

THE SEMINAL RECEPTACLES AND ACCESSORY
GLANDS OF THE DIPTERA, WITH SPECIAL
REFERENCE TO THE ACALYPTERAE

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(Continued from Vol. XXXIII, page 215)

SCIOMYZIDÆ. Subfamily Sciomyzinæ. Wesché described two spermathecae in *Pherbellia cinerella* (Fallén) [*Sciomyza*], "remarkably horny, covered with short barbs, and with strongly chitinized stalks." I have seen *Pherbellia nana* (Fallén), which has two spherical black spermathecae, with relatively short ducts.

SUBFAMILY TETANOCERINÆ. Dufour described *Sepedon sphegeus* (Fabricius), *Limnia stictica* (Fabricius) [*Tetanocera*], and *Elgiva albiseta* (Scopoli) [*Tetanocera aratoria*]. In *Limnia* and *Elgiva* he reported three chitinized spermathecae, and in the latter two parovaria. In *Sepedon* there were two non-chitinized bodies, enlarged near their bases and narrower at the apices. Dufour identified these as parovaria, but was unable to find spermathecae—which he suggested were nevertheless present.

I have dissected *Dictya umbrarum* (Linné), *Hoplodictya setosa* (Coquillett), *Limnia saratogensis* (Fitch), and *Sepedon armipes* Loew?). In the first three, representing the old genus *Tetanocera*, there are two chitinized spermathecae, subspherical, and each enclosed in a separate envelop of the usual type of columnar

examined by Sturtevant 1926

cells. But in all three genera there is a brown envelop surrounding both the columnar ones, so that at first sight both spermathecae appear to be enclosed in a single envelop. In *Dictya* and in *Hoplodictya* there are two rounded parovaria, somewhat larger than the spermathecae, and each with a large central cavity. Active sperm were found in the spermathecae of *Hoplodictya*. *Sepedon* also has two subspherical chitinized spermathecae, and two parovaria. There is no common spermathecal envelop, and the parovaria resemble those described by Dufour for *S. sphegeus* rather than the others that I have observed in the subfamily. Each has a rather thick basal duct, then a swollen region that gradually tapers to a diameter about that of the duct. Then follows another swollen region that gradually tapers to the slender cylindrical apex of the gland. The whole organ is somewhat longer than the spermathecal ducts, and the two swollen regions are each about the size of a spermatheca with its columnar-cell envelop.

PSILIDÆ. Dufour described *Loxocera ichneumonca* (Linné) and *Chyliza permixta* Rondani [*leptogaster*]. In the former he recorded two subsessile chitinized spermathecae and a single stalked parovarium. For the latter he stated that the parovaria were oval, with long ducts.

I have dissected *Pseudopsila collaris* (Loew) and *Psila lateralis* Loew. In both genera the spermathecae have the curious form shown in figure 9. Each duct bears a single branched tube that is surrounded by the usual envelop cells. In *Pseudopsila* no type of branching other than that figured was found in the specimens studied. One of the three specimens of *Psila* had spermathecae of just the same type, another had one of the four branches forked near its apex, while in the third three branches were thus forked. In *Pseudopsila* the ventral receptacle resembles a spermathecal duct in size and shape. Sperm were found in it and also in the spermathecal ducts. The large ventral uterine pouch shown in the figure was observed in both genera. Its walls are muscular like those of the uterus. Two small parovaria occur in *Pseudopsila*, but only one was observed in *Psila*—the other may have been overlooked.

DIOPSIDÆ. I have studied *Sphyracephala brevicornis* Say. There are three chitinized spermathecae, attached to two rather short ducts, and two pear-shaped parovaria with ducts that are longer than those of the spermathecae. No ventral receptacle was observed, so if one is present it is probably not heavily chitinized.

SEPSIDÆ. Dufour described *Themira putris* (Linné) [*Cheli-gaster*] as having three spermathecae. He suspected that a parovarium was present, but failed to find it. Two of the supposed spermathecae were described and figured as stalked, the third one as sessile. The latter and one of the stalked ones were chitinized, but the second stalked one was not. From my own observations on this genus it is clear that the non-chitinized body was really the parovarium, and that both spermathecae are stalked (i.e., have longish ducts), but are adherent to the oviduct. Dufour also described *Nemopoda cylindrica* (Fabricius). He stated that there were three spermathecae, but that only one of them was chitinized, and that a single parovarium was present. My own dissection of this species has yielded a different result (see below).

I have dissected *Nemopoda cylindrica* (Fabricius), *Saltella scutellaris* (Fallén), *Sepsis* spp., and *Themira* sp. In all cases there are two spherical chitinized spermathecae, equal in size except in *Nemopoda*, where one is clearly larger than the other. In all four genera the spermathecal ducts are bent down toward the oviduct, and in all except *Saltella* the spermathecal envelopes are adherent to the oviduct just anterior to the insertion of the ducts. Sperm were present in the spermathecae of *Sepsis* and *Themira*. The parovaria are subspherical and about the same size as the spermathecal envelopes. Two were found in *Nemopoda* and *Themira*, one in *Saltella* and *Sepsis*. No ventral receptacle was detected in this group.

PIOPHILIDÆ. Dufour described *Piophila casei* (Linné) [*peta-sionis*] as having a single large sessile chitinized spermatheca and two pairs of parovaria, the members of one pair being ovoid and stalked, those of the other long, curved, and attached to fine

ducts. I have not studied this species; but, judging from the forms described below, the sessile chitinized body was the ventral receptacle, while one pair of supposed parovaria was really a pair of spermathecae.

I have dissected two undetermined species of *Piophila*, and *Prochyliza xanthostoma* Walker. In these forms there are two chitinized spermathecae, elliptical in *Prochyliza*, spherical and telescoped basally in one species of *Piophila*, and curved and tapering in the second *Piophila*. The parovaria are two in number, and are hollow and oval. A very weakly chitinized ventral receptacle is present in all three forms. In *Prochyliza*, at least, its apex is directed posteriorly. Sperm were found in this group only in the spermathecae of *Prochyliza*. In *Piophila* the ventral wall of the uterus is very thick and muscular, much as in the Sapromyzidae.

ODINIIDÆ. *Traginops irrorata* Coquillett has two spherical chitinized spermathecae and a backward curved ventral receptacle that is chitinized only on its anterior face. Sperm were found in the ventral receptacle. No parovaria were found, but a single parovarial duct was present.

CHIROMYIDÆ. I have a cleared preparation of *Chiromyia* sp. that shows two chitinized spermathecae, telescoped at each end very much like those of *Aulacigaster*.

SAPROMYZIDÆ. Dufour stated that *Sapromyza rorida* Fallén has two spermathecae, of which one has two pockets—i.e., there are three, but only two ducts.

