

of Tullgren. Pendergrast (1957) placed the Piesmidae in the same group as the Lygaeidae. As already stated, the Piesmidae can be placed in the Lygaeoidea on the structure of the female genitalia. The Tingidae, together with the Vianaididae, form a group here considered to warrant superfamily status.

SALDOIDEA

SALDIDAE

Previous descriptions : Ekblom, 1926 ; Leston, 1956*d* ; Snodgrass, 1933.

Species examined : *Salda littoralis* (L.) (figs. 54-56), *Saldula saltatoria* (L.), *Aepophilus bonnairei* Sign.

Paratergite VIII firmly united to dorsal edge of first gonocoxa ; individuality of sclerites associated in this fusion lost in *Aepophilus* ; paratergite IX not separated from tergum IX ; first gonapophyses joined by membrane, elongate and sclerotized, tips serrate on dorsal margin, each gonapophysis partially split longitudinally ; rami sclerotized and interlocking ; second gonapophyses sclerotized and united except at apex, terminally truncate and not tapering like first gonapophyses ; anterior strut of gonangulum rather short, broad and flattened ; second gonocoxa elongate, sclerotized, with dorsal edge thickened ; gonoplaes broad and flat, sclerotized and united by membrane, except proximally where united by sclerotized mesad projections ; gonoplaes not so united in *Aepophilus* ; single median spermatheca present.

LEPTOPODIDAE

Species examined : *Valleriola greeni* Dist. (figs. 59, 60), *Patapus spinosus* (Rossi).

Sternum VII produced posteriorly and covering genitalia ; paratergites VIII fused to first gonocoxae, in *Valleriola* sclerites still distinct ; paratergites IX rounded posteriorly and separate ; first gonapophysis triangular and sclerotized and partially split longitudinally ; rami sclerotized and interlocking ; anterior strut of gonangulum short and partially sclerotized ; second gonocoxa slender and partially sclerotized ; second gonapophysis rather flattened and partially sclerotized, longer in *Valleriola* ; gonoplaes sclerotized, broad, flat but not united ; median spermatheca present ; wall of genital chamber surrounding opening of spermathecal duct with an elongate diamond-shaped sclerite.

MESOVELIIDAE

Previous descriptions : Ekblom, 1928 ; Neering, 1954.

Species examined : *Mesovelica furcata* Muls. and Rey (figs. 57, 58), *M. vittigera* Horv., *Mesoveloidea williamsi* Hungerf.

Anterior margin of sternum VII in mid-line produced antero-internally as a long apodeme ; paratergite VIII completely fused to first gonocoxa ; first gonapophysis elongate, lacinate and sclerotized, with serrations ventro-laterally, each gonapophysis partially split longitudinally ; rami sclerotized and interlocking ; anterior strut of gonangulum rather broad and flat ; second gonocoxa elongate, broad and flat, sclerotized and with dorsal edge slightly thickened ; second gonapophyses elongate, sclerotized and lacinate, united except at apex and without serrations ; gonoplaes triangular in shape, sclerotized and attached to second gonocoxae, dorsal and ventral edges slightly curved mesad ; median spermatheca with accessory fecundation canal.

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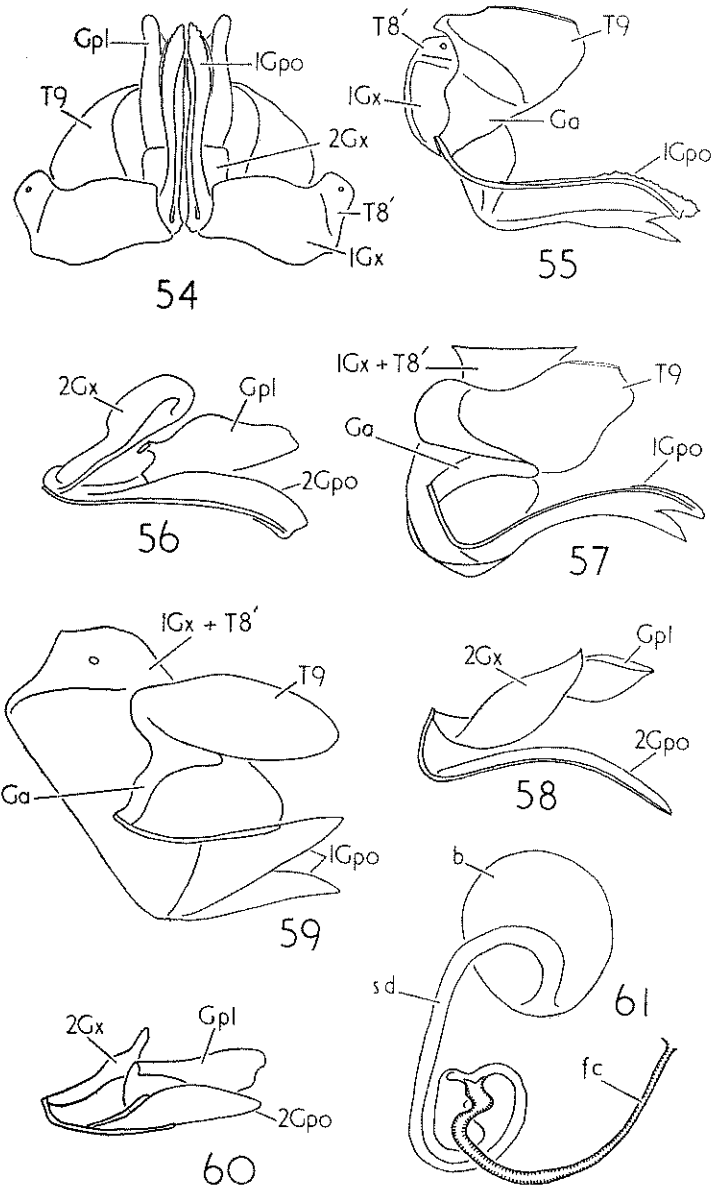
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FIGS. 54-61.—(54)-(56) *Salda littoralis* (L.) (Saldidae): (54) ventral view of female terminalia; (55) first (56) second gonocoxa and associated parts; (57)-(58) *Mesovelina furcata* Muls. and Rey (Mesoveliidae); (57) first (58) second gonocoxa and associated parts; (59)-(60) *Valleriola greeni* Dist. (Leptopodidae): (59) first (60) second gonocoxa and associated parts; (61) *Leotichus speluncerum* China (Leotichidae): spermatheca.

Esaki and China (1927) erected a group, the Telmatobia, to contain the Ochteridae, Galgulidae (= Gelastocoridae), Velocipedidae, Leptopodidae and Saldidae (includes Aepophilidae). Pendergrast (1957) has shown that this is not a natural group. He has removed the Ochteridae, Galgulidae and Velocipedidae and has stated that the Saldoidea should contain the Saldidae and Leptopodidae only. The study of the female genitalia supports this, but suggests that the Saldoidea should perhaps also include the Mesoveliidae. Pendergrast (1957) has shown that the Mesoveliidae possess a fecundation canal, as do the Hydro-metridae, Hebridae, Gerridae and Veliidae. He has, therefore, considered these to represent a monophyletic group. However, there is a strong suggestion of convergence. I have found a fecundation canal to be present in *Leotichius speluncerus* China. In the Pentatomoidea, Leston has suggested that a structure, probably functioning as a fecundation canal, is present in *Hotea subfasciata*. If such a canal can arise by convergent evolution in these species, there is no reason to suppose that it could not arise independently in the Mesoveliidae and the other families mentioned. It has evolved independently in the Carabidae (Coleoptera) (Stein, 1847). Since the female genitalia are similar to those of the Saldidae and quite different from those of the Gerridae, Veliidae, etc., the Mesoveliidae is here considered within the Saldoidea.

Pendergrast (1957) has further noted that the internal male genitalia of the Mesoveliidae possess accessory glands and thus they differ from the other families he considered to belong to the same group. He noted also that accessory glands (mesadenes) were present in the Saldidae.

The present study has also shown that the female genitalia of the Aepophilidae are extremely similar to those of the Saldidae, thus supporting the inclusion of this group within the Saldidae (Leston, 1956d).

