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## The Anatomy of the Oligochaete *Enchytraeus albidus*, with a Key to the Species of the Genus *Enchytraeus*

BY A. WEIR BELL<sup>1</sup>

The small whiteworm (*Enchytraeus albidus*) is used almost universally as a convenient source of food for small fishes. In nature these worms are found in all kinds of environment—in top soil, peat moss, and debris of all kinds along the shores of salt- and fresh-water bodies. They have been collected from every continent and almost every climate. In the laboratory they are raised on moist peat moss or other moist plant fibers at room temperature. Their food is an occasional bit of mashed potato, bread crumbs, or (preferably) rolled oats. They may be found abundant in sewage-treatment beds, and, when placed on moldy bread, they soon reduce the mold. Although some horticulturists suspect them of damaging the live roots of plants, the writer has yet to find an authentic case of such activity; their presence on the dead roots attests only to their action in the reduction of dead plant tissues.

Since the author first began to study this family of worms, the Enchytraeidae, numerous workers (biologists, horticulturists, and one publisher of a book on fishes) have sent worms to be identified. In all but one case the worms were found to be *Enchytraeus albidus*; the exception, which was thought to be *Enchytraeus albidus*, turned out to be *Enchytraeus fonteinensis* Michaelsen. In this case the original stock was supplanted by a contaminating species. More recently Dr. Libbie

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<sup>1</sup> Los Angeles City College.

H. Hyman of the American Museum of Natural History sent the writer some worms which proved to be *Enchytraeus albidus*. In the course of correspondence she suggested that the present paper be written, in order that other persons can more easily recognize the white-worms they use, either as fish food or in biological research.

When Henle first described this species in 1837, the significant characteristics of the several genera were not fully appreciated or recognized. Many species originally included in the genus *Enchytraeus* have now been removed to other genera; on the other hand a number of species of this genus formerly thought to be different are now included in the species *albidus*. The early investigators ignored certain fundamental characteristics, especially of the reproductive system, such as size of sperm funnels, length of sperm duct, shape of spermatheca, presence of diverticles on the spermathecal ampulla, and presence and extent of glands on the ectal duct of the spermatheca. Later investigators, finding new and nearly related species, were compelled to observe and record these previously overlooked diagnostic characters. The following diagnosis is based on the observations to date of a number of scientists (see References).

#### DIAGNOSIS

**EXTERNAL ANATOMY:** *Enchytraeus albidus* is one of the larger species of the genus, ranging in size from 10 to 35 mm. in length and from 0.5 to 1.0 mm. in diameter. It is pure white (rarely yellowish), often transparent under the microscope. The number of segments varies from 52 to 74. The head pore is located in the furrow between the prostomium and the first segment; this location is referred to as 0/I. There are no other dorsal pores. The clitellum is found on the whole of segments XII and XIII. The setae, three to five per bundle, occur in four bundles each on all but the first and last segments; they are straight except at the proximal end where they may be slightly or sharply curved.

**INTERNAL ANATOMY:** The brain is approximately one and one-half times as long as broad, converges anteriorly, and is indented both anteriorly and posteriorly. The ventral nerve cord is large, without marked ganglionated swellings, and shows a single canal (neurochord) middorsally in cross section. A pair of postpharyngeal ganglia extend posteriorly from the roof of the pharynx into the coelome of segment III. The gut is free of any diverticula or glands other than the septal glands and peptonephridia noted below. On the floor of the mouth is a "tongue"; the pharynx consists of typically elevated palisade cells in

