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Vol. 109. Part 1. Pp. 1-63. 122 figs.

15th June, 1957

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 4s. 0d.

STUDIES ON THE REPRODUCTIVE ORGANS OF THE HETEROPTERA
WITH A CONSIDERATION OF THEIR BEARING ON
CLASSIFICATION.

By J. G. PENDERGRAST.

(*Department of Zoology, Auckland University College, New Zealand.*)*

Manuscript received 4th June, 1956.

(Read 5th December, 1956.)

With 122 Text-figures.

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I. INTRODUCTION, ACKNOWLEDGMENTS AND TECHNIQUE.

The aim of this investigation has been to accumulate information on the morphology of the reproductive organs in as large a range of families of the Heteroptera as possible, in order to attempt to estimate the value of the reproductive organs as characters in systematics.

In the females it was found that there is, in general, little diversity in the form of the organs except the spermatheca. Therefore the work in this sex has been concerned, in the main, with this organ. It has a cuticular lining which retains its form in dried specimens. This has enabled the writer to study it in a larger number of families than was possible with the male organs, which have to be examined in fresh or suitably fixed material. A body of pure anatomical and histological information has been collected from these studies, especially in regard to the male organs, but, as much of it is not of direct value in considering the bearing of the organs on classification, it will not be included in the present paper.

* The greater part of the work described here was carried out in the Department of Zoology and Applied Entomology, Imperial College of Science, London.

The writer would like to stress that the study is not an attempt to base a new system of classification on one set of characters. It is realised that an adequate classification of the Heteroptera will be possible only after many characters have been studied in detail throughout the suborder. This study can be regarded only as a preliminary investigation in this field. It will be necessary to examine many more representatives from each group before an adequate appraisal of the value of the reproductive organs in the classification of the Heteroptera can be made.

The reproductive organs were studied by dissection of fresh or fixed material. Bouin's fluid was found to be the most useful fixative because it is often possible to carry out adequate dissections on material treated with it and it also serves as a good general fixative for sectioning. Sections were prepared by ordinary paraffin imbedding, double imbedding with celloidin or by the methyl benzoate-celloidin method. The spermathecae from fresh or preserved specimens were dehydrated, cleared and mounted in balsam. This treatment did not remove epithelia and muscle tissue. Spermathecae from dried material were examined after the abdomen had been boiled in ten per cent. caustic potash and the organ dissected out, stained and mounted in the usual way.

The writer desires to express his gratitude to Professor O. W. Richards, his supervisor, for guidance and criticism; and to Mr. R. G. Davies for helpful suggestions and advice. His thanks are also due to the authorities of the British Museum (Natural History) for the loan of specimens, and especially to Dr. W. E. China for ready assistance at all times. The writer had many valuable discussions on points of classification with Mr. Dennis Leston, who also generously donated many specimens from his collection.

He would also gratefully acknowledge the help of the following, mainly in providing material for study: Dr. G. L. Arora, Punjab, India; Dr. J. Carayon, Paris; Mr. A. J. P. Goodchild, London; Mr. G. H. Caswell, Ibadan, Nigeria; Mr. D. K. McE. Kevan, Nottingham; Professor T. W. Kirkpatrick, Trinidad; Dr. J. E. Morton, London; Dr. T. R. E. Southwood, London; Professor R. L. Usinger, San Francisco; Dr. T. E. Woodward, Brisbane, Australia.

Finally, he would like to acknowledge his indebtedness to his wife for translations of German works and help in many other ways.

Reference should be made here to the excellent pioneer studies of Dufour (1833) on the internal anatomy of the Hemiptera. Considering the standard of the optical equipment of the time, the quality of this work is all the more remarkable.

II. THE FEMALE ORGANS.

The female reproductive organs of most Heteroptera are, except for details of the spermatheca, of somewhat uniform character. There are two laterally-placed ovaries of the acrotrophic type, each consisting of a number of ovarioles. Ovariole numbers have been investigated by Woodward (1950) and Carayon (1950a). As Woodward pointed out, although families may be characterised by certain prevailing numbers, there are usually exceptions. For example, in the Pentatomidae there are often seven ovarioles, but six and four have also been noted. Even within a single genus differences have been observed (Pendergrast 1950). The two lateral oviducts from the ovaries converge and form a median common oviduct which is continuous posteriorly with a passage, the

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vagina, opening to the exterior. The vagina is ectodermal and possesses a cuticular lining.

When a spermatheca, or spermathecae, is present it arises from the dorsal wall of this duct. It is lined with a chitinous intima which may be thin and membranous, thick but unsclerotised or sclerotised. In some Heteroptera the organ is a simple thin-walled sac, whilst in others it shows varying degrees of complexity. It is generally possible to recognise a spermathecal duct leading from the vagina to a dilated sperm storage region, the spermathecal bulb. In some groups this bulb, or part of it, is invested by secretory cells located outside the spermathecal epithelium. In many the cuticle of the bulb can be seen to be traversed by extremely fine radial canals which are continued out as delicate tubules into the secretory cell layer. In many bugs a spermathecal pump is present. This can be a simple muscular investment of the bulb or it may be a more complex specialisation of part of the spermathecal duct. The Gerroidea possess a type of spermatheca not found elsewhere in the Heteroptera. In some groups (e.g. Miridae, Nabidae and Velocipedidae), where a spermatheca is not present, the vagina is modified to form a chamber, the bursa copulatrix, with thick cuticular walls.

Accessory glands may be present, opening into the common oviduct or into the vagina. In the latter case the gland is lined with a chitinous intima.

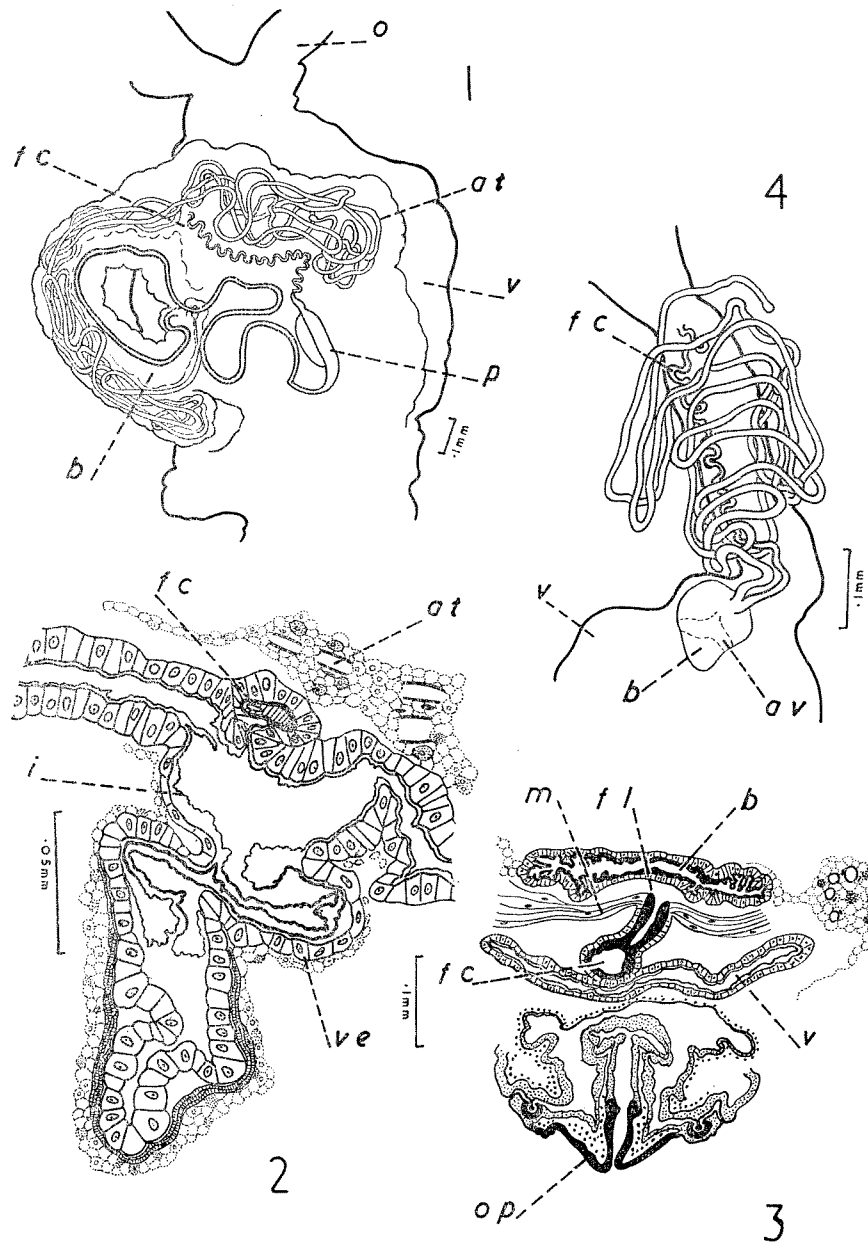
The types of spermatheca noted.

Most of the spermathecae examined have been placed into a few definite groups without difficulty. However, in some cases this has not been possible. The spermathecae of the Lygaeidae are extremely diverse and it has proved quite impossible to list spermathecal characters for the group. Some Lygaeid spermathecae are obviously close to the type found in the Berytidae and Pentatomidae, but the majority show no such affinity. The spermathecae of the Colobathristidae and Piesmididae resemble those of some Lygaeidae but the diversity is so great in this family that it would be unwise to stress relationship here.

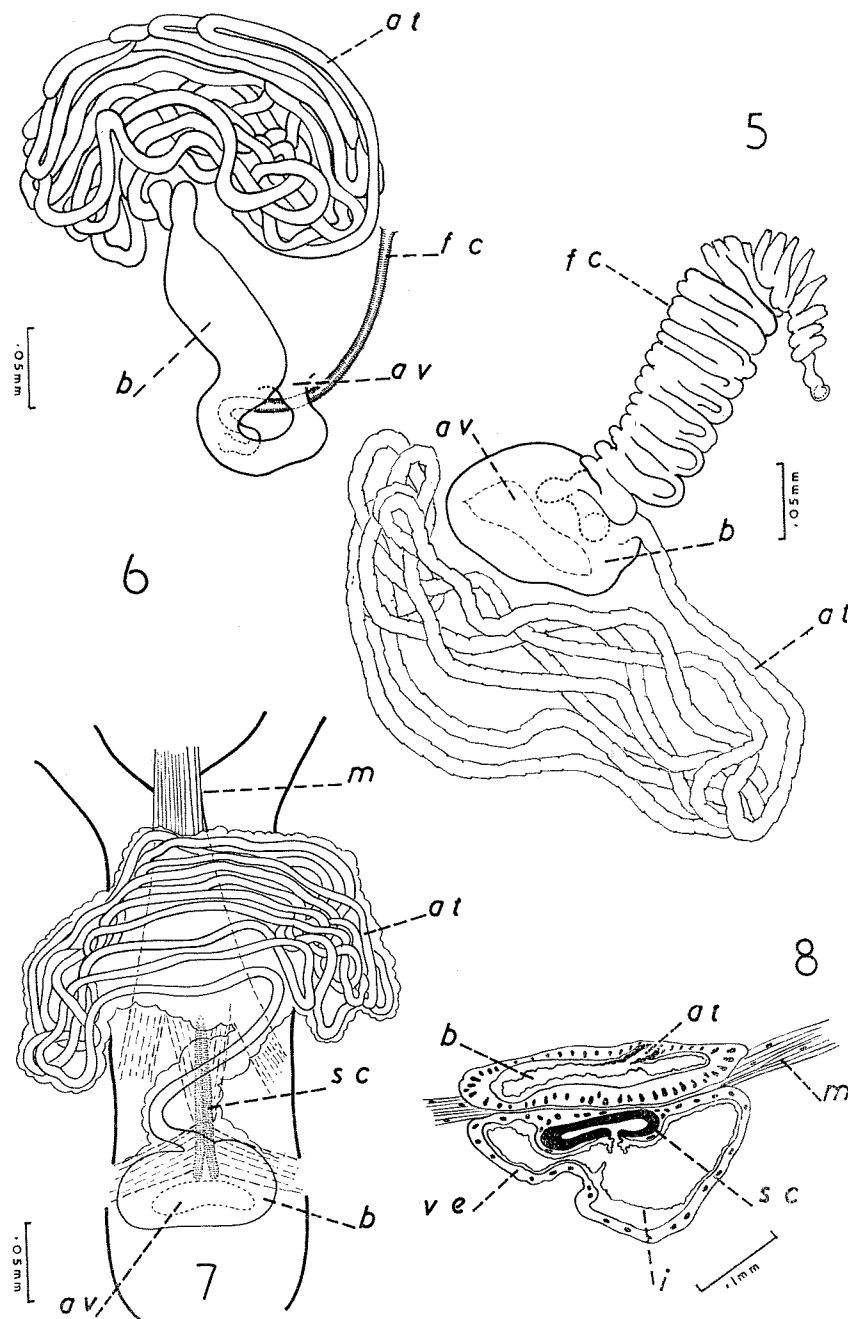
Where there is no spermatheca the type of fecundation and the form of the bursa copulatrix have been considered.

1. Gerridae, Veliidae, Hydrometridae, Mesoveliidae, Hebridae (figs. 1-9).

These groups have a spermatheca of a type not found elsewhere in the sub-order. The organ consists of a basal spermathecal bulb (*b*), which is in direct communication with the vagina, and an extremely long narrow apical tube (*at*) much folded and imbedded in a mass of glandular cells and fat body. In all the species examined, except *Velia* (where it is, perhaps, present in a rudimentary form), there is a feature apparently unique in the Heteroptera—a narrow sclerotised duct (*fc*) leading forwards from the basal bulb of the spermatheca to the anterior end of the vagina. A similar structure has been noted in the Carabidae (Coleoptera) by Stein (1847) (quoted by Imms, 1948, and Heberdey, 1931). Here, it is termed the "fecundation canal", and it is believed to allow the direct passage of spermatozoa from the spermatheca to eggs in the common oviduct. The disposition of the canal in the Gerroidea points to a



FIGS. 1-4.—(1) *Gerris lacustris*, vagina and spermatheca (Gerridae). (2) *G. lacustris*, transverse section anterior region vagina, common oviduct and spermatheca. (3) *G. lacustris*, transverse section vagina, spermatheca and ovipositor at level of spermathecal pump. (4) *Hydrometra stagnorum*, vagina and spermatheca. Potash (Hydrometridae). (For key to lettering of figures see page 63.)



