

1959

copy to LIAK

cataloged

Vol. 111. Pt. 14. Pp. 405-467. 103 figs. 31st December, 1959.

THE
TRANSACTIONS
 OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
 OF
LONDON

World List abbreviation: Trans. R. ent. Soc. Lond.

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LONDON:

**PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.**

Price £1 5s. 0d.

THE FEMALE GENITALIA OF THE HETEROPTERA: MORPHOLOGY
AND BEARING ON CLASSIFICATION¹

By G. G. E. SCUDDER

(*Department of Zoology, University of British Columbia, Canada.*)

Manuscript received 19th February, 1959

(Read 6th May, 1959)

With 103 Text-figures

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¹ Part of a dissertation presented in partial fulfilment of the Degree of Doctor of Philosophy in the University of Oxford.

I. INTRODUCTION

DUPUIS AND CARVALHO (1956) have given a general account of the structure of the female genitalia in the Heteroptera. Elsewhere (Scudder, 1957*e*, 1957*f*, 1959), I have given a new interpretation of the ovipositor in the Hemiptera. This scheme is followed here.

The musculature of most of the British families has been examined and that of six is figured here, though not described in detail, the labelling being self explanatory. Larsén (1938) has studied the musculature in the aquatic Heteroptera. The musculature has been very useful in confirming homologies. Only muscles associated with and affecting the interpretation of the female genitalia are here labelled.

The value of the female genitalia in the systematics of the group is considered. In the text, families are placed in superfamilies on the basis of the structure of the female genitalia. This is *not* an attempt to erect a system of classification on this evidence alone, but is adopted for simplicity in presentation, so that the results may be assessed easily by other workers who might wish to use this morphological study in further systematic work. Usually, however, the arrangement agrees with established custom. Where this is otherwise, a discussion is given.

The spermatheca in the Heteroptera has been described and discussed by Pendergrast (1957) and will not be treated in detail here. However, some additional information on this organ in some families has been obtained and so is described and discussed in the appropriate places in the text.

II. MATERIAL AND METHODS

The female genitalia were examined from dried museum material after the abdomen had been removed from the specimen and boiled in 10 per cent. potassium hydroxide solution. Material was passed through glacial acetic acid, stained in acid fuchsin and cleared in beechwood creosote. The musculature was studied from dissections of fresh material. Specimens were dissected under 50 per cent. alcohol immediately after having been killed in ethyl acetate vapour.

All drawings were made by using a squared graticule eyepiece. The drawings are not to scale.

III. SOME ASPECTS OF THE GENERAL STRUCTURE

The female genitalia of the Heteroptera may be homologised with the structure seen in the Lepismidae (Thysanura) (Scudder, 1957*e*, 1957*f*). The terminology in this paper follows the scheme proposed by Scudder (1957*f*).

The ovipositor is situated on abdominal segments VIII and IX. The ventrolateral parts of tergum VIII are often separated from the median part, as separate sclerites, paratergites VIII, which carry spiracles VIII. Ventrolaterally on either side of segment VIII, beneath the paratergite, is located a basal sclerite or first gonocoxa. This carries ventrally and caudally the first gonapophysis. The dorsal edge of the latter is heavily sclerotized and forms the grooved first ramus. This ramus is often produced anteriorly beyond the

base of the first gonapophysis internally. Segment IX carries a pair of second gonocoxae, to which are attached a pair of second gonapophyses. The ventral edge of each second gonapophysis is heavily sclerotized and forms the ridged second ramus; this interlocks with the first ramus. Attached to the internal part of the first gonapophysis or to the base of the first ramus is the gonangulum. In the Heteroptera and the other Hemipteroid groups, the gonangulum is fused posteriorly to tergum IX. It is triangular or often \wedge -shaped. The anterior limb or edge of this sclerite is the part fusing with the first ramus or gonapophysis. The posterior limb or side is fused either partially or completely with tergum IX. The ventral angle of the posterior side or limb articulates near the mid-point of the dorsal edge of the second gonocoxa. This articulation forms the fulcrum on which the second gonocoxa pivots and is rocked by opposing muscles (figs. 98-103, 1 and 3). The extensor muscle of the gonapophyses (muscle 1) is attached to the posterior part of the second gonocoxa, behind the fulcrum, and the retractor muscle of the second gonapophysis (muscle 3) is attached to the anterior part of the second gonocoxa, anterior to the fulcrum.

A characteristic feature of the Heteroptera is the difference in shape and size of the two pairs of gonocoxae. The second gonocoxae are more slender than the first pair.

The structure called the "outer ramus of the first valvula" and labelled *rivlo*, by Snodgrass (1933), has caused some confusion. Snodgrass regards the first gonapophysis (= first valvula) as possessing two rami, an inner and an outer. The inner is a sclerotization of and prolongation of the first gonapophysis, to which is attached the gonangulum: this is here termed the first ramus and interlocks with the second ramus which is part of the second gonapophysis and connects it with the second gonocoxa. The "outer ramus" of the first gonapophysis is not an analogous structure, but a thickened sclerotization of the ventral edge of the first gonapophysis. It is the theoretical homologue of the second ramus, but does not connect the first gonapophysis to the first gonocoxa. The first ramus is without a homologue on the second genital segment. Whilst the first and second rami are analogous, they cannot be regarded as homologous structures.

IV. ARRANGEMENT OF FAMILIES AND SUPERFAMILIES AS SUGGESTED BY THE FEMALE GENITALIA, EXCLUDING THE SPERMATHECA

Pentatomoidea

Cydnidae
Urostylidae
Brachyplatidae
Scutelleridae
Canopidae
Tessarotomidae
Acanthosomidae
Dinidoridae
Eumenotidae
Pentatomidae

Pyrrhocoroidea

Pyrrhocoridae

Coreoidea

Coreidae
Colobathristidae
Rhopalidae
Alydidae

Lygaeoidea

Lygaeidae
Stenocephalidae
Largidae
Berytinidae
Piesmidae

Aradoidea

Aradidae
Dysodiidae

Cimicoidea

Nabidae
Velocipedidae
Miridae
Isometopidae
Anthocoridae
Cimicidae
Microphysidae
Thaumastocoridae
Polycetenidae

Dipsocoroidea

Dipsocoridae

Reduvisoidea

Reduviidae
Phymatidae

Tingoidea

Tingidae
Vianaididae

Saldoidea

Saldidae
Leptopodidae
Mesoveliidae

Gerroidea

Veliidae
Hebroveliidae
Macroveliidae
Gerridae
Hydrometridae
Hebridae

Nepoidea

Nepidae
Belostomatidae

Naucoroidea

Naucoridae
Aphelocheiridae

Notonectoidea

Notonectidae
Pleidae

Ochteroidea

Ochteridae

Corixoidea

Corixidae

Incertae sedis I

Leotichidae
Helotrephidae
Galgulidae

Incertae sedis II

Aneuridae
Enicocephalidae
Schizopteridae
Termitaphididae
Joppeicidae

V. SYSTEMATIC CONSIDERATION OF THE FEMALE GENITALIA OF THE
FAMILIES AND SUPERFAMILIES OF HETEROPTERA

PENTATOMOIDEA

CYDNIDAE

Sehirinae

Previous description : Leston, 1956a.

Species examined : *Sehirus luctuosus* Muls. and Rey (figs. 1-3), *S. bicolor* (L.), *S. dubius* (Scop.), *S. biguttatus* (L.), *Geotomus punctulatus* (Costa).

Female genitalia having an almost directly posterior aspect ; sternum VII complete, not cleft and not obscuring terminalia ; paratergites VIII continuous above anus and free from first gonocoxae ventrally ; paratergites IX, broad, flattened and almost meeting in mid-line beneath anus ; first gonocoxa large, rounded and with antero-dorsal corner produced as an apodeme ; first gonapophyses small, flap-like and membranously united ; sclerotized first and second rami distinct and curved ; anterior strut of gonangulum long and slender ; second gonocoxae slender and curved round posteriorly to meet in mid-line beneath paratergites IX, where they are enlarged and produced dorsally ; second gonocoxae joined to paratergite IX along whole of ventral edge of latter ; second gonapophyses membranous and flap-like and partially fused to membrane between second gonocoxae—the inter-gonocoxal membrane ; gonoplacs absent ; genital chamber large and sacciform, with a dorsal pouch posteriorly within precincts of segment VIII ; pair of ring sclerites present in posterior wall of dorsal pouch ; median spermatheca present with duct opening into dorsal pouch ; area of attachment of posterior dilator muscle of genital chamber often sclerotized.

The musculature of *S. luctuosus* and *S. bicolor* has been examined and the latter figured (fig. 98).

Cydninae

Species examined : *Cydnus aterrima* Forst.

Similar to structure in Sehirinae, but with paratergites VIII contiguous posteriorly ; gonapophyses larger and more sclerotized ; second gonapophyses united dorsally by membrane ; ring sclerites and gonoplacs absent.

Coriomelaeinae

Previous description : McAtee and Malloch, 1933.

Species examined : *Thyreocoris scarabaeoidea* (L.), *Coriomelana pulicarius* (Germ.), *Galgupha atra* A. & S. (fig. 5).

(a) *Thyreocoris scarabaeoides* : female genitalia similar to those of Sehirinae, but with gonapophyses heavily sclerotized and appearing as curved rods connected by membrane ; rami well developed and paratergites VIII fused in mid-line posteriorly.

(b) *Coriomelana pulicarius* and *Galgupha atra* : similar to Sehirinae in general shape, in fusion of paratergites VIII, etc., but lacking rami and anterior strut of gonangulum ; second gonapophyses unrecognisable as such ; paired elongate sacs attached to base of second gonocoxae, the surface of the former being covered with minute projections ; ring sclerites and gonoplacs absent.

The Sehirinae and Cydnidae are very similar, with plate-shape type of female genitalia and with sclerotized rami. Those of *Thyreocoris* are also similar, but characteristically more sclerotized. The female genitalia in the other Coriomelaeinae are very different. Apart from *Thyreocoris*, the female genitalia in the latter subfamily are very specialised and indicate a homogeneous group. This may indicate that *Thyreocoris* is placed in the wrong subfamily, but, alternatively, it may be that *Thyreocoris* represents a remnant of the early Coriomelaeinae stock, isolated in the Palaearctic from the rest of the subfamily, which are mostly tropical.

UROSTYLIDAE

- ✓ Previous descriptions : Yang, 1938a, 1938b, 1939.
 ✓ Species examined : *Urolabida tenera* Hope.

First gonocoxae enlarged and obscuring rest of terminalia from external view ; paratergites VIII large, apically rounded and not contiguous posteriorly ; first and second rami present and interlocking ; first gonapophyses rather large, flap-like and membranously united ventrally ; gonapophyses and connecting membrane, posteriorly bordered by a fringe of long, dense hairs ; first gonapophyses apically free from first gonocoxae ; anterior strut of gonangulum slender ; second gonapophyses partially sclerotized, rather flap-like and membranously joined to each other, except at extreme apex ; second gonapophyses joined to inter-gonocoxal membrane ; second gonocoxae continuous beneath anus, the fused part being separate from the part of the gonocoxa attached to the second ramus ; an area of sclerotization attached to junction of second gonocoxa and second gonapophysis, carries the ring sclerite and supports the genital chamber ; U-shaped sclerite present around opening of spermatheca into genital chamber ; gonoplaes absent.

BRACHYPLATIDAE

Species examined : *Libyaspis* sp.