I have studied *Camptoprosopella vulgaris* (Fitch), *Lauxania cylindricornis* (Fabricius), *L. trivittata* Loew, *Minettia longipennis* (Fabricius), *M. lupulina* (Fabricius), *M. valida* (Walker), *Sapromyza bispina* Loew, and *S. compedita* Loew. These forms all have three chitinized spermathecae attached to two ducts. In *Minettia longipennis* it is clearly the right duct that is branched. The organs are pear-shaped in *M. longipennis* and *M. valida*, spherical in all the others. Sperm were found in them in *M. lupulina*. The parovaria are small, and oval in

shape. Two (or at least two ducts) were found in each genus examined. In all these species the ventral wall of the uterus is very thick, muscular, and opaque. A chitinized ventral receptacle is not present; but sections of *Lauxania trivittata* show that there is a non-chitinized one that contains sperm. It is probably present throughout the group.

OCHTHIPHILIDÆ. I have dissected *Leucopis* spp. and *Ochthiphila polystigma* Meigen. In each genus there are two spermathecal ducts, each bearing two spherical chitinized spermathecae. No ventral receptacle nor sperm were found. *Leucopis* has two parovaria, but only one has been found in any of the numerous dissections of *Ochthiphila*. Sections of *Ochthiphila* have not been found to show a ventral receptacle; but as this species is parthenogenetic (Sturtevant, 1923), the organ may still be present in other members of the group.

HELOMYZIDÆ. Dufour described *Helomyza ferruginea* Meigen [*rufa*] as having two ducts, each with two spermathecae—as in the *Conopidae* and *Ochthiphilidae*. Wesché reported four spermathecae in *Helomyza similis* Meigen.

I have examined *Anorostoma marginata* Loew, *Helomyza quinquepunctata* Say, *Leria pectinata* (Loew), and *Oecothoa fenestralis* (Fallén). In *Helomyza* there are two ducts and four chitinized spermathecae, as described by Dufour. In the present species the spermathecae are corkscrew-shaped. In the other three genera there are three chitinized spermathecae, attached to two ducts. The organs are spherical in all three genera, but have a small apical papilla in *Leria*. In *Leria* there is a large dorsal pouch to the uterus, from the apex of which arise the spermathecal ducts. Just posterior to the pouch arise the ducts of the two oval parovaria. The only other parovarium found in the group was a single one in *Oecothoa*. A small non-chitinized ventral receptacle much like that of the *Chloropidae* was found in *Anorostoma* and in *Leria*. In both of these genera sperm were found both in the ventral receptacle and in the spermathecae.

TRIXOSCELIDÆ. A cleared preparation of *Trixoscelis frontalis* (Fallén) shows three chitinized spermathecae.

CLUSIIDÆ. I have studied *Clusia lateralis* (Walker), *Clusiodes johnsoni* Malloch, and *Heteromeringia nitida* Johnson. In all these there are two chitinized spermathecae, spheroid in shape, and, in *Clusiodes*, strongly telescoped at each end. In all three cases the envelop is much thinner apically than over the rest of the spermatheca. The ducts are very short in *Clusiodes* and *Heteromeringia*, longer in *Clusia*. *Clusia* has two large cylindrical parovaria, each of which has a weakly chitinized duct throughout its length. In *Clusiodes* a single small pear-shaped parovarium was found. The ventral receptacle is a large thick-walled organ, not chitinized, in *Clusia*. In *Clusiodes* it is longer, and the apical region has an enlarged cavity with a chitinized floor. In *Heteromeringia* the organ is still longer, and is tightly curled up as in some *Drosophilids*. In this last genus it also has a basal enlargement, in which sperm were found. Sperm were present both in the spermathecae and in the ventral receptacle of *Clusia*.

CÆLOPIDÆ. Wesché reported three chitinized spermathecae in *Cælopa* sp. I have dissected *Cælopa parvula* Haliday. Three chitinized spermathecae, telescoped basally, were present. The specimen was not fresh, and it was not found possible to trace the ducts. A single parovarium was found. No ventral receptacle was seen.

ANTHOMYZIDÆ. I have dissected *Anthomyza variegata* (Loew) and *Mumetopia occipitalis* Melander. In the former there are two ovoid chitinized spermathecae with long slender ducts. One parovarial duct was found. No sperm nor ventral receptacle were seen. *Mumetopia* also has two chitinized spermathecae. They are spherical, with the basal halves covered with basally directed papillae. The two parovaria are spherical, each with a short swollen duct. These ducts are inserted laterally with respect to the spermathecal ducts, rather than posterior to them. There is present a small weakly chitinized ventral receptacle. Sperm were found in the spermathecae and in the ventral receptacle.

OPOMYZIDÆ. Wesché reported two chitinized spermathecae in *Geomyza combinata* (Linné) [*Balioptera*] and in *G. tripunctata* Fallén. I have a cleared preparation of *Opomyza germinationis* (Linné) (collected in England) that likewise has two chitinized spermathecae.

DIASTATIDÆ. I have dissected *Diastata repleta* (Walker) [= *pulchra* Loew]; and have a cleared preparation of *Curtonotum gibba* (Fabricius), which seems to me to be best placed in this family. In *Curtonotum* there are two slender chitinized spermathecae; no chitinized ventral receptacle appears. In both genera the rectal glands are heavily chitinized, thimble-shaped, and covered with small spines. They are mentioned here because they can easily be mistaken for spermathecae in cleared specimens, and because they serve to strengthen the conclusion that the two genera should be placed close together. In *Diastata* there are two short spermathecal ducts with unusually heavy internal spiral thickenings. Each duct ends blindly, and the usual spermathecal envelop cells are present at its apex. That is, the spermathecae themselves are entirely missing, just as in the Ephydridæ. There is a large heavily chitinized ventral receptacle, in which sperm were found. This receptacle differs from that of the Ephydridæ in that it curves posteriorly and then dorsally, making almost a complete circle. The apex is somewhat enlarged, and is slightly telescoped.

PERISCCELIDÆ. I have studied *Periscelis annulata* (Fallén) and *Sphyroperiscelis wheeleri* Sturtevant. Both genera are anomalous among the Acalypteræ in that only a single spermathecal duct is present, while this duct bears at its apex three spherical chitinized spermathecae. In *Sphyroperiscelis* two pear-shaped parovaria were observed, each gland being about the size of a spermathecal envelop. In *Periscelis* only one parovarial duct was seen; the gland itself was not found. There is a rather long non-chitinized ventral receptacle in *Periscelis*, which is unusual in that it lies along the ventral side of the oviduct. The only sperm found in the group were in this organ.

In both genera the mature eggs are dark brownish-black, resembling those of Ochthera.