its roof, from which a duct passes posteriorly on each side to drain the septal glands lying on the walls of septa IV/V, V/VI, and VI/VII; peptonephridia (salivary glands) arise from a dorsal diverticulum behind the pharynx, each gland being a sac-like, elongated pouch, unbranched but with rugose walls; the esophagus gradually widens into the midgut. The circulatory system consists of a dorsal vessel arising in segments XIV to XVII, a series of commissurals (aortic arches) in segments II, III, IV, and V, and a ventral (subintestinal) vessel extending from the second segment to the caudal end. A number of lymphocytes (coelomocytes) are found in the body cavities; they are flat, varying from spindle to pear-shaped, but mostly elliptical. Nephridia begin in segment VII; they consist of a small anteseptal part composed of a funnel only and a large postseptal part, from the hind end of which an excretory duct passes almost directly to the surface just anterior to the ventral setae. The testes are found in segment XI; the ovaries, in XII. The sperm funnel is about six times as long as broad; its duct is quite long, extending as far back as segment XXI in some records. The penial apparatus consists of a central, muscle-covered, penial bulb surrounded by a colony of 20 to 30 accessory glands, between which the strands of the retractor penis muscles from the dorsolateral body wall are inserted. The sperm duct, instead of passing through the penial bulb as in other genera (*Fridericia*, *Lumbricillus*), lies lateral to the bulb and reaches the surface at the base of the invagination (ectodermal infolding). The penial bulb and its accessory glands all empty into this invagination. The spermathecae open externally at intersegmental furrow IV/V. They consist of an ampulla and ectal duct of equal length. The spermathecal ampulla is a sac-like pouch, distinctly set off from the ectal duct, uniting mesially with the esophagus in segment V, and possessing a dorsal or lateral diverticulum, which rarely may be divided. The ectal duct of the ampulla is supplied along its distal half by a large number of pear-shaped glands.

In order that persons interested in raising these small worms may be better able to identify their cultures, the writer submits herewith a detailed account of the essential diagnostic characteristics of *Enchytraeus albidus*, based on the worms sent by Dr. Hyman; in addition a key to the accepted species of the genus is given in order that any contaminating species in the cultures can be recognized. Should the worms fall outside the genus *Enchytraeus*, the investigator must refer to other genera in such references as Michaelsen (1900), Stephenson (1930), and Cernovitov (1937). If anyone is interested in investigations on these worms it is imperative that he make serial sections of some of them

to get the details of internal organs. This involves fixation (in Zenker's or Bouin's fluid) of the worm in as straight a line as possible, dehydration in alcohols, clearing in oil, embedding in paraffin, sectioning in an unbroken series, mounting on slides, and staining differentially.

#### DETAILED DESCRIPTION

The worms sent from the American Museum of Natural History fall well within the diagnosis of *Enchytraeus albidus* as worked out by other scientists. They are white in color; 15 to 20 mm. in length; 0.5 to 1.0 mm. in diameter; and have from 52 to 65 segments. There are no special external markings or glands; the clitellum is slightly elevated and lies on segments XII and XIII. The setae are in four bundles of three to five per bundle, except on the first and last segments; sexually mature worms lose the setae on segment XII as a rule. The setae (fig. 3) are straight, except at the proximal end where they may be slightly curved. They measure approximately 10  $\mu$  in diameter and vary from 95  $\mu$  to 110  $\mu$  in length.

**NERVOUS SYSTEM:** The brain is roughly one and one-half times as long as wide, one careful measurement from a reconstruction from sections (fig. 2) being 120  $\mu$  wide and 180  $\mu$  long. It is indented posteriorly and concave anteriorly; its side walls diverge caudad. The ventral nerve cord (fig. 1) is fairly cylindrical, not enlarged segmentally as in some enchytraeids; a canal (probably a neurochord) is present in its middorsal region from segment VII caudad. A pair of postpharyngeal ganglia project posterodorsally from the end of the pharynx.

**ALIMENTARY TRACT:** The mouth (in segments I and II) has a small mass on its floor which is commonly called the tongue (fig. 1). The pharynx (in segment III) has the characteristic roof of palisade cells, a diagnostic feature of the family Enchytraeidae. From the dorsal tips of these cells a duct passes posteriorly to drain the septal glands lying on the faces of septa IV/V, V/VI, and VI/VII. The septal glands are easily seen in the living animal, and in histological preparations they are darkly stained. Behind the pharynx in segment III a dorsal diverticulum from the gut gives rise to a pair of glands known as peptonephridia or "salivaries." At first single, the peptonephridium divides as it passes through the septum into segment IV, each branch forming an elongated, sac-like structure, unbranched but with rugose walls, lying against the septal gland behind and extending to the ventral reaches of the coelome in IV. The esophagus enlarges gradually to become the midgut; it has no other diverticula or glands. The chloragog