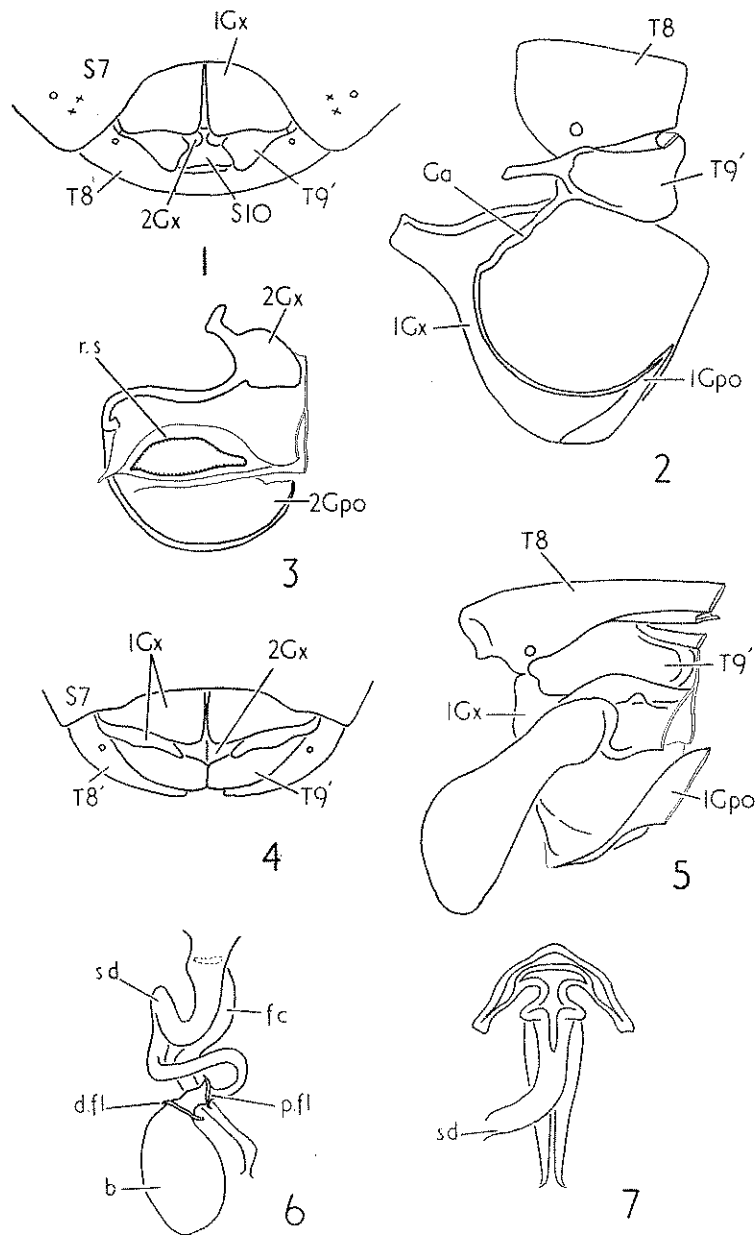
General shape and structure similar to Sehirinae ; paratergites not contiguous posteriorly ; paratergites VIII ventrally in contact with first gonocoxae ; anterior apodeme of first gonocoxa short ; first gonapophyses large and rami absent ; anterior strut of gonangulum broad and well sclerotized ; second gonocoxae joined in mid-line, but still possessing well developed apodemes ; a flat sclerotization attached to anterior of second gonocoxae is presumably the second gonapophyses ; two ring sclerites present ; wall of genital chamber without sclerotizations ; gonoplaes absent.

SCUTELLERIDAE

Scutellerinae

Species examined : *Anoplogonius nigricollis* Sign.

Paratergites VIII and IX about same size ; first gonocoxa large with antero-dorsal apodeme very large and antero-ventral part rather membranous and produced anteriorly ; sclerotized rami present and interlocking ; anterior strut of gonangulum complete and slender ; first and second gonapophyses large and flap-like and membranous ; first pair united ; second gonapophyses attached to inter-gonocoxal membrane ; second gonocoxae fused posteriorly, not fusing with paratergite IX, but freely pivoting on posterior strut of gonangulum ; genital chamber without ring sclerites, but with complicated sclerites around opening of spermathecal duct ; gonoplaes absent.



FIGS. 1-7.—(1)-(3) *Schirus luctuosus* Muls. and Rey (Cydnidae): (1) ventral view of female terminalia; (2) inner view of first gonocoxa and associated parts; (3) inner view of second gonocoxa and associated parts. (4) *Agonosoma flavolineatum* Lap. (Scutelleridae); ventral view of female terminalia; (5) *Galgupha atra* A. and S. (Cydnidae): inner view of right half of female genitalia; (6) *Hotea subfasciata* (Westw.) (Scutelleridae): spermatheca; (7) *H. curculionoides* (H.-S.): anchor-shaped sclerite surrounding opening of spermathecal duct.

Eurygastrinae

Species examined: *Eurygaster maurus* (L.).

Genitalia similar to those of Scutellerinae, but less sclerotized; with paratergites very large and contiguous posteriorly; rami partially reduced and anterior strut of gonangulum membranous.

Pachycorinae

Species examined: *Chelysoma variabilis* H.-S., *Deroplax redtenbacheri* (Mayr), *Hotea curculionoides* (H.-S.), *H. subfasciata* Westw., *Pachycoris torridus* Scop., *Agonosoma flavolineatum* Lap. (fig. 4).

Paratergites VIII and IX about same size; paratergites VIII almost meeting in mid-line posteriorly in *Chelysoma*, *Deroplax*, *Hotea* and *Agonosoma*; paratergites IX contiguous posteriorly; first gonocoxae ventrally nonsclerotized; first gonapophyses small and flap-like, completely membranous in *Agonosoma* only; membrane connecting first gonapophyses partially sclerotized in *Deroplax* and *Hotea*; rami and anterior strut of gonangulum present and sclerotized in *Deroplax*, partially sclerotized in *Hotea curculionoides*, but more or less membranous in rest; gonoplas absent; ring sclerites present in *Agonosoma*, *Chelysoma*, and *Pachycoris*, absent in others; dorsal wall of postero-dorsal pouch of genital chamber partially sclerotized in *Deroplax*, *Agonosoma* and *Hotea curculionoides*; anchor-shaped sclerite situated in genital chamber wall, around entry of spermathecal duct, in *Chelysoma*, *Pachycoris*, *Deroplax* and *Hotea curculionoides* (fig. 7); also present in *Tectocoris diophthalmus* (Thunb.) (Pendergrast, 1957).

In *Deroplax redtenbacheri* and *Hotea curculionoides* the spermatheca is identical with a very long duct. In *Hotea subfasciata* the spermatheca is peculiar in possessing two ducts (fig. 6). In this species also there is a special sac developed as an invagination in the intersegmental membrane between sterna VII and the first gonocoxae. Mr. D. Leston (*in litt.*) states that the anterior part of this sac often has an irregular hole dorsally and this opening is almost opposite the opening of the accessory canal of the spermatheca which opens into the dorsal wall of the genital chamber, anterior to the opening of the spermathecal duct. The spermatheca in *Agonosoma* has the proximal part of the spermathecal duct similar to *H. subfasciata*, but there is neither an accessory duct nor a ventral sac. Externally in *Agonosoma* above the first gonocoxae there are finger-like processes (fig. 4), probably subdivisions of the gonocoxae as they are attached to them.

In the Pachycorinae, the nature of the spermatheca and sclerotizations of the genital chamber suggest that the systematic placing of the two species *H. curculionoides* and *H. subfasciata* in the same genus needs reinvestigation. The anchor-shaped sclerites present in *Chelysoma*, *Pachycoris*, *Deroplax*, *Tectocoris* and *H. curculionoides* suggest a monophyletic group.

Leston states that the special sac in *H. subfasciata* and the associated accessory duct to the spermatheca suggest that copulation may be abnormal in this species. The irregular hole sometimes present in the sac may be caused by the aedeagus being inserted into this sac, penetrating the dorsal wall and wall of the genital chamber; Leston (1952) has commented on the uniqueness of the aedeagus in this species. Sperm then liberated into the genital chamber

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could migrate up the accessory canal into the spermatheca. The aperture of the accessory duct is not wide enough to permit the insertion of the aedeagus.

The sclerotized nature of the dorsal wall of the pouch of the genital chamber in many Pachycorinae is probably to prevent rupture of the chamber during copulation. The conjunctival appendages of the aedeagus press against the wall during copulation. The function of the other sclerotizations at the opening of the spermatheca is unknown.

CANOPIDAE

Species examined: *Canopus impressus* (F.).

Similar to *Sehirinae* with rami distinct and well sclerotized; gonocoxae and paratergites of similar shape; paratergites VIII not continuous posteriorly.

A special feature of the Canopidae is the possession of rectal sacs.

TESSAROTOMIDAE

Previous descriptions: Leston, 1953a; Yang, 1935.

Species examined: *Eusthenes robustus* Lap., *Phloea corticata* Drury, *Piezosternum calidum* F.

Paratergites VIII and IX about same size in *Piezosternum*, paratergites IX the larger in *Eusthenes*; paratergites VIII the larger in *Phloea* and partially fused to sternum VII which is cleft; rami sclerotized and interlocking; gonapophyses flap-like, but not membranous in *Phloea*; rami and gonapophyses membranous in *Piezosternum*; ring sclerites present in *Piezosternum*; second gonocoxae rather membranous and more or less inseparable from inter-gonocoxal membrane in *Phloea*; gonoplaes absent.

ACANTHOSOMIDAE

Previous description: Rosenkranz, 1939.

Species examined: *Acanthosoma haemorrhoidale* (L.) (fig. 8), *Elasmostethus interstinctus* (L.).

Paratergites VIII and IX contiguous posteriorly; former larger than latter; second gonocoxae contiguous posteriorly; anterior strut of gonangulum very short and broad; both pairs of rami sclerotized and interlocking; rami bearing membranous flaps—flap on first ramus of one side being opposed by flap on second ramus of same side, thus forming an incomplete sac; gonoplaes absent.

DINIDORIDAE

Previous description: Yang, 1940.

Species examined: *Coridius* (= *Aspongopus*) *janus* (F.).

Paratergites IX larger than paratergites VIII and contiguous posteriorly; broad sclerotized rami present and gonapophyses partially sclerotized; second gonocoxae continuous posteriorly; anterior strut of gonangulum weakly sclerotized; cup-shaped sclerotization present in wall of genital chamber near opening of spermathecal duct; gonoplaes absent.

EUMENOTIDAE

Previous description: Esaki, 1930.

Species examined: *Eumenotes obscura* Westw.

Paratergites as in Dinidoridae; general shape of female genitalia like those in *Megymenum*; rami and gonapophyses partially sclerotized; second gonocoxae apparently completely membranous, rami thus not firmly fused to a dorsal sclerite; first ramus free from short and broad anterior strut of gonangulum; ring sclerites and gonoplacs absent; genital chamber without sclerotizations.

PENTATOMIDAE

Previous descriptions¹: Bonnemaison, 1952; Trukhanov, 1947; Jeannel, 1920; Vodjdani, 1954; Leston, 1955a, 1956b; Lacaze-Duthiers, 1853; Santoro, 1954; Dupuis, 1951; Puchkova, 1958.

Species examined: *Acoloba lanceolatum* (F.), *Palomena prasina* (L.), *Pentatoma rufipes* (L.), *Picromerus bidens* (L.), *Podops inuncta* (F.), *Stollia fabricii* Kirk.

Paratergites VIII continuous above anus in *Podops*, *Acoloba*, *Picromerus* and *Stollia*; rami and anterior strut of gonangulum membranous or absent; gonapophyses membranous in most cases; first gonapophyses often rather large and joined together by a large triangular shaped membrane—the triangulum of Verhoeff (1893); antero-ventral corner of first gonocoxa produced forwards; retractor muscle of first gonapophysis and retractor muscle of second gonapophysis absent; goblet-like sclerotized structures often attached to wall of genital chamber; gonoplacs absent.

The female genitalia of the Pentatomidae are very constant and are always without sclerotized rami. The first gonapophyses are joined by the triangulum and both retractor muscles of the gonapophyses are absent, this being associated with the loss of the anterior strut of the gonangulum and the rami. Pendergrast (1957) has shown that the spermatheca of this family is constant and characteristic and I have confirmed this.