The large gonoplaes, the fusion of paratergites VIII and the first gonocoxae and the partially divided and often serrate nature of the first gonapophyses appear to be characters distinguishing the Saldoidea.

GERROIDEA

VELIIDAE

Previous description : Ekblom, 1926.

Species examined : *Velia caprai* Tam. (figs. 62-64), *V. sauli* Tam., *V. currens* (F.), *Microvelia reticulata* (Burm.), *M. pulchella* Westw., *Rhagovelia tenuipes* Champ. (fig. 65).

Tergum IX forming an anal plate or lid covering posterior of abdomen and obscuring genitalia in *Velia* spp., but only partially so in *Microvelia* spp.; in *Rhagovelia* tergum IX not forming an anal lid; sternum VII anteriorly produced as an apodeme in mid-line, extending to anterior margin of sternum VI; first gonocoxa and paratergite VIII fused; first gonapophyses elongate, lacinate and sclerotized; rami sclerotized and interlocking; second gonapophyses elongate, lacinate and sclerotized, united by a Y-shaped sclerotized bar about one third of way from base in *Velia* spp.; second gonapophyses covered with hairy projections apically; gonangulum more or less triangular in shape with posterior angle elongately produced posteriorly and fused to paratergite IX, which is very small; second gonocoxae sclerotized and elongate, very closely associated with gonangulum and paratergite IX; gonoplaes absent; median spermatheca with an accessory fecundation canal.

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HEBROVELIIDAE

Previous description: Lundblad, 1939.

Species examined: *Hebrovelia singularis* Lundbl.

Identical in structure with Veliidae, but with tergum IX not forming an anal lid; genitalia externally appearing as in *Rhagovelia*, with first gonocoxae visible.

MACROVELIIDAE

Species examined: *Macrovelia horni* Uhl., *Ocellovelia germari* Dist.

Female genitalia as in Hebroveliidae.

GERRIDAE

Previous descriptions: Carpenter, 1906; Ekblom, 1926; Guthrie, 1954; Imms, 1936.

Species examined: *Gerris najas* (Deg.) (figs. 66, 67), *G. notabilis* D. & H., *G. incurvatus* D. & H., *G. lacustris* (L.), *G. gibbifer* Schum., *Brachymetra albinervis* A. & S., *Cylindrostethus productus* Spin.

Almost identical with Veliidae; with apodeme of sternum VII longer; tergum IX not forming an anal lid; second gonapophyses without feathery projections; apodeme of first gonocoxae smaller and narrower; second gonocoxae and gonoplacs absent.

HYDROMETRIDAE

Previous descriptions: Ekblom, 1926; Sprague, 1956.

Species examined: *Hydrometra stagnorum* (L.) (figs. 68, 69).

Tergum IX forming an anal lid; anterior margin of sternum VII in mid-line produced as an apodeme; paratergite VIII ventrally completely united with first gonocoxa; first gonapophysis small, triangular and sclerotized; small portion of rami at base of gonapophyses sclerotized and interlocking, otherwise membranous; anterior strut of gonangulum membranous; second gonapophysis triangular and membranous; second gonocoxa quadrate in shape and sclerotized posteriorly, the anterior projection connecting with second gonapophysis, almost completely membranous; gonoplacs apparently absent; median spermatheca with accessory fecundation canal.

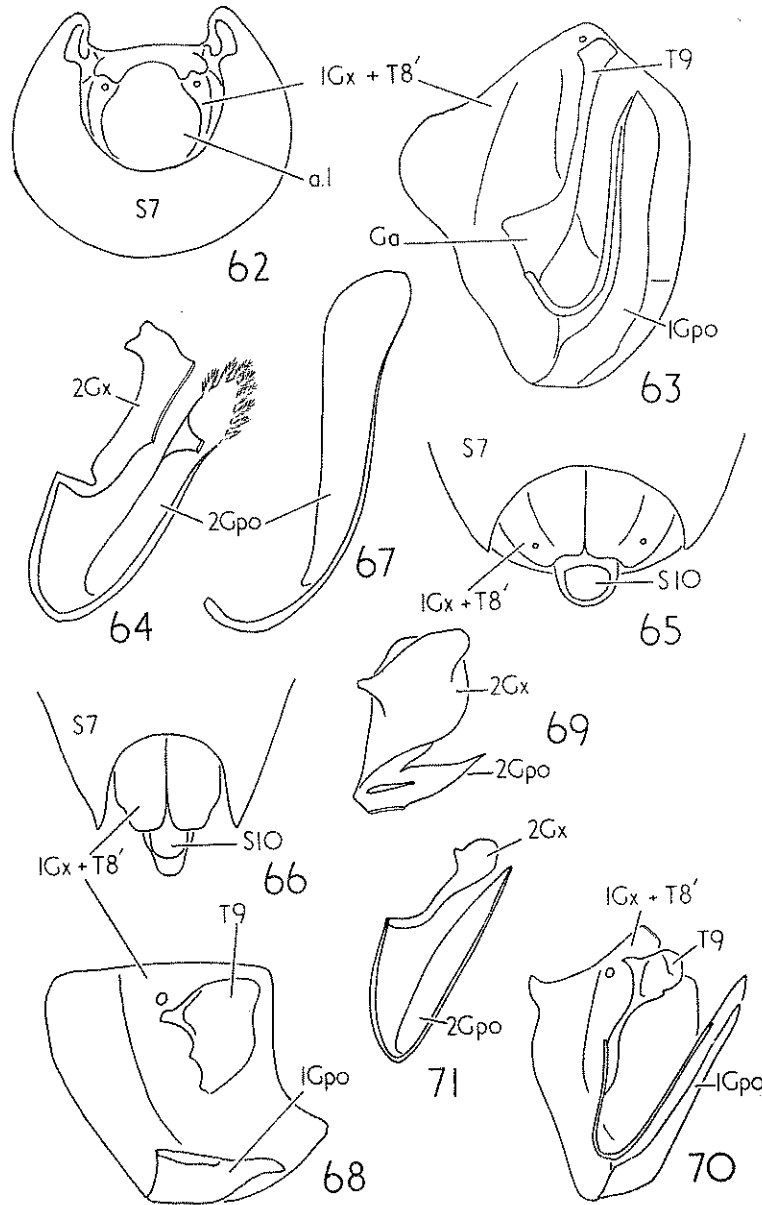
I consider the female genitalia to be of the lacinate type and not the plate-shaped type, as stated by Dupuis (1955).

HEBRIDAE

Species examined: *Hebrus ruficeps* (Thoms.) (figs. 70, 71).

Tergum IX not forming an anal lid; paratergite VIII fused with first gonocoxa; gonapophyses partially sclerotized, elongate and with sclerotized and interlocking rami; anterior strut of gonangulum partial, sclerotized; paratergite IX and second gonocoxa about same size, quadrate in shape and sclerotized; paratergite IX sclerotized posteriorly only; gonoplacs absent; median spermatheca with accessory fecundation canal.

McKinstry (1942) has given a table of characters separating the families here considered in the Gerroidea. He also included the Mesoveliidae, but this has already been considered in the Saldoidea. China and Usinger (1949) have



FIGS. 62-71.—(62)-(64) *Velia caprai* Tam. (Veliidae): (62) posterior view of female terminalia; (63) first (64) second gonocoxa and associated parts; (65) *Rhagovelia tenuipes* Champ. (Veliidae): ventral view of female terminalia; (66)-(67) *Gerris najas* (Deg.) (Gerridae): (66) ventral view of female terminalia; (67) second gonapophysis; (68)-(69) *Hydrometra stagnorum* (L.) (Hydrometridae): (68) first (69) second gonocoxa and associated parts; (70)-(71) *Hebrus ruficeps* (Thoms.) (Hebridae): (70) first (71) second gonocoxa and associated parts.

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reduced the Hebroveliidae and Macroveliidae to subfamily rank within the Veliidae. The present work has shown that, whereas the Veliinae have tergum IX forming an anal lid, the Microveliinae have the terminalia only partially obscured by tergum IX and the Rhagoveliinae are without an anal lid. If these three subfamilies are retained within the Veliidae, there appears no reason why the Hebroveliidae and Macroveliidae should not also be included. The anal lid character has not been used in the systematics of this group. It appears to be a very reliable character and warrants further study.

