NOTES ON THE MORPHOLOGY OF CAMBARINCOLA MACRODONTA ELLIS*

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INTRODUCTION AND CLASSIFICATION

THE BRANCHIOBDELLIDAE (Discodrillidae) are a family of oligochaetes living as parasites or commensals on crayfish. All are similar in possessing a sucker or acetabulum at the posterior end which serves to attach the animal firmly to the host. All are reported to be hermaphroditic, and all possess a lower and an upper dental plate sufficiently variable to be a valuable aid in classification. The body is always composed of a constant number (usually eleven) of segments.

The group has generally been neglected by zoologists so that even the classification has been unsettled until recently. The name formerly applied to the family was Discodrillidae, but Hall (1914) and Ellis (1912, 1918) have favored the abandonment of this name for that given above and taken from the type genus Branchiobdella described by Odier in 1823. Hall (1914) listed five North American genera in the family including a new genus and species. Ellis (1918) added another genus containing one species and a new species to each of two already recognized genera. Adding new forms discovered by Ellis to those given in a key by Hall, the classification of the Branchiobdellidae stands at present as follows:

Branchiobdella Odier 1823
- *B. americana*
- *B. tetradonta*

Bdellodrilus Moore 1895
- *Bd. illuminatus*
- *Bd. instabilis*
- *Bd. pulcherrimus*

Pterodrilus Moore 1895
- *Pt. alcicornus*
- *Pt. disticlius*
- *Pt. durbini*

Cambarincola Ellis 1912
- *C. philadelphica*
- *C. macrodonta*
- *C. vitrae*

Ceratodrilus Hall 1914
- *Cr. thysanosomus*

Xironodrilus Ellis 1918
- *X. formosus*

Of these thirteen species occurring in North America, Moore (1895) has given a detailed account of one, namely, *Bd. illuminatus*. Smallwood (1906) under the title "Notes on Branchiobdella" gave some interesting observations on *Bd. instabilis*. These same observations, however, were concerned mainly with oogenesis and spermatogenesis and his material

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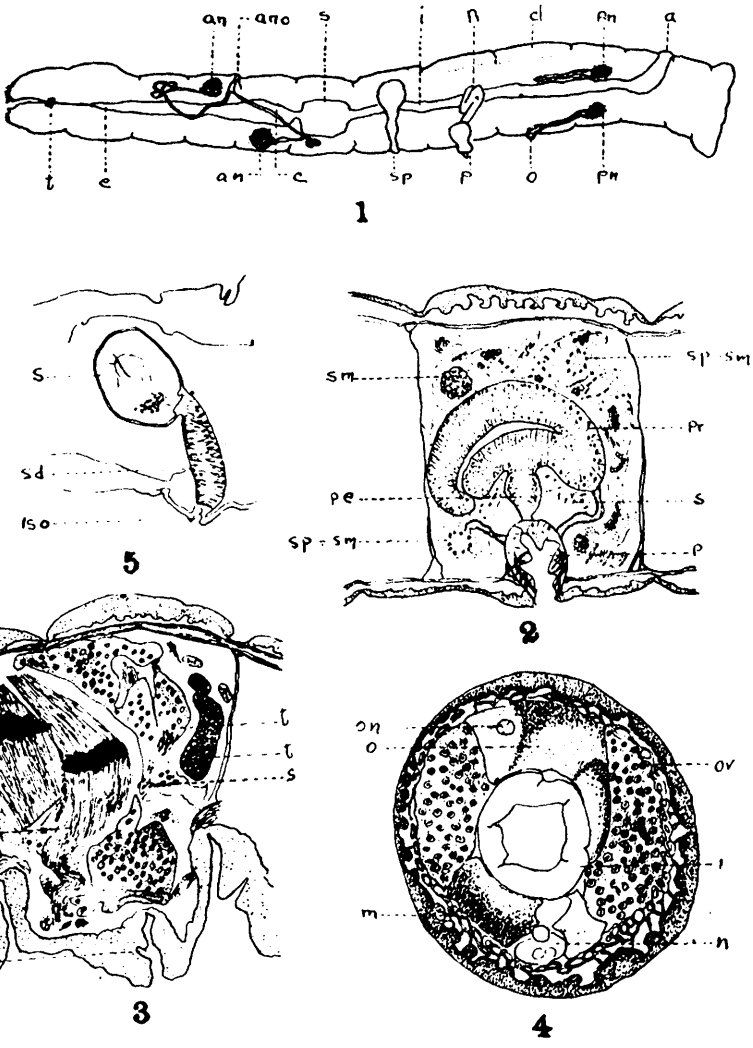

was insufficient to permit a complete study of these processes. Since only one species in the family has been described further than to fix its systematic position, it has seemed worth while to investigate another, namely, *Cambarincola macrodonta* first identified by Ellis in 1912.

