming tegen predatoren) hebben geleid tot afzetting van het ei in vertikale stand. Het bereiken van een bepaalde fase in de evolutie van de embryogenese kan eveneens tot deze verandering in positie geleid hebben.

3.4.3 Rotatie van het ei

Wij beredeneren (p. 336) dat het Protoheteropteron dat geen lange legboor bezat, de bipotentie had voor ei-afzetting 'naar achteren' en 'naar voren'. De verschillende theoretische mogelijkheden van ovipositie worden binnen de centrale cirkel van fig. 281 aangegeven. Saldidae (p. 10) en Mesoveliidae (p. 48) bezitten een krachtige 'concave' legboor en zetten het ei zodanig af, dat rotatie van het ei 180° rondom zijn lengte-as binnen het moederdier verondersteld moet worden. *Gerris* (p. 66) regelt of niet-geroteerde, dan wel-geroteerde eieren afgezet worden in afhankelijkheid van de ovipositie óp, resp. onder het substraat. Voorbeelden van 90° rotatie van het ei leveren enkele Pentatomidae (*Aeliomorpha*, *Macrina*, p. 118) en de eivorm is met deze legwijze in overeenstemming

3.4.4 Vergelijking van de embryogenesen volgens gestandaardiseerde schema's

Het vaststellen van een bepaalde eizijde als morfologisch dorsaal of ventraal wordt zeer bemoeilijkt door rotatie van het ei. Aan de hand van de embryogenesetypen (fig. 276) en de eitypen, op gestandaardiseerde wijze afgebeeld (fig. 282–285), wordt bepaald welke eieren 180° geroteerd werden afgezet. Het blijkt dat rotatie van het ei door veel meer soorten wordt toegepast, dan op grond van eerdere aanwijzingen werd vermoed.

3.4.5 De dorsoventrale polariteit van het eisysteem

Uitgaande van het oorspronkelijkste type der embryogenese (fig. 276a) en van eiafzetting 'achterwaarts', zonder rotatie, wordt de polariteit van het afgezette ei in relatie tot de hoofdassen van het wijfje bepaald. De zijde van het ei waar het 'pro-

embryo' in het blastoderm zich ontwikkelt wordt als ventraal aangeduid. Wij stellen de volgende regels op: 1. Alle oppervlakkig afgezette eieren, welke een 180° embryorotatie vertonen, worden met de ventrale zijde tegen het substraat geplakt; de manier van eiafzetting (volgens beide methoden van *Gerris* of volgens die van *Mesovelia*) heeft hierop geen invloed; het volgroeide embryo ligt met de buikzijde tegen de dorsale eizijde. 2. Eieren zonder embryorotatie liggen eveneens ventraalwaarts tegen het substraat, behoudens wanneer het ei 180° geroteerd wordt afgezet; de morfologische zijden van het volgroeide embryo vallen samen met die van het ei. Dezelfde regels gaan op voor rechtopstaande of voor in planteweefsel geboorde eieren, wanneer zij worden afgebeeld als zijnde horizontaal afgezet (fig. 283J; 284N). Een beschouwing wordt gewijd aan enige mogelijke interacties tussen de evolutie van de embryogenese, de plaatsing van het ei en verandering van de eivorm.

3.4.6 Discussie

Asymmetrieën

De vele soorten asymmetrieën in het eisysteem der Hydrocorisae worden in verband gebracht met asymmetrische verschijnselen in het adulte stadium. Het opmerkelijke vouwpatroon van antennen en poten van de prolarve is een karakteristiek van de hemipteroide Orden.

Afgezette eieren in situ

De oorspronkelijke vrije afzetting van eieren wordt aangetroffen in Psocoptera en in de meeste groepen der Homoptera.

Polariteit van het ei

De bipotentie om het legapparaat aan te wenden voor achterwaartse of voorwaartse eiafzetting komt ook in andere Orden voor (Thysanoptera, Hymenoptera, Diptera). Rotatie van het ei is dus waarschijnlijk een meer algemeen entomologisch verschijnsel; deze kan echter alleen indirect aangetoond worden, wanneer de embryogenese en de positie van het wijfje ten opzichte van het afgezette ei bekend zijn. Op p. 340–344 hebben wij getracht criteria te vinden om de polariteit van het eisysteem te bepalen. De in talrijke publikaties aangehaalde zgn. wet van HALLEZ (1886) wordt aan een kritische analyse onderworpen. Wij besluiten tot de volgende gewijzigde formulering: de oriëntatie van de longitudinale en transversale assen van het afgezette ei en het ingesloten pro-embryo correspondeert met die van het leggende wijfje, tenzij de eieren worden afgezet in geroteerde (dwarse of longitudinale) toestand. Deze wetmatigheid geldt ook voor de oriëntatie van de prolarve, wanneer het embryo niet van positie is veranderd. Literatuurgegevens over abnormale oriëntaties van eieren of prolarven worden besproken.

4 Voorlopige discussie over de fylogenie der Heteroptera

4.1 De consequenties van onze gegevens voor de supragenerieke classificatie

De groepskenmerken, ontleend aan het eisysteem, worden besproken per hoofdafdeling. De Leptopodoidea vormen een natuurlijke, van de overige Heteroptera scherp begrensde groep. De Amphibicorisae blijken heterogener dan op grond van andere combinaties van kenmerken kon worden aangenomen en omvatten zeker meer dan één superfamilie. Mesoveliidae en Hydrometridae wijken belangrijk af van het groepstype. Gerridae en Veliidae worden duidelijker tegen elkaar afgegrensd. *Macrovelia* en andere aberrante genera vertonen grote verwantschap met de Veliidae en zeker niet met de Mesoveliidae.

De Pentatomomorpha vormen een natuurlijke groep families, exclusief de Idiostolidae. Elke familie is gekarakteriseerd door een verschil in anagenetische hoogte, zowel in de differentiaties der eischaal als in de embryogenese. De oorsprong der Pentatomoidea gaat verder terug dan die van de overige superfamilies, terwijl de anagenese verder is voortgeschreden. De relaties tussen de families in de lygaeide-coreide vertakking zijn in recente tijd vele malen onderwerp geweest van levendige discussies, resulterend in een zich wijzigend systeem van superfamilies. Onze bevindingen brengen vooral anagenetische trends aan het licht. De Piesmatidae staan in de totaalanagenese basaal, gevolgd door de Stenocephalidae. In tegenstelling tot de meningen, geuit in de jongste literatuur, zijn de Stenocephalidae meer lygaeide- en de Colobathristidae meer coreide-achtig, althans wat het eistadium betreft. Malcidae zijn door cladogenese gescheiden van Piesmatidae. De eieren van Pseudophloeinae en *Hydara* komen overeen met die der Alydidae.

Men rekent tot de Cimicomorpha de volgende groepen: Reduvioidea, Cimicoidea, Joppeicidae, Thaumastocoridae en, onder voorbehoud, de Dipsocoroidea. Ons onderzoek toont aan dat alleen de families, die wij voorlopig gemakshalve in de Cimicoidea in breedste zin samenvatten, tot de Cimicomorpha gerekend kunnen worden (de monotypische Joppeicidae werden door ons niet onderzocht). De kloof tussen de embryogenese der Reduviidae en der Cimicoidea is even groot als die tussen elk van deze groepen en de Pentatomomorpha. De betekenis van de overeenkomsten en verschillen in de structuren van het chorion in de Reduviidae en Cimicoidea wordt belicht. Op basis der eieren verdienen de Bryocorinae (met uitsluiting van de *Helopeltis*-groep) veeleer de status van familie. Verscheidene Miridae genera moeten waarschijnlijk in andere subfamilies ondergebracht worden. Velocipedidae en Pachynomidae hebben nabide-achtige eieren. Thaumastocoridae, Dipsocoroidea en Enicocephalidae nemen alle, wat de eistructuren betreft, een geïsoleerde positie in. Het is niet juist de beide laatste tot een groep, de Dipsocorimorpha, te verenigen.

De mening van verschillende auteurs om de Corixidae van de Hydrocorisae te isoleren en zelfs geheel apart van de rest van de Heteroptera te plaatsen, is niet gerechtvaardigd op grond van het eisysteem. Hydrocorisae, inclusief de Ochteridae en

Gelastocoridae, hebben een uniforme embryogenese en ei-ontsluiting. Daarentegen zijn zij heterogeen wat de chorionische architectuur betreft. Een overzicht wordt gegeven van de zeer verschillende indelingen in superfamilies. Onze argumentatie leidt tot de opvatting dat de stamvorm der Hydrocorisae gezocht moet worden in de tak der Naucoridae en niet in de Ochteridae. Verschillende taxa welke tot nu toe als subfamilies werden opgevat, zullen waarschijnlijk tot families verheven moeten worden (Potamocorinae, Aphelocheirinae, Diaprepocorinae, Micronectinae).

4.2 De betrekkingen tussen de hoofdgroepen der Heteroptera

De gebruikelijke indeling van de Heteroptera is die in Geocorisae, Amphibicorisae en Hydrocorisae. De eerste groep werd door LESTON, PENDERGRAST and SOUTHWOOD (1954) gesplitst in Pentatomomorpha en Cimicomorpha. Wij geven een overzicht van de verwarringen die daardoor optraden toen andere auteurs de morpha-naamgeving uitbreidden tot de overige hoofdgroepen. De resultaten van onze studie leiden tot het onderkennen van de volgende min of meer equivalente hoofdgroepen: Amphibicorisae, Leptopodoidea, Cimicomorpha *s.str.*, Dipsocoroidea, Enicocephalidae, Reduviidae, Thaumastocoridae, Pentatomomorpha en de Hydrocorisae. De terrestrische Heteroptera blijken een sterk polyfyletische oorsprong te hebben, zodat de naam Geocorisae als taxonomische eenheid beter kan vervallen. Een definitieve indeling met nomenclatorische consequenties zal pas worden gegeven aan het eind van Deel III van het gehele werk.

Een voorlopige projectie van de fylogenie der hoofdafdelingen geven wij in fig. 306. Het basale deel van dit diagram wordt gevormd door de Amphibicorisae. De overige 8–9 groepen vonden hun oorsprong in de stamvormen van de Amphibicorisae; zij worden voorgesteld als onafhankelijke stralen reikend tot verschillende anagenetische hoogten. De verantwoording van deze voorstelling van zaken wordt gegeven op p. 361.

4.3 Uitbreiding van het onderzoek

Dit hoofstuk geeft een beknopt overzicht van nieuwe aspecten van de vergelijkende morfologie, die in Deel II en III behandeld zullen worden. De organen en structuren, waarvan de evolutie en fylogenetische betekenis wordt nagegaan, zijn: a. het oog van het eerste larvale stadium (p. 363), b. trichobothria (p. 364), c. praetarsus (p. 365), d. geurklieren (p. 366–369), e. reproductie-organen en ectodermalia (p. 369–372), f. chromosomen (p. 372–374), g. speekselklieren (p. 375), h. darmsysteem (p. 376), i. stigmata (p. 377–378).

References

ALTSON, A. M.	1933	The effects of absence of humidity on the eggs of *Dysdercus* spp. in the field. *Ent. mon. Mag.* 69: 83–85.
ANDERSON, D. S.	1960	The respiratory system of the egg-shell of *Calliphora erythrocephala*. *J. Ins. Physiol.* 5: 120–128.
ANDO, H.	1962	The comparative embryology of Odonata with special reference to a relic dragonfly *Epiophlebia superstes* Selys. *The Japan Society for the promotion of Science, Tokyo* 205 pp.
ANDRE, F.	1934	Notes on the biology of *Oncopeltus fasciatus* (Dallas). *Iowa St. Coll. J. Sci.* 9: 73–87.
ANDREWARTHA, H. G. and L. C. BIRCH	1954	The distribution and abundance of animals. *Chicago* 782 pp.
ANNANDALE, N.	1905	The egg and early larval stages of a Coreid bug, probably *Dalader acuticosta* Amyot et Serv.; with a note on its Hymenopterous parasite. *Trans. ent. Soc. Lond.* 1905: 55–59.
ATWAL, A. S.	1959	The oviposition behaviour of *Bagrada cruciferarum* Kirk. (Pentat.: Heteroptera) and the influence of temperature and humidity on the speed of development of eggs. *Proc. nat. Inst. Sci. India* 25: 65–67.
BADONNEL, A.	1943	Psocoptères. *Faune de France* 42: 1–164.
BAKER, A. C.	1921	The practical significance of the revolution of the embryo in Aphid eggs. *Science, Lancaster* 54: 133–135.
BANKS, C. J.	1939	Records of captures of *S. germari* Fieb. and *C. panzeri* Fieb. (Hemiptera, Corixidae) in Hamsphire and Wiltshire; with a note on the eggs of *S. germari*. *J. Soc. Brit. Ent.* 2: 34–36.
BANKS, C. J.	1949	The absorption of water by the eggs of *Corixa punctata* Illig. (Hem. Corixidae) under experimental conditions. *J. exp. Biol.* 26: 131.
BARANOWSKI, R. M.	1958	Notes on the biology of the royal palm bug, *Xylastodoris luteolus* Barber (Hemiptera, Thaumastocoridae). *Ann. ent. Soc. Amer.* 51: 547–551.
BARTH, R.	1961	Sobre o órgão abdominal glandular de *Arilus carinatus* (Forster, 1771) (Heteroptera, Reduviidae). *Mem. Inst. Osw. Cruz.* 59: 37–43.
BARTH, R. and H. MUTH	1958	Estudos anatômicos e histológicos sôbre a subfamília Triatominae (Heteroptera, Reduviidae). VIII. parte: Observações sôbre a superfície dos ovos das espécies mais importantes. *Mem. Inst. Osw. Cruz.* 56: 197–208.
BAUDISCH, K.	1958	Beiträge zur Zytologie und Embryologie einiger Insektensymbiose. *Z. Morph. Ökol. Tiere* 47: 436–488.
BEAMENT, J. W. L.	1946a	The formation and structure of the chorion of the egg in an Hemipteran, *Rhodnius prolixus*. *Quart. J. micr. Sci.* 87: 393–439.

BEAMENT, J. W. L. 1946b The waterproofing process in eggs of *Rhodnius prolixus* Stål. *Proc. roy. Soc.* (B) 133: 407–418.

BEAMENT, J. W. L. 1947 The formation and structure of the micropylar complex in the egg-shell of *Rhodnius prolixus* Stål. (Heteroptera: Reduviidae). *J. exp. Biol.* 23: 213–233.

BEAMENT, J. W. L. 1949a The penetration of insect egg-shells. I: Penetration of the chorion of *Rhodnius prolixus* Stål. *Bull. ent. Res.* 39: 359–383.

BEAMENT, J. W. L. 1949b The penetration of insect egg-shells. II: The properties and permeability of sub-chorial membranes during development of *Rhodnius prolixus* Stål. *Bull. ent. Res.* 39: 467–488.

BEAMENT, J. W. L. 1951 The structure and formation of the egg of the fruit tree Red Spider mite, *Metatetranychus ulmi* Koch. *Ann. appl. Biol.* 38: 1–24.

BEHRENDT, K. 1963 Über die Eidiapause von *Aphis fabae* Scop. (Homoptera, Aphididae). *Zool. Jb. Physiol.* 70: 309–398.

BOBB, M. L. 1951 Life history of *Ochterus banksi* Barb. (Hemipt. Ochteridae). *Bull. Brookl. Ent. Soc.* 46: 92–100.

BOCK, E. 1939 Bildung und Differenzierung der Keimblätter bei *Chrysopa perla* L. *Z. Morph. Ökol. Tiere* 35: 615–702.

BONHAG, P. F. and J. R. WICK 1953 The functional anatomy of the male and female reproductive systems of the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Heteroptera: Lygaeidae). *J. Morph.* 93: 177–283.

BÖRNER, C. 1904 Zur Systematik der Hexapoden. *Zool. Anz.* 27: 511–533.

BÖRNER, C. 1930 Beiträge zu einem neuen System der Blattläuse. *Arch. Klass. Phylog. Ent.* 1: 115–194.

BOSELLI, F. B. 1932 Studio biologico degli Emitteri che attaccano le nocciuole in Sicilia. *Boll. Lab. Zool. Portici* 26: 142–309.

BOURNIER, A. 1960 Sur l'existence et l'évolution du corps dorsal secondaire dans l'ontogénèse de *Caudothrips buffai* Karny (Thysanoptera Tubulifera). *C.R. Acad. Sci., Paris* 250: 1347–1348.

BOURNIER, A. 1961 Sur l'existence et l'évolution d'un mycétome au cours de l'embryogenèse de *Caudothrips buffai* Karny. *Verh. XI int. Kongr. Ent. Wien 1960*, 1: 352–354.

BRANDT, A. 1869 Beiträge zur Entwicklungsgeschichte der Libelluliden und Hemipteren, mit besonderer Berücksichtigung der Embryonalhülle derselben. *Mém. Acad. Imp. Sci. St. Pétersb.* 13 (1): 1–33.

BRINDLEY, M. D. H. 1930 On the metasternal scent glands of certain Heteroptera. *Trans. ent. Soc. Lond.* 78: 199–207.

BRINDLEY, M. D. H. 1934 A note on the eggs and breeding habits of *Salda littoralis* L. *Proc. R. ent. Soc. Lond.* 9: 10–11.

BRINKHURST, R. O. 1960 Studies on the functional morphology of *Gerris najas* Degeer (Hem. Het. Gerridae). *Proc. zool. Soc. Lond.* 133: 531–559.

BROCHER, F. 1913 L'aquarium de Chambre. Introduction à l'étude de l'Histoire Naturelle, *Paris*: 248–281.

BROOKES, H. M. 1952 The morphological development of the embryo of *Gryllulus commodus* Walker (Orthoptera: Gryllidae). *Trans. roy. Soc. S. Austr.* 75: 150–159.

BROWN, E. S. 1948 The ecology of Saldidae (Hemiptera-Heteroptera) inhabiting a salt marsh, with observations on the evolution of aquatic habits in insects. *J. Anim. Ecol.* 17: 180–188.

BUCHNER, P. 1923 Studien an intracellulären Symbionten. IV. Die Bakteriensymbiose der Bettwanze. *Arch. Protistenk.* 46: 225–263.

BUCHNER, P. 1953 Endosymbiose der Tiere mit pflanzlichen Mikroorganismen. *Stuttgart* 771 pp.

BUCHNER, P. 1957 Endosymbiosestudien an Schildläusen VI. Die nicht in Symbiose lebende Gattung *Apiomorpha* und ihre ungewöhnliche Embryonalentwicklung. *Z. Morph. Ökol. Tiere* 46: 481–528.

BUENO, I. R. DE LA TORRE 1906 Life histories of North-American water bugs. *Canad. Ent.* 38: 189–197; 242–252.

BUTLER, E. A. 1923 A Biology of the British Hemiptera-Heteroptera. London VIII + 682 pp.

BUTT, F. H. 1949 Embryology of the Milkweed Bug, *Oncopeltus fasciatus* (Hemiptera). *Cornell Univ. Agric. Exp. Station* 283: 1–43.

BUTENANDT, A. 1955 Wirkstoffe des Insektenreiches. *Nova Acta Leop.* 17: 445–471.

CAPPE DE BAILLON, P. 1920 Contribution anatomique et physiologique à l'étude de la reproduction chez les Locustiens et les Grilloniens. *La Cellule* 31: 1–245.

CARAYON, J. 1948 Dimorphisme sexuel des glandes odorantes métathoraciques chez quelques Hémiptères. *C.R. Acad. Sci., Paris* 227: 303–305.

CARAYON, J. 1949a L'ootheque d'Hémiptères Plataspides de l'Afrique tropicale. *Bull. Soc. ent. Fr.* 54: 66–69.

CARAYON, J. 1949b Observations sur la biologie des Hémiptères microphysides. *Bull. Mus. Hist. nat. Paris* 21: 710–716.

CARAYON, J. 1950a Observations sur l'accouplement, la ponte et l'éclosion chez des Hemiptères Hénicocéphalidés de l'Afrique tropicale. *Bull. Mus. Hist. nat. Paris* 22: 739–745.

CARAYON, J. 1950b Caractères anatomiques et position systématique des Hémiptères Nabidae. (Note préliminaire). *Bull. Mus. Hist. nat. Paris* 22: 95–101.

CARAYON, J. 1950c Nombres et disposition des ovarioles dans les ovaires des Hémiptères-Hétéroptères. *Bull Mus. Hist. nat. Paris.* 22: 470–475.

CARAYON, J. 1954a Organes assumant les fonctions de la spermathèque chez divers Héteroptères. *Bull. Soc. zool. Fr.* 79: 189–197.

CARAYON, J. 1954b Un type nouveau d'appareil glandulaire propre aux mâles de certains Hémiptères Anthocoridae. *Bull. Mus. Hist. nat. Paris* 26: 602–606.

CARAYON, J. 1961 La viviparité chez les Hétéroptères. *Verh. XI. int. Kongr. Ent. Wien 1960* 1: 711–714.

CARAYON, J. 1962 Observations sur l'appareil odorifique des Hétéroptères, particulièrement celui des Tingidae, Vianaididae et Piesmatidae. *Cahiers des Nat.* 18: 1–16.

CARAYON, J.; R. L. USINGER and P. WYGODZINSKY 1958 Notes on the higher classification of the Reduviidae, with the description of a new tribe of the Phymatinae (Hemiptera-Heteroptera). *Rev. Zool. Bot. afr.* 57: 256–281.

CHEN, S. H. and B. YOUNG 1943 Further remarks on the carriage of eggs on the elytra by the males of *Sphaerodema rusticum*. *Sinensia* 14: 49–53.

CHINA, W. E. 1955a The evolution of the waterbugs. Bull. Symposium on organic evolution. *Nat. Inst. Sci. India, New Delhi* 7: 91–103.

CHINA, W. E. 1955b A reconsideration of the systematic position of the family Joppeicidae Reuter (Hemiptera-Heteroptera), with notes on the phylogeny of the suborder. *Ann. Mag. nat. Hist.* 8: 353–370.

CHINA, W. E. 1955c A new genus and species representing a new subfamily of Plataspidae, with notes on the Aphylidae (Hemiptera, Heteroptera). *Ann. Mag. nat. Hist.* 8: 204–210.

CHINA, W. E. 1957 The marine Hemiptera of the Monte Bello Islands, with descriptions of some allied species. *J. Linn. Soc. (Zool.)* 43: 342–357.

CHINA, W. E. and N. C. E. MILLER 1959 Check-list and keys to the families and subfamilies of the Hemiptera-Heteroptera. *Bull. Brit. Mus. (Nat. Hist.) Ent.* 8: 1–45

CHINA, W. E. and R. L. USINGER 1949 Classification of the Veliidae (Hemiptera) with a new genus from South Africa. *Ann. Mag. nat. Hist.* 2: 343–354.

CHRISTOPHERS, C. R. 1945 Structure of the *Culex* egg and egg raft in relation to function (Diptera). *Trans. R. ent. Soc. Lond.* 95: 25–34.

COBBEN, R. H. 1957 Beitrag zur Kenntnis der Uferwanzen (Hem. Het., Fam. Saldidae). *Ent. Ber.* 17: 245–257.

COBBEN, R. H. 1961 A new genus and four new species of Saldidae (Heteroptera). *Ent. Ber.* 21: 96–107.

COBBEN, R. H. 1965a The functional morphology of the leptopodoid phallus: a case of rectilinear evolution in Saldidae (Hem.-Heteroptera). *Proc. XII Int. Congr. Ent., London* 1964: 162–163.

COBBEN, R. H. 1965b Egg-life and symbiont transmission in a predatory bug, *Mesovelia furcata* Ms & Rey (Heteroptera, Mesoveliidae). *Proc. XII Int. Congr. Ent., London* 1964: 166–168.

COBBEN, R. H. 1965c Das aero-mikropylare System der Homoptereneier und Evolutionstrends bei Zikadeneiern (Hom. Auchenorhyncha). *Zool. Beitr. Berlin* 11: 13–69.

COOKER, R.; V. MILLSAPS and R. RICE 1936 Swimming plume and claws of the broad-shouldered water-strider *Rhagovelia flavicincta* Bueno. *Bull. Brookl. ent. Soc.* 31: 81–84.

CORBY, H. D. L. 1947 *Aphanus* (Hem., Lygaeidae) in stored ground-nuts. *Bull. ent. Res.* 37: 609–617.

COUNCE, S. J. 1959a Micropyle structure in the eggs of several *Drosophila* species. *Drosophila Inform. Serv.* 33: 126–127.

COUNCE, S. J. 1959b Spermatozoa in *Drosophila* eggs. *Drosophila Inform. Serv.* 33: 127–128.

COUNCE, S. J. 1961 The analysis of insect embryogenesis. *Annu. Rev. Ent.* 6: 295–312.

DASHMAN, T. 1953a Terminology of the pretarsus. *Ann. ent. Soc. Amer.* 46: 56–62.

DASHMAN, T. 1953b The unguitractor plate as a taxonomic tool in the Hemiptera. *Ann. ent. Soc. Amer.* 46: 561–578.

DAVEY, K. G. 1965 The physiology of reproduction in insects. *Ann. ent. Soc. Québec* 10: 13–25.

DAVIS, CH. C. 1961 A study of the hatching process in aquatic invertebrates. II. Hatching in *Ranatra fusca* P. Beauvois (Hemiptera, Nepidae). *Trans. Amer. microsc. Soc.* 80: 230–234.

DAVIS, CH. C. 1964 A study of the hatching process in aquatic invertebrates. VII. Observations on hatching in *Notonecta melaena* Kirkaldy (Hemiptera, Notonectidae) and on *Ranatra absona* D. & Dec. (Hemiptera, Nepidae). VIII. The hatching process of *Amnicola*(?) *hydrobioides* (Ancey) (Prosobranchia, Hydrobiidae). *Hydrobiologia* 23: 253–266.

DAVIS, CH. C. 1965 A study of the hatching process in aquatic invertebrates. XII. The eclosion process in *Trichocorixa naias* (Kirkaldy) (Heteroptera, Corixidae). *Trans. Amer. microsc. Soc.* 84: 60–65.

DAVIS, N. T. 1956 The morphology and functional anatomy of the male and

female reproductive systems of *Cimex lectularius* L. (Heteroptera, Cimicidae). *Ann. ent. Soc. Amer.* 49: 466–493.

DAVIS, N. T. 1957 Contributions to the morphology and phylogeny of the Reduvioidea (Hemiptera: Heteroptera). Part I. The morphology of the abdomen and genitalia of Phymatidae. *Ann. ent. Soc. Amer.* 50: 432–443.

DAVIS, N. T. 1966 Contributions to the morphology and phylogeny of the Reduvioidea (Hemiptera: Heteroptera). Part III. The male and female genitalia. *Ann. ent. Soc. Amer.* 59: 911–924.

DEGRANGE, CH. 1956 Sur les micropyles des oeufs des Ephéméroptères. *Bull. Soc. ent. Fr.* 61: 146–148.

DEGRANGE, CH. 1957 L'oeuf et le mode d'éclosion de quelques Plécoptères. *Trav. Lab. Hydrobiol. Grenoble* 48–49: 37–49.

DEGRANGE, CH. 1960 Recherches sur la reproduction des Ephéméroptères. *Trav. Lab. Hydrobiol. Grenoble* 50–51: 7–193.

DEGRANGE, CH. 1961 Processus cinétique de l'éclosion chez les Ephéméroptères. *Trav. Lab. Hydrobiol. Grenoble* 52–53: 1–6.

DELMAS, R. 1926 Notes sur la biologie de *Pristiphora conjugata* Dahlbom. *Bull. biol.* 60: 447–472.

DENIS, R. 1949 Apterygota. In: Grassé's *Traité de Zoologie* 9: 113–275.

DISPONS, P. und W. STICHEL 1959 Illustrierte Bestimmungstabellen der Wanzen. II. Europa (Hemiptera-Heteroptera Europae). *Berlin* 3, Heft 3–6: 81–185.

DOESBURG, P. H. VAN 1964 *Termatophylidea opaca* Carvalho, a predator of thrips. *Ent. Ber.* 24: 248–253.

DRAKE, C. J. and J. M. CAPRILES 1952 Water-striders from territoria Amazones of Venezuela (Hemiptera: Hydrometridae, Veliidae). *Great Basin Nat.* 12: 47–54.

DRAKE, C. J. and N. T. DAVIS 1958 The morphology and systematics of the Piesmatidae (Hemiptera), with keys to World genera and American species. *Ann. ent. Soc. Amer.* 51: 567–581.

DRAKE C. J. and N. T. DAVIS 1960 The morphology, phylogeny, and higher classification of the family Tingidae, including the description of a new genus and species of the subfamily Vianaidinae (Hemiptera: Heteroptera). *Ent. amer.* 39: 1–100.

DRAKE, C. J. and J. A. ROZE 1955 A new species of *Veloidea* from Venezuela (Hemiptera: Veliidae). *Bull. Brooklyn ent. Soc.* 50: 106–109.

DRAKE, C. J. and J. A. SLATER 1957 The phylogeny and systematics of the family Thaumastocoridae (Hemiptera: Heteroptera). *Ann. ent. Soc. Amer.* 50: 353–370.

DUFOUR, L. 1833 Recherches anatomiques et physiologiques sur les Hémiptères. *Mém. prés. Acad. Sci., Paris* 4: 3–333.

DUPUIS, C. 1947 Données sur la morphologie des glandes dorso-abdominales des Hémiptères-Hétéroptères. Historiques et discussion. *Feuille Nat. Paris.* 2: 13–21; 49–52.

DUPUIS, C. 1955 Les génitalia des Hémiptères Hétéroptères (Génitalia externes des deux sexes; voies ectodermiques femelles). Revue de la morphologie. Lexique de la nomenclature. Index bibliographique analytique. *Mém. Mus. nat. Hist. Nat., Zool.* 6: 183–278.

DUPUIS, C. 1963 L'étude bio-taxinomique des insectes entomophages: l'exemple des diptères Phasiinae. *Cahiers natur., Bull.* 19: 1–20.

EDWARDS, J. S. 1961 Spitting as a defensive mechanism in a predatory reduviid. *Verh. XI int. Kongr. Ent. Wien* 1960. 3: 259–263.

EDWARDS, J. S. 1962 Observations on the development and predatory habit of two

reduviid Heteroptera, *Rhinocoris carmelita* Stål and *Platymeris rhadamanthus* Gerst. *Proc. R. Ent. Soc. Lond.* 37: 89–98.

EICHHORN, O. 1961 Zur Embryonalentwicklung der Adelgiden (Hemipt.). *Anz. Schädlingsk.* 34: 20–26.

EKBLOM, T. 1926 Morphological and biological studies of the Swedish families of Hemiptera-Heteroptera. Part I. The families Saldidae, Nabidae, Lygaeidae, Hydrometridae, Veliidae and Gerridae. *Zool. Bidr., Uppsala* 10: 29–179.

EKBLOM, T. 1930 Morphological and biological studies of the Swedish families of Hemiptera-Heteroptera. Part II. The families Mesoveliidae, Corizidae and Corixidae. *Zool. Bidr. Uppsala* 12: 113–150.

EKBLOM, T. 1941 Chromosomenuntersuchungen bei *Salda littoralis* L., *Calocoris chenopodii* Fall. und *Mesovelia furcata* Muls. and Rey., sowie Studien über die Chromosomen bei verschiedenen Hemiptera-Heteroptera im Hinblick auf phylogenetische Betrachtungen. *Chromosoma* 2: 12–35.

EMEIS, W. 1915 Über Eientwicklung bei den Cocciden. *Zool. Jb., Anat.* 39: 27–78.

ESAKI, T. and W. E. CHINA 1927 A new family of aquatic Heteroptera. *Trans. ent. Soc. Lond.* 75: 279–295.

ESAKI, T. and S. MIYAMOTO 1959 A new or little known *Hypselosoma* from Amami-Oshima and Japan, with the proposal of a new tribe for the Genus (Hemiptera). *Sieboldia* 2: 109–120.

EYLES, A. C. 1963 Descriptions of the immature stages of five Rhyparochrominae (Heteroptera-Lygaeidae). *Trans. Soc. Brit. Ent.* 15: 277–294.