FIGS. 5-8.—(5) *Mesovelgia furcata*, spermatheca, apical tube displaced posteriorly to expose fecundation canal. Potash (Mesoveliidae). (6) *Hebrus ruficeps*, spermatheca. Potash (Hebridae). (7) *Velia caprai*, vagina and spermatheca (Veliidae). (8) *V. caprai*, transverse section vagina and base of spermatheca.

similar function, although there is no other evidence to support this. Nevertheless, it has been found convenient to refer to this duct as the fecundation canal.

In the Gerridae the arrangement of the spermatheca and fecundation canal is more complex than in the other families, although the same elements are present. The basal bulb is a long sac lined with a thin cuticle. Proximally it is as wide as the spermatheca into which it opens by a wide aperture, while distally it narrows and is bent upon itself. At its distal end arise the long, tangled glandular tube and the fecundation canal. The latter is narrow and heavily sclerotised. By examining a series of microscope sections of the organ it can be seen that, as in the other Gerroidea, its cuticle is continuous with that lining the basal sac and the vagina (fig. 2). That is, it is to be regarded as a specialisation of the walls of these structures. About two-thirds of the way along its length is a pump (*p*). This is a greatly dilated region of the canal, the dorso-lateral parts of which are extended as a pair of wing-like flanges (fig. 3, *fl*). To each of these is attached a stout bundle of muscle fibres running out across the vaginal wall (fig. 3, *m*). From the pump the fecundation canal continues, now in the vaginal wall, in a series of small regular sinuous curves to its point of entry into the vagina.

In all the other families the apical glandular tube has a fairly constant structure. The form of the fecundation canal differs from family to family. In the Hydrometridae (fig. 4) it is short, simple and sinuous. In the Mesoveliidae (fig. 5) it is heavily sclerotised and its coils are fused to form a compact cylindrical structure. In the Hebridae (fig. 6) the canal is short and straight. *Velia* (fig. 7) does not possess a fecundation canal but sclerotised structures (*sc*) in the vaginal wall, to which muscle fibres are attached, are possibly homologous with it. This conclusion is reached from consideration of the position of these structures and from their relationships seen in transverse sections (fig. 8, *sc*). *Macrovelia* (fig. 9), however, which China and Usinger (1949) consider to be a relict which may provide a clue to the ancestral type from which the Veliidae are derived, has a fecundation canal which is close to that of *Mesovelia*.

Species examined :

- GERRIDAE : *Gerris lacustris* L., *Halobates* sp.
 VELIIDAE : *Velia caprai* Tamanini, *Macrovelia horni* Uhler.
 HYDROMETRIDAE : *Hydrometra stagnorum* (L.).
 MESOVELIIDAE : *Mesovelia furcata* Mulsant and Rey.
 HEBRIDAE : *Hebrus ruficeps* (Thomson).

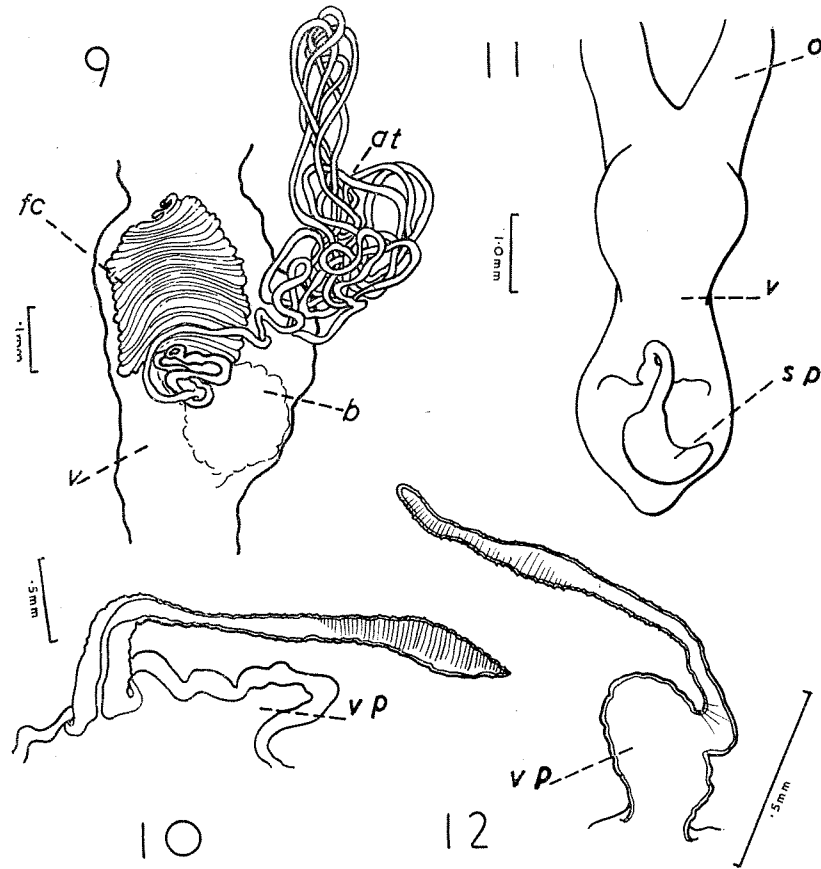
2. Nepidae, Belostomatidae (figs. 10-12).

Larsén (1938) has described the spermatheca of *Nepa*. In these two families the organ is a simple bent pointed tube. It is usually short but in the Belostomatidae it may be longer and narrow. It is lined with an unsclerotised cuticle which is marked with transverse striations. At the base of the organ the vaginal wall may be raised to form a pouch (the "Vaginaltasche" of Larsén).

Species examined and from the literature :

- BELOSTOMATIDAE : *Lethocerus niloticus* Stål (fig. 10), *Benacus griseus* Say (fig. 11), *Sphaerodema rusticum* (Fabricius) (fig. 12).
 NEPIDAE : *Nepa cinerea* L. [Larsén, 1938].

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FIGS. 9-12.—(9) *Macrovelia horni*, vagina and spermatheca (Veliidae). (10) *Lethocerus niloticus*, spermatheca. Potash (Belostomatidae). (11) *Benacus griseus*, vagina and spermatheca (Belostomatidae). (12) *Sphaerodema rusticum*, spermatheca. Potash (Belostomatidae).

3. Notonectidae, Pleidae, Helotrephidae, Gelastocoridae (figs. 13-16).

A detailed account of the spermatheca of *Notonecta glauca* L. has been given by Larsén. In these families the organ is long and with an unsclerotised cuticle. The spermathecal duct is coiled and its basal parts usually lined with a characteristic thick cuticle. This part of the duct may have a glandular epithelium when the cuticle is traversed by fine canals (*Notonecta*, *Neotrepbes*, *Mononyx*). The apical bulb has a thin lining and is surrounded by muscle fibres. The apical surface of the bulb is flattened, usually expanded and cap-like. This apical surface has been found to be invested by secretory cells in *Notonecta* and *Neotrepbes*.

Species examined and from the literature :

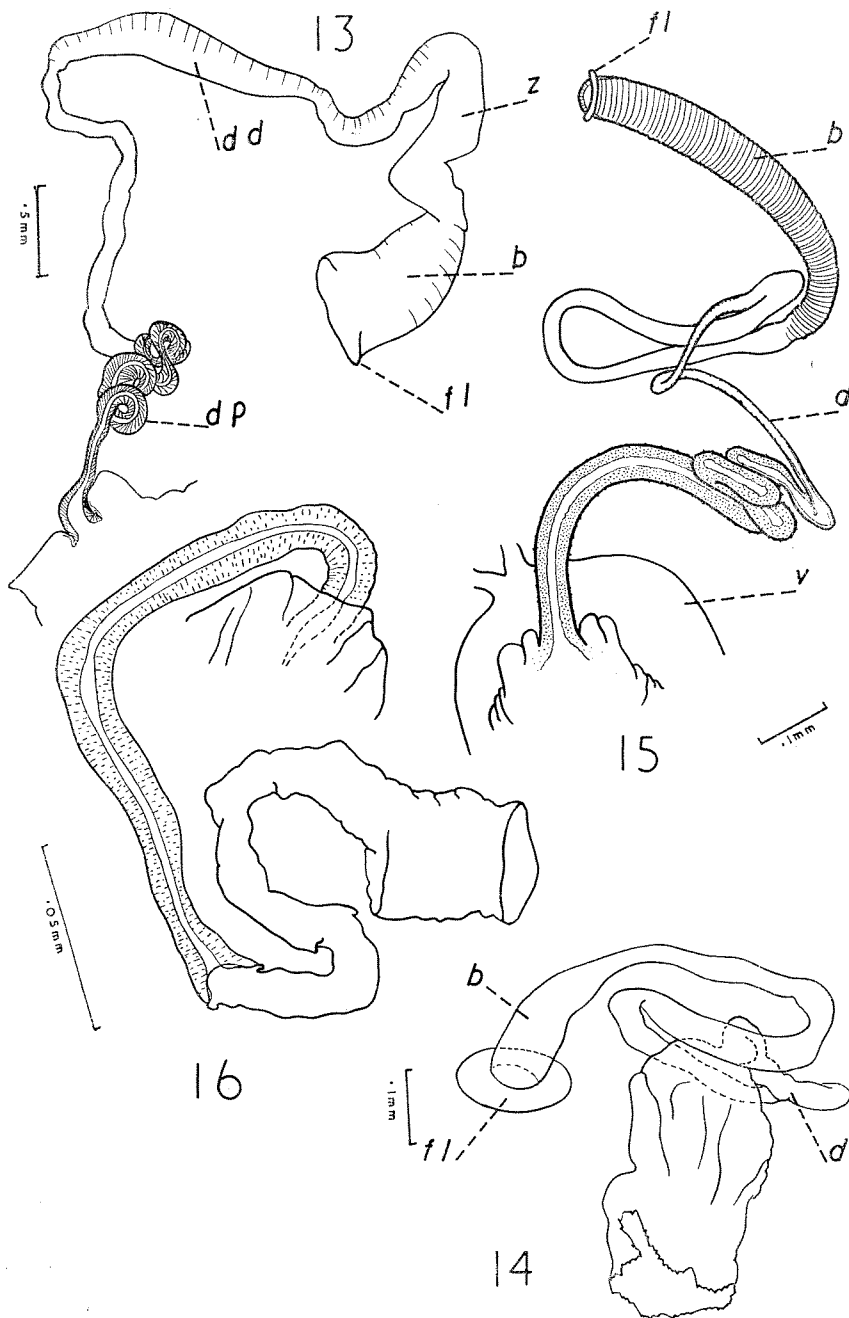
NOTONECTIDAE: *Notonecta glauca* L. [Larsén], *Notonecta obliqua* Gallen (fig. 13).

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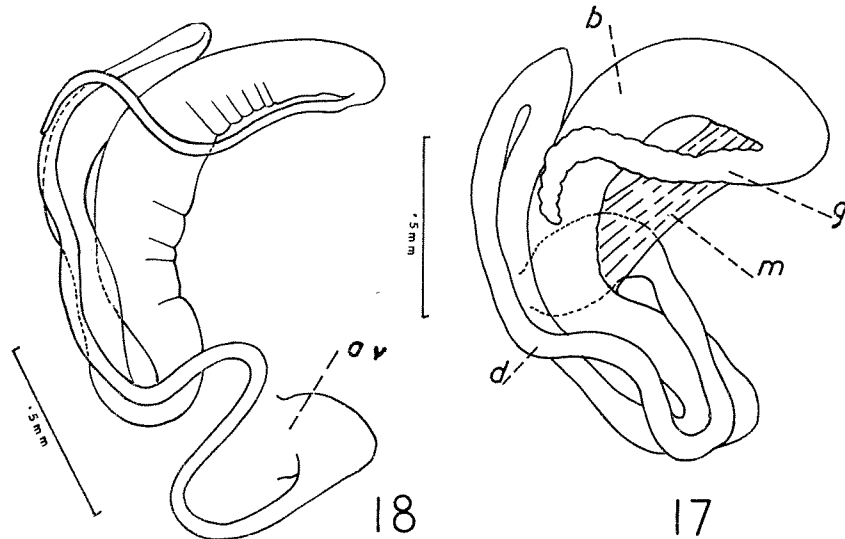


FIGS. 13-16.—Spermathecae. Potash. (13) *Notonecta obliqua* (Notonectidae). (14) *Plea leachi* (Pleidae). (15) *Neotrepes usingeri* (Helotrephidae). (16) *Mononyx annulipes* (Gelastocoridae).

PLEIDAE : *Plea leachi* MacGregor (fig. 14), *Plea* sp.
 HELOTREPHIDAE : *Neotrepes usingeri* China (fig. 15).
 GELASTOCORIDAE : *Mononyx annulipes* Horvath (fig. 16).

4. Naucoridae, Aphelocheiridae, Corixidae, Ochteridae (figs. 17, 18).

Larsén has described the reproductive organs of *Naucoris*, *Aphelocheirus*, *Corixa* and *Sigara*. The spermatheca in these families has a narrow duct leading to a fusiform sperm bulb (*b*). The apex of the bulb is drawn out and surrounded by secretory cells (*g*). In the Naucoridae and Ochteridae it has the form of a vermiform tube bent on the sperm bulb. In the Corixidae the tube is very



FIGS. 17, 18.—*Ochterus marginatus*, spermatheca (Ochteridae): (17) Whole mount. (18) Potash.

