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

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Introduction

It was estimated by Williston (1908) that more than half of the living Diptera belong to the large group that is variously known as Muscidae, Myodaria, Muscoidea, Oligoneura, Eumyiidae, etc. The division of this group into smaller units is an extremely difficult task, though there is fairly general agreement that two main series are present: the Calyptera, Schizometopa, or Thecostomata, and the Acalyptera, Holometopa, or Haplostomata. It is difficult to draw up satisfactory definitions of these series, and there are a number of forms that are near the border-line and may be placed on either side of it. Nevertheless, there is general agreement that the separation into these two series represents a valid and useful conception.

The Acalypterate series includes from twenty to forty more or less generally recognized families, perhaps better called subfamilies. Scarcely any two authors agree either as to the number of these families or as to their limits, and there are current several widely different sequences of arranging them. The older authors classified the group chiefly according to the venation of the wings, the structure of the arista, and the number and

arrangement of the bristles. Loew and others used the structure of the ovipositor in some cases; and Hendel, Czerny and Melander have also used the shape and arrangement of the external sclerites of the head. Frey (1921) has made a detailed study of the mouth-parts, and has contributed a large amount of new and suggestive data. His arrangement of the Acalypterate families seems to me the best that has yet been proposed, and has been followed in the present paper. The reader is also referred to Frey's paper for a full historical account of the classification of the group.

For some years it has seemed to me desirable to make use of new characters for checking up the existing systems of classification. The careful work of Nonidez (1920) on the internal genital apparatus of Drosophila showed that the seminal receptacles were strikingly different from those of the Calypteræ; and the accounts of Weschè indicated differences within the Acalypteræ. My own examination of several species of Drosophilidæ suggested that that group was rather uniform, and a dissection of *Leria pectinata* (Helomyzidæ) showed that form to represent a new and quite distinct type. Accordingly it was determined to make a comparative study of the apparatus in all the Acalypteræ of which living females could be obtained. After many of the dissections were made the important early work of Dufour (1851) was examined. This paper furnishes data on several groups that I have not dissected, and greatly increases the available information on many other groups, especially as it gives a comprehensive view of the forms other than Acalyptera—of which I have examined only a few scattered genera.

Another reason for carrying out a comparative study of the receptacles and accessory glands was that the functions of these parts are only very imperfectly understood. It was hoped that some light might be thrown on this general problem, and that species might be found that would be favorable for further study of the question.

PREVIOUS WORK

The point of departure for all comparative studies on the internal organs of the Diptera is the extensive and painstaking work of Dufour (1851). In the special part of the present paper

Dufour's descriptions of the "appareil séminal et sébifique" of the forms studied by him are incorporated with the material collected by later workers, including myself. The large number of species that he studied, and the way in which later work has verified his findings, will be apparent from that account. There are, however, a few points that should be explained concerning Dufour's descriptions. He called the seminal receptacles and their ducts the "glande sébifique," and the spermathecæ themselves the "orbicelles," while the parovarium was termed the "reservoir séminal." That is to say, he reversed the function of these organs as now generally understood. There can now be no question that sperm are stored in the "orbicelles" and not in the "reservoirs séminals," since improved optical apparatus enables us to see the sperm directly instead of inferring its position from the structure of the organs concerned. But, as will be shown below, I am inclined to suppose that Dufour was correct in ascribing a glandular function to the spermathecæ. Dufour notes the color of the center of the spermatheca, *i.e.*, of the sac as opposed to its envelop. I have inferred from this as to whether or not the sac is chitinized—a point not specifically stated by Dufour. Weschè (1906) has published the only other extensive account of the internal parts of the female reproductive organs of the Diptera. The parts here discussed were not the primary object of Weschè's study, and his accounts are accordingly incomplete in many respects. His work was done with cleared material, and so only chitinized parts were observed. His data are thus useful to us only in indicating the number and shape of chitinized spermathecæ present. In the case of the Ephydridæ he did observe the chitinized ventral receptacles, but owing to failure to trace the soft parts he interpreted them as spermathecæ.

Lowne (1890–1895), Cholodkovsky (1909), Pantel (1910), Townsend (1911), and others have studied the Calypteræ in some detail. This literature is summarized briefly in the descriptive portion of the present paper.

Nonidez (1920) has presented perhaps the fullest account of the structure and physiology of these organs, based on *Drosophila melanogaster* Meigen. His conclusions were drawn from exten-

sive dissections, sectioned material, and in vitro studies of freshly dissected specimens. It was this author who first described and correctly interpreted the ventral receptacle.

NOMENCLATURE OF THE FORMS DESCRIBED

I am responsible for the identification of the species that I have myself dissected. In cases where I could not be practically certain of the species I have refrained from applying any specific name at all. These determinations have been made largely by the use of the published synopses of the various groups; but my use of these keys has been controlled by applying them to my own collection of over 8,000 Acalypterate specimens. This collection is fairly extensive for the regions around Woods Hole and New York and for southern Alabama, the three regions where most of the specimens here described were collected, and also contains much material from Europe, California, Cuba, Central America, and elsewhere. In several of the subfamilies—the ones in which are most of the species here described—I have also studied much of the material in the United States National Museum, the American Museum of Natural History, the Boston Natural History Society, the Loew collection at Harvard, the Walker and Williston collections at the British Museum, and the collections of Messrs. J. M. Aldrich and C. W. Johnson.