Leston (1956b) has described an exerted ovipositor in this family, in *Birket-smithia*; he states that the exerted valves are not homologous with the exerted valves of the Lygaeid-type of ovipositor, but are modified gonocoxae.

The female genitalia of this superfamily may be considered as the plate-shaped type (see Dupuis, 1955), with a directly posterior or postero-ventral aspect; members of this group usually oviposit on the surface of leaves, trunks, etc. The paratergites are very large and together with the first gonocoxae are the most conspicuous parts of the terminalia. The gonapophyses are small and usually membranous and flap-like. In most families the rami are sclerotized, gently curved and interlocking. Ring sclerites may be present. The first gonocoxa is not fused to paratergite VIII and gonoplacs are absent. Paratergites VIII and IX and the second gonocoxae meet in the mid-line posteriorly. Paratergites VIII, when fusing, form a broad sclerite dorsal to the anus. The second gonocoxae, when fusing, form a narrow bridge-like sclerite immediately

¹ Additional references to this and other families may be found in the following paper, received since the completion of this manuscript:

Štys, P., 1958, A guide to the literature on the female ectodermal genitalia of Heteroptera. *Acta Musei Reginaehradecensis S.A.L.* 1958: 45-64.

beneath the anus and sternum X; even when not fusing, they appear as a bridge-like sclerite and characterise the genitalia of the Pentatomoidea.

There is a tendency for the development of additional sclerotizations in the wall of the genital chamber, especially around the opening of the spermathecal duct and at the attachment of the posterior dilator muscle of the genital chamber. Other special structures associated with the transmission of symbionts may be present.

The musculature in the group is rather constant and characteristically all species seem to be without the retractor muscle of the first gonapophyses. In species without sclerotized rami, the retractor muscle of the second gonapophysis is also absent (fig. 99).

There is nothing in the morphology of the female genitalia to support or disprove the division of the superfamily into two groups, as suggested by Leston (1956c, 1958). Several families by the presence of ring sclerites and/or the retention of sclerotized and interlocking rami, can probably be regarded as the least specialised. The female genitalia of the Pentatomidae, by their reduced nature, suggest that this family is the most highly evolved in the taxon. This is supported by the constant and specialised structure of the spermatheca (Pendergrast, 1957).

Leston (1955a, 1956a, 1956b) has misinterpreted the second gonocoxa in his accounts of the female genitalia of the Pentatomoidea, but applies a consistent nomenclature in the group. What he calls the second gonocoxa (= second valvifer) is paratergite IX. His "ventral sclerites of segment 9" (Leston, 1956a) are the fused second gonocoxae, as is the median bridge-like piece he figures (Leston, 1955a) in *Piezodorus lituratus* (F.) beneath sternum X.

There is general agreement that this is a natural group, but at the family and subfamily level, however, this is not so. The families recognised in this study follow Leston (*unpublished*). Only in the Pentatomidae do the female genitalia provide a set of useful delimiting characters.

PYRRHOCOROIDEA

PYRRHOCORIDAE

Previous descriptions: Gupta, 1951; Ludwig, 1926; Mayer, 1875; Seidel, 1924; Pruthi, 1924.

Species examined: *Dysdercus cingulatus* (F.), *D. fasciatus* Sign. (figs. 28, 29), *Pyrrhocoris apterus* (L.).

Paratergites VIII small, triangular, well separated from each other and not fused to first gonocoxae; paratergites IX large, almost contiguous posteriorly; first gonocoxae rather rounded in outline with an antero-dorsal apodeme; first gonapophyses membranous and flap-like and ventrally united by membrane; rami short, sclerotized, slightly curved and interlocking; anterior strut of gonangulum slender; second gonocoxae broad and flattened, curved round posteriorly, apically turned ventrally and fusing in mid-line, forming an M-shaped structure; second gonocoxae partially fused to paratergites IX along ventral edge of latter; second gonapophyses membranous, flap-like and partially fused to inter-gonocoxal membrane; gonoplares absent; median spermatheca present; genital chamber large and with a dorso-posterior pouch.

The musculature of *D. fasciatus* has been investigated and is shown in figure 100. All muscles appear to be present.

The female genitalia of this superfamily are of the plate-shaped type and rather similar to those of the Pentatomoidea. There is a median spermatheca, but gonoplacs are absent. The shape and complete fusion of the second gonocoxae, together with the presence of the retractor muscle of the first gonapophysis, precludes the inclusion of the Pyrrhocoridae in the Pentatomoidea. Since they have not the lacinate type of ovipositor, the Pyrrhocoroidea cannot be included in the Lygaeoid-Coreoid complex; the ovipositor is not of the true lacinate type as stated by Leston (1955b). All three pairs of ovipositor valves are not present as stated by Gupta (1951), who calls the gonocoxae the basivalvulae, and the gonangulum the valvifer.

Since the ovipositor of the Largidae is unlike that of the Pyrrhocoridae, but like that of the Lygaeidae, family status for the Largidae, first proposed by China (1954), has been accepted and the family treated in the Lygaeoidea, thus leaving the Pyrrhocoridae as the only family in the superfamily. The present work supports Southwood (1956a) in the erection of a superfamily. Southwood also included Largidae, but stated that more information was required on this family before its taxonomic position could be fully ascertained.

COREOIDEA

COREIDAE

Previous descriptions: Brown, 1955; Snodgrass, 1933; Tower, 1913.

Species examined: *Coreus marginatus* (L.) (figs. 9, 10), *Leptoglossus occidentalis* Heid.

Sternum VII cleft, but not to base; paratergites IX rather large and rounded and almost contiguous posteriorly; paratergites VIII triangular, small and separate from first gonocoxae; first gonocoxae large and rounded with anterior apodeme in middle of anterior edge; first gonapophyses rather elongate and sclerotized and with short, obliquely angled, sclerotized rami; anterior strut of gonangulum short, flattened and with a distinctly projecting apodeme anteriorly; second gonocoxae broad, rather flat and freely pivoting on ventral end of posterior strut of gonangulum, which is fused to paratergite IX; second ramus sclerotized and interlocking with first; second gonapophysis slender proximally, but apically expanded where it forms an incomplete cylindrical structure and in *Coreus* is joined to its opposite number; small sclerites at base of and attached to second gonocoxae; ring sclerites present; gonoplacs absent; median functional spermatheca present; a small spherical sac attaches to membrane between first gonapophysis and first gonocoxa in *Coreus*.

COLOBATHRISTIDAE

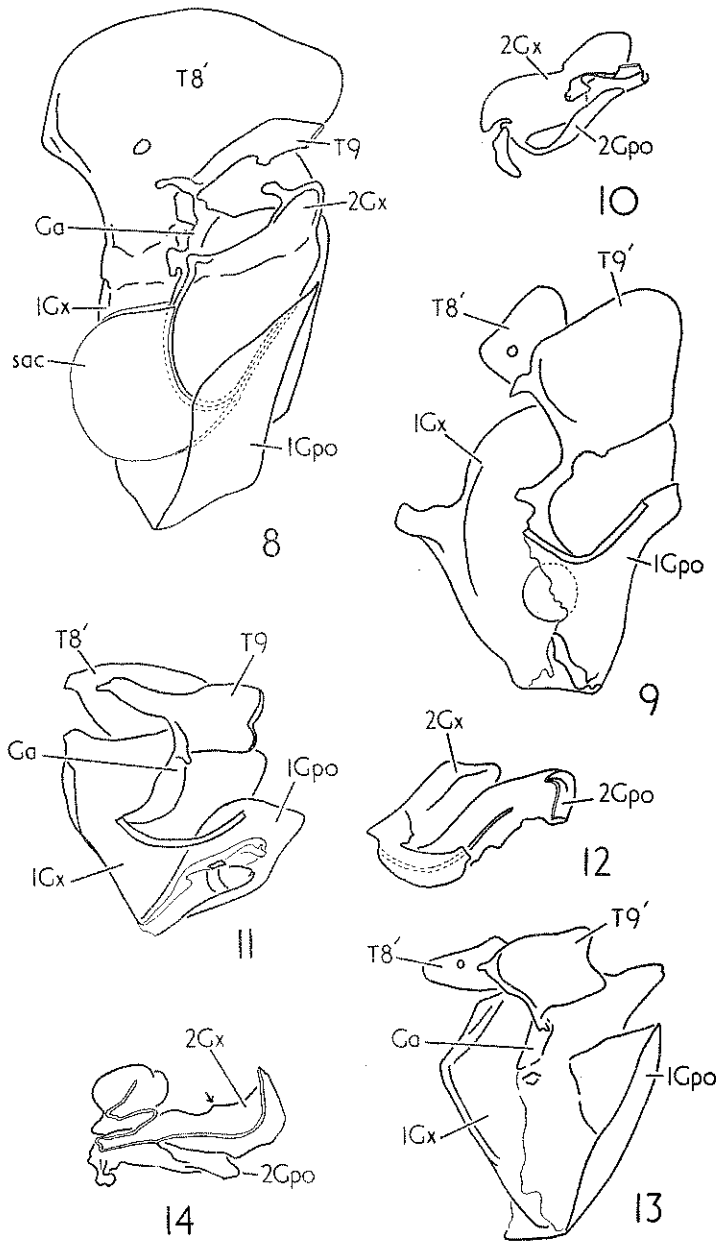
Species examined: *Phaenacantha* sp. (figs. 19, 20).

Very similar to general structure in *Coreus*; first gonocoxa without distinct anterior projecting apodeme; first gonapophyses short antero-posteriorly, but broad dorso-ventrally; rami sclerotized, but rather short; second gonocoxa and gonapophysis as in *Coreus*, but both structures joined to their opposite number; gonoplacs absent; without sclerotized expansions supporting genital chamber.

RHOPALIDAE

Previous description: Woolley, 1949.

Species examined: *Myrmus miriformis* (Fall.), *Rhopalus subrufus* (Gmel.)



Figs. 8-14.—(8) *Acanthosoma haemorrhoidale* (L.) (Acanthosomidae): inner view of right half of female genitalia; (9)-(10) *Coreus marginatus* (L.) (Coreidae): (9) first (10) second gonocoxa and associated parts; (11)-(12) *Rhopalus subrufus* (Gmel.) (Rhopalidae): (11) first (12) second gonocoxa and associated parts; (13)-(14) *Alydus calcaratus* (L.) (Alydidae): (13) first (14) second gonocoxa and associated parts.

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(figs. 11, 12), *Stictopleurus crassicornis* (L.), *Harmostes reflexulus* (Say), *Leptocoris trivittatus* (Say).

Genitalia usually withdrawn well into and obscured by sternum VII, which is not cleft; apodeme at dorsal angle of gonangulum very large and produced anteriorly; rami sclerotized, obliquely angled and interlocking; first rather rounded, but sclerotized and joined ventrally by membrane, variously folded and carrying characteristically a U-shaped sclerite; second gonocoxae rather short, broad, sclerotized and not meeting in mid-line posteriorly; second gonapophyses broad, sclerotized, carrying rami on outer face and joined apically and to second gonocoxae dorsally; gonoplacs absent; median spermatheca present; wide sclerotized expansions present at base of second gonocoxae.

The musculature of *Rhopalus subrufus* and of *Myrmus miriformis* has been examined. The retractor muscle of the first gonapophysis is present and the posterior dilator muscle of the genital chamber appears to have split into two.

In *Stictopleurus* and *Harmostes* the genitalia, instead of being rather flattened as in *Rhopalus* and *Myrmus*, are rather elongate dorso-ventrally. The terminal view of the abdomen (posterior margin of segment VII) is triangular in *Stictopleurus* and *Harmostes* and semicircular in the other genera mentioned. This accounts for the difference in shape of the female genitalia.