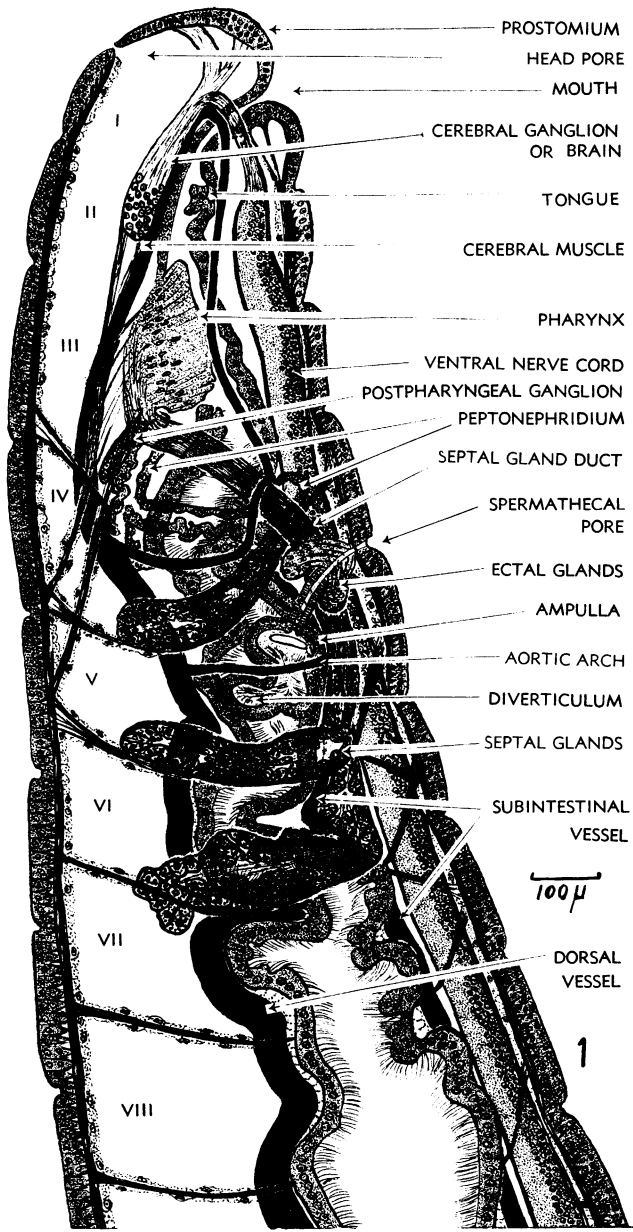
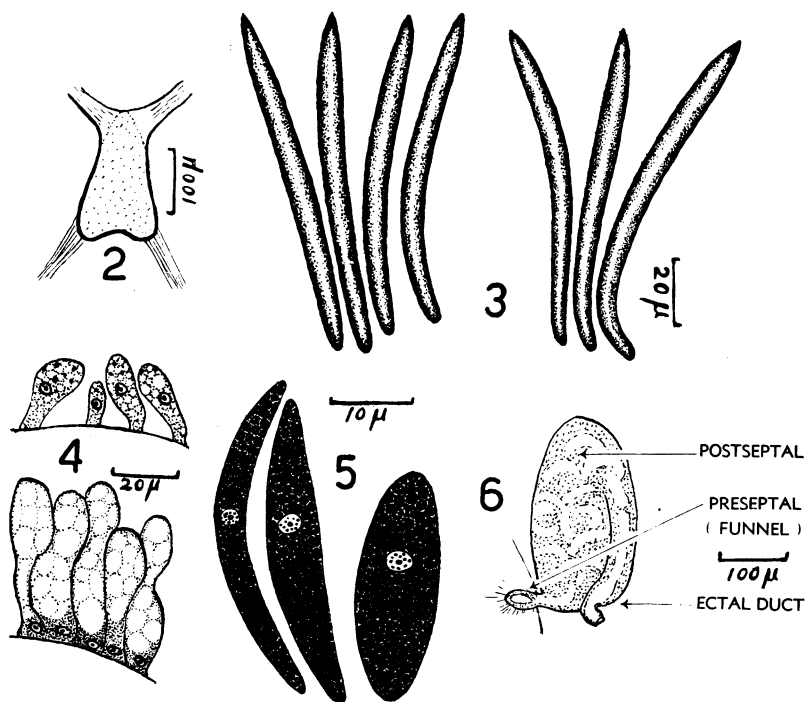


