

MORPHOLOGY OF THE INTERNAL REPRODUCTIVE SYSTEM OF FEMALE *CORETHRELLA* (DIPTERA: CHAOBORIDAE)

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Abstract. The morphology of the internal reproductive system of female *Corethrella*, based on whole mounts, serial sections, and SEM preparations of *C. appendiculata*, *C. brakeleyi*, and *C. wirthi*, is described and illustrated for the first time. Two large accessory glands empty by a common duct into the dorsal end of a cylindrical bursa copulatrix that has a thick wall of elastin. The duct of a single spermatheca opens on the anteromedial surface of the lumen of the bursa. The proximal $\frac{1}{3}$ of the length of this duct bears 10–20 cylindrical, 2-segmented projections from its intima. Approximately 20 cuticular pores are randomly distributed over the entire spermatheca.

The family Chaoboridae, a subfamily of Culicidae until given family status by Stone (1956), consists of 7 extant genera. Cook (1956) listed *Chaoborus* Lichtenstein, *Corethrella* Coquillett, *Cryophila* Edwards, *Eucorethra* Underwood, *Mochlonyx* Loew, *Neochaoborus* Edwards, and *Promochlonyx* Edwards. Of these, *Neochaoborus* is presently regarded as a subgenus of *Chaoborus*. Freeman (1962) described an additional genus, *Australomochlonyx*. In all species of the family, larvae are predaceous and adult mouthparts are much shorter than those of Culicidae.

Belkin (1962) considered short mouthparts to be an insufficient character in separating Chaoboridae from Culicidae. He retained the original classification, with Corethrellini, Chaoborini, and Eucorethrini as tribes of Chaoborinae. He considered all Corethrellini to be members of *Corethrella*, a view shared by Miyagi (1975) and Cranston (1980) but in contrast to Lane (1953), who placed several species of the tribe in *Lutzomiops* Lane. Belkin indicated that Corethrellini differed sufficiently from the other 2 tribes to be given subfamily status, but he did not do so. Saether (1970) recognized the family status of Chaoboridae and, accordingly, raised the tribes recognized by Belkin to subfamilies. He concurred with Belkin that Corethrellinae have little in common with other Chaoboridae, and stated that they might deserve full family status.

A distinctive morphological characteristic of *Corethrella*, which is not shared by other genera of Chaoboridae, is the presence in the female of mouthparts adapted for feeding on blood, including the presence of toothed mandibles (Miyagi 1975, McKeever & Pound 1979, Cranston 1980). The fact that members of this genus are truly hematophagous has been confirmed by Williams & Edman (1968), Miyagi (1974), McKeever (1977), and Cranston (1980). The genus consists of 61 species; most species

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are Neotropical, but some have been reported from each of the other zoogeographic realms (Belkin 1962, Cranston 1980).

Descriptions of the morphology of the female reproductive system of Culicidae have been given by Christophers (1923) for culicids in general, and by Christophers (1960) and Parks & Larsen (1965) for *Aedes aegypti* (L.). To my knowledge, no comparable study has been made of *Corethrella*. This report presents a description of internal reproductive structures of female *Corethrella*, based upon specimens of *C. appendiculata* Grabham, *C. brakeleyi* (Coquillett) and *C. wirthi* Stone.

MATERIALS AND METHODS

Specimens of *C. brakeleyi* and *C. wirthi* were collected as described by McKeever & Hartberg (1980). Specimens of *C. appendiculata* were reared from larvae obtained at Vero Beach, Florida.

Most specimens that were used for histological sections were etherized, killed in aqueous Bouin's fixative, plus 5 drops of Photo-Flo® (Eastman Kodak Company, Rochester, New York) per 100 ml, at 50 °C, dehydrated in a graduated ethanol series, cleared in Histosol® (National Diagnostics, Somerville, New Jersey), embedded in paraplast, serial sectioned at 5 µm, and stained with Masson's trichrome or paraldehyde-fuchsin as described by Meola (1970) or basic fuchsin, acid fuchsin, fast green, and Harris' hematoxylin. Some specimens were killed in 2% glutaraldehyde in 0.067 M aqueous sodium cacodylate, embedded in plastic, sectioned at 2 µm, and stained in Harris' hematoxylin.