ALYDIDAE

Species examined: *Alydus calcaratus* (L.) (figs. 13, 14), *A. pluto* Uhler, *Megalotomus 5-spinosus* (Say), *Tollius curtulus* (Stål).

Paratergite VIII small, triangular and free from first gonocoxa; paratergite IX large and quadrate; first gonocoxa produced posteriorly; first gonapophysis with exposed part sclerotized, but rest of this elongate structure only partially so; first ramus absent; anterior strut of gonangulum represented by a faint trace of sclerotization; second gonocoxae broad, sclerotized, boat-shaped and fused posteriorly; second gonapophyses sclerotized, shorter than and fused to second gonocoxae; second ramus and gonoplacs absent; sclerotized expansions at base of second gonocoxae fusing in mid-line to form a complete and complicated support to genital chamber; median spermatheca present.

The genitalia in the Coreoidea have usually a posterior aspect and are of the plate-shaped type in *Rhopalus* and *Myrmus*, but other genera studied appear somewhat closer to the laciniate type. The first gonocoxa is not fused to paratergite VIII and gonoplacs are absent. The second gonocoxae, if fusing in the mid-line posteriorly, do not form a median narrow bridge-like sclerite as in the Pentatomoidea, nor an M-shaped sclerite as in the Pyrrhocoroidea. Sclerotized and interlocking rami are usually present, except in the Alydidae. Ring sclerites may be present.

The retractor muscle of the first gonapophysis is present, at least in species with sclerotized rami and anterior strut of the gonangulum present. This is not the case in Pentatomoidea. There is a tendency for the development of sclerotized expansions at the base of the second gonocoxae; these support the genital chamber and are most complicated in the Alydidae.

The study of the female genitalia supports the conclusion of Reuter (1912) that the Rhopalidae and the Alydidae should be of family rank. The Coreoidea are the more primitive in retaining ring sclerites, in having the second gonocoxae free from each other and in having elongate gonapophyses and only small

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sclerotizations supporting the genital chamber. The Alydidae appear to be the most specialised as they have lost the rami, have the second gonocoxae fused with each other and with the second gonapophyses and have very complicated sclerotized expansions supporting the genital chamber. The Rhopalidae, by possessing the U-shaped sclerite between the first gonapophyses, are very distinct. This family also has the posterior dilator muscle of the genital chamber divided into two, but this may also be so in the other families of the Coreoidea. Southwood (1956a) finds, on egg structure, the Rhopalidae to be more specialised than the Alydidae.

If the two superfamilies, Lygaeoidea and Coreoidea, are kept separate, the Colobathristidae appear more correctly placed in the latter on the character of the female genitalia. Pendergrast (1957) was unable to associate the Colobathristidae with other families on the characters of the spermatheca. Southwood (1956a) states that the egg is quite different from that in the Lygaeidae.

LYGAEOIDEA

LYGAEIDAE

Previous descriptions: Bonhag and Wick, 1953; Ekblom, 1926; Ludwig, 1926; Scudder, 1957g.

Species examined: this family has been investigated more completely than any other in order to examine the structural stability of the female genitalia within a single family. In all about 320 species, comprising 247 genera have been examined. *Gastrodes grossipes* (Deg.) (Rhyparochrominae) is figured (figs. 21, 22).

Sternum VII usually cleft to base; paratergite VIII triangular and separate from first gonocoxa; all parts of ovipositor complex, usually sclerotized (save gonapophyses in Lygaeinae); first gonocoxa more or less triangular in shape, to which elongate, lacinate first gonapophyses attach ventrally; first and second rami long, rod-like, acutely angled and interlocking; first and second gonapophyses usually united longitudinally, the former almost always in basal two-thirds only; anterior strut of gonangulum rather broad and flattened; second gonocoxa crescentic in shape, slightly flattened, free posteriorly and articulating with ventral end of posterior strut of gonangulum at its mid-point; second gonapophyses sclerotized and lacinate; median spermatheca present; ring sclerites often present; sclerotizations in wall of genital chamber otherwise usually absent; gonopods absent.

The musculature of *Oncopeltus fasciatus* (Dall.), *Ischnodemus sabuleti* (Fall.), *Scolopostethus thomsoni* Reut. and *Gastrodes grossipes* has been examined and found to be the same as that in *Dicranocephalus* (Scudder, 1957a).

Within the Lygaeidae the structure of the female genitalia is remarkably constant, differing in very few genera. In the Pachygronthinae, Oxycareninae and Heterogastrinae (in part) and to a lesser extent in the Cyminae, the first gonocoxae are conspicuously elongate dorso-ventrally and appear to extend half way along the abdomen ventrally. The Oxycareninae are distinct in having the abdomen conspicuously truncate posteriorly.

In *Harmostica ornata* (Dist.) (Rhyparochrominae: Stygnocorini) the female genitalia are atypical and the ovipositor is not long and lacinate. Instead it is short and the second gonapophyses are very broad.

In *Bubaces castaneus* Dist. (Rhyparochrominae: Lethaeini) there is an additional hook-like sclerotized projection to the inside of the second gonocoxae.

The female genitalia of the Lygaeinae are distinct. There is a reduction of the sclerotization of the gonapophyses with the formation of isolated sclerites and broadening and folding of the membranous parts of the gonapophyses. This is adequately illustrated by Bonhag and Wick (1953).

In Malcinae a short laciniated ovipositor is present. The anterior strut of the gonangulum is parallel to the gonapophyses and paratergite IX therefore appears more posterior than usual. The second gonocoxa is a rather large quadrate structure and ring sclerites are present.

The female genitalia of this group are distinct in shape and structure, as described above. Although the elongation in the Pachygronthinae, Oxycareninae and Heterogastrinae may indicate a close affinity of these three subfamilies, supported by the position of dorsal abdominal gland openings and abdominal spiracles, the lack of such elongation in some genera (e.g. *Masoas* (Heterogastrinae)) introduces the need for caution in this grouping. The truncate terminalia in Oxycareninae characterises this group and isolates them from other subfamilies. The structure in Lygaeinae suggests that this subfamily should be placed apart from the rest. That the Lygaeinae are distinct has been shown by Nuorteva (1956) in their salivary gland structure, and Manna (1951) has pointed out that they are unique in their loss of the m-chromosomes, characteristic of all other Lygaeoidea (and Coreoidea). The Orsillinae have the typical Lygaeid type of genitalia and do not have the gonapophyses modified as in the Lygaeinae. I consider that the former should be moved from the Lygaeinae and placed as a separate subfamily. Ashlock (1957), from a study of the male genitalia, has also concluded that the Lygaeini and Orsillini are not at all closely related.

Pendergrast (1957), in stating that "The spermatheca of the Lygaeidae are extremely diverse and it has proved quite impossible to list spermathecal characters for the group", and further, "there is a bewildering diversity in its form even amongst members of the same subfamily", was in fact demonstrating the unworkable nature of the then accepted supra-generic grouping in Lygaeidae. The present study, by abandoning some of the traditional supra-generic divisions, shows, in fact, that the spermatheca can provide valuable taxonomic characters in this family.

I have examined representatives of the majority of the world genera of the Lygaeidae and have been able to establish the value of the spermatheca in most subfamilies. It is of use at different taxonomic levels in the different subfamilies. All members of the Oxycareninae examined have a similar type of spermatheca; this may indicate that it provides a good subfamily character in this group. In the Heterogastrinae various generic types are found and in *Dinomachus* it is a good specific character (Scudder, 1957c). In the Orsillinae and Ischnorhynchinae, good generic characters are seen. Perhaps the most interesting use of the spermatheca has been in the tribal classification of the Rhyparochrominae (Scudder, 1957d). Here tribes suggested by the position of spiracles, trichobothria and in part by chromosome number, were clearly delimited on spermathecal structure, especially in the Rhyparochromini. The independent work of Ashlock (1957) on the aedeagus in general also supports the classification based on the above characters. In the Rhyparochromini,

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the spermatheca cannot satisfactorily be used below the tribal level, but in the other tribes of the Rhyparochrominae, good generic characters are evident.

STENOCEPHALIDAE

Previous description: Scudder, 1957a.

Species examined: *Dicranocephalus agilis* (Scop.), *D. albipes* (F.), *D. insularis* (Dallas), *D. lauticeps* (Stal), *D. lateralis* Sign., *D. marginatus* (Ferrari), *D. medius* (Muls. & Rey), *D. punctipes* (Stål), *D. testaceus* (Stål), *D. tunetanus* Horv., *D. pallidus* Sign., *Psotilnus mucronifer* Stål.

Identical in structure with the female genitalia of Lygaeidae.

LARGIDAE

Species examined: *Largus cinctus* H.-S., *Lohita grandis* (Gray).

Identical in structure with Lygaeidae, but having the gonapophyses more sclerotised, especially the second pair.

The ovipositor is of the lacinate type and not the plate-shape type as stated by Southwood (1956a).

BERYTINIDAE

Species examined: *Berytinus minor* (H.-S.), *B. clavipes* (F.), *Gampsocoris punctipes* (Germ.), *Metatropis rufescens* (H.-S.) (figs. 15, 16).

The female genitalia are almost identical in structure with those of the Lygaeid subfamily Malcinae, but have the second gonocoxae crescentic instead of quadrate in shape.

PIESMIDAE

Previous description: Wille, 1929; Drake and Davis, 1958.

Species examined: *Piesma maculata* (Castel.) (figs. 17, 18).

Sternum VII cleft to base; paratergite IX and first gonocoxa about same size, with paratergite VIII smaller; otherwise very similar to Lygaeidae, with gonapophyses shorter and broader, but nevertheless lacinate.

The female genitalia of the Lygaeoidea have a ventral aspect and the superfamily may be said to have a lacinate type of ovipositor, without gonoplaes and with paratergite VIII not fused to the first gonocoxa. A median spermatheca is present and ring sclerites may also occur.

The genitalia of most Lygaeidae, Largidae and Stenocephalidae are almost indistinguishable. The Malcinae (Lygaeidae) and Berytinidae seem to be related on the structure of the female terminalia. The Piesmidae are very similar to the Lygaeidae on the one hand and to the Berytinidae on the other; they undoubtedly belong in the Lygaeoidea and not in the Tingoidea, as believed until comparatively recently. The general shape of the sclerites visible externally (paratergites VIII and IX and first gonocoxae) in the Berytinidae and Malcinae is very similar to that seen in families possessing the plate-shape type of ovipositor.

Manna (1951) pointed out that the Lygaeoidea and Coreoidea were unique in the Heteroptera in possessing a pair of m-chromosomes. The Lygaeoidea generally have a low chromosome number and an XY sex-determining mechanism, whilst the Coreoidea have a higher chromosome number and an XO sex-determining mechanism. These appear to be fairly reliable characters. The Stenocephalidae were placed close to the Lygaeidae (Scudder, 1957a) on morphological grounds and a recent investigation of the cytology of *Dieranocephalus agilis* (Scop.) (Lewis & Scudder, 1958) shows it to have a diploid chromosome number of $12A + X + Y$, a Lygaeoid complement and sex-determining mechanism.