FIG. 1. Camera lucida drawing of longitudinal section through the anterior end; a composite of several sections.

cells (fig. 4) invest the gut, beginning with segment V. In this segment they are small ( $20\ \mu$ ), with a few granules; from segment VI caudad they are much taller ( $50\ \mu$ ) and clear. The clear, hyaline character of these cells is a striking character and probably accounts for the transparency of the worm and the reason for the name *albidus*.

**CIRCULATORY SYSTEM:** The dorsal blood vessel arises in the region between segment XIII and segment XVII. The specimens from the American Museum had segments XIII and XIV as the source. The dorsal vessel (fig. 1) extends forward without special swellings or valves



FIGS. 2-6. Details of structure. 2. Dorsal view of the brain, reconstructed from serial sections. 3. Ventral setae of segment VI (left) and of segment LII (right). 4. Chloragogen cells from segment V (above) and from segment VI (below). 5. Coelomocytes. 6. Reconstruction of a nephridium from segment VII.

(heart bodies) and comes to lie beneath the brain in segment II; here it divides with the commissural nerves, the branches (also called commissurals) passing ventrad and caudad to the third segment, where they unite to form the subintestinal vessel. Commissural vessels have also been recorded in segments III, IV, and V, but the writer has

found them only in IV and V (when empty, they are difficult to follow). The body cavity contains a large number of elliptical corpuscles called coelomocytes or lymphocytes (fig. 5). These are flat ( $4\text{ }\mu$  thick), varying in surface view from elliptical to spindle-shaped, and measure from  $10\text{ }\mu$  by  $25\text{ }\mu$  to  $7\text{ }\mu$  by  $35\text{ }\mu$ .

**EXCRETORY SYSTEM:** The first nephridia (fig. 6) are in segment VII, with the nephridiostome in segment VI. This organ consists of two parts: the preseptal, composed of the funnel (nephridiostome) and the stalk; the postseptal, composed of a mass of fine, ciliated tubules bound into a solid body, from the surface of which the excretory duct passes to the surface. In these worms the preseptal consists of the funnel only (about  $50\text{ }\mu$  long); the postseptal is relatively large, in surface