China (1957) has given a summary of characters separating the Veliidae and Gerridae. To this may be added the loss of the second gonocoxae in the Gerridae and the presence of feathery projections on the gonapophyses in some Veliidae. The second gonocoxa is present in the Veliidae and not absent, as stated by Ekblom (1926).

Pendergrast (1957) has shown the Gerroidea (including the Mesoveveliidae) to be distinct from all other Heteroptera in possessing a fecundation canal.

NEPOIDEA

NEPIDAE

Previous descriptions : Berlese, 1909 ; Dufour, 1821 ; Hamilton, 1931 ; Larsen, 1938 ; Locy, 1884 ; Marshall and Severin, 1904 ; Verhoeff, 1893.

Species examined : *Nepa cinerea* L. (figs. 72, 73).

Sternum VII produced posteriorly, covering genitalia ; paratergite VIII elongate, projecting beyond end of abdomen and forming a respiratory siphon ; paratergite IX rather small, elongate and not separate from tergum IX ; first gonocoxa quadrate with antero-dorsal angle produced anteriorly as a long broad apodeme ; first gonapophysis broad, elongate and sclerotized ; sclerotized rami on dorsal edge of first gonapophyses on basal two-thirds ; gonangulum triangular in shape, sclerotized and fused to paratergite IX posteriorly ; second gonapophyses elongate, sclerotized and fused at base ; second ramus extending along basal two-thirds of second gonapophysis and interlocking with first ramus ; second gonocoxa slender, curved dorsally in posterior half and joined by sclerotized bridge across middle with opposite number ; gonoplac sclerotized and rather stylus-like ; single median spermatheca present.

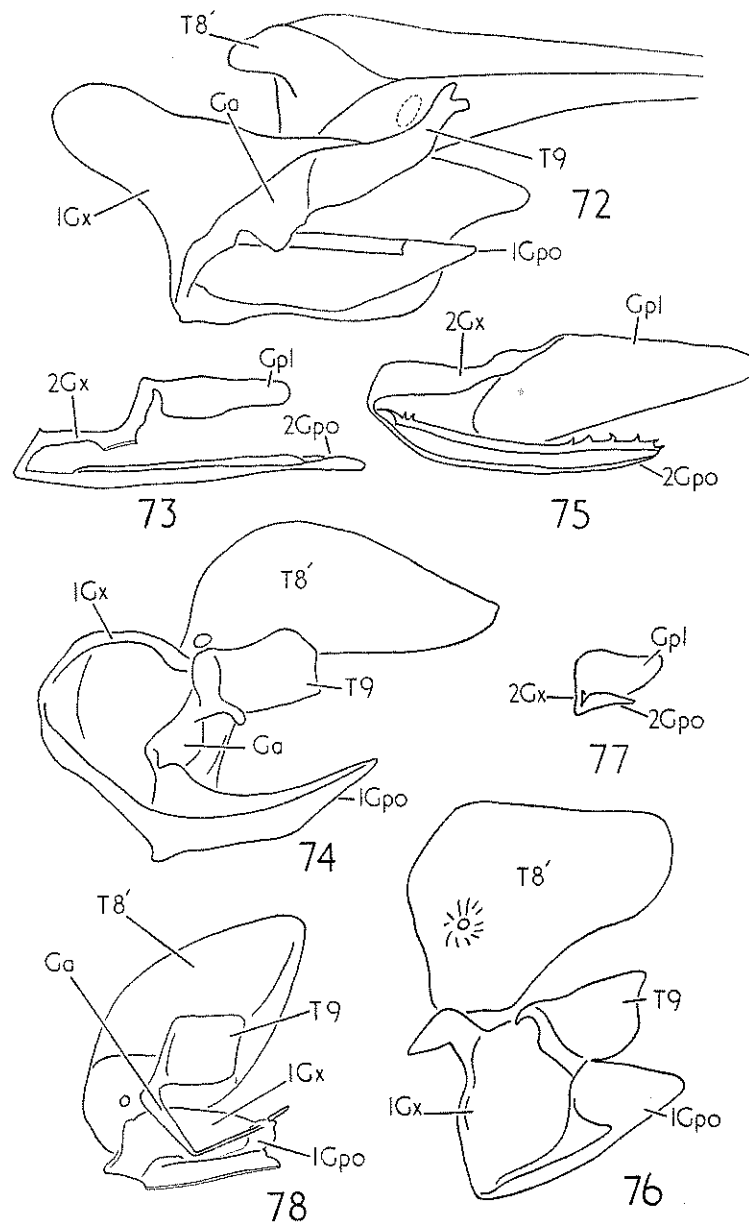
BELOSTOMATIDAE

Species examined : *Lethocerus grandis* (F.).

Paratergite VIII elongate, projecting beyond end of abdomen and forming a respiratory siphon ; paratergite IX small and quadrate ; first gonocoxa triangular and slightly produced posteriorly ; antero-dorsal corner of first gonocoxa produced as a short, broad apodeme ; first gonapophysis slender, elongate, triangular in shape, sclerotized and with a distinct shallowly grooved ramus ; anterior strut of gonangulum slender and sclerotized ; gonoplac rather stylus-like ; single median spermatheca present.

Börner (1934) and Pendergrast (1957) considered the Nepoidea to contain only the Nepidae and Belostomatidae, whereas Esaki and China (1927), Beier (1938) and Poisson (1951) include the Naucoridae and Aphelocheiridae also. The study of the female genitalia supports the conclusions reached by Börner and Pendergrast. They are characterised by the very long paratergites VIII forming a respiratory siphon and the stylus-like gonoplacs.

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FIGS. 72-78.—(72)-(73) *Nepa cinerea* L. (Nepidae): (72) first (73) second gonocoxa and associated parts; (74)-(75) *Ilyocoris cimicoides* (L.) (Naucoridae): (74) first (75) second gonocoxa and associated parts; (76)-(77) *Aphelocheirus montandoni* Horv. (Aphelocheiridae): (76) first (77) second gonocoxa and associated parts; (78) *Sigara dorsalis* Leach (Corixidae): first gonocoxa and associated parts.

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NAUCOROIDEA

NAUCORIDAE

Previous descriptions : Heymons, 1899 ; Larsen, 1938 ; Rawat, 1939.

Species examined : *Ilyocoris cimicoides* (L.) (figs. 74, 75).

Paratergite VIII large, broad and flattened, free from first gonocoxa ; first gonocoxa almost triangular in shape, with a broad apodeme antero-dorsally ; first gonapophysis lacinate, sclerotized with a well defined grooved ramus ; anterior strut of gonangulum broad, flat and sclerotized ; second gonapophysis long, slender and sclerotized with short blunt spines apically and with a distinct ridged ramus ; second gonocoxa flat, narrow and elongate ; gonoplac broad and flat, subequal to paratergite VIII ; single median spermatheca present.

APHELOCHEIRIDAE

Previous description : Larsen, 1938.

Species examined : *Aphelocheirus montandoni* Horv. (figs. 76, 77).

Paratergite VIII large, broad and flattened, not fused to first gonocoxa ; first gonocoxa rather quadrate in shape with an elongate apodeme antero-dorsally ; first gonapophysis short and triangular and all but fused to paratergite IX ; anterior strut of gonangulum apparently absent ; second gonapophyses very small and fused and without rami ; second gonocoxa very small and slender ; gonoplac quite large and flat, about as large as paratergite IX ; single median spermatheca present.

The genitalia of the Aphelocheiridae I consider to be of the lacinate and not the plate-shaped type, as stated by Dupuis (1955).

The two families here considered in the Naucoroidea were included in the Notonectoidea by Oshanin (1916), Pruthi (1925), Börner (1934) and Stichel (1955). Esaki and China (1927), Beier (1938) and Poisson (1951) have included them in the Nepoidea. Esaki and China (1927) did, however, consider the Naucoridae and Aphelocheiridae more closely related to each other than to either the Nepidae or Belostomatidae.