HABITS AND EXTERNAL APPEARANCE

Cambarincola macrodonta, like other Branchiobdellidae is found living as an external parasite or commensal on crayfish. The posterior extremity of the body is modified to form a sucker which firmly attaches the animal to the host. They are found most frequently attached in this manner to the anterior ventral side of the abdomen or to the first two or three swim-

merets. Almost as frequently they may be found beneath the rostrum in the region where the green glands open and around the bases of the antennae. Less frequently they occur on the thorax at the base of the walking legs, on the maxillipeds, or sometimes on the legs themselves. They are never found in the gill chambers.

Though the animals are attached so firmly to the host that it is very unlikely that any activity of the crayfish could dislodge them, they can move quite freely from place to place over the host. When a parasitized crayfish is held dorsal side downward, the worms may be seen migrating from their now exposed position to the dorsal side of the host or to some other part away from the light. Their movements and speeds in these migrations much resemble those of the caterpillars commonly called "measuring worms." On undisturbed crayfish the worms seldom change their point of attachment and are always found on the ventral side of the host

The worms are found on both male and female crayfish in equal numbers, mature crayfish being commonly hosts to the greater numbers. It is difficult or impossible to determine the number infesting a single animal but it certainly varies from zero to thirty or more. Crayfish carrying no parasites were frequently taken from the same water with specimens heavily infested.

The worms are white in color and vary in extended length from two to twelve millimeters, depending on the state of maturity. The body is composed of ten plainly marked segments (Fig 1) and a terminal acetabulum probably made up of an eleventh segment. Each of the body segments except the acetabulum is biannulate (Fig. 2, 3); the anterior portion making up about two thirds of the segment. This biannulate condition, while plainly visible externally is evident in the body wall only. Internally only the first nine of the body segments are apparent, the tenth and eleventh being nearly filled with the muscle strands controlling the acetabulum. There is no hint of metamerism in the head except that the prostomium is distinct from the larger hinder part of the head. The entire body except the head and acetabulum is capable of great extension and contraction. In contracting the anterior larger part of each annulus telescopes slightly over the posterior part and at the same time the entire segment shortens markedly.

The body is narrowest in the first post cephalic segment and gradually increases in diameter until it becomes largest in the seventh. Since the greater length of the body rests parallel to the surface of the crayfish, and since the acetabulum is joined in a vertical position, the body is generally flexed rather sharply in the region of the ninth and tenth segments.

The posterior segment, the acetabulum, is expanded to form a disc concave on the terminal surface and provided internally with the strong muscle strands already mentioned. The acetabulum serves to attach the worms firmly to the host by a sort of suction governed entirely by these muscles. That the attachment is a very firm one is shown by the fact that worms loosened from the host and permitted to attach themselves to a common dissecting needle, cannot be dislodged from the needle by the most violent shaking or stirring in a dish of water. The sucker has no other function than that of keeping the worm so firmly attached to the host.

Little is known of the food of this group of worms. Smallwood (1906) thinks that they are not parasitic at all but feed upon the microscopic

organisms in the water. Older ones, he suggests, might be able to bite off with their strong teeth the fine hairs found on the swimmerets and other parts of the crayfish. Hall (1914) says of them that they are not parasitic when young but as they get older they break the chitinous covering of the host and suck the blood. He found voluntary muscle of the crayfish in the stomachs of some specimens. A Mr. Haley who collected *Ceratodrilus thysanosomus* for him had given him the information that older females carrying eggs "seemed to weaken and die" if badly infested.

In the case of *Cambarincola macrodonta* there has never been any indication that it is ever a parasite. Specimens detached from the host and kept in finger bowls for as long as two weeks could be induced to eat no part of the crayfish body, nor could there be found any evidence on the body of the most highly infested host of any gnawing or feeding of the worms. The writer kept numbers of live crayfish in aquaria for several months and never once noted the death of any animal heavily infested. The only ones which did die, in fact, were the smaller ones which were killed and eaten by their fellows.

THE DIGESTIVE SYSTEM

The digestive system (Fig. 1, Plate II) is composed of a terminal mouth, an esophagus widely expanded to form a crop as it proceeds backward, a stomach, and a straight intestine ending in anus located in the dorsal part of the body between segments nine and ten.