Whole mounts were made from specimens that were etherized, dissected in physiological saline, fixed with 2% glutaraldehyde, stained in aceto-orcein, briefly destained in 70% ethanol-1% HCl, and mounted in acid fuchsin-CMC® (Turtox, Chicago).

Specimens examined by scanning electron microscopy (SEM) were placed in 10% KOH at 60 °C for 2 h, dissected in water, dehydrated in a graduated ethanol series, air dried, and gold coated.

All measurements were made of specimens of *C. wirthi* that had completed at least one gonadotrophic cycle and that had not had a recent blood meal. Measurements were made with an ocular micrometer. Average values, ± 2 standard errors, are expressed in µm.

RESULTS

The female reproductive organs of *Corethrella* consist of the ovaries, paired lateral oviducts, a median common oviduct, a vagina, and a terminal atrium that opens by the vulva. A bursa copulatrix opens into the atrium; it extends dorsally from the atrium and receives a duct from a single spermatheca and a common duct from paired accessory glands (Fig. 1-3).

Two cylindrical to fusiform ovaries, 425.9 ± 34.0 long \times 139.0 ± 14.9 wide, $n = 12$, are located in the 3rd, 4th and 5th abdominal segments (Fig. 1). Each ovary is

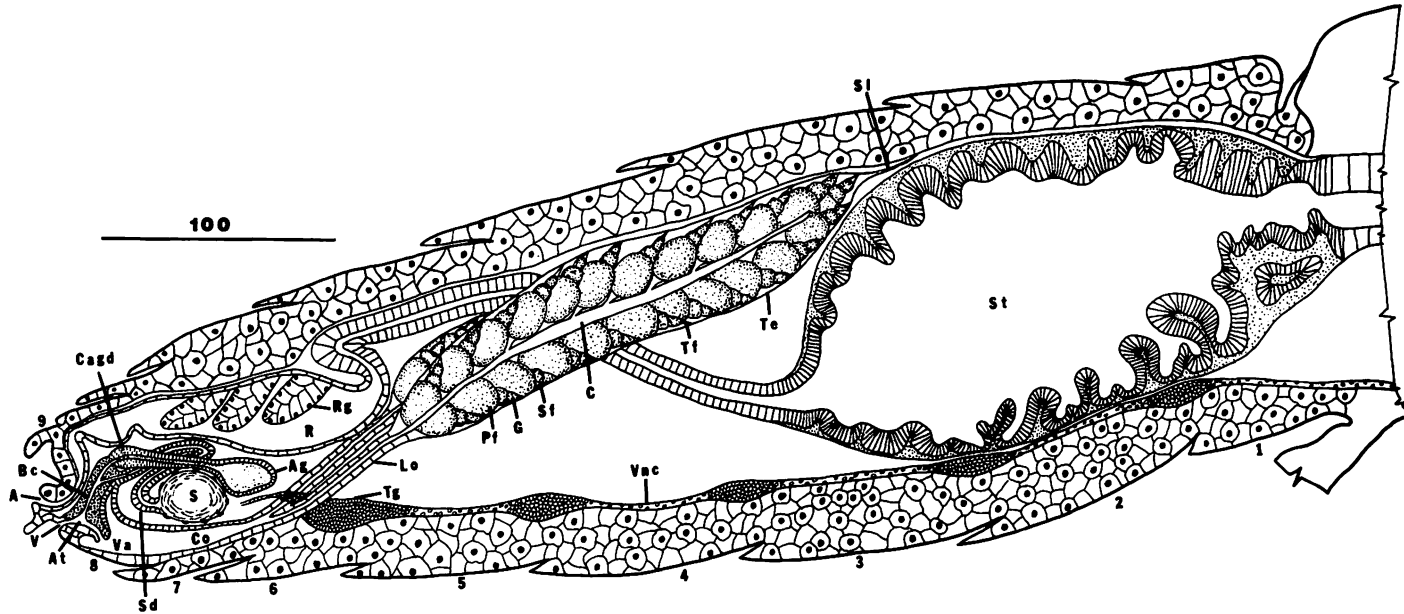


FIG. 1. Diagram of sagittal section of entire abdomen of *Corethrella* from histological sections. Scale value in μm . Structures: A, anus; Ag, accessory gland; At, atrium; Bc, bursa copulatrix; C, calyx; Cagd, common accessory gland duct; Co, common oviduct; G, germarium; Lo, lateral oviduct; Pf, primary follicle; R, rectum; Rg, rectal gland; S, spermatheca; Sd, spermathecal duct; Sf, secondary follicle; Sl, suspensory ligament; St, stomach; Te, tunica externa; Tf, terminal filament; Tg, terminal ganglion; V, vulva; Va, vagina; Vnc, ventral nerve cord; 1-9, abdominal segments.

surrounded by a thick membranous epithelial sheath, the tunica externa, which extends anteriorly beyond the ovary as the suspensory ligament. This ligament anchors the ovary to the anterior dorsal body wall of the 3rd abdominal segment. Associated with the epithelial sheath are muscle cells whose elongated nuclei are less than $\frac{1}{2}$ as large as the spherical nuclei of the epithelium. Processes from these cells branch and anastomose to form a network of fibers around the ovary. In addition, each ovary is invested by a network of tracheoles. Main tracheal trunks from spiracles of the 4th and 5th abdominal segments join each ovary on its midlateral surface and at its base, respectively. A membrane similar to the tunica externa lines the egg passage, or calyx, in the center of each ovary.