EYLES, A. C. and R. E. BLACKITH 1965 Studies on hybridization in *Scolopostethus* Fieber (Heteroptera: Lygaeidae). *Evolution* 19: 465–479.

FERNANDO, C. H. and C. Y. LEONG 1963 Miscellaneous notes on the biology of Malayan Corixidae (Hem.: Heteroptera) and a study of the life histories of two species, *Micronecta quadristrigata* Bredd. and *Agraptocorixa hyalinipennis* (F.). *Ann. Mag. nat. Hist.* 13: 545–558.

FEWKES, D. W. 1963 The effect of exposure to dry conditions on the eggs of *Aeneolamia varia saccharina* (Hom. Cercopidae). *Ann. ent. Soc. Amer.* 56: 719–720.

FLUITER, H. J. DE en P. A. BLIJDORP 1935 De grauwe dennensnuitkever *Brachyderes incanus* L. *Med. Landb. Hogesch. Wageningen* 39: 3–72.

FROESCHNER, R. C. 1960 Cydnidae of the Western Hemisphere. *Proc. U.S. nat. Mus. Washington* 111: 337–680.

GALLIARD, H. 1934 Rôle de la mue embryonnaire des Réduvidés hématophages dans le processus d'éclosion. *Ann. Parasit.* 12: 345–349.

GIBSON, W. W. 1965 An observation on the oviposition habits of *Mydas clavatus* (Diptera: Mydaidae). *Journ. Kans. ent. Soc.* 38: 196–197.

GIESE, R. L. and L. WILSON 1957 Diapause, and the embryo of the Saratoga spittlebug. *Trans. Wisc. Acad. Sci. Madison* 46: 255–259.

GOODCHILD, A. J. P. 1966 Evolution of the alimentary canal in the Hemiptera. *Biol. Rev.* 41: 97–140.

GOOT, P. VAN DER 1929 Eenige dierlijke vijanden van *Vigna hosei* en *Calopogonium mucunoides*. *Landbk. Tijdschr. Ned. Ind.* 4: 753.

GOSS, R. J. 1952 The early embryology of the book louse, *Liposcelis divergens* Badonnel (Psocoptera; Liposcelidae). *J. Morph.* 91: 135–167.

GOSS, R. J. 1953 The advanced embryology of the book louse, *Liposcelis divergens* Badonnel (Psocoptera; Liposcelidae). *J. Morph.* 92: 157–191.

GOSS, R. J. 1954 Ovarian development and oogenesis in the book louse, *Liposcelis divergens* Badonnel (Psocoptera, Liposcelidae) *Ann. ent. Soc. Amer.* 47: 190–207.

GRASSÉ, P. P. 1949 Isoptera. *Traité de Zoologie* 9: 408–544.

GRIFFITH, M. E. 1945 The environment, life history and structure of the water boatman, *Rhamphocorixa acuminata* (Uhler) (Hemiptera, Corixidae). *Kansas Univ. Sci. Bull.* 30: 241–366.

GULDE, J. 1902 Die Dorsaldrüsen der Larven der Hemiptera-Heteroptera. *Ber. Senkenberg Ges. Frankfurt* 1902: 85–136.

GUPTA, A. P. 1961 A critical review of the studies on the so-called stink or repugnatorial glands of Heteroptera with further comments. *Canad. Ent.* 93: 482–486.

GUPTA, A. P. 1963a A consideration of the systematic position of the Saldidae and Mesoveliidae. *Proc. ent. Soc. Wash.* 65: 31–38.

GUPTA, A. P. 1963b Comparative morphology of the Saldidae and Mesoveliidae (Heteroptera). *Tijdschr. Ent.* 106: 169–196.

HAGAN, H. R. 1931 The embryogeny of the Polyctenid, *Hesperoctenes fumarius* Westwood, with reference to viviparity in insects. *J. Morph.* 51: 3–92.

HAGAN, H. R. 1951 Embryology of the viviparous insects. *New York* 472 pp.

HALE, H. M. 1924 Notes on eggs, habits and migration of some Australian aquatic bugs (Corixidae and Notonectidae). *S. Aust. Nat.* 5: 133–135.

HALKKA, O. 1959 Chromosome studies on the Hemiptera Homoptera Auchenorrhyncha. *Ann. Acad. Sci. Fenn.* 43: 1–72.

HALLEZ, P. 1886 Loi de l'orientation de l'embryon chez les insectes. *C.R. Acad. Sci. Paris* 103: 606–608.

HANDLIRSCH, A. 1899 Wie viele Stigmen haben die Rhynchoten? Ein morphologischer Beitrag. *Verh. zool. bot. Ges. Wien* 49: 499–510.

HARTLEY, J. C. 1961 The shell of Acridid eggs. *Quart. J. micr. Sci.* 102: 249–255.

HARTLEY, J. C. 1962 The egg of *Tetrix* (Tetrigidae, Orthoptera) with a discussion on the probable significance of the anterior horn. *Quart. J. micr. Sci.* 103: 253–259.

HARTLEY, J. C. 1964 The structure of the egg of the British Tettigoniidae (Orthoptera). *Proc. R. ent. Soc. Lond.* (A) 39: 111–117.

HARWOOD, R. F. and W. R. HORSFALL 1959 Development, structure, and function of coverings of eggs of floodwater mosquitoes. III. Functions of coverings. *Ann. ent. Soc. Amer.* 52: 113–116.

HASE, A. 1917 Die Bettwanze *(Cimex lectularius* L.), ihr Leben und ihre Bekämpfung. *Monogr. Angew. Ent. No. 1. Z. Angew. Ent.* 4, Beih. 1, 144 pp.

HENRICI, H. 1938 Die Hautdrüsen der Landwanzen (Geocorisae), ihre mikroskopische Anatomie, ihre Histologie und Entwicklung. Teil I. Die abdominalen Stinkdrüsen, die Drüsenpakete und die zerstreuten Hautdrüsen. *Zool. Jb. Anat.* 65: 141–228.

HERTEL, R. 1955 Zur Kenntnis der Systematik, Biologie und Morphologie von *Neides tipularius* L. (Heteroptera Neididae). *Abh. Mus. Tierk. Dresden* 22: 111-183.

HESLOP-HARRISON, G. 1949 The subfamily Liviinae Löw of the Homopterous Psyllidae. Part 2. *Ann. Mag. nat. Hist.* 2: 241–270.

HESLOP-HARRISON, G. 1952 The number and distribution of the spiracles of the adult Psyllidae. *Ann. Mag. nat. Hist.* 5: 248–260.

HESSE, A. J. 1947 A remarkable new dimorphic isometopid and two other new

species of Hemiptera predatory upon the red scale of citrus. *J. ent. Soc. S. Afr.* 10: 31–45.

HEYMONS, R. 1899 Beiträge zur Morphologie und Entwicklungsgeschichte der Rhynchoten. *Nova Acta. Abh. K. Leop.-Carol. deut. Akad. Naturf.* 74: 351–456.

HEYMONS, R. 1926 Über Eischalensprenger und den Vorgang des Schlüpfens aus der Eischale bei den Insekten. *Biol. Zentralbl.* 46: 51–63.

HINTON, H. E. 1960a The structure and function of the respiratory horns of the eggs of some flies. *Philos. Trans. Roy. Soc. Lond.* 243: 45–73.

HINTON, H. E. 1960b Plastron respiration in the eggs of blowflies. *J. Ins. Physiol.* 4: 176–183.

HINTON, H. E. 1961a The structure and function of the egg-shell in the Nepidae (Hemiptera). *J. Ins. Physiol.* 7: 224–257.

HINTON, H. E. 1961b How some insects, especially the egg stages, avoid drowning when it rains. *Proc. S. London ent. nat. Hist. Soc.* 1960: 138–154.

HINTON, H. E. 1962a The structure of the shell and respiratory system of the eggs of *Helopeltis* and related genera (Hemiptera, Miridae). *Proc. zool. Soc. Lond.* 139: 483–488.

HINTON, H. E. 1962b A key to the eggs of the Nepidae (Hemiptera). *Proc. R. ent. Soc. Lond.* (A) 37: 65–68.

HINTON, H. E. 1962c The fine structure and biology of the egg-shell of the wheat bulb fly, *Leptohylemyia coarctata. Quart. J. micr. Sci.* 103: 243–251.

HINTON, H. E. 1962d Respiratory systems of insect egg-shells. *Sci. Progr. Lond.* 50: 96–113.

HINTON, H. E. 1963 The respiratory system of the egg-shell of the blowfly *Calliphora erythrocephala* Meig., as seen with the electron microscope. *J. Ins. Physiol.* 9: 121–129.

HINTON, H. E. 1964 Sperm transfer in insects and the evolution of haemocoelic insemination. *Insect Reproduction Symp.* No. 2., Lond. 1964: 95–107.

HINTON, H. E. and S. Cole 1965 The structure of the egg-shell of the cabbage root fly, *Erioischia brassicae. Ann. appl. Biol.* 56: 1–6.

HUGHES-SCHRADER, S. 1958 The DNA content of the nucleus as a tool in the cytotaxonomic study of insects. *Proc. 10th int. Congr. Ent. Montreal* 1956 2: 935–944.

HUNTER, R. E. and T. F. LEIGH 1965 A laboratory life history of the consperse stink bug *Euschistus conspersus* (Hemiptera: Pentatomidae). *Ann. ent. Soc. Amer.* 58: 648.

HUNGERFORD, H. B. 1918 Notes on the oviposition of some semiaquatic Hemiptera *(Hebrus, Salda, Lampracanthia). Journ. ent. Soc.* 26: 12–18.

HUNGERFORD, H. B. 1919 The biology and ecology of aquatic and semiaquatic Hemiptera. *Kans. Univ. sci. Bull.* 11: 3–335.

HUNGERFORD, H. B. 1922 The life history of the Toad Bug, *Gelastocoris oculatus* Fabr. *Kans. Univ. sci. Bull.* 14: 145–171.

HUNGERFORD, H. B. 1923 Notes on the eggs of Corixidae. *Bull. Brooklyn Ent. Soc.* 18: 13–16.

HUNGERFORD, H. B. 1948 The eggs of Corixidae (Hemiptera). *J. Kans. ent. Soc.* 21: 141–146.

HUSSEY, P. B. 1926 Studies on the pleuropodia of *Belostoma flumineum* and *Ranatra fusca* with a discussion of these organs in other insects. *Ent. Amer.* 7: 1–80.

IDRIS, B. E. M. 1960 Die Entwicklung in normalen Ei von *Culex pipiens* L. (Diptera). *Z. Morph. Ökol. Tiere* 49: 387–429.

ILLINGWORTH, J. F. 1921 The linear bug, *Phaenacantha australica* Kirkaldy: a new pest of sugar cane in Queensland. *Bull. Div. Ent. Sug. Exp. Sta. Qd.* 14: 11 pp.

IMMEL, R. 1955 Zur Biologie und Physiologie von *Reduvius personatus* L. *Z. Morph. Ökol. Tiere* 44: 163–195.

JACKSON, D. J. 1957 A note on the embryonic cuticle shed on hatching by the larvae of *Agabus bipustulatus* L. and *Dytiscus marginalis* L. (Coleoptera: Dytiscidae). *Proc. R. ent. Soc. Lond.* (A) 32: 115–118.

JACKSON, D. J. 1959 The association of a slime *Bacterium* with the inner envelope of the egg of *Dytiscus marginalis* (Coleoptera) and the less common occurrence of a similar *Bacterium* on the egg of *D. semisulcatus*. *Quart. Journ. micr. Sci.* 150: 433–443.

JANDE, S. S. 1959 An analysis of the chromosomes in four species of the family Belostomatidae (Heteroptera, Cryptocerata). *Res. Bull. Panjab Univ., Hoshiarpur* 10: 24–34.

JANES, M. J. and A. HAGER 1936 Studies on the incubation of the Chinch Bugg egg. *Iowa St. College Journ. Sc.* 10: 395–402.

JEANNEL, R. 1942 Les Hénicocéphalidés. Monographie d'un group d'Hémiptères hématophages. *Ann. Soc. entom. France*, 110: 273–366.

JENTSCH, S. 1939 Die Gattung *Ectopsocus* (Psocoptera). *Zool. Jb. Syst.* 73: 1–46; 111–128.

JOHANNSEN, O. A. and F. H. BUTT 1941 Embryology of insects and Myriapods. *London* 462 pp.

JOHANSSON, A. S. 1957 The functional anatomy of the metathoracic scent glands of the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Heteroptera: Lygaeidae). *Norsk ent. Tidsskr.* 10: 95–109.

JOHNSON, C. G. 1934a Note on the oviposition of *Notostira erratica* L. (Hem., Capsidae). *J. Soc. Brit. Ent.* 1: 7–8.

JOHNSON, C. G. 1934b On the eggs of *Notostira erratica* L. (Hemiptera, Capsidae). I. Observations on the structure of the egg and the sub-opercular yolk-plug, swelling of the egg and hatching. *Trans. Soc. Brit. Ent.* 1: 1–32.

JOHNSON, C. G. 1937 The absorption of water and the associated volume changes occurring in the eggs of *Notostira erratica* L. (Hemiptera, Capsidae) during embryonic development under experimental conditions. *J. exp. Biol.* 14: 413–421.

JOHNSON, C. G. 1940 Development, hatching and mortality of the eggs of *Cimex lectularius* L. (Hemiptera) in relation to climate, with observations on the effects of preconditioning to temperature. *Parasitology* 32: 127–173.

JONES, B. M. 1956a Endocrine activity during insect embryogenesis. Function of the ventral head glands in Locust embryos *(Locustana pardalina* and *Locusta migratoria*, Orthoptera). *Journ. exp. Biol.* 33: 174–185.

JONES, B. M. 1956b Endocrine activity during insect embryogenesis. Control of events in development following the embryonic moult *(Locusta migratoria* and *Locustana pardalina*, Orthoptera). *Journ. exp. Biol.* 33: 685–696.

JONES, P. A. and H. C. COPPEL 1963 Immature stages and biology of *Apateticus cynicus* Say. (Hemiptera: Pentatomidae). *Can. Ent.* 95: 770–779.

JORDAN, K. H. C.	1932	Zur Kenntnis des Eies und der Larven von *Microvelia schneiderі. Z. wiss. Insekt. Biol.* 127: 18–22.
JORDAN, K. H. C.	1933	Beiträge zur Biologie heimischer Wanzen (Heteroptera). *Stettin. Ent. Ztg.* 94: 212–236.
JORDAN, K. H. C.	1935	Beitrag zur Lebensweise der Wanzen auf feuchten Böden (Heteroptera). *Stettin. ent. Ztg.* 96: 1–26.
JORDAN, K. H. C.	1937	Lebensweise und Entwicklung von *Micronecta minutissima* L. (Hem. Het.). *Ent. Jahrb.* 46: 173–177.
JORDAN, K. H. C.	1958	Die Biologie von *Elasmucha grisea* L. (Heteroptera: Acanthosomidae). *Beitr. Ent.* 8: 385–397.
JORDAN, K. H. C. und A. WENDT	1938	Zur Biologie von *Salda littoralis* L. (Hem.: Het.). *Stettin. ent. Ztg.* 99: 273–292.
KALSHOVEN, L. G. E.	1950	De plagen van de cultuurgewassen in Indonesië. *'s-Gravenhage-Bandoeng* 1, 512 pp.
KEILBACH, R.	1935	Über asymmetrische Flügellage bei Insekten und Ihre Beziehungen zu anderen Asymmetrien. *Z. Morph. Ökol. Tiere* 29: 1–44.
KELLEN, W. R.	1959	Notes on the biology of *Halovelia marianarum* Usinger in Samoa (Veliidae: Heteroptera). *Ann. ent. Soc. Amer.* 52: 53–62.
KELLEN, W. R.	1960	A new species of *Omania* from Samoa, with notes on its biology (Heteroptera: Saldidae). *Ann. ent. Soc. Amer.* 53: 494–499.
KERSHAW, J. C. and G. W. KIRKALDY	1910	A memoir on the anatomy and life-history of the homopterous insect *Pyrops candelaria* (or "Candle-fly"). *Zool. Jahrb., Syst.* 29: 105–124.
KING, R. C.	1964	Further information concerning the envelopes surrounding dipteran eggs. *Quart. J. micr. Sci.* 105: 209–211.
KING, R. C. and E. A. KOCH	1963	Studies on the ovarian follicle cells of *Drosophila. Quart. J. micr. Sci.* 104: 297–320.
KIRITSHENKO, A. N.	1951	True Hemiptera of European USSR. Keys and bibliography. [In Russian] *Opred. Faune SSSR, Moscow* 42: 1–423.
KOGAN, M.	1960	*Corythaica cyathicollis* (Costa, 1864). Aspectos sistemáticos, biológicos e econômicos (Hemiptera, Tingidae). *Mem. Inst. Osw. Cruz* 58: 59–88.
KÖHLER, A.	1903	Über die Bildung des Chorions bei *Pyrrhocoris apterus. Zool. Anz.* 26: 633–636.
KÖHLER, A.	1907	Untersuchungen über das Ovarium der Hemipteren. *Ztschr. wiss. Zool.* 87: 337–381.
KORMILEV, N. A.	1955	Una curiosa familia de Hemípteros nueva para la fauna argentina. Thaumastotheriidae (Kirkaldy, 1907). *Rev. Soc. ent. argent.* 18: 5–10.
KORSCHELT, E.	1884	Die Bildung des Chorions bei einigen Wasserwanzen. *Zool. Anz.* 7: 500–504.
KRAUSE, G.	1939	Die Eitypen der Insekten. *Biol. Zbl.* 59: 495–536.
KRAUSE, G.	1958	Neue Beiträge zur Entwicklungsphysiologie des Insektenkeimes. *Verh. dtsch. Zool. Ges., Leipzig* 1957: 396–424.
KULLENBERG, B.	1942	Die Eier der schwedischen Capsiden (Rhynchota) I. *Ark. Zool.* 33 (A) (15): 1–16.
KULLENBERG, B.	1943	Die Eier der schwedischen Capsiden (Rhynchota) II. *Ark. Zool.* 34 (A) (15): 1–8.
KULLENBERG, B.	1946	Studien über die Biologie der Capsiden. *Zool. Bidr., Uppsala* 23: 1–522.

KUMAR, R. 1961 Studies on the genitalia of some aquatic and semi-aquatic Heteroptera. *Ent. Tidskr., Lund* 82: 163–179.

KUMAR, R. 1962a Morpho-taxonomical studies on the genitalia and salivary glands of some Pentatomoidea. *Ent. Tidskr.* 83: 44–88.

KUMAR, R. 1962b Morpho-taxonomical studies on the genitalia and salivary glands of some Cimicomorpha (Rhynchota, Hemiptera). *Tijdschr. Ent.* 105: 1–28.

KUMAR, R. 1964a On some internal organs in Enicocephalidae, Leptopodidae and Ochteridae (Hemiptera). *Proc. Roy. Soc. Queensl.* 75: 39–44.

KUMAR, R. 1964b Anatomy and relationships of Thaumastocoridae (Hemiptera: Cimicoidea). *Journ. Ent. Soc. Queensl.* 3: 48–51.

KUMAR, R. 1965 Aspects of the morphology of Coreoidea and their value in its higher classification. *Proc. roy. Soc. Queensl.* 76: 27–91.

LARSÉN, O. 1927 Über die Entwicklung und Biologie von *Aphelocheirus aestivalis* Fabr. *Ent. Tidskr.* 48: 181–206.

LARSÉN, O. 1930 Biologische Beobachtungen an Schwedischen *Notonecta*-Arten. *Ent. Tidskr.* 51: 219–247.

LATTIN, J. D. 1955 The eggs of *Corimelaena virilis* (McAtee and Malloch) (Hemiptera: Cydnidae: Corimelaeninae). *Pan-Pac Ent.* 31: 63–66.

LAUGHLIN, R. 1957 Absorption of water by the egg of the garden chafer, *Phyllopertha horticola* L. *J. exp. Biol.* 34: 226–236.

LE BERRE, J. R. 1952 Le phénomène de la blastocinèse dans les oeufs à diapause de *Locusta migratoria gallica* Rem. *C.R. Acad. Sci., Paris* 234: 1487–1489.

LE BERRE, J. R. 1959 Caractères biologiques des *Locusta* de la faune de France et étude d'un exemple de diapause embryonnaire. *Ann. Epiph.* 10: 101–254.

LEBRUN, D. 1960 Recherches sur la biologie et l'éthologie de quelques Hétéroptères aquatiques. *Ann. Soc. ent. France* 129: 179–199.

LENT, H. and J. JURBERG 1966 Os estádios larvares de '*Phloeophana longirostris*' (Spinola, 1837) (Hemiptera, Pentatomoidea). *Rev. Brasil, Biol.* 26: 1–4.

LEONARD, D. E. 1966 Biosystematics of the '*Leucopterus Complex*' of the genus *Blissus* (Heteroptera: Lygaeidae). *Bull. Connecticut Agr. Exp. Stat.* 677: 5–47.

LEONG, C. Y. 1962 The life-history of *Anisops breddini* Kirkaldy (Hemiptera, Notonectidae). *Ann. Mag. nat. Hist.* (13) 5: 377–383.

LESTON, D. 1953 Notes on the Ethiopian Pentatomoidea (Hemiptera). XVI: an Acanthosomid from Angola, with remarks upon the status and morphology of Acanthosomidae Stål. *Publ. cult. Cia Diamant, Angola* 16: 123–132.

LESTON, D. 1955a Notes on the Ethiopian Pentatomoidea (Hem.). XVIII: The eggs of three Nigerian Shieldbugs, with a tentative summary of egg form in Pentatomoidea. *Ent. mon. Mag.* 91: 33–36.

LESTON, D. 1955b Miscellaneous biological notes on British Corixidae and Notonectidae (Hem.). *Ent. mon. Mag.* 91: 92–95.

LESTON, D. 1957 Cyto-taxonomy of Miridae and Nabidae (Hemiptera). *Chromosoma* 8: 609–616.

LESTON, D. 1958 Chromosome number and the systematics of Pentatomomorpha (Hemiptera). *Proc. 10th int. Congr. Ent. Montreal* 1956 2: 911–918.

LESTON, D. 1961 Testis follicle number and higher systematics of Miridae (Hemiptera-Heteroptera). *Proc. zool. Soc. London* 137: 89–106.

LESTON, D.; PENDERGRAST, J. G. and T. R. E. SOUTHWOOD 1954 Classification of the terrestrial Heteroptera (Geocorisae). *Nature, London* 174: 91–92.

LEUCKART, R. 1855 Ueber die Micropyle und den feinern Bau der Schalenhaut bei den Insekteneiern. *Arch. Anat. Physiol. wiss. Med.* 1855: 90–253.

LEWIS, K. R. and G. G. E. SCUDDER 1957 The chromosomes of *Dicranocephalus agilis* (Hemiptera: Heteroptera). *Cytologia* 23: 92–104.

LIN, S.; HODSON, A. C. and A. G. RICHARDS 1954 An analysis of threshold temperatures for the development of *Oncopeltus* and *Tribolium* eggs. *Physiol. Zool.* 27: 287–311.

LINCOLN, D. C. R. 1961 The oxygen and water requirements of the egg of *Ocypus olens* Müller (Staphylinidae, Coleoptera). *J. Ins. Physiol.* 7: 265–272.

LINLEY, J. R. 1965 The ovarian cycle and egg stage in *Leptoconops (Holoconops) becquaerti* (Kieff.) (Diptera, Ceratopogonidae). *Bull. ent. Res.* 56: 37–56.

LINSENMAIR, K. E. und R. JANDER 1963 Das 'Entspannungsschwimmen' von *Velia* und *Stenus*. *Naturwiss.* 50: 1–2

LIVINGSTONE, D. 1962 On the biology and immature stages of a sap-sucker on *Zizyphus jujuba*, *Monosteira minutula* Mont., a species new to India (Hem.: Tingidae). *Agra Univ. Journ. of Research (Science)* 11: 117–129.

LUDWIG, W. 1936 Bestimmung und Vererbung der Asymmetrieformen (Rechts-Links-Problem). *Verh. dtsch. zool. Ges.* 1936: 21–73.

LUNDBECK, W. 1914 Some remarks on the eggs and egg-deposition of *Halobates*. *Mindeskrift for Japetus Steenstrup* 27: 13 pp.

MAHR, E. 1960a Normale Entwicklung, Pseudofurchung und die Bedeutung des Furchungszentrums im Ei des Heimchens *(Gryllus domesticus)*. *Z. Morph. Ökol. Tiere* 49: 263–311.

MAHR, E. 1960b Experimente zur Analyse der Blastokinese des Embryo im Ei von *Gryllus domesticus*. *Verh. dtsch. zool. Ges.* 1960: 99–113.

MAHR, E. 1961 Bewegungssysteme in der Embryonal-entwicklung von *Gryllus domesticus*. *Roux' Arch. Entwickl.-Mech.* 152: 662–724.

MALHOTRA, C. P. 1958 Bionomics of *Serinetha augur* Fabr. and its association with *Dysdercus cingulatus* Fabr., the red cotton bug. *Indian For.* 84: 669–671.

MAMMEN, H. 1912 Ueber die Morphologie der Heteropteren und Homopterenstigmen. *Zool. Jahrb., Anat* 34: 121–178.

MANNA, G. K. 1958 Cytology and inter-relationships between various groups of Heteroptera. *Proc. 10th int. Congr. Ent. Montreal* 1956 2: 919–934.

MANNA, G. K. 1962 A further evaluation of the cytology and inter-relationships between various groups of Heteroptera. *Nucleus* 5: 7–28.

MAO-HUA, P. 1963 A preliminar study on the small brown planthopper, *Delphacodes striatella* Fall. in South Kiangsu [In Chinese with summary]. *Acta Ent. Sinica* 12: 117–136.

MARSHALL, J. F. 1938 The British mosquitoes. *London, Brit. Mus. (Nat. Hist.)* 341 pp.

MATSUDA, R. 1960 Morphology, evolution and a classification of the Gerridae (Hemiptera-Heteroptera). *Kansas Univ. sci. Bull.* 41: 25–632.

MATTHÉE, J. J. 1951 The structure and physiology of the eggs of *Locustana pardalina* Walk. *Sci. Bull. Dep. Agric. Un. S. Afr., Pretoria* 316, 83 pp.

MCFARLANE, J. E. 1960 Structure and function of the egg shell as related to water absorption by the eggs of *Acheta domesticus* L. *Canad. J. Zool.* 38: 231–241.

McFarlane, J. E. and C. P. Kennard 1960 Further observations on water absorption by the eggs of *Acheta domesticus* L. *Can. J. Zool.* 38: 77–85.

McKinstry, A. P. 1942 A new family of Hemiptera-Heteroptera proposed for *Macrovelia hornii* Uhler. *Pan-Pacif. Ent.* 18: 90–96.

Mecznikov, E. 1866 Embryologische Studien an Insekten. *Z. wiss. Zool.* 16: 128–132; 389–500.

Mellanby, H. 1935 The early embryological development of *Rhodnius prolixus*. *Quart. J. micr. Sci.* 78: 71–90.

Mellanby, H. 1936 The later embryology of *Rhodnius prolixus*. *Quart. J. micr. Sci.* 79: 1–42.

Michalk, O. 1935 Zur Morphologie und Ablage der Eier bei den Heteropteren, sowie über ein System der Eiablagetypen. *Dtsch. ent. Z.* 1935: 148–157.

Miller, A. 1940 Embryonic membranes, yolk cells, and morphogenesis of the stonefly *Pteronarcys proteus* Newman (Plecoptera: Pteronarcidae). *Ann. ent. Soc. Amer.* 33: 437–477.

Miller, N. C. E. 1934 The developmental stages of some Malayan Rhynchota. *J. Fed. Malay St. Mus.* 17: 502–525.

Miller, N. C. E. 1953 A note on the ova of Urostylidae (Hem., Heteroptera). *Ent. mon. Mag.* 89: 137.

Miller, N. C. E. 1956 The biology of the Heteroptera. *London* 162 pp.

Miller, P. L. 1964 The possible rôle of haemoglobin in *Anisops* and *Buenoa* (Hemiptera: Notonectidae). *Proc. R. ent. Soc. Lond. (A)* 39: 166–175.

Miyamoto, S. 1953 Biology of *Heloptrephes formosanus* Esaki et Miyamoto, with descriptions of larval stages. *Sieboldia* 1: 1–10.

Miyamoto, S. 1957 List of ovariole numbers in Japanese Heteroptera. *Sieboldia* 2: 69–82.

Miyamoto, S. 1959 Additions and correction to my 'List of ovariole numbers in Japanese Heteroptera', (1). *Sieboldia* 2: 121–123.

Miyamoto, S. 1961 Comparative morphology of alimentary organs of Heteroptera, with the phylogenetic consideration. *Sieboldia* 2: 197–259.

Möllring, F. K. 1956 Autogene und anautogene Eibildung bei *Culex* L. Zugleich ein Beitrag zur Frage der Unterscheidung autogener und anautogener Weibchen an Hand von Eiröhrenzahl und Flügellänge. *Z. Tropenmed. Parasit.* 7: 15–48.

Muir, F. and J. C. Kershaw 1911 On the later embryological stages of the head of *Pristhesancus papuensis*. *Psyche* 18: 75–79.

Muir, F. and J. C. Kershaw 1912 The development of the mouthparts in the Homoptera, with observations on the embryo of *Siphanta*. *Psyche* 19: 77–89.

Müller, H. J. 1951 Über das Schlüpfen der Zikaden (Homoptera Auchenorrhyncha) aus dem Ei. *Zoologica* 37: 1–41.

Müller, H. J. 1961a Erster Nachweis einer Eidiapause bei den Jassiden *Euscelis plebejus* Fall. und *lineolatus* Brullé (Homoptera Auchenorrhyncha). *Z. ang. Ent.* 48: 233–241.

Müller, H. J. 1961b Über die Abhängigkeit der Oogenese von *Stenocranus minutus* Fabr. (Hom. Auchenorrhyncha) von Dauer und Art der täglichen Beleuchtung. *Verh. II. int. Kongr. ent. Wien* 1960 1: 678–689.

Müller, H. J. 1965 Probleme der Insektendiapause. *Verh. Dtsch. Zool. Ges. Jena* 1965: 192–222.

Myers, J. G. 1926 Biological notes on New Zealand Heteroptera. *Trans. N.Z. Inst.* 56: 449–511.

NEEDHAM, J. G. 1907 The eggs of *Benacus* and their hatching. *Ent. News* 18: 113–116.

NGUYEN BAN, J. 1964 Étude de la biologie de *Graphosoma lineata*. *Bull. Soc. Hist. nat. Toulouse*. 99: 325–340.

ODHIAMBO, T. R. 1959 An account of parental care in *Rhinocoris albopilosus* Sign. (Hem.-Het. Reduviidae), with notes on its life history. *Proc. R. ent. Soc. London (A)* 34: 175–185.

OHM, D. 1956 Beiträge zur Biologie des Wasserwanzen *Aphelocheirus aestivalis* F. *Zool. Beitr. N.F.* 2: 359–386.

PANTEL, J. 1913 Recherches sur les Diptères à larves entomobies-II. Les enveloppes de l'oeuf avec leurs dépendances, les dégâts indirects du parasitisme. *La Cellule* 29: 1–289.

PARKER, A. H. 1965 The maternal behaviour of *Pisilus tipuliformis* Fabr. (Hem. Reduviidae). *Ent. exp. & appl.* 8: 13–19.

PARSONS, M. C. 1962 Skeleton and musculature of the head of *Saldula pallipes* (F.) (Heteroptera: Saldidae). *Trans. R. ent. Soc. London* 114: 97–130.

PARSONS, M. C. 1966 Clypeal modification in some littoral and aquatic Heteroptera. *Can. J. Zool.* 43: 161–166.

PATAY, R. 1941 Sur un dispositief aérifère de l'embryon de *Pediculus vestimenti* Nitzsch. *Bull. Soc. zool. Fr.* 66: 182–189.

PEARMAN, J. V. 1928 Biological observations on British Psocoptera. *Ent. mon. Mag.* 64: 209–218; 239–243; 263–268.