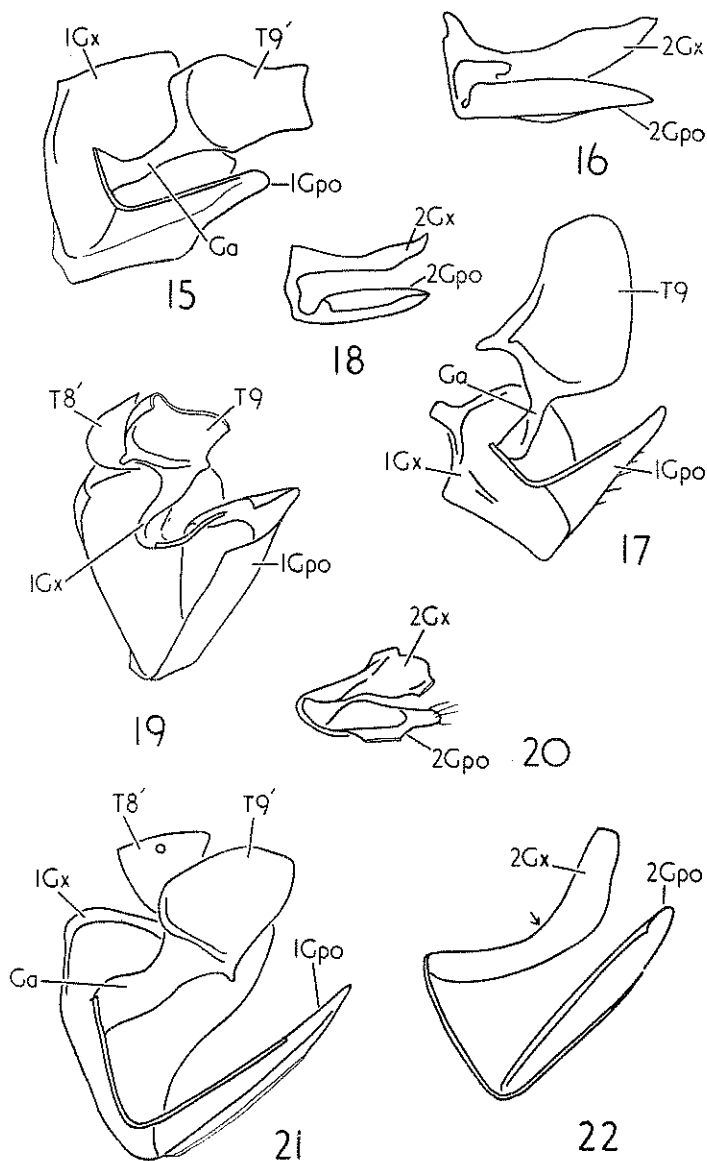
Pruthi (1925) stated that the male genitalia of the Lygaeidae can be distinguished by the total absence of conjunctival appendages. Ashlock (1957) states that conjunctival appendages in the Lygaeidae, if present, are in the form of relatively small inflatable lobes or, as in some Myodochina, in the form of spines borne on the conjunctiva or on inflatable lobes. The Lygaeidae (except the Heterogastrinae and Pachygronthinae) have the terminal part of the vesica, that part called by Ashlock "the gonoporal process of the vesica", long, flagellum-like with the sclerotized ejaculatory duct within. No such vesica has yet been demonstrated in the Coreoidea. Elsewhere, I have shown (Scudder, 1957a) that the Stenocephalidae possess the long, flagellum-like vesica together with conjunctival appendages. The Coreoidea are characterised by having conjunctival appendages. Pruthi (1925) stated that the Berytinidae were without any distinct conjunctival appendages and have a flagellum-like vesica. He based his conclusions on *Berytinus minor* and *Hubertiella cardamoni*. I have erected and examined the aedeagus of *Berytinus minor*, *B. clavipes*, *Gampsocoris punctipes* and *Metatropis rufescens* and find that the conjunctiva has a pair of small, rounded and partially sclerotized lateral appendages, what Pruthi called "insignificant thick patches in the lateral region". Also the vesica has long finger-like appendages and the gonoporal process of the vesica is flagellum-like.

The Largidae are said to be without conjunctival appendages and with a flagellum-like vesica (Pruthi, 1925), but *Lohita grandis* has two acicular conjunctival appendages. It thus appears that the Lygaeidae only; and not the Lygaeoidea as a whole, lack conjunctival appendages, and even in this family, conjunctival lobes and spines may be present.

From this it can be seen that the male genitalia of the Coreoidea and Lygaeoidea are not distinct. There is a gradual loss of conjunctival appendages as one passes successively through the families Stenocephalidae, Largidae, Berytinidae, Lygaeidae to the Piesmididae, where they are completely absent, except in *Miespa* (Drake and Davis (1958).)

Pendergrast (1957) has shown that the Coreoidea are characterised by the absence of a proximal spermathecal pump flange. In the Lygaeidae a proximal flange is usually present. In the Berytinidae it is absent or poorly developed, but in the Colobathristidae, Largidae and Stenocephalidae it is present.

The division between the Coreoidea and Lygaeoidea suggested by the nature of the principal salivary gland (Southwood, 1956b), does not coincide with the division obtained when other characters are considered. Whilst the Piesmididae and Lygaeidae (except Lygaeinae) have three lobes to the principal salivary



FIGS. 15-22.—(15)–(16) *Metatropis rufescens* (H.-S.) (Berytinidae): (15) first (16) second gonocoxa and associated parts; (17)–(18) *Piesma maculata* (Castel.) (Piesmidae): (17) first (18) second gonocoxa and associated parts; (19)–(20) *Phaenacantha* sp. (Colobathristidae): (19) first (20) second gonocoxa and associated parts; (21)–(22) *Gastrodes grossipes* (Deg.) (Lygaeidae): (21) first (22) second gonocoxa and associated parts.

gland, the Coreidae, Rhopalidae, Alydidae and Stenocephalidae have four. The number of lobes in the Largidae is not known.

As mentioned earlier, the female genitalia of the Colobathristidae are similar to those of the Coreidae, but have some affinities with the Lygaeidae. Pruthi (1925), however, regarded the male genitalia as showing that hardly more than subfamily status in the Lygaeidae was warranted for this group.

The position of the trichobothria on the abdomen, perhaps the best morphological character for distinguishing the Coreoidea from the Lygaeoidea, is probably only of minor importance and not sufficient to justify separate status if other characters so warrant a single superfamily. At present the Lygaeoidea are characterised by possessing the abdominal trichobothria on sterna V, VI and VII in the outer thirds of the sterna, whilst the Coreoidea have the corresponding organs in the median thirds. The antennal insertion character, often stated to separate the Lygaeoidea and Coreoidea, does not hold good; it breaks down in the Ninini (Lygaeidae, Cyminae) (Scudder, 1957*b*). The membranar venation in the Coreoidea is stated to consist of numerous and anastomosing veins, whilst the Lygaeoidea is said to possess only a few veins. It should be noted that the Stenocephalidae have a large number of anastomosing veins (Scudder, 1957*a*).

The above facts suggest that there may only be one superfamily involved, with the Coreidae and Lygaeidae or the Piesmidae as the two extremes.

ARADOIDEA

DYSODIIDAE

Species examined: *Dysodius crenulatus* Stål (figs. 23, 24).

Sternum VII cleft almost to base; paratergite IX larger than paratergite VIII, first gonocoxa triangular in shape, closely associated with but not fused to paratergite VIII and bearing the lacinate and sclerotized first gonapophyses; rami long, sclerotized, acutely angled and interlocking; second gonocoxae crescentic in shape, free posteriorly and not particularly closely applied to paratergites IX; anterior strut of gonangulum slender; large apodeme conspicuous at dorsal corner of gonangulum; gonoplacs absent; median spermatheca present.

ARADIDAE

Previous descriptions: Leston, 1955*b*; Tamanini, 1950, 1955; Tropin, 1951.

Species examined: *Aradus cinnamomeus* (Panz.), *A. depressus* (F.) (figs. 25-27), *A. debilis* Uhl., *A. blaisdelli* van D.

Terminalia flattened; sternum VII partially cleft; paratergites VIII very large and projecting well beyond end of abdomen, and not fused with first gonocoxae; paratergites IX small, smaller than first gonocoxae; first gonapophyses elongate and sclerotized; anterior strut of gonangulum very slender; both pairs of rami sclerotized, rather obliquely angled and interlocking; second gonapophyses elongate, heavily sclerotized distally, with a dense covering of long, fine hairs and often apically bifid or trifid; second gonocoxae often joined dorsally in the mid-line posteriorly, partially sclerotized, rather elongate and closely associated with paratergites IX; gonoplacs absent; median spermatheca present; often M-shaped sclerite present at opening of spermathecal duct into genital chamber.

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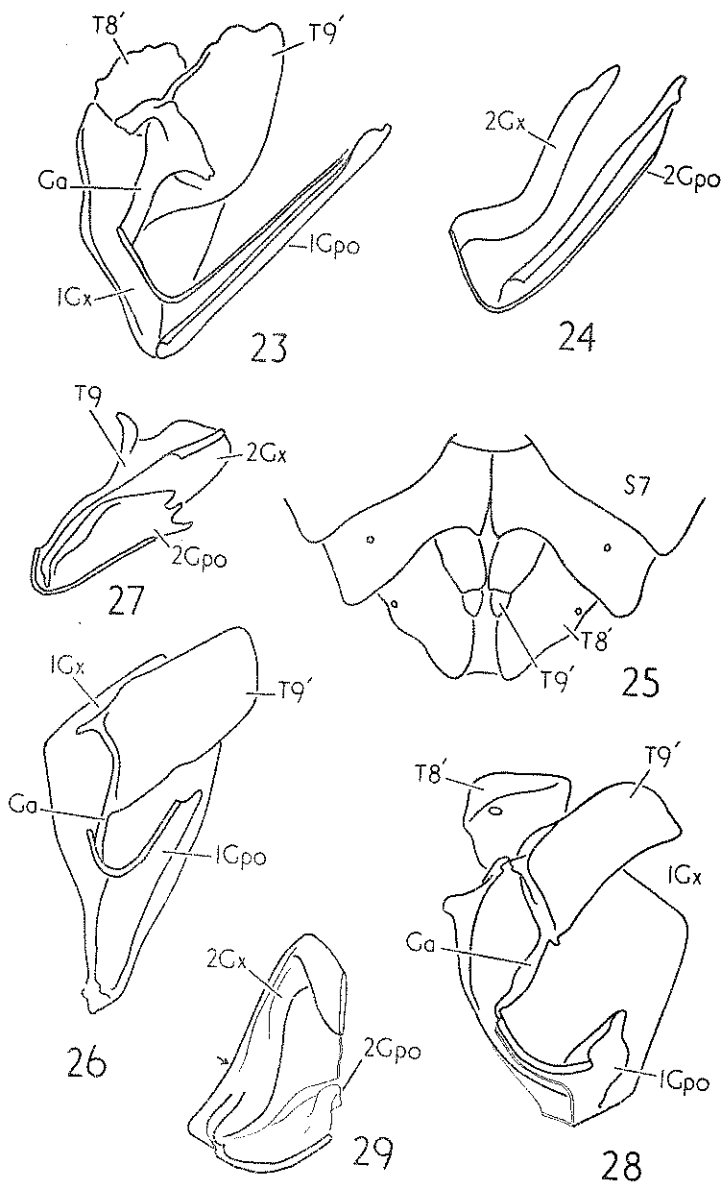
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Figs. 23-29.—(23)-(24) *Dysodius crenulatus* Stal (Dysodiidae): (23) first (24) second gonocoxa and associated parts; (25)-(27) *Aradus depressus* (F.) (Aradidae): (25) ventral view of female terminalia; (26) first (27) second gonocoxa and associated parts; (28)-(29) *Dysdercus fasciatus* Sign. (Pyrrhocoridae): (28) first (29) second gonocoxa and associated parts.

Dupuis (1955) states that the genitalia are of the plate-shaped type and Leston (1955b) states that the female genitalia of the Aradidae are of the same general type as in the Pentatomoidea and Coreoidea and he associated the Aradidae with these, especially with the latter. I find this relationship to be true in so far as the genitalia are flattened and externally resemble the plate-shaped type. Internally, however, the genitalia are closer to the lacinate type of ovipositor. The gonapophyses are sclerotized and the second pair are quite unlike the condition in the Coreoidea. Leston (1955b) has interpreted paratergite IX as the second gonocoxa. The sclerite he calls the "inter-valvifer sclerite" is the bridge connecting the dorsal part of the second gonocoxae.

CIMICOIDEA

NABIDAE

Previous descriptions: Ekblom, 1926; Kullenberg, 1947.