Dufour's material was identified by Macquart. I have translated these names into modern terminology so far as I was able, using mainly Becker, Bezzi, Kertész, and Stein (1903–1907). In the descriptions I have given the modern term, followed by Dufour's term enclosed in brackets, when the names differ.

The sequence of groups adopted in the descriptive portion of this paper is that used by Williston (1908), except within the Acalypterate group. In the latter forms I have followed Frey (1921), with a few minor changes.

SPERMATHECÆ

The spermathecal ducts arise from the anterior portion of the dorsal wall of the uterus—in fact I have considered their insertion as marking the point of separation for the oviduct and uterus. The ducts usually have internal trachea-like spiral

thickenings lining their lumens, though these are often faint or perhaps entirely absent. Each duct has a thin cellular envelop throughout its length.

The spermatheca itself is usually a more or less spherical, heavily chitinized sac attached to the apex of its duct. The form is, however, variable—it may be cylindrical, telescoped, or cork-screw-like; often the sac is not chitinized (probably in reality only very weakly chitinized); and in some forms there is no special sac at the end of the spermathecal duct. Typically the spermatheca is surrounded by a characteristic envelop of large columnar cells that contain large vacuoles. In those forms that have no differentiated spermatheca these envelop cells still persist as a cap on the end of the duct.

PAROVARIA (= *colleterial glands*)

The parovarial ducts arise from the dorsal wall of the uterus, just posterior (or rarely lateral) to the insertion of the spermathecal ducts.

The parovarium itself is never chitinized; in form it is most often a pear-shaped body with a small lumen, but it may be nearly spherical, long and cylindrical, or may have a more complex form. Its cells are very large and contain vacuoles; but these are easily broken by pressure, the cells then appearing granular. The cells are not columnar as are the spermathecal envelop cells, but are roughly hexagonal in optical section. This peculiarity is sufficient to enable one to distinguish the two organs in almost any dissection.

VENTRAL RECEPTACLE

This organ has been found only in certain of the Acalypterate subfamilies. It arises from the anterior ventral portion of the uterus. In form it varies from a simple pocket in the uterine wall to a very long, fine, and much coiled tube, or a large, heavily chitinized, telescoped pouch. Its structure seems to be of considerable taxonomic importance. The direction in which the tube bends and its degree of chitinization appear to be the two most significant characters for systematic use.

The ventral receptacle was described and figured for certain Ephydridæ by Wesché, and was apparently seen in *Piophila*

casei by Dufour (1851). In both of these cases it was identified as a spermatheca. It was accurately described and figured in *Phytomyza* by Miall and Taylor (1907), and was seen but not accurately understood or figured in *Drosophila* by Unwin (1907). In neither of these cases was its function surmised. It was correctly described in detail, and also figured, and its function clearly proved, in *Drosophila* by Nonidez (1920).

In some forms there is a ventral pouch to the uterus that simulates a ventral receptacle; but the two types of organs appear to be very distinct. While the ventral receptacle may lie embedded in the uterine wall, it never has a muscular wall of its own, but is supplied only with a thin cellular envelope. The uterine pouches, on the other hand, have the same type of strongly muscular wall as the uterus itself.

INTRASPECIFIC VARIABILITY IN NUMBER OF SPERMATHECÆ

Nonidez (1920) found occasional specimens of *Drosophila* with three spermathecæ, though two is the usual number throughout the Drosophilidæ. I have dissected 330 specimens of various wild stocks of *D. melanogaster*, 321 *D. simulans*, 20 hybrids between these two species, 38 *D. funebris*, 33 *D. immigrans*, and 19 each of *D. buskii* and *D. repleta*. In these series there were two specimens with three spermathecæ (one *melanogaster* and one *simulans*); all the others had two spermathecæ.

The above totals do not include the data obtained from a certain stock of *D. melanogaster* originally collected in Sweden, nor from several mutant stocks that may be descended in part from the Swedish stock. Eighty-four females of this Swedish stock were dissected, and fourteen of them were found to have three spermathecæ. The inheritance of this character is now being studied; only a preliminary account of the race can yet be given. Selection for increased spermatheca-number has been effective in that a race is now established in which from 25% to 75% of the females have three spermathecæ, and a few specimens with four have been found. There is evidence that at least two Mendelian genes are concerned in the production of the extra spermathecæ, but the genetic analysis is still incomplete.

In some specimens of this race there are only two spermathecæ present, but one is distinctly larger than the other, and is shaped as though it were a double organ. In other specimens one spermatheca is normal, but the other is replaced by two small spermathecæ attached to a single duct. In still other specimens—apparently those in which the duct branches nearer its base—all three spermathecæ are equal in size. Finally, in some specimens there are three equal spermathecæ, each with a separate duct, so that there are three distinct ducts opening into the uterus. In those cases in which one spermatheca is clearly doubled, either the right or the left organ may be so affected.

The specimens with four spermathecæ have not yet been studied in detail.