PENDERGRAST, J. G. 1957 Studies on the reproductive organs of the Heteroptera with a consideration of their bearing on classification. *Trans. R. ent. Soc. London*. 109: 1–63.

PENDERGRAST, J. G. 1958 An egg-burster in *Rhopalimorpha* Dallas (Hem., Acanthosomidae). *Ent. mon. Mag.* 94: 72.

PENDERGRAST, J. G. 1959 The occurrence of the family Mesoveliidae in New Zealand (Hemiptera, Heteroptera). *N.Z. Ent.* 2: 28.

PENDERGRAST, J. G. 1962 The internal anatomy of the Peloridiidae (Homoptera: Coleorrhyncha). *Trans. R. ent. Soc. Lond.* 114: 49–65.

PENDERGRAST, J. G. 1963 Observations on the biology and immature stages of *Antestia orbona* Kirk. *N.Z. Ent.* 3: 19–25.

PESSON, P. 1951 Homoptères. In: Grassé's *Traité de Zoologie* 10: 1390–1656.

PETERSON, A. 1962 Some eggs of insects that change color during incubation. *Fla. Ent.* 45: 80–87.

PFALER-COLLANDER, E. 1941 Vergleichend-karyologische Untersuchungen an Lygaeiden. *Acta Zool. Fenn.* 30: 1–119.

POINAR, G. O. 1965 Observations on the biology and ovipositional habits of *Aleurocybotus occiduus* (Hom.: Aleyrodidae) attacking grasses and sedges. *Ann. ent. Soc. Amer.* 58: 618–620.

POISSON, R. 1923 Accouplement, ponte et éclosion des hémiptères aquatiques. *Bull. biol. Fr. et Belg.* 57: 89–97.

POISSON, R. 1924 Contribution à l'étude des Hémiptères aquatiques. *Bull. biol. Fr. et Belg.* 58: 49–305.

POISSON, R. 1926 *L'Anisops producta* Fieb. Observations sur son anatomie et sa biologie. *Arch. Zool. exper. gen.* 65: 181–208.

POISSON, R. 1933 Quelques observations sur la structure de l'oeuf des insectes Hémiptères-Hétéroptères. *Bull. Soc. Sc. Bretagne* 10: 1–38.

POISSON, R. 1951 Hétéroptères. In: Grassé's *Traité de Zoologie* 10: 1657–1803.

POISSON, R. 1957 Hemiptera Heteroptera: Hydrocorisae & Geocorisae-Gerroidea. *S. Afr. Animal Life, Uppsala* 4: 327–373.

POISSON, R.	1959	Sur un nouveau représentant africain de la faune terrestre commensale des biotopes hygropétriques: *Madeovelia guineensis* nov. gen., nov. sp. (Insecte Hétéroptère). *Bull. de l' I.F.A.N.* 21: 658–663.
POLIVANOVA, E. N.	1965	Resistance of embryos of *Eurygaster integriceps* and other stinkbugs to different moisture conditions at different temperatures (Hemiptera, Pentatomoidea) [In Russian with English summary]. *Zool. Ž.* 45: 1170–1174.
POPHAM, E. J.	1960	On the respiration of aquatic Hemiptera Heteroptera with special reference to the Corixidae. *Proc. zool. Soc. Lond.* 135: 209–242.
POPHAM, E. J.	1962	On the salivary pump of *Dysdercus intermedius* Dist. (Hemiptera Heteroptera) and other bugs. *Proc. zool. Soc. Lond.* 139: 489–493.
PRIESNER, H.	1964	Ordnung Thysanoptera (Fransenflügler, Thripse) *Bestimmungsbücher zur Bodenfauna Europas.* 2: 1–242.
PUCHKOV, V. G. and L. V. PUCHKOVA	1956	A key to the eggs and larvae of Hemiptera-Heteroptera injurious to crops [In Russian]. *Trud. vsesoyuzn. ent. Obshch.* 45: 218–342.
PUCHKOVA, L. V.	1955	Eggs of Hemiptera-Heteroptera. I. Coreidae. [In Russian]. *Ent. Obozr.* 34: 48–55.
PUCHKOVA, L. V.	1956	Eggs of Hemiptera-Heteroptera. II. Lygaeidae. [In Russian]. *Ent. Obozr.* 35: 262–284.
PUCHKOVA, L. V.	1957	Eggs of Hemiptera-Heteroptera. III. Coreidae (Supplement), IV. Macrocephalidae [In Russian]. *Ent. Obozr.* 36: 44–58.
PUCHKOVA, L. V.	1959	The eggs of true bugs (Hemiptera-Heteroptera), V. Pentatomoidea [In Russian with English summary]. *Ent. Obozr.* 38: 634–648.
PUCHKOVA, L. V.	1966*	The morphology and biology of the egg of the terrestrial bugs (Hemiptera) [In Russian]. *Horae Soc. Ent. Un. Sovet.* 51: 75–132.
RAKSHPAL, R.	1962a	Morphogenesis and embryonic membranes of *Gryllus assimilis* (Fabr.). (Orthoptera: Gryllidae). *Proc. R. Ent. Soc. Lond. (A)* 37: 1–12.
RAKSHPAL, R.	1962b	The effect of cold on pre- and post-diapause eggs of *Gryllus pennsylvanicus* Burm. (Orthoptera: Gryllidae). *Proc. R. Ent. Soc. Lond. (A)* 37: 117–120.
Rastogi, S. C.	1965	The food pump and associated structures in *Coridius janus* (Fabr.) (Heteroptera: Dinidoridae). *Proc. R. Ent. Soc. Lond. (A)* 40: 125–134.
RATHKE, M. H.	1861	Studien zur Entwicklungs-Geschichte der Insekten. *Stett. Ent. Zeit.* 22: 169–191.
RAVEN, CHR. P.	1961	Oogenesis: The storage of developmental information. *Intern. Ser. of Monogr. Div. Zoology* 10 274 pp.
RAWAT, B. L.	1939	On the habits, metamorphosis and reproductive organs of *Naucoris cimicoides* L. (Hemiptera-Heteroptera). *Trans. R. Ent. Soc. Lond.* 88: 119–138.
RAYMENT, T. A.	1955	Historic pole 346. *Proc. R. zool. Soc. N.S. W.* 1953–54: 63–66.

* Unfortunately a discussion on this important Russian publication could not be incorporated in the text.

REMANE, R. 1961 Revision der Gattung *Mocydiopsis* Ribaut (Hom. Cicadellidae). *Abh. Akad. Wiss. Lit. Mainz. (Math.-Nat.).* 1961: 101–149.

REMOLD, H. 1962 Über die biologische Bedeutung der Duftdrüsen bei den Landwanzen (Geocorisae). *Zts. f. vergl. Phys.* 45: 636–694.

REMPEL, Y. G. and N. S. CHURCH 1965 The embryology of *Lytta viridana* La Conte (Coleoptera: Meloidae). I. Maturation, Fertilization and Cleavage. *Can. Journ. Zool.* 43: 915–925.

REUTER, O. M. 1910 Neue Beiträge zur Phylogenie und Systematik der Miriden nebste inleitenden Bemerkungen über die Phylogenie der Hetero ropterenfamilien. *Acta Soc. Sci. fenn.* 37: 2–172.

REUTER, O. M. 1912 Bemerkungen über mein neues Heteropterensystem. *Ofv. Finska Vetensk.-Societ. Forh.* 54: 1–62.

RICE, L. A. 1954 Observations on the biology of ten Notonectoid species found in the Douglas Lake, Michigan Region. *Amer. Midl. Naturalist* 51: 105–132.

RICHARDS, O. W. and R. G. DAVIES 1957 A.D. Imms. A general textbook of Entomology. *London* 886 pp.

RIMES, G. D. 1951 Some new and little-known shore-bugs (Heteroptera-Saldidae) from the Australian region. *Trans. roy. Soc. S. Aust.* 74: 135–145.

ROONWAL, M. L. 1935 Über das Schneiden dotterreicher Eier. *Zool. Anz.* 110: 17.

ROSAY, B. 1959 Gross external morphology of embryos of *Culex tarsalis* Coquillett (Diptera: Culicidae). *Ann. ent. Soc. Amer.* 52: 481–484.

ROSENKRANZ, W. 1939 Die Symbiose der Pentatomiden (Hem. Het.). *Z. Morph. Ökol. Tiere* 36: 279–309.

ROTH, L. M. 1961 A study of the odoriferous glands of *Scaptocoris divergens* (Hemiptera: Cydnidae). *Ann. ent. Soc. Amer.* 54: 900–911.

RYCKMAN, R. E. 1962 Biosystematics and hosts of the *Triatoma protracta* complex in North America (Hemiptera: Reduviidae) (Rodentia: Cricetidae). *Univ. Calif. Publ. Ent.* 27: 93–189.

SALT, R. W. 1953 The influence of food on cold hardiness of insects. *Canad. Ent.* 85: 261–269.

SANDER, K. 1956 The early embryology of *Pyrilla perpusilla* Walker (Homoptera), including some observations on the later development. *Aligarh. Mus. Univ. Publ. (Z.S.)* 4: 1–61.

SANDERS, W. 1962 Das Verhalten der Mittelmeerfruchtfliege *Ceratitis capitata* Wied. bei der Eiablage. *Z. Tierpsychol.* 19: 1–28.

SANDS, W. A. 1957 The immature stages of some British Anthocoridae (Hemiptera). *Trans. R. Ent. Soc. Lond.* 109: 295–310.

SATTLER, W. 1957 Beobachtungen zur Fortpflanzung von *Gerris najas* De G. (Heteroptera). *Z. Morph. Ökol. Tiere* 45: 411–428.

SAUER, H. W. 1966 Zeitraffer-Mikro-Film-Analyse embryonaler Differenzierungsphasen von *Gryllus domesticus*. *Z. Morph. Ökol. Tiere* 56: 143–251.

SCHAEFER, C. W. 1963 Remarks on Scudder's classification of the lygaeoid-coreoid complex of the Heteroptera. *Can. J. Zool.* 41: 1174–1175.

SCHAEFER, C. W. 1964 The morphology and higher classification of the Coreoidea (Hemiptera – Heteroptera): Parts I and II. *Ann. ent. Soc. Amer.* 57: 670–684.

SCHAEFER, C. W. 1966 The morphology and higher systematics of the Idiostolinae (Hemiptera: Lygaeidae). *Ann. ent. Soc. Amer.* 59: 602–613.

SCHANZ, G.	1965	Entwicklungsvorgänge im Ei der Libelle *Ischnura elegans* und Experimente zur Frage ihrer Aktivierung. Eine Mikro-Zeitraffer-Film-Analyse. *Inaugural-Dissertation Marburg/Lahn* 1965: 92 pp.
SCHERF, H.	1960	Progressive Eiverfärbung bei Curculioniden und ihre Problematik. *Zool. Anz.* 165: 47–54.
SCHNEIDER, G.	1940	Beiträge zur Kenntnis der symbiontischen Einrichtungen der Heteropteren. *Z. Morph. Ökol. Tiere* 36: 595–644.
SCHNETTER, M.	1934	Morphologische Untersuchungen über das Differenzierungszentrum der Honigbiene. *Z. Morph. Ökol. Tiere* 29: 114–195.
SCHÖLZEL, G.	1937	Die Embryologie der Anopluren und Mallophagen. *Z. Parasitenk.* 9: 730–770.
SCHORR, H.	1957	Zur Verhaltensbiologie und Symbiose von *Brachypelta aterrima* Först. (Cydnidae, Heteroptera). *Z. Morph. Ökol. Tiere* 15: 561–602.
SCUDDER, G. G. E.	1955	Review: Illustrierte Bestimmungstabellen der Wanzen. II. Europa (Hemiptera-Heteroptera Europae), by Wolfgang Stichel, Pts 1–4. *Ent. mon. Mag.* 91: 47.
SCUDDER, G. G. E.	1957	The systematic position of *Dicranocephalus* Hahn, 1826 and its allies (Hemiptera: Heteroptera). *Proc. R. ent. Soc. Lond. (A)* 32: 147–158.
SCUDDER, G. G. E.	1959	The female genitalia of the Heteroptera: morphology and bearing on classification. *Trans. R. ent. Soc. Lond.* 111: 405–467.
SCUDDER, G. G. E.	1962	Results of the royal society expedition to Southern Chile, 1958–59: Lygaeidae (Hemiptera), with the description of a new subfamily. *Canad. Ent.* 94: 1064–1075.
SCUDDER, G. G. E.	1963	Adult abdominal characters in the lygaeoid-coreoid complex of the Heteroptera, and the classification of the group. *Can. J. Zool.* 41: 1–14.
SEIDEL, F.	1924	Die Geschlechtsorgane in der embryonalen Entwicklung von *Pyrrhocoris apterus* L. *Z. Morph. Ökol. Tiere* 1: 429–450.
SEIDEL, F.	1960	Körpergrundgestalt und Keimstruktur. Eine Erörterung über die Grundlagen der vergleichenden und experimentellen Embryologie und deren Gültigkeit bei phylogenetischen Überlegungen. *Zool. Anz. Leipzig* 164: 245–305.
SEIDEL, F.	1965	Das Eisystem der Insekten und die Dynamik seiner Aktivierung. *Verh. dtsch. zool. Ges.* 1965: 166–187.
SEIDLER, B.	1940	Vergleichend morphologische Untersuchungen der Eistruktur nahe verwandter Käferarten. *Z. Morph. Ökol. Tiere* 36: 677–744.
SHARAN, R. K. and S. L. SAHNI	1960	Provisional embryonic cuticles of *Dysdercus singulatus* (Hemiptera: Pyrrhocoridae). *Ann. ent. Soc. Amer.* 53: 538–541.
SHAROV, A. G.	1966	Basic Arthropodan Stock, with special reference to insects. *Intern. Ser. of Monogr. Div. Zoology* 30 271 pp.
SIKES, E. K. and V. B. WIGGLESWORTH	1931	The hatching of insects from the egg, and the appearance of air in the tracheal system. *Quart. J. micr. Sci.* 74: 165–192.
SINGH-PRUTHI, H.	1925	The morphology of the male genitalia in the Rhynchota. *Trans. ent. Soc. Lond.* 1925: 127–267.
SLATER, FL. W.	1899	The egg-carrying habit of *Zaitha*. *Amer. Nat.* 33: 931–933.

SLATER, J. A. and C. J. DRAKE	1958	The systematic position of the family Thaumastocoridae (Hemiptera: Heteroptera). *Proc. 10th int. Congr. Ent. Montreal* 1956 1: 321–323.
SLIFER, E. H.	1932a	Insect development. III. Blastokinesis in the living grasshopper egg. *Biol. Zbl.* 52: 223–229.
SLIFER, E. H.	1932b	Insect development. IV. External morphology of grasshopper embryos of known age and with a known temperature history. *J. Morph.* 53: 1–21.
SLIFER, E. H.	1934	Insect development. VI. The behavior of grasshopper embryos in anisotonic balanced salt solutions. *J. exp. Zool.* 67: 137–157.
SLIFER, E. H.	1938	The formation and structure of a special water-absorbing area in the membranes covering the grass-hopper egg. *Quart. J. micr. Sci.* 80: 437–457.
SLIFER, E. H.	1945	Removing the shell from living grasshopper eggs. *Science* 102: 282.
SLIFER, E. H.	1946	The effects of xylol and other solvents on the diapause in the grasshopper egg; together with a possible explanation for the action of these agents. *J. exp. Zool.* 102: 333–356.
SLIFER, E. H.	1949	Changes in certain of the grasshopper egg coverings during development as indicated by fast green and other dyes. *J. exp. zool.* 110: 183–203.
SLIFER, E. H.	1956	Specialized areas on the body surface of grass-hoppers and locusts (Orthoptera, Acrididae). *Proc. 10th int. Congr. Ent. Montreal* 1956, 1: 531–534.
SLIFER, E. H. and R. L. KING	1933	Grasshoppers eggs and the paraffin method. *Science* 78: 366.
SLIFER, E. H. and S. S. SEKHON	1963	The fine structure of the membranes which cover the eggs of the grasshopper, *Melanoplus differentialis*, with special reference to the hydropyle. *Quart. J. micr. Sci.* 104: 321–334.
SOUTHWOOD, T. R. E.	1955	The morphology of the salivary glands of terrestrial Heteroptera (Geocorisae) and its bearing on classification. *Tijdschr. Ent.* 98: 77–84.
SOUTHWOOD, T. R. E.	1956*	The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. *Trans. R. ent. Soc. Lond.* 108: 163–221.
SOUTHWOOD, T. R. E. and D. LESTON	1959	Land and water bugs of the British Isles. *The Wayside and Woodland Series. London* 436 pp.
SOUTHWOOD, T. R. E. and G. G. E. SCUDDER	1956	The bionomics and immature stages of the thistle lace bugs *(Tingis ampliata)* H.-S. and *T. cardui* L.; (Hem., Tingidae). *Trans. Soc. Brit. Ent.* 12: 93–112.
SPEYER, W.	1929	Die Embryonalentwicklung und das Ausschlüpfen der Junglarve von *Psylla mali* Schm. *Z. wiss. Insectenbiol.* 24: 215–220.
SPRAGUE, I. B.	1956	The biology and morphology of *Hydrometra martini* Kirkaldy. *Univ. Kans. Sci. Bull.* 38: 579–693.
STEELE, H. V.	1941	Some observations on the embryonic development of *Austroicetes cruciata* (Acrididae) in the field. *Trans. roy. Soc. S. Afr.* 65: 329–332.
STICHEL, W.	1955	Illustrierte Bestimmungstabellen der Wanzen. II. Europa (Hemiptera-Heteroptera Europae). *Berlin* 1 Heft 1–5: 1–160.

* Our list of references should be supplemented by the comprehensive bibliography of SOUTHWOOD's publication.

STICHEL, W. 1956 Illustrierte Bestimmungstabellen der Wanzen. II. Europa (Hemiptera-Heteroptera Europae). *Berlin* 1, Heft 6–15: 161–480.

STICHEL, W. 1957 Illustrierte Bestimmungstabellen der Wanzen. II. Europa (Hemiptera-Heteroptera Europae), *Berlin* 4, Heft 2–10: 60–293.

STRÜBING, H. 1960 Eiablage und photoperiodisch bedingte Generationfolge von *Chloriona smaragdula* Stål und *Euidella speciosa* Boh. (Homoptera – Auchenorrhyncha). *Zool. Beitr. N.F.* 5: 301–332.

ŠTUSÁK, J. M. 1957 Beitrag zur Kenntnis der Eier der Tingiden (Heteroptera: Tingidae). *Beitr. Ent.* 7: 20–28.

ŠTUSÁK, J. M. 1958 Zweiter Beitrag zur Kenntnis der Eier der Tingiden (Hemiptera-Heteroptera, Tingidae). *Acta Soc. ent. Čsl.* 55: 361–371.

ŠTUSÁK, J. M. 1961 Dritter Beitrag zur Kenntnis der Eier der Tingiden (Heteroptera, Tingidae). *Acta Soc. ent. Čsl.* 58: 71–88.

ŠTUSÁK, J. M. 1962 Immature stages of *Elasmotropis testacea* (H.-S) and notes on the bionomics of the species (Het. Tingidae). *Acta Soc. ent. Čsl.* 59: 19–27.

ŠTYS, P. 1961 Morphology of the abdomen and female ectodermal genitalia of the trichophorous Heteroptera and bearing on their classification. *Verh. II. int. Kongr. Ent. Wien* 1960 1: 37–43.

ŠTYS, P. 1962 Venation of metathoracic wings and notes on the relationships of Microphysidae (Heteroptera). *Acta Soc. ent. Čsl.* 59: 234–239.

ŠTYS, P. 1964a The morphology and relationships of the family Hyocephalidae (Heteroptera). *Acta Zool. Acad. Sci. Hungar.* 10: 229–262.

ŠTYS, P. 1964b Thaumastellidae – a new family of pentatomoid Heteroptera. *Acta Soc. ent. Čsl.* 61: 238–253.

ŠTYS, P. 1965 General outline of the phylogeny of Coreoidea (Heteroptera). *Proc. 12th int. Congr. Ent. London* 1964: 74.

SWAMMERDAM, J. 1737 Bijbel der Natuure. Historie der insecten. *Leyden* 910 pp.

SWEET, M. H. 1964 The biology and ecology of the Rhyparochrominae of New England (Heteroptera: Lygaeidae). Part I. *Ent. Amer.* 43: 1–124.

TAMANINI, L. 1956 Osservazioni biologiche e morfologiche sugli *Aradus betulinus* Fall., *A. corticalis* L., *A. pictus* Bär. (Hem. Heteroptera, Aradidae). *Stud. Trent. Sci. Nat.* 33: 3–53.

TELFORD, D. 1957 The pasture *Aedes* of central and northern California. The egg stage: gross embryology and resistance to desiccation. *Ann. ent. Soc. Am.* 50: 537.

TEYROVSKÝ, V. 1924 Das Ei und Eiablage von *Cymatia coleoptrata* F. *Jubilejní sborník Čsl. entomol. společn* 1924: 100–101.

THONTADARYA, T. S. and C. G. P. BASAVANNA 1959 Mode of egg-laying in Tingidae (Hem.). *Nature* 184: 289–290.

TIEGS, O. W. 1942a The 'dorsal organ' of Collembolan embryos. *Quart J. micr. Sci.* 83: 153–169.

TIEGS, O. W. 1942b The 'dorsal organ' of the embryo of *Campodea*. *Quart. J. micr. Sci.* 84: 35–47.

TIMONIN, M. 1961 The interaction of plant, pathogen, and *Scaptocoris talpa* Champ. *Can. J. Botan.* 39: 695–703.

TISCHLER, W. 1960 Studien zur Bionomie und Ökologie der Schmalwanze *Ischnodemus sabuleti* Fall. (Hem., Lygaeidae). *Z. wiss. Zool.* 163: 168–209.

TONAPI, G. T. 1959 A note on the eggs of *Gerris fluviorum* F. with a brief description of its neanide. (Hem. Gerrididae). *Ent. mon. Mag.* 95: 29–31.

TRUCKENBRODT, W. 1964 Zytologische und entwicklungsphysiologische Untersuchungen am besamten und am parthenogenetischen Ei von *Kalotermes flavicollis* Fabr. *Zool. Jb. Anat.* 81: 359–434.

TUFT, P. H. 1950 The structure of the insect egg-shell in relation to the respiration of the embryo. *J. exp. Biol.* 26: 327–334.

TULLGREN, A. 1918 Zur Morphologie und Systematik der Hemipteren I. *Ent. Tidskr.* 39: 113–132.

ULJANIN, W. M. 1874 Observations on the development of thrips (Physopoda). [In Russian]. *Izv. Imp. Ob. Liubit. Estest. Anth. Ethnogr.* 10: 39–44.

USINGER, R. L. 1945 Biology and control of Ash plant bugs in California. *J. econ. Ent.* 38: 585–591.

USINGER, R. L. 1946 Notes and descriptions of *Ambrysus* Stål with an account of the life history of *Ambrysus mormon* Montd. (Hemiptera, Naucoridae). *Kans. Univ. Sci. Bull.* 31: 185–210.

USINGER, R. L. 1956 Aquatic Hemiptera. In: Usinger, Aquatic insects of California. *Berkeley* 182–228.

USINGER, R. L. and R. MATSUDA 1959 Classification of the Aradidae (Hemiptera-Heteroptera). *Brit. Mus. (Nat. Hist.)* 410 pp.

USINGER, R. L.; P. WYGODZINSKY and R. E. RYCKMAN 1966 The biosystematics of Triatominae. *Annu. Rev. Ent.* 11: 309–330.

VAN EMDEN, F. 1925 Zur Kenntnis der Eizähne der Arthropoden ins besondere der Coleopteren. *Z. wiss. Zool.* 126: 622–654.

VODJDANI, S. 1954 Contribution à l'étude des punaises de Cereales et en particulier *d'Eurygaster integriceps* Put. (Hemiptera, Pentatomidae, Scutellerinae). *Ann. Epiphyt.* 1954: 105–160.

WAGNER, E. 1961 Heteroptera-Hemiptera. In: *Die Tierwelt Mitteleuropas* 4 (10a): 1–172.

WAGNER, E. 1963 Eine neue Reduviiden-Art vom Tschadseegebiet (Hem. Het.). *Z. Arbeitsgem. österr. Ent.* 15: 65–67.

WAGNER, E. 1966 Wanzen oder Heteropteren. I. Pentatomorpha. In: *Die Tierwelt Deutschlands* 45: 1–235.

WAGNER, W. 1963 Dynamische Taxionomie, angewandt auf die Delphaciden Mitteleuropas. *Mitt. Hamburg. Zool. Mus. Inst.* 60 (1962): 111–180.

WALTON, G. A. 1962 The egg of *Agraptocorixa gestroi* Kirkaldy (Hemiptera-Heteroptera: Corixidae). *Proc. R. ent. Soc. Lond. (A)* 37: 104–106.

WARREN, B. C. S. 1956 On the recognition of the species. *Proc. 10th int. Congr. Ent. Montreal* 1: 111–123.

WEBER, H. 1930 Biologie der Hemipteren. *Biologische Studienbücher, Berlin* 11: 1–543.

WEBER, H. 1931 Lebensweise und Umweltbeziehungen von *Trialeurodes vaporariorum* (Westwood). (Homoptera-Aleurodina). Erster Beitrag zu einer Monographie dieser Art. *Z. Morph. Ökol. Tiere* 23: 575–753.

WEBER, H. 1939a Beiträge zur Kenntnis der Überordnung Psocoidea: 5. Zur Eiablage und Entwicklung der Elefantenlaus *Haematomyzus elephantis* Piaget. *Biol. Zbl.* 59: 98–109.

WEBER, H. 1939b Beiträge zur Kenntnis der Überordnung Psocoidea: 6. Lebendbeobachtungen an der Elefantenlaus *Haematomyzus*, nebst

vergleichenden Betrachtungen über die Lage des Embryos im Ei und das Auskriechen. *Biol. Zbl.* 59: 397–409.

WEBER, H. 1954 Grundriss der Insektenkunde. *Stuttgart* 428 pp.

WEBSTER, F. M. and W. J. PHILLIPS 1912 The spring grain-aphis or Green bug. *U.S. Dept. Agr., Bur. Ent. Bull.* 110: 94–103.

WEFELSCHEID, H. 1912 Über die Biologie und Anatomie von *Plea minutissima* Leach. *Zool. Jahrb.* 32: 389–474.

WESENBERG-LUND, C. 1943 Biologie der Süsswasserinsekten. *Kopenhagen:* 106–149.

WHEELER, W. M. 1889 Über drüsenartige Gebilde im ersten Abdominalsegment der Hemipterenembryonen. *Zool. Anz.* 12: 500–504.

WHITE, M. J. D. 1954 The chromosomes. *London* 124 pp.

WIELOWIESKI, H. 1884 Zur Kenntnis der Eibildung bei der Feuerwanze. *Zool. Anz.* 8: 369–375.

WIGGLESWORTH, V. B. 1950a Principles of insect physiology. *London* 554 pp

WIGGLESWORTH, V. B. 1950b The new method for injecting the tracheae and tracheoles of insects. *Quart. J. micr. Sci.* 91: 217–224.

WIGGLESWORTH, V. B. 1964 The life of insects. *London* 360 pp.

WIGGLESWORTH, V. B. 1965 The principles of insect physiology. *London* 741 pp.

WIGGLESWORTH, V. B. and J. W. L. BEAMENT 1950 The respiratory mechanisms of some insect eggs. *Quart. J. micr. Sci.* 91: 429–452.

WIGGLESWORTH, V. B. and J. W. L. BEAMENT 1960 The respiratory structures in the eggs of higher Diptera. *J. Ins. Physiol.* 4: 184–189.

WIGGLESWORTH, V. B. and M. M. SALPETER 1962 The aeroscopic chorion of the egg of *Calliphora erythrocephala* Meig. (Diptera). Studied with the electron microscope. *J. Ins. Physiol.* 8: 635–641.

WILBRINK, G. 1912 De Kedirische wortelwants. *Stibaropus molginus* (Schiodt). *Meded. Proefst. Java-Suikerind.* 22: 639–651.

WILCKE, J. 1941 Biologie en morphologie van *Psylla buxi* L. *Tijdschr. Pl.Ziekt.* 47: 41–89.

WILEY, G. O. 1922 Life history notes on two species of Saldidae (Hemiptera) found in Kansas. *Kansas Univ. Sci. Bull.* 14: 299–310.

WILL, L. 1885 Bildungsgeschichte und morphologischer Werth des Eies von *Nepa cinerea* L. und *Notonecta glauca* L. *Z. wiss. Zool. 1885* 41: 311–389.

WILLE, J. 1929 Die Rübenblattwanze *Piesma quadrata* Fieb. *Monogr. Pflsch.* 2: 1–116.

WOODROFFE, G. E. 1963 Biological notes on British Hemiptera-Heteroptera captured during 1962. *Ent. mon. Mag.* 4: 161–162.

WOODWARD, T. E. 1950 Ovariole and testis follicle numbers in the Heteroptera. *Ent. mon. Mag.* 86: 82–84.

WOODWARD, T. E. 1952 Studies on the reproductive cycle of three species of British Heteroptera, with special reference to the overwintering stages. *Trans. R. ent. Soc.* 103: 171–218.

WRÓBLEWSKI, A. 1958 The Polish species of the genus *Micronecta* Kirk. (Heteroptera, Corixidae). *Ann. zool., Warsaw* 17: 247–381.

WYGODZINSKY, P. 1943 Contribuição ao conhecimento do gênero '*Stenolemus*' Signoret 1858 (Ploiariinae, Reduviidae, Hemiptera). *Rev. brasil. Biol.* 3: 443–451.

WYGODZINSKY, P. 1950 Schizopterinae from Angola (Cryptostemmatidae, Hemiptera). *Publ. cult. Mus. Dundo, Comp. Diam. Ang.* 7: 9–47.

WYGODZINSKY, P. 1953 Cryptostemmatinae from Angola (Cryptostemmatidae, Hemiptera). *Publ. cult. Mus. Dundo, Comp. Diam. Ang.* 16: 29–47.

YAJIMA, H. 1960 Studies on embryonic determination of the Harlequinfly, *Chironomus dorsalis*.
I. Effects of centrifugation and of its combination with constriction and puncturing. *J. Embryol. exp. Morph.* 8: 198–215.

YAMADA, Y. 1914 On *Urostylus westwoodii* Scott. [In Japanese]. *Insect World* 18: 138–142.

YAMADA, Y. 1915 On *Urostylus striicornis* Scott. [In Japanese]. *Insect World* 19: 313–316.

YOUNG, E. C. 1965 Flight muscle polymorphism in british Corixidae: ecological observations. *J. Animal. Ecol.* 34: 353–389.