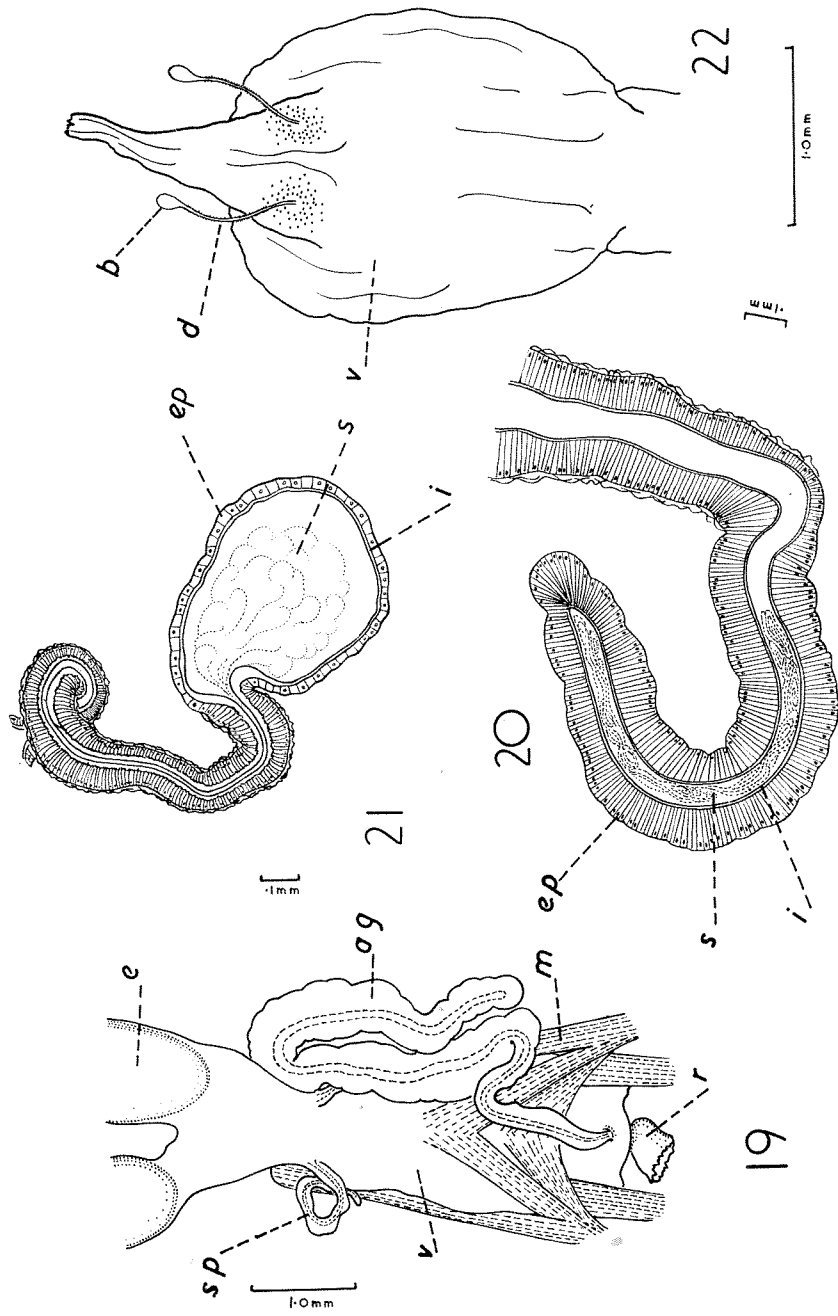
long and follows a twisted course amongst the mass of secretory cells. In *Aphelocheirus*, however, the glandular region is short, being merely the pointed apex of the sperm bulb. The sperm bulb of the Naucoridae, Aphelocheiridae and Corixidae is completely invested by muscle fibres, but in *Ochterus* the fibres form a stout muscle (*m*) stretched between the two ends of the curved sperm bulb.

Species examined and from the literature :

- OCHTERIDAE : *Ochterus marginatus* (Latreille) (fig. 17, 18).
 NAUCORIDAE : *Naucoris cimicoides* (L.) [Larsén].
 APHELOCHEIRIDAE : *Aphelocheirus aestivalis* Fabricius [Larsén].
 CORIXIDAE : *Corixa dentipes* (Thomson) [Larsén], *Sigara salbergi* Fieber [Larsén].

5. Reduviidae, Phymatidae, Tingidae (figs. 19–26).

All the species of Reduviidae examined, and those described by other workers, have two spermathecae. These are usually small and simple sacs

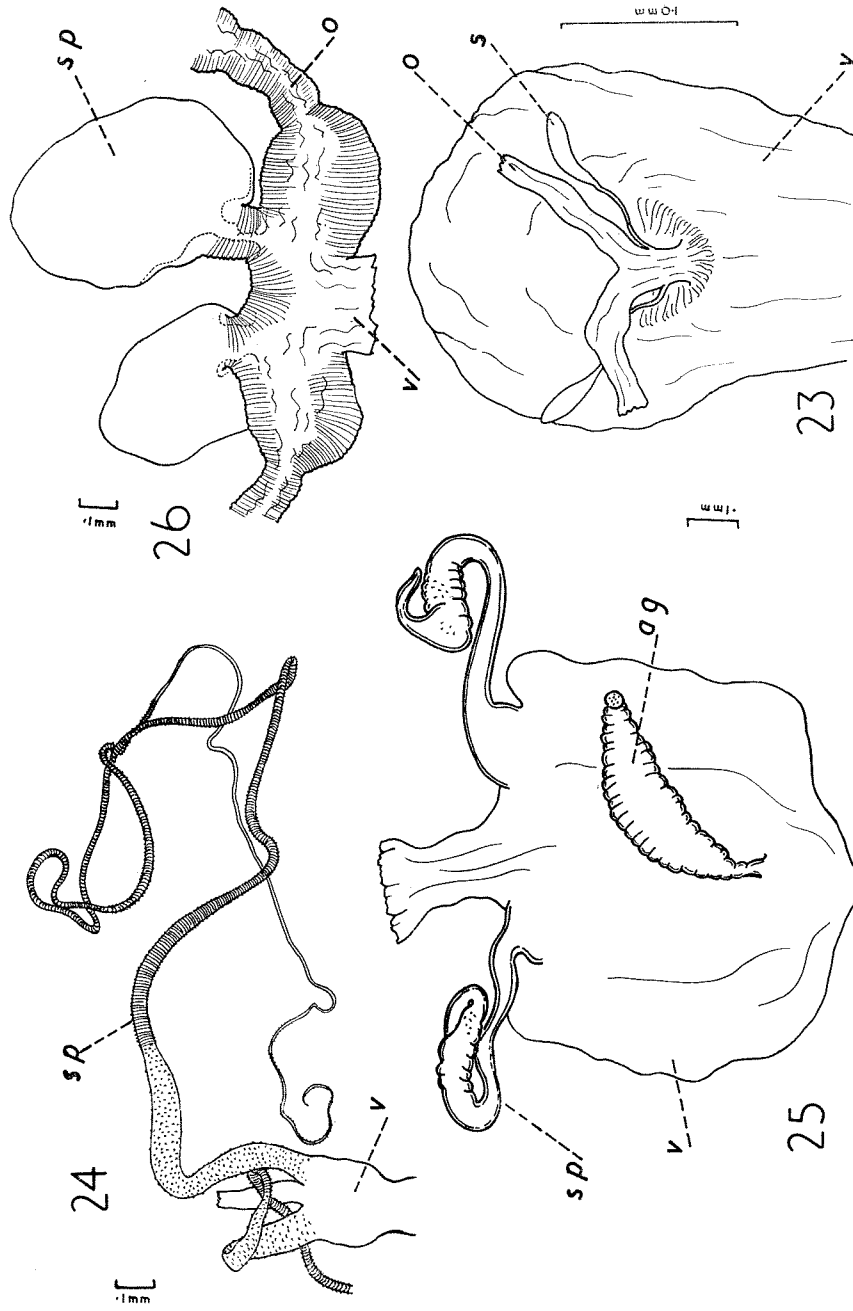


Figs. 19-22.—(19) *Rhodnius prolixus*, female reproductive organs (Triatominae, Reduviidae). (20) *R. prolixus*, spermatheca; cleared specimen in optical section. (21) *Triatoma infestans*, spermatheca; cleared and in optical section (Triatominae, Reduviidae). (22) *Coranus subapterus*, vagina and spermathecae. Potash (Harpactorinae, Reduviidae).



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Figs. 19-22.—(19) *Rhodnius prolixus*, female reproductive organs (Triatominae, Reduviidae). (20) *R. prolixus*, spermatheca; cleared specimen in optical section. (21) *Triatoma infestans*, spermatheca; cleared and in optical section (Triatominae, Reduviidae). (22) *Coranus subapterus*, vagina and spermathecae. Potash (Harpactocorinae, Reduviidae).



Figs. 23-26.—(23) *Reduvius personatus*, vagina and spermatheca. Potash (Reduviinae, Reduviidae). (24) *Empicoris vagabundus*, vagina and spermatheca. Potash (Emesinae, Reduviidae). (25) *Phymata erosa*, vagina, spermatheca and accessory gland. Potash (Phymatidae). (26) *Tingis ampliata*, spermathecae. Potash (Tingidae).

or tubes opening near the anterior end of the vagina. Galliard (1935) did not observe that the spermathecae are cuticular structures in *Rhodnius* and *Triatoma* but these studies have shown that a thin unsclerotised lining is present (figs. 20, 21, *i*). The vagina is usually very large and consists of a short narrow neck-like anterior part leading into an expanded saccular posterior part. The vaginal intima is thin and unsclerotised. In *Rhodnius* and *Triatoma* the expanded vagina serves for the reception and temporary storage of spermatophores (Khalifa, 1950). Some Reduviidae have accessory glands (*ag*) opening into the posterior part of the vagina. In some there is a single gland (e.g. *Rhodnius*), in others there are two glands (e.g. *Sycanus*, described by Kershaw, 1909). The spermathecae of *Empicoris vagabundus* (Emesinae) (fig. 24) are of interest. Each is an exceedingly long, narrow, twisted tube which decreases in diameter to become thread-like distally.

The spermathecae and single accessory gland of *Phymata* (Phymatidae) (fig. 25) are similar in form to those of the Reduviidae, although the cuticle is considerably thicker.

In the Tingidae there are two saccular spermathecae arising from an expanded region at the junction of the vagina and lateral oviducts. In *Tingis* and *Stephanitis* the cuticular lining of the genital ducts is extended for some distance into the lateral oviducts.

Species examined and from the literature :

REDUVIIDAE: *Rhodnius prolixus* Stål [Galliard and personal obs.] (figs. 19, 20), *Triatoma infestans* Klug (fig. 21), *T. rubrovaria* Blanchard [Galliard], *T. vitticeps* Stål [Galliard], *T. dimidiata* (Latrielle) [Galliard], *T. protracta* Uehler [Galliard], *Coranus subapterus* (De Geer) (fig. 22), *Sycanus croceovivattus* Dohrn [Kershaw], *Reduvius personatus* (L.) (fig. 23), *Empicoris vagabundus* (L.) (fig. 24).

PHYMATIDAE: *Phymata erosa* L. (fig. 25).

TINGIDAE: *Tingis ampliata* (Herrich-Schaeffer) (fig. 26), *Stephanitis rhododendri* Horvath.

6. Miridae, Anthocoridae, Microphysidae, Cimicidae,
Polycetenidae, Nabidae, Velocipedidae.

There is no spermatheca. In many, very interesting methods of haemocoelic fecundation have been demonstrated by other workers. In the Miridae, Nabidae and Velocipedidae the vagina is enlarged and its intima thickened and partially sclerotised to form a structure usually termed the bursa copulatrix.

The following are the main studies on reproduction in these families: Kullenberg (1947), Miridae; Carayon (1952*d*, 1953*a, b*), Anthocoridae; Carayon (1949), Microphysidae; Berlese (1898), Cragg (1920), Abraham (1934), Mellanby (1939), Carayon (1952*d*), Cimicidae; Hagan (1931), Ferris and Usinger (1939), Jordan (1922), Polycetenidae; Kullenberg (1947), Carayon (1952*a, b, c*), Nabidae.

In addition the following species were examined by the writer:

NABIDAE: *Nabis rugosus* (L.).

VELOCIPEDIDAE: *Scotomedes alienus* Distant.

MIRIDAE: *Leptoterna dolobrata* (L.).

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7. Saldidae, Leptopodidae, Aradidae, Berytidae, Pyrrhocoridae, Coreidae, Pentatomidae, Urolabidae, Phloeidae, Cydnidae, Plataspidae (figs. 27-68).

Although there is considerable diversity in detail, the spermathecae of these families have certain common features.

There is a spermathecal duct, which may be simple or complex, leading to an apical sperm receptacle or bulb surrounded by a mass of secretory cells (fig. 42, *g*). Between the receptacle and the main part of the duct is a muscular pump consisting of a cylinder of muscle fibres surrounding the central duct. The fibres are attached at least at one end and often at both to a cuticular flange or flanges, projecting from the duct wall (fig. 42, *fd, fp*). When one flange is absent the fibres are attached to the duct wall or to the base of the sperm bulb.

The differences in detail often correspond to family or subfamily groupings. It is not proposed to describe them in full in this present paper. The following are the main characteristics of the spermathecae examined in these families:

SALDIDAE: There is a single deep pump flange, the fibres being attached distally to the bulb.

LEPTOPODIDAE: In *Leptopus* the proximal pump flange is deep and narrow (as in the Saldidae). There is a disc-like proximal flange at the base of the bulb.

ARADIDAE: A short cylindrical apical bulb with a distal pump flange encircling its base and with a fairly long stout pump region. The spermathecal duct is bent acutely where it leaves the pump region with the result that one side of the proximal flange is reduced.