The only other species in which variations of this nature have been found is *Psila lateralis* (see the descriptive part of this paper); but in very few species have more than five to ten specimens been dissected. On the other hand, in the cases in which more than one species of a genus has been studied the spermatheca-number of all such species has turned out to be the same. The only exceptions to this rule are *Calobata* and *Limnia*, and in both these genera Dufour examined one of the species while I saw the other, so that the discrepancies may not be real. Further, there are relatively few cases in which variations occur within a family.

On the whole it seems probable that the number of spermathecæ is a relatively constant character—though it is clear that results based on one or a very few specimens may at times turn out to be misleading; and, by analogy with other characters, it is likely that some forms will be found much more variable than others. *Psila lateralis* presumably represents such a condition.

DESCRIPTIONS, FORMS OTHER THAN ACALYPTERÆ

TIPULIDÆ. Dufour described *Tipula oleracea* Linné in detail and also figured it. There are three chitinized spermathecæ, with separate ducts that unite to form a single long common duct. The two parovaria also have a common duct, opening into the oviduct near the opening of the spermathecal duct. In *Ctenophora* Dufour also reported three chitinized spermathecæ.

CULICIDÆ. Dufour described and figured *Culiseta annulata* (Schrank) [Culex]. There are three chitinized spermathecæ with separate ducts, and one large parovarium. Neveu-Lemaire (1902) reported a single spermatheca in *Anopheles*, two in *Mansoniodes*, three in *Culex*. Howard, Dyar, and Knab (1912) described one in *Uranotaenia* and *Aedeomyia*, three in *Mansonia*.

Von der Brelje (1924) has studied several genera, and also discusses the work of Kulagin (1901) and of Macfie and Ingram (1922). There is one spermatheca in *Anopheles* and in *Dixa*, three in *Aedes*, *Corethra*, *Culex*, *Mansoniodes*, *Mochlonyx*, and *Theobaldia*. In *Mochlonyx* the three ducts are entirely separate; in *Mansoniodes* they are not described; in the other four genera two of them are united near the base, and in *Culex* and *Corethra* the third is united to this common duct still further basally. In *Mansoniodes* one spermatheca is smaller than the other two. In all these genera the spermathecæ are spherical and chitinized, but the chitin has small thin spots in it, that appear like holes in *Anopheles*. There is a single parovarium in *Aedes*, *Anopheles*, *Culex*, *Theobaldia*, and *Mochlonyx;* in the last-named genus the gland is forked apically. In *Corethra* there are two parovaria, with a common duct, while in *Dixa* there are two with ducts that are separate apically but join before they reach the uterus. In *Dixa* there is also present a pair of glands anterior to the spermatheeal duct. Both the parovarial and the spermatheeal ducts open into the posterior region of the uterus in this family, though in the higher members of the order this relation has never been observed. Posterior to these openings there is, in *Aedes*, *Anopheles*, *Culex*, *Mochlonyx*, and *Theobaldia*, a large dorsal pouch of the vagina, which v. d. Brelje calls the bursa copulatrix—though its function is only surmised.

CHIRONOMIDÆ. Weseché failed to find any chitinized spermathecæ in *Chironomus;* he reported three in *Ceratopogon*. Miall and Hammond (1900) described two spherical spermathecæ and a single large parovarium in *Chironomus*.

MYCETOPHILIDÆ. Dufour described a number of members of this family. *Ceroplatus dispar* Dufour has two spermathecæ (apparently not chitinized) and two large parovaria. *Bolitophila fusca* Meigen [*Macrocera hybrida*] has the same number of organs, but the spermathecæ are heavily chitinized. *Mycetophila amabilis* Dufour has two spermathecæ, not chitinized, and one parovarium. *Sciara ingenua* Dufour has two non-chitinized spermathecæ and two parovaria.

BIBIONIDÆ. Dufour reported three chitinized spermathecæ in *Bibio marci* Linné. Weseché confirmed this for *B. hortulanus* Linné and *Dilophus febrilis* (Linné). In *Scatopse notata* (Linné) Weseché described and figured a single chitinized spermatheca.

SIMULIIDÆ. Weseché reported a single chitinized spermatheca in *Simulium*.

LEPTIDÆ. Dufour described and figured *Leptis tringaria* Linné. There are three non-chitinized spermathecæ, whose ducts are united basally to form a long common duct. There are two long parovaria.

I have examined *Chrysopila* sp. and *Leptis* sp. There are three spermathecæ in each species. They are spheroid and heavily chitinized in *Chrysopila*, with the usual type of envelop cells. The three ducts are united basally, and have a common envelop even in the region where they are separate. In *Leptis* the spermathecæ are long and narrow, with the lumen scarcely larger than that of the ducts. Each spermatheca is chitinized only in a few small plates near its apex. The spermatheeal envelop is unusually thin—scarcely thicker than the envelop of the duct.

STRATIOMYIDÆ. According to Dufour there are three chitinized spermathecæ and two parovaria in *Beris vallata* Forster, *Odontomyia tigrina* Fabricius, *Sargus cuprarius* (Linné), *Chrysomyia* sp., and *Pachygaster leachii* Curtis [*Vappo pallipennis*]. In *Ephippiomyia ephippium* (Fabricius) [*Ephippium thoracicum*] there are only two spermathecæ. The form of the spermatheca shows great variation from species to species in this family.