The mouth is guarded in front by the very mobile prostomium which is divided into equal dorsal and ventral portions by a slight notch on each lateral anterior border. Back of the prostomium and the front portion of the mouth are the upper and lower teeth lying in the same vertical plane. The upper teeth are seen as five points projecting from a broad slightly crescentic base The lower are four points on a smaller less crescentic base.

About the middle of the anterior-posterior length of the head the mouth narrows abruptly and the esophagus begins. It continues nearly straight backward (Fig. 1 e) through the first, second, and third annuli, gradually becoming larger until in the third segment its diameter is nearly as great as that of the stomach. In live specimens the surface of the esophagus in these last two annuli is folded or ridged slightly. In view of this fact and in view of its being so widely expanded, it might more properly be called a crop (Fig. 1 c.). Stained preparations show its walls to be distinctly glandular.

The stomach (Fig. 1 s.) lies entirely in segment four. It is separated in front from the esophagus and behind from intestine by distinct constrictions. The intestine passes from the stomach straight through the body to the anus (Fig. 1 a.).

No separate glandular organs connected to any part of the alimentary tract were seen. In most specimens just removed from the crayfish and compressed under a cover glass, distinct chlorogogue cells (Moore 1895) were seen lying over the crop, stomach, and a large part of the length of the intestine. These were always light brown in color with distinct polygonal outlines and quite apparent nuclei.

THE REPRODUCTIVE SYSTEM. MALE ORGANS

The male reproductive glands consist of two pairs of testes, one pair in segment five and the other in segment six. In mature specimens these

are so large as to completely fill the body cavity in this region except for the space occupied by the intestine and other organs to be described. In such mature specimens every section through the testes showed mature spermatazoa which were generally grouped in small clumps and might be found in any region of the testis (Fig. 2 s, 3 s). In material properly fixed, cysts of dividing spermatocytes (Fig. 2 sm) or spermatids (Fig. 2 sp-sm) were often encountered. The greater part of the testes, however is made up of a homogeneous mass of resting cells (Fig. 3 t) slightly oval in outline and with indistinct nuclei.

The copulatory organs occupy segment six. They consist of a copulatory bursa or atrium, a penis, and a large distinct prostrate gland. The atrium or bursa is a pear shaped organ opening to the exterior on the midventral line (Fig. 2 p). Its walls are very thick, particularly in its expanded upper portion, and its cavity quite irregular. Muscles controlling the organ are very distinct around its external opening.

The prostrate gland (Fig. 2 pr.) is a large forked structure whose two rami generally lie in a vertical plane in live specimens rather than horizontally as shown in the figure. The walls are thick and the lumen scarcely perceptible in some median sections through it. One of the rami of the prostrate gland forks a second time (Fig. 2 pe) in a manner best described by the figure. This second branch appears no different structurally from the rest of the gland, except that it narrows considerably at its outer end. It proceeds but a short distance until this outer end joins the bursa in the dorsal expanded region of that organ. This portion of the prostrate serves as a penis. Running from the lateral border of the bursa to the unbranched end of the prostrate gland is a very small tube serving as a second connection between these two organs. What function this may have has not been determined. A second tube similar in size and appearance to this leaves the other lateral border of the bursa but it has been impossible to discover its function or to follow its course.

Worms were repeatedly removed from crayfish in numbers and placed in finger bowls in hopes that the process of copulation might be observed. In such circumstances the worms always attached themselves to the bottom in clumps, wound and unwound their bodies intimately around each other, and finally after a few minutes came to rest in a compact mass. After a few hours, the individuals of such a mass always separated from each other and never again seemed to be aware of the existence of their fellows. During none of this time was copulation noted, though the worms were very active at first and the penis is so small that there are many difficulties attending such an observation. These observations were intended to disclose the function of the bursa. Moore (1895) found that in *Bdellodrilus illuminatus* it could be everted through the male genital opening if sufficient pressure were applied, but that it always carried to the outside with it the sixth ganglion. In Cambarincola very slight pressure was sufficient to cause the bursa to be everted with the penis (Figure 1 p) and never was the nerve cord carried to the outside. It seems, then, that eversion of the bursa is natural in this form as in *Cambarincola philadelphica* (Moore 1895).

There is a pair of sperm ducts in each of segments five and six as shown by the clumps of spermatazoa (Fig. 3 s) within the ducts (Fig. 3 sd.). These clumps of spermatazoa present a very striking appearance, being a solid mass except for the edges where a few isolated cells may be

found. These were encountered in practically every specimen sectioned, though not all preparations show it so strikingly as the one figured.