DROSOPHILIDÆ. Wesché reported two chitinized spermathecae in *Drosophila funebris* (Fabricius). Unwin (1907) verified this, and also saw the ventral receptacle, but did not correctly interpret it. Nonidez (1920) has given a full account of the genital organs of both sexes of *Drosophila melanogaster* Meigen, with brief notes on the ventral receptacles of *D. obscura* Fallén and *D. virilis* Sturtevant. I have figured (Sturtevant, 1921) the spermathecae of many species of the family, studied from cleared material.

I have dissected *Amiota leucostoma* Loew, *Chymomyza amœna* (Loew), *C. procnemis* (Williston), *Drosophila affinis* Sturtevant, *D. busckii* Coquillett, *D. funebris* (Fabricius), *D. immigrans* Sturtevant, *D. melanogaster* Meigen [*ampelophila* Loew], *D. obscura* Fallén, *D. quinaria* Loew, *D. repleta* Wollaston, *D. robusta* Sturtevant, *D. simulans* Sturtevant, *D. testacea* Roser [putrida Sturtevant], *D. transversa* Fallén, *D. virilis* Sturtevant, *D. willistoni* Sturtevant, *Leucophenga maculosa* (Coquillett), *Mycodrosophila dimidiata* (Loew), *Scaptomyza adusta* (Loew), *S. graminum* (Fallén), and *Stegana vittata* (Coquillett). In addition I have cleared preparations of *Leucophenga varia* (Walker), *Zaprionus vittiger* Coquillett, *Zygothrica dispar* (Wiedemann), and a series of additional species of *Drosophila*.

All of these have the same type of female genitalia. There are two chitinized spermathecae. In *Chymomyza*, *Drosophila*, *Mycodrosophila*, and *Scaptomyza* they are more or less spherical and are telescoped at the base (rarely also at the apex). In *Amiota* and *Leucophenga* they are cylindrical, not telescoped, and have external transverse thickenings similar to those of *Lonchæa* and *Scatophaga*. In *Stegana* the spermathecae are nearly spherical, not telescoped, and the chitin is perforated by numerous small holes. In this genus there is also a slender non-chitinized tube that arises from the apex of each spermatheca, passes through the envelop, and reaches a length greater than that of the spermatheca plus its short duct. Sperm were found in the spermatheca here, but were not present in this apical tube. No similar structure has been seen elsewhere among the Acalypteræ.

Two parovaria were observed in *Chymomyza procnemis*, in ten species of *Drosophila*, in *Amiota*, and in *Scaptomyza graminum*;

a single one was seen in *Stegana*. It is probable that two occur throughout the group. In form the glands are subspherical, with a more or less distinct central lumen. They are usually smaller than a spermathecal envelop—in several species smaller than the chitinized spermatheca itself. The ducts are in nearly all cases shorter than the spermathecal ducts, and have internal spiral thickenings that are very faint in most species.

A non-chitinized ventral receptacle is present in all the species dissected. In *Drosophila obscura* and in *Amiota* it is a broad recurved pocket; in *D. melanogaster* and *D. simulans* it is longer, narrower, and lies in a loose coil of about two turns; in *D. busckii* it is still longer and narrower, and lies in a coil of about three turns; *D. affinis* and the two species of *Scaptomyza* show it still longer and in a somewhat more complex coil—roughly three superposed U's in *D. affinis*; in *D. willistoni*, *Leucophenga*, and *Mycodrosophila* it has become extremely long and narrow, and lies in a very tight coil; in *Chymomyza*, *D. funebris*, *D. immigrans*, *D. quinaria*, *D. repleta*, *D. robusta*, *D. testacea*, *D. transversa*, *D. virilis*, and *Stegana* it is quite as long and narrow as in the preceding group, and does not lie in a single definite coil, but is very tightly curled and closely bound together in a complex tangle. When drawn out straight in *D. robusta* (one of the largest species) it was found to be about twice the length of the entire fly.

Active sperm were found in the spermathecae of *Stegana*; in the ventral receptacle of *Mycodrosophila* and *Scaptomyza*; and in both organs in *Chymomyza procnemis* and ten of the species of *Drosophila*. There can be no doubt that both organs function as sperm reservoirs in all the genera here described.

I have previously discussed (Sturtevant, 1921) the eggs of various Drosophilids. I may here add that anterior filaments are lacking in *Amiota*, *Leucophenga*, and *Stegana*. Four rather short tapering filaments are present in *Mycodrosophila*. Incidentally it may be noted that there are four long slender anterior filaments on the eggs of *Desmometopa m-nigrum* (Milichiiidæ), that two very short ones occur in *Parallelomma* (Cordyluridæ), and that in *Sepsis* sp. (Sepsidæ) there is a single very long slender apical one. No special attempt was made to examine the eggs

of the various Acalyptera dissected, but in no other instances outside the Drosophilidae were any filaments noticed.

EPHYDRIDÆ. Dufour dissected *Ochthra mantis* (Degeer), and noted the blackish color of the fully grown ovarian eggs (a point that I have verified), but did not describe the receptacles and accessory glands. Wesché recorded a single chitinized receptacle in all the members of the family he examined, mentioning specifically *Hydrellia griseola* Fallén and *Parydra coarctata* Fallén. From his descriptions and the figure of the latter species, compared with my own dissections in both these genera, it is clear that the single body Wesché saw was the ventral receptacle, not the spermatheca as he naturally supposed it to be.

I have dissected the following species: *Dichæta caudata* (Fallén), *Dimecænia spinosa* (Loew), *Discocerina leucoprocta* Loew, *D. obscurella* (Fallén), *Ephydra subopaca* Loew, *Gastrops nebulosus* Coquillett, *Glenanthe* sp., *Gymnopa tibialis* Cresson, *Hydrellia formosa* Loew, *H. hypoleuca* Loew, *Ilythea spilota* Curtis, *Notiphila* sp., *Ochthra mantis* (Degeer), *Paralimna appendiculata* Loew, *Parydra* sp., *Philygria debilis* Loew, *P. opposita* Loew, *Psilopa atrimana* Coquillett, *P. fulvipennis* Hine, *Scatella* sp., *Scatophila mesogramma* (Loew).