Explanation of figure lettering

a	antenna
ab	antennal bud
ac	air cleft
ae	aft side of egg
ai	air
ail	aerostatic inner layer
ais	airsponge
am	amnion
amf	amniotic fluid
amp	aero-micropylar process
an	anteclypeus
ap	aeropyle
api	aeropylar inner opening
apo	aeropylar outgrowth
apoo	aeropylar outer opening
apop	opercular respiratory horn
apr	rim respiratory horn
asg	abdominal scent gland
b	brain
bas	borderline of amnion and serosa
bp	blastopore
br	brown ring (symbionts?)
bth	blastodermal thickening
c	chorion
cbe	canals branching entad
cd	chorionic dome
ce	compound eye
cel	chorionic eclosion line
cer	chorionic eclosion rupture
ces	cephalic strand
cg	chorionic globule
ch	chorionic hydropyle
cil	chorionic inner layer
cim	chorionic inner meshwork
cl	chorionic lid
clw	chorionic line of weakness
co	cephalic organ
col	chorionic outer layer
com	chorionic outer meshwork
cop	chorionic operculum
copr	opercular process
cose	conceptaculum seminis
cp	chorionic partition
cps	chorionic porous substance
cr	chorionic reticulation
crc	chorionic rim collar
cri	chorionic rivet
crw	chorionic ring of weakness
cry	crystal
cst	chorionic strut
csta	chorionic stalk
cy	contracted yolk body
d	dorsal side egg
dem	dorsal side embryo
do	dorsum
ec	embryonic cuticle
ecer	ec eclosion rent
ecf	ec cephalic frame-work
eco	ec outgrowth
ecv	ec vesicle
enc	end chamber
esf	extraserosal fluid
ex	exposed area of shell
fas	fusion of amnion and serosa
fcb	binucleate follicle cell
fe	fore side of egg
fis	filament of serosal cell
fob	first ovipositor blades
fr	frons
fr-ptc	fronto-postclypeal region

gb	germ band
gc	germ cells
gm	germarium
gs	gluing substance
h	head
hb	hexagonal boundary
isd	thread-like intima of stomodaeum
l 1–3	1st–3rd legs
lc	larval cuticle
lecd	ecdysial line of larva
lg	ligature
li	labium
lo	larval organ
lov	lateral oviduct
lr	labrum
lu	lumen
mb	membrane of unknown origin
md	mandible
mp	micropyle
mpa	micropylar area
mpi	internal micropylar canal
mpia	internal micropylar appendage
mpin	intrachorionic micropylar canal
mpo	micropylar outer opening
mpp	imprint of micropyle
mpr	micropylar process
mx_1	maxilla
mx_2	labium
myc	mycetome
nc	nerve cord
ng	neural groove
nuc	nutritive cord
om	ommatidium
oo	oocyte
pc	pore canal
pcd	proctodaeum
pd	pedestal
ped	pedicel
pf	protoplasmic fibrillae
pi	point of invagination
pl	protocephalic lobes
pla	prolarva
pls	plastron
po	postclypeus
pop	posterior pole
pp	pleuropodium
pr	pronotum
ps	pseudoperculum
pt	pit, indentation of dorsal apodeme
ra	respiratory area
rco	rudimentary cephalic organ
ro	ruptor ovi (egg-burster)
roc	clypeal ruptor
rof	frontal ruptor
roi	imprint of ruptor ovi
s	serosa
sb	sealing bar
sc	serosal cuticle
scb	sc bladder
scc	serosal cone cell
scd	degenerating serosal cells
scer	sc eclosion rupture
sch	sc hydropyle
sci	sc inward projection
scil	sc inner layer
scl	clustering serosal cells
sco	contracting serosal cells
scol	sc outer layer
scop	sc operculum
scp	sc black pigment
scw	sc wedge
sd	stomodaeum
sdr	disrupted serosa
sed	secondary dorsal organ
sem	semen
sgb	intersegmental border
sh	serosal hydropyle
shr	rudiment serosal hydropyle
sn	serosal cell nucleus
sp	serosal plug
spb	spiny band
st	stigma
sub	substrate
sul	suprachorionic layer
sw	serosal window
sy	symbionts

syb	symbiont ball
syp	symbiont pellet
tb	trichobothrium
tf	terminal filament
tg	thoracic ganglion
v	ventral side of egg
ve	vertex
vem	ventral side of embryo
vi	vitellarium
y	yolk
yn	yolk nucleus

Photographs

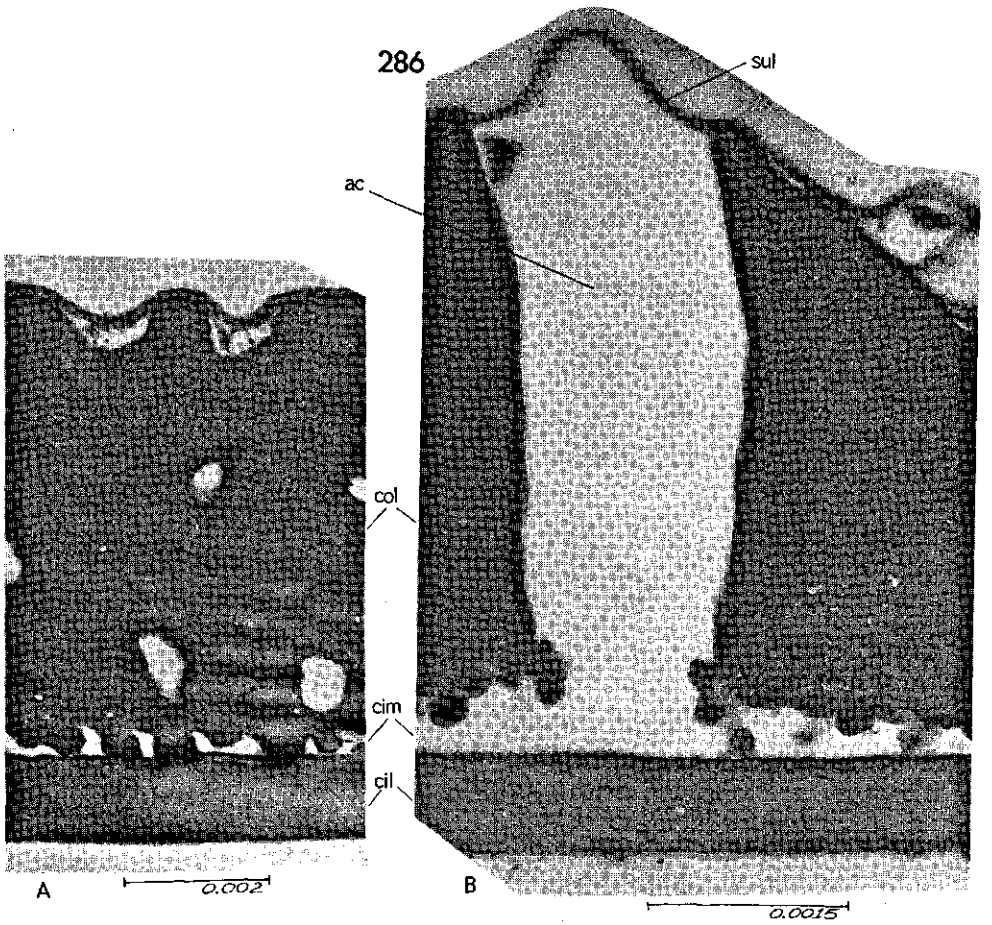


Fig. 286–305. Micrographs of chorionic structures (transmission electron microscope); unless otherwise stated, the figures refer to transverse sections.
Fig 286. *Saldula palustris*, deposited egg; A: close to posterior pole; B: aeropylar region close to anterior pole.

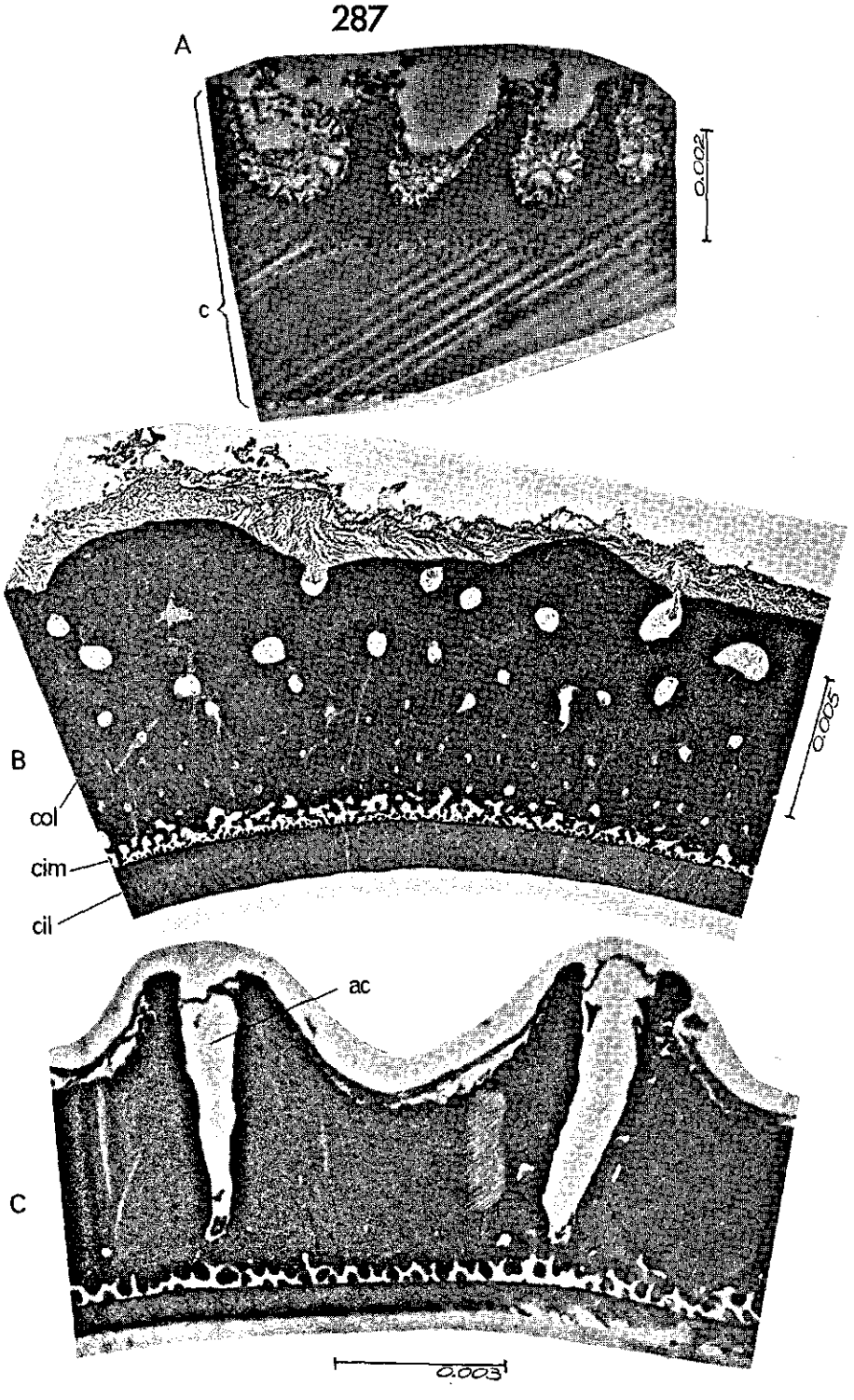


Fig. 287A: *Aepophilus bonnairei*, mid part of ovarian egg; B: *Orthophrys pygmaeum*, ovarian egg, anterior lateral part; C: *Saldula palustris*, as fig. 286B.

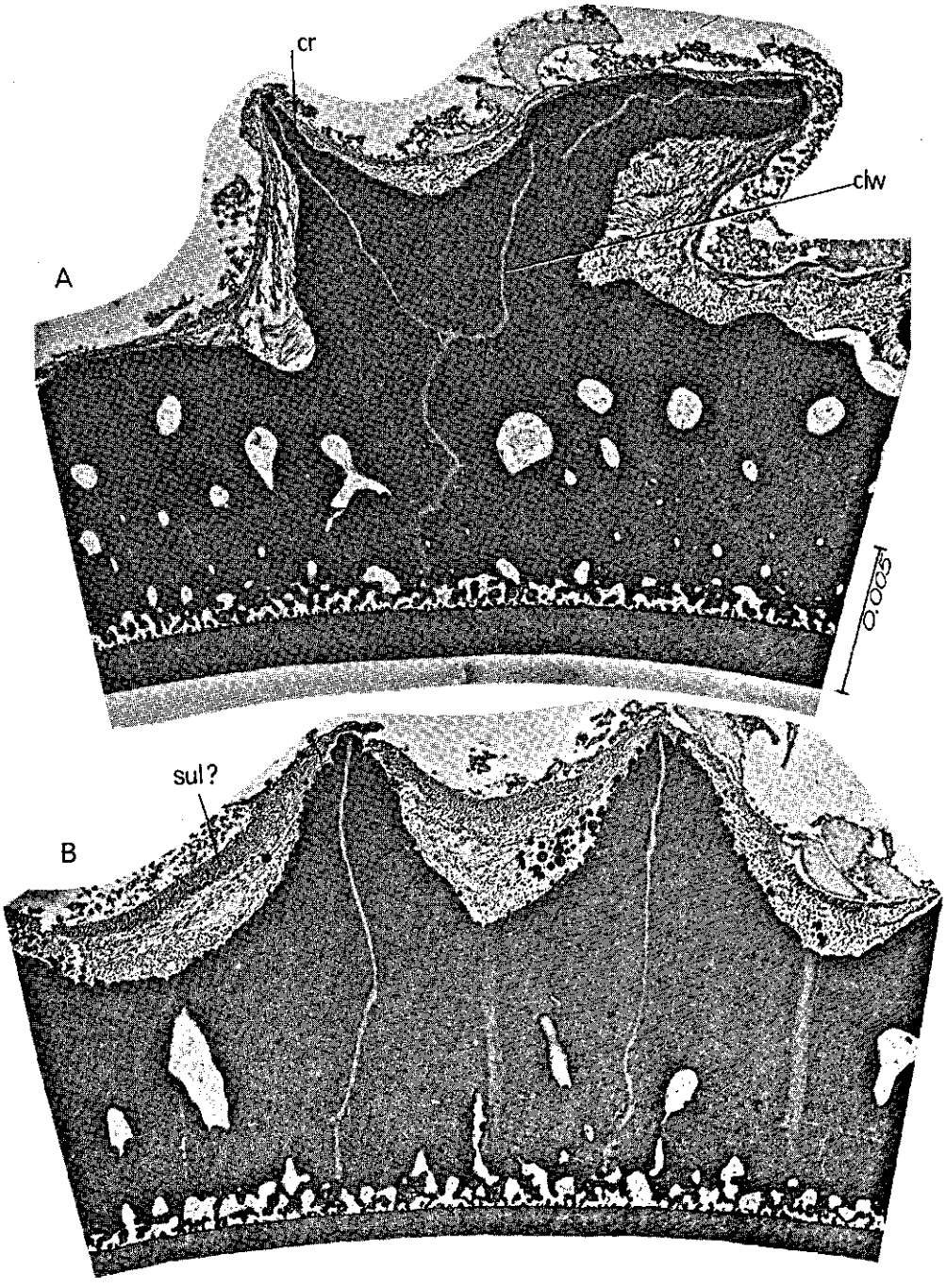


Fig. 288A, B: *Orthophrys pygmaeum*, ovarian egg, reticulated area (compare fig. 10).

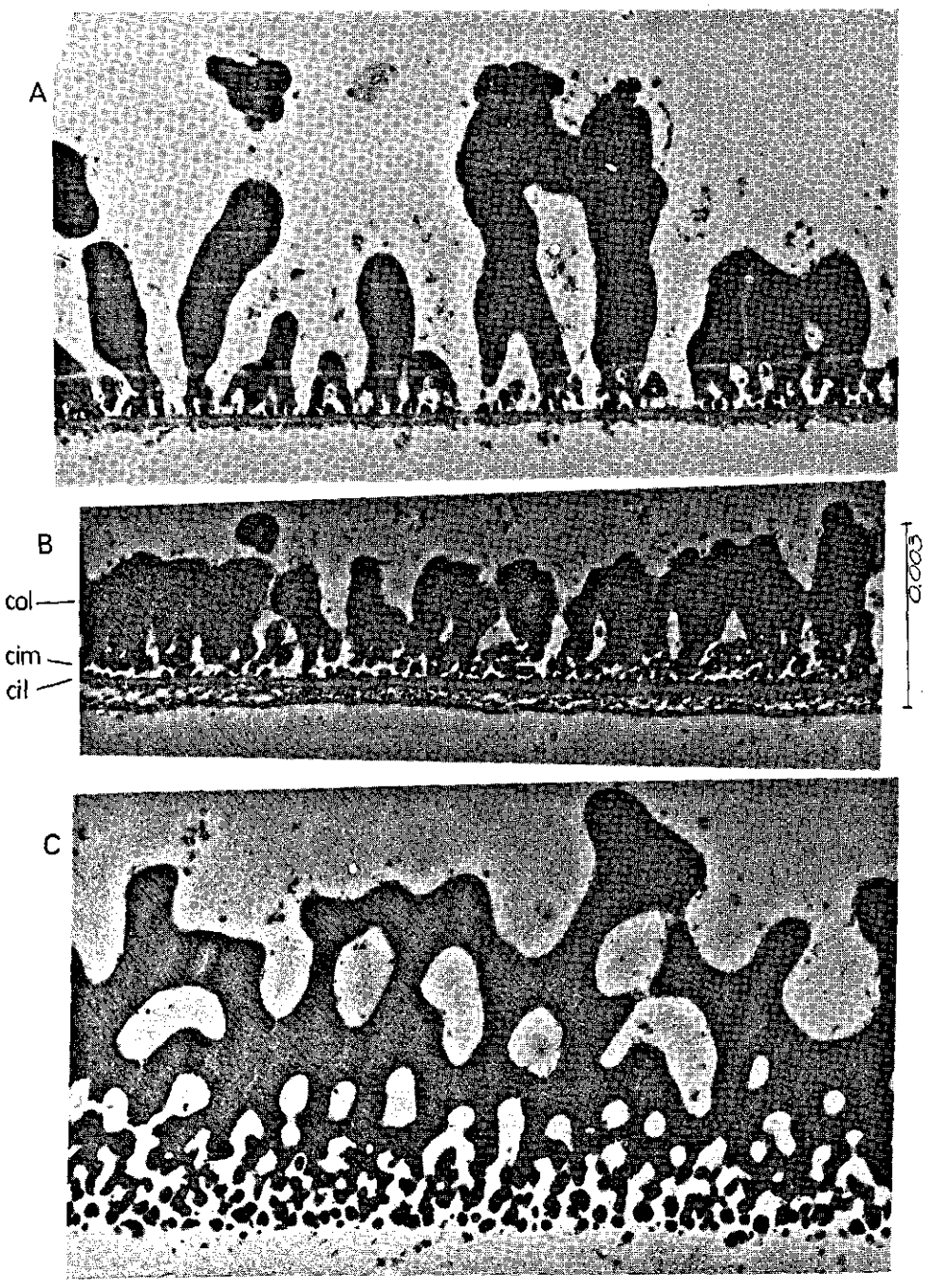


Fig. 289A–C: *Pentacora signoreti*, ovarian egg; A: fore side of anterior pole (compare fig. 6); B: lateral side; C: oblique section through chorionic outer layer.

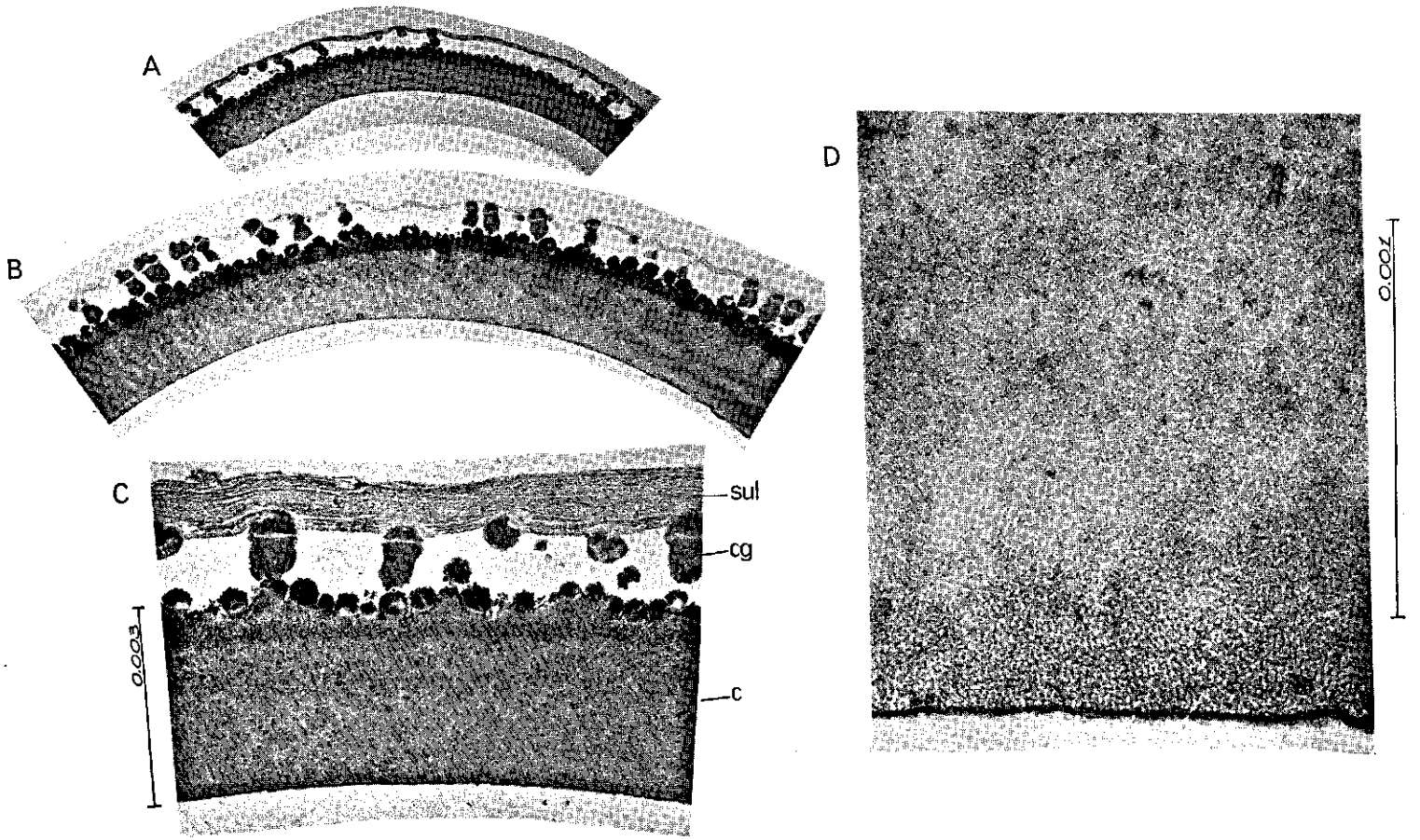


Fig. 290A–D: *Hebrus elimatus*, mid part of ovarian egg (stained with $KMnO_4$); D: high magnification of inner part of shell.

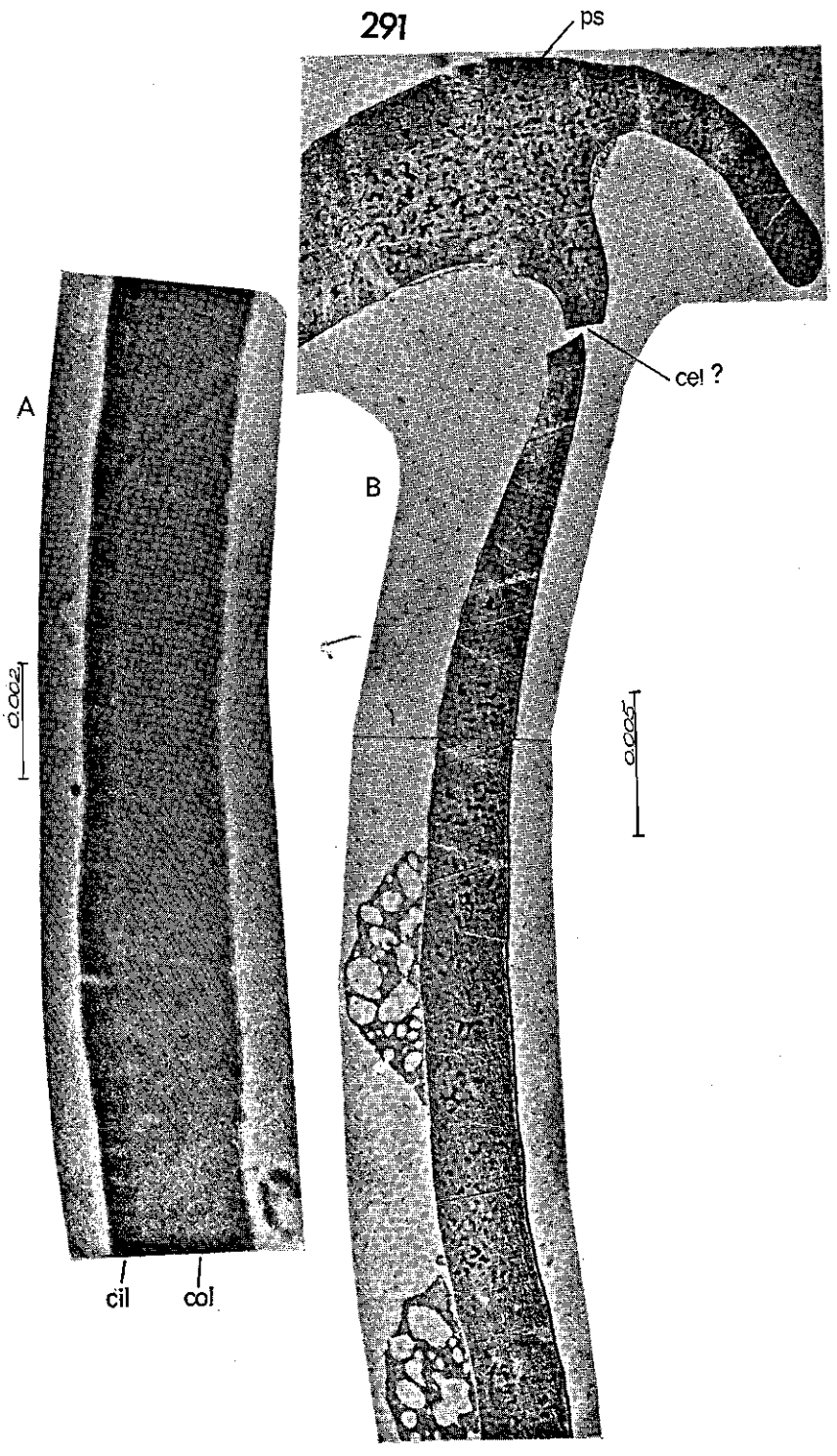


Fig. 291A: *Pachycoleus rufescens*, ovarian egg, lateral side; B: *Mesovelia furcata*, ovarian egg, longitudinal section through upper edge of anterior pole.

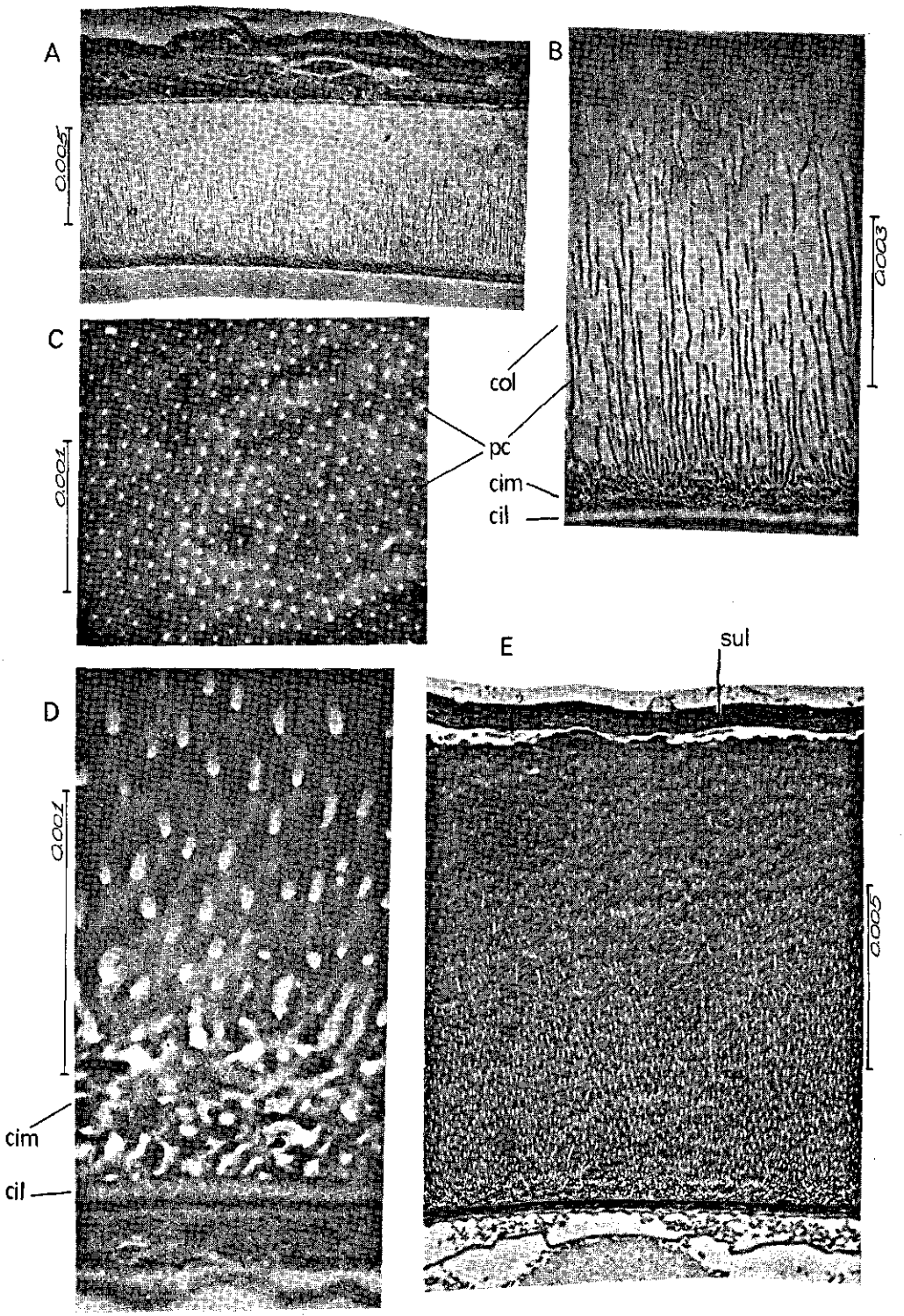


Fig. 292A, B: *Aquarius paludum*, anterior half of ovarian egg; C–E: *Gerris thoracicus*, deposited egg, close to anterior pole; C: horizontal section; D: basal part of section E. (The dark appearance of the intrachorionic canals in A and B is due to the embedding material: Vestopal; in C–E, Metacryllate was used.)

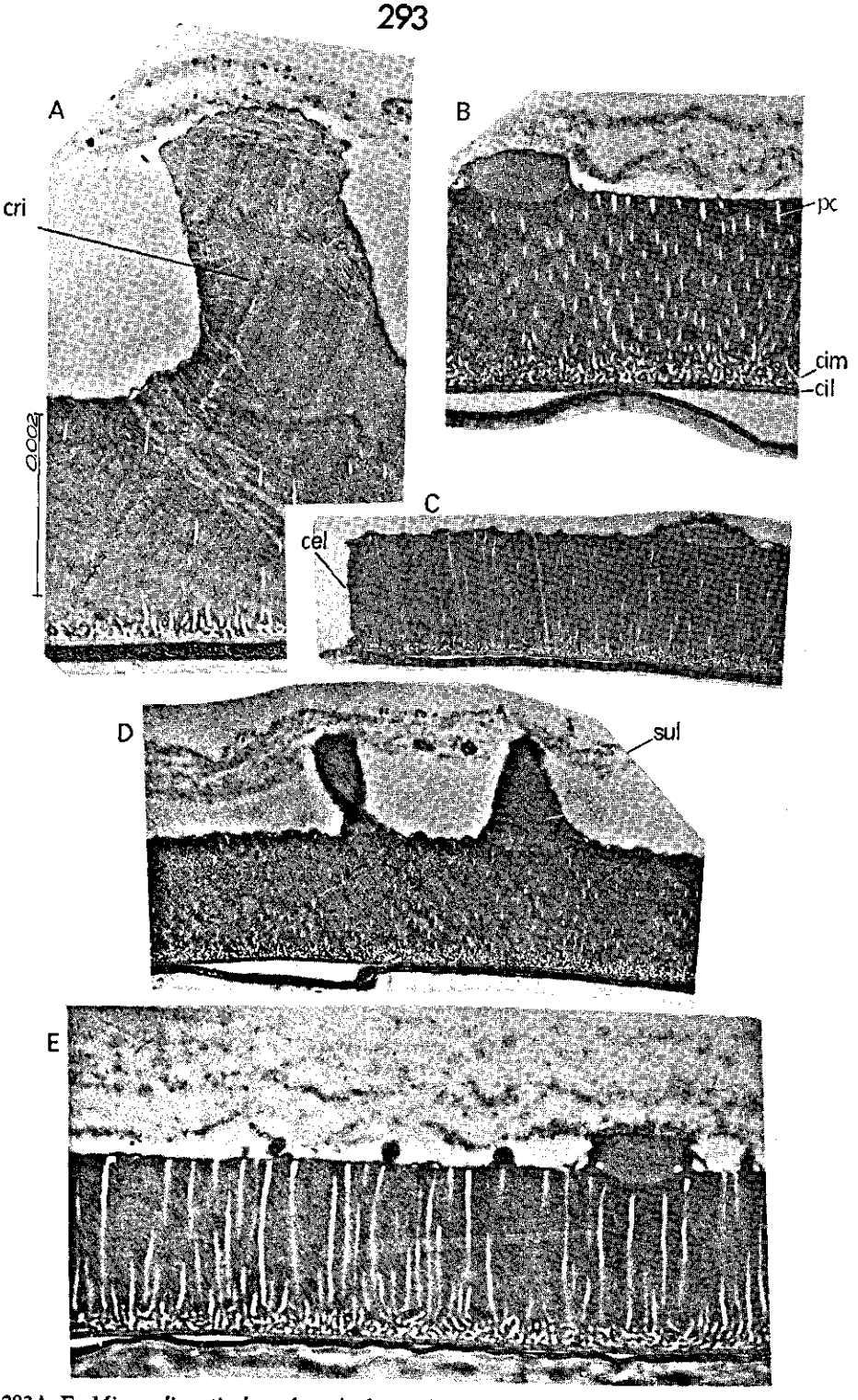


Fig. 293A–E: *Microvelia reticulata*, deposited egg; A–D: anterior half, fore side; E: lateral side.