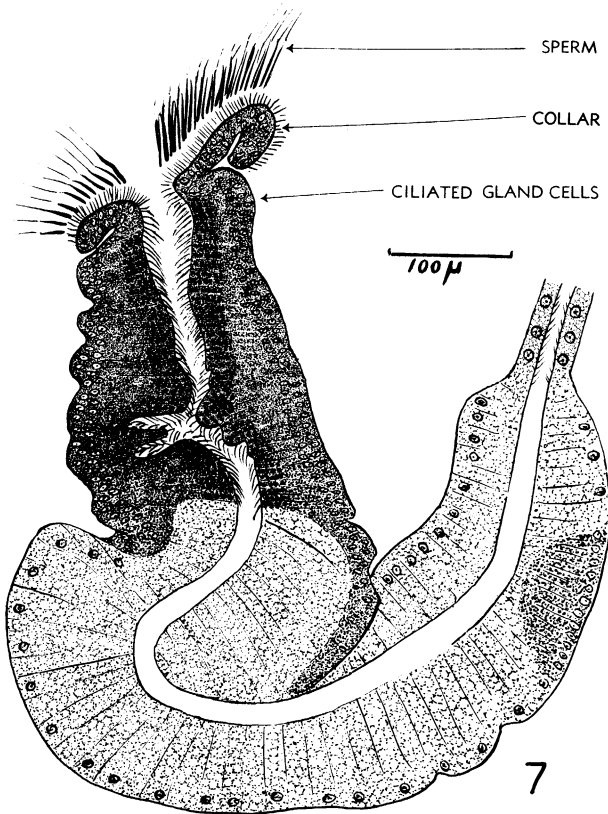
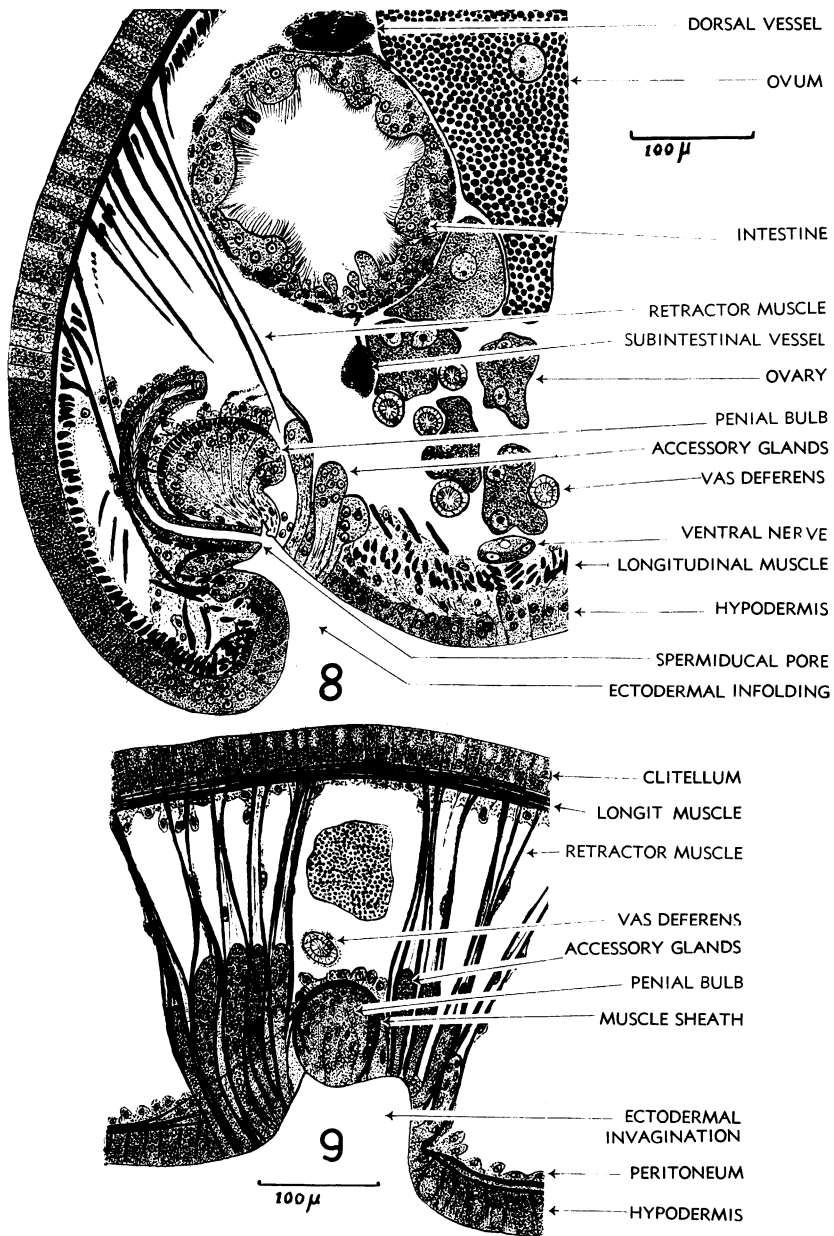


FIG. 7. Sperm funnel.



FIGS. 8, 9. Male system. 8. Cross section through segment XII, showing relationship of penial bulb, vas deferens, accessory glands, and related structures. 9. Longitudinal section through the penial bulb, showing related structures.



view measuring about  $150\ \mu$  by  $250\ \mu$ , in thickness  $50\ \mu$ . The excretory duct arises from the end of the postseptal part and passes directly to the surface just anterior to the ventral setae. There is a small enlargement near the end of the excretory duct, sometimes referred to as the bladder.