TABANIDÆ. There are three small chitinized spermathecæ in *Pangonia marginata* Fabricius, *Tabanus bovinus* Linné, *Hæmatopota pluvialis* (Linné), and *H. crassicornis* Wahlberg -the first

two reported by Dufour, the last three by Wesché (both saw *T. bovinus*). In the two species examined by him, Dufour also described two parovaria.

I have dissected *Chrysops* sp. There are three spermathecæ, chitinized apically but not basally. They are long ovoid in shape, and have the usual envelop cells. Sperm were observed in them.

ASILIDÆ. Dufour described the spermathecæ as three chitinized coiled tubes in *Asilus crabroniformis* Linné, *Dioctria nigritarsis* Dufour, and *Laphria fulva* Meigen. He also recorded two parovaria in these forms. I have found similar spermathecæ in *Atomosia* sp., and in *Dasyllis* sp. In two species of *Asilus* they are coiled, but irregularly so and not chitinized. In *Erax* sp., and in *Proctacanthus* sp., they are spherical and chitinized. In all these forms, except *Proctacanthus*, three spermathecæ were seen. In *Proctacanthus* only two were seen, but only one poor dissection was obtained, so a third is probably present. It may be noted that Wesché stated that he had found three globular spermathecæ in the family—genus not specified.

THEREVIDÆ. Dufour described three non-chitinized spermathecæ in *Thereva* spp., but only two in *Psilocephala ardea* Fabricius [*Thereva confinis*].

SCENOPINIDÆ. Dufour described and figured *Scenopinus fenestralis* Linné. There are two spermathecæ, each with a long coiled duct, the two coils apparently being separate. Each spermatheca is adherent to the single parovarium.

BOMBYLIIDÆ. Wesché stated that *Comptosia ocellata* has spermathecæ similar in number and arrangement to those of the Tabanidæ. Dufour described three chitinized spermathecæ and two parovaria in *Bombylius major* Linné, *B. cruciatus* Fabricius, *B. minor* Linné, *Systoechus ctenopterus* Mikn [*Bombylius*] and *Usia aenea* Rossi. In *S. cruciatus* there is also a pair of long slender tubes attached just posterior to the parovaria. I have myself observed three coiled chitinized spermathecæ in *Systropus macer* Loew, suggestive of the type found by Dufour in the

Asilidæ. However each spermatheca here has a separate series of coils, whereas Dufour's figure shows all three coiled together in *A. crabroniformis*. In *Systropus* there is a common envelop for the three spermathecæ. Active sperm were found in the basal portions of the spermathecæ.

EMPIDIDÆ. Dufour recorded a single spermatheca and two parovaria in *Empis livida* Linné, *E. unicolor* Brullé, and *Ramphomyia sulcata* Meigen. Wesché also stated that he had observed only one spermatheca in the family.

DOLICHOPODIDÆ. Wesché failed to find the spermatheca, since it is not chitinized. Dufour described and figured it for *Dolichopus nitidus* Fallén. There is a single organ consisting of a non-chitinized bulb, attached to a long slender duct that is coiled into a spool-like form. Two parovaria are present. I have examined an unidentified species of *Dolichopus*, and can confirm Dufour's account of the spermatheca, though my species differed in having a conspicuous transverse constriction in the spermatheca itself. I have also observed active sperm in the portion of the organ basal to the constriction. The long duct has, at least in the greater part of its length, two longitudinal ribs on opposite sides, which give it the appearance of two fused ducts. I am disposed to conclude that such is really its nature. I have also dissected specimens of the genera *Gymnopternus*, *Hydrophorus*, *Paraclius*, *Pelastoneurus*, *Sciapus*, and *Thrypticus*. All these agree in having a single non-chitinized spermatheca. The duct is coiled in *Gymnopternus* and *Paraclius*. In *Sciapus* it is quite short; in *Pelastoneurus* it is much larger at the base, and is less so in *Dolichopus* and in *Paraclius*. The spermatheca itself is a simple sac in *Sciapus;* dumb-bell shaped more or less as in *Dolichopus*, in *Hydrophorus*, *Paraclius*, and *Pelastoneurus*. In *Thrypticus* there is no constriction, but there appears to be a basal and an apical chamber. Sperm were seen in the organ in *Gymnopterus*, *Hydrophorus*, *Pelastoneurus*, and *Sciapus*. It seems likely that the spermathecæ of this family would repay careful study.

PHORIDÆ. Wesché failed to find any spermathecæ here. Dufour found in *Phora abbreviata* v. Roser [*sordidipennis*] a single non-

chitinized spermatheca and two parovaria. I have observed the same relations in two species of *Aphiochæta*. Sperm were present in the spermatheca.