The Nepidae and Belostomatidae have already been considered. Pendergrast (1957) found that the Naucoridae and Aphelocheiridae, together with the Corixidae and Ochteridae, could be grouped together on the evidence of the spermatheca.

The study of the female genitalia suggests that the Naucoroidea should contain only the Naucoridae and Aphelocheiridae. The structure of the gonoplacs and paratergites VIII, with the reduced second gonocoxae and gonangulum, characterise the superfamily.

NOTONECTOIDEA

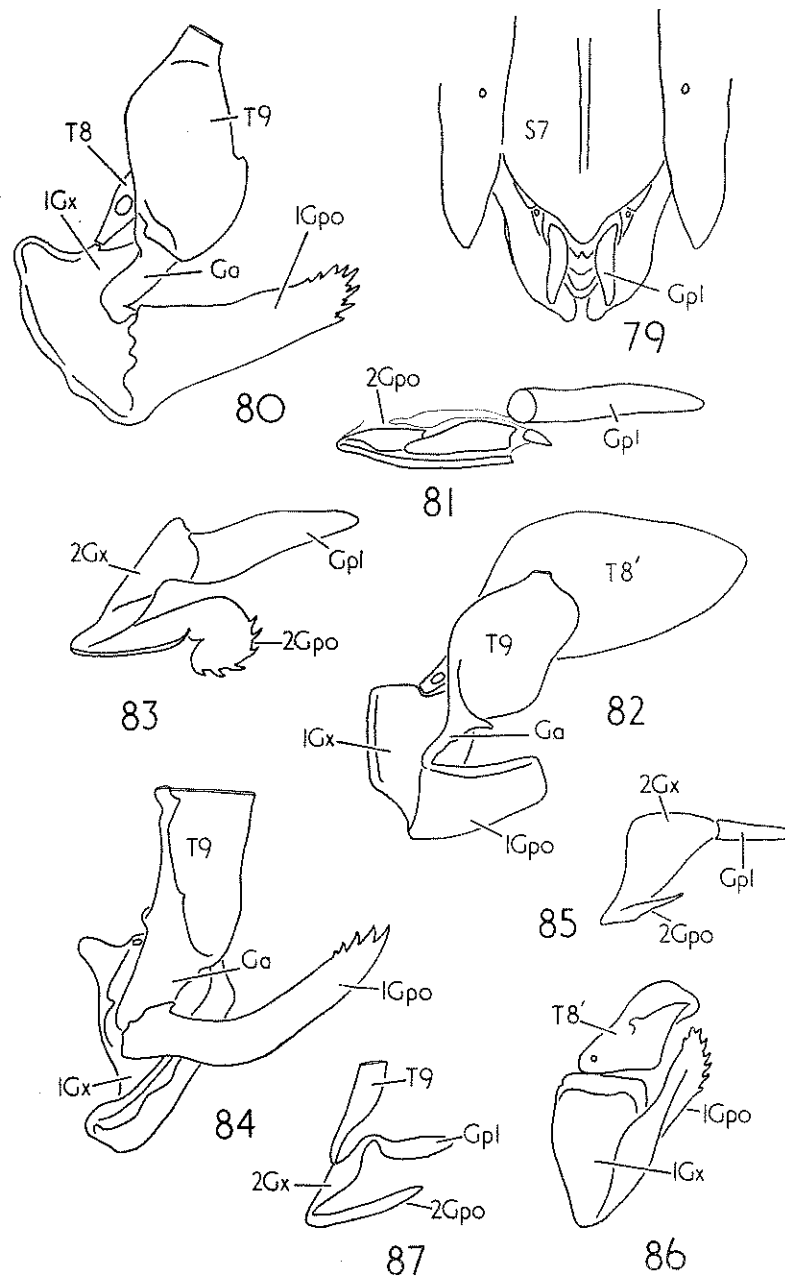
NOTONECTIDAE

Notonectinae

Previous descriptions : Berlese, 1909 ; Larsen, 1938.

Species examined : *Notonecta glauca* L. (figs. 79-81), *N. undulata* Say, *Enithares lineatipes* Horv. (figs. 82, 83).

Sternum VII produced posteriorly, partially covering genitalia ; paratergite VIII large and conspicuous, with spiracle VIII close to attachment with first gonocoxa ; paratergite



FIGS. 79-87.—(79)–(81) *Notonecta glauca* L. (Notonectidae): (79) ventral view of female terminalia; (80) first (81) second gonocoxa and associated parts; (82)–(83) *Enithares lineatipes* Horv. (Notonectidae): (82) first (83) second gonocoxa and associated parts; (84)–(85) *Buenoa antigone* Kirk. (Notonectidae): (84) first (85) second gonocoxa and associated parts; (86)–(87) *Plea atomaria* (Pall.) (Pleidae): (86) first (87) second gonocoxa and associated parts.

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IX smaller and not separated from tergum IX ; first gonocoxa almost triangular in shape, anterior margin thickened, but without projecting apodeme ; first gonapophysis rather broad and sclerotized, with spines at apex ; first rami indistinct ; gonangulum triangular in shape and sclerotized ; second gonocoxa slender and only partially sclerotized ; second ramus present and sclerotized ; second gonapophysis sclerotized—in *Notonecta* consisting of two separate sclerites, in *Enithares* heavily sclerotized throughout, bent ventrally at apex and with spines ; gonoplacs separate and stylus-like ; single median spermatheca present.

Anisopinæ

Species examined : *Anisops niveus* (F.), *Buenoa antigone* Kirk. (figs. 84, 85), *B. pallens* Champ.

Sternum VII produced posteriorly as in *Notonecta* ; paratergite VIII fused to first gonocoxa and spiracle VIII located on extreme dorsal edge of latter ; paratergite IX rather membranous ; first gonocoxa triangular in shape, with posterior margin swollen, reflexed and heavily sclerotized ; antero-dorsal corner of first gonocoxa produced forward as an apodeme ; first gonapophysis heavily sclerotized, as an elongate, curved rod with spines apically ; rami absent ; gonangulum triangular in shape, heavily sclerotized, posteriorly fused to paratergite IX and extending dorsally to meet its opposite number in mid-line ; second gonocoxa rather membranous ; second gonapophyses united at base, very short, lacinate and membranous ; gonoplacs separate, short and stylus-like ; single median spermatheca present.

The female genitalia of the two subfamilies considered here appear to be quite different and distinctive, supporting the divisions of the family adopted at present. The structure in the Anisopinæ appears to be the more specialised.

PLEIDAE

Previous description : Wefelscheid, 1912.

Species examined : *Plea atomaria* (Pall.) (figs. 86, 87).

Abdominal sterna keeled in mid-line ; sternum VIII large and covering genitalia ; paratergite VII produced posteriorly ; paratergite VIII rather large, not fused to first gonocoxa ; paratergite IX much smaller than paratergite VIII and not separated from tergum IX ; first gonocoxa rather triangular in shape, larger than paratergite VIII and anterior margin without projecting apodeme ; first gonapophysis rather broad and sclerotized, apically armed with sclerotized teeth ; first ramus indistinct ; anterior strut of gonangulum absent ; second gonocoxa crescentic in shape ; second gonapophyses much smaller than first and united ; gonoplacs separate and rather stylus-like ; single median spermatheca present.

Reuter (1912), Oshanin (1916) and Pruthi (1925) included the Notonectidae, Naucoridae, Nepidae and Belostomatidae in this group. Börner (1934) considered the Notonectoidea to contain the Naucoridae, Aphelocheiridae, Notonectidae and Pleidae. Stichel's (1955) Notonectoidea contains the Pleidae, Notonectidae, Naucoridae, Belostomatidae, Nepidae and Ranatridae. The position of the Nepidae (including the Ranatridae), Belostomatidae, Naucoridae and Aphelocheiridae has already been discussed. Pendergrast (1957) has suggested a redefinition of the Notonectoidea to include the Notonectidae, Pleidae, Helotrephidae and Galgulidae.

view of female
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The study of the female genitalia suggests that only the Pleidae and Notonectidae should be included in this superfamily. However, although the Galgulidae and Helotrephidae do not appear to be allied to these two families, it has been found impossible to place them in any other superfamily on the structure of the female genitalia.