There is no apparent relation between the current subdivisions of this group, based on external characters, and the structure of the parts here studied. Accordingly the group will be discussed as a whole. There is great uniformity in the essential features of the seminal receptacles here. All the forms examined have two short spermathecal ducts, with rudimentary spermathecae; and a large heavily chitinized ventral receptacle which is essentially a short hollow tube, bent forwards near its base. These characters not only occur in all the Ephydridæ examined, but no combination at all similar occurs elsewhere except in *Diastata*. It is true that only one spermatheca was found in *Gastrops*, *Ilythea*, and *Parydra*, and none in *Paralimna*; but in these genera only one or a very few specimens each were examined, and these were not altogether satisfactorily dissected. The Ephydrid spermathecal duct ends blindly, without any constriction or enlargement at its apex, and the usual type of columnar envelop

cells radiate from this apex. The only other type of spermatheca observed in the family was in *Discocerina obscurella* (*D. leucoprocta* being normal). In this form there is a long fine crooked duct, at least twice as long as the usual heavier duct that is basal to it; around this fine duct the envelop cells form a large cylinder, similar to that found in the Psilidæ. In all cases the spermathecal ducts are relatively short, have a large lumen, and show clearly the internal spiral thickenings. In both species of *Hydrellia* they are much swollen in the middle portion of their length.

Two spherical or oval parovaria were seen in *Dichæta*, *Discocerina*, *Ephydra*, *Hydrellia*, *Ilythea*, *Notiphila*, *Ochthra*, and *Psilopa*; only one was found in *Dimecænia*, *Glenanthe*, *Gymnopa*, *Philygria*, *Scatella*, and *Scatophila*. In *Hydrellia* the ducts are of the same length and structure as those of the spermathecae (though they are not swollen in the middle as are the spermathecal ducts of this genus), and the glands themselves are nearly the same shape and size as the spermathecal envelops. The two types of organ can thus be distinguished only from the appearance of the envelop cells and the insertion of the ducts on the uterus. In the other forms studied the parovaria were in most cases smaller than the spermathecal envelops; if they were of the same size their ducts showed less conspicuous spiral thickenings.

The heavily chitinized ventral receptacle has a large thimble-shaped apical cap on it in *Dichæta*, *Gastrops*, *Gymnopa*, *Hydrellia*, *Notiphila*, *Ochthra*, *Paralimna*, *Parydra*, *Psilopa*, *Scatella*, and *Scatophila*; a smaller apical cap in *Dimecænia*, *Ephydra*, and *Ilythea*; and no cap at all but only an enlarged apex in *Discocerina*, *Glenanthe*, and *Philygria*. Sperm have been found in this organ in *Dimecænia*, *Discocerina*, *Hydrellia*, *Ilythea*, and *Philygria*. In no case in this family have any sperm been found in any other part of the female reproductive system.

In each species of *Discocerina* examined there is a large ventral uterine pouch, as large as the uterus itself or nearly so, and with muscular walls of the same type as those of the uterus. It arises just posterior to the opening of the ventral receptacle into the uterus. This structure is quite similar to the ventral pouches that occur in the Psilidæ and Tethinidæ.

CANACEIDÆ. I have dissected *Canace* sp. There are two chitinized spermathecae, and two pear-shaped parovaria. No ventral receptacle was identified with certainty, though a small non-chitinized one is perhaps present. Sperm were found in the spermathecae. It will be seen that this form is quite distinct from the Ephyrinidæ, with which it has often been united.

TETHINIDÆ. I have studied *Pelomyia mallochii* Sturtevant, *Tethina albula* (Loew), and *T. parvula* (Loew). There are two spheroidal chitinized spermathecae, attached to short ducts, and two short cylindrical parovaria that taper basally to their insertions on the uterus. The spermathecae of *Pelomyia* are telescoped both basally and apically. In *Tethina parvula* there is almost certainly a small non-chitinized ventral receptacle. In the other two species there is a large muscular-walled ventral receptacle like that of the Psilidæ or of Discocerina.

BORBORIDÆ. Dufour described *Borborus equinus* (Fallén) as having two chitinized spermathecae and two tubular parovaria. Wesché stated that *Borborus* has two spermathecae, *Leptocera* three. I can confirm both these results.

I have dissected *Borborus equinus* (Fallén), *B. (Borborillus) sordidus* (Zetterstedt) [*brevisetus* Malloch], *Leptocera (Coproica) ferruginata* (Stenhammar), *L. (Scotophilella)* sp., *L. (Thoracochaeta) brachystoma* (Stenhammar), *Sphærocera pusilla* (Fallén), and *S. subsultans* (Fabricius). In *Borborus* and *Sphærocera* there are two chitinized spermathecae, more or less spherical in shape and attached to short ducts. In all except *Borborillus* the envelop is drawn out into an apical process. In *Leptocera* one of the spermathecae is double—i.e., one duct bears two, and these two are heavily chitinized down to a common base. Two parovaria occur in all three genera. In *Coproica* each gland is oval; in the other forms studied the glands are long, slender, and cylindrical. No ventral receptacle was found, but the small size and muscular surroundings of the uterus render this result of little significance. Sperm were present in the spermathecae of *Coproica* and *Sphærocera*.

AULACIGASTER. I have been unable to find any satisfactory group to receive *Aulacigaster leucopeza* Macquart, and shall therefore describe it and the following genus as appendices to the Acalypteræ.

In *Aulacigaster* there are three telescoped chitinized spermathecae, attached to two relatively short ducts. There are two parovaria, with ducts that are slightly longer than the spermathecal ducts. The parovaria themselves are about as long as their ducts; each has a narrow crooked weakly chitinized central tube, about which are grouped large cells with huge vacuoles, forming a cylinder similar to that found in the Agromyzidæ, but without a sac-like enlargement. No ventral receptacle was observed in the eight specimens dissected; four of them had sperm in the spermathecae, but no sperm could be found elsewhere. Sections have also failed to show any ventral receptacle.

CRYPTOCHÆTUM. *Cryptochætum iceryæ* (Williston) (bred from *Icerya* collected in California, and received through the kindness of Dr. S. H. Schrader) has proved to have very puzzling internal genitalia. There are two non-chitinized spermathecae and two parovaria—but it remains doubtful which is which. The small pear-shaped organs are typical parovaria, but no spermathecae at all like the large organs have been seen elsewhere. The small size of the fly prevented an accurate determination of the insertion points of the ducts, and no sperm were seen; so it is necessary to merely guess that this identification is correct. As shown in the figure, these supposed spermathecae are cylindrical, each with an apical papilla. No envelop cells were identified. What appears to be a small weakly chitinized ventral receptacle is present, but its structure could not be made out satisfactorily. A large muscular pouch, that apparently may contain at least one egg at times, arises from the posterior ventral region of the uterus.

THE CLASSIFICATION OF THE ACALYPTERÆ

It is my opinion that systems of classification can be justified only on grounds of convenience. A classification has an excuse for existence if it serves to simplify the task of learning and remembering the characteristics of a series of organisms, or if

it serves as a guide to the probable nature of those characters of an organism that are not yet investigated. From this point of view, the ideal classification is the one that brings together most closely those species that are similar in the largest number of diverse kinds of characters, and in which the successively larger groups indicate correspondingly fewer agreements in such diverse characters.

