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National Oceanic and Atmospheric Administration
National Marine Fisheries Service

Marine Flora and Fauna of the Northeastern United States. Annelida: Oligochaeta

DAVID G. COOK and RALPH O. BRINKHURST

SEATTLE, WA
May 1973

National Marine Fisheries Service, Circulars

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U.S. DEPARTMENT OF COMMERCE
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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
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NATIONAL MARINE FISHERIES SERVICE

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FOREWORD

This issue of the "Circulars" is part of a subseries entitled "Marine Flora and Fauna of the Northeastern United States." This subseries will consist of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the Northeastern United States. Manuals will be published at irregular intervals on as many taxa of the region as there are specialists willing to collaborate in their preparation.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R. I. Smith, published in 1964, and produced under the auspices of the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass. Instead of revising the "Woods Hole Keys," the staff of the Systematics-Ecology Program decided to expand the geographic coverage and bathymetric range and produce the keys in an entirely new set of expanded publications.

The "Marine Flora and Fauna of the Northeastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual will be based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each major taxon, treated in a separate manual, will include an introduction, illustrated glossary, uniform originally illustrated keys, annotated check list with information when available on distribution, habitat, life history, and related biology, references to the major literature of the group, and a systematic index.

These manuals are intended for use by biology students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. In many instances the manuals will serve as a guide to additional information about the species or the group.

Geographic coverage of the "Marine Flora and Fauna of the Northeastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Virginia, but may vary somewhat with each major taxon and the interests of collaborators. Whenever possible representative specimens dealt with in the manuals will be deposited in reference collections of the Gray Museum, Marine Biological Laboratory, and other universities and research laboratories in the region.

After a sufficient number of manuals of related taxonomic groups have been published, the manuals will be revised, grouped, and issued as special volumes. These volumes will thus consist of compilations of individual manuals within phyla such as the Coelenterata, Arthropoda, and Mollusca, or of groups of phyla.

CONTENTS

MARINE FLORA AND FAUNA OF THE NORTHEASTERN UNITED STATES
Annelida: Oligochaeta

DAVID G. COOK[1] and RALPH O. BRINKHURST[2]

ABSTRACT

The manual includes an introduction on the general biology, an illustrated key, an annotated systematic list, a selected bibliography, and an index to the marine Oligochaeta of the East Coast of North America. The Families Naididae, Tubificidae, Enchytraeidae, and Megascolecidae are treated.

INTRODUCTION

The Oligochaeta, a group of predominantly terrestrial and freshwater annelids, includes a number of species which have adapted well to the marine benthic environment. Despite the fact that these organisms may occur in great numbers in the sea (densities of up to a million per m^2 have been reported) the information on their ecology and taxonomy is comparatively sparse. The available data do suggest, however, that the intertidal zone, the subtidal zone, the continental shelf, and even the abyssal plain, all have characteristic oligochaetes associated with them.

Four families of oligochaetes occur along the east coast of North America, namely, the Megascolecidae (with 2 species), Naididae (8 species), Enchytraeidae (13 species), and Tubificidae (22 species); members of the first named family are known as megadriles and the last three as microdriles (to which much of the following discussion applies).

Definition and Diagnostic Characters

Oligochaeta are typically vermiform, cylindrical, segmented, bilaterally symmetrical, hermaphroditic annelids with a spacious coelom, a prostomium, an anterior ventral mouth, and a posterior anus. Conventionally segments are numbered in Roman numerals, beginning at the anterior end with the peristomium as segment I. Each segment, except the persistomium, usually bears four bundles of setae, two dorsolateral, and two ventrolateral (shortened to dorsal and ventral in the key) which are implanted directly in the body wall; parapodia are absent. There are two basic types of setae whose number and morphology in the various body regions are taxonomically important: (a) crochets, which can be straight, curved or sigmoid, may or may not possess a more or less median thickening (the node or nodulus) and which may have rounded, simple-pointed or bifid (forked) distal ends; crochets are found in all oligochaete families; (b) hair setae, which are elongate, simple-pointed structures, without a node, and whose surface may be smooth, finely serrated, or invested with a number of very fine lateral hairlets; hair setae are found only in the dorsal bundles of some Naididae and Tubificidae among the families with marine species. At sexual maturity the epidermis of a few anterior segments is thickened, forming a dorsolateral or annular clitellum which secretes the cocoon containing one to several eggs. Oligochaetes do not have a larval stage, and juveniles resembling small adults emerge from the cocoons after a few weeks or months of development. A double ganglionated ventral nerve cord extends through the length of the body: anteriorly it divides