OCHTEROIDEA

OCHTERIDAE

Previous description : Jaczewski, 1934.

Species examined : *Ochterus marginatus* (Latr.) (figs. 88, 89).

Sternum VII produced posteriorly, with posterior margin indented in mid-line ; paratergite VIII not fused to first gonocoxa, indistinctly separated from tergum VIII which is divided into two mid-dorsally ; antero-ventral angle of paratergite VIII elongately produced ; paratergites IX quadrate in shape and very weakly sclerotized ; first gonocoxa quadrate with a very large finger-like anteriorly projecting apodeme ; first gonapophysis triangular and sclerotized ; rami sclerotized and interlocking ; rather straight and first ramus with groove rather shallow ; anterior strut of gonangulum slender and sclerotized ; second gonocoxa slender, sclerotized with dorso-posterior margin, except extreme apex, fused to ventral margin of paratergite IX ; gonoplaes rectangular in shape ; single median spermatheca present.

Paratergite VIII in *Ochterus* is similar to that in the Notonectidae ; Jaczewski (1934) stated that the female genitalia were reminiscent of those of Notonectidae, but the ovipositor is not as reduced as he indicated. The gonoplaes are similar to those in the Saldidae ; the first gonapophysis and gonocoxa are different from those in the Saldidae and appear quite distinctive.

Reuter (1912) included the Ochteroidea in his division Hydrobiotica and placed in it three families, Ochteridae, Galgulidae and Peloridiidae, the latter being set apart from the two former. Oshanin (1916) and Pruthi (1925) followed this scheme and included only the Ochteridae and Galgulidae. The Peloridiidae were placed in a new series of Hemiptera, the Coleorrhyncha, by Myers and China (1929) and this is placed in the Homoptera on the same status as the Auchenorrhyncha. A study of the female genitalia of *Hemiodocus fidelis* Evans leads me to the same general conclusion, although it is not possible to draw a sharp distinction between the type of ovipositor in the Homoptera as distinct from the Heteroptera.

CORIXOIDEA

CORIXIDAE

Previous descriptions : Crampton, 1929 ; Griffith, 1945 ; Hagemann, 1910 ; Höregott and Jordan, 1954 ; Larsen, 1938 ; Poisson and Jaczewski, 1928.

Species examined : *Corixa punctata* (Ill.), *Sigara dorsalis* Leach (figs. 78, 90, 91).

Tergum VIII divided in mid-line ; paratergites VIII very large and carrying spiracles ; sternum VIII more or less undivided ; first gonapophyses finger-like and each bearing a stylus-like structure ; anterior strut of gonangulum present ; second gonocoxae probably

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membranous and fused to second gonapophyses; second gonapophyses rather large and meeting beneath anus, but not fusing in mid-line; gonoplaes absent; single median spermatheca present.

Crampton (1929) considers the stylus-like structure at the apex of the first gonapophysis to be a true gonostyle. The anterior strut of the gonangulum is called the S-shaped strut by Larsen (1938).

The female genitalia in this group are very characteristic and fairly constant in structure.

Börner (1904) erected the group Sandaliorrhyncha for the Corixidae. Many later authors have considered this family to be separate from the rest of the Heteroptera. China (1955*b*) has given a full survey of the systematic position of the Corixidae and states that he at one time considered that they might even be aquatic Homoptera.

On the structure of the female genitalia it would appear that the Corixidae should be placed quite apart from the rest of the Heteroptera.

INCERTAE SEDIS I

This group includes families with genitalia having Cimicoid affinities, but which cannot be placed in any of the present superfamilies on the structure of these organs.

LEOTICHIDAE

Species examined: *Leotichus speluncorum* China (figs. 61, 94, 95).

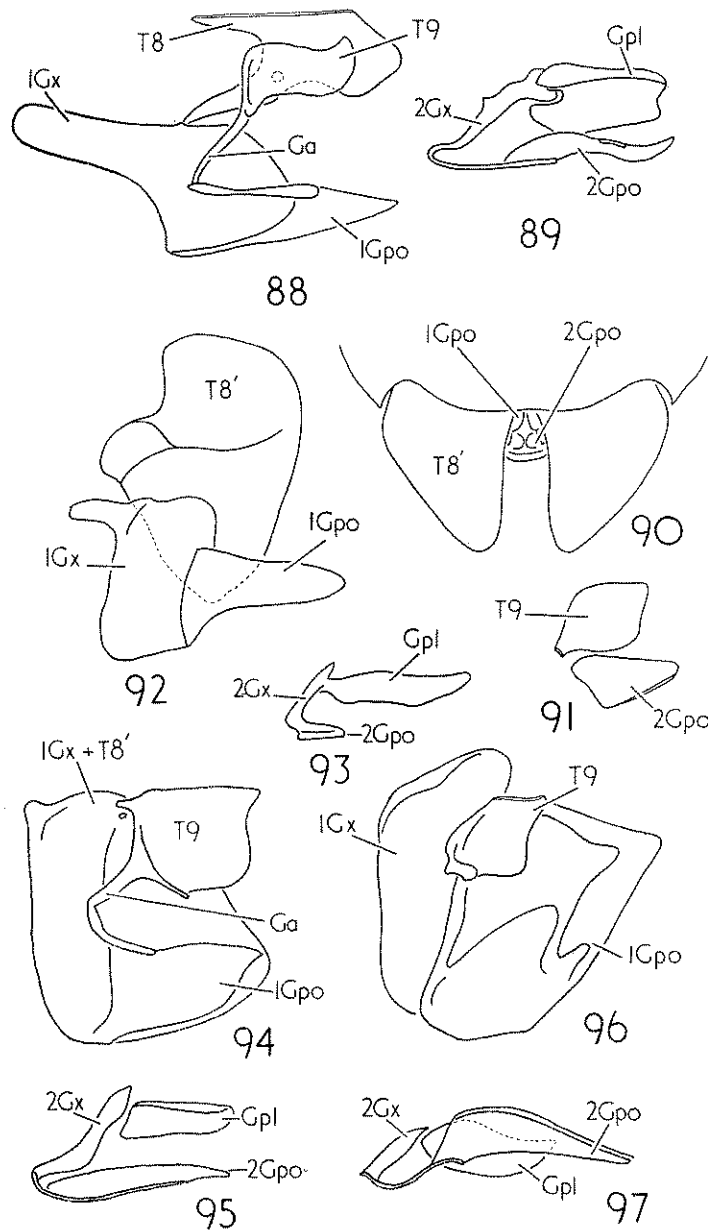
Paratergite VIII completely fused with first gonocoxa; paratergite IX rounded posteriorly and separate from opposite number; first gonapophysis broad and almost triangular in shape and heavily sclerotized; rami sclerotized and interlocking; anterior strut of gonangulum slender and sclerotized; second gonapophysis elongate and sclerotized; gonoplaes elongate rectangular and not united; median spermatheca with accessory fecundation canal.

China (1933) when he erected this family placed it close to the Saldidae. Whilst there appear to be many characters supporting this systematic placing, the structure of the female genitalia, especially the nature of the first gonapophyses, does not concur. However, there is little doubt that the Leotichidae should be placed with the other aquatic Heteroptera. Pendergrast (1957) did not examine the spermatheca of the Leotichidae. In *Leotichus speluncorum* (fig. 61) I have found a median spermatheca with an accessory fecundation canal. Pendergrast would thus have included this family in the Amphibicorisae; he would not have related it to the Saldidae as the latter lack such a canal. The structure of this canal in the Leotichidae is very similar to that in the Hebridae; the female genitalia are quite unlike those of the Hebridae.

HELOTREPHIDAE

Species examined: *Neotrepheus usingeri* China (figs. 96, 97).