Between the tunica externa and lining of the calyx are 35–58 ovarioles (49.4 ± 4.4 , $n = 10$). Each ovariole is pyramidal in shape (Fig. 1, 4) and consists of an epithelial tube, the tunica propria and its enclosed cells. An attenuated apical portion of the tube, the terminal filament, is attached to the tunica externa. A basal portion, the pedicel, is attached to the epithelial lining of the calyx; lumens of the pedicel and calyx are confluent. Lying within the tunica propria are the apical germarium that will produce oogonia, and the basal vitellarium.

In the formation of an oocyte, an oogonium becomes surrounded by a layer of follicular cells within the germarium. It undergoes 3 divisions and produces 1 oocyte and 7 nurse cells; these, with the surrounding follicular cells, constitute a follicle. The vitellarium normally consists of a large basal primary follicle, 42.0 ± 3.7 long \times 36.3 ± 3.0 wide at its base, $n = 25$, and a small secondary follicle which, with the germarium, is 20.9 ± 1.8 long \times 16.1 ± 1.3 wide at its base, $n = 25$.

Walls of the lateral oviducts consist of a continuation of the propria externa and epithelial lining of the calyx, with smooth muscles between these 2 membranes. These ducts unite immediately posterior to the terminal ventral ganglion and form a median common oviduct. The latter is lined with cuboidal cells anteriorly. Cells on its ventral surface decrease in height posteriorly and become squamous as the vagina is approached; those on its dorsal surface are cuboidal throughout.

Posteriorly the genital passage becomes progressively wider and develops a pronounced dorsal pouch immediately anterior to the bursa copulatrix. This portion of the passage, the vagina, is lined throughout with squamous epithelium; no sclerotized intima is evident.

Posterior to the vagina is the atrium, a dorsoventrally constricted passage that increases in transverse width until it reaches its external orifice, the vulva, at the posterior edge of the 8th sternite. Except for their median areas, both dorsal and ventral walls of the atrium are covered with a sclerotized intima. In cross section the intima appears as a folded ribbon, but a surface view shows that it consists of tufts alternating with depressions. The ventral wall of the atrium is formed from a flaplike structure that extends anteriorly from the vulva above a posterior extension of the vagina. Its dorsal surface topography corresponds to the dorsal wall of the atrium.