BERYTIDAE: The apical bulb is large, ovoid or globular, and with a thin intima. A well-developed distal pump flange encircles its base. The proximal flange is absent or poorly developed and the spermathecal duct is fairly short.

PYRRHOCORIDAE: There is no distal flange to the pump, the fibres being attached around the basal edge of the bulb.

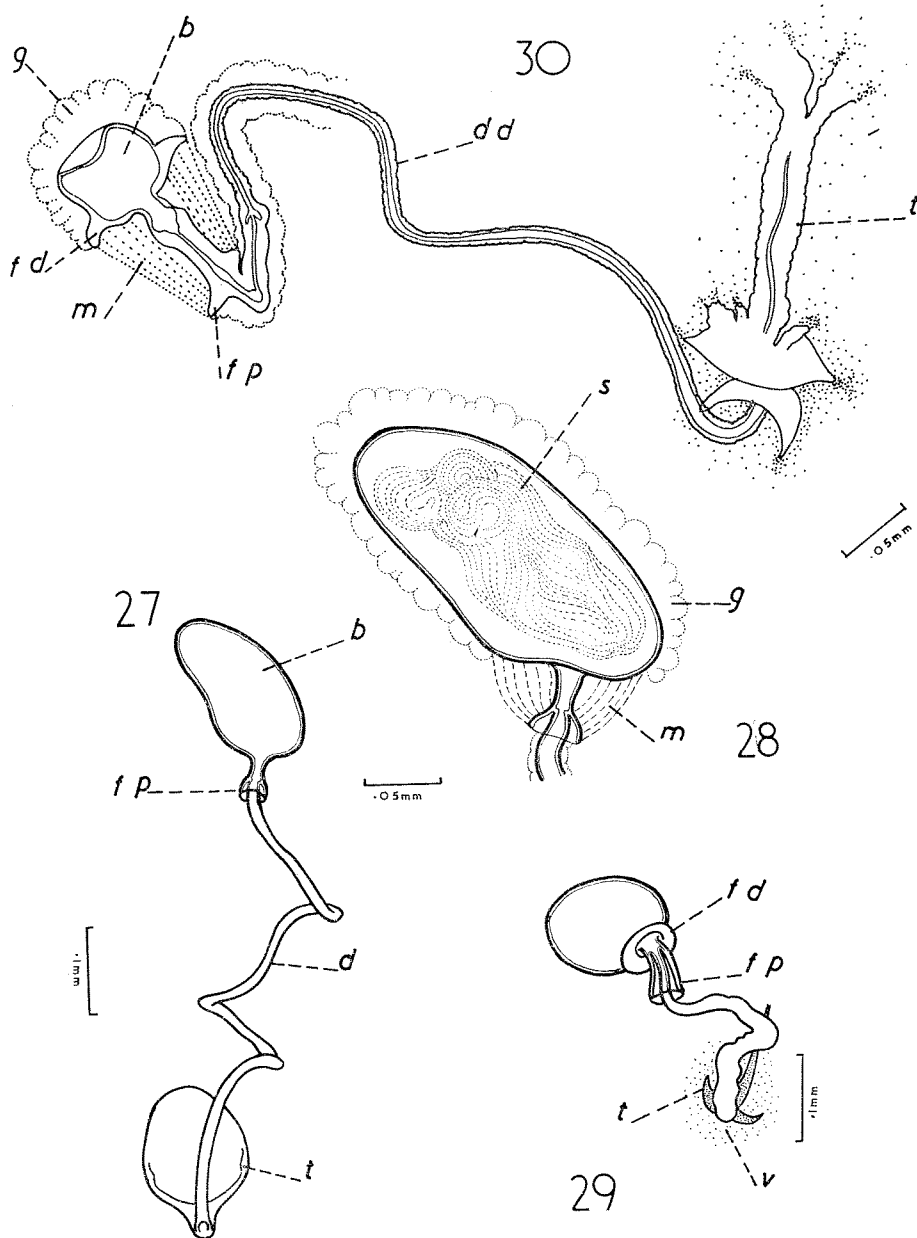
COREIDAE: There is no distal flange, the muscle fibres being attached to a coiled mass of the distal parts of the spermathecal duct. Behind the pump the spermathecal duct is short or fairly short. The cuticular lining is usually thick.

PENTATOMIDAE: There is a well-developed pumping region with two definite flanges. In this family the rest of the organ has a considerable range of form from the relatively simple type of, for example, the Acanthosominae, to the complex organ of the Pentatominae. The differences in detail will be obvious from the figures and, in addition, those considered to be of importance will be mentioned in a later section (VII) where the classification of the family is considered.

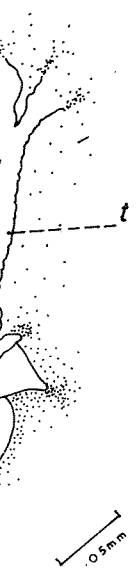
UROLABIDAE: In *Urolaba* the spermatheca is simple and small with a short duct. There is a single pump flange (the proximal) and the flattened sperm bulb has a blind tubular apical projection.

PHLOEIDAE: 'The long pump region in *Phloeophana* has two flanges.' The middle third of the spermathecal duct has the form of a hollow ovoid dilation.

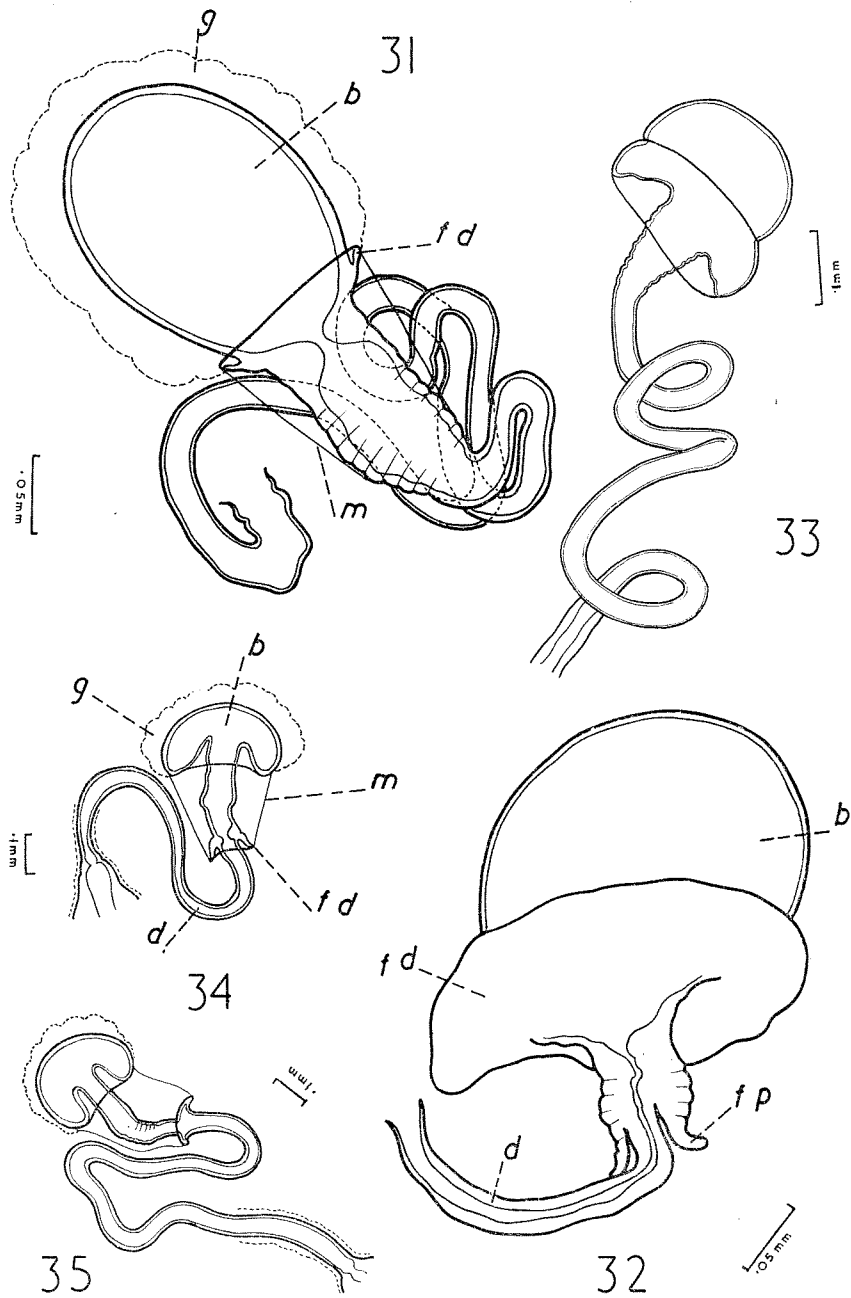
CYDNIDAE: The spermatheca is small. There are two flanges and the spermathecal duct has its base modified by partial invagination to form a double-walled dilation. Fusion and sclerotisation may partially obscure the structure. In one species examined (*Galgupha ovalis*) the spermathecal duct has a large thin-walled sac-like diverticulum.



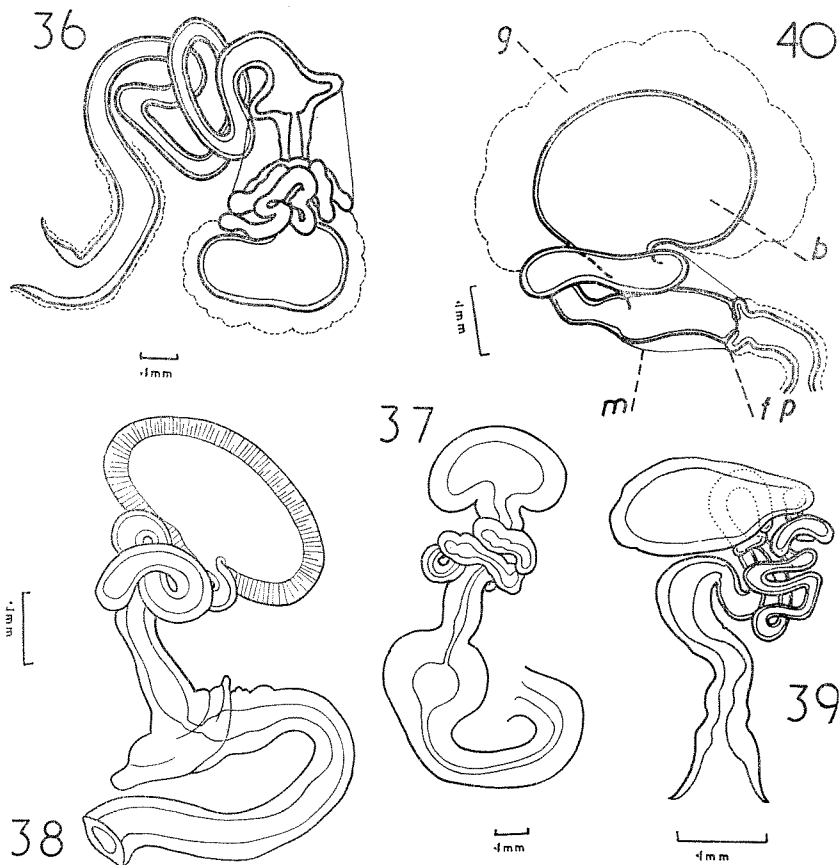
FIGS. 27-30.—(27) *Saldula saltatoria*, spermatheca. Potash (Saldidae). (28) *S. saltatoria*, spermathecal bulb and pump; cleared specimen. (29) *Leptopus marmoratus*, spermatheca. Potash (Leptopodidae). (30) *Aradus cinnamomeus*, spermatheca. Potash (Aradidae).



S. saltatoria,
atus, spermatheca. Potash



FIGS. 31-35.—Spermathecae : (31) *Berytinus minor*, cleared. (Berytidae). (32) *Metacanthus pluto*, potash (Berytidae). (33) *Metatropis rufescens*, potash (Berytidae). (34) *Pyrrhocoris apterus*, cleared (Pyrrhocoridae). (35) *Dysdercus fuscatus*, cleared (Pyrrhocoridae).



FIGS. 36-40.—Spermathecae: (36) *Coreus marginatus*, cleared (Coreinae, Coreidae). (37) *Anoplocnemis* sp., potash (Coreinae, Coreidae). (38) *Acantholybas brunneus*, potash (Coreinae, Coreidae). (39) *Coriomeris denticulatus*, potash (Pseudophloeinae, Coreidae). (40) *Myrmus miriformis*, cleared (Rhopalinae, Coreidae).

PLATASPIDAE: The spermatheca is simple. There are two stout pump flanges and the duct is short.

Species examined and from the literature:

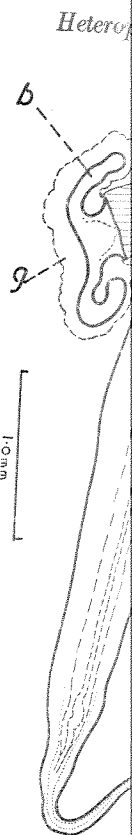
SALDIDAE: *Saldula saltatoria* (L.) (figs. 27, 28), *S. littoralis* (L.).

LEPTOPODIDAE: *Leptopus marmoratus* Goeze (fig. 29).

ARADIDAE: *Aradus cinnamomeus* Panzer (fig. 30), *A. debilis* Uehler.

BERYTIDAE: *Berytinus minor* (Herrich-Schaeffer) (fig. 31), *Metacanthus pluto* Gross (fig. 32), *Metatropus rufescens* (Herrich-Schaeffer) (fig. 33).

PYRRHOCORIDAE: *Pyrrhocoris apterus* (L.) (fig. 34), *Dysdercus fasciatus* Signoret (fig. 35), [Freeman, 1947, figures spermathecae of 6 other species of *Dysdercus*].