Paratergite VIII not fused to first gonocoxa and not separated from tergum VIII; first gonocoxa and first gonapophysis both triangular in shape, sclerotized and about same



FIGS. 88-97.—(88)–(89) *Ochterus marginatus* (Latr.) (Ochteridae): (88) first (89) second gonocoxa and associated parts; (90)–(91) *Sigara dorsalis* Leach (Corixidae): (90) ventral view of female terminalia; (91) second gonapophysis and associated parts. (92)–(93) *Nertha grandicollis* Germ. (Galgulidae): (92) first (93) second gonocoxa and associated parts; (94)–(95) *Leotichus speluncerum* China (Leotichidae): (94) first (95) second gonocoxa and associated parts; (96)–(97) *Neotrepheus usingeri* China (Helo-trephidae): (96) first (97) second gonocoxa and associated parts.

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size ; first ramus and anterior strut of gonangulum membranous ; second gonocoxa small, elongate, rectangular and partially sclerotized ; paratergite IX fused to posterior strut of gonangulum which attaches to proximal end of second gonocoxa ; second ramus almost membranous ; second gonapophyses sclerotized and united dorsally, edges curved round ventrally to form an incomplete cone, extreme apices free ; gonoplares rather large, sclerotized, free and somewhat stylus-like ; median spermatheca present.

China (1933, 1955a, 1955b) grouped the Helotrephidae with the Pleidae and Notonectidae. Pendergrast (1957), after a study of the spermatheca, supported this. The female genitalia of *Neotrephus* are unlike those in the latter two families, but they are also unlike those in any other family, although they clearly have some characters of the aquatic bugs.

GALGULIDAE

Species examined : *Nertha grandicollis* Germ. (figs. 92, 93).

Paratergite VIII free from first gonocoxa, prism-shaped with posterior angle produced ; first gonapophysis finger-like and sclerotized, larger than gonoplares ; rami and anterior strut of gonangulum membranous ; posterior strut of gonangulum fused to partially sclerotized paratergite IX ; second gonocoxa small rectangular in shape and partially sclerotized ; second gonapophyses united in mid-line and to inter-gonocoxal membrane, not projecting as valves posteriorly ; gonoplares sclerotized, elongate and rectangular, not united ; median spermatheca present.

As stated when discussing the Ochteroidea, the female genitalia of *Nertha* do not appear similar to those of *Ochterus*, although they fall within the type of structure present in many of the water bugs.

INCERTAE SEDIS II

This group includes families which have the female genitalia so specialised as to make any systematic placing based on this structure impossible. In almost all cases an ovipositor is absent.

ANEURIDAE

Species examined : *Aneurus laevis* (F.), *A. avenius* (Duf.).

In this family it is not possible to trace any structures of the female genitalia. The ovipositor and associated sclerites are absent. There is no sign of the typical median spermatheca, but there is a simple small diverticulum in the dorsal wall of the genital chamber. Pendergrast (1957) states that this diverticulum is surrounded by tall glandular cells and that the sperm lies within this sac and in the anterior part of the chamber.

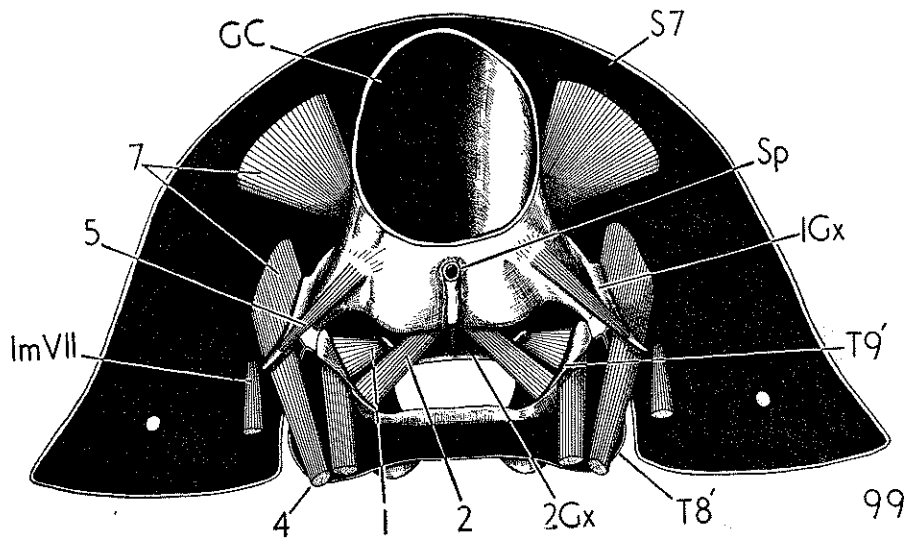
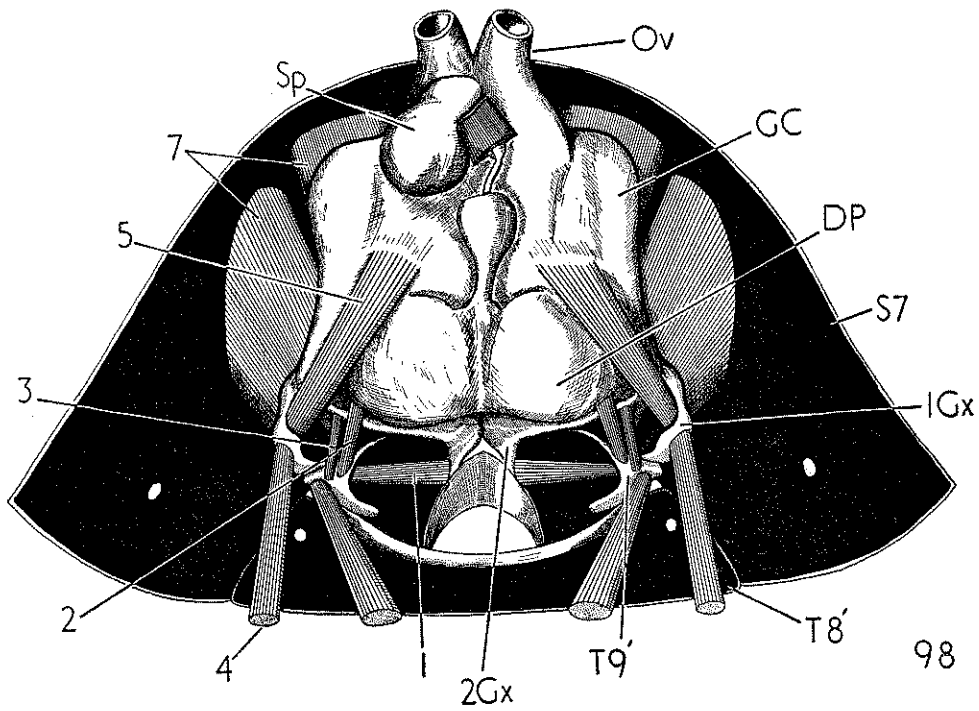
Leston, Pendergrast and Southwood (1954) point out that a true spermatheca is absent in *Aneurus* ; this is a Cimicoid character. However, Southwood (1956a) has shown that the structure of the egg is Pentatomoid in nature, with micropylar processes. All recent authors include the Aneuridae in the Aradoidea.

ENICOCEPHALIDAE

Previous description : Carayon, 1950a.

Species examined : undetermined species from New Guinea.

Because of extreme reduction, an interpretation of the female genitalia of this family has proved so difficult that the account here given is very brief.



FIGS. 98-99.—Internal view of musculature of female terminalia of: (98) *Sehirus bicolor* (L.) (Cydnidae); (99) *Picromerus bidens* (L.) (Pentatomidae).

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There is what appears to be a paratergite IX and three ventral sclerites, the homology of which cannot be ascertained on present information. A single median spermatheca is absent.

Carayon (1950a) has noted a small median seminal receptacle. Pendergrast (1957) has stated that this would indicate that the family was not allied to the Reduviidae. Leston, Pendergrast and Southwood (1954) have stated that the Enicocephalidae are apparently Geocorisae, but have pointed out that the wing venation suggests a distinct relationship with the Hydrocoridae. Stichel (1955) has erected a division, the (H) Enicocephalomorpha, for the Enicocephalidae, a group to be of equal status with the Pentatomomorpha and Cimicomorpha, but the female genitalia do not appear to help in the elucidation of this problem.

SCHIZOPTERIDAE

Species examined : *Schizoptera* sp.

In this family an ovipositor is apparently absent, but a true median spermatheca is present. The latter is an invaluable taxonomic character (Wygodzinsky, 1950).