Species examined: *Nabis ferus* (L.) (figs. 30, 31), *N. limbatus* Dahl., *N. major* Costa, *N. rugosus* (L.), *N. rufusculus* Reut., *Pagasa fusca* (Stein).

Paratergite VIII small, triangular and ventrally joined to first gonocoxa; paratergite IX large and rounded; first gonocoxa large and triangular with dorso-anterior corner produced as a short flat apodeme; dorsally first gonocoxa fused with paratergite IX; first gonapophysis elongate, lacinate and sclerotized, with minute serrations apically on dorsal edge; first ramus sclerotized and on apical half of first gonapophysis runs on interior face, on basal half on dorsal edge; anterior strut of gonangulum sclerotized, broad and flat; second gonocoxa broad, flat and sclerotized with dorsal edge thickened; second ramus sclerotized and interlocking with first ramus, thus running on ventral edge of basal half of second gonapophysis and on outer face of apical half; second gonapophysis elongate and lacinate with coarse serrations on dorsal edge; gonoplaes firmly attached to apex of second gonocoxae, short with dorsal and ventral edges turned inwards forming incomplete boat-shaped structures; true median spermatheca absent; pseudospermathecae absent; genital chamber with pouched "seminal depository".

The musculature in *N. limbatus* is shown in figure 102.

The female genitalia of this family are of the lacinate type, eggs being deposited in plant tissue. The first gonocoxa in the Nabidae is fused to paratergite IX, but paratergite VIII is not completely fused to the first gonocoxa. The true median spermatheca and pseudospermathecae are absent, the sperm receiving function being taken over by the pouch of the genital chamber termed the seminal depository.

Carayon (1952a, 1952b, 1952c, 1952d, 1954, 1955) has described various modifications of the genital chamber associated with the phenomenon of haemocoelic fecundation practised in some Nabidae belonging to the subfamily Prostemminae. These modifications are mostly the development of accessory pouches and tissues associated with the genital chamber and the transmission of sperm.

The presence of longitudinal intersegmental muscles in the abdomen is indicative of a generalised structure.

VELOCIPEDIDAE

Species examined: *Scotomedes alienus* Dist.

The female genitalia of *Scotomedes* are almost identical with the structure in the Nabidae.

MIRIDAE

Previous descriptions: Davis, 1955; Knight, 1941; Kullenberg, 1946, 1947; Lacaze-Duthiers, 1853; Slater, 1950; Southwood, 1953; Wagner, 1952; Stichel, 1955.

Species examined: *Calocoris norvegicus* (Gmel.) (figs. 32, 33), *C. fulvomaculatus* (Deg.), *Lygus rugulipennis* Popp., *Liocoris tripustulatus* (F.), *Stenodema laevigatum* (L.), *Leptopterna dolabrata* (L.), *Monalocoris filicis* (L.), *Dicyphus stachydis* Reut., *Orthotylus ochrotrichus* Fieb., *Plagiognathus arbustorum* (F.).

Sternum VII in mid-line often produced as a small flap-like subgenital plate; paratergite VIII completely fused to first gonocoxa and individuality of sclerites completely lost; paratergites IX large and rounded posteriorly; first and second gonapophyses long, lacinate and sclerotized, occasionally with minute serrations; second gonapophyses often with a bulbous base; rami sclerotized and running along gonapophyses as in Nabidae; anterior strut of gonangulum slender and sclerotized; second gonocoxa long, broad and sclerotized, dorsal edge thickened and with two transverse thickened ridges, one at point of articulation with posterior strut of gonangulum, and other near base; gonoplac small, curved with dorso-internal angle produced anteriorly as an apodeme; genital chamber with various thickenings and sclerotizations including paired ring sclerites; genital chamber with ventral pouched "seminal depository"; median spermathecal gland (accessory gland) present.

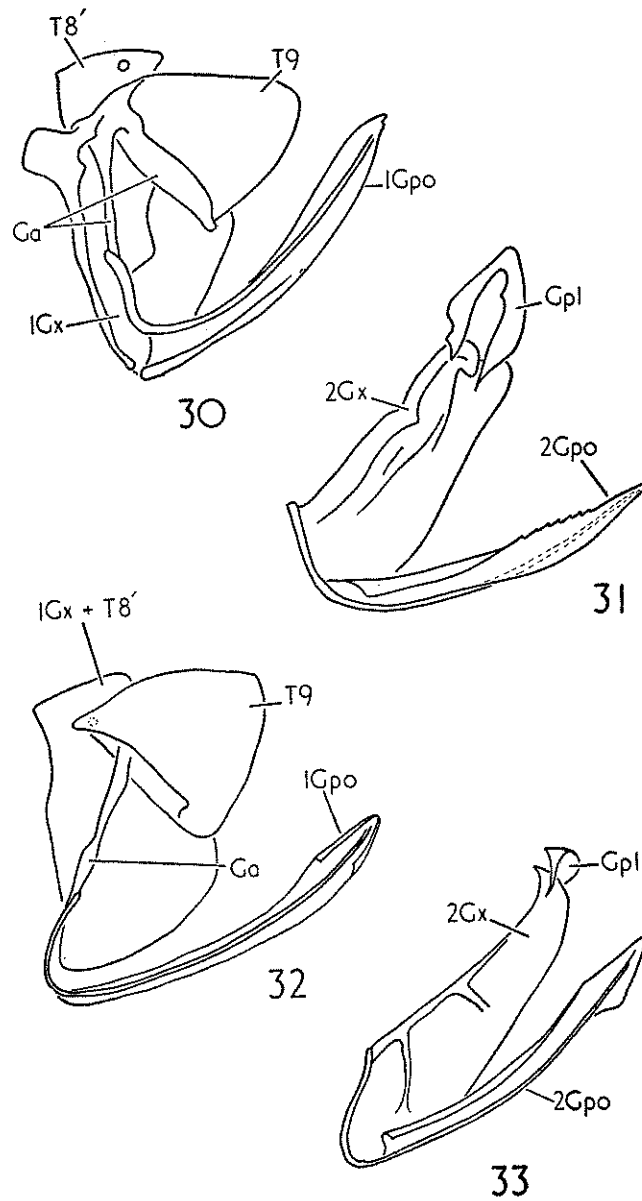
The musculature of *L. dolabrata* is shown in figure 103.

The female genitalia of the Miridae are similar to those of the Nabidae, but have the first gonocoxa and paratergite VIII completely fused, the first gonocoxa being free from paratergite IX. Also there is a median spermathecal gland and the second gonocoxa and genital chamber have different thickenings. The gonoplacs are also different.

As pointed out elsewhere (Scudder, 1956b), I do not agree with the interpretation of the first gonocoxa (= first valvifer) of Southwood (1953) and Davis (1955). The structure called the "eighth paratergum" by these authors, is the fused first gonocoxa and paratergite VIII. This interpretation is supported by the musculature.

The posterior strut of the gonangulum is called the "ramal plate" by Davis (1955). Davis considered the anterior strut of the gonangulum and the first ramus as one structure, an elongation of the processes from the base of the first gonapophyses, and did not agree with Kullenberg (1947) who thought that there were two parts involved. Kullenberg (1947) followed Snodgrass (1933) and considered that the ramus of the first gonapophysis extended anteriorly as the "fibula" and fused with an outgrowth of paratergite IX, the connecting piece or "verbindungstück". The thickened dorsal edge of the second gonocoxa, Davis (1955) called the valviferal apodeme. He further considered that the serrations of the gonapophyses probably reflected the oviposition habit of the various species. If this were true, species such as *Calocoris fulvomaculatus* ovipositing in woody tissue would be expected to have gonapophyses conspicuously more serrate than types ovipositing in softer tissue. Comparative studies suggest that this is not so.

The various thickenings and sclerotizations of the genital chamber have been described and illustrated by Davis (1955), and Slater (1950) has shown that these structures may be used as taxonomic characters and in demonstrating phylogenetic relationships. Slater and Davis (1952), Southwood (1953) and



FIGS. 30-33.—(30)–(31) *Nabis ferus* (L.) (Nabidae): (30) first (31) second gonocoxa and associated parts; (32)–(33) *Calocoris norvegicus* (Gmel.) (Miridae): (32) first (33) second gonocoxa and associated parts.

Kelton (1955*a, b, c*) have given further instances of their value in this field so they will not be considered further.

The spermathecal gland is homologous with the true median spermatheca seen in such families as the Lygaeidae, Pentatomidae, etc. The seminal depository of the Miridae may be homologous with that in the Nabidae, but cannot be regarded as homologous with the sac-like pseudospermathecae in the Tingidae.

There is apparently little range of structure in the female genitalia in the Miridae, excluding the genital chamber. There is nothing to support or at variance with the system of classification of the Miridae by Carvalho (1956), Leston (1957), etc.

ISOMETOPIDAE

Species examined: *Lindbergiola aureopilosa* Carv.

The female genitalia are almost identical with the structure in the Miridae, but the genital chamber is not as complicated and is apparently without a median spermathecal gland.

ANTHOCORIDAE

Previous descriptions: Carayon, 1952*e*, 1953*a*, 1953*b*; China and Myers, 1929; Gomez-Menor Guerrero, 1956.

Species examined: *Anthocoris confusus* Reut., *A. gallarum-ulmi* (Deg.), *A. nemorum* (L.) (figs. 34-36), *Lycocoris campestris* (F.).

Sternum VII very slightly produced posteriorly in mid-line; paratergite VIII triangular and free from first gonocoxa; paratergite IX rounded posteriorly, with a longitudinal split ventrally near second gonocoxa; paratergite IX partially fused to first gonocoxa; anterodorsal corner of first gonocoxa produced forwards as an apodeme; first gonapophysis long, lacinate, sclerotized and with serrations on dorsal edge of apical half; each first gonapophysis appears to be partially split longitudinally, the mesad parts being fused; rami sclerotized, extending along edges of gonapophyses and interlocking; anterior strut of gonangulum slender and sclerotized; second gonocoxa elongate, broad and sclerotized, with dorsal margin thickened; second gonapophysis long, lacinate and sclerotized, with both dorsal and ventral edge at extreme apex with minute serrations; gonoplae small and sclerotized, with mesad projecting apodeme; median spermatheca absent.

The female genitalia of the Anthocoridae are very similar to those of the Nabidae, differing especially in the split nature of the first gonapophyses and in rami running on the edges of the same.

An ovipositor is not always present in this family. China and Myers (1929) have shown that various stages in the reduction can be demonstrated in different species. In this family haemocoelic fecundation takes place (Carayon, 1953*a*, 1953*b*) and accessory structures may be developed (Carayon, 1952*e*).

MICROPHYSIDAE

Species examined: *Loricula elegantula* (Baer.).

Almost identical with Anthocoridae, but with the gonapophyses elongate, parallel-sided with rounded apices and without serrations; ring sclerites and gonoplae present; paratergite VIII fused to first gonocoxa; median spermatheca absent.

CIMICIDAE

Previous descriptions : Abraham, 1934 ; Berlese, 1898 ; Carayon, 1953c ; Christophers & Cragg, 1922 ; Cragg, 1920 ; Davis, 1956 ; Hase, 1918 ; Heymons, 1899 ; Landois, 1869 ; Mather, 1952 ; Mellanby, 1939 ; Murray, 1914 ; Ribaga, 1897 ; Rothschild, 1912.

Species examined : *Cimex lectularius* L. (figs. 37, 38).

Paratergites VIII and IX and first gonocoxa rather quadrate in shape and about same size ; paratergite VIII not completely fused to first gonocoxa ; first gonocoxa partially fused to paratergite IX ; first gonapophysis short, broad and flat, but pointed and not rounded and flap-like ; first ramus partially sclerotized ; anterior strut of gonangulum absent ; second gonocoxa almost completely fused to paratergite IX ; second gonapophysis very reduced, rather flap-like ; second ramus hardly recognisable and not interlocking with first ; gonoplaes not recognisable as such ; median spermatheca absent ; Ribaga's organ present.