FIGS. 41-45.—(41) *N. viridula*, spermatheca. (42) *N. viridula*, spermatheca. (43) *N. viridula*, spermatheca. (44) *N. viridula*, spermatheca. (45) *N. viridula*, spermatheca.

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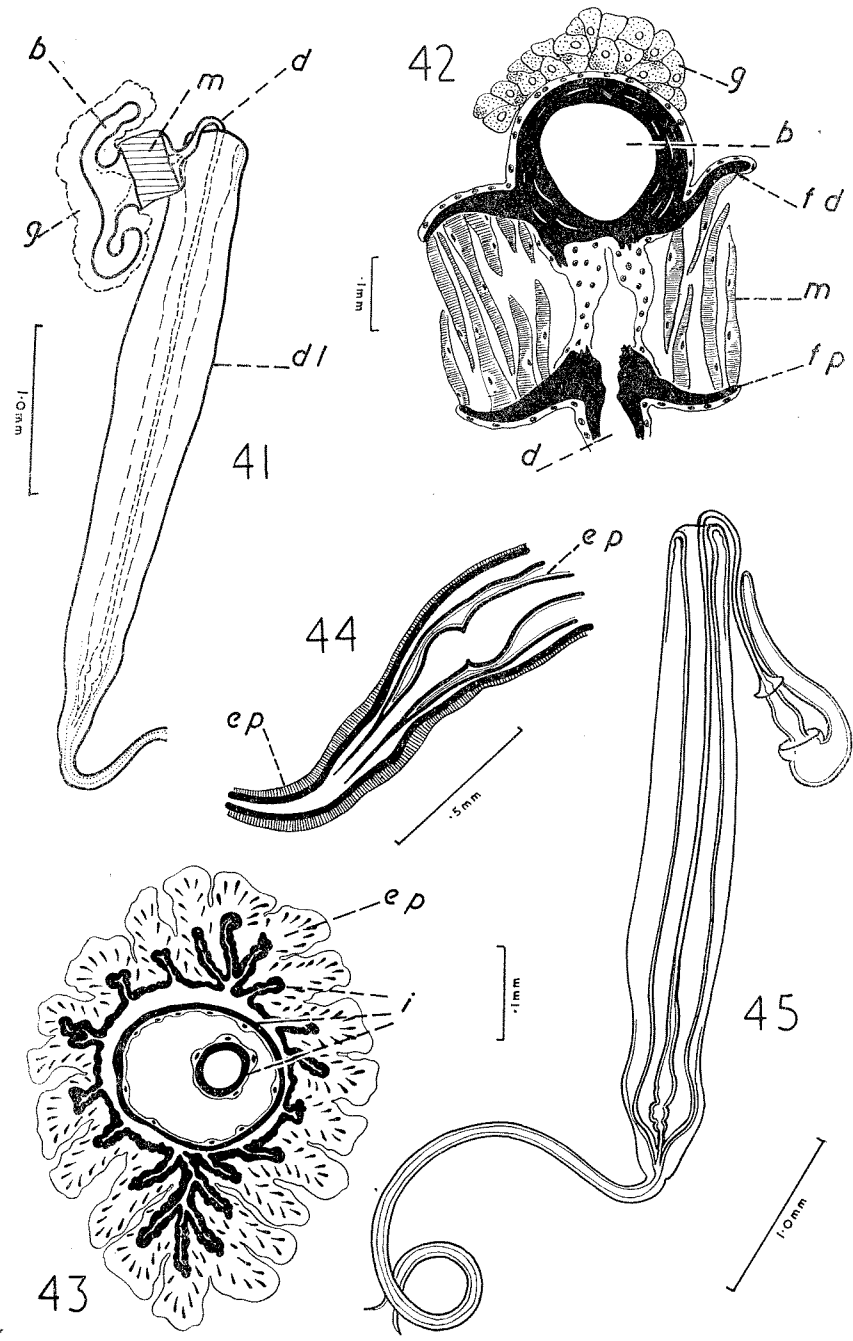
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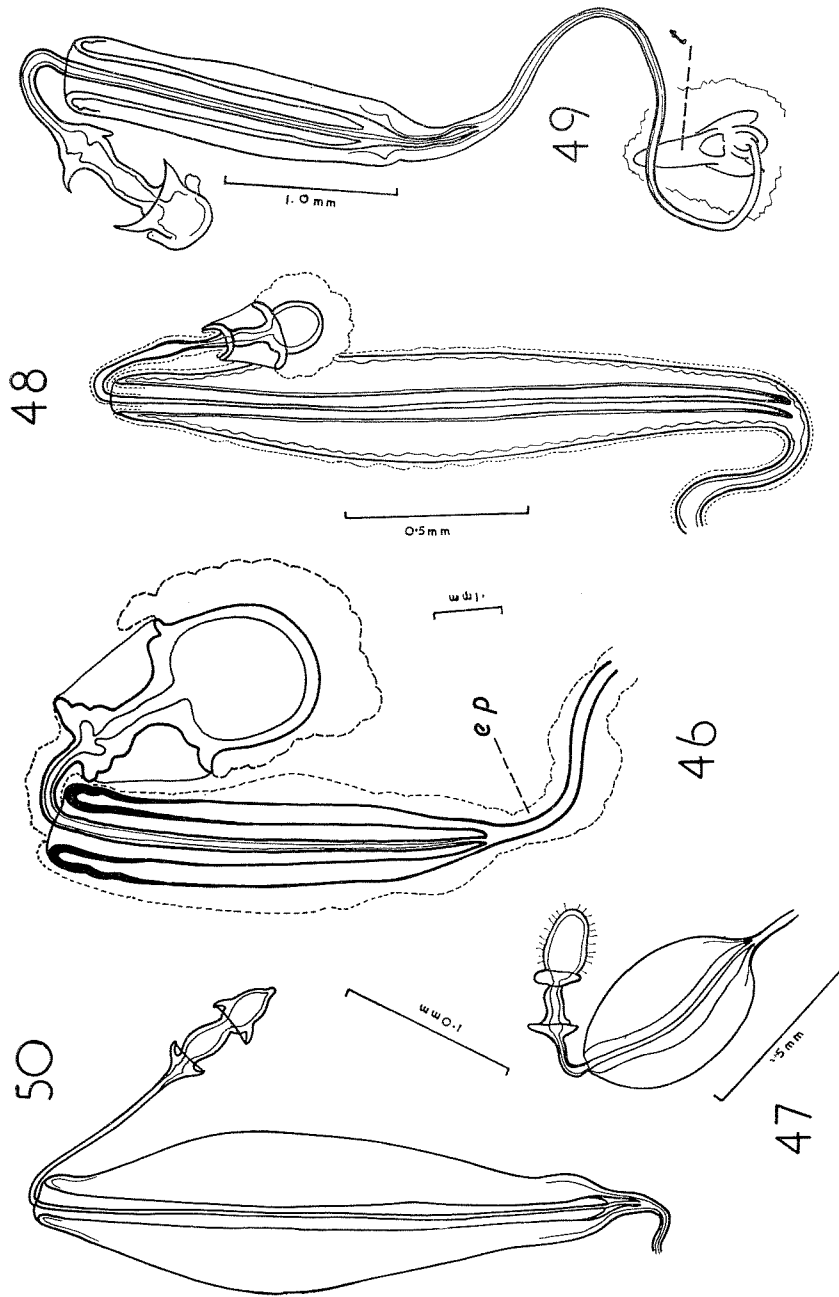
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FIGS. 41-45.—(41) *Nezara viridula*, spermatheca. Cleared (Pentatominae, Pentatomidae). (42) *N. viridula*, longitudinal section through spermathecal bulb and pump. (43) *N. viridula*, transverse section spermathecal duct dilation. (44) *N. viridula*, base of spermathecal duct dilation. Cleared and in optical section. (45) *Theseus modestus*, spermatheca. Potash (Pentatominae, Pentatomidae).



Figs. 46-50.—Spermathecae: (46) *Cermatulus nasalis*, cleared (Asopinæ, Pentatomidae). (47) *Hoploxya coeruleus*, potash (Asopinæ, Pentatomidae). (48) *Podops vivanta*, cleared (Graphosomatinae, Pentatomidae). (49) *Dalsira costalis*, potash (Phyllocephalinae, Pentatomidae). (50) *Platycarenum humilis*, potash (Discocephalinae, Pentatomidae).

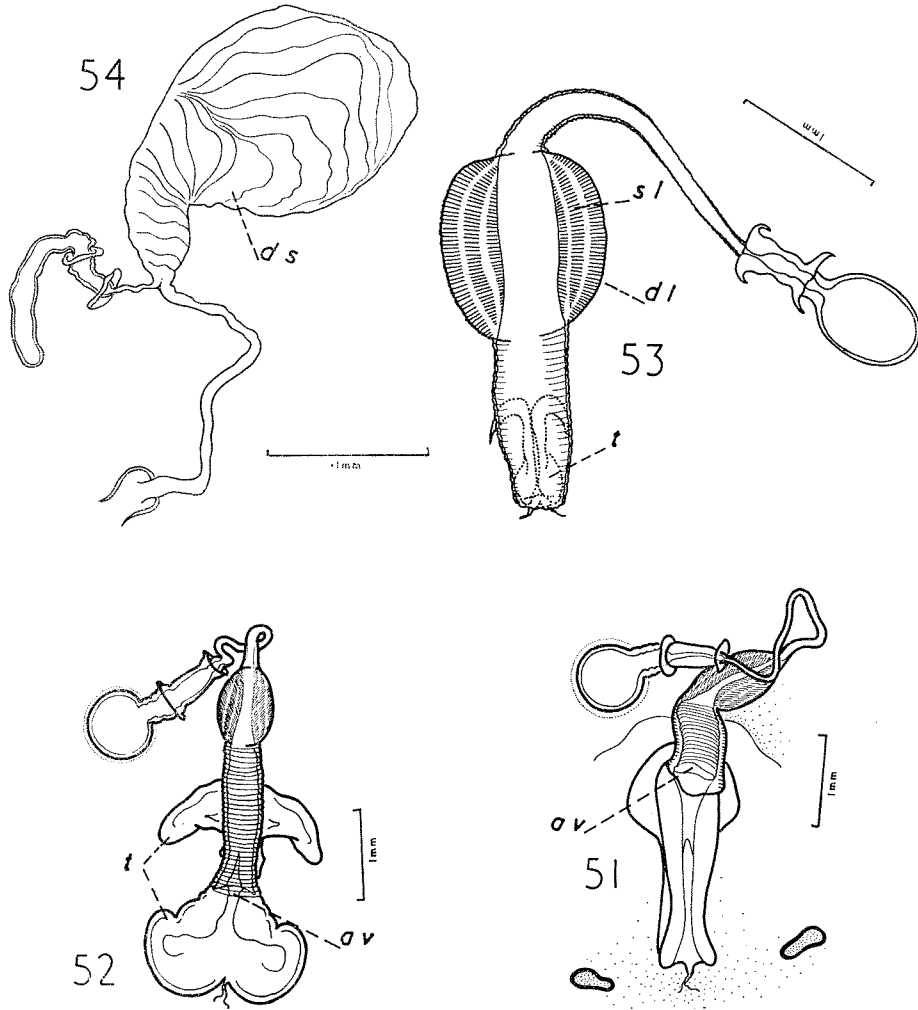
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COREIDAE: *Coreus marginatus* (L.) (fig. 36), *Anoplocnemis* sp. (fig. 37), *Acantholybas brunneus* Breddin (fig. 38), *Coriomeris denticulatus* (Scopoli) (fig. 39), *Myrmus miriformis* (Fallén) (fig. 40).

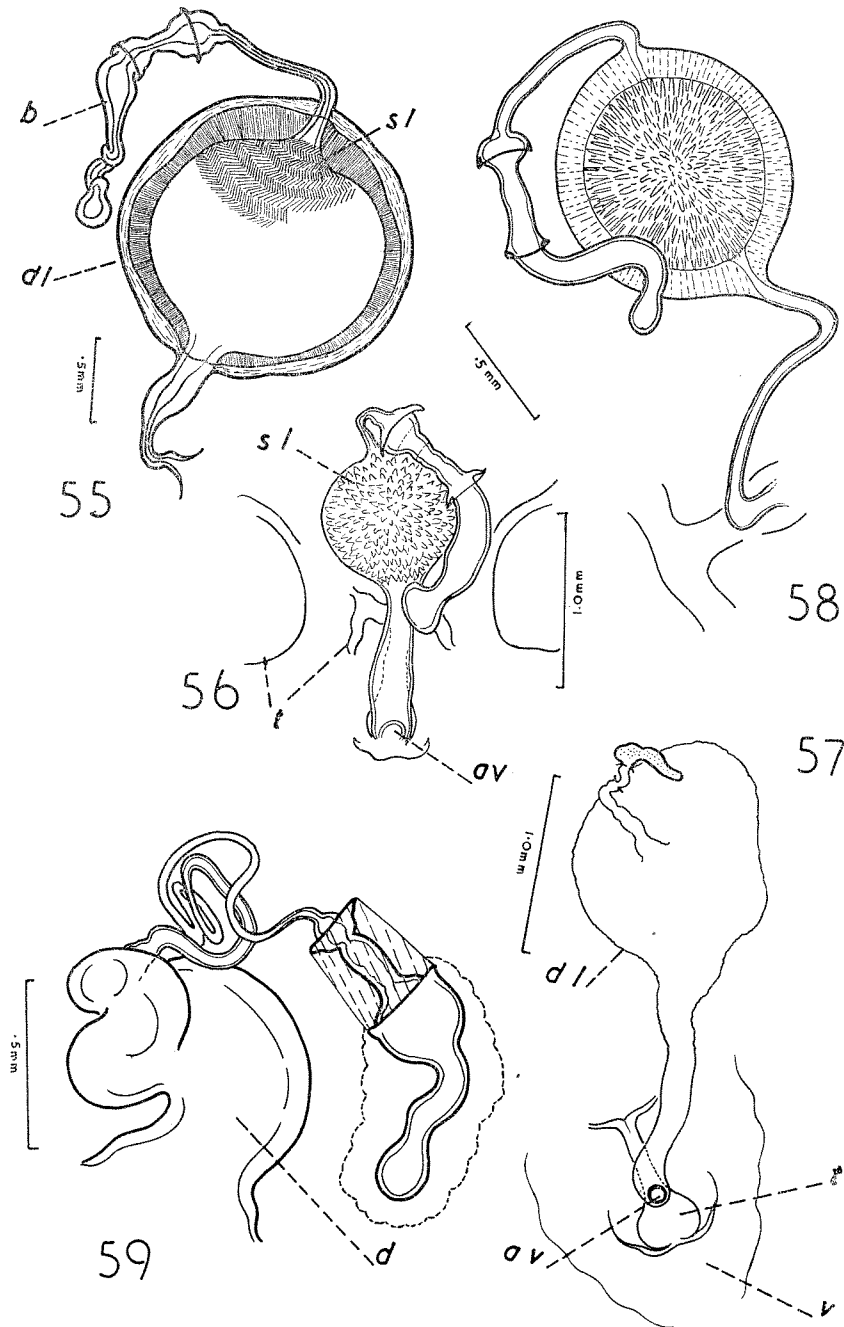
PENTATOMIDAE:

Pentatominae: *Nezara viridula* (L.) [Malouf, 1933 (inaccurate) and personal observations] (figs. 41-44), *Glaucius amyoti* (Dallas), *Dictyotus caenosus* (Westwood), *Carpocoris fuscispina* Boheman, *Eurydema ventralis* Kolenati [Bonnemaison, 1952, and personal observation], *E. ornata* (L.), *Theseus modestus* (Stål) (fig. 45).