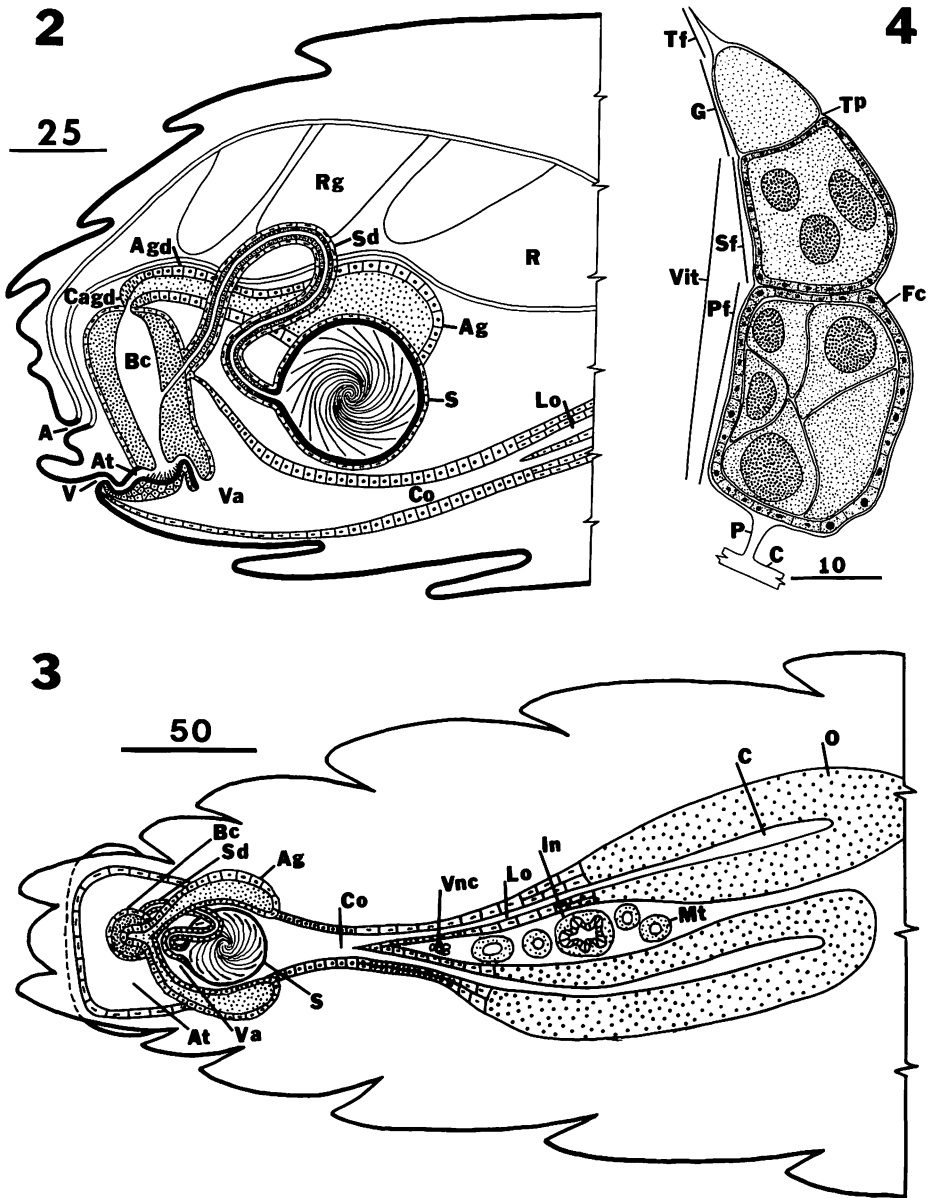


FIG. 2-4. Diagrams of reproductive structures of *Corethrella* from histological sections. 2, Sagittal section of terminal abdominal segments. 3, Frontal section of posterior abdomen. 4, Longitudinal section of ovary. Scale values in μm . Structures: A, anus; Ag, accessory gland; Agd, accessory gland duct; At, atrium; Bc, bursa copulatrix; C, calyx; Cagd, common accessory gland duct; Co, common oviduct; Fc, follicle cell; G, germarium; In, intestine; Lo, lateral oviduct; Mt, malpighian tubule; O, ovary; P, pedicel; Pt, primary follicle; R, rectum; Rg, rectal gland; S, spermatheca; Sd, spermathecal duct; Sf, secondary follicle; Tf, terminal filament; Tp, tunica propria; V, vulva; Va, vagina; Vit, vitellarium; Vnc, ventral nerve cord.