**REPRODUCTIVE SYSTEM, MALE:** The testes are located at the base of septum X/XI in segment XI. These organs are at first enveloped by a peritoneal membrane, but at sexual maturity the latter is soon ruptured

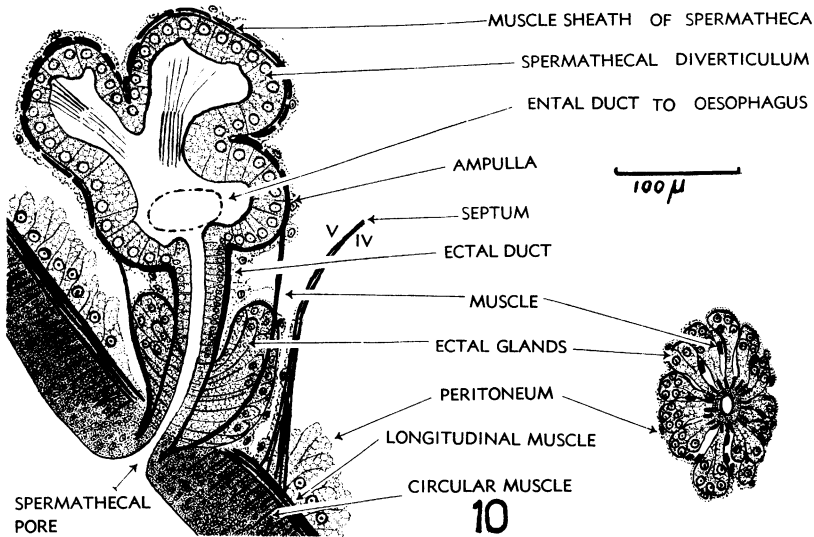


FIG. 10. Camera lucida drawings of sections through the spermatheca; longitudinal view from several adjacent sections (left), cross section through the ectal duct (right).

by the prodigious growth of spermatogenic tissue. In sexually mature worms the entire coelome is laden with sexual products; apparently the other sex organs, especially the enormous sperm funnels, do not allow enough space for such prodigality, because large sperm sacs extend forward, filling the coelome of segment X. The large size of the sperm funnels (fig. 7) is a striking feature of this species. These measure approximately  $200\ \mu$  wide by  $1200\ \mu$  long; each is folded upon itself, lying beside the gut in segment XI. At the orifice of the funnel there is a distinct ciliated collar, broader on one side than on the other. In sexually mature worms one finds vast numbers of mature sperm cells, lying parallel to one another and directed towards the entrance of the funnel. The cavity of the funnel is greater and ciliated in its first

quarter. The sperm duct begins at the end of the funnel, where it measures about 50  $\mu$  in diameter, and extends for some distance posteriorly before making its exit at the penial apparatus in segment XII, where it has decreased in diameter to about 25  $\mu$ . One of the features of these worms is the passage of the long, coiled sperm duct posteriorly beyond the clitellum; the sperm ducts in the present worms varied in extent from segment XVI to segment XX. The structure of the penis or penial apparatus of this worm is an important diagnostic feature (figs. 8 and 9). This organ consists of a central penial bulb enveloped in a muscular sheath. Unlike the lumbricilline penial bulb, however, the sperm duct passes not through it, but lateral to it. Surrounding this bulb there is a large number of accessory glands (20 to 30 or more), evidently modified hypodermal cells, which empty, together with the sperm duct, into a deep depression called the ectodermal invagination or infolding. This infolding is probably caused by the pull of the retractor penis muscles, which lie between the accessory glands and take their origin from the dorsolateral body wall. These muscles are derived from the circular muscles of the body wall, the latter often being completely absent where the retractor penis muscles are well developed.

**FEMALE ORGANS:** The ovaries lie in segment XII at the base of septum XI/XII, just anterior to the penial apparatus. As in other enchytraeids small masses of oocytes ("*Teilovaria*") are liberated into the body cavity; from these, single cells develop, one at a time, into the large eggs (fig. 8, ovum). When mature, the eggs are so large that they require two or more segments to contain them and are visible to the naked eye. There is no oviduct or funnel, or specialized ovisac for temporary storage of the ovarian products. The eggs are liberated directly to the surface through an inconspicuous pore which lies caudal to the male pore. The spermathecae (fig. 10) are important diagnostic structures in this species. The external pore is located at intersegmental furrow IV/V, at the level of the lateral setae. The organ itself consists of an ectal duct, about 30  $\mu$  to 40  $\mu$  in diameter and 200  $\mu$  long, and an ampulla of about the same length. The ampulla is sac-like, with a fairly large diverticulum which may pass forward, laterally, or caudad, and sometimes up over the gut. The ental duct is very short, the ampulla being essentially connected directly to the side of the esophagus. The ectal duct possesses a rich covering of glands over its distal half; these are modified epithelial cells of the duct itself, for here the duct epithelium is wanting; moreover, the whole organ is covered by peritoneum. Of interest is the muscle sheath enveloping the ampulla and

the ectal duct; it lies next to the epithelial layer, except that along the ectal duct there is an additional number of fibers which run between the pear-shaped ectal glands at some distance from the duct proper.