This view of the nature and object of classification differs from the traditional one, *i.e.*, that the classification should correspond to the genetic relationship of the forms concerned—to their phylogeny. It is, of course, obvious that the two points of view will usually lead to similar results. But, at least in the absence of large series of fossil forms, phylogenies must always remain wholly hypothetical. Accordingly it seems to me more desirable to base systems of classification frankly on grounds of convenience.

It is for these reasons that the following discussion is not concerned with the question of which are the "highest" groups, nor with the construction of hypothetical family trees. All that is attempted is to offer some suggestions as to methods of making the classification of the group more useful as a mnemonic scheme and for purposes of prediction.

Frey's (1921) classification of the group, based chiefly on mouth-parts, may be summarized as follows:

Series 1. Conopiformes.

Conopidae, Neriidae, Micropezidae, Chloropidae, Milichiidae.

Series 2. Ortalidiformes.

Agromyzidae, Lonchæidae, Ortalidae, Richardiidae, Ulidiidae, Pterocallidae, Tanypezidae, Pyrgotidae, Platystomidae, Tephritidae.

Series 3. Sciomyzæformes.

The 28 remaining subfamilies—Rhopalomeridae to Borboridae.

Hendel (1922) has proposed a somewhat different arrangement, as follows:

I. Sciomyzomorphæ.

1. Sciomyzoidea. (Rhopalomeridae, Sciomyzidae, Dryomyzidae, Neottiophilidae.)

2. Sepsoidea. (Megameridae, Sepsidae, Diopsidae, Pionophilidae, Thyreophoridae, Psilidae.)

II. Tephritomorphæ.

3. Tyloidea. (Micropezidae, Neriidae.)
4. Tephritoidea. (Lonchæidae, Tanypezidae, Ulidiidae, Pterocallidae, Ortalidae, Platystomidae, Richardiidae, Phytalmyidae, Tephritidae, Tachiniscidae, Pyrgotidae.)

III. Lauxaniomorphæ.

5. Lauxanioidea. (Lauxaniidae, Celyphidae, Oechthiphiidae.)
6. Helomyzoidea. (Cælopidæ, Helomyzidae, Trixoseellidae.)
7. Anthomyzoidea. (Chiromyidae, Clusiidae, Anthomyzidae, Opomyzidae.)

IV. Drosophilomorphæ.

8. Ephydroidea. (Canaceidae, Ephydridæ, Borboridae, Tethinidae.)
9. Drosophiloidæ. (Drosophilidae, Astiidae, Perisceiidae.)
10. Milichioidea. (Odiniidae, Agromyzidae, Carnidae, Milichiidae.)
11. Chloropoidea. (Chloropidae.)

My own views, based in part on the new data presented in the present paper, are in some respects a compromise between these two systems. I agree with Hendel that Frey's "Conopiformes" do not form a convenient group, and that the Conopidae are probably best treated as not belonging to the Acalypteræ. That the Neriidae and Micropezidae are to be placed in the "Ortalidiformes" or "Tephritomorphæ" seems to me also a reasonable view. But I cannot agree that the remaining two groups—Chloropidae and Milichiidae—should be placed near the other forms included in Hendel's "Milichioidea." The rudimentary seminal receptacles with long fine ducts, and the pocket-like ventral receptacle indicate that these two groups are close to each other and remote from the Agromyzidae and the other members of Hendel's "Drosophilomorphæ." In my opinion a special group ("Chloropiformes"), corresponding to Frey's "Conopi-

formes," should be made for the reception of these two groups. In that they possess coiled spermathecal ducts, the Milichiidae are more like the Botanobiinae than like the Chloropinae.

The "Ortalidiformes" or "Tephritomorpha" are clearly marked off from the rest of the Acalypterae by the structure of the ovipositor. On this basis the group should include the Agromyzidae—as it does in Frey's system—and also the Micropezidae, as it does in Hendel's scheme. On the same basis, the Odiniinae must be removed from the Agromyzidae—a conclusion that is clearly borne out by the internal female reproductive organs. I have followed Frey and Hendel not only in this latter respect, but also in separating *Periscelis* from the Lonchæidae, to which I formerly referred it. It does not have the Ortalidiform ovipositor, and also has a unique spermathecal apparatus.

Frey's group *Sciomyzæformes* is made up simply of the rest of the families after the exclusion of the groups just discussed. Hendel has formed three series and eight superfamilies of this assemblage. This treatment does not seem to me altogether satisfactory; more data on various characters will be needed to elaborate a satisfactory system. For the present I shall merely discuss the indications derived from my own work.

The Sapromyzidae (Lauxaniidae of Hendel and others) and Oechthiphilidae are often placed near each other, and have even been united. The external characters usually used for classification do in fact suggest that the groups are very close, though the two groups may be separated by an examination of the preapical tibial bristles (well-developed in the Sapromyzidae, minute or absent in the Oechthiphilidae). Frey reports differences in the mouth-parts; and the accounts above show that there are three spermathecae and a thick muscular uterine wall in the Sapromyzidae, but four spermathecae and a normal uterine wall in the Oechthiphilidae. Another striking difference occurs in the males. The Oechthiphilidae (*Leucopis* and *Pseudodinia* examined) have two simple unbranched paragonia, or accessory reproductive glands. This is the usual condition among the Acalypterae, as among the Diptera in general. I have observed it in the Agromyzidae, Borboridae, Drosophilidae, Ephydriidae, Micropezidae, Milichiidae, Ortalidae, Sciomyzidae, Sepsidae, and Uli-

diidae. But in the Sapromyzidae (genera *Caliope*, *Camptoprosopella*, *Lauxania*, *Minettia*, *Sapromyza*, and *Steganolauxania* examined) the paragonia are repeatedly branched, and form so dense a tangle that I have been unable to make out whether there are only two (i.e., two insertion points), or many. It may be added that this is the only case in which I have found what appears to be a good diagnostic character for a large group in the soft parts of the male genitalia.

The old family Geomyzidae has here been broken up, following Frey and Hendel, into the Opomyzidae, Diastatidae, Chiromyidae, Anthomyzidae, Trixoseclidæ, and Tethinidae. Of these, Hendel would include the Diastatidae under the Drosophilidae, ally the Trixoseclidæ with the Helomyzidae, and the Tethinidae with the Borboridae and Ephydriidae, leaving the remaining three groups as related to each other and to the Clusiidae. I have not sufficient data on the genital organs of the Opomyzidae, Chiromyidae, or Trixoseclidæ to warrant a discussion of them. Diastata suggests the Ephydriidae rather than the Drosophilidae in its female genitalia. But I should remove *Curtonotum* from the Drosophilidae and place it with Diastata, on the basis of the peculiar rectal glands occurring in both, as well as the common external characters of pectinate costa, similar auxiliary vein, and bristly mesopleura. The female genitalia of the Anthomyzidae do not specially suggest those of any other group. Those of the Tethinidae certainly do not speak for Milichiid affinities, nor for Ephydrid ones. There are, however, suggestions of the Borboridae in the shape of the parovaria, the short spermathecal ducts, and the shape of the spermathecal envelopes.