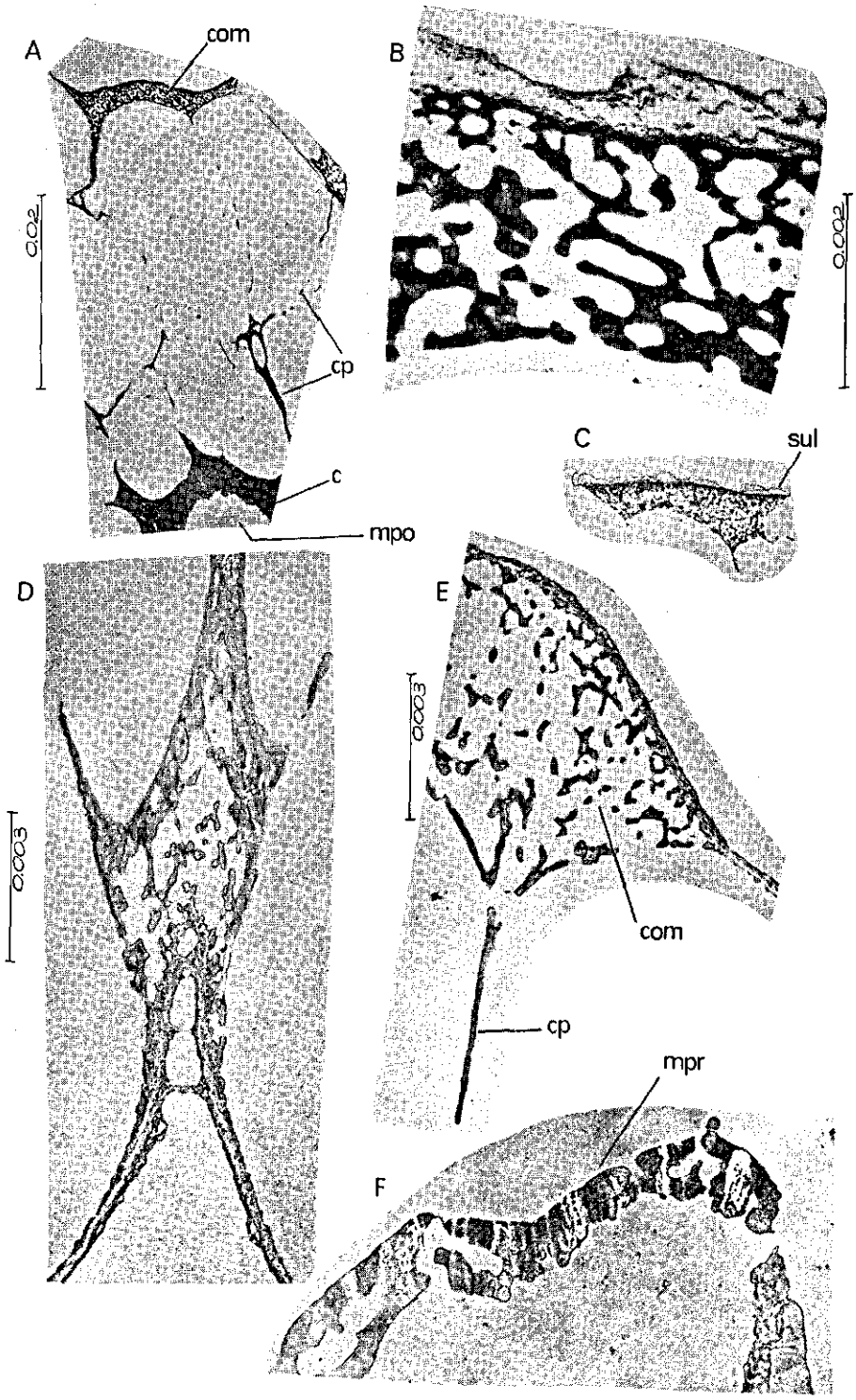


Fig. 294A–F: *Hydrometra stagnorum*, deposited egg; A: transverse section near the base of the micropylar stalk; B, C, E: outer meshwork of the chorionic blisters; D: junction of partitions dividing the lumina of the outer layer; F: wall of micropylar tube just below its apex (compare fig. 50, 51).

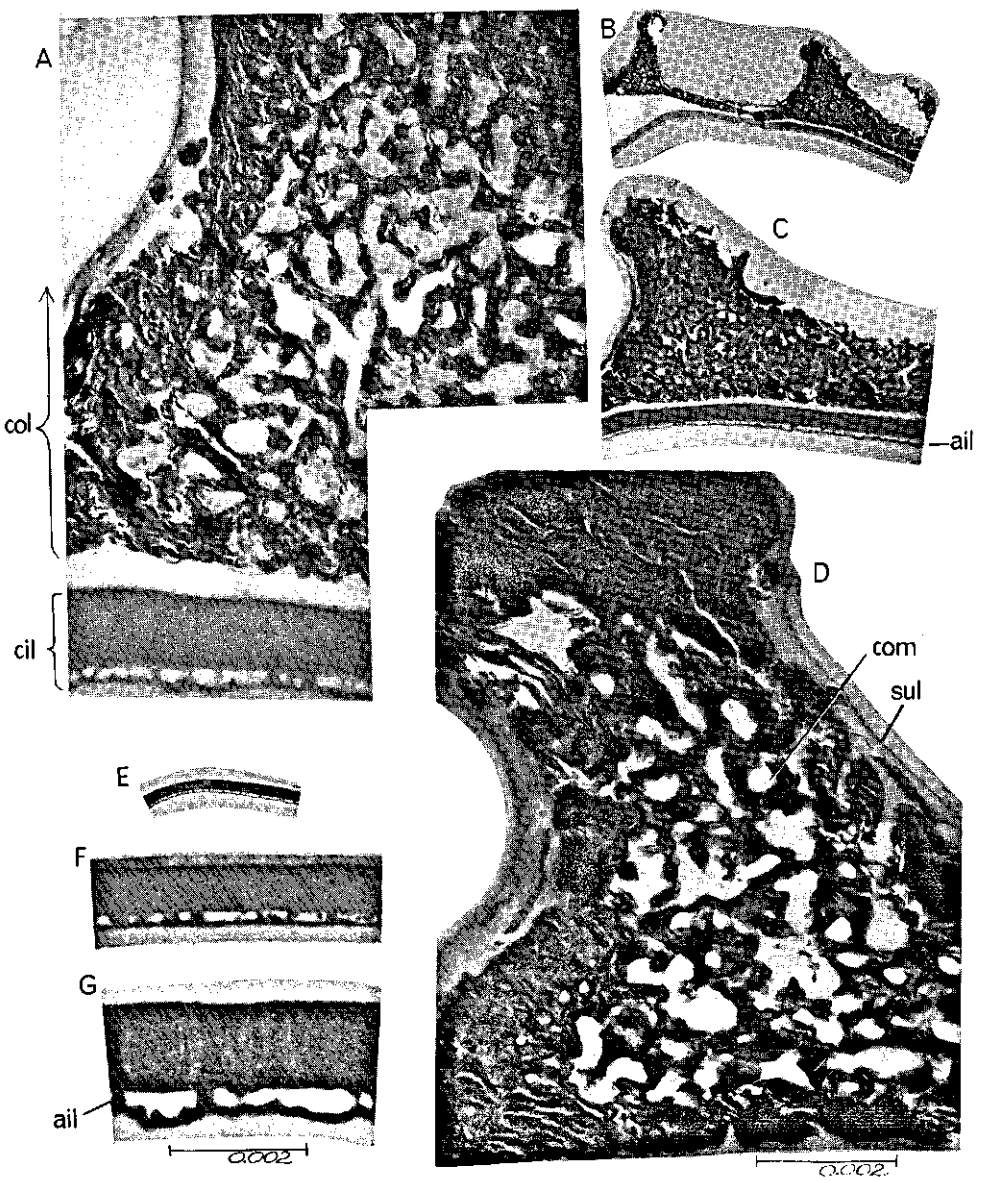


Fig. 295A–G: *Neuroctenus* sp., mid part of deposited egg, note the interspace between outer and inner layer (compare fig. 65D).

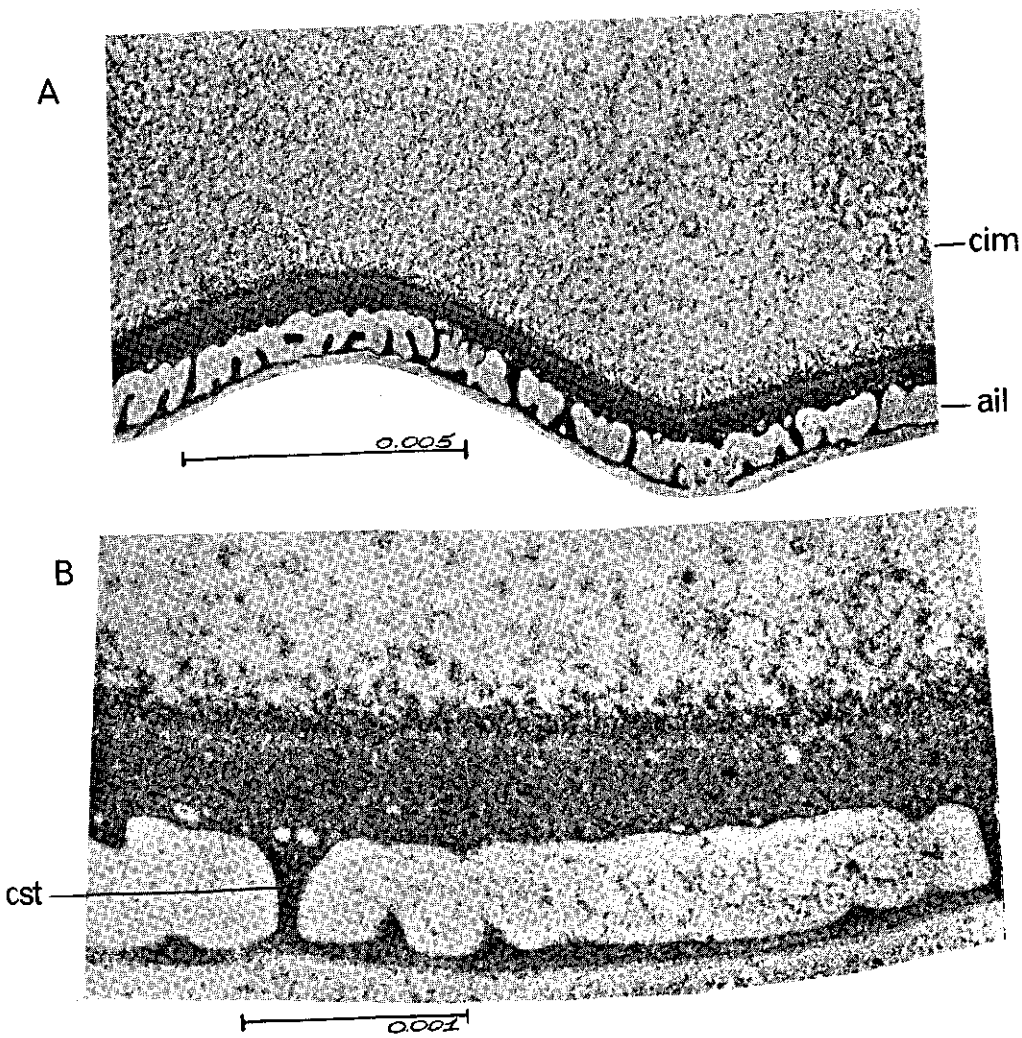


Fig. 296A, B: *Coptosoma* sp., internal part of shell of deposited egg. (The side of the egg sectioned was not determined.)

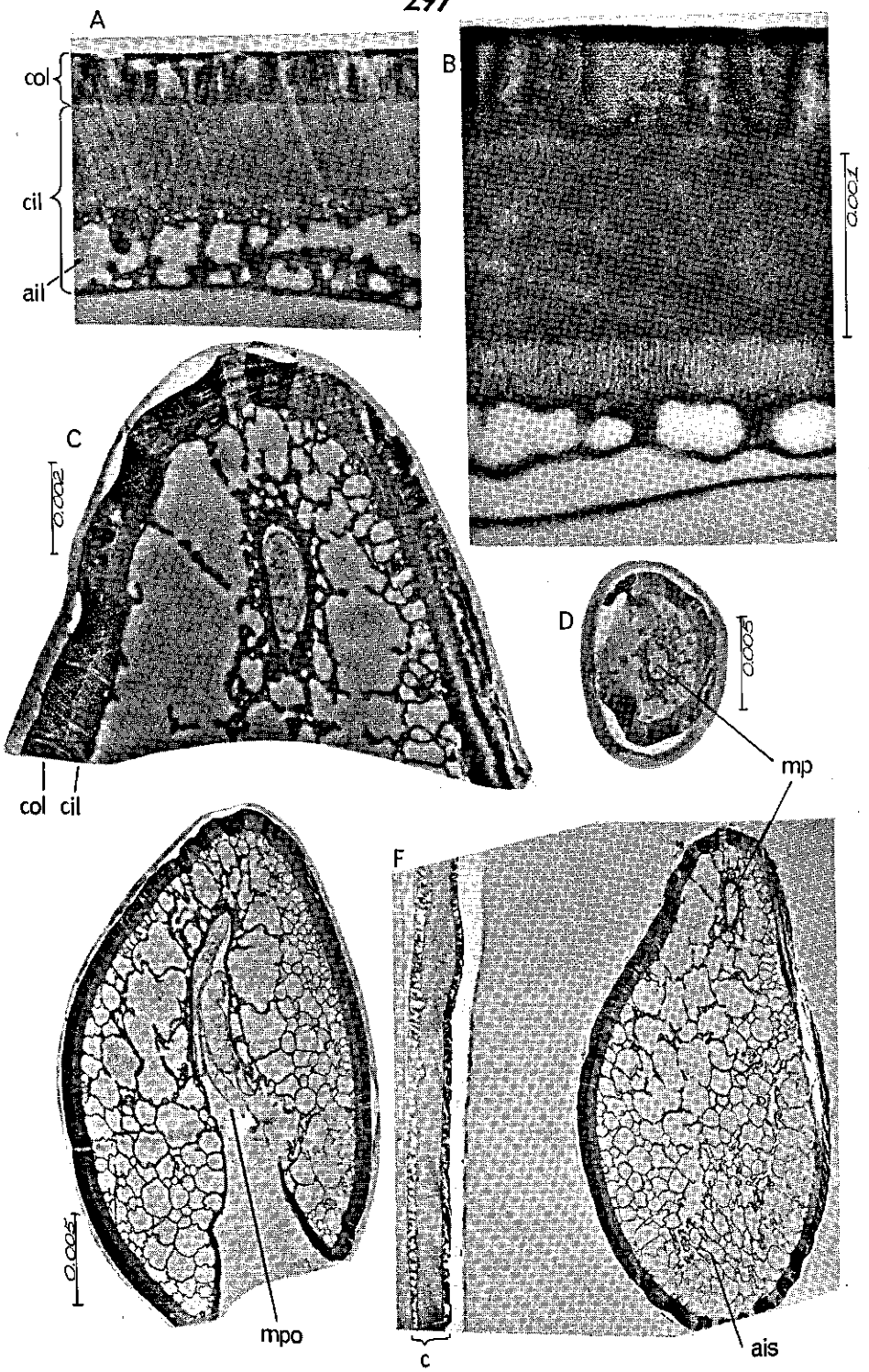


Fig. 297A–F. *Oncopeltus fasciatus*, longitudinal sections of anterior pole, deposited egg; A: close to micropyle; B: closer to pole; C, E, F: aero-micropylar cup; D: stem region of cup.

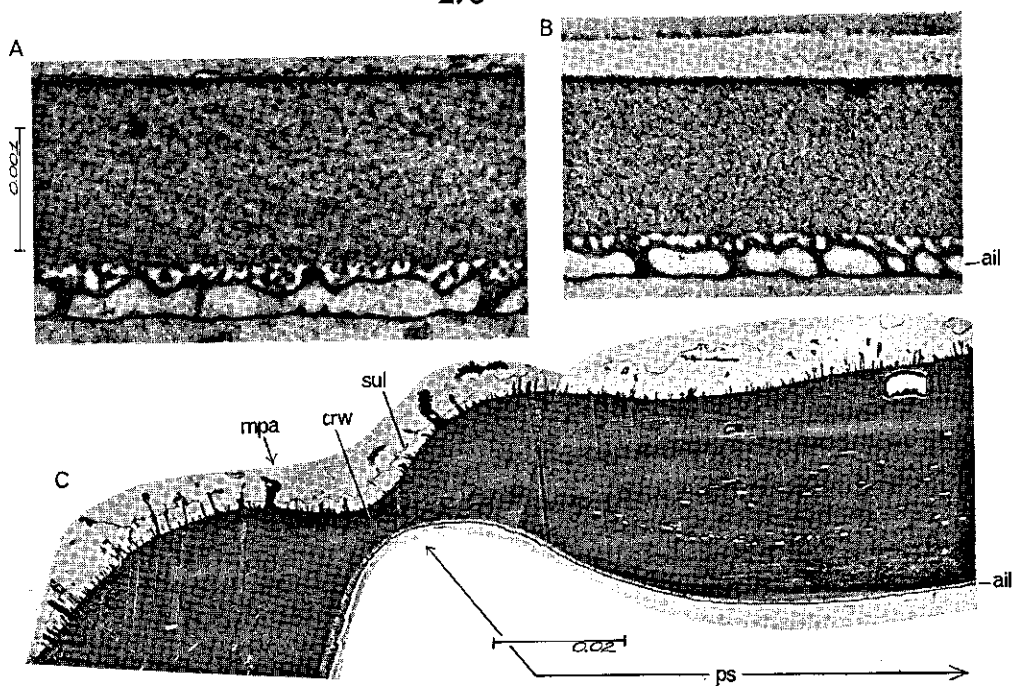


Fig. 298A, B: *Elasmucha grisea*, deposited egg, anterior pole; C: *Macrina juvenca*, deposited egg, longitudinal section of edge of anterior pole.

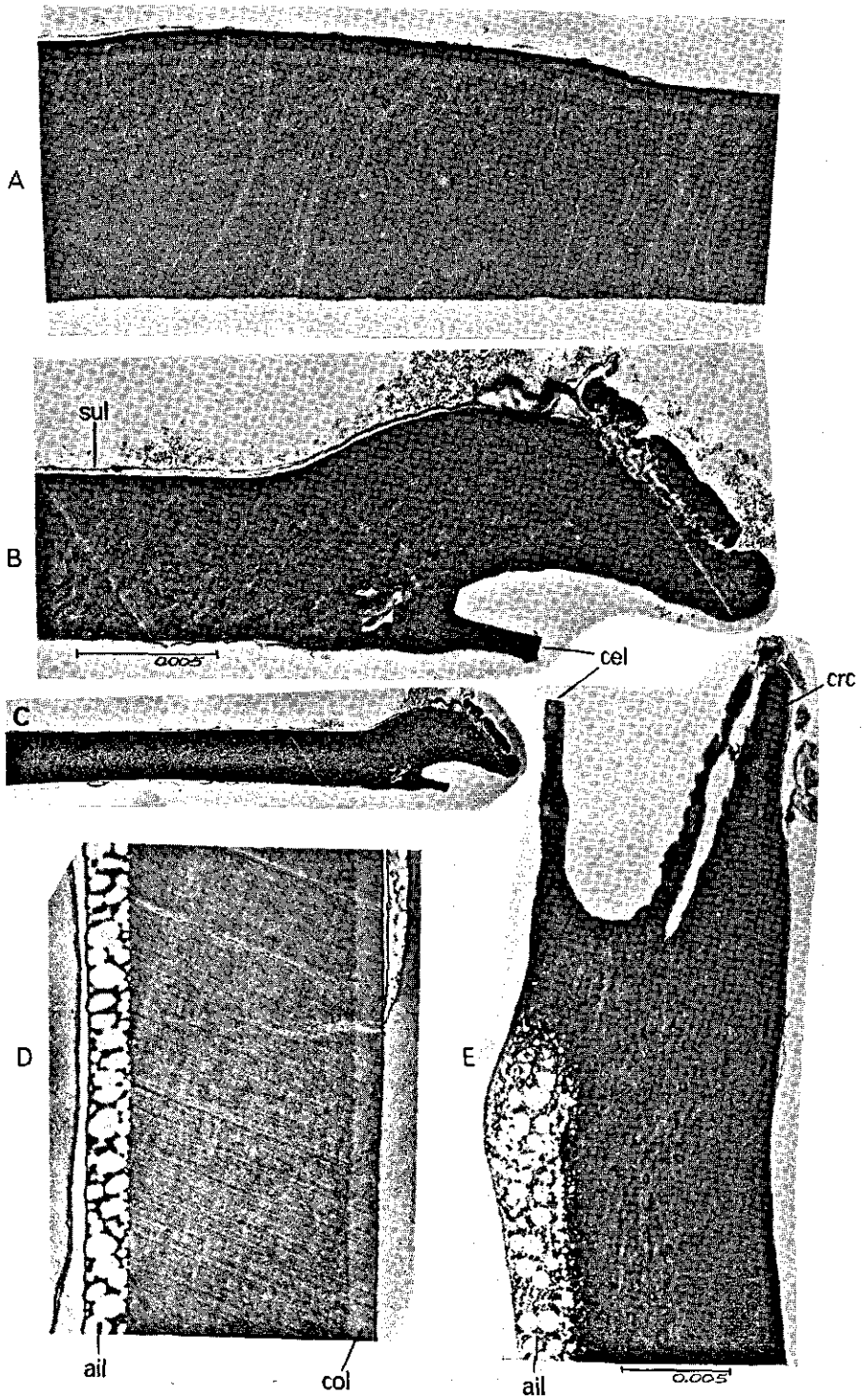


Fig. 299A–E: *Reduvius personatus*, vacated egg, longitudinal section of anterior pole; A: mid part of operculum; B, C: margin of operculum; D: shell some distance posterior to the eclosion split; E: rim region of shell.

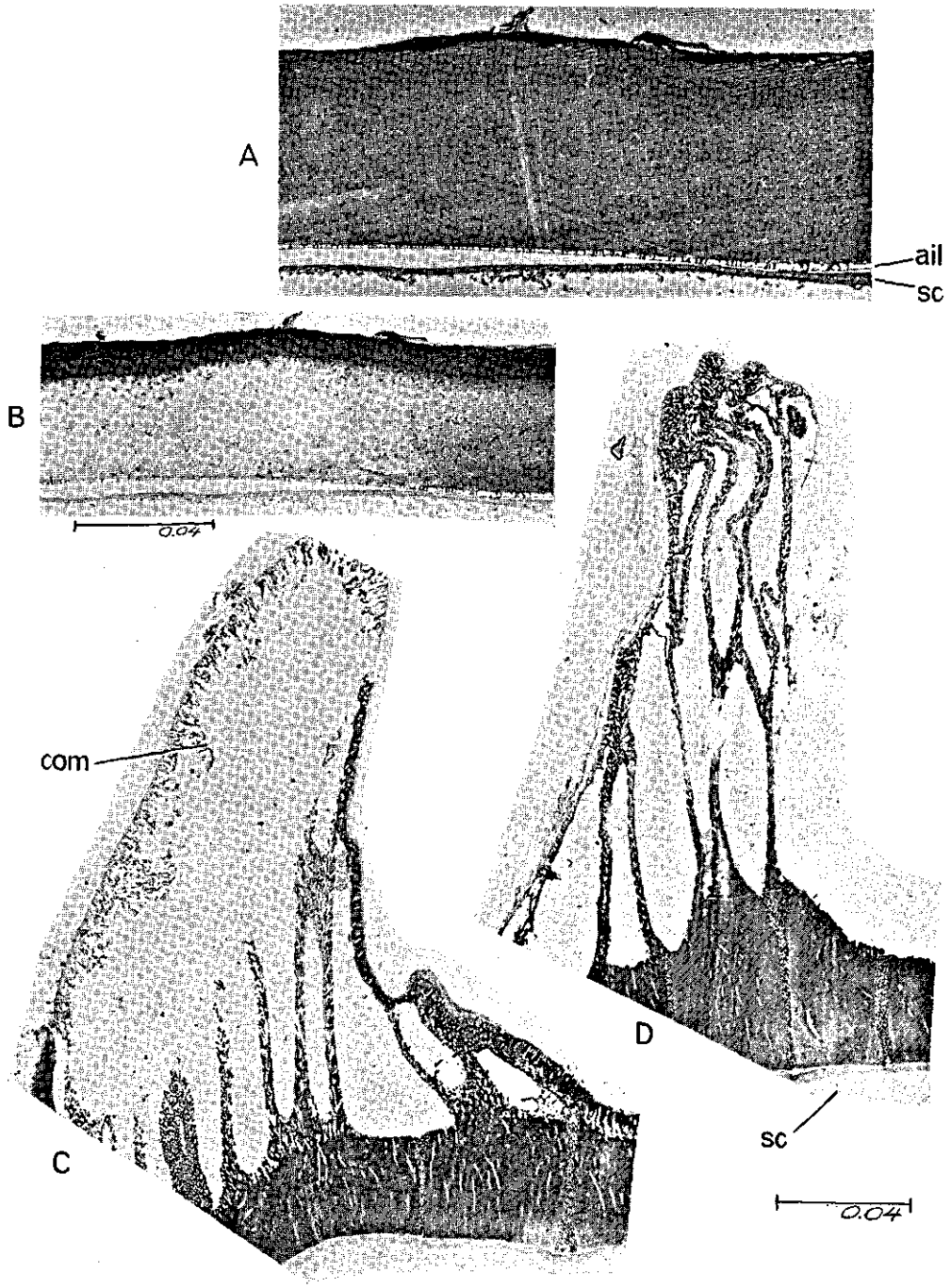


Fig. 300A–D: *Coranus aegyptius*, deposited egg, longitudinal section of anterior pole; A, B: shell some distance below the eclosion rupture; B, stained with $KMnO_4$; C, D: collar of opercular rim.

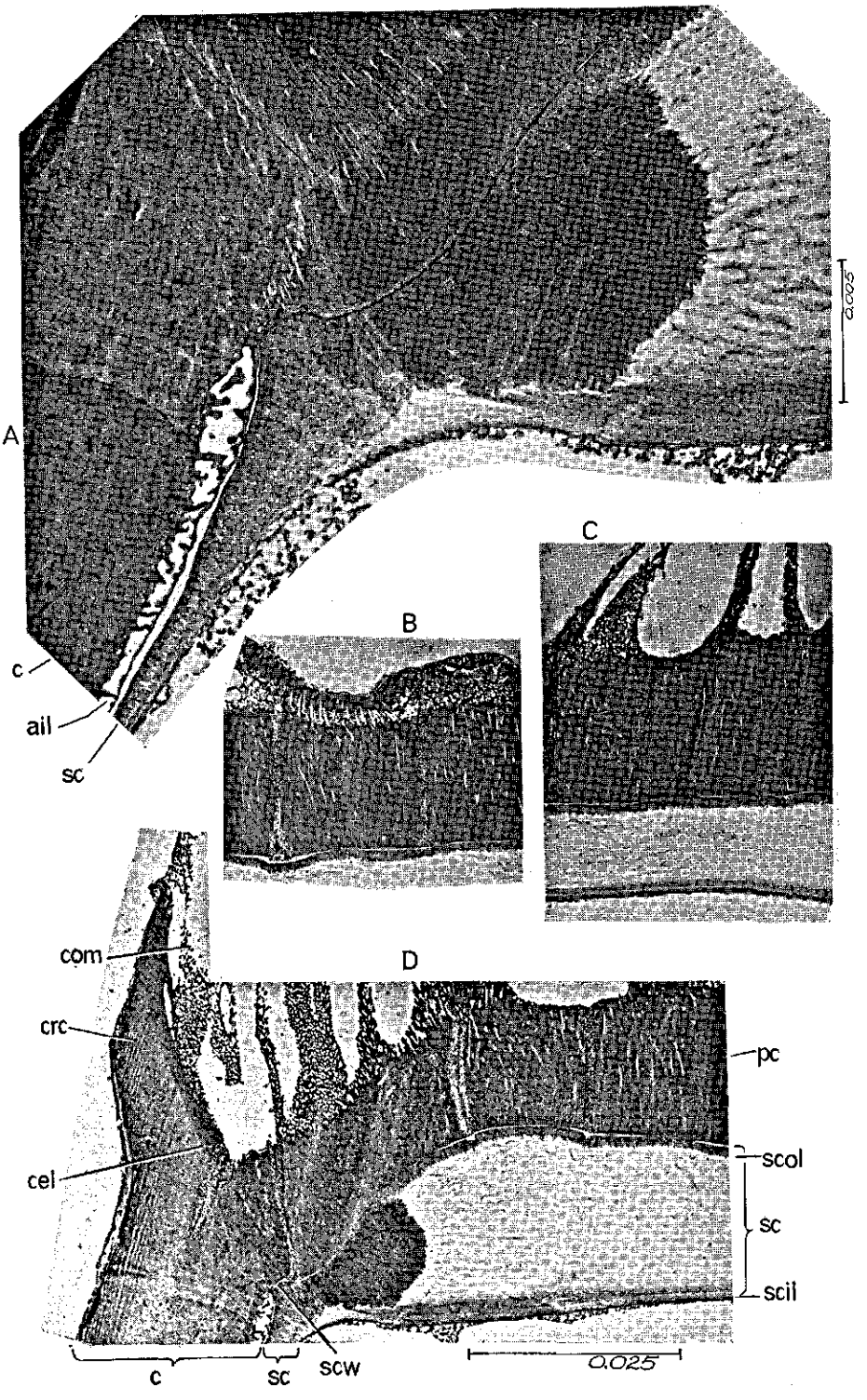


Fig. 301A–D: *Coranus aegyptius*, deposited egg, longitudinal section of anterior pole; A, D: egg orifice and operculum with underlying serosal cuticular wedge (compare fig. 211); B, C: operculum between the margin and the centre.