LONCHOPTERIDÆ. Wesché failed to find the spermathecæ, but they were described and figured in the same year by de Meijere (1906). In *Lonchoptera lutea* Panzer and *L. furcata* Fallén, de Meijere found two ducts, each with a border of large cells at its apex, forming a cylindrical envelop. In *L. lutea* the duct is long and slender, and sperm were found throughout its length. In *L. furcata* the whole organ was smaller, the duct shorter, and sperm were never found. *L. furcata* appears to reproduce parthenogenetically and de Meijere believed the spermathecæ to be rudimentary organs.

PLATYPEZIDÆ. I have dissected *Platypeza* sp. It has three spherical chitinized spermathecæ, with the usual envelop cells and with rather long ducts that are entirely separate.

SYRPHIDÆ. Dufour described and figured *Volucella zonaria* Poda and *Eristalis tenax* (Linné). In both there are three spherical chitinized spermathecæ with long ducts and two parovaria. *Eristalis* is unique in that the parovaria are much branched. Wesché also recorded three chitinized spermathecæ in *E. tenax* and in *Syritta pipiens* Linné. I have studied *Criorhina decora* (Macquart), *Eristalis aeneus* (Scopoli), *E. arbustorum* (Linné), *Ferdinandea dives* (Osten-Sacken), *Helophilus similis* Macquart, *Melanostoma mellinum* (Linné), *Mesogramma marginata* (Say), *Paragus* sp., *Pipiza pistica* Williston, *Platychirus* sp., *Rhingia nasica* Say, *Sericomyia chrysotoxoides* Macquart, *Sphærophoria* sp., *Syrphus* sp., and *Xylota ejuncida* Say. In all these the spermathecæ are three in number. They are chitinized in all but *Helophilus* and *Xylota;* spherical in all except *Xylota,* but drawn out into a chitinized stalk in *Sphærophoria.* In *Xylota* it is probably best to describe the spermatheca as spherical, but just basal to it the duct is much swollen, forming a cavity somewhat larger than that of the spermatheca itself. The apical region is surrounded by typical envelop cells, while the cells around the basal swelling rather resemble parovarial cells. The only other unusual relation of envelop cells found in this family is that occurring in *Eristalis* and *Helophilus,* where the spermathecæ are covered with a very thin layer of cells, while the duct just basal to them is surrounded by a layer of typical large envelop cells. In *Criorhina* one spermatheca is much smaller than the other two; elsewhere the three are equal in size. In *Criorhina, Ferdinandea,* and *Sericomyia* the chitin of the spermatheca is perforated by numerous small holes; in *Melanostoma* it is covered with small papillæ; in the other forms with chitinized spermathecæ the surface is smooth and not perforated.

The spermathecal ducts are entirely separate in *Criorhina* and *Pipiza,* and probably so in *Xylota.* In *Eristalis* they are separate, but two of them are enclosed in a common envelop from their bases to the point where the shifted spermathecal envelop begins. The ducts were not studied in *Helophilus* or *Sericomyia;* in all the other eight genera two of them unite basally, so that only two ducts enter the uterus. This fusion is very near the base in *Sphærophoria,* but in all the other forms the fused portion is at least as long as either separate branch. In *Paragus* the entire duct is relatively short, and is much thickened basally. Sperm were noted in the spermathecæ of *Helophilus, Paragus, Rhingia,* and *Sericomyia.*

Parovaria were observed only in *Ferdinandea, Platychirus,* and *Syrphus.* In all three forms they were long and unbranched. Two were found in *Syrphus* and probably in *Platychirus,* only one in *Ferdinandea.* It is possible that two occur in all the forms studied, since the long telescoped ovipositor made it difficult to dissect such a delicate organ as this.

CONOPIDÆ. Dufour described *Myopa dorsalis* Fabricius [*ferruginea*] and *Physocephala rufipes* Fabricius [*Conops*]. In each there are two spermathecal ducts, each of which bears two chitinized spermathecæ. Two parovaria also occur in each species. Pantel (1910) also stated that the members of this group have two ducts, each with twin spermathecæ. I have observed the same relation in *Zodion* sp., the only Conopid I have dissected.

ŒSTRIDÆ. According to Wesché there are two spermathecæ in *Gastrophilus equi* (Clark). These, as also the two parovaria, had already been observed by Dufour.

MUSCIDÆ CALYPTERATÆ. A full account of the reproductive organs of *Calliphora erythrocephala* Meigen is given by Lowne (1890–1895), and of *Musca domestica* Linné by Hewett (1914). Dufour, Wesché, Cholodkovsky (1909), Pantel (1910), Townsend (1911), and Minchin (1905) have described numerous other Calypteræ. It appears from these accounts that there are commonly three chitinized spermathecæ with separate ducts (*Echinomyia, Gonia, Gymnosoma, Phasia, Winthemia, Helicobosca, Dexia, Prosena, Sarcophaga, Lucilia, Calliphora, Mesembrina, Musca, Rhyncomyia, Aricia, Ophyra, Lispa, Anthomyia, Homalomyia, Pegomyia,* etc.). Only two are reported in *Siphona* spp. and in the group of *Stomoxyiidæ* (*Stomoxys, Hæmatobia, Glossina*). Pantel described only one in *Tachina* [*Chætotachina*]. In all cases reported there are two parovaria, except in *Aricia urbana* Meigen, [*Mydæa*], which according to Dufour has three. I have found three chitinized spermathecæ with separate ducts in *Fucellia* sp., which is usually placed in the family Anthomyidæ, but shows points of resemblance to the Cordyluridæ.