Close apposition of the anterior dorsal and ventral walls would constitute a valve between atrium and vagina (Fig. 2).

The bursa copulatrix is located in the posterior region of the 8th segment. It is ventrodorsally elongated, circular in cross section, and covered with squamous epithelium. Inside the epithelium is a thick noncellular layer that gives a positive reaction to elastin stain. There is no sclerotized lining of its patent, stellate, or circular distensible lumen. The lumen serves as a common passage for secretions from the accessory glands and for sperm passing to and from the spermathecal duct; it opens on the medial dorsal wall of the atrium.

On the medial ventral wall of the atrium, directly below the opening of the bursa copulatrix, is a circular depression that has a dense covering of hairlike structures. Sagittal and cross sections reveal that these hairs are short in the center and increase in length toward the edge of the depression. They resist action of KOH and apparently are chitinized.

Two pyriform accessory glands, 76.5 ± 5.4 long \times 31.6 ± 3.9 wide, $n = 10$, lie in the posterior 6th and anterior 7th segments, lateral to and above the spermatheca. Their walls are composed of cuboidal to squamous epithelium that produce a homogenous secretion that fills the large lumen. During active periods, discrete globules of secretion are evident within the cells. A duct composed of cuboidal epithelium leads from each gland. These ducts unite and form a common accessory gland duct that joins the dorsal end of the bursa copulatrix. The wall of the common duct consists principally of a thick layer of circumferentially oriented muscles.

A smooth, dark brown, spherical spermatheca, 23.8 ± 0.9 in diameter, $n = 22$, is located medially in the 7th segment, just dorsal to the vagina and common oviduct. Its wall is composed of simple squamous epithelium that covers a thick, dark brown cuticle. This cuticle extends $5\text{--}9 \mu\text{m}$ into the spermathecal duct. Approximately 20 pores, which penetrate the cuticle, are randomly distributed over the entire surface of the spermatheca. They are approximately $3 \mu\text{m}$ in diameter and have an aperture that is ca. $0.75 \mu\text{m}$ in diameter. Examination of histological sections reveals that a dark outer and a light inner zone surround the aperture. In SEM preparations the light and dark zones are reversed (Fig. 5). No chitinized projection from the pore's rim was detected by either SEM or light microscopy and no specialized cells were observed to be associated with the pores.

The spermathecal duct is 3.8 ± 0.3 in diameter, $n = 23$, with a patent lumen that is 0.9 ± 0.1 in diameter, $n = 25$. Its wall consists of an outer simple squamous epithelium that is continuous with epithelial coats of the spermatheca and bursa copulatrix, a single layer of circumferential muscles, and a lining of cuticle, the intima.

When placed in 10% KOH at 60°C for 2 h, epithelial and muscular coats of the duct are removed. On the exposed surface of the intima, for approximately $\frac{1}{3}$ of its length proximal to the spermatheca, are 10–20 randomly distributed cylindrical structures (Fig. 6). They have a basal portion that is approximately $1.5 \times 1.5 \mu\text{m}$ and