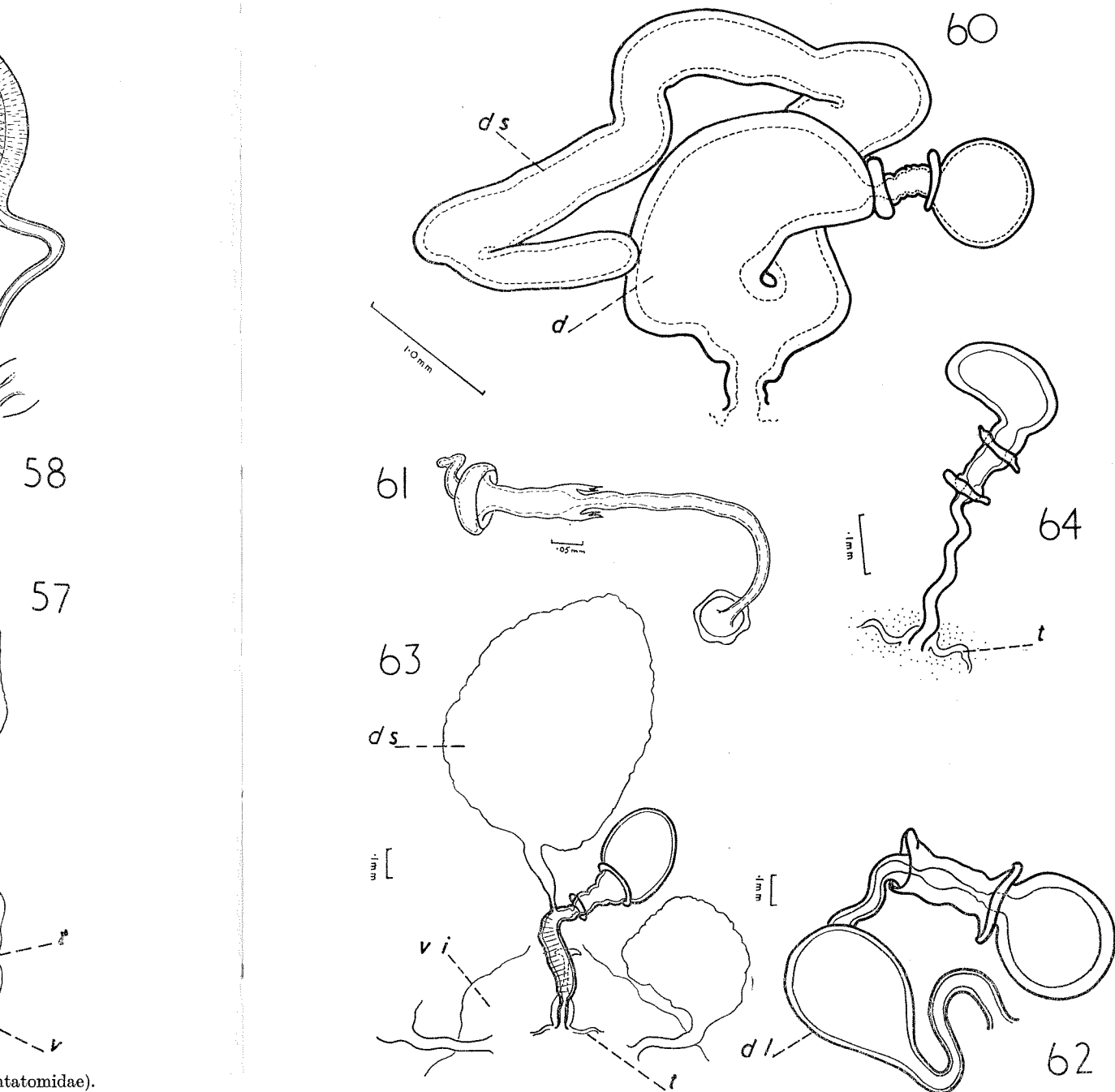
Figs. 46-50.—Spermathecae: (46) *Cermatulus nasalis*, cleared (Asopinae, Pentatomidae). (47) *Hoplocys coeruleus*, potash (Asopinae, Pentatomidae). (48) *Podops inuncta*, cleared (Graphosomatinae, Pentatomidae). (49) *Dalsira costalis*, potash (Phyllocephalinae, Pentatomidae). (50) *Platycarenum humilis*, potash (Discocephalinae, Pentatomidae).



FIGS. 51-54.—Spermathecae. Potash (All Tessaratominae, Pentatomidae). (51) *Tessaratomia javenica*. (52) *Carpona imperialis*. (53) *Phyllocoris acuta*. (54) *Rhoecocoris sulciventris*.



Figs. 55-59.—Spermathecae. (55) *Cryptacrus comes*, potash (Scutellerinae, Pentatomidae). (56) *Scutiphora pedicellata*, potash (Scutellerinae, Pentatomidae). (57) *Tectocoris diophthalmus*, potash (Scutellerinae, Pentatomidae). (58) *Sphaerocoris annulus*, potash (Scutellerinae, Pentatomidae). (59) *Acanthosoma haemorrhoidale*, cleared (Acanthosominae, Pentatomidae).



FIGS. 60-64.—Spermathecae. Potash. (60) *Aspongopus viduatus* (Dinidorinae, Pentatomidae). (61) *Urolaba tenera* (Urolabidae). (62) *Phloeophana longirostris* (Phloeidae). (63) *Galgapha ovalis* (Cydnidae). (64) *Coptosoma inclusa* (Plataspidae).

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- Asopinae: ✓ *Cermatulus nasalis* (Westwood) (fig. 46), ✓ *Hoplocxys coeruleus* Dallas (fig. 47), ✓ *Glypsus conspicuus* (Westwood).
- Graphosomatinae: ✓ *Graphosoma italicum* Mueller [Berlese, 1899, and personal observation], ✓ *Podops inuncta* Fabricius [Leston, 1953a, and personal observations] (fig. 48).
- Phyllocephalinae: ✓ *Dalsira costalis* (Germar) (fig. 49).
- Discocephalinae: ✓ *Platycarenum humilus* (Herrich-Schaeffer) (fig. 50).
- Tessaratominae: ✓ *Tessarotoma javenica* (Thunberg) (fig. 51), ✓ *Carpona imperialis* (Dohn) (fig. 52), ✓ *Phyllocoris acuta* Jeannel (fig. 53), ✓ *Rhoecocoris sulciventris* (Stål) (fig. 54).
- Scutellerinae: ✓ *Cryptacrus comes* (Fabricius) (fig. 55), ✓ *Scutiphora pedicellata* (Kirby) (fig. 56), ✓ *Calidea dregii* Germar, ✓ *Tectocoris diophthalmus* (Thunberg) (fig. 57), ✓ *Sphaerocoris annulus* (Fabricius) (fig. 58).
- Acanthosominae: ✓ *Acanthosoma haemorrhoidale* (L.) (fig. 59), ✓ *Rhopalimorpha lineolaris* Pendergrast, ✓ *R. obscura* White.
- Dinidorinae: ✓ *Aspongopus viduatus* (Fabricius) (fig. 60).
- UROLABIDAE: *Urolaba tenera* Westwood (fig. 61).
- PHOEBIDAE: *Phloeophana longirostris* (Spinola) (fig. 62).
- CYDNIDAE: *Galgupha ovalis* Huss (fig. 63), *Sehirus bicolor* (L.) (fig. 65), *Macroclytus brunneus* Fabricius (fig. 66), *Thyreocoris scarabaeoides* (L.) (fig. 67).
- PLASTASPIDAE: *Coptosoma inclusa* Stål (fig. 64), *Libyaspis flavosparsa* (Montandon) (fig. 68).

8. Families in which the spermatheca shows little affinity with any of the above types.

AËPOPHILIDAE.

Unsatisfactory mounts of the spermatheca of *Aëpophilus bonnairei* Signoret were prepared and the author has not had further opportunity to examine females of this species. The organ seems to have a long globular apical bulb and a short wide duct. It has not been possible to determine whether there is a pumping mechanism.

CRYPTOSTEMMATIDAE.

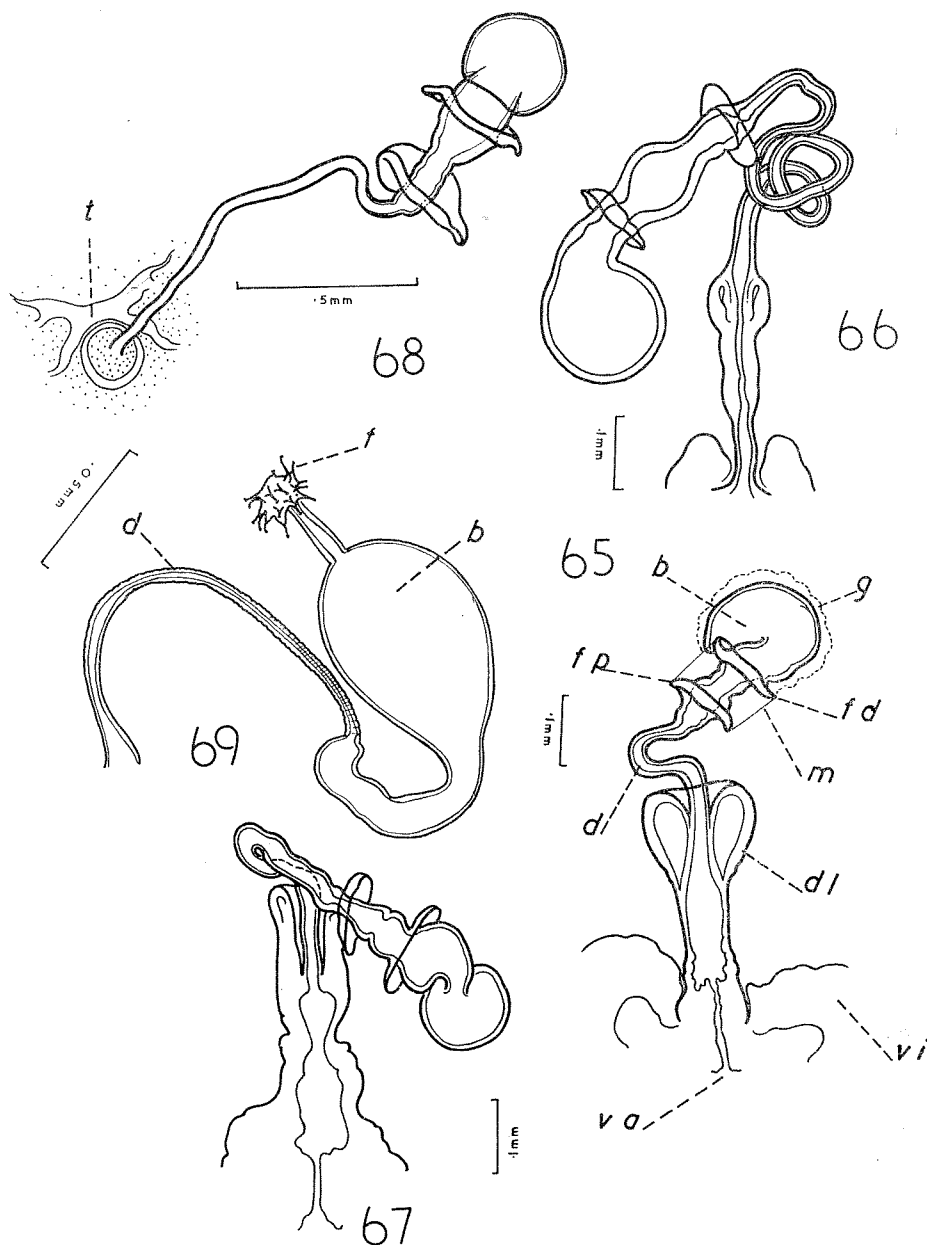
The dried spermatheca of *Ceratocombus australiensis* Gross (fig. 69) has a short duct with an ovoid bulb bearing a short narrow apical canal with an expanded cap bearing a mass of ducteoles (*f*). Similar spermathecae have been figured by Wygodzinsky (1951 and 1953) for *Trichotonannus makilingensis* Wygodzinsky, *T. dundo* Wygodzinsky, *Guapinannus bierigi* Wygodzinsky and *Peloridinannus margaritatus* Wygodzinsky.