In *Musca domestica* there are two small pouches arising from the anterior ventral portion of the uterus; apparently these are useful during copulation.

As is well known, numerous forms among the Calypteræ are viviparous. Since in the majority of the Diptera there is only space for a single egg in the uterus, it is evident that there must be present some different arrangement in those forms in which numerous larvæ develop at once within the body of the mother. Dufour showed that in the viviparous Tachinidæ examined by him the uterus itself is enlarged and contains the developing eggs and larvæ; in *Sarcophaga* two large pockets are given off from the uterus, and here the developing eggs and larvæ are to be found. These have been studied in detail by Cholodkovsky (1909). Pantel (1910) and Townsend (1911) have dissected large numbers of Calypteræ, and Townsend has proposed a general scheme of classification of this group based chiefly on characters of the internal genital apparatus of the females. These papers contain a very great amount of valuable data; but for our present purpose they are chiefly useful in showing that at least that part of the group studied by Pantel and Townsend (*i. e.*, excluding the Anthomyiidæ) is remarkably uniform with respect to the characters that have proved useful in working over the Acalypteræ.

The above account of the Calypteræ does not include the Cordyluridæ, which have been commonly referred to the Acalypteræ, but seem to me to be best placed near the Anthomiidæ. They may now be discussed. Wesché reported three chitinized spermathecæ in *Scatophaga lutaria* (Fabricius) and in *S. stercoraria* (Linné). In the former they are telescoped at the base; in the latter they are cylindrical with spiral striations, like those of *Lonchæa* or *Leucophenga*. I have examined *Cordylura* sp., *Parallelomma* sp., *Scatophaga furcata* (Say), and *S.* sp. All four forms have three chitinized spermathecæ, with spiral striations. In *Parallelomma* there is an apical unstriated region; in *Scatophaga* sp. there is a deep apical invagination. In all of these species there are three short ducts, entirely separate to their bases. This last character furnishes confirmation for the view that the group should be placed with the Calypteræ rather than with the Acalypteræ.

Two parovaria occur in *Cordylura* and in *Parallelomma*. In the former they are about four or five times the length of a spermatheca; in the latter they are spheroid and slightly shorter than a spermatheca. Two parovarial ducts were found in *Scatophaga furcata*, but the organs themselves were not seen. In *S.* sp. only one parovarium was found. It was ovoid, and slightly larger than a spermatheca. No sperm nor ventral receptacles were found in this group.

HIPPOBOSCIDÆ. According to Berlese (1909) there are two branched parovaria in *Melophagus*. No spermatheca nor ventral receptacle is present, the sperm lying in the oviduct itself. A separate copulation is required to fertilize each egg.

ACALYPTERÆ

MICROPEZIDÆ. Dufour recorded *Calobata cothurnata* Panzer as having two spermathecæ, apparently not chitinized, and with

long ducts. I have studied *Calobata univitta* Walker. There are three chitinized spermathecæ, that are pear-shaped, each with a small indentation at the apical (broad) end. Two of them are attached to a common duct, and this fact probably led Dufour to report them as a single organ. As will soon appear, the attachment of two spermathecæ to a single duct (which has already been described in the Syrphidæ) is very common in the Acalypteræ. In *Calobata*, as in most of the other Acalypteræ in which the relation occurs, the common duct branches just basal to the spermathecæ, so that their envelopes are closely apposed.

CHLOROPIDÆ. Subfamily Chloropinæ. Wesché failed to find any chitinized spermathecæ in this subfamily. I have examined *Chloropisca glabra* (Meigen), *Diplotoxa* (*versicolor* Loew?), and *Meromyza pratorum americana* (Fitch). All three have two rudimentary spermathecæ attached to long fine ducts, two rather long narrow parovaria tapering gradually to their insertions on the uterus, and a single non-chitinized pocket-like ventral receptacle that has its blind end anterior to its opening into the uterus. In *Chloropisca* and *Meromyza* the spermathecæ are adherent, each to the mesial surface of the corresponding ovary. In the former the organ consists of a continuation of the narrow duct, loosely twisted, and bordered (on one side only) by a row of the usual columnar envelop cells. In this form the basal portion of each spermathecal duct is enlarged for a distance about equal to the length of a parovarium. Active sperm were seen in these basal enlargements and in the ventral receptacle, but not elsewhere. In *Diplotoxa* and *Meromyza* there is a minute spherical mass of chitin at the apex of each spermathecal duct, and the envelop cells are arranged radially about this mass, to form a small sphere. There are no basal thickenings in the spermathecal ducts. In *Diplotoxa* sperm were found in the ventral receptacle and not elsewhere.