One of the most distinct subfamilies, as judged by the female genitalia, is the Ephydriidae. The absence of spermathecae, short spermathecal ducts, and heavily chitinized ventral receptacle occur together only in the Ephydriidae (where they were found in all 17 genera examined) and in Diastata; and Diastata differs from all the Ephydriidae in that its ventral receptacle curves posteriorly, so that the apex lies behind the base. Of these three characteristics, only the least important one (short duct) occurs in Canace, which has been referred to the Ephydriidae until recently. The erection of a family Canaceidae is thus made still

more desirable. *Gymnopa* has been referred to the Chloropidæ; and Cresson (1922), in a recent account of the genus, has concluded that it is probably related to the Chloropidæ, Ephydridæ, and Agromyzidæ, but that it is doubtful if it can properly be included in any of these families. The female genitalia of *Gymnopa* are perfectly normal Ephydrid organs, and show no trace of Chloropid or Agromyzid characters. Frey's studies on the mouth-parts also indicate that the genus is a typical Ephydrid. It must surely be left in the group where it is now usually placed.

An unexpected result of these studies is the similarity that exists between the Clusiidæ and the Drosophilidæ. The ventral receptacle is much alike in the two groups—that of *Heteromeringia* being especially Drosophilid in appearance—and is not approached in any other family. The spermathecae of *Clusiodes* are also of the telescoped type that is so frequent in the Drosophilidæ. However, the two families are scarcely to be placed near together, since they differ in most of the characters that are usually considered of primary importance in the Acalypteræ—postverticals, auxiliary vein, costal breaks, cruciate frontals, insertion of arista, and filter apparatus in the œsophagus.

The two unplaced genera—*Aulacigaster* and *Cryptochaetum*—should probably be made the types of new subfamilies. An examination of the mouth-parts of a cleared specimen of *Aulacigaster* shows the following characters: filter-apparatus and palpal bristles absent; five pseudotracheæ on each side, no common pseudotracheal duct; mentum with no median furrow. Among the forms described by Frey it agrees best with *Diastata*, from which it differs most obviously in the number of pseudotracheæ (ten to eleven in *Diastata*). The two forms agree in the structure of the stipes and galea (except that the latter is shorter in *Aulacigaster*), the mentum (including its six bristles), and in the small bristles of the fulcrum. The two forms are, however, too distinct in external characters and in female genitalia to be placed in the same family.

Melander (1913) referred *Cryptochaetum* to the Agromyzidæ. I am unable to agree with his contention that the postverticals can be recognized among the numerous hair-like vertical bristles;

and the type certainly does not have an Agromyzid ovipositor. The genus has also been referred to the Chloropidæ and to the Oehlthipidæ. It requires considerable modification of family characters to place it in either of these, or in any other group. No data on the mouth-parts are available, and the female genitalia are unique. My observations indicate that the antennæ do not lack an arista, as supposed. A single cleared and dissected specimen makes it probable that the third antennal joint is very small, and that what appears to be this joint is really the arista, which is a thin chitinized plate shaped like the cover of a book and completely enfolding the third joint.

LITERATURE CITED

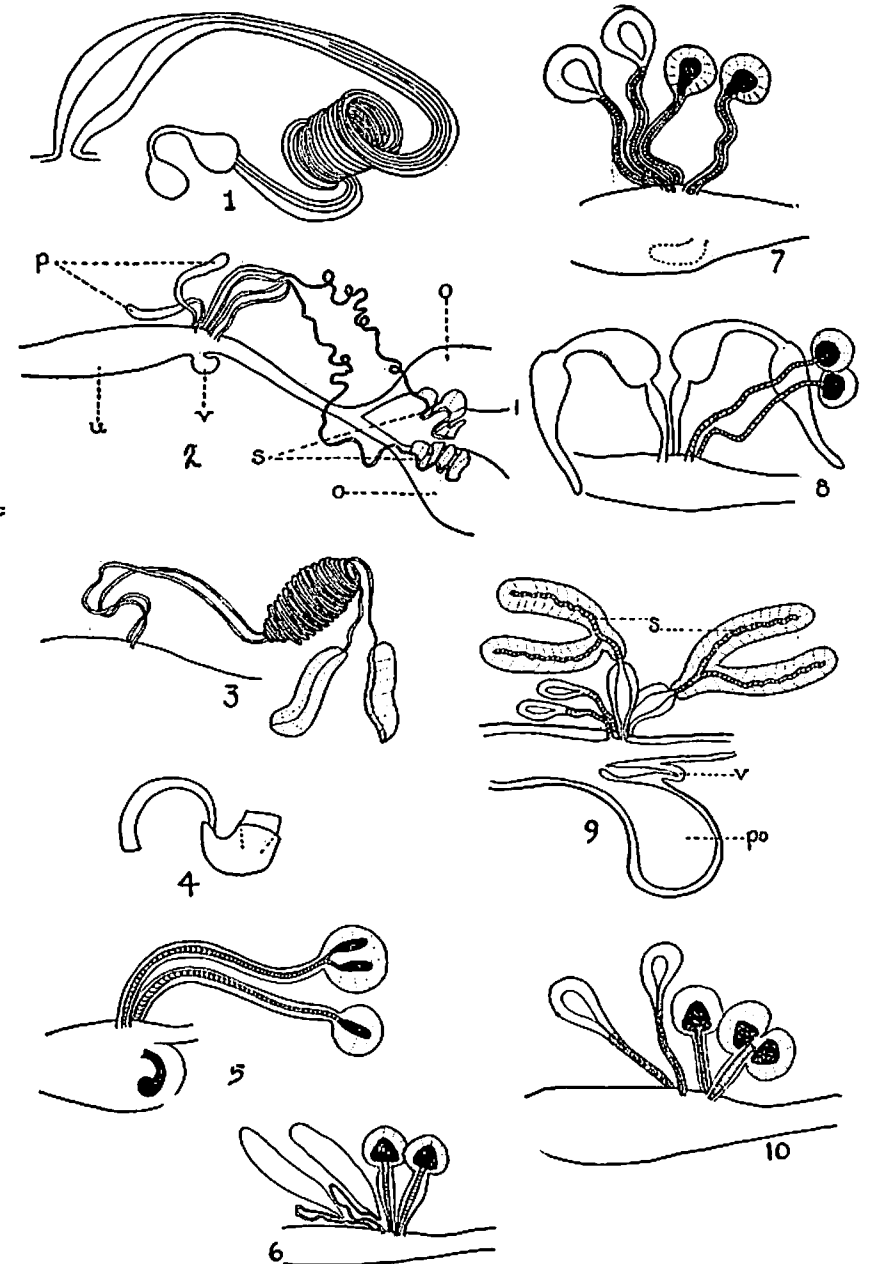
- BECKER, T., M. BEZZI, K. KERTESZ, and P. STEIN. 1903-1907. Katalog der paläarktischen Dipteren. Budapest. 4 vols.
 BERLESE, A. 1909. Gli Insetti. Milan. Vol. 1, 1004 pp.
 VON DER BRELJE, R. 1924. Die Anhangsorgane des weiblichen Geschlechtsorganes der Stechmücken (Culicidæ). Zool. Anz. 61: 73-80.
 CHOLODKOVSKY, N. 1909. Zur Kenntniss des weiblichen Geschlechtsapparates der Musciden. Zeits. wiss. Insektenbiol. 5: 333-337.
 COLLIN, J. E. 1910. Additions and corrections to the British list of Muscidæ Acalyptatæ. Ent. Mo. Mag., 2d ser., 21: 169-178.
 CRESSON, E. T., JR. 1922. Studies in American Ephydridæ. III. Trans. Amer. Ent. Soc. 47: 325-343.
 DUFOUR, L. 1851. Recherches anatomiques et physiologiques sur les diptères. Mem. Acad. Sci. France 11: 171-360.
 FREY, R. 1921. Studien über den Bau des Mundes der niederen Diptera Schizophora. Act. Soc. Faun. Flora Fenn. 48, no. 3, 247 pp.
 HENDEL, F. 1922. Die paläarktischen Muscidæ acalyptatæ = Haplostomata nach ihren Familien und Gattungen. I. Die Familien. Konowia 1: 145-160, 253-265.
 HEWETT, C. G. 1914. The house-fly, *Musca domestica*; its structure, habits, development, relation to disease and control. Cambridge. 382 pp.
 HOWARD, L. O., H. G. DYAR, and F. KNAB. 1912. The mosquitoes of North and Central America and the West Indies. Carnegie Inst. Washington, publ. 159. 3 vols.
 KULAGIN, N. 1901. Der Bau der weiblichen Geschlechtsorgane bei Culex und Anopheles. Zeits. wiss. Zool. 69: 578-597.
 LOWNE, B. T. 1890-1895. The anatomy, physiology, morphology, and development of the blow-fly, *Calliphora erythrocephala*. London. 778 pp.
 MACPHE, J. W. S., and A. INGRAM. 1922. On the genital armature of the female mosquito. Ann. Trop. Med. Parasitol. 16: 157-188.