This family is placed with the Dipsocoridae in the Dipsocoroidea, but this appears to be based solely on superficial resemblances.

TERMITAPHIDIDAE

Species examined : *Termitaphis* sp., *Termitaradus* sp.

This family is without an ovipositor. China (1955a) places it with the Aradiidae.

JOPPEICIDAE

Species examined : *Joppeicus paradoxus* Put.

An ovipositor is apparently absent in this family. China (1955a) has considered the systematic position and morphology of the Joppeicidae and concluded that it is closely related to the Reduviidae.

VI. HISTORICAL ACCOUNT OF THE CLASSIFICATION OF THE HETEROPTERA

Kiritshenko (1951) has adequately compared the various classifications of the Heteroptera proposed prior to 1950 ; this will not be repeated here.

Leston, Pendergrast and Southwood (1954), in a consideration of the higher classification of the Geocorisae, recognised two distinct groups, the Pentatomomorpha and the Cimicomorpha. This was based on a study and re-evaluation of the male genitalia, abdominal trichobothria, wing venation, spermatheca, salivary glands and egg structure. Their Pentatomomorpha coincides with Pruthi's (1925) Pentatomid-type male genitalia group and with Tullgren's (1918) Heteroptera trichophora. China (1955a) expressed doubts on the validity of this division of the Geocorisae into two, but he adopts a similar division himself in his phylogenetic diagram in the same paper.

Stichel(1955) considers that there are five divisions of the Heteroptera ; these he calls the Hydrocoriomorpha, Amphibicoriomorpha, Henicocephalomorpha,

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Cimicomorpha and Pentatomomorpha. I have elsewhere (Scudder, 1956a) commented on the naming of these divisions.

China (1955b) has discussed the evolution of the Amphibicorisae and Hydrocorisae and their relationships. Pendergrast (1957) has shown, by a study of the spermatheca, that the Amphibicorisae appear to be a monophyletic group, all possessing an accessory fecundation canal.

Many families have been continually moved from one division to another in the classifications and a large number of authors have made suggestions on the relationships of odd families. For example, Sahlberg (1920) and Ekblom (1928) removed the Hebridae and Mesoveliidae from the Anonycha, where they were placed by Reuter (1912) and placed them in the Amphibicorisae. The Saldidae seem always to have been a problem to the systematists and Leston, Pendergrast and Southwood (1954) and Southwood (1956a) were unable to place this family with any conviction; Leston and Scudder (1956) placed it in the Geocorisae, but China (1955b) considered it correctly placed in the Amphibicorisae.

VII. THE FEMALE GENITALIA AND CLASSIFICATION OF THE HETEROPTERA

The families in the foregoing account have been arranged, as far as possible, under superfamilies. A discussion or summary of the type of structure within each superfamily is given where possible.

The type of ovipositor appears to be dependent on the oviposition site and habit. Those ovipositing in plants, etc., have a lacinate type of ovipositor with lanceolate gonapophyses and the anterior strut of the gonangulum present and heavily sclerotized, whilst those ovipositing on the surface of leaves, trunks, etc., have a plate-shaped type of ovipositor with flap-like gonapophyses and the anterior strut of the gonangulum reduced and often completely membranous or absent. It is found that, within limits, the type and structure of the ovipositor is constant within the lower groups (*e.g.* superfamily or family), as members of these categories usually have the same oviposition habit. Thus the ovipositor can be employed, with other characters, in the delimiting of families and superfamilies. An example of this has already been published (Scudder, 1957a).

A survey of the superfamilies, excluding the Corixoidea and the "Incertae sedis II", shows that, on the basis of the female terminalia, they fall into two apparently distinct groups. No single character satisfactorily indicates this grouping, but a complex of characters is present: their separation is expressed as below.

- (i) Gonoplac always absent; no fusion of paratergite VIII and first gonocoxa; single median spermatheca present and functioning as a sperm-receiving and storage organ; pseudospermathecae absent; fecundation normal. PENTATOMOIDEA, COREOIDEA, LYGAEOIDEA, ARADOIDEA, PYRRHOCOROIDEA
- (ii) Gonoplac usually present; paratergite VIII often fused with first gonocoxa; median spermatheca present or absent, if present sometimes functioning as in (i), at other times losing its functions of receiving and storing sperm and serving as a secretory organ; pseudospermathecae sometimes present; fecundation generally normal, but haemocoelic fecundation occasionally occurring
CIMICOIDEA, REDUVIOIDEA, TINGOIDEA, SALDOIDEA, DIPSOCOROIDEA, GERROIDEA, NOTONECTOIDEA, NEPOIDEA, NAUCOROIDEA, OCHTEROIDEA, INCERTAE SEDIS I.

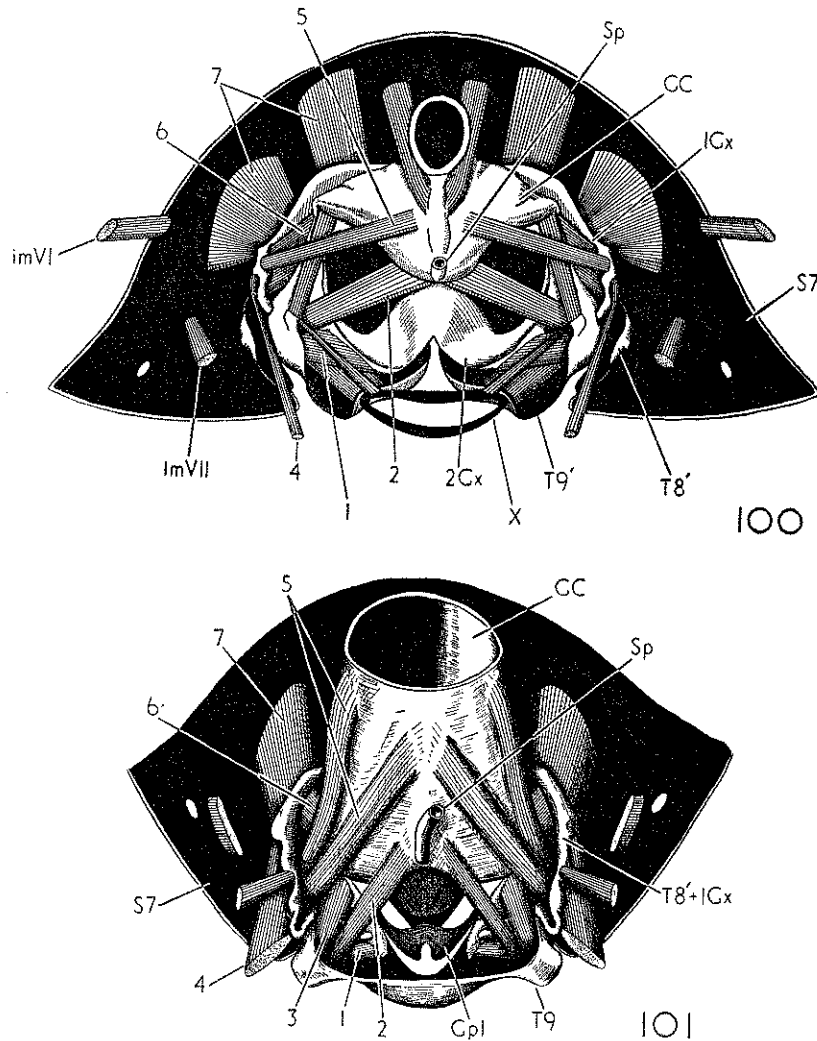
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It will be seen that the grouping based on the female genitalia coincides, more or less, with that based by Pruthi (1925) on the male genitalia.

Southwood (1956b) has shown that the Pentatomomorpha have characteristically a tubular type of accessory salivary gland and usually a convoluted or coiled accessory duct, whereas the Cimicomorpha have a vesicular type of accessory salivary gland and a rather straight accessory duct. Dissections of



Figs. 100-101.—Internal view of musculature of female terminalia of: (100) *Dysdercus fasciatus* Sign. (Pyrrhocoridae); (101) *Rhodnius prolixus* Stål (Reduviidae).