NOTE ON CIRCULAR MUSCLES: In a number of studies of enchytraeid worms in the past the writer has noted that the epidermis, especially in the anterior end, is loosely organized, with no definite basement membrane. In these cases the circular muscles lie interspersed with hypodermal cells and in many instances can be seen to reach to the surface cuticle. In *Enchytraeus albidus* this is true; moreover, it is especially evident in the origins and insertions of the retractor penis muscles (fig. 9). Thus to some extent in this family of worms there exists a plastic exoskeleton.

# KEY TO THE SPECIES OF THE GENUS *Enchytraeus*

1. Penial apparatus loosely arranged, without a common lumbricilline bulb; or, if present, the sperm duct does not pass through it but opens directly on the surface between penial papillae .....2  
Penial apparatus consists of a penial bulb, a solid mass of glandular cells enveloped by a muscular sheath through which the sperm duct passes .....12
2. Body deeply constricted at intersegmental furrow IV/V.....*constrictus* Backlund  
Body not so constricted .....3
3. Spermathecae lacking, a few gland cells about male pore .....*florentinus* Bell  
Spermathecae present, male apparatus with glands .....4
4. Small and slender in relation to segment number (i.e., 9.0 mm. long, 0.35 mm. thick, 80 segments); parasitic in crabs; prostomium bent (peptonephridia not mentioned; may belong to genus *Stephensoniella*).....*parasiticus* Baylis  
Larger, not parasitic, prostomium normal .....5
5. Spermathecae without diverticles .....6  
Spermathecae with diverticles .....8
6. Spermathecae without patent connection with esophagus; segments, 38-44; length 11 mm. or less; dorsal vessel arises in segment XII or XIII; sperm duct limited to segment XII; spermathecal duct covered with peritoneum only .....*liejdeensis* Stephenson  
Spermathecae with patent connection with esophagus; ectal duct completely covered with glandular cells; segments, 49-75; length up to 15 to 18 mm.; dorsal vessel arises in segment XV, or farther posteriorly; sperm duct reaches posteriorly to segments XVI to XX .....7
7. Spermathecal ampulla wide and spherical, with ectal duct of same length and short ental duct; excretory duct from terminus of postseptal; segments, to 48; setae, to three; sperm duct not mentioned as having atrial enlargement .....*sabulosus* Southern  
Spermathecal ampulla not much broader than ectal duct which is rel-