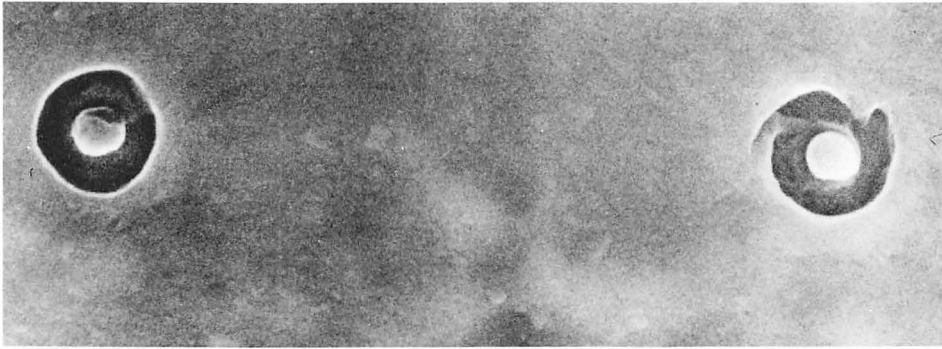


FIG. 5. SEM photomicrograph of pores in the cuticle of the spermatheca of *Corethrella wirthi*. $\times 6765$.

a distal portion that is $1.5 \text{ long} \times 1.0 \text{ } \mu\text{m}$ wide. The distal portion has the general appearance of a light bulb, with a constricted neck where it joins the basal portion. The basal portion is hollow and its lumen is confluent with the lumen of the duct. The distal portion also appears to be hollow, but whether or not it is could not be determined with certainty. These structures were observed in some histological sections; they extend to the surface of the duct and a tuft on the distal portion projects above the epithelium. They could not be distinguished in whole mounts not treated with KOH.

The spermathecal duct joins the anterior surface of the bursa copulatrix immediately dorsal to the dorsal projection of the vagina. Its lumen passes posteroventrally through the thick wall of the bursa and opens on the midanterior surface of the lumen of the bursa.

DISCUSSION

Since midges belonging to *Corethrella* were originally classified as members of the Culicidae, their reproductive structures are compared and contrasted with those of *Aedes* Meigen, from which they differ in several respects. An outstanding difference is the arrangement of openings of accessory glands, spermatheca, and bursa copulatrix into the genital canal. Snodgrass (1935) stated that in Diptera the vagina receives the spermathecal ducts and, in an illustration, showed that it also receives accessory gland ducts. Christophers (1960) divided the posterior genital canal of *Ae. aegypti* into vagina and atrium; he stated that separate ducts from each of 3 spermathecae open into the former, and a duct from a single, small accessory gland opens into the latter. Curtin & Jones (1961) studied the same species and found that the atrium receives a common duct from 2 lateral spermathecae, a large duct from the medial spermatheca, a duct from a single accessory gland, and the opening of a bursa copulatrix. All of these open into the atrium through a common structure that they termed the