- DE MEIJERE, J. C. H. 1906. Die Lonchopteren des paläarktischen Gebietes. Tijds. v. Ent. 49: 44-98.
- MELANDER, A. L. 1913. A synopsis of the Dipterous groups Agromyzinae, Milichiinae, Ochthiphilinae, and Geomyzinae. Jour. N. Y. Ent. Soc. 21: 219-273, 283-300.
- MIALL, L. C., and A. R. HAMMOND. 1900. The structure and life-history of the Harlequin fly. Oxford. 196 pp.
- MIALL, L. C., and T. H. TAYLOR. 1907. The structure and life-history of the holly-fly. Trans. Ent. Soc. London 1907: 259-283.
- MINCHIN, E. A. 1905. Report on the anatomy of the tsetse-fly (*Glossina palpalis*). Proc. Royal Soc. 76 B: 531-547.
- NEVEU-LEMAIRE, M. 1902. Sur les réceptacles séminaux de quelques Culicidés. Bull. Soc. Zool. Franco 27: 172-175.
- NONDEZ, J. F. 1920. The internal phenomena of reproduction in *Drosophila*. Biol. Bull. 39: 207-230.
- PANTEL, J. 1910. Recherches sur les Diptères a larves entomblies. La Cellule 26: 25-216.
- STURTEVANT, A. H. 1921. The North American species of *Drosophila*. Carnegie Inst. Washington, publ. 301. 150 pp.
- . 1923. The probable occurrence of parthenogenesis in *Ochthiphila polystigma*. Psyche 30: 22-27.
- TOWNSEND, C. H. T. 1911a. Review of work by Pantel and Portchinski on reproductive and early stage characters of Muscoid flies. Proc. Ent. Soc. Wash. 13: 151-170.
- . 1911b. Announcement of further results secured in the study of muscoid flies. Ann. Ent. Soc. Amer. 4: 127-152.
- UNWIN, E. 1907. The vinegar-fly (*Drosophila funebris*). Trans. Ent. Soc. London, 1907. 285-302.
- WESCHÉ, W. 1906. The genitalia of both the sexes in Diptera, and their relation to the armature of the mouth. Trans. Linn. Soc. London, Zool., 2d series, 9: 339-386.
- WILLISTON, S. W. 1908. Manual of North American Diptera. New Haven. 405 pp.