SUBFAMILY BOTANOBIINÆ. I have examined *Botanobia coxendix* (Fitch), *B. frit pusilla* (Meigen), *Crassiseta* sp., *Hippelates flavipes pusio* (Loew), *H. nitidifrons* Malloch, *H. texanus* Malloch, *Melanochæta* (*longula* Loew?), and *Siphonella oscinina* (Fallén). All of these forms have two rudimentary spermathecæ as in the Chloropinæ, and also a ventral receptacle that is of the same type as that of the Chloropinæ. A single parovarium was found in *Botanobia* (both species), the single gland resembling the two of the Chloropinæ. In *Melanochæta* and *Siphonella* two parovarial ducts were observed, but the organs themselves were not found. In the other forms no parovaria were detected, but at least one was probably present. The most striking characteristic of this subfamily is that the two very fine spermathecal ducts are (in all the species dissected) rolled into a single heavy spool-like coil, within which lie the spermathecæ themselves. No trace of such a coil was seen in the Chloropinæ, but it is characteristic of the Milichiidæ. Sperm were found only in Crassiseta, where they were in the ventral receptacle, and in *Hippelates nitidifrons*, in which they were present in the basal portion of the spermathecal duct, though there is no basal enlargement corresponding to that of Chloropisca. The chitinized core of the spermatheca is always very small, and has little if any lumen. It is spherical in *Botanobia*, pear-shaped in *Siphonella*, a short cylinder in *Hippelates*, spheroidal and with a much roughened surface in *Crassiseta* and *Melanochæta*.

MILICHIIDÆ. I have examined *Desmometopa m-nigrum* (Zetterstedt), *Mallochiella halteralis* (Coquillett), *Milichiella lacteipennis* (Loew), *Paramyia nitens* (Loew), *Pholeomyia indecora* (Loew), and *Phyllomyza* sp. In all of these there are two very long fine spermathecal ducts, and these are rolled into a single spool-like coil that is usually somewhat looser than that found in the Botanobiinæ, but nevertheless reminds one of that subfamily. The spermathecæ themselves have been seen only in *Mallochiella* and *Pholeomyia*. In both forms they are two in number, and each consists of a slender very weakly chitinized tube—merely a continuation of the duct—surrounded in a single plane by the usual columnar envelop cells. The whole organ thus has a feather-like appearance. Parovaria were found only in *Mallochiella*, where two are present. The ducts have internal spiral thickenings that are much more conspicuous than those of the spermathecal ducts. The duct is shorter than the gland, which is about the length of a spermatheca, and is roughly cylindrical in shape, tapering to its base.

The above account was drawn up from fresh dissections, in which neither sperm nor ventral receptacles were found. Both were, however, discovered in fixed and sectioned material of *Milichiella*. The ventral receptacle is non-chitinized, and is evidently the functional sperm-reservoir. It is probably present also in the other members of this subfamily.

AGROMYZIDÆ. Miall and Taylor (1907) described *Phytomyza aquifolii* Goureau. There are two spherical spermathecæ, and two parovaria. The ventral receptacle was also described and figured. The figure agrees well with that given here for the same genus, and the authors also made out that the sac opened into the ventral wall of the uterus. They concluded their account of it thus: " . . . we are unable to explain the function of this organ."

I have examined *Agromyza* spp., *Cerodonta dorsalis* (Loew), and *Phytomyza* sp. In all three genera there are two nearly spherical chitinized spermathecæ, two parovaria, and a chitinized ventral receptacle. Sperm have been found in the spermathecæ of *Agromyza* and *Cerodonta*, and in the ventral receptacle of the latter. The parovaria, in all three genera, consist of a short basal duct, containing an internal spiral thickening, then a fairly large, thin-walled spherical sac. The apical portion of the organ consists of an irregular weakly chitinized duct, surrounded by very large cells that contain huge vacuoles. This portion is somewhat longer than all the rest of the parovarium taken together. The ventral receptacle of *Cerodonta* is a simple pocket, horse-shoe-shaped when seen from the side, with the opening at the posterior end and with the blind anterior end somewhat enlarged. In *Agromyza* and in *Phytomyza* the opening is also posterior. The structure is similar in the two genera, and may be understood from the figure as well as from a description. This receptacle lies embedded in the ventral wall of the uterus. A similar organ occurs in *Phytomyza bicolor* Coquillett, of which I have a cleared preparation.

In *Cerodonta* the two spermathecal ducts fuse near their bases to form a short common duct that is broader than either single duct. This relation seems not to occur in the other two genera.

LONCHAEIDÆ. According to Dufour, *Palloptera ustulata* Fallén [*Sapromyza*] has three chitinized spermathecæ. Wesché recorded two for *Lonchæa* sp. I have examined *Lonchæa polita* Say and *L.* sp. In each species there are three chitinized spermathecæ that are cylindrical and have spiral ridges like those of the Cordyluridæ or of *Leucophenga*. In *L. polita* there are only two ducts, the right one being branched at its apex to bear two spermathecæ. In the undetermined species there are only two ducts at the base, but one of them branches very near the base—so that this species comes nearer having three separate ducts than any other Acalypterate yet observed. Two parovarial ducts were observed in this form, but the glands themselves were not seen in either species. A chitinized ventral receptacle is present in each species. In *L. polita*, where a better dissection was obtained, it is retort-shaped, and lies embedded in the unusually thick muscular ventral wall of the uterus. Sperm were found only in the unidentified species, where they were in the spermathecæ.