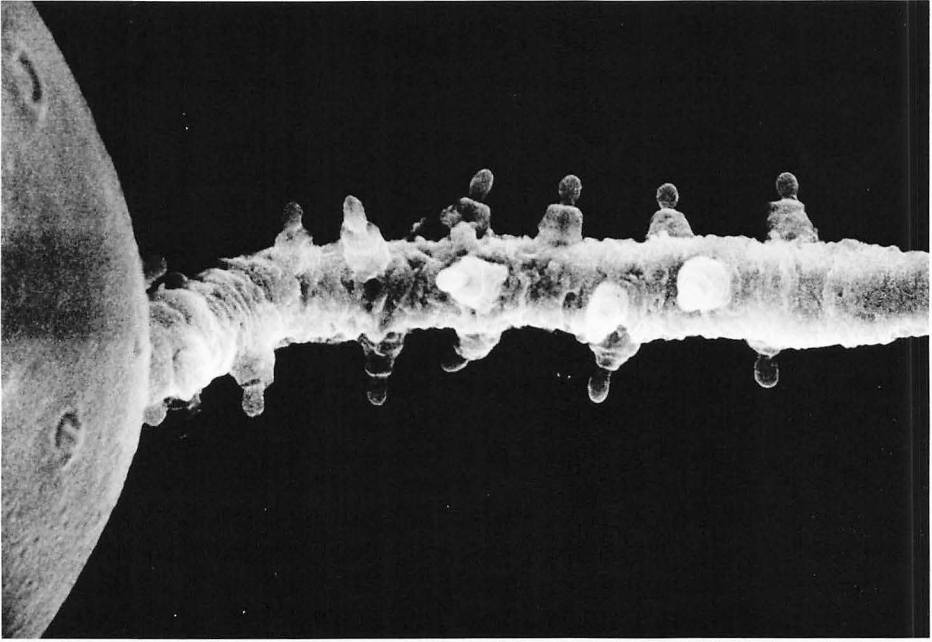


FIG. 6. SEM photomicrograph of the posterior spermatheca of *Corethrella wirthi*, showing pores in the cuticle and projections from the cuticular intima of the spermathecal duct after removal of epithelial and muscular coats with KOH. $\times 3925$.

“dorsal plate.” Parks & Larsen (1965) also worked with *Ae. aegypti* and found a single common duct from all 3 spermathecae that opens into the atrium at a spermathecal eminence.

Christophers (1923) described the bursa copulatrix as a cul-de-sac of the atrium and thought that, in mosquitoes, the accessory gland opens into it. Hodapp et al. (1960) described the bursa copulatrix of *Ae. aegypti* as a large, nonmuscular, distensible dorsal sac that opens on the dorsal wall of the vagina. They also mentioned a slitlike orifice between the postpygidial plate and dorsal vaginal lip. Curtin & Jones (1961) gave a more detailed description of a direct orifice to the bursa; they believed that the male inserts its aedeagus into this orifice during copulation. Jones & Wheeler (1965) stated that, in *Ae. aegypti*, the male fills the bursa with sperm during copulation, and the sperm later swim to the opening of the bursa, make a U-turn into the vestibule, and swim up the spermathecal ducts.

In contrast to the foregoing, *Corethrella* have 2 accessory glands that open by a common duct into the bursa copulatrix. A duct from a single spermatheca also opens into the bursa. The opening of the bursa is sufficiently close to the vulva for a male to insert his aedeagus into the lumen of the bursa and deposit sperm. These sperm would have direct access to the spermathecal duct without leaving the bursa, as they must do in *Aedes*.

Jones & Sheffield (1970) examined the bursa of *Ae. aegypti* with the electron microscope and found that it was a single-cell-layered sac. All cells were of the same type and were separated from the hemocoel by an extremely thin basal lamina. They made no mention of a lining of thick elastin that is present in *Corethrella*.

Anterior dorsal and ventral walls of the atrium of *Corethrella* appear similar in configuration to structures designated as vaginal valves in *Ae. aegypti* by Jones & Wheeler (1965); they probably serve as valves between atrium and vagina. There are 2 ventral valves in *Aedes*, but only 1 in *Corethrella*. Hairlike structures that occur in a depression on the medial ventral wall of the atrium of *Corethrella* have not been described in mosquitoes. They probably serve as sensory structures during copulation and/or oviposition.

Parks & Larsen (1965) described perforations on a circular area near the base of the spermathecae of *Ae. aegypti*. This area fits into a cuplike receptacle of cells that probably are Clements & Potter's (1967) glandular cells and Jones & Fischman's (1970) basal gland cells. The latter authors stated that these cells are highly secretory and that their secretion was present in the spermathecae of fertilized *Ae. aegypti*. Each cell releases its secretion through a flask-shaped structure described by Clements & Potter (1967) as a cuticular ductule that connects to a pore in the spermathecal cuticle. Thus, pores in the spermatheca of *Aedes* serve as a passageway through the cuticle for secretions of basal gland cells.

For comparison with the foregoing description of the spermatheca of *Ae. aegypti* and with observations of the structure in *Corethrella*, spermathecae of *Eucorethra underwoodi* Underwood, *Chaoborus astictopus* Dyar & Shannon, *Aedes sollicitans* (Walk.), *Culex* sp. L., and *Anopheles* sp. Meigen, were examined by light microscopy. *Anopheles* had 1 spermatheca with 50–70 pores randomly distributed over its entire surface. As in *Corethrella*, there is no projection of the pore's rim. The other 4 species examined each had 3 spermathecae, but only those of *Ae. sollicitans* had pores. These were located on the basal $\frac{1}{3}$ of the spermatheca and each pore had flask-shaped cuticular projections from the edge of its rim. These projections undoubtedly are the same as the cuticular ductule described in *Ae. aegypti* by Clements & Potter (1967). In view of their structure, and the fact that they do not connect with gland cells, pores in the cuticle of *Corethrella* probably serve to exchange nutrients and gasses between fluids in the spermatheca and hemocoel.