Davis (1956) has reviewed the literature and work on the Cimicidae and has done much original work. The female genitalia in this family are very reduced, but traces of the ovipositor, probably a lacinate one, are present, although China (1955a) states that such a structure is absent. Dupuis (1955) states that the Cimicidae have the plate-shape type of ovipositor. The occurrence of haemocoelic fecundation in this family suggests a close affinity with the Anthocoridae. The presence of a Ribaga's organ in the Cimicidae may be compared with a similar, perhaps homologous, structure present in some Anthocoridae (Carayon, 1952e).

THAUMASTOCORIDAE

Previous description : Drake and Slater, 1957.

Species examined : *Baclozygum depressum* Bergr.

Female genitalia very reduced ; paratergite VIII large and sclerotized ; small sclerotizations ventro-posteriorly probably represent reduced first gonocoxae ; paratergites IX not separate from tergum IX ; all other parts of genitalia derived from genital segments apparently absent ; median spermatheca absent ; genital chamber large and sac-like with two ventral sclerotized pouches.

This family has been placed next to the Lygaeidae ; it is quite unlike this family morphologically. The ventral sclerotized pouches to the genital chamber may be pseudospermathecae. The loss of parts of the genitalia and absence of a true median spermatheca, together with the absence of abdominal trichobothria, indicate that the Thaumastocoridae should be placed close to the Cimicidae. This is in agreement with the findings of Kormilev (1955a) and Drake and Slater (1957).

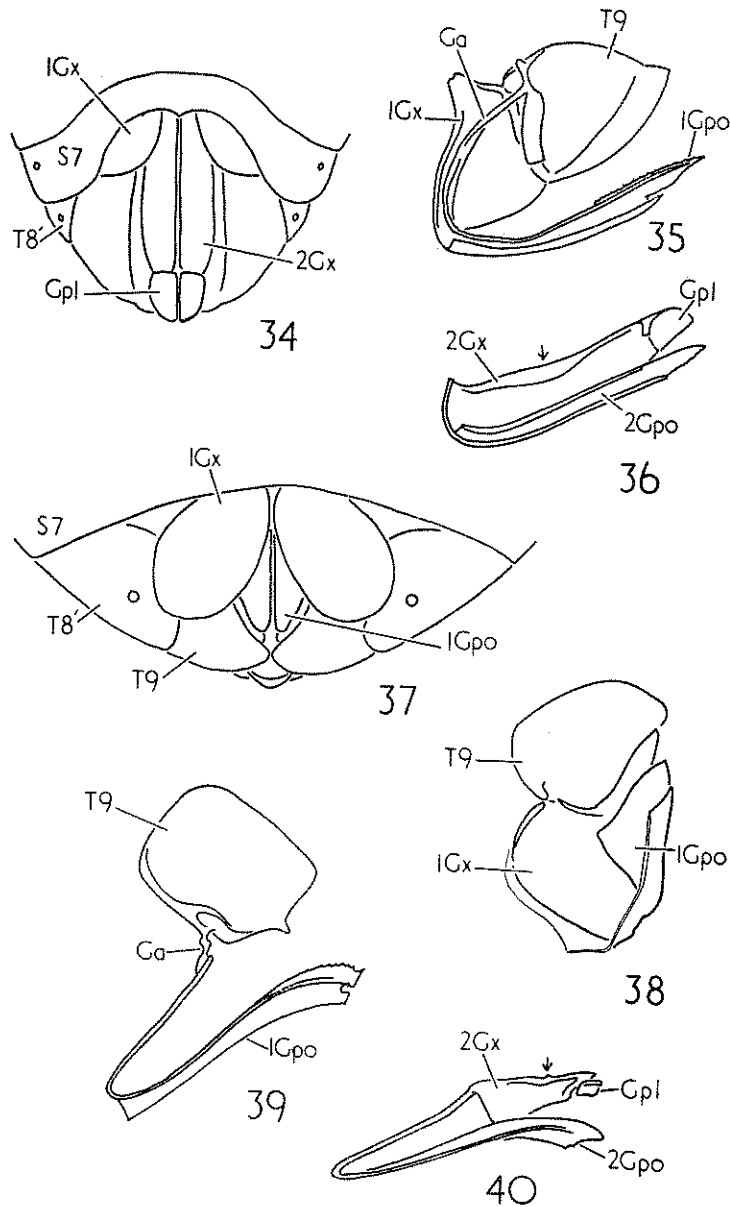
POLYCTENIDAE

Previous descriptions : Ferris and Usinger, 1939 ; Hagan, 1931 ; Jordan, 1912.

Species examined : *Hesperoctenes* sp.

First gonocoxae, only, distinguishable in the species examined ; median spermatheca absent.

Hagan (1931) found that a spermatheca was absent in this family. Pseudospermathecae are also apparently absent. What may be regarded as the analogue



Figs. 34-40.—(34)–(36) *Anthocoris nemorum* (L.) (Anthocoridae): (34) ventral view of female terminalia; (35) first (36) second gonocoxa and associated parts; (37)–(38) *Cimex lectularius* L. (Cimicidae): (37) ventral view of female terminalia; (38) first gonocoxa and associated parts; (39)–(40) *Ceratocombus coleoptratus* (Zett.) (Dipso-coridae): (39) first (40) second gonocoxa and associated parts.

of a Ribaga's organ has been demonstrated in one species (Ferris and Usinger, 1939). This family is probably closely related, therefore, to the Cimicidae.

The Cimicoidea have the genitalia visible ventrally and primitively have a lacinate type of ovipositor for oviposition in plant tissue (e.g. Nabidae, Miridae and some Anthocoridae). The ovipositor may be reduced in some families (Cimicidae, some Anthocoridae, Thaumastocoridae), this being associated with oviposition on the surface and not in tissue. The ecto-parasitic viviparous Polycytenidae have lost almost all trace of an ovipositor.

In types with a well developed ovipositor, gonoplacs are present and the first gonocoxa is more or less fused to paratergite VIII. Distinct sclerotized rami are also present. The sperm receiving and storage function of the median spermatheca has been lost and when the latter is present it serves as a secretory organ. Sperm is received and stored in other analogous accessory structures (pseudospermathecae). Haemocoelic fecundation occurs in several families (Nabidae, Anthocoridae, Cimicidae, Polycytenidae) with the modification and specialization of organs accordingly.

Carayon (1950*b*, etc.) and Pendergrast (1957) suggest that the Cimicoidea be redefined to include the Nabidae and Velocipedidae, together with the Cimicidae, Anthocoridae, Microphysidae, Miridae, Isometopidae and Polycytenidae. The present work strongly supports this grouping and also suggests the inclusion of the Thaumastocoridae, a family placed in this superfamily by Drake and Slater (1957).

The female genitalia of the Velocipedidae further support the opinion of Blöte (1945), followed by Leston, Pendergrast and Southwood (1954), that this is probably a subfamily of the Nabidae.

DIPSOCOROIDEA

DIPSOCORIDAE

Species examined: *Cryptostemma alienum* H.-S., *Ceratocombus coleoptratus* (Zett.).

Ceratocombus coleoptratus (figs. 39, 40): sternum VII large and produced posteriorly to cover terminalia; paratergite VIII incompletely separated from tergum VIII; paratergite IX not separate from tergum IX; first gonocoxa indistinct, probably represented by an area of sclerotization folded back on sternum VII internally; first gonapophyses partially split and mesad portions membranously joined, otherwise elongate and sclerotized and tips with minute serrations on dorsal edge; rami sclerotized and interlocking; second gonapophyses elongate, sclerotized and united except at extreme apex; second gonocoxa broad, flat and sclerotized; anterior strut of gonangulum slender and sclerotized, posterior strut fused to paratergite IX with ventral end projecting well below edge of paratergite, forming a conspicuous fulcrum for the second gonocoxa; gonoplacs small, flap-like and membranously united in midline; median spermatheca present.

Cryptostemma alienum: similar to *Ceratocombus coleoptratus* in general structure; paratergites VIII and IX not separate from respective terga; first gonocoxa almost completely membranous; gonapophyses much shorter and less sclerotized; gonoplacs fused to paratergites IX, appearing as ventral extensions of latter.

Saunders (1892) and Handlirsch (1908) placed the Dipsocoridae as a subfamily of the Cimicidae. Reuter (1912) erected a distinct series, the Trichotelocera, for this family and was followed by Oshanin (1916) and Pruthi (1925).

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Pruthi (1925) stated that there was no similarity between the male genitalia of the Dipsocoridae and Cimicidae, but that there was a partial resemblance to the Reduviidae. Leston, Pendergrast and Southwood (1954), however, stated that the Dipsocoroidea were probably allied to the Cimicomorpha, and Stichel (1955) has placed the family in this division, in the Cimicoidea. Pendergrast (1957) has shown the Dipsocoridae to possess a true median spermatheca which has little affinity with that of other forms.

On the shape and structure of the gonapophyses, together with the possession of a median spermatheca and gonoplacs, this superfamily appears to be related to the Saldidae. The modification of the first gonocoxae, which appear to have fused to form an invaginated plate attached to sternum VII posteriorly, and the small size of the gonoplacs, distinguish this superfamily.

REDUVIOIDEA

REDUVIIDAE

Dr. N. T. Davis of the University of Connecticut is at present studying the female genitalia and systematics of this group. I have studied *Rhodnius prolixus* Stål in some detail, and an account of this is presented together with a few observations on other species.

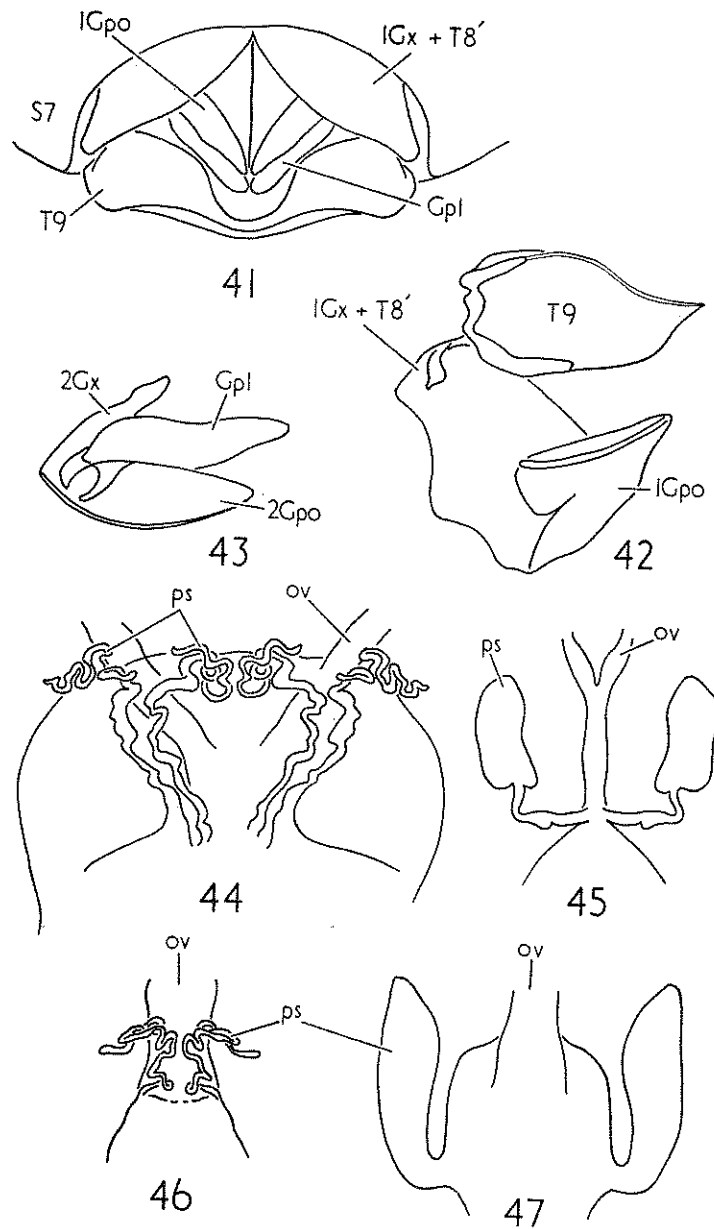
Previous descriptions: Davis, 1957; Galliard, 1935; Kershaw, 1909; Wigglesworth, 1948.