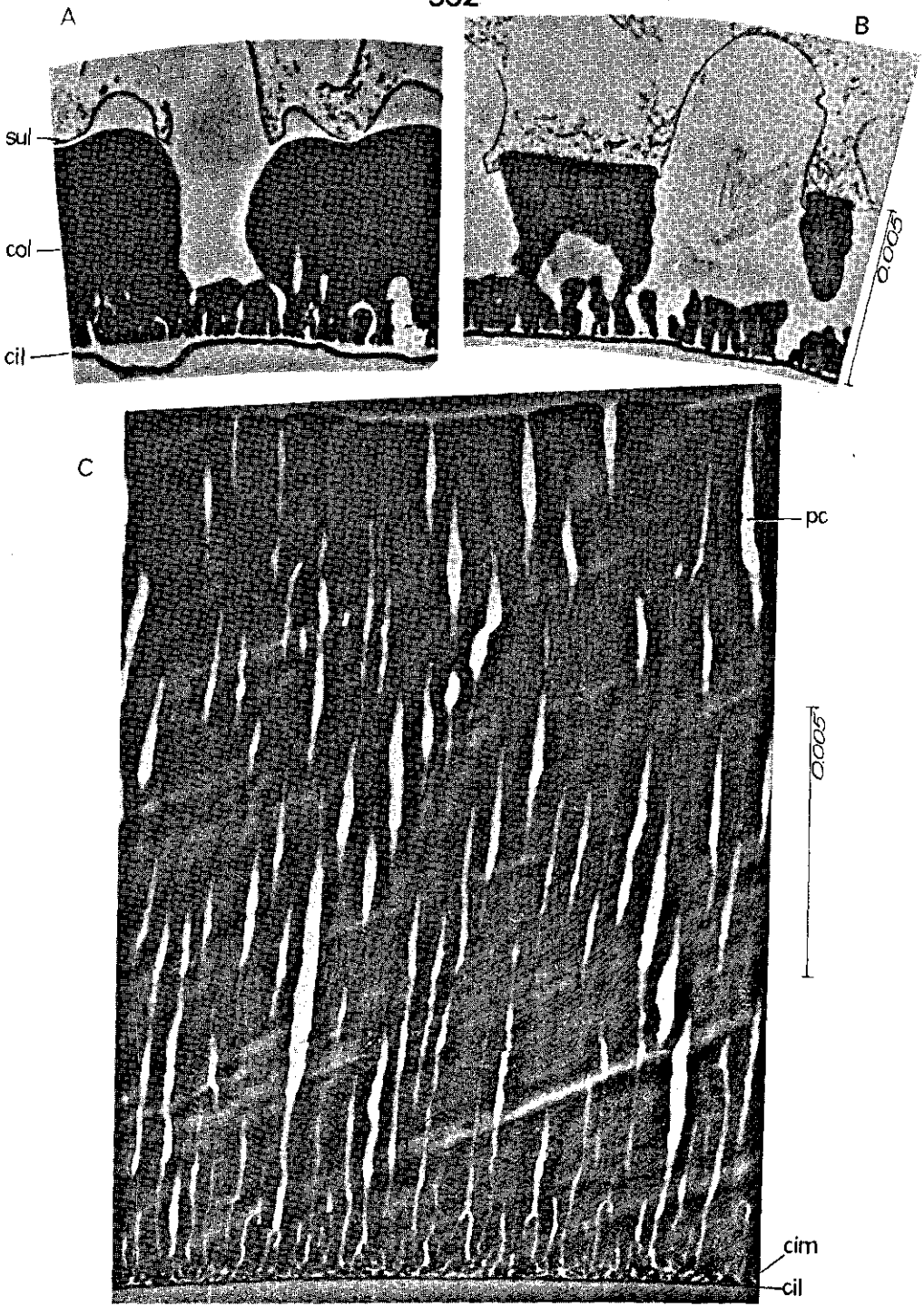


Fig. 302A, B: *Micronecta* sp., fore side (A), lateral side (B) of anterior part of deposited egg; C: *Corixa punctata*, mid part of ovarian egg.

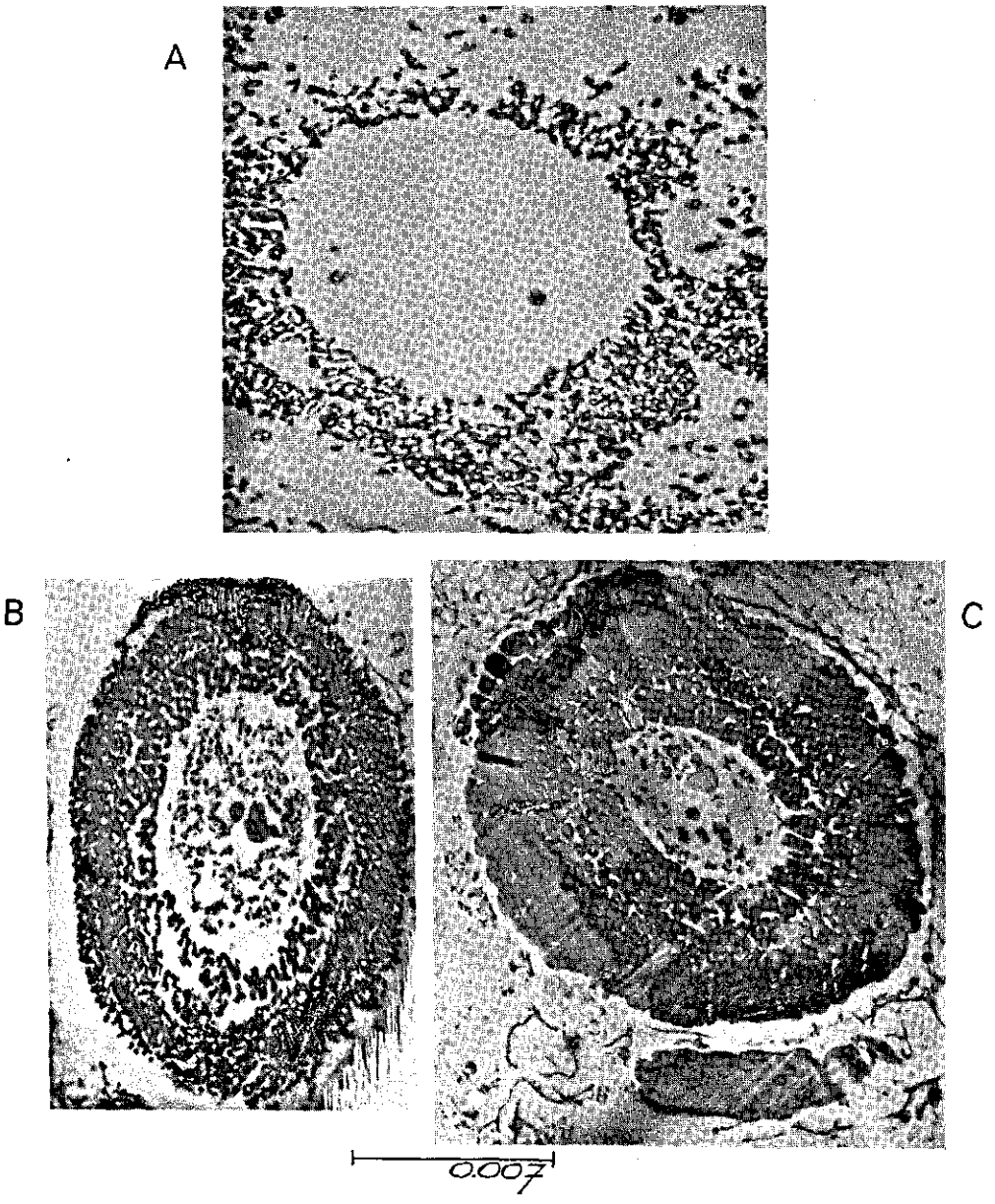


Fig. 303A–C: *Notonecta glauca*, deposited egg, micropylar horn at the apex (A), at the base (C).

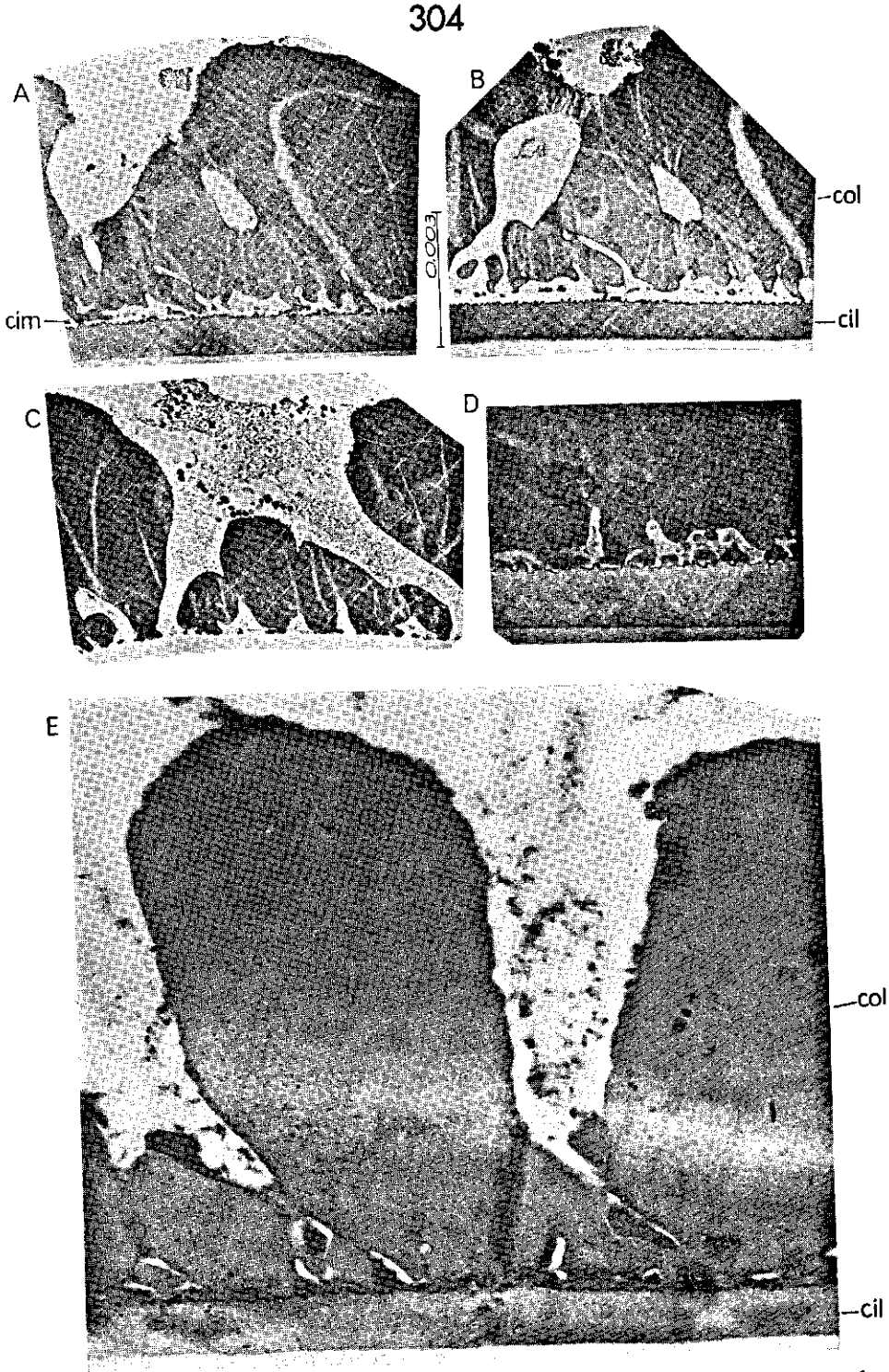


Fig. 304. *Ochterus marginatus;* A–D: mid part of ovarian egg, compare fig. 255H (The outer layer in B and C is detached from the inner layer.); E: pseudoperculum.

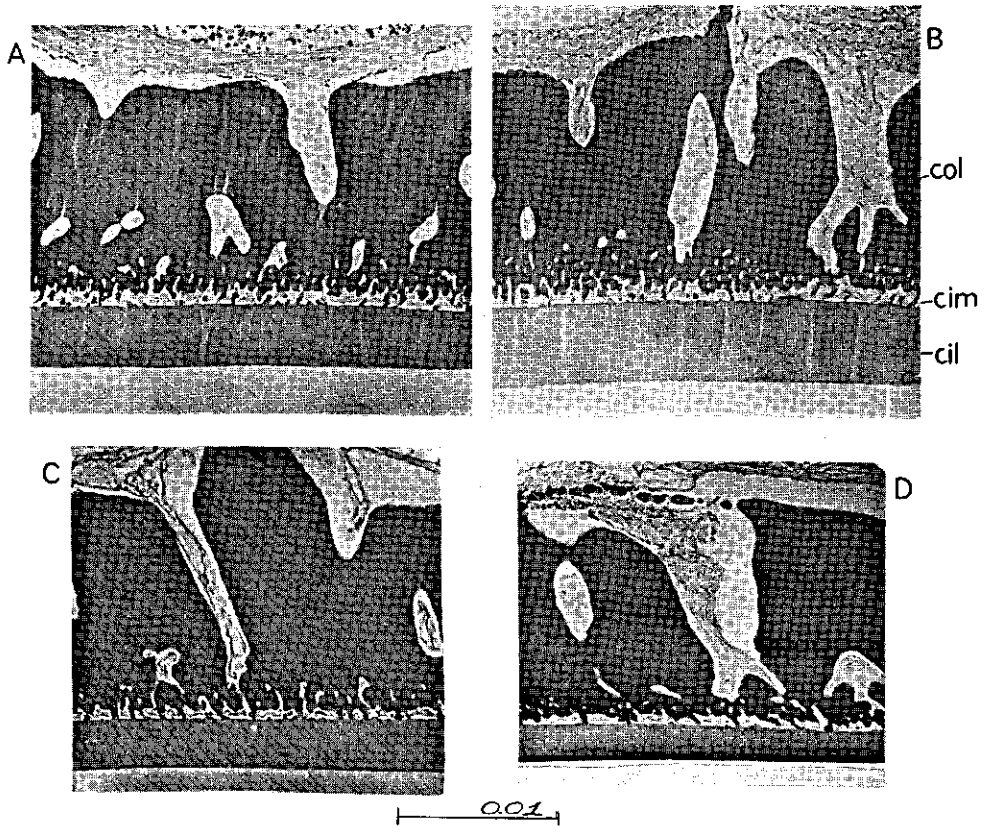


Fig. 305A–D: *Nerthra laticollis*, section close to anterior pole. (The inner part of the microsection in D shrunk during photographing.)

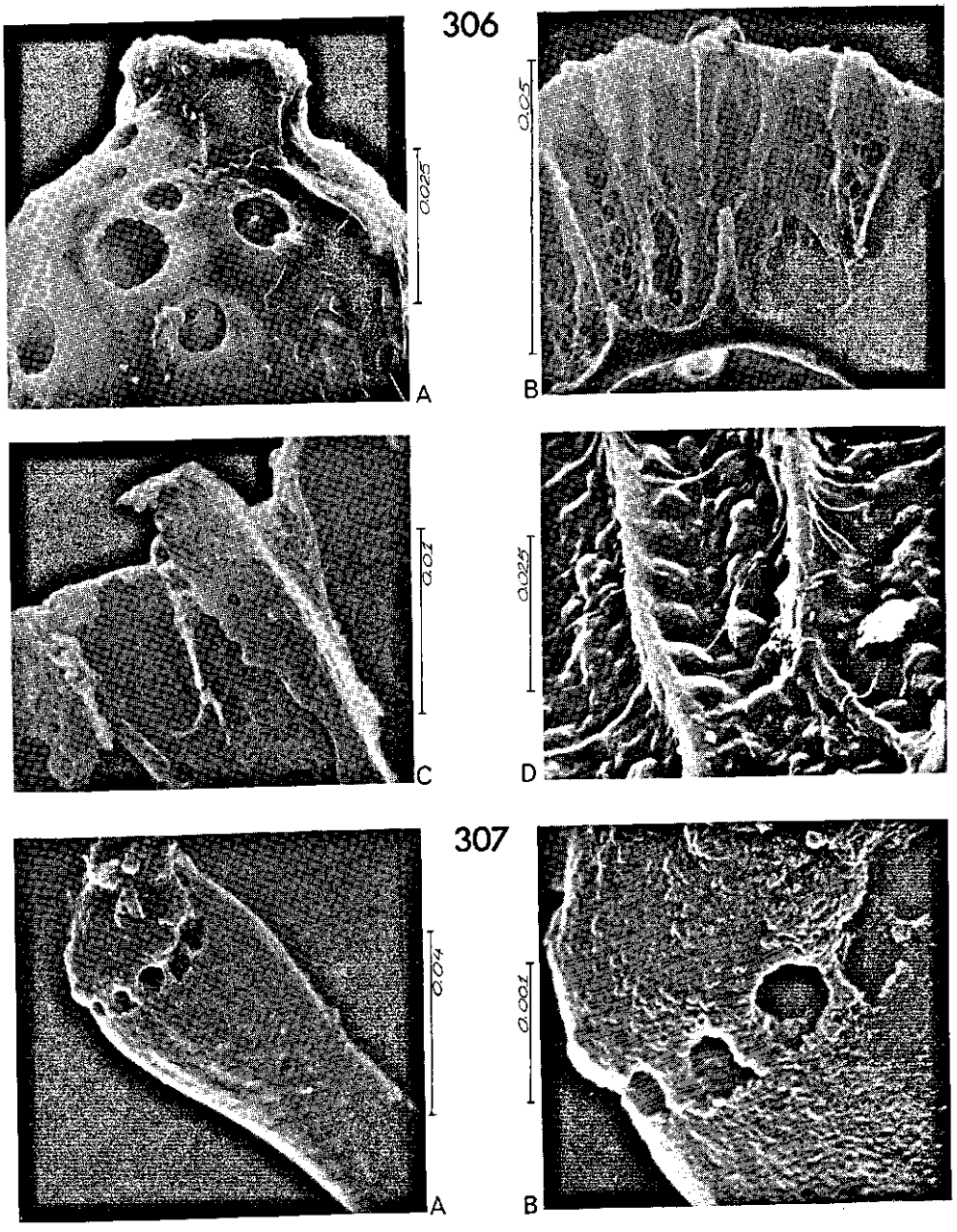


Fig. 306–316. Micrographs of chorionic structures (Scanning electron microscope).
Fig. 306, 307. 306A–D: *Hydrometra gracilenta*, deposited egg; A: anterior pole with aero-micropylar cup, side view; B: oblique cross-section through anterior part of actual shell (compare fig. 51); C: the external meshwork (compare fig. 294); D: outer surface of shell at the egg's waist. Fig. 307A, B: *Ranatra* sp. (Ivory Coast), deposited egg, apex of respiratory horn (compare fig. 231).

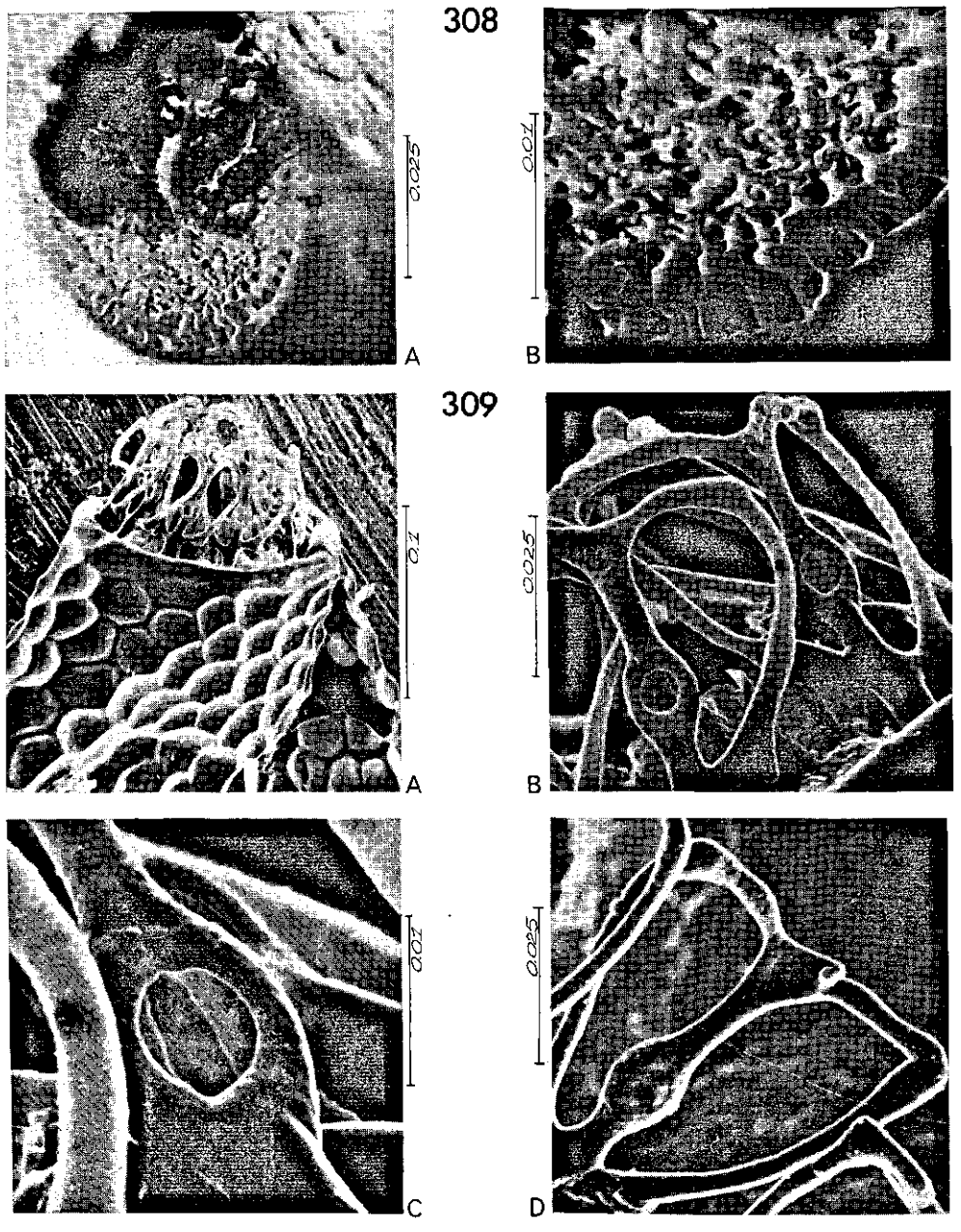


Fig. 308, 309. 308A, B: *Ranatra* sp. (Ivory Coast), cross section half way up the respiratory horn. Fig. 309A–D: *Kleidocerys championi*, ovarian egg; A: anterior pole, side view; B–D: aero-micropylar process; B, C: outer view with aperture; D: inner view.

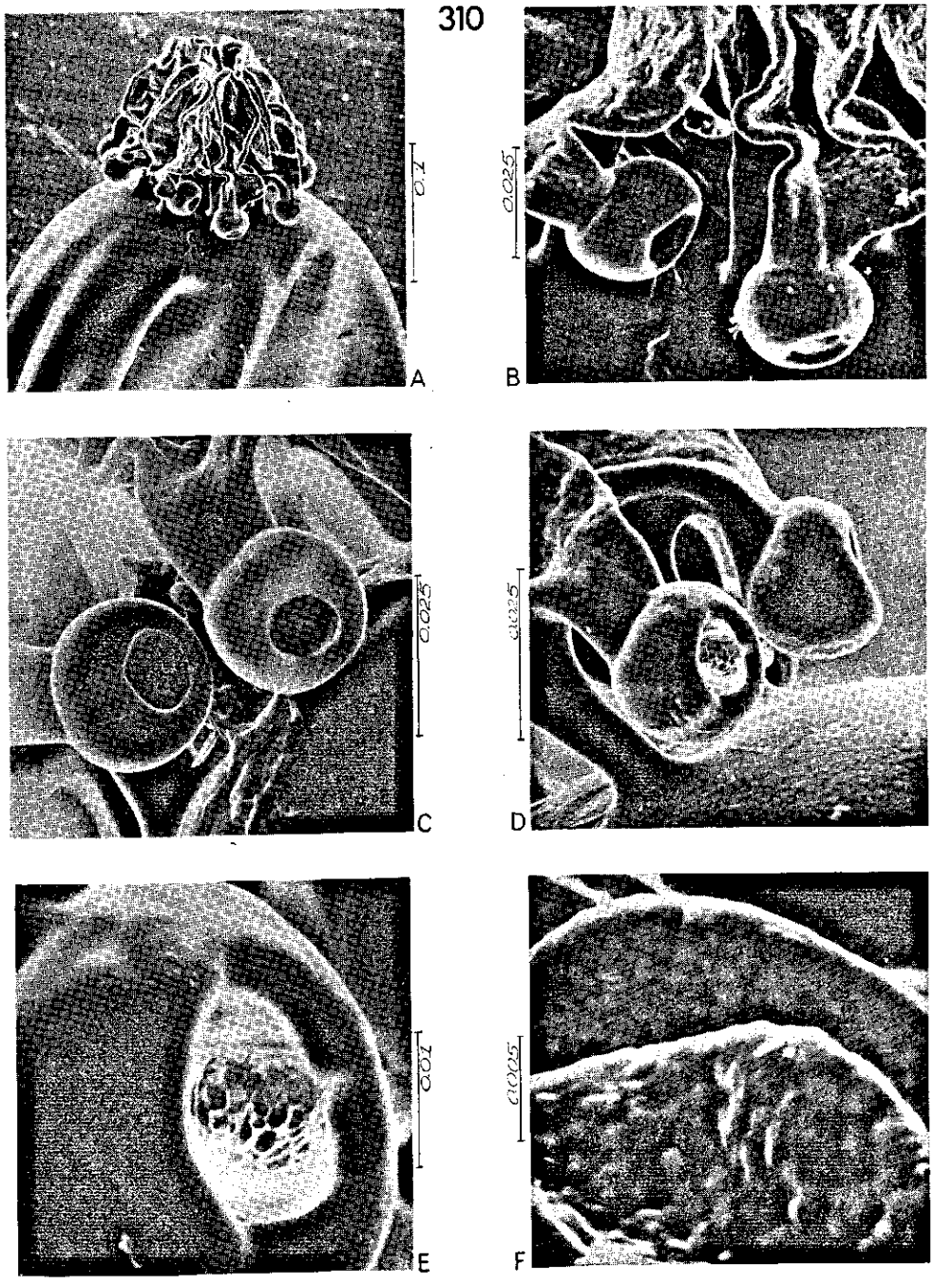


Fig. 310A–F: *Ortholomus punctipes*, ovarian egg; A: anterior pole, side view; B–E: aero-micropylar process, showing the internal air-sponge in E; F: part of the upper air-sponge proliferation.

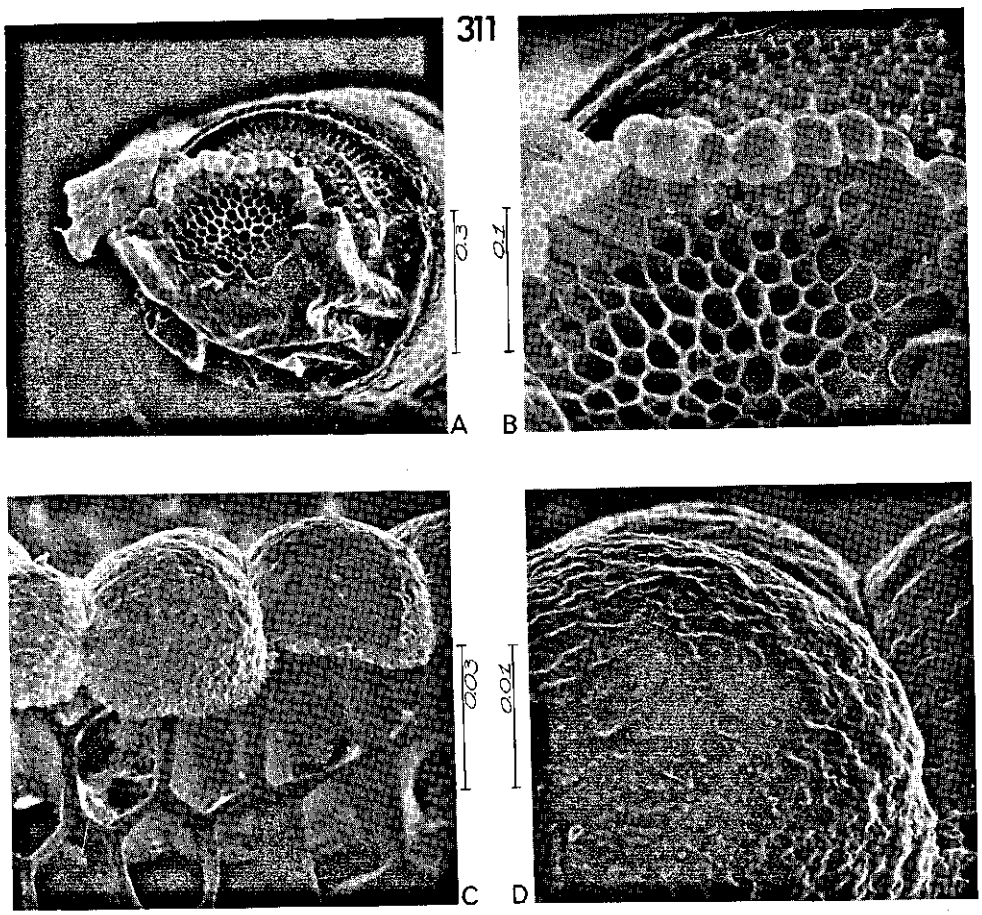


Fig. 311A–D: *Rhinocoris* sp. (Ivory Coast), deposited egg; A: anterior pole, obliquely from above. The outer veil, connecting the chorionic rim of the egg's mouth with the ring of mushroom-like structures upon the operculum, is partly removed (compare fig. 208). B, C and D: the mushroom-like bodies under increasing magnification.

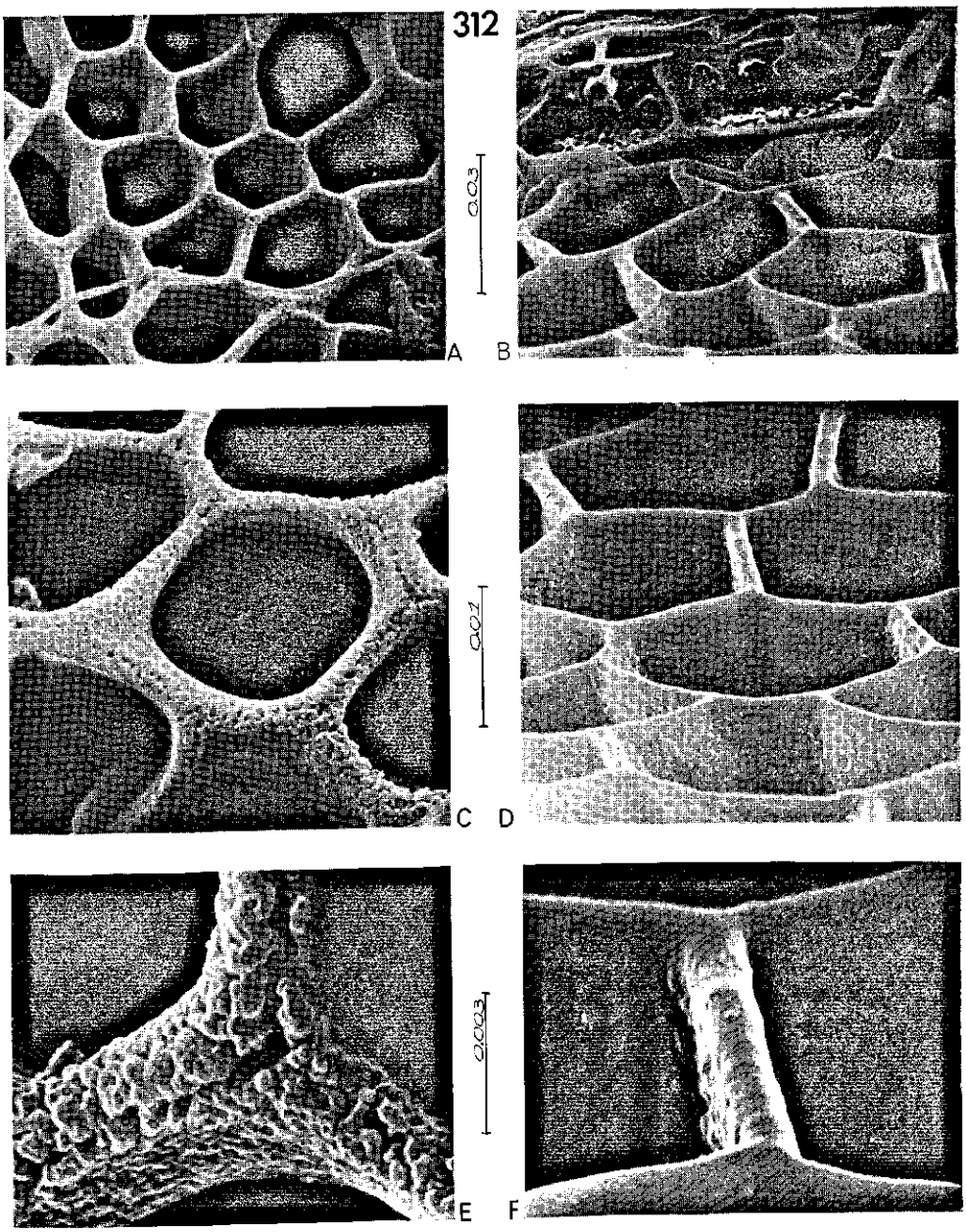


Fig. 312A–F: *Rhinocoris* sp. (Ivory Coast), chorionic structure of the opercular honeycomb (see fig. 311), within the ring of mushroom-like bodies (A, C, E) and outside this ring (B, D, F).