In order to determine whether cylindrical structures that protrude from the intima to the surface of the spermathecal duct of *Corethrella* are present in other Chaoboridae or Culicidae, spermathecal ducts of *E. underwoodi*, *C. astictopus*, *Ae. sollicitans*, *Culex* sp., and *Anopheles* sp. were treated with KOH and examined by light microscopy. None of these species had any type of protuberance from the intima. Clements & Potter (1967) described glandular cells located outside the muscular sheath of the spermathecal duct near the spermatheca of *Ae. aegypti*. These cells discharge their secretion into the lumen of the spermathecal duct through a long cuticle-lined ductule. They probably are the same as Jones & Fischman's (1970) periductal cells.

Projections from the spermathecal duct of *Corethrella* bear no resemblance to glandular cell ductules described and illustrated by Clements & Potter (1967) and by Jones & Fischman (1970). The function of the structures present in *Corethrella* is unknown.

Jones & Fischman (1970) described an epithelial layer between the muscular layer and cuticle of the spermathecal duct. This was evident in sections cut at 0.5–1.0 μm and examined by light microscopy, as well as in material examined with the electron microscope. While such a layer probably is present in *Corethrella*, it could not be distinguished in 5 μm sections.

A single, small, globular accessory gland that is filled with fine to large droplets or granules occurs in *Ae. aegypti*. Its duct is thick and hyaline with a thick brown lining of cuticle where it enters the reproductive canal (Curtin & Jones 1961). Rossignol et al. (1977) studied the accessory gland by transmission electron microscopy and found that it consisted of 15–20 cells, each of which surrounded an extracellular cavity that was filled with granular material. Its cuticular duct was surrounded by a thick layer of muscle cells, and the cuticle was thickened to form a thick tube where it shares a common opening into the atrium with the spermathecal vestibule.

In *Corethrella* there are 2 large accessory glands filled with a homogenous secretion. Their ducts are formed from cuboidal epithelial cells that are similar to, but smaller than, the cells which form the gland. There is no evidence of hyalinization or of a cuticle in either the individual ducts or common duct. Further, the common duct opens into the dorsal end of the bursa rather than directly into the atrium as it does in *Aedes*.

According to Snodgrass (1935) ovariole (=terminal) filaments unite to form a suspensory ligament of the ovary. Christophers (1960) stated that terminal filaments originate from the peritoneal membrane (=tunica externa) in *Ae. aegypti*. Parks & Larsen (1965) worked with the same species and determined that the suspensory ligament consisted of an extension of the tunica externa, not terminal filaments; this is also true for *Corethrella*. Christophers (1923) found the ligament attached to the dorsal body wall of the 4th and 5th segments, but Curtin & Jones (1961) traced it to alary muscles of the 2nd segment in *Aedes*. In *Corethrella* it extends to the anterior dorsal body wall of the 3rd segment.

A network of branching striated muscle fibers covers the ovary of both *Ae. aegypti* (Hodapp et al. 1960) and the midge *Chironomus plumosus* L. (Wensler & Rempel 1962). A similar network is present in *Corethrella*, but no striations could be discerned. Trachea that supply the ovaries of *Corethrella* originate in the 4th and 5th segments as they do in *Aedes* (Parks & Larsen 1965).

A connecting column of flattened cells occurs between successive follicles, and similar cells form a plug in the pedicel and ovarioles of both *Ae. aegypti* (Christophers 1960, Parks & Larsen 1965), and *Chironomus plumosus* (Wensler & Rempel 1962). Neither interfollicular cells nor a plug of cells in the pedicel could be discerned in *Corethrella*.

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