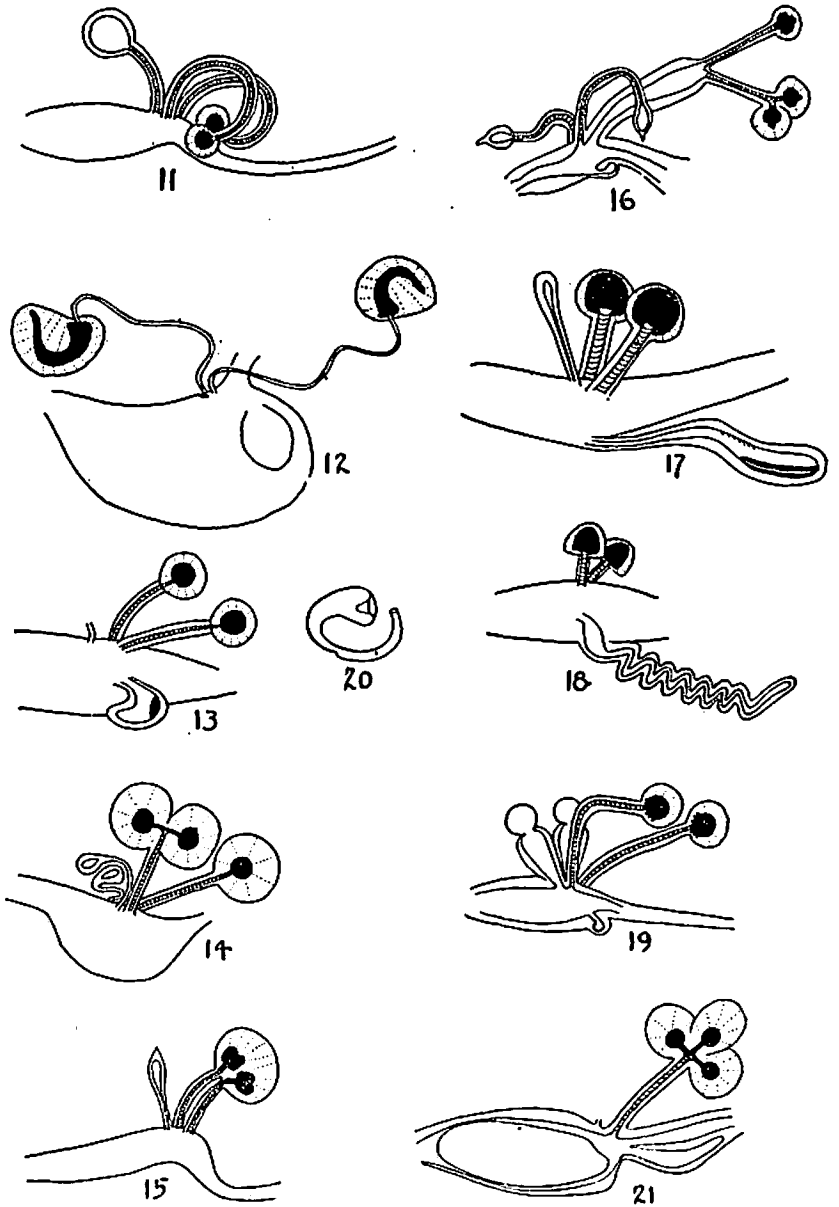
EXPLANATION OF PLATES I, II, III

- Figure 1. *Dolichopus* sp. Spermatheca and its duct.
- Figure 2. *Chloropisca glabra*. o, ovary; p, parovarium; s, spermatheca; u, uterus; v, ventral receptacle.
- Figure 3. *Pholcomyia indecora*.
- Figure 4. *Phytomyza bicolor*. Ventral receptacle.
- Figure 5. *Lonchaea polita*.
- Figure 6. *Chaetopsis apicalis*.
- Figure 7. *Straussia longipennis*.
- Figure 8. *Sepedon armipes*.

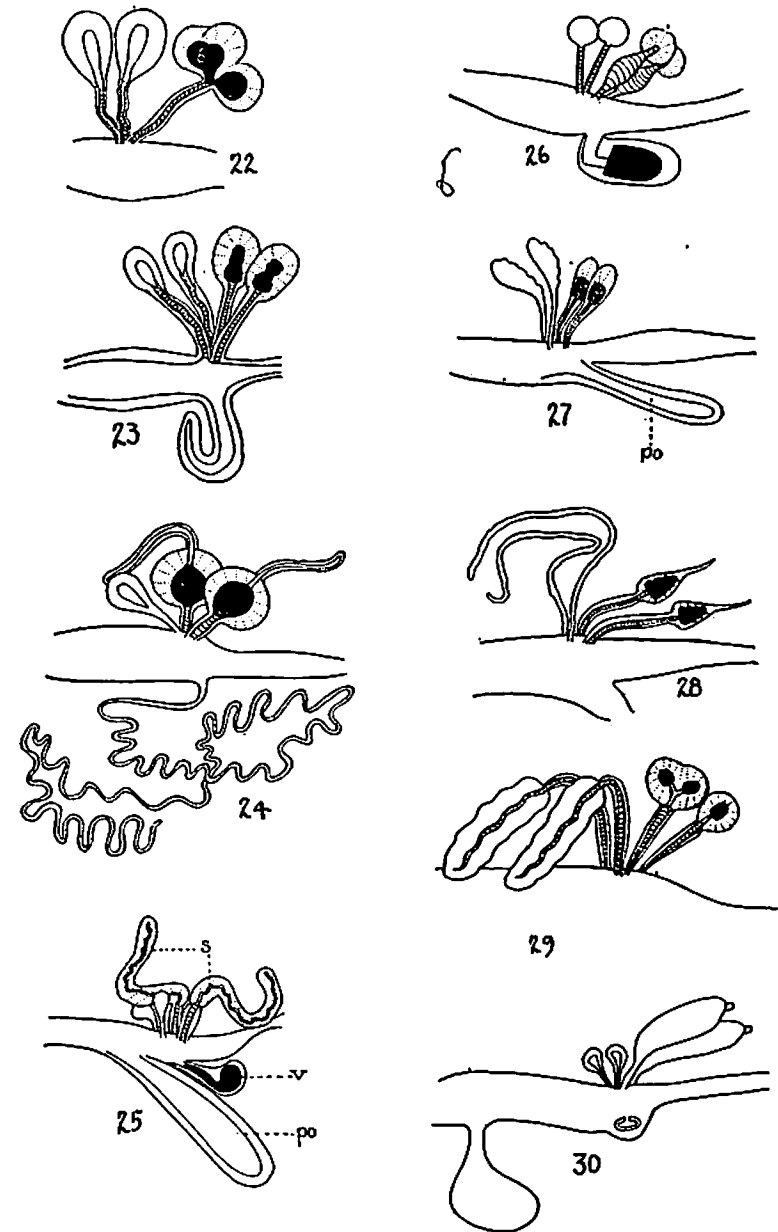
- Figure 9. *Pseudopsila collaris*. po, ventral pouch; s, spermatheca; v, ventral receptacle.
- Figure 10. *Sphyracephala brevicornis*.
- Figure 11. *Sepsis* sp.
- Figure 12. *Piophilus* sp.
- Figure 13. *Traginops irrorata*.
- Figure 14. *Minettia lupulina*.
- Figure 15. *Ochthiphila polystigma*.
- Figure 16. *Leria pectinata*.
- Figure 17. *Clusiodes johnsoni*.
- Figure 18. *Heteromeringia nitida*.
- Figure 19. *Mumetopia occipitalis*.
- Figure 20. *Diastata repleta*. Ventral receptacle.
- Figure 21. *Periscelis annulata*. An egg is shown in the uterus.
- Figure 22. *Sphyroperiscelis wheelcri*.
- Figure 23. *Amiota leucostoma*.
- Figure 24. *Stegana vittata*.
- Figure 25. *Disocercina obscurella*. po, ventral pouch; s, spermatheca.
- Figure 26. *Hydrellia hypoleuca*.
- Figure 27. *Pelomyia mallochii*. po, ventral pouch.
- Figure 28. *Borborus equinus*.
- Figure 29. *Aulacigaster leucopexa*.
- Figure 30. *Cryptochaetum iceryæ*.



SEMINAL RECEPTACLES AND ACCESSORY GLANDS
OF THE DIPTERA



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