ENICOCEPHALIDAE.

A single dried female of *Systelloderes maclachlani* Kirkaldy and a few specimens of *S. angustatus* (Champ.) were examined and no spermathecae were found. Carayon (1950*b*) examined fresh specimens of *Oncyclocotis curculio* Karsch and reported that there is a tubular genital chamber on the dorsal wall of which is a small seminal receptacle. From the brief description it is



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FIGS. 65-69.—Spermathecae. (65) *Sehirus bicolor*, cleared (Cydnidae). (66) *Macrocytus brunneus*, potash (Cydnidae). (67) *Thyreocoris scarabaeoides*, potash (Cydnidae). (68) *Libyaspis flavosparsa*, potash (Plataspidae). (69) *Ceratocombus australiensis*, potash (Cryptostemmatidae).

not clear whether the structure is a true spermatheca or a simpler specialisation of the dorsal vaginal wall.

LYGAEIDAE.

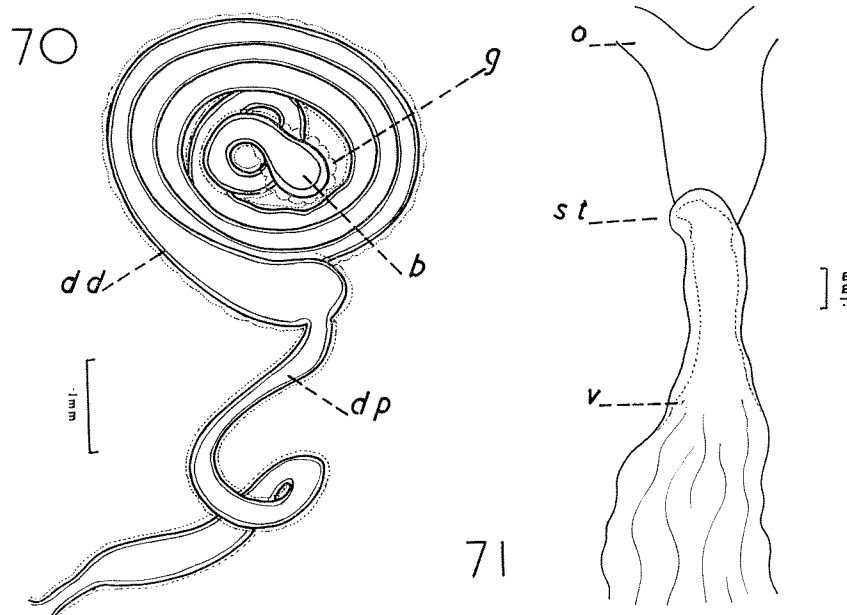
Fourteen genera from seven subfamilies were examined. A definite spermatheca was found in all these but there is a bewildering diversity in its form even amongst members of the same subfamily. It is intended to deal with this family in a separate publication.

COLOBATHRISTIDAE.

The spermatheca of *Phaenacantha sedula* Horvath is simple with a globular apical bulb and a very long irregularly-coiled duct.

PIESMIDAE.

The spermatheca of *Piesma quadratus* (Fieber) (fig. 70) has the form of a long tube with its distal parts closely coiled in a flat spiral of about four



FIGS. 70, 71.—(70) *Piesma quadratus*, spermatheca. Cleared (Piesmidae). (71) *Aneurys laevis*, vagina and common oviduct (Dysodiidae).

whorls. Its apex, which is held in the centre of the spiral, is globular and surrounded by a mass of secretory cells. Wille (1929) figured the spermatheca ("Vaginalrohr") of this species. He did not show an apical bulb and the whorls of the duct are held in a very open coil.

DYSODIIDAE.

The spermatheca of *Mezira pacifica* Usinger is very similar to that of the Aradidae. In *Aneurys laevis* (Fabricius) (fig. 71) and *Ctenoneurus hochstetteri*

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(Mayr), on the other hand, there is a simple small diverticulum of the dorsal wall of the vagina. It is surrounded by tall glandular cells. Sections of this region show sperm lying in masses of secretion in the diverticulum as well as within the anterior parts of the vagina.

9. Families for which information on the spermatheca is lacking.¹

LEOTICHIDAE	SCHIZOPTERIDAE	ISOMETOPIDAE
TERMITAPHIDIDAE	THAUMASTOTHERIIDAE	HYOCEPHALIDAE
APHYLIDAE	JOPPEICIDAE	

III. THE MALE ORGANS.

The male organs consist of paired testes connected by vasa deferentia with a median ductus ejaculatorius. In many groups there is a dilated region, the bulbus ejaculatorius, at the anterior end of the ductus. Accessory glands are often present. These may be of mesodermal origin (mesadenes) and open into the vasa, or ectodermal (ectadenes), in which case they are diverticula of the ductus ejaculatorius.

Except for the number of follicles or sperm tubes present, the structure of the testis is fairly uniform throughout the suborder. It consists of a number of follicles arranged more or less longitudinally and bound together by an investing peritoneal sheath. The numbers of follicles in the testes of a large number of Heteroptera have been noted by Woodward (1950), and others have been observed during this present study. These range from a single follicle in *Velia caprai* Tamanini to eight in some Miridae. Woodward has noted that in most species examined the numbers of testis follicles and ovarioles are the same. When they differ the number is usually only one greater in one sex than in the other.

The vas deferens is a simple tube with an epithelium usually invested by a muscularis of circular fibres which may become greatly thickened posteriorly. In some Heteroptera the vas is dilated apically to form a vesicula seminalis. In others it is the middle or the base which is enlarged. Where accessory glands are absent the epithelium of the vesicula may be glandular. When mesadene accessory glands are present they are usually attached to the basal half of each vas, often just prior to its entry into the bulbus ejaculatorius (e.g. fig. 100, *mg*). The gland does not pour its contents into the vas immediately, but the two canals, vas and accessory gland duct, pass back to the bulbus side by side, bound together by peritoneal membrane and often by the same muscle coat. When no bulbus ejaculatorius is present, as in the water bugs and the Gerroidea, the anterior end of the ductus ejaculatorius has a well-developed muscle coat and an epithelium of extremely tall columnar secretory cells often arranged in distinct folds (figs. 73, 78, 83). This epithelium has the same appearance as that lining the lumen of the bulbus ejaculatorius in those bugs possessing one.

¹ Since the completion of these studies, Carayon (1954) has described the sperm storage apparatus in certain families including the Isometopidae and the Joppeicidae. His observations on the families investigated by the present writer, viz. Reduviidae, Phymatidae, Tingidae and Aradidae (including Dysodiidae), in general confirm this account, although he does not regard the dorsal diverticulum in *Aneurus* as a sperm storage organ. In his studies Carayon distinguishes between a true spermatheca and other sperm storage organs.

The bulbus ejaculatorius is the complex dilated anterior end of the ductus ejaculatorius. Preliminary developmental studies indicate that the structure (with the exception of its musculature and the mesodermal vasa and mesadene ducts which enter it) is of ectodermal origin, as are the ectadenes which develop as lateral outgrowths of its dorsal wall. In its simplest form (as in the Saldidae, fig. 86) the bulbus consists of an outer saccular epithelium, termed here the investing layer (ep_1), which is continuous with that of the ductus ejaculatorius. This secretes a chitinous intima (i) which usually becomes separated from the cell layer and lies loosely encircling the central parts of the organ. Posteriorly it forms a tube which traverses the ductus to the aedeagus. Within the investing epithelium and its intima are two concentric epithelial layers forming a central core to the organ. The outer one, termed the middle layer (ep_2), is usually cuboidal and secretory and its cells discharge into the space within the intima. The inner layer, or lining epithelium (ep_3), is composed of very tall cells often arranged in folds. These cells are secretory and their products enter the central lumen of the bulbus which, because of the extreme tallness of the cells, is often considerably constricted. This central canal forms the duct for sperm and for mesadene secretions, the vasa and accessory gland ducts having entered it near its anterior end. As they pass back the two inner layers become reduced in diameter, fuse and eventually disappear. Thus the contents of the central canal and the products of the middle epithelium are deposited eventually within the cuticular tube of the ductus ejaculatorius through which they pass back to the aedeagus.

In some families the condition of the bulbus is not as simple as that described above. Anteriorly, the investing epithelium does not always cover the ventral side of the central core of the organ but forms, rather, a sac-like investment of its dorsal surface only, the ventral parts being invested by a thick mass of muscle fibres. This is the condition, for example, in *Dysdercus* and *Rhopalimorpha* (figs. 101, 115). In such a case the middle epithelium is also confined to the dorsal side of the lining layer and may be continuous with the investing epithelium, or almost so. When ectadenes are present they open into this dorsal sac of the bulbus. In some cases there may be large bladder-like diverticula of the dorsal sac into which the ectadenes may, or may not, open (figs. 109, *er*; 110, *es*).

The ductus ejaculatorius is a simple, thin-walled tube with an epithelium continuous with the investing layer of the bulbus (fig. 102). The cuticular lining (fig. 103*i*), which is the continuation of the loose intima of the bulbus, is usually separated from the epithelium and forms a central tube carrying the sperm and secretions of the mesadenes, the lining epithelium and the middle layer back to the aedeagus. The secretions of the ectadenes and the investing epithelium of the bulbus are, however, confined to the region outside this tube.

Although the male organs have been examined in some detail, for the purposes of classification they are probably best considered primarily on the basis of the three following characters: (*a*) the presence or absence of a definite bulbus ejaculatorius, (*b*) the presence or absence of accessory glands and, if they are present, the type of gland and (*c*) the number of follicles in the testis. Secondary characters which will be discussed are the form of the testis, the position of the vesicula seminalis, the form of the vas deferens, the presence or absence of ectodermal sacs associated with the bulbus ejaculatorius.

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The types of male reproductive organs noted.

Using the three main characters it is possible to divide the types of male reproductive organs into four major groups.

1. Gerridae, Veliidae, Hydrometridae, Mesoveliidae, Hebridae (figs. 72-80).

There is no bulbus ejaculatorius, the long vas deferentia uniting to form a simple ductus ejaculatorius. The number of testis follicles is small (1 or 2). Accessory glands are absent (except in *Mesovelgia*, where they are small and saccular).

In *Gerris lacustris* L. (figs. 72, 73) the reproductive organs are elongated, correlated perhaps with the lack of accessory glands. Each testis comprises two completely separate lobes, each consisting of a single follicle. Half-way along each follicle arises a short vas efferens. The vasa deferentia, vesiculae seminales and ductus ejaculatorius are all lined with a secretory epithelium.

In *Velia caprai* Tamanini (figs. 77, 78) each testis is large, ovoid and consists of a single follicle. As in *Gerris*, the ducts have a secretory epithelium. The ductus ejaculatorius is very long.

In *Hydrometra stagnorum* L. (fig. 76) the testes are long and fusiform. It is probable that each consists of a single follicle. The vesiculae seminales are long but the ductus ejaculatorius is short and narrow.

The organs in *Mesovelgia furcata* Mulsant and Rey (figs. 79, 80) differ from the others in this group in being less elongated and in possessing two pairs of accessory glands which enter the dorsal aspects of the ductus ejaculatorius. Their presence causes some elaboration in the structure of the anterior parts of the ductus, which thus outwardly resembles the complex bulbus found in land bugs. However, sectioning shows this resemblance to be superficial. The testes are spherical and each comprises a single follicle. The vesiculae seminales are united at the anterior end of the ductus to form a median saccular structure.

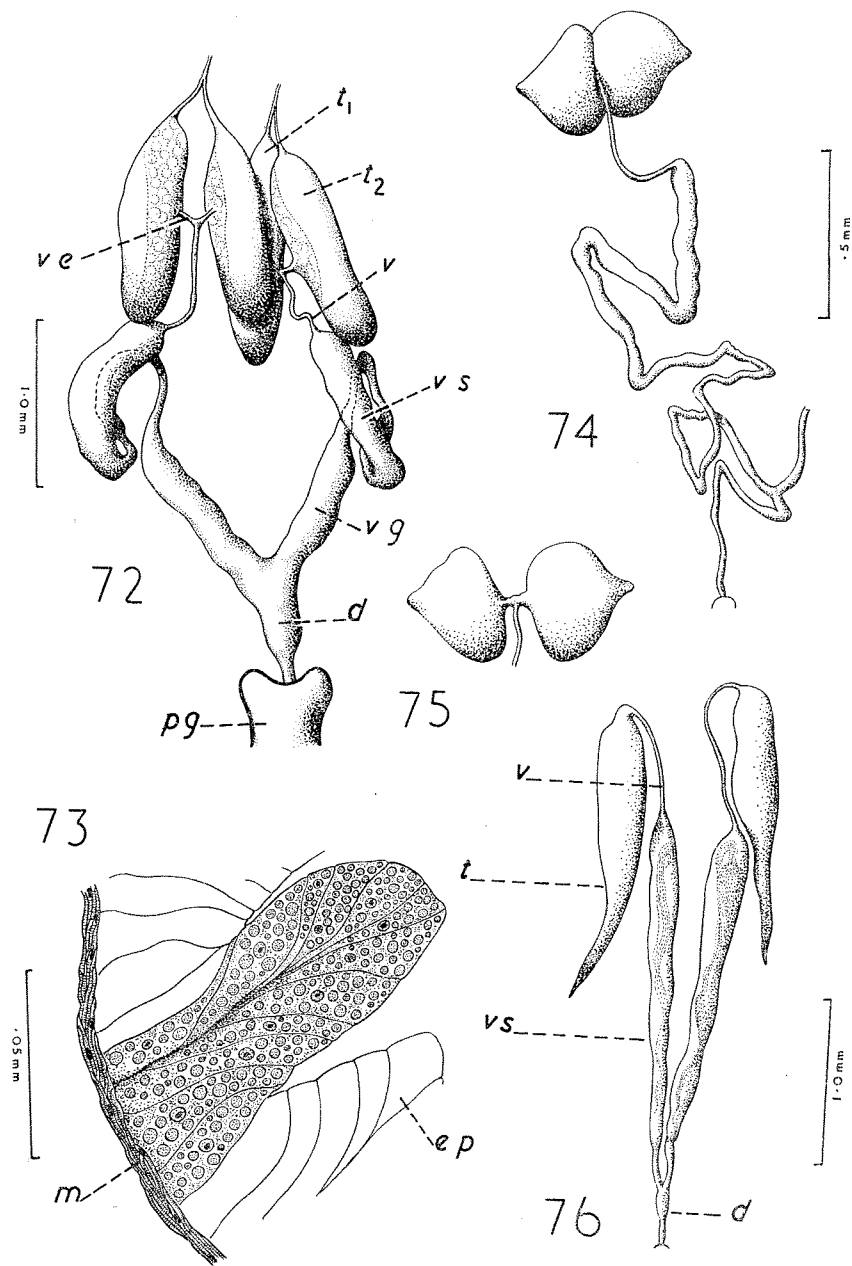
The reproductive organs of *Hebrus ruficeps* (Thomson) (figs. 74, 75) consist of a pair of bilobed testes, extremely long vasa deferentia and vesiculae seminales and a long narrow ductus ejaculatorius. Each testis consists of two conical lobes set base to base. Each lobe probably comprises a single follicle. There is a marked resemblance between the organs in *Gerris* and *Hebrus*.