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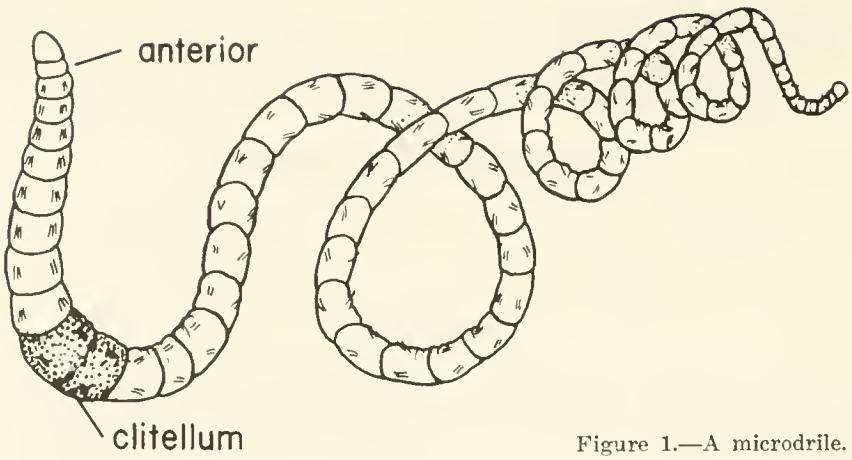


Figure 1.—A microdrile.

and passes upwards on either side of the pharynx to, or just posteriorly to, the peristomium where it joins a dorsal bilobed cerebral ganglion (or brain). The gut begins as a short narrow esophagus, then widens into a simple tube (constricted by the septa dividing each segment) which extends throughout the body length. Just posteriorly to the esophagus, the Enchytraeidae, Naididae, and Tubificidae (microdriles) possess a thickened pad of cells dorsally (the pharynx) which can be extruded through the mouth and to which, presumably, food particles adhere. In the Megascolecidae (megadriles) a muscular thickening of the gut wall, the gizzard, is usually situated near the anterior end of the esophagus. In the microdrile families bundles of darkly staining secretory cells, the pharyngeal glands, are found associated with the septa and gut in the region of segments III to VII. In Tubificidae and Naididae these glands are usually diffuse cell masses located laterally and dorsally, or dorsally, to the gut. In Enchytraeidae, however, the pharyngeal glands are discrete organs with a characteristic appearance and distribution. Peptonephridia, found only in some genera of Enchytraeidae, are also glandular organs associated with the anterior part of the gut; the term is used in the sense of Nielsen and Christensen (1959) to denote paired, tubular diverticulae which arise at the esophageal-pharyngeal junction. The vascular system consists of dorsal and ventral blood vessels which are connected in each segment either directly by dorsoventral commissures or indirectly through a blood plexus surrounding the gut. Excretion is by means of segmentally arranged paired nephridia. Each nephridium consists of a ciliated funnel which opens in the coelom, and a convoluted tubule which communicates with the exterior through a nephridiopore located ventrally on the adjacent posterior segment. Nephridia are usually absent in a variable number of anterior segments, in the region of the genitalia, in some posterior segments, and in some species they may be reduced to one, or a few, in number. The coelom is usually a simple cavity filled with coelomic fluid; in some genera and species the latter contains large numbers of coelomocytes which are large, spherical to ovoid, free cells. The genital system consists basically of male, female, and spermathecal components. The male component consists of one or two, rarely more, pairs of testes whose products (sperm) are conducted to the exterior by a more or less complex set of male genitalia. The sperm from each pair of testes is collected by a pair of male funnels (located on the posterior septum of the testis segment) which each open into a tubular vas deferens. The latter usually join paired ectodermal storage and intromittant organs (the atria and penes), or only one of these, which open to the exterior through the male pores (see also Fig. 2 and under "microdriles" and "Megascolecidae" below). The female system is composed of one or two pairs of ovaries and small female funnels which are situated ventrolaterally just posteriad to the last testes segment. The spermathecal component, whose function is to store sperm after copulation, consists typically of a pair of ectodermal pouches, the spermathecae, which are located near the region of the gonads (except in the Enchytraeidae where they are