Species examined: *Rhodnius prolixus* Stål (figs. 41-43).

Posterior margin of sternum VII folded backwards and inwards and provided with muscles; first gonocoxa fused completely with paratergite VIII, the non-functional spiracle VIII being found at dorsal edge of the fused structure; paratergites IX large, rounded, not meeting in mid-line posteriorly and not separate from tergum IX; first gonapophysis short, triangular and almost completely membranous; rami sclerotized, short and interlocking; anterior strut of gonangulum membranous; second gonocoxa slender, sclerotized and articulating with ventral end of posterior strut of gonangulum, about third of way from distal end; second gonapophysis broad, flattened and antero-medially with mesad projection; second gonapophyses apically united and basally connected by continuation of inter-gonocoxal membrane; gonoplacs broad and very similar to fused second gonapophyses in shape, united except at extreme apex and completely free from second gonocoxae; genital chamber large and sac-like; median spermathecal gland present; a pair of lateral finger-like pseudospermathecae present; ring sclerites absent.

The musculature of the female genitalia of *R. prolixus* is shown in figure 101. A conspicuous feature is the divided anterior dilator muscle of the genital chamber.

An examination of other species from various subfamilies of the Reduviidae shows a great variation in the structure of the median spermathecal gland and pseudospermathecae. This was also noted by Pendergrast (1957). He stated, however, that all the species of Reduviidae examined, and those described by other workers, have two pseudospermathecae ("spermathecae"). I have found a species of *Petalochirus* from Uganda to possess four pseudospermathecae (fig. 44). The median spermathecal gland is not present in all Reduviidae, but in some it is said to be paired (Kershaw, 1909). The types of pseudospermathecae, some of which are illustrated in figures 44-47, show the range of structure in the various subfamilies and suggest that they could be of great value as taxonomic characters in this group.



FIGS. 41-47.—(41)-(43) *Rhodnius prolixus* Stål (Reduviidae): (41) ventral view of female terminalia; (42) first (43) second gonocoxa and associated parts; (44)-(47) pseudo-spermathecae of: (44) *Petalochirus* sp. (Reduviidae, Salyavatinae); (45) *Ischnobaena* sp. (Reduviidae, Emesinae); (46) *Ptilocnemus* sp. (Reduviidae, Holoptilinae); (47) *Glymmatophora* sp. (Reduviidae, Ectichodinae).

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PHYMATIDAE

Previous description : Davis, 1957.

Species examined : *Phymata erosa* (L.).

A central and two lateral sclerites only visible from exterior, central being terga VIII and IX and the lateral the fused paratergites VIII and first gonocoxae, which appear as semicircular structures ; first gonapophyses very reduced, very small, membranous and flap-like structures at base of first gonocoxae, and attached to broad ventral membrane connecting the two first gonocoxae ; paratergites IX not separated from tergum IX ; two partially sclerotized, joined structures attached to tergum IX probably represent the second gonapophyses ; second gonocoxae either fused to tergum IX or absent ; gonoplaes apparently absent ; genital chamber large and sacciform with a median spermathecal gland and paired lateral pseudospermathecae as in *Rhodnius*.

The female genitalia in the Reduivoidea are of the plate-shaped type, oviposition taking place on the surface of the substratum and not usually in plant tissue. The median spermatheca serves as a secretory gland only and it is known as the colleterial gland when present, its secretion serving as an adhesive to attach the eggs firmly to the substratum. Paired lateral pseudospermathecae are usually present and receive and store sperm. There is a fusion of paratergite VIII and the first gonocoxa, spiracle VIII becoming non-functional ; gonoplaes are usually present.

The paired lateral pseudospermathecae are reminiscent of the lateral pouches present in many other groups of insects (e.g. Collembola, *Grylotalpa*, Siphunculata, Megaloptera, etc. (Heberdey, 1931)). They may not be homologous throughout the Reduivoidea.

In the past there was considerable discussion regarding the families to be included in the Reduivoidea. The study of the female genitalia indicates that it should include only the Reduviidae and Phymatidae. Pendergrast (1957) has reviewed earlier groupings in this superfamily and has concluded that it should contain the Reduviidae and Phymatidae, with the Tingidae as a possible addition. The present work indicates that the Tingidae should be placed with the Vianaididae in a separate superfamily.

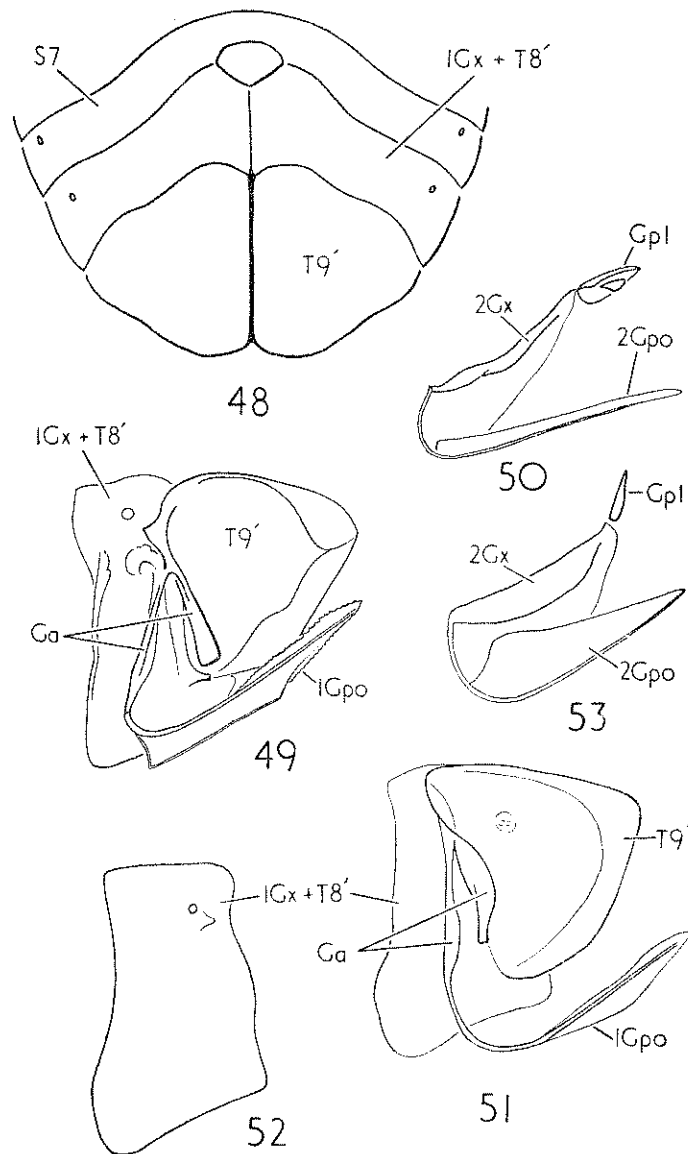
TINGOIDEA

TINGIDAE

Previous descriptions : Feldman and Bailey, 1952 ; Sharga, 1955.

Species examined : *Tingis reticulata* H.-S. (figs. 48-50), *T. cardui* (L.), *T. ampliata* (H.-S.), *Acalypta parvula* (Fall.), *Agramma laeta* (Fall.), *Corythuca padi* Drake.

Small triangular sclerite attached in mid-line to posterior margin of sternum VII and overlapping base of genitalia ; paratergites VIII fused to dorsal edge of first gonocoxae, but individuality of sclerites still recognisable ; paratergites IX large and conspicuous ; gonapophyses elongate, lacinate and sclerotized ; first gonapophyses united in basal part and terminally with serrate ridges ; second gonapophyses united but not ridged ; first gonocoxae postero-ventrally slightly produced ; second gonocoxae rather crescentic in shape and free from each other posteriorly ; gonoplaes present, each often composed of two separate sclerites ; gonangulum fused to paratergite IX at dorsal angle only, anterior strut long, slender and posterior strut free from paratergite IX, rather flat ; gonangulum



FIGS. 48-53.—(48)-(50) *Tingis reticulata* H.-S. (Tingidae): (48) ventral view of female terminalia; (49) first (50) second gonocoxa and associated parts; (51)-(53) *Anommatocoris minutissimus* China (Vianaididae): (51) first gonocoxa and associated parts; (52) fused first gonocoxa and paratergite VIII; (53) second gonocoxa and associated parts.

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at dorsal angle also fused to first gonocoxa and paratergite VIII, where the latter two sclerites fuse; rami sclerotized and interlocking; single ring sclerite present posteriorly in dorsal wall of genital chamber; true median spermatheca absent; paired sac-like pouches—pseudospermathecae—present anteriorly in genital chamber.

VIANAIDIDAE

Species examined: *Anommatocoris minutissimus* China (figs. 51-53), *Vianaida coleopterata* Korm.

Similar to Tingidae, but with genital chamber sacciform, large and without anterior sac-like pseudospermathecae; ring sclerite absent; gonoplacs present, but almost completely desclerotized; fusion of paratergite VIII and first gonocoxa complete, with loss of individuality of sclerites; posterior strut of gonangulum fused to paratergite IX; gonangulum not fused to first gonocoxa + paratergite VIII; conical projection on paratergite VIII incompletely fused to paratergite IX.

China (1945) described *Anommatocoris*, a new genus of Heteroptera, and placed it as an aberrant member of the subfamily Oxycareninae (Lygaeidae), the genus having lost the ventral abdominal trichobothria. Kormilev (1955b) erected a new family, the Vianaididae, for a new genus, *Vianaida*, and in this he also included *Anommatocoris*. Examination of the female genitalia enables the systematic position of these genera to be ascertained. In the fusion of paratergite VIII and the first gonocoxa, the presence of gonoplacs, the absence of a true median spermatheca and the presence of the triangular sclerite at the base of the genitalia, the family Vianaididae is found to be quite distinct from the Lygaeidae and close to the Tingidae. The drawings by the two authors of the female terminalia, seen from the exterior, are not alike. Kormilev has omitted to insert the line delimiting the fused first gonocoxa and paratergite VIII.

It appears that the Vianaididae is a good family close to the Tingidae, but my studies suggest that *Vianaida* and *Anommatocoris* are congeneric.

The female genitalia of the Tingoidea have a ventral aspect and appear rather flattened and plate-like, but a well developed lacinate ovipositor is present, eggs usually being laid in plant tissue. There is no median spermatheca, sac-like pseudospermathecae being present in the Tingidae. The latter family is unique in the Heteroptera examined, in having the posterior strut of the gonangulum not fused to paratergite IX, except at its dorsal angle. The first gonocoxa and paratergite VIII are fused and gonoplacs are present. The rami are sclerotized, complete and interlocking and there is a small triangular sclerite at the base of the ovipositor. There is also a connection between paratergite VIII and paratergite IX and/or the gonangulum.

Reuter (1912), China (1933), Börner (1934), Beier (1938) and Poisson (1951) considered the Tingidae and Piesmididae to be closely related. Tullgren (1918) was the first to show that these families were quite separate. Whilst the second possessed abdominal trichobothria, they were absent in the first. Subsequently, most studies have shown the Tingoidea, as previously constituted, to be an unnatural group. Leston (1953b) noted the similarity between the Tingid and Mirid egg. Leston, Pendergrast and Southwood (1954) suggested that the Tingidae were related to the Reduvioidea, but were unable to place the Piesmididae for certain in any superfamily of the Heteroptera Trichophora