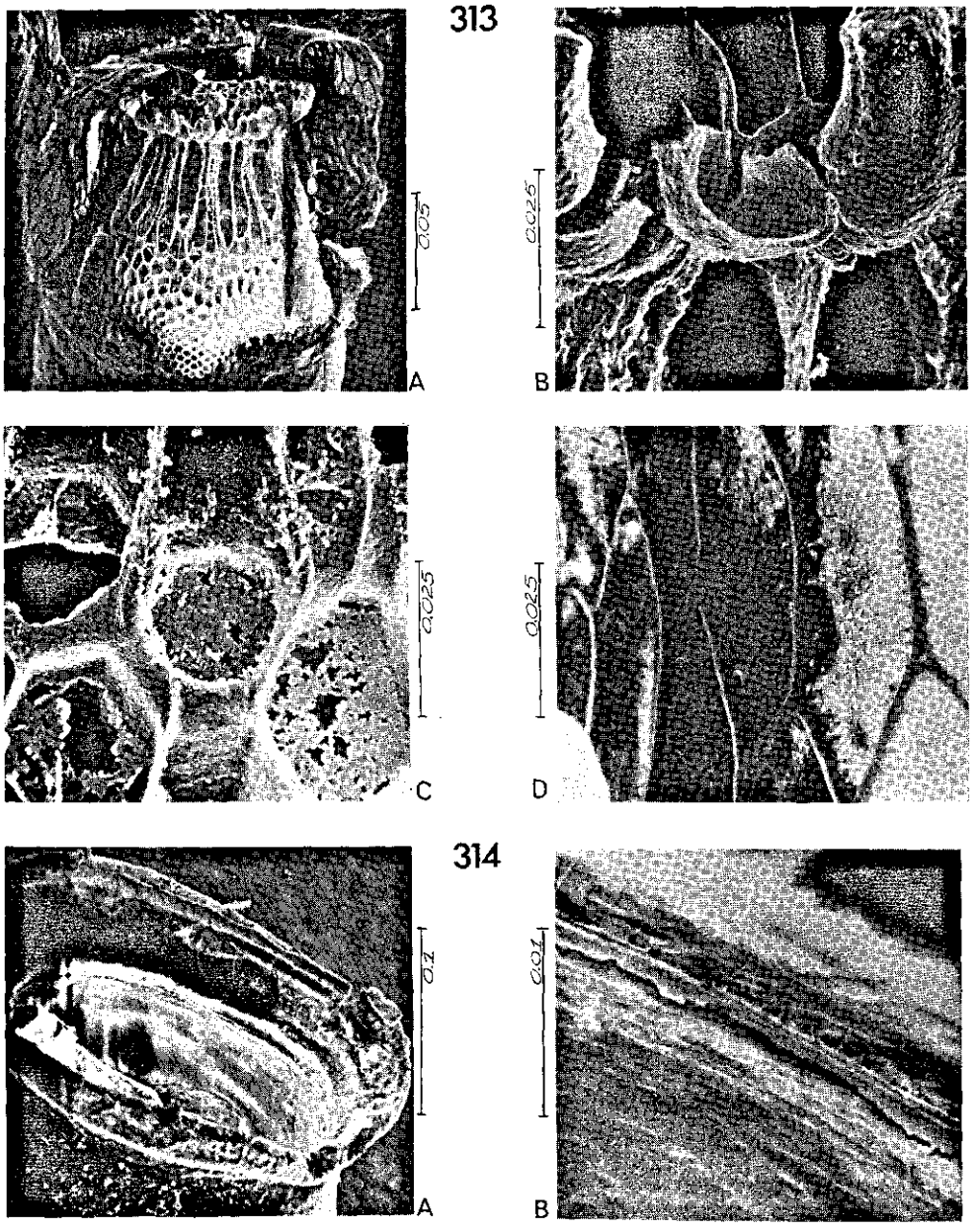


Fig. 313, 314. 313A–D: *Rhinocoris iracundus*, deposited egg; A: anterior pole, side view; half of outer veil removed; B: mushroom-like bodies; C: honeycomb of the marginal opercular upgrowth; D: internal view of outer veil. 314A–B: *Nabis rugosus*, deposited egg; A: orifice obliquely from above; operculum pushed off; B: innerside of orifice (fragment of A) with aerostatic inner layer.

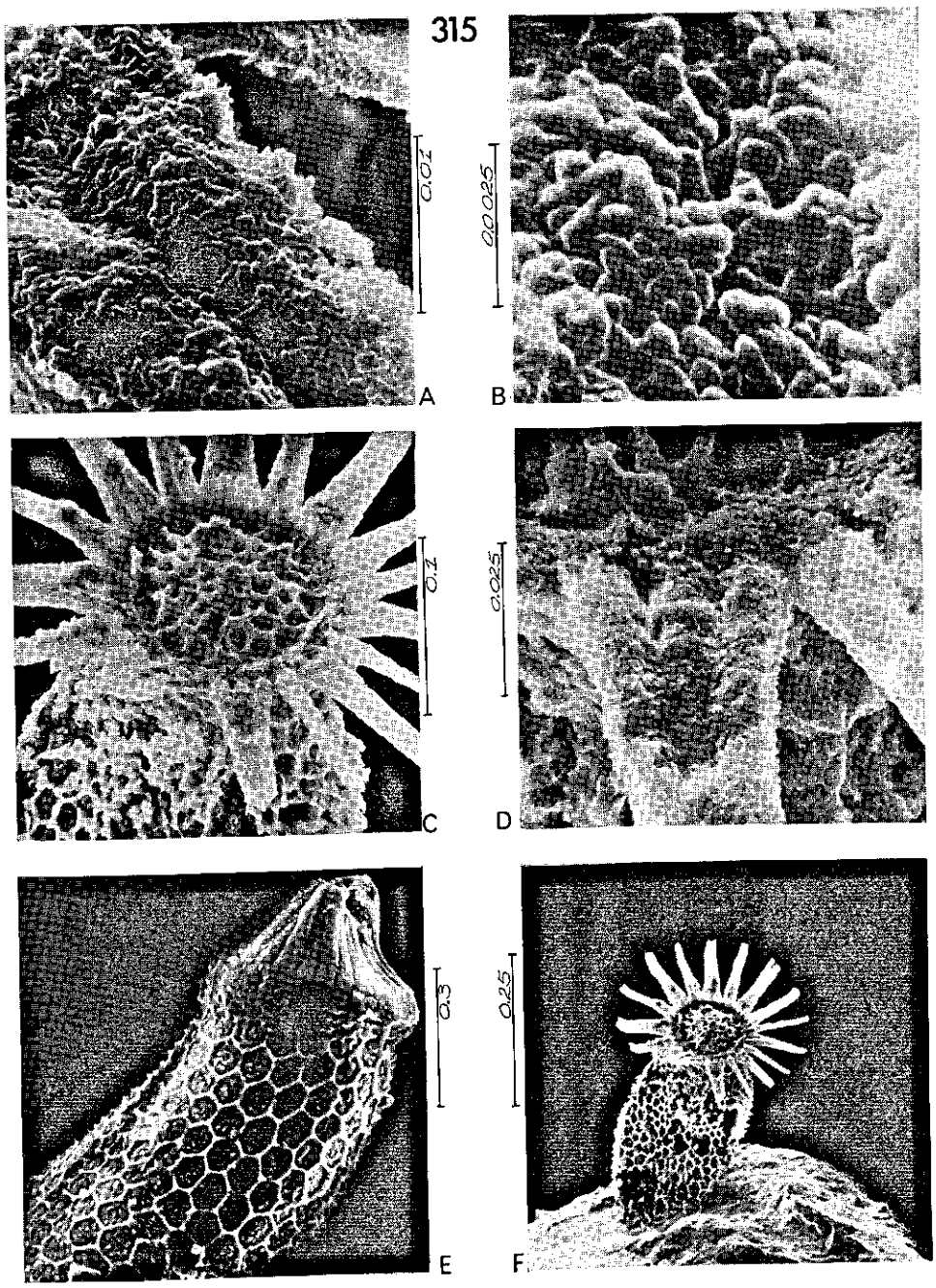
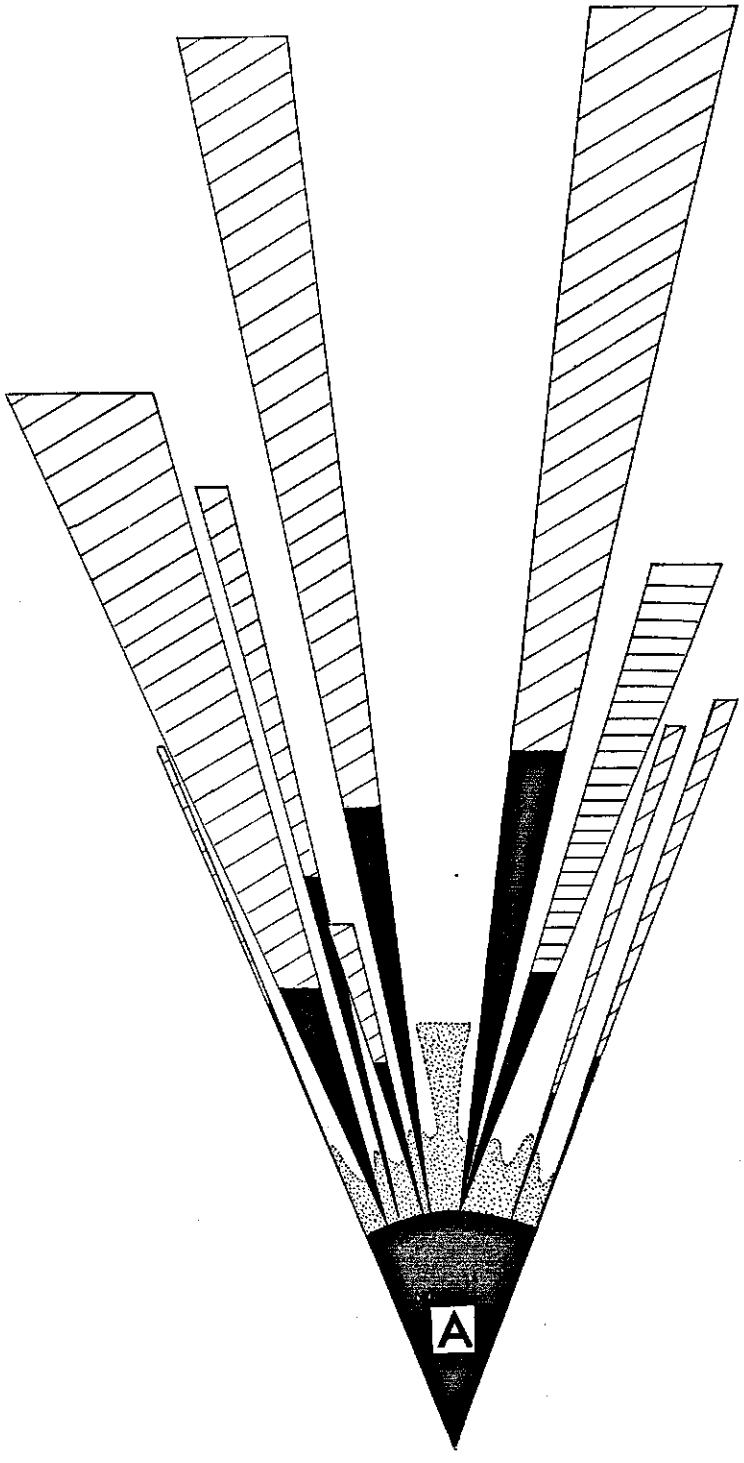


Fig. 315A–F: *Loricula*, ripe egg dissected from ovariole. E: *L. elegantula* under humid conditions (compare fig. 148). A–D, F: *L. pselaphiformis*, under dry conditions; the aeropylar filaments are spread out; the inner face of the base of one filament is shown with increasing magnification from D through A to B.

Fig. 316. Diagram of the hypothetical phylogeny of Heteroptera. The terrestrial groups (obliquely lined areas) and the Hydrocorisae (horizontally lined area) are presented as radiations from an extinct Amphibicorisal stock (A). The arborescence of the individual lineages is not indicated. The undulating stippled area at the base refers to modern Amphibicorisae. Black areas are unknown ancestors. For further explanation, see text.

316



Author index

Anderson 283
Ando 286, 306, 307, 309, 310, 312, 324, 325, 345, 364.
Andre 94
Andrewartha 306
Annandale 102
Atwal 290, 291

Badonnel 345
Baker 306
Balbiani 284
Banks 198, 311
Baranowski 168
Barth 183, 369
Basavanna 338
Baudisch 307, 311, 324
Beament 183, 184, 250, 265, 278, 279, 288, 289, 321, 325
Behrendt 306
Birch 306
Blijdorp 346
Bobb 238, 292
Bock 278
Bolle 95
Bonhag 371
Börner 357, 364
Bournier 309
Brandt 72, 73, 196, 198, 200
Brindley 7, 297, 367, 368
Brinkhurst 73, 253, 367, 369
Brocher 206
Brown 362
Buchner 136
Bueno 206, 218
Butler 94, 138, 198
Butt 73, 88, 94, 184, 301, 302, 303, 305, 307, 309
Buttenandt 369

Cappe de Baillon 286
Capriles 365
Carayon 136, 138, 164, 248, 284, 324, 356, 357, 362, 366, 367, 368, 369
China 100, 351, 352, 357, 358, 359, 362, 364, 366, 367, 368, 371, 376, 377
Christophers 288
Church 288
Cobben 36, 50, 257, 258, 265, 266, 272, 281, 282, 302, 307, 323, 326, 332, 345, 348, 362, 368, 370, 371, 374, 376
Cole 306
Cooker 365
Corby 93
Counce 269, 288

Dashman 365
Davey 372
Davies 286, 307
Davis, Ch. 200, 206, 229, 230
Davis, N. 134, 356, 366, 367, 371, 377
Degrange 286, 288, 324, 325, 326, 344, 349
Delmas 346
Denis 286
Dispons 357
Doesburg, van 164, 334
Drake 168, 256, 357, 365, 366, 367, 371, 377
Dufour 198, 360
Dupuis 348, 352, 366, 372

Edwards 183, 290, 369
Eichhorn 305
Ekblom 7, 365, 374
Emden, van 122, 319, 326
Esaki 248, 358

Fernando 198, 200
Fluiter, de 346
Froeshner 108

Gibson 346
Goodchild 376
Goot, van der 84
Goss 286, 307, 309, 346, 348
Grant 354

Grassé 286
Griffith 200
Gulde 366
Gupta 362, 364, 365, 366, 368, 371, 377

Hagan 301, 309, 324
Hager 291
Hale 200
Halkka 374
Hallez 347, 348
Handlirsch 377
Hartley 4, 125, 164, 251, 252, 253, 286, 310, 324
Harwood 278
Hase 136
Henrici 366
Hertel 84
Heslop-Harrison 345, 377
Heymons 136, 206, 218, 326
Hille Ris Lambers 348, 349, 364
Hinton 125, 164, 184, 194, 200, 201, 206, 209, 250, 257, 260, 278, 279, 280, 282, 283, 286, 306, 325, 372
Horsfall 278
Hughes-Schrader 373
Hungerford 7, 47, 54, 66, 71, 198, 200, 206, 209, 218, 229, 234, 240, 334
Hussey 206, 209

Idris 278, 307, 325, 348
Illingworth 95
Immel 290, 303

Jackson 324, 325
Jande 374
Jander 368
Janes 291
Jeannel 248
Jentsch 258
Johannsen 305, 307, 309
Johansson 367
Johnson 130, 136, 164, 166, 290, 291, 310, 313, 321, 322, 323
Jones 307, 324, 325
Jordan 7, 47, 66, 93, 94, 102, 109, 200, 297
Jurberg 351

Kalshoven 104
Keilbach 344
Kellen 42, 43, 66
Kennard 310
Kershaw 184, 326, 338, 348
King 288, 325
Kiritshenko 360
Kirkaldy 338, 348
Koch 288
Kogan 141, 320, 363
Köhler 95, 206
Korschelt 206, 229
Krause 307, 308
Kullenberg 162, 164, 166, 313, 322, 323, 338, 366
Kumar 168, 249, 352, 354, 357, 371, 375

Larsén 218, 229
Lattin 108, 294, 371
Laughlin 310
Le Berre 312, 345
Lebrun 47, 66, 71, 200, 206, 218
Le Grelle 311
Lent 351
Leonard 373
Leong 198, 200, 229, 230
Leston 112, 114, 198, 229, 294, 297, 352, 360, 362, 364, 369, 371, 372, 373, 374, 378
Leuckart 66, 71, 198, 206, 286, 288
Lewis 373
Lin 291
Lincoln 283
Lindskog 295
Linley 284
Linsemaier 368
Livingstone 125, 141, 363
Ludwig 328
Lundbeck 71

Mahr 307, 312, 346
Malhotra 106
Mammen 377
Manna 372, 373
Mao-Hua 307
Marshall 280
Masson 220
Matsuda 78, 366, 367
Matthée 311, 345
McFarlane 280, 310, 325
McKinstry 365
Mecznikov 71, 196, 198, 200
Mellanby 183, 184, 302, 303, 305, 313, 325
Michalk 331
Miller, A. 308, 311, 324, 325, 326
Miller, N. 95, 100, 109, 114, 130, 172, 182, 183, 333, 351, 352
Millsaps 365

Miyamoto 66, 248, 284, 357, 360, 375, 376
Muir 184, 326
Müller 297, 306, 307, 311, 323, 324, 325, 326
Muth 183
Myers 248

Ohm 290

Pantel 278, 288
Parker 333
Parsons 318, 376
Pearman 307, 345
Pendergrast 109, 272, 322, 352, 357, 358, 360, 362, 376
Pesson 284
Peterson 324
Pfaler-Collander 372
Philips 311
Poinar 284
Poisson 7, 54, 61, 66, 71, 198, 200, 206, 209, 210, 229, 357, 358, 362, 365
Polivanova 291
Popham 375, 377
Priesner 345
Puchkov 106, 122, 162, 366
Puchkova 82, 93, 94, 101, 102, 104, 106, 108, 109, 110, 122, 162, 366

Rakshpal 306, 324
Rastogi 376
Rathke 198
Raven 344, 346
Rawat 218
Rayment 345
Readio 182
Remane 295
Remold 369
Rempel 288
Reuter 357, 365, 366
Rice 229, 365
Richards 286, 307
Rimes 7, 11
Rosay 278, 307, 325
Roth 324, 369
Roze 365
Ryckman 183, 372

Sahni 95, 315, 324
Salpeter 250
Salt 278
Sander 307, 311, 326
Sands 136
Sattler 73, 272, 328
Sauer 286
Schaefer 353, 354, 355, 373
Schanz 312
Scherf 325
Schneider 90, 94
Schölzel 307, 308, 309, 311, 326, 349
Schorr 108, 333
Scudder 78, 94, 353, 354, 357, 358, 360, 362, 363, 372, 373
Seidel 73, 95, 302, 310, 324
Sekhon 278
Sharan 95, 315, 324
Sharov 309, 310
Sikes 136, 322, 326
Singh-Pruthi 369, 370, 371
Slater 168, 256, 357
Slifer 278, 307, 311, 312, 324
Southwood 44, 73, 78, 82, 84, 93, 94, 95, 101, 102, 104, 106, 108, 109, 110, 114, 122, 124, 125, 130, 136, 138, 141, 162, 182, 183, 198, 246, 248, 249, 250, 255, 256, 270, 272, 288, 289, 294, 297, 306, 313, 319, 322, 331, 352, 354, 356, 360, 362, 363, 372, 374, 375
Sprague 61
Stammeshaus 95
Steele 307, 308
Stichel 354, 357, 358, 360
Strübing 297
Štusák 141, 363
Štys 353, 354, 355, 357, 364, 377
Swammerdam 206
Sweet 93, 292, 294, 296, 297, 333

Tamanini 78
Telford 278, 325
Teyrovsky 198
Thomas 138
Thontadarya 338
Tiegs 304, 324
Timonin 369
Tischler 292
Tonapi 73
Truckenbrodt 286
Tuft 279, 280
Tullgren 364

Uljanin 324
Usinger 78, 209, 218, 240, 313, 351, 369, 372

Vodjdani 110

Wagner, E. 351, 357, 358

Wagner, W. 323, 326, 373, 374
Walton 200
Weber 82, 200, 284, 286, 305, 307, 308, 309, 311, 326, 348
Webster 311
Wefelscheid 234
Wendt 7, 297
Wesenberg-Lund 71
Wheeler 206
White 373, 374
Wick, 371
Wigglesworth 4, 136, 250, 278, 322, 326
Wilbrink 108
Wilcke 311, 326
Wiley 7
Wille 82
Willis 324
Woodroffe 295
Woodward 284, 297
Wróblewski 198
Wygodzinsky 246, 248, 369, 372

Yajima 307
Yamada 109
Young 292, 293

Subject Index

Page numbers in bold print denote drawings, in italic type denote electron-micrographs; numerals in ordinary print refer to text pages.

The data on chorion, embryogeny and hatching, reappearing in regular sequence in the descriptive sections by families (pp. 6–249), are omitted from the index.

Subfamily and family names and higher categories mentioned in chapters 3 and 4 are not listed in entirety but are only selectively indexed by subjects.

abdominal scent gland 36
Abedus 209
Abedus ovatus 206
Abedus signoreti 206
Acalypta 140, 292
Acanthaspis 168, 181, **175**
Acanthocelides 346
Acanthocinus 288
Acanthocoris 96
Acanthomia 290
Acanthomia hystrix 96, **97**
Acanthosoma haemorrhoidale 108, **107**
Acanthosomatidae 108, 109
Acheta 280, 306, 310, 312, 324, 346
Acompocoris 134, 136, **329**
Acompocoris pygmaeus 132, 134, **133**
Aedes 325
Aeliomorpha 116–118, 122, 336, **115**
Aepophilus 7, 8, 11, 12, 16, 20, 42, 251, 252, 259, 260, 266, 272, 331, 350, 363, 365, 366, 368, 375, **15**, **261**, *432*
aeropyle 251–264
aerostatic innerlayer 251–264
Aethus 292
Afrius figuratus 116
Agapophyta viridula 112, 114, **113**
Aganosoma 110, **115**
Agramma laeta **139**
Agraptocorixa 200, 266, 275
Agraptocorixa hyalinipennis 185, 198, 200, **193**
Agrion puella 288
air cleft 20–22, 24
alimentary canal 376
Alloetomus 158, 160
Alloetomus germanicus 141
Alydidae 102–104
Alydus calcaratus 102, 104, 340, **99**
Ambrysus 209, 210, 218, 266, **215**
Amphibicorisae
—, observations 44–74
—, chorion 252–254
—, phylogeny 350, 351
ampulla, in Mesovelia 52
Ancyrosoma 118
Ancyrosoma albolineatum 116
Aneurus 363
Anisops 218, 229, 230
Anommatocoris minutissimus 140, **139**
Anoplocnemis 96, 98, **100**, 120, 290, 343, **101**, **105**, **329**
Antestia 363
Anthocoridae 132–134
Anthocoris 134, 136, 142, 303, 377
Anthocoris confusus 132
Anthocoris nemorum 132, **133**
Antiteuchus 118
Antiteuchus mixtus 116
Aphanus rolandri 86, **87**
Aphelinus 345
Aphelocheirus 218, 265, 266, 276, 290, 366
Aphis 306, 348
Aphylidae 124
Aphylum bergrothi 124
Apis 346
Apterygota 286, 289
Aquarius najas 74, 328
Aquarius paludum 66, *437*
Arachnocoris 331, 356

Arachnocoris dispar 125, 130, **131**
Aradidae 75–78
Aradus 292
Aradus cinnamomeus 363
Archipsocus fernandi 309
Arctocorisa germari 198
Arilus 369
Arvelius 116, **115**
Aspongopus 112, 274, 320, **113**
asymmetries 327–331, 344
Austroicetes 307

Baclozygum depressum 166, **169**
Bagrada 290, 291
Banchus 345
Belostoma 257, 258
Belostoma anura 206
Belostoma flumineum 209
Belostoma micantula 206
Belostomatidae 206–209
Beosus maritimus 86, **81**
Berytinidae 84
Berytinus 82, 84, 301, 340, **329**
Berytinus crassipes 84, **91**
Berytinus signoreti 84, **83**
blastoderm 301, 302
blastokinesis 30–33, 298, 304, 305
blastopore 301
Blatta 346
Blissus 92, 93, 291, 373
Blissus leucopterus insularis 86, 90
borax carmine 5, 27
Brachycarenus tigrinus 106
Brachypelta aterrima 108
Bryocoris 152, 156, 158, 162, 164, 256, 268, 270, 272, 275, 289, 321, 322, 325, 327, 356
Bryocoris pteridis 141, 150, 162, 256, 313, **151**
Buenoa 218, 228, 229, 276, **231**

Calacanthia 10, 12, 16, 20, 251, 331
Calacanthia alpicola 8
Calidea hutereanae 109
Calliphora 283
Calocoris roseomaculatus 141
Calopteryx atrata 286
Campodea 286
Camptopus 104
Camptopus lateralis 102, **99**
Campyloneura virgula 141, 158, 165
Cantacader 140
Capsodes 158, 160
Capsodes gothicus **141**
Capsus 158
Capsus ater 141, 313
Carpocoris 120, 315, 322, **329**
Carpocoris pudicus 116, 290, **119, 121**
Catorhintha 96, 98, 102, 268, 274, 336, 355, **101**
cephalic organ 28–30, 304
Ceraleptus 100, 270, 355
Ceraleptus gracilicornis 96, 100, **97**
Cerataphis orchidearum 348
Ceratocombus 244, 246, 258, 276, 314, 316, 336
Ceratocombus coleoptratus 240, 242, **245**
Ceratocoris 122, 124, 270
Ceratocoris bucephalus 122, **121**
Cethera 182, 183, 290, 340
Cethera musiva 168, 174, **175**
Chartoscirta 11, 22, 36, 40
Chartoscirta cincta 8, 34, 290, **15, 29, 34**
Chartoscirta cocksi 8
Chartoscirta elegantula 8, **35**
Chauliops bisontula 82, 84
Chauliops rutherfordi 82, **81**
Chepuvelia 254, 269, 336, 351, 362, 365, 366, 370
Chepuvelia usingeri 61, 64, **67**
Chilacis 86, 92
Chiloxanthus pilosus 7, 8, 12, 21, 36, 251, 252, 290, 292, 294, 297, 374, **9, 19, 27, 35**
Chiloxanthus stellatus 7, 14
Chironomus 307
Chlamydatus 66, 304, 312, **329**
Chlamydatus evanescens 141, 142, 294, 313, **144**
Chlamydatus saltitans 141, 142, 162, **143**
chorion
—, aeration 281
—, aeropylar system 251–264
—, Amphibicorisae 252–254
—, architecture 251–264
—, chemical analysis 278, 279
—, Cimicomorpha 255, 256
—, confusion of layers 278
—, darkening 280
—, Dipsocoridae, Schizopteridae, Enicocephalidae 258, 259
—, disadvantages of chemical applicants 250
—, discussion 278–289
—, Hydrocorisae 257, 258
—, Leptopodoidea 251, 252
—, main types 259–264
—, Pentatomomorpha 254, 255
—, relation hexagons, egg size, female size 283, 284

Chorosoma 314, **330**
Chorosoma shillingi 104, **99**
Chorthippus 252, 310
Chrysopa 278
Cicadella 323
Cimex 132, 134, 136, 275, 290, 291, 303, 322, **329**
Cimex lectularius 134, 290, **135**
Cimicidae 134–136
Cimicomorpha
—, chorion 255, 256
—, observations 124–184
—, phylogeny 355–357
Cixius 326
Cletus unifasciatus 96
Coleoptera 288
Coleopterocoris 258, 265, 276, 358, 364, 366, 371
Coleopterocoris kleerekoperi 209, **211**
Collembola 324, 325
Colobathristidae 95
Coptosoma 122–124, 301, **121**, *441*
Coranus 176, 178, 180, 181, 183, 184, 278, 279, 298, 300, 303, 308 309, **330**, **341**
Coranus aegyptius 168, 178, **179**, **263**, *445*, *446*
Coranus subapterus 168, 178, 180, **179**
Coreidae 96–102
Coreus 96, 100, 102, 104, 268, 327, 340, **329**
Coreus marginatus 96, **101**, **103**
Corixa 186, 194, 196, 238, 240, 250, 257, 258, 275, 288, 305, 322, 344
Corixa panzeri 185, 192, **197**
Corixa punctata 185, 192, **193**, **195**, **197**, **264**, *447*
Corixidae 6, 185–200
Corythaica cyathicollis 141
Cosmolestes 95
Cosmolestes annulipes **91**
Cossutia 96
Cryphocricos barozzi 209, 216
Cryptostemma 244, 258, 260, 278
Cryptostemma japonica 240, 242, **243**
crystalline products 214, 216, 305
Culex 288, 307, 325, 348, 349
Culicidae 278, 307
Cydnidae 106–108
Cylindrostethus 66, 72
Cyllecoris histrionicus 141, 158
Cymatia 186, 190, 198, 200, 257–259, 275, 280
Cymatia americana 200
Cymatia bonsdorffi 185, 190, **191**
Cymatia coleoptrata 188, **191**, **193**
Cymus 92
Cymus glandicolor 86, **81**
Cypraea 241
cytotaxonomy 372–374

Dalader acuticosta 96, 102, **103**
Dalpada 274, 322
Deraeocoris 160
Deraeocoris cordiger 141, 158
Deraeocoris olivaceus 141, 158, **157**
Deraeocoris ruber 141, 158
Deraeocoris serenus 141
Dermatinus 94, 95, **91**
Dermestes 310
diapause 291, 292, 294–298, 306, **293**
Diaprepocoris 257, 258, 275, 312, 321, 359, **329**, **343**
Diaprepocoris zealandiae 185, 188, **189**, **191**
Dicranocephalus 373
Dicranocephalus medius 94
Dictyla symphyti **140**, **139**
Dictyoptera 286
Dicyphus 144, 152, 158, 162, 166
Dicyphus annulatus 141
Dicyphus epilobii 141
Dicyphus globulifer 141
Dicyphus pallicornis 141, 144, 290, 292, 313, **147**
Dicyphus pallidus 141, **144**
Dinidoridae 112
Dipsocoridae 240–246, 258
Dipsocoroidea
—, chorion 258
—, observations 240–248
—, phylogeny 357
Diptera 286, 288, 345, 346
Discocoris 166, 168, 254
Discocoris vianai 166, **169**
Dolerus 345
Dolichonabis limbatus 130, 313
dorsal organ 33, 305, 312
dorsoventral polarity 340, 342, 344–349, **337**, **339**, **341**, **343**
Dorycoris pavoninus 116
Drosophila 269, 288, 346
Drymus unus 292
Dryophilocoris flavoquadrimaculatus 158
Dysdercus 94, 95, 290, 315, 324, 363, 375
Dytiscus 324

eclosion
—, act 38, 39, 52, 126, 128, 146, 150, 176, 196, 198, 204, 216, 226, 312–326