THE REPRODUCTIVE SYSTEM. FEMALE ORGANS

The single pair of ovaries (Fig. 4 ov.) occupies segment seven. On the surface nearest the intestine and on the dorsal and ventral portions of these organs are found eggs (Fig. 4 o) in various stages of growth. Often eggs were seen whose bulk quite equaled that of all the remaining portion of the ovary, and whose nuclei were so distinct that they could be seen through the body walls in living animals (Fig. 4 on). About half the bulk of the remaining part of the ovary is made up of small spherical oocytes with distinct condensed nuclei. Each is separated from the other by a considerable amount of connective tissue.

Eggs pass to the outside through a pair of ovipores in the ventral body wall of segment seven. These openings were for a long time overlooked in sectioned material because of their small size. They were first noted in live compressed animals when frequently a portion of one of the posterior nephridia was squeezed through the opening (Fig. 1 o). They show plainly enough in some of my material sectioned later. In *Bdellodrilus illuminatus* Moore found the ovipores to be a pair of similar openings but situated on the dorsal side of segment seven.

On the ventral side of the fifth segment is found the opening of the spermatheca (Fig. 1 sp., Fig. 5 so). A slight thickening of the tissues nearby forms a protuberance around the opening. The spermatheca proceeds dorsally for half the depth of the body as a thick walled glandular structure (Fig. 5 sd) much resembling a portion of the prostrate gland. At its upper end this glandular portion enlarges and becomes a thin walled sac (Fig. 5 s), whose diameter quite equals that of the intestine and whose cavity is directly connected to that of the tubular portion below. This also, is different from the same organ in *Bd. illuminatus*. The spermatheca in that form is bifid and apparently without a large sac like cavity. In the case of Cambarincola the form of the spermatheca can be easily made out in live specimens that have been starved. In the figure, which is drawn from a Delafield's haematoxylin preparation, sperm cells were found in the vesicular portion.

In segments six and seven the dorsal and lateral body walls are thickened to form a clitellum (Fig. 1 cl).

THE EXCRETORY SYSTEM

The excretory system consists of two pairs of nephridia. The anterior pair is situated asymmetrically, one member lying in segments one and two and the other in three and four (Fig. 1 an, an). The more anterior member of this pair originates in a tightly wound coil in the dorsum of segment two. About this coil is a small amount of tissue so heavily pigmented in live specimens that the nephrostome could never be seen. Stained and sectioned material has likewise failed to show the nephrostome. From this coiled position in segment two the tubule passes forward into segment one where it again coils about itself but loosely enough that its course may be followed. From here the tubule again passes backward and empties to the outside on the dorsal portion of the body between segments two and three.

The posterior member of the anterior pair of nephridia begins in a manner similar to the first but in the ventral region of the third segment. From this first coil the tubule proceeds backward to form a second coil in the

ventral region of the fourth segment. It then proceeds dorsally and anteriorly until it meets the duct of the first nephridium and joins with it just before the latter opens to the outside (Fig. 1 ano).

Both of the posterior pairs of nephridia are found in segment eight. Pigmented tissue so completely conceals their course that it has been impossible to follow them further than to determine that both tubules pass forward into segment seven (Fig. 1 pn).

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PLATE II

Figure 1. Free hand sketch drawn from a single specimen compressed under a cover glass. a. anus; an. anterior nephridia; ano. opening of anterior nephridia; c. crop; cl. clitellum; e. esophagus; i. intestine; o. ovipore with posterior nephridia forced through opening; p. penis; pn. posterior nephridia; pr. prostate gland; s. stomach; sp. spermatheca; t. dental plates.

Figure 2. Longitudinal section through segment six showing testis, male copulatory organs, and prostate gland. P. copulatory bursa; pe. penis; pr. prostate gland; s. spermatazoa; sm. dividing spermatocytes, sp-sm. spermatids.

Figure 3. Longitudinal section through the sixth segment showing the sperm ducts. P. genital opening; s. spermatazoa; sd. sperm ducts; t. testis.

Figure 4. Cross section through segment seven showing ovaries and mature eggs. l. intestine; m. muscles of body wall; n. nerve cord; o. egg; on. germinal vesicle; ov. ovary.

Figure 5. Longitudinal section through segment five showing spermatheca. s. vesicular portion of spermatheca; sd. duct; so. opening.