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several members of the Amphibicorisae and Hydrocorisae, together with the account by Baptist (1941), show that the salivary gland characters may be extended to the aquatic and semi-aquatic Heteroptera. The Amphibicorisae and Hydrocorisae have accessory salivary glands and ducts as in the Cimicomorpha. These two water-bug groups are also without ventral abdominal trichobothria and thus similar to Cimicomorpha.

Leston, Pendergrast and Southwood (1954) and Pendergrast (1957) state that the spermatheca is absent in the Cimicomorpha. As stated above, a homologue is present, but is usually modified as a secretory organ, the functions of receiving and storing sperm being usually taken over by analogous accessory structures, the pseudospermathecae.

The Cimicomorpha, as now defined, does not always have the true median spermatheca non-functional as such. It is feasible to consider the more primitive members as possibly having a functional spermatheca, or, conversely, to consider the modifications seen in most terrestrial Cimicomorpha as special features. There is ample evidence to suggest that a typical feature of certain land Cimicomorpha is the anomalous method of fecundation. Further, the pseudospermathecae throughout this division are not homologous. It does not seem inconsistent, therefore, to include the Amphibicorisae and Hydrocorisae (excluding Corixoidea) within the Cimicomorpha.

The female genitalia and the many other characters of the Corixoidea, in my opinion, indicate that this superfamily should be set apart from the rest of the Heteroptera. I would suggest that it be placed in a division of equal status with the Pentatomomorpha.

Owing to the reduced nature of the female genitalia of the "Incertae sedis II", no attempt has been made to place these families in the systematic arrangement.

VIII SUMMARY

The structure of the female terminalia in the Heteroptera has been studied and their value in the systematics of the group is considered.

The current classification into families and superfamilies is supported, with few exceptions: *viz.* the family Stenocephalidae is distinct from the Alydidae and close to the Lygaeidae; the Cydnid subfamily Coriomelaeinae and the Scutellerid subfamily Pachycorinae are perhaps heterogeneous; the Colobathristidae are very similar to the Coreidae, and the Thaumastocoridae and Vianaididae are placed in the Cimicoidea and Tingoidea, respectively. The Mesoveliidae appear close to the Saldidae.

In the higher classification of the Heteroptera, the female genitalia suggest that the superfamilies fall into two groups, these groups coinciding with the division based by Pruthi (1925) on the male genitalia. In this grouping the Pentatomoid superfamilies are placed together as the Pentatomomorpha and the Cimicoid superfamilies, together with the aquatic and semi-aquatic bugs, as the Cimicomorpha. It has been found that the structure of the salivary glands also supports this grouping.

It has not been possible to place the Leotichidae, Galgulidae and Helotrephidae in any of the known superfamilies, but all three have definite relationships with the aquatic bugs. A number of families, owing to their specialized nature

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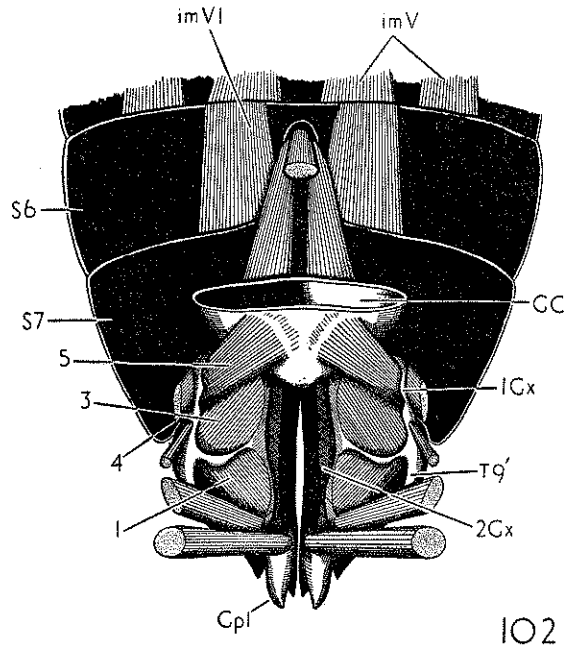
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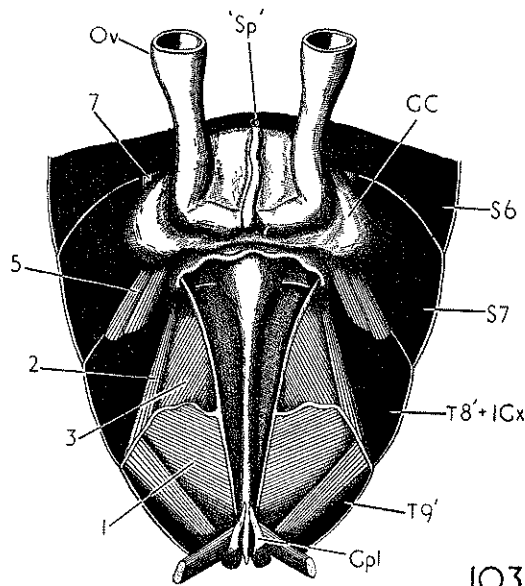
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FIGS. 102-103.—Internal view of musculature of female terminalia of: (102) *Nabis limbatus* Dahl. (Nabidae); (103) *Leptopterna dolabrata* (L.) (Miridae).

and lack of an ovipositor, have not been placed at all in the present work. The structure of the female genitalia, and the many other peculiar characters of the Corixidae, suggest that the latter need a higher category of their own, perhaps on the same level as the Pentatomomorpha.

It is seen that in both the Pentatomomorpha and Cimicomorpha, the type of ovipositor is dependent on the oviposition site and habit. Those ovipositing in plant or animal tissue have a lacinate type of ovipositor with sclerotized, lanceolate blades and the anterior strut of the gonangulum heavily sclerotized. Those ovipositing on the surface of leaves, trunks, etc. have a plate-shaped type of ovipositor with membranous flap-like gonapophyses and the anterior strut of the gonangulum often membranous or completely absent.

IX. ACKNOWLEDGMENTS

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XI. KEY TO LETTERING OF FIGURES

a.l., anal lid.
b., spermathecal bulb.
d.fl., distal flange.
DP, dorsal pouch.
fc, fecundation canal.
Ga, gonangulum.
GC, genital chamber.
Gpl, gonoplac.
im V, *im VI*, intersegmental longitudinal muscles of segments V and VI.
lm VII, lateral intrasegmental muscle of segment VII.
Ov, *ov*, oviduct.
p.fl., proximal flange.
ps, pseudospermatheca.
r.s., ring sclerite.
sac, ramal sac.
sd, spermathecal duct.
Sp, spermatheca.
 "Sp", accessory gland (homologue of true median spermatheca).
S6, *S7*, *S10*, Sterna VI, VII, X.
T8, *T9*, terga VIII and IX.
T8', *T9'*, paratergites VIII and IX.
X, segment X.

1Gpo, *2Gpo*, first and second gonapophysis.
1Gx, *2Gx*, first and second gonocoxa.
 1, extensor muscle of gonapophysis (homologous to 29 IX in Scudder, 1959).
 2, posterior dilator muscle of genital chamber.
 3, retractor muscle of second gonapophysis (homologous to 28 IX in Scudder, 1959).
 4, tergal muscle of first gonocoxa (probably homologous to 28 VIII in Scudder, 1959).
 5, anterior dilator muscle of genital chamber.
 6, retractor muscle of first gonapophysis (homologous to 14 VIII in Scudder, 1959).
 7, retractor muscle of first gonocoxa (homologous to 15 VII and in some cases, where two muscles are present, also to 14 VII in Scudder, 1959).

Acanthoso
 Alydidae,
 Aneuridae,
 Anthocori
 Aphelocor
 Aradidae,
 Belostoma
 Berytinida
 Brachypla
 Canopidae
 Cimicidae,
 Colobathri
 Coreidae,
 Corixidae,
 Cydnidae,
 Dinidorida
 Dipsocorida
 Dysodiidae
 Enicoceph
 Eumenotid
 Galgulidae
 Gerridae,
 Hebridae,
 Hebrovelii
 Helotreph
 Hydromet
 Isometopic
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