—, rupture of chorion 272–278, 289, **271**, **273**, **277**
Ectrichodea 182
Ectrichodea antennalis 170, 182, **175**
Edessa 116–118, 274, **115**
Edocla 168, 174, 340, **175**
egg-burster 316–326
egg rotation 334–338
egg shell, see chorion
Elasmostethus 254
Elasmostethus interstinctus 108, **107**
Elasmucha 108, 254, 284, 301, 307, 319, 329
Elasmucha fieberi 108
Elasmucha grisea 108, **107**, **243**, **262**, *443*
electron microscope
—, scanning 4
—, transmission 4
Elvisura 110
Embiophila 152, 256, 259, 260, 272, 275, 321, 356
Embiophila myersi 138, 256
embryogenesis
—, embryo position 300, 301
—, embryo shape 301
—, embryonic types compared 338–340
—, Heteroptera 298–305
—, other insects 307–310
—, phylogeny 302, **299**
—, rotations 298–300, 307, 308
embryonic cuticle 6, 39, 46, 315, 316, 318–320, **317**
embryonic envelopes
—, see embryonic cuticle and serosal cuticle
—, uncertain origin 314, 315
Empicoris 170, 172, 181, 183, 184, 254, 265, 289, 301, 302, 340, **330**
Empicoris culiciformis 168, 170, 275, 290, **171**
Enicocephalidae 258, 260
—, chorion 259
—, observations 248, 249
—, phylogeny 357
Enisthares 220
Enisthares maculata 218
Ephemeroptera 286, 289, 309, 326
Erianotus lanosus 368
Erioischia brassicae 306
Esakiella hutchinsoni 230, 234
Eumenotes 120, 274
Eumenotes obscura 116, 118
Eupelix cuspidata 326
Eurydema cyaneum 116
Eurygaster 110, 363, **329**
Eurygaster integriceps 110, **111**
Euscelis 297
Eusthenes robustus 114
Eutermis 346
Exolygus 146
Exolygus rugulipennis 141, 157
extrachorion 251
eye
—, embryonic development 28, 303
—, first larval instar 363, 364
—, trichobothria 363, 364

flexing patterns, see prolarva
Fieberocapsus 158, 162
Fieberocapsus flaveolus 141

Gampsocoris punctipes 84
Gelastocoridae 238–240
Gelastocoris 240, 269
Gelastocoris nebulosus 238, 240, 241
Gelastocoris oculatus 240
Gellia dilatata 116
genitalia 369–372
Geocoris 90, 363
Geocoris dispar 84, 86, 90, **85**, **87**
Geocoris grylloides 84
germ cells 22, 303
Gerridae 66–74
Gerris 6, 48, 64, 72, 192, 250, 253, 282, 291, 300, 303, 304, 310, 311, 314, 316, 318, 326, 328, 331, 334, 336, 342, 349, 351, 360, 363, **329**
Gerris fluviorum 74
Gerris gibbifer 66
Gerris lacustris 66, 72, 290
Gerris odontogaster 66, 72, **71**
Gerris thoracicus 66, 72, 74, **69**, **73**, **261**, *437*
Glaenocorisa propinqua 185
Globiceps sphegiformis 141
Gorpis deliensis 125, 128
Graphosoma lineatum 290
Graptopeltus lynceus 86
grumorium, see hydropyle
grumulus, see hydropyle
Gryllidae 286
guarding of egg 333

haemoglobin 230
Hallez's law 347, 348
Halobates 72, 334
Halobates princeps 368
Halosalda lateralis 8, 36, 297, **9**
Halovelia 284

Halovelia hilli 61, 64
Halovelia marianarum 66
Halticus 142, 158
Halticus apterus 141
Halticus major 141
Haploprocta sulcicornis 96
Harpocera 158
Harpocera thoracica 141, 296
hatching mechanism, see eclosion
Hebridae 44–48
Hebrovelia 61, 64, 254, 265, 269, 351, 362, 363, 374, **67**
Hebrus 48, 52, 253, 260, 268, 282, 302, 314, 316, 318, 331, 336, 340, 350, 351, 363, 365, 366, 367, 374, 375, 376, 377, **329**
Hebrus concinnus 48
Hebrus elimatus 44, 46, 261, **47**, *435*
Hebrus pusillus 48
Hebrus ruficeps 44, 48, 374, **45, 47**
Helopeltis 154, 158, 160, 164, 255, 256, 270, 356
Helopeltis antonii 141, 164, **163**
Helotrephes 230, 234, 257, 276, **235**
Helotrephidae 234
Hemimetabola 306, 309, 310
Henestaris laticeps 86
Hermatobates 366
Hesperocorixa 310, **329**
Hesperocorixa linnei 185, **199**
Hesperoctenes 284, 300, 301, 309
Heterocleptes 362, 366, 368, 370
Heterocorixa 200
Heterogaster 90, 92
Heterogaster urticae 86
Heterotoma 142, 158
Heterotoma planicornis 141
hibernation, see diapause
Himacerus apterus 5, 125, 128, 296, **129, 131**
Holometabola 306, 309, 310, 324, 325
Homoeocerus 290
Homoeocerus paleus 96
Homoeocerus schoutedeni 96, 263
Homoptera 281, 284, 289, 307, 308, 309, 311, 323, 326, 345, 346, 348, 349
Hoplomachus 158
Hoplomachus thunbergi 141
Hotea 290, 371, 372
Hotea curculionoides 109, 110, 371, **111**
Hotea subfasciata 109, **111**
Hyaliodes 141, 158, 160, 165, 356
Hydara 290, 301, 355
Hydara tenuicornis 96, 100, **97**
Hydrocorisae
—, chorion 257, 258
—, observations 184–240
—, phylogeny 357–359
Hydrocyrius columbiae 209, 269
Hydrometra 6, 60, 72, 253, 260, 261, 270, 280, 281, 283, 291, 300, 303, 311, 314, 316, 318, 328, 331, 351, 363, 364, 367, 370, 374, 376, **329**
Hydrometra gracilenta 54–56, **57**, **63**, *451*
Hydrometra martini 61
Hydrometra stagnorum 54, 290, **57, 59, 262**, *439*
Hydrometridae 54–61
Hydrophilus 347
hydropic structure, see hydropyle
hydropyle
—, chorionic 201, 209
—, serosal 28, 29, 40, 46, 50, 70, 222–224, 288, 304, 310, 311
Hymenoptera 286, 345, 346
Hyocephalidae 351, 354
Hypselosoma 246, 269, 276, **247**
Hypselosoma hirashimai 248
Hyrcanus 44, 48, 350, **47**

Idiocerus 323
Idiostolidae 78
Idiostolus 78, 255, 259, 260, 353, 371, **79**
Ilyocoris 194, 210, 214, 222, 224, 226, 228, 229, 230, 232, 258, 259, 266, 269, 302, 304, 305, 308, 310, 312, 322, 324, 325, 327, 340, 343 358, 366, 377, **330, 343**
Ilyocoris cimicoides 209 210 216, 218, 276, 290 374, **211, 213, 215, 217, 219**
incubation 290, 291, 305, 306
intraspecific variation 18
Ischnodemus 90, 92, 94, 301
Ischnodemus sabuleti 86, 90, 290, 292
Ischnura 310, 312
Isometopus 158, 162, 255
Isometopus intrusus 141, 373, 374, **163**
Isoptera 286
Isyndus heros 183

Joppeicus paradoxus 357

Kalotermes 286
Kelisia 323, 326
Kleidocerys 92, 93, 354
Kleidocerys championi 86, 92, **89**, *452*
Kleidocerys resedae 86, 92, **91**
Krizousacorixa 200

Laccotrephes 202, 203
Laccotrephes calcaratus 200
Laccotrephes fabricii 200
Lachnus 326, 348
lactic acid 4, 5
Largus fulvipes 94
larval organ 36
Leotichius 368, 372
Lepidoptera 286
Lepisma 286, 310
Leptoconops 284
Leptocoris 104, 106
Leptocoris augur 106
Leptocorisa 102, 104, 355, **97**, **101**
Leptoderma 183
Leptoglossus 98, 290, 343
Leptoglossus membranaceus 96
Leptohylemyia 306
Leptopodidae 40–43
Leptopodoidea
—, chorion 251, 252
—, observations 7–43
—, phylogeny 350
Leptopus 252, 265, 272, 291, 318, 328, 363, **317**
Leptopus hispanus 42, 252
Leptopus marmoratus 40, 42, 252, 311, 368, 374, 375, **41**, **43**
Leptoterna dolabrata 141, 313, **155**
Leptoterna ferrugata 141, **155**
Lethocerus 209, 257, 258, 269, 372
Lethocerus indicus 206, 208, 369, **211**
life cycles 292–297
Ligyrocoris diffusus 296
Limnobatodes 253
Limnobatodes paradoxus 54, 61, **59**
Liocoris 146, 148, 166, 313, 321, 323
Liocoris tripustulatus 141, 146, 290, 312, 313, **149**
Liposcelis 346, 348
Lisarda 174, 181, 321, 340, **330**
Lisarda vandenplasi 168, 172, **173**, **177**
Lisyphlebus 345
Livia 345
Locusta 253, 307, 312, 324
Locustana 307, 324
Lorichius umbonatus 125, 128
Loricula 314
Loricula elegantula 138, **137**, *457*
Loricula pselaphiformis 136, 138, *457*
Lyctocoris campestris 132
Lygaeidae 84–94
Lygaeus 90, 92
Lygaeus equestris 86
Lytta 288

Machadonannus ocellatus 238
Machilis 310
Macrina 118, 120, 122, 264, 336
Macrina juvenca 116, 117, 255, 336, **115**, **263**, *443*
Macrocephalus 182
Macrocephalus cimicoides 170
Macrolophus 142, 156, 158
Macrolophus nubilus 141, 292, **155**, **163**
Macroplax fasciata 86
Macrotylus paykulli 141
Macrovelia 54, 64, 254, 265, 269, 351, 361, 362, 365, 366, 367, 368, 370
Macrovelia horni 61, 294, **69**
Madeovelia 362
major classification 360–362, **459**
Malacocoris 255, 331
Malacocoris chlorizans 141, 160, 313
Malcidae 82–84
Malcus 84
Malcus flavidipes 82
Malcus tuberculatus 82
Mallophaga 286, 289, 307, 309, 311, 326, 349
Martiniola madagascariensis 336
Megacoelum 160, 162
Megacoelum beckeri 141, 160, **161**
Megacoelum infusum 141, 160, **161**
Megaloceraea recticornis 141
Megalocoleus 141, 158, 162
Megalocoleus molliculus 141, 156, **155**
Megalonotus chiragra 86, **87**
Megochterus nasutus 234, 236, 238
Megymenum subpurpurascens 112
Melanocoryphus 90, 92
Melanocoryphus albomaculatus 86
Melanoplus 278, 307, 312, 324, 325
Melophagus 346
Mesovelia 10, 48, 50, 52, 54, 126, 176, 253, 259, 266, 268, 269, 302, 303, 304, 305, 314, 316, 318, 319, 320, 321, 327, 328, 331, 348, 350, 351, 361, 363, 365, 366, 367, 370, 374, 376, 377, **329**
Mesovelia furcata 48, 54, 290, 294, **49**, **51**, **53**, **262**, *436*
Mesovelia horvathi 48, **55**
Mesovelia mulsanti 48, 54, **55**
Mesoveliidae 48–54
Mesoveloidea 5, 253, 336, 350, 370
Mesoveloidea williamsi 48, 54, **55**
Metapterus 181

Metapterus banksii 168, 181, **173**
Metatetranychus 288
Metatropis 84
Metopoplax 90
Metopoplax ditomoides 86
Mevaniomorpha hystrix 96, **97**
Mezira 301
Mezira rugosa 75, 76, **77**
Micronecta 185, 186, 188, 257, 258, 259, 268, 275, 359, **187**, **264**, *447*
Micronecta browni 185, 186, **187**
Micronecta meridionalis 185, 186, 198
Micronecta poweri 185
Micronecta quadristrigata 198
Micronecta scutellaris 185, 186, **187**
Microphysidae 137, 138
micropyle 265–270
—, displacement 266–268, **271**, **273**
—, function 288
—, number Heteroptera 265, 266, **271**, **273**
—, number other insects 284–288
—, orientation 268–270
—, structure 268–270
—, transverse canal 270, **271**
Microvelia 44, 48, 61, 64, 65, 66, 68, 250, 253, 266, 300, 308, 314, 316, 318, 319, 328, 331, 351, 363, 376, **329**, **337**
Microvelia longipes 61, 63
Microvelia pulchella 61, 63
Microvelia reticulata 61, 290, 340, 374, **63**, **65**, **67**, **261**, *438*
Microvelia signata 61, 64, 269, **67**
Mictis 98
Mictis metallica 96, **101**
Miridae 141–166
Miridius quadrivirgatus 141
Miris 162
Mirperus 104
Mirperus jaculus 102
Mocydiopsis 295
Monalocoris 152, 160, 164, 268, 270, 274, 275, 289, 327, 356
Monalocoris filicis 141, 256, **151**
Monosynamma maritima 141
Mydas 345
Myrmedobia 255
Myrmedobia coleoptrata 138, **137**
Myrmedobia tenella 138
Myrmus 104, 106, 314, 316
Myrmus miriformis 104, 294, **99**
Myzus 348
Nabidae 125–130
Nabis 126, 134, 140, 176, 255, 303, 305, 320, 322, 363, **329**
Nabis rugosus 125, 128, 290, 300, **127**, **129**, *456*
Nagusta punctaticollis 168, 178, **175**
Nannocoris 246, 258
Naucoridae 209–218
Naucoris maculatus 216, 218, 276
Neoborus illitus 313
Nepa 202, 204, 206, 212, 276, 328, 360, 377, **330**
Nepa rubra 200, 201, 206, 290, **203**, **264**
Nepidae 200–206
Nerthra 238, 269, **239**
Nerthra colaticollis 238, 240
Nerthra laticollis 238, 240, **450**
Nerthra martini 240
Nerthra terrestris 238, **239**
Neuroctenus 75, 76, 78, 82, 86, 108, 255, 260, 272, 301, 340, **77**, **262**, **339**, *440*
Neuroctenus pseudonymus 78
Neuroptera 286
Nezara 116
Notonecta 204, 212, 214, 216, 218, 222, 224, 230, 232, 234, 258, 259, 260, 268, 269, 276, 290, 294, 302, 304, 305, 306, 314, 315, 324, 325, 326, 340, 358, 375, 377, **223**, **330**, **343**
Notonecta glauca 218, 220, 222, 224, 228, 229, 290, 328, **221**, **223**, **225**, **227**, **229**, **231**, **264**, *448*
Notonecta lutea 218, 222, 294, 314
Notonecta maculata 218, 220, 222, 224, 226, 234, 296, 314, **223**, **231**, **343**
Notonecta melaena 230
Notonecta obliqua 218, 220, 228, 290, 328, **221**
Notonecta reuteri 218, 222, 294
Notonecta viridis 218, 220
Notonectidae 218–230
Notostira 141, 156, 166, 310, 313, 321, 322, 323
Notostira elongata 141, 164, 290, 313, **155**
Nysius 136, 354
Nysius californicus 86
Nysius helveticus 86
Nysius thymi 86, 90, 291, **83**, **293**

Ocellovelia 336, 351, 362, 368, 370
Ocellovelia germari 61, 64, **67**
Ochteridae 234–238
Ochterus 240, 257, 259, 276, 290, 301, 302, 303, 314, 358, 366, **330**, **343**
Ochterus banksi 238, 292
Ochterus marginatus 234, 238, 374, **237**, **263**, *449*

Ochterus perbosci 236, **237**
Ocypus 283
Odonata 286, 288, 289, 307, 309–312, 324, 325
Odontoscelis 110, 292, 371
Odontotarsus 110, 371, **111**
Oliarius 326
Omania 252, 265, 266, 336, 350, 368, 372
Omania marksae 42, **43**
Omania samoensis 42
Oncopeltus 90, 92, 94, 95, 108, 184, 255, 270, 272, 290, 291, 301, 302, 303, 305, 331, 367, 371, 377, **217**, 329
Oncopeltus fasciatus 74, 86, 290, **83**, **91**, **262**, *442*
Oncotylus 158
Oncotylus punctipes 141
Oncylocotis 259, 327
Oncylocotis curculio 248, **247**
Onymocoris hackeri 166
operculum 288, 289
Oravelia 254, 351, 362, 366, 367, 368, 370
Oravelia pege 61, 64, **69**
Orius 132, 136
Orsillus 90, 354
Orsillus depressus 86, **77**
Orthocephalus 142
Orthocephalus mutabilis 141, 158
Ortholomus 90, 92, 283
Ortholomus jamaicensis 86
Ortholomus punctipennis 86, 90, **85**, *453*
Orthonotus 162
Orthonotus rufifrons 141
Orthophrys **21**
Orthophrys pygmaeum 7, 8, **11**, 12, 16, **21**, **15**, **261**, *432*, *433*
Orthoptera 286, 307, 308, 312, 324, 346
Orthotylus diaphanus 141, 158
Orthotylus ericetorum 141, 158, 162
Orthotylus flavosparsus 313
Orthotylus marginalis 141
Orthotylus virescens 141
oviposition 331–334, **335**
Oxycarenus pallens 86

Pachycoleus 242, 244, 246, 258, 259, 260, 278, 340, 374, **341**
Pachycoleus rufescens 240, 241, 374, **243**, **263**, *436*
Pachynomidae 132
Pachynomus 356
Pachynomus brunneus 132, 265
Pantilius 141, 166, 297, 321, 325
Pantilius tunicatus 141, 156, 296, **155**, **159**, **293**
Paraphrynovelia 362
parental care 333
Pelocoris 218
Pelocoris femoratus 216
Pentacora 11, 18, 20, 42, 251
Pentacora hirta 7, 18
Pentacora leucographa 7, 11, 12, 16, **15**
Pentacora ligata 7, 18
Pentacora mexicana 7, 18
Pentacora signoreti 7, 8, 16, 17, 18, 252, **14**, **261**, *434*
Pentacora sphacelata 7, 18
Pentatoma 292
Pentatomidae 116–122
Pentatomomorpha
—, chorion 254, 255
—, observations 74–124
—, phylogeny 351–355
Perillus bioculatus 116, **117**
Perithous 345
Peritrechus geniculatus 86
Peritropis 141, 165
Phaenacantha 95
Phasmida 286
Phimodera 371
Phloeidae 351
Phtyia **105**
Phyllomorpha 281, 334
Phyllopertha 310
Phymata 182
Phymata crassipes 170, 182
Phytocoris ulmi 141
Picromerus bidens 116, 120
Piesma 82, 92, 93, 275
Piesma cinereum 80, 82
Piesma maculatum 80, 82, **83**
Piesma quadratum 80, **81**
Piesmatidae 80–82
Piocoris erythrocephalus 84
Pisilus 333
Pithanus 158
Pithanus maerkeli 141
Plagiognathus 142
Plagiognathus arbustorum 141, 156, **155**, **163**
Plagiognathus chrysanthemi 141
plastron 20, 42, 58, 92, 138, 160, 201, 204, 251, 255, 256, 281, 282, **14**, **43**, **85**, **167**, **179**, **203**
Plataspidae 122–124
Plataspis 122
Platycnemis 307, 308, 346
Platygaster 345

Platymeris rhadamanthus 183, 290
Plea 258, 268, 274, 276, 292, 300, 301, 302, 304, 314, 327, 328, 344, 358, **330**
Plea atomaria 4, 230, 234, 276, 290, 292, 327, 328, 374, **233**
Plea puella 230, 234, **233**
Plea striola 234
Plecoptera 286, 289, 308, 325, 326
Pleidae 230–234
pleuropodia 33, 226, 228, 324,
Plokiophilidae 138
Podops 363
Poissonia 208
Poissonia longifemorata 206
polarity, see dorsoventral polarity
Polymerus 158
Polymerus holosericeus 141
polyspermy 288
position of released eggs 331–334, **335**
pregerm 342, 346
pretarsus 365, 366
Pristhesancus papuensis 184
Pristiphora 346
Procilia morgani 109
prolarva, posture of 36, 38, 41, 328, **329**, **330**
Prostemma 125, 130, **131**
Proto-Ochteridae 358
Pseudoloxops 255, 331
Pseudoloxops coccineus 141, 160, **144**
pseudoperculum 288, 289
Pseudosaldula 7
Psocoptera 286, 289, 309, 311, 326, 345, 348
Pteronarcys 308, 346
Ptilomera 68
Ptilomera assamensis 66
Pycanum ruber 114
Pyrilla 307, 326
Pyrops 338, 348
Pyrrhocoridae 94, 95
Pyrrhocoris 74, 95, 272, 302, 363, **329**
Pyrrhocoris apterus 94, **91**

Ranatra 200, 202, 204, 206, 207, 230, 276, 281, 290, 310, *451*, *452*
Ranatra absona 206
Ranatra fusca 206, 209
Ranatra linearis 200, 201, **203**, **205**
Ranatra parvipes 200
Ranatra vicina 200
Reduviidae 168–184
Reduvius 178, 180, 278, 279, 292, 364, 375
Reduvius personatus 168, 181, 290, 303, **263**, *444*
reproductive organs 369–372
respiratory area 12–22, 42
respiratory horn 255–257, 282
revolution 311
Rhagadotarsus 66, 72, 332, **69**
Rhinocoris 174, 178, 181, 183, 184, **330**, **341**, *454*, *455*
Rhinocoris albopilosus 168
Rhinocoris bicolor 168
Rhinocoris carmelita 168
Rhinocoris iracundus 168, 176, 328, **177**, *456*
Rhinocoris obtusus 168, **177**
Rhinocoris rapax 168
Rhodnius 181, 183, 184, 250, 251, 265, 278, 279, 280, 289, 302, 303, 305, 325, 326, **177**
Rondania 346
rotations, see embryogenesis
—, see egg rotation
ruptor ovi, see egg-burster
rupture of chorion, see eclosion

Saga 286
Sahlbergella 156, 164, 312, 321, 356
Sahlbergella singularis 141, 154
Salda anthracina 7
Salda crassicornis 7, 8, 11
Salda littoralis 7, 8, 11, 12, 14, 16, 20, 29, 36, 290, 297, 374, **9**, **17**, **24**, **25**, **26**, **35**, **37**
Salda lugubris 7
Salda morio 8, 11
Saldidae 7–39
—, absorption of serosa 33–36
—, cephalic organ 28–30
—, chorion 10–22
—, eclosion 38, 39
—, egg-burster 39
—, embryogenesis 22–36
—, embryonic cuticle 39
—, literature 7
—, material 7
—, micropyle 12
—, oviposition 10
Saldoida armata 8
Saldoida slossoni 8, 21
Saldula 8, 11, 18, 20, 22, 36, 251, 290, 291, 305
Saldula aberrans 8, 12, 21
Saldula arenicola 8
Saldula brevicornis 7
Saldula c-album 8, 374, **9**

Saldula coorongensis 7
Saldula fucicola 8, **9**, **20**, **23**, **24**, **27**, **28**, **31**
Saldula horvathi 20, 48, 54
Saldula jihafana 8, 12, 21, **17**
Saldula madonica 8, 20, 251, 282, **14**
Saldula marginalis 8, 11, 36, 290, 297
Saldula orthochila 8, 252, 290, 291, 295, 297, **9**
Saldula pallipes 7, 8, 290, 291
Saldula palustris 8, 12, 16, 20, **9**, **20**, **35**, **37**, **261**, *431*, *432*
Saldula politus 8, 12, 21
Saldula psammobia 7
Saldula rivularia 8, 10, 18, **13**
Saldula saltatoria 7, 8, 22, 38, 290, 291, 374, **37**
Saldula scotica 8, 10, 11, 18, 20, 251, 331, 342, 374, **9**, **13**
Saldula variabilis 8, 20, **17**
salivary system 375
Sakuntula 256
Sakuntula ravana 140, **139**
Scaptocoris 369
scent apparatus 366–369
Schidium 340
Schidium callipygum 168, 172, **173**
Schizopteridae 246–248
Sciocoris 116, 117, 274, 340, 344, **339**
Sciocoris cursitans 116, **117**
Scotomedes alienus 130
Scotomedes minor 130, 265, **131**
Scutelleridae 109, 110
sealing bar 288, 289
seasonal types 292–297
Sehirus 270, 319, **329**
Sehirus biguttatus 106, 290, 363, **107**
Serinetha 265, 269
serosal cuticle 6, 289, 313, 314, 322–325, **317**
serosal plug 33
—, absorption 34–36, 224, 305
—, persistent 312, 313
shell, see chorion
Sieboldius 286
Sigara 200
Sigara fossarum 185
Sigara nigrolineata 198
Sigara striata 198
Siphanta 326
Siphnus 112, 114
Siphnus alcides **113**
Siphonaptera 288
Siphunculata 286, 289, **307**, 309, 311, 326, 349
Spathocera dalmani 96, **102**
Spathocera laticornis 96
Speovelia 253, 336
Speovelia maritima 54
Sphaerocoris 290
Sphaerocoris annulus 109
Sphaerodema 206, 208, 209, **207**
Sphaerodema ampliatum 206, 208
Sphaerodema annulatum 206
Sphaerodema rusticum 206, 208
Sphedanovarus 340
Sphedanovarus camerunensis 168, **175**
spiracles 377, 378
Stalia 125
Stalia boops **131**
Steganocerus multipunctatus 109
Sthenarus roseri 141
Stenocephalidae 94
Stenocorixa protrusa 200
Stenocranus 297, 323
Stenolemus arachniphagus 334
Stenus 368
Stibaropus 108
Stictopleurus abutilon 106
Strongylocoris 141, 160, 331
Strongylocoris leucocephalus 141, 160
Strongylocoris luridus 141, 160, **157**, **159**
Strongylocoris obscurus 141, 160
Stygnocoris 292, 306
Stygnocoris pedestris 86, 294, 296, 297, **83**
Sulpicia 98
Sulpicia distincta 96, 116, **103**
suprachorionic layer 16, 251, 253
symbionts 50–52, 90, 136, 305
Symphylus 110, **111**
Syrtis 182
Syrtis pennsylvanica 170, 174
Systellonotus triguttatus 141

Tachycines 346
Tantia 117, **115**
Tantia striata 116
Tanypteryx 312
Temnostethus 132, 136
Temnostethus gracilis 132, 295
Temnostethus pusillus 132, 295
Tenagobia 257, 258, 275
Tenagobia incerta 185, 186, 200, **189**
Tenagobia selecta 198
Tenebrio 346
Teratodella 160
Teratodella brevicornis 141, 160, **167**

Termatophylidea 158, 160, 164, 256, 270, 282, 356
Termatophylidea opaca 141, 158, **159**
Tessaromerus licenti 109
Tessarotoma 114, 266
Tessarotoma javanica 112
Tessarotomidae 112–116
Tetrix 324
Tettigonia 347
Thaumastella aradoides 78, 80, 255, 353, **79**
Thaumastellidae 78–80
Thaumastocoridae 166–168, 256, 357
Thaumastocoris australicus 166, 168, 256
Thaumastocoris hackeri 168
Themonocoris 369
Thysanoptera 309, 345
Thysanura 309, 310
Tingidae 140, 141
Tiphotrephes 234, 276
Tiphotrephes indicus 230, 234, **235**
Trapezonotus 377
Trapezonotus arenarius 86, **87**
Trepobates 66, 72
Trepobates taylori 66
Triatoma 364
Triatoma maculata 168, 182
Triatoma protracta 183
trichobothria 363–365
Trichoptera 326
Trichotonannus 246, 258

Urentius 140, 320, **137**
Urochela nigropunctata 109, **113**
Urostylidae 109
Urostylis 109, **113**

Valleriola 282, 368
Valleriola moesta 42, **43**
Vanda 348
Velia 66
Velia caprai 61, 63, 294
Veliidae 61–66
Velocipedidae 130
Ventidius 72
Ventidius distanti 66
vestopal 4
Vestula 178
Vestula lineaticeps 168, 178, **175**
Vianaididae 140, 141
Vilhenannus angolensis 248

Wagneripteryx 282
water absorption, see hydropyle

Xylastodoris 166, 168
Xylastodoris australicus 168
Xylastodoris luteolus 166, 168, 363, **169**

Yolk plug, see serosal plug

STELLINGEN

I

De huidige theorieën over de evolutie van de insektenembryogenese (bijv. SHAROV, 1966) berusten op gegevens verkregen van te weinig species. Een 'horizontale' benadering van het probleem biedt de ontwikkelingsfysioloog een leidraad bij het selecteren van proefmateriaal.

SHAROV, A. G., Intern. Ser. of Monogr. Div. Zoology 30, 271 pp., 1966
Dit proefschrift

II

De time-lapse microfotografie, zoals toegepast door SCHANZ (1965) voor het filmen van embryologische processen, geeft gemakkelijk aanleiding tot verkeerde conclusies ten aanzien van de oorzakelijke verklaringen van dooierbewegingen.

SCHANZ, G., Inaugural-Dissertation. Marburg/Lahn 92 pp., 1965
Dit proefschrift

III

De storingen in de embryogenese, die optreden na behandeling van *Pyrrhocoris*-eieren met mimetica van het juveniel hormoon, worden op onjuiste gronden door NOVÁK (1967) geïnterpreteerd ten gunste van zijn 'gradient-factor theorie'.

NOVÁK, V. J. A., in: Insects and Physiology: 119–132, 1967

IV

De opvatting dat overdracht van sperma via een spermatofoor bij insekten duidt op een primitief gebeuren (HINTON, 1964; DAVEY, 1965), is in zijn algemeenheid niet juist.

HINTON, H. E., Insect Reproduction Symp.: 95–107, 1964
DAVEY, K. G., Ann. ent. Soc. Québec 10:13–25, 1965
Dit proefschrift

V

Het ontstaan van haemocoelische inseminatie bij wantsen is waarschijnlijk door divergerende evolutie van het mannelijke en vrouwelijke geslachtsapparaat ingeleid.

VI

In het onderzoek over de biologische aspecten van plantevirussen en mycoplasma's in cicaden wordt te weinig aandacht besteed aan de endosymbionten.

SMITH, K. M., Insect Virology: 195–230, 1967

VII

Gebrek aan voedingsstoffen is als verklaring voor fungistase in de bodem onvoldoende.

JACKSON, R. M., in: Ecology of soil-borne plant pathogens: 363–369, 1965

VIII

Kennis van de wilde flora dient een verplicht onderdeel te zijn van het studieprogramma van de richting Plantenziektenkunde.

IX

Het is te verwachten dat vooral de entomologie in toenemende mate bijdragen zal leveren tot een beter inzicht in de wetmatigheden, die de macroevolutie sturen.

X

Behalve door geur en smaak kunnen 'odd substances' ook door middel van mechanisch-fysische eigenschappen een rol spelen in de waardplantkeuze van insekten.

XI

Randpopulaties van een soort met een groot areaal zijn genetisch armer dan centrale populaties. Het is van belang hiermee rekening te houden bij het importeren van insekten ten behoeve van biologische bestrijdingsprogramma's.

XII

Met het oog op het groeiend belang van onderzoek in het kader van geïntegreerde bestrijding en natuurbehoud en de daaruit voortvloeiende behoefte aan taxonomische specialisten, zou het wenselijk zijn bekwame amateur-entomologen voor dit onderzoek vrij te maken door middel van aantrekkelijk gesalarieerde werkgelegenheid.

XIII

Het is voor het onderwijs en het natuurwetenschappelijk onderzoek noodzakelijk dat de Landbouwhogeschool naast conventionele proefvelden de beschikking krijgt over rijk gevarieerde en goed beheerde natuurterreinen in de omgeving van Wageningen.

R. H. Cobben
Wageningen, 21 juni 1968