2. Naucoridae, Aphelocheiridae, Belostomatidae, Nepidae, Notonectidae, Pleidae, Corixidae, Gelastocoridae, Ochteridae (figs. 81-83).

There is no bulbus ejaculatorius. Where determined, the number of testis follicles ranges between four and seven. There may be long, tubular accessory glands entering the apex of the ductus.

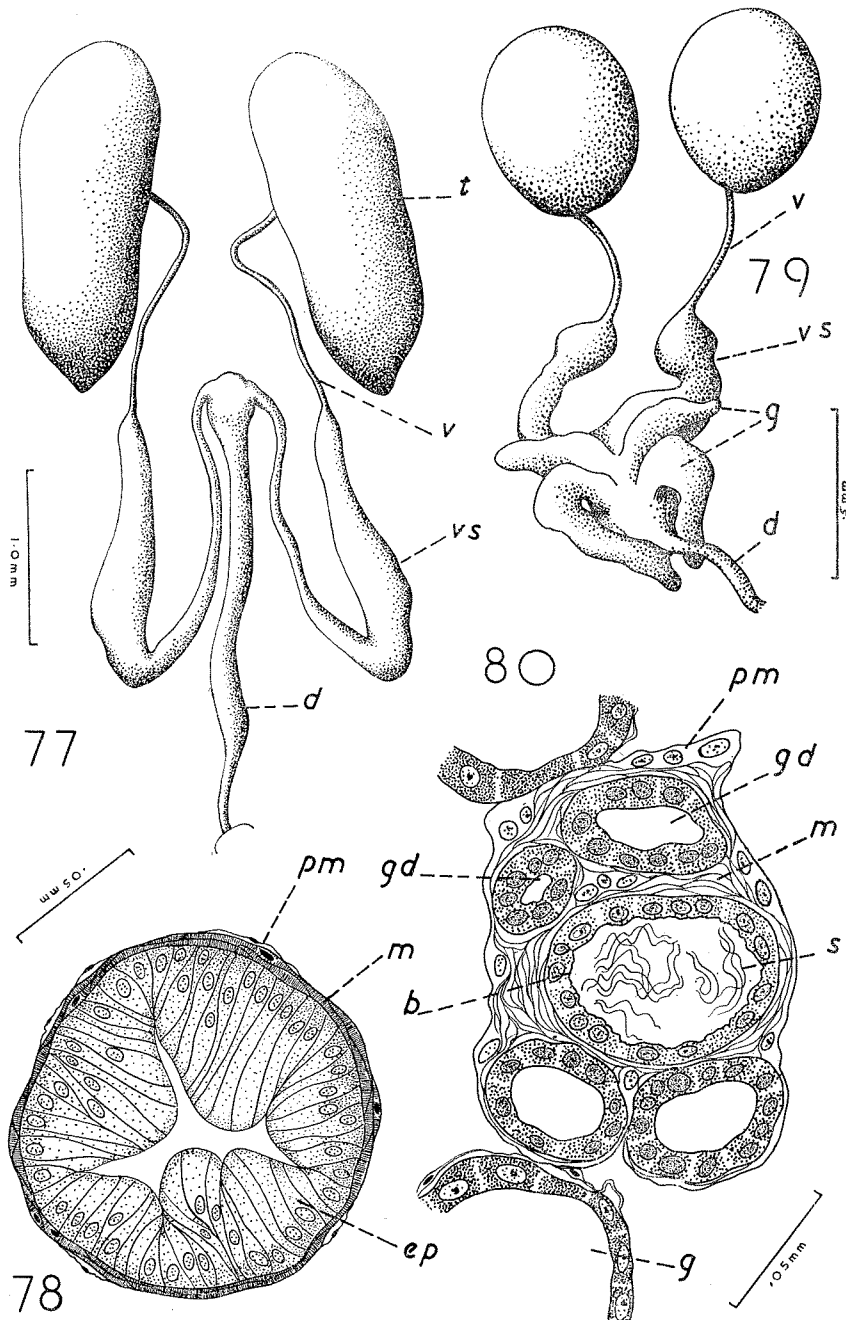
Larsén (1938) has given a full account of the reproductive organs in *Naucoris cimicoides* L., *Aphelocheirus aestivalis* Fabricius, *Nepa cinerea* L., *Notonecta glauca* L. and *Corixa dentipes* Thomson. Also, Rawat (1939) has described the organs in *Naucoris cimicoides*, Kerkis (1926) in *Plea atomaria* and Hamilton (1931) in *Nepa cinerea*.

Fixed material of *Mononyx terrestris* Kevan (Gelastocoridae) was examined (fig. 81). Each testis comprises two very long lobes, the apices of which are



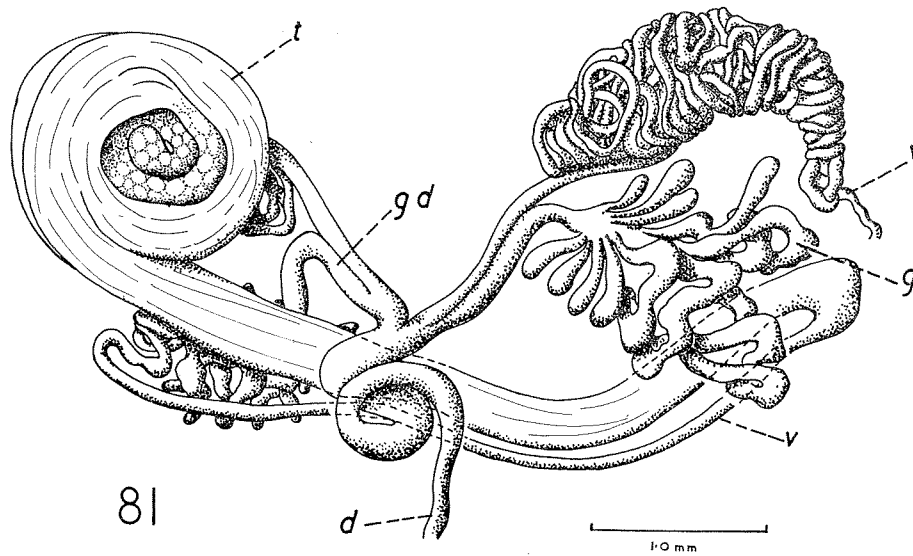
FIGS. 72-76.—(72) *Gerris lacustris*, male reproductive organs (Gerridae). (73) *G. lacustris*, transverse section to show part of wall of ductus ejaculatorius. (74) *Hebrus ruficeps*, male reproductive organs. Right testis and vas deferens omitted (Hebridae). (75) *H. ruficeps*, testis with lobes separated. (76) *Hydrometra stagnorum*, male reproductive organs (Hydrometridae).

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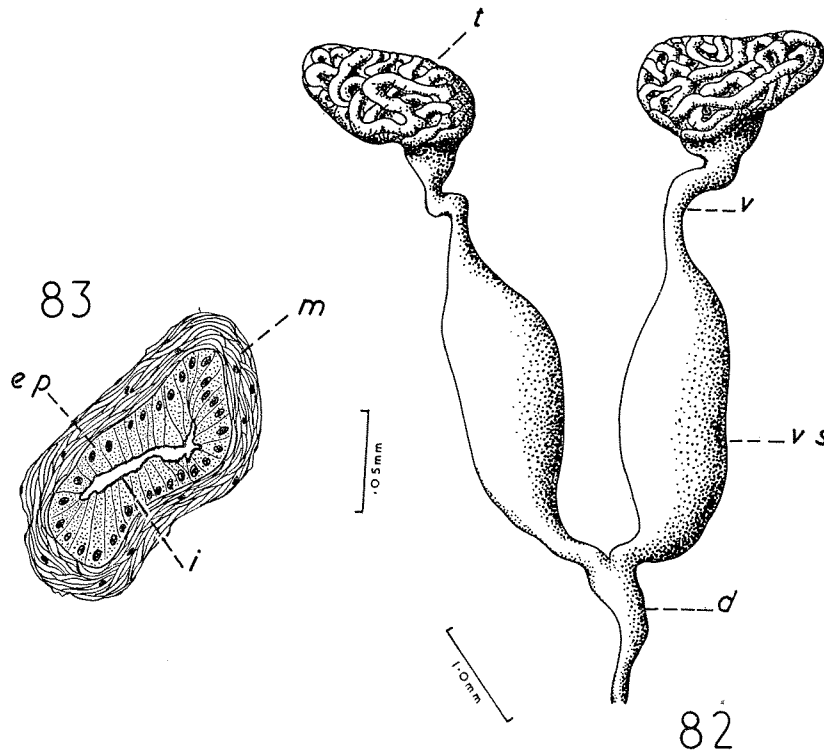


Figs. 77-80.—(77) *Velia caprai*, male reproductive organs (Veliidae). (78) *V. caprai*, transverse section anterior end ductus ejaculatorius. (79) *Mesovelia furcata*, male reproductive organs (Mesoveliidae). (80) *M. furcata*, transverse section anterior end ductus ejaculatorius.

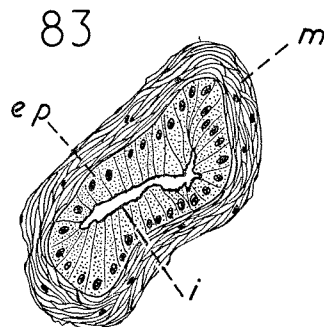
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Figs. 81-83.—(81) *Mononyx terrestris*, male reproductive organs. Right testis and distal parts of vas deferens omitted (Gelastocoridae). (82) *Sphaerodema rusticum* male reproductive organs (Belostomatidae). (83) *S. rusticum*, transverse section ductus ejaculatorius.

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coiled together in a spiral in the same manner as in the Notonectidae. Basally a long strap-like uncoiled part crosses the abdomen to the other side of the body to give rise to the vas deferens, which is an irregularly-coiled duct. Ducts from a pair of accessory glands enter the apex of the long coiled ductus ejaculatorius at the same point as the vasa deferentia.

An alcohol specimen of *Ochterus marginatus* (Latreille) (Ochteridae) was examined. However, the organs were badly preserved and only the following features were noted: each testis consists of two lobes having the helical form seen in the Gelastocoridae and Notonectidae and there are probably two sets of accessory glands. The ductus ejaculatorius is very long.

The reproductive organs of *Sphaerodema rusticum* Fabricius (Belostomatidae) (figs. 82, 83) have many points of similarity with those of the Nepidae. The testes resemble those of *Ranatra* described by Larsén. As in the Nepidae, each vas deferens is dilated to form a large vesicula seminalis. *Sphaerodema* resembles *Ranatra* but differs from *Nepa* in the absence of accessory glands.

3. Saldidae, Aëophilidae, Nabidae, Reduviidae, Phymatidae, Anthocoridae, Cimicidae, Aradidae, Dysodiidae, Lygaeidae, Berytidae, Pyrrhocoridae, Coreidae, Piesmidae, Tingidae, Pentatomidae, Cydnidae, Plataspidae (figs. 84-122).

The system is, in general, considerably shorter than in the two previous groups. There is a complex bulbus ejaculatorius which has basically the same form throughout these families. Mesadenes are present (except in *Piesma*) and ectadenes are sometimes present. The number of follicles is variable but usually the number falls in the range six to eight.

SALDIDAE.

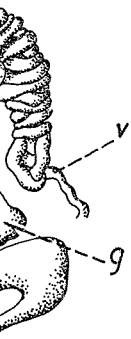
In *Saldula saltatoria* (L.) (figs. 84-87) each testis has two lobes with three and four follicles respectively. The basal half of each vas forms a vesicula seminalis. Bound to it by peritoneal membrane (fig. 85) is a dilated tubular mesadene gland opening into the apex of the bulbus. The bulbus ejaculatorius is made up of the three epithelial layers described above (fig. 86). Unlike the condition in most other families in this group, the chitinous intima secreted by the outer epithelial layer and by the epithelium of the ductus ejaculatorius remains more or less applied to the cells.

AËOPHILIDAE.

The organs of *Aëophilus bonnairei* Signoret (figs. 88, 89) resemble those of *Saldula*. Each testis has seven follicles held in two lobes of three and four follicles each.

NABIDAE.

The male organs have been described by Woodward (1949) and Carayon (1951). Ectadenes and mesadenes are present. Carayon has given an account of the internal structure of the bulbus. The description is not accompanied by illustrations, but it seems apparent that the organ is of the same complex type found in other families of this group.



— v s

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verse section