ORTALIDÆ. I have dissected *Melicria similis* Loew. There are three chitinized spermathecæ, resembling those of *Lonchæa*, and attached to two ducts as in *L. polita*. Owing to the heavily chitinized ovipositor, dissection is very difficult in this and related families. For this reason the ventral receptacle remains uncertain, though probably a weakly chitinized one was present. Sperm were not found.

CEPHALIDÆ. I have a cleared preparation of *Camptoneura picta* (Fabricius) that shows three chitinized spermathecæ. It is likely from their position that two of them arise from a common duct, but the ducts are not visible.

PLATYSTOMIDÆ. Dufour's account of *Platystoma umbrarum* Fabricius gives that species two rather long tapering parovaria, and three chitinized spermathecæ. Dufour also figured three spermathecal ducts that enter the uterus separately. This latter observation can hardly be accepted until verified, since such a relation has not been observed in any other undoubted Acalypterate. It does not occur in the only Platystomid that I have

examined—*Rivellia viridulans* Desvoidy. In this form there are three chitinized spermathecæ, each of which is spherical but strongly telescoped basally—closely resembling the form characteristic for *Drosophila*. The spermathecal ducts are two in number, and each has a conspicuous oval swollen region just basal to the spermatheca. One of them branches apically from the swelling, to bear two spermathecæ. Difficulty of dissection prevented any satisfactory attempt to see if a ventral receptacle is present.

ULIDIIDÆ. Weseché figured three chitinized spermathecæ for *Ulidia nigripennis* Loew (stated by Collin (1910) to be really *U. erythrophthalma* Meigen). These were telescoped at the base. Weseché also figured the spermathecæ of *Seoptera vibrans* (Linné). These were four in number, but only two ducts were present, each bearing two spermathecæ at its apex. Dufour described and figured *Chrysomyza demandata* (Fabricius) [*Ulidia*]. There are three spherical chitinized spermathecæ, two of them arising from a common duct, and two pear-shaped parovaria with long fine ducts.

I have dissected *Chaetopsis ænea* (Wiedemann), *C. apicalis* Johnson, *C. fulvifrons* (Macquart), *Chrysomyza ænea* Wiedemann, *C. demandata* (Fabricius), *Eumetopiella rufipes* (Macquart), *Seoptera vibrans* (Linné), and *Stenomyia tenuis* Loew. My observations on *Chrysomyza* and *Seoptera* agree with those of Dufour and Weseché, except that in *Seoptera* I have also seen two parovaria, and a suggestion of a brownish ventral receptacle. In all the other forms studied there are only two chitinized spermathecæ, more or less spherical in shape. Sperm were found in the spermathecæ of *Chætopsis apicalis, Eumetopiella,* and *Stenomyia*. Two rather long parovaria with very fine ducts were found in *Chætopsis ænea* and *C. apicalis,* while in *Eumetopiella* and *Stenomyia* only a single small gland was seen—though the difficulty of dissection is so great that it is quite likely that two are present. Because of this same difficulty it is probably not significant that no trace of a ventral receptable was found except as noted above for *Seoptera*; sections have in fact shown that *Chætopsis* has a non-chitinized ventral receptacle, in which sperm were present.

PTEROCALLIDÆ. I have examined *Callopistromyia annulipes* (Macquart) and *Pseudotephritis vau* (Say). In each there are three spherical chitinized spermathecæ, attached to two ducts. No sperm nor ventral receptacles were found, but the latter may have been present and not chitinized. *Pseudotephritis* has two rather long cylindrical parovaria, and a large heavy-walled uterus like that of the Lonchaeidæ or Sapromyzidæ.

TEPHRITIDÆ. I have a cleared preparation of *Ensina picciola* (Bigot), and have dissected *Euaresta bella* Loew, *Eurosta comma* (Wiedemann), *Neaspilota achilleæ* Johnson, *Procecidochares* (*Oedaspis*) sp., ~~*Straussia longipennis*~~ (Wiedemann), *Terellia palposa* (Loew), *Trypanea daphne* (Wiedemann), and *Zonosema flavonotata* (Macquart). In all these there are present two pear-shaped chitinized spermathecæ. They bear small knobs in *Euaresta,* and numerous larger papillæ in *Procecidochares.* In *Terellia* there are enlargements of the ducts just basal to the spermathecæ and about the same size as a spermatheca. The only sperm found in the group were in these enlargements. The ducts are long and fine, but with heavy envelopes, in all the forms dissected. No ventral receptacle has been definitely observed in dissections, but it is probable that a very weakly chitinized one is present in *Neaspilota* and *Straussia,* while sections of *Euaresta* show a non-chitinized one, with the apex directed anteriorly and with sperm present. The organ is probably present in the rest of the group, but was not found because of the difficulty of dissection characteristic of this and the preceding seven families. Two parovaria were found in *Neaspilota, Procecidochares, Straussia,* and *Terellia.* In *Zonosema* and *Trypanea* only one was found but a second was perhaps present. In *Neaspilota* and *Procecidochares* they are long, with a thin-walled spherical enlargement suggestive of that found in the Agromyzidæ. In the other forms named the parovaria are spherical or pear-shaped.

(*To be continued*)