- actively very short; former opens directly into esophagus; short excretory duct from anterior end of postseptal; setae four ventrally; segments, to 75; sperm duct with atrial-like enlargement ..... *krumbachi* Cejka
8. Spermathecal ampulla with single outpocketing; ectal duct not more than half covered with glands ..... 9  
Spermathecal ampulla with two diverticles, one dorsal and one ventral; ectal duct completely covered with gland cells ..... 11
9. Penial apparatus of a number of glandular masses; spermathecal ampulla with laterally projecting bulge; sperm duct extends as far posteriorly as segment XXI; sperm funnel up to eight times as long as broad; setae, up to six ..... *albidus* Henle  
Penial apparatus of two glandular papillae; spermathecal ampulla with dorsally projecting pouch; sperm duct confined to segment XII; sperm funnel, up to four times as long as broad; setae, up to four ..... 10
10. Brain anteriorly straight across, posteriorly slightly emarginate; spermathecal ampulla with stalked sac extending above the ental duct, and ectal duct with distal half covered with gland cells ..... *metlakatlensis* Eisen  
Brain concave anteriorly and convex posteriorly; spermathecal ampulla converges to point dorsally and to ectal opening ventrally, where there is a circlet of ectal gland cells ..... *kincaidi* Eisen
11. Dorsal outpocketing very large, without muscular sheath; brain much longer than wide; penial apparatus with about 10 accessory glands ..... *multiannulatus* Altman  
Dorsal outpocketing not so large, and covered by a muscular sheath; brain only twice as long as wide; penial apparatus with 18 to 20 accessory glands ..... *multiannulatoides* Altman
12. Clitellum and all associated sex organs displaced three segments anterior to usual position (testes in segment VIII, ovaries in IX, and so on) ..... *gordioides* Cernovsikov  
Clitellum and sex organs normally located ..... 13
13. Large worms, 60 to 125 segments, 15 to 40 mm. long, 0.6 to 1.0 mm. thick ..... 14  
Small worms, not more than 42 segments; 4 to 10 mm. long, up to 0.3 mm. in thickness ..... 16
14. Quite large, as many as 125 segments, to 40 mm. in length; spermathecal ectal duct with a few gland cells; parasitic in crabs ..... *carcinophilis* Baylis  
Not so large, up to 90 segments, to 26 mm. in length; spermathecal ectal duct without glands; not associated with crabs ..... 15
15. Brain posteriorly convex; up to 90 segments, to 26 mm. in length; sperm duct reaches posteriorly to segment XXI and has atrial enlargement near penial bulb ..... *mediterraneus* Michaelsen  
Brain posteriorly concave; up to 65 segments, to 15 mm. in length; sperm duct confined to segment XII; no atrial enlargement ..... *alaskae* Eisen
16. Segments, to 42; spermathecal ampulla with lateral bulge ..... *australis* Stephenson

- Segments, to 35; spermathecal ampulla without outpocketing. . . . .17
17. Spermatheca with sac- or purse-like ampulla and ectal duct beset with gland cells . . . . .18  
Spermatheca with small spherical ampulla, not much broader than ectal duct which has no ectal glands . . . . .21
18. Ectal duct with small circlet of gland cells only . . . . .19  
Ectal duct with complete covering of gland cells . . . . .20
19. Ectal duct long; sperm duct ends in "prostate" (probably the penial bulb); setae, to two only; dorsal vessel arises in segment X . . . . .*silvestris* Bretscher  
Ectal duct short; sperm duct with large "bursa propulsoria" (also probably the penial bulb); setae, to three (rarely four), dorsal vessel arises posterior to clitellum . . . . .*buchholzi* Vejdovsky
20. Brain quadrate; spermathecal ampulla several times as long as ectal duct; ectal duct covered with thick layer of glands. . . . .*buchholzi suecicus* Backlund  
Brain twice as long as wide; spermathecal ampulla spherical; ectal glands like a thin covering of peritoneum only. . . . .*gillettensis* Welch
21. Spermathecal ampulla without esophageal communication . . . . .22  
Spermathecal ampulla with esophageal communication. . . . .*fonteinensis* Michaelsen
22. Brain slightly convex behind; peptonephridia in segment IV only; first nephridium in segment V; spermathecal ampulla one-third of the length of the ectal duct . . . . .*indicus* Stephenson  
Brain truncate posteriorly; peptonephridia extend into segment V; first nephridium in segment VII; spermathecal ampulla the length of ectal duct . . . . .*harurami* Stephenson

## REFERENCES

CERNOSVITOV, L.

1937. System der Enchytraeiden. Bull. Assoc. Russe Rech. Sci. Prague, Sect. Sci. Nat. Math., no. 34, pp. 263-295.

MICHAELSEN, WILHELM

1900. Oligochaeta. In F. Schulze (ed.), Das Tierreich. Berlin, Friedländer und Sohn, no. 10, xxix+575 pp., 13 figs.

STEPHENSON, JOHN

1913. On some littoral Oligochaeta of the Clyde. Trans. Roy. Soc. Edinburgh, vol. 48, pp. 31-65, 2 pls.
1925. The Oligochaeta of Spitzbergen and Boar Island. Some additions and a summary. Proc. Zool. Soc. London, pp. 1293-1322, 8 figs.
1930. The Oligochaeta. Oxford, Clarendon Press, xiv+978 pp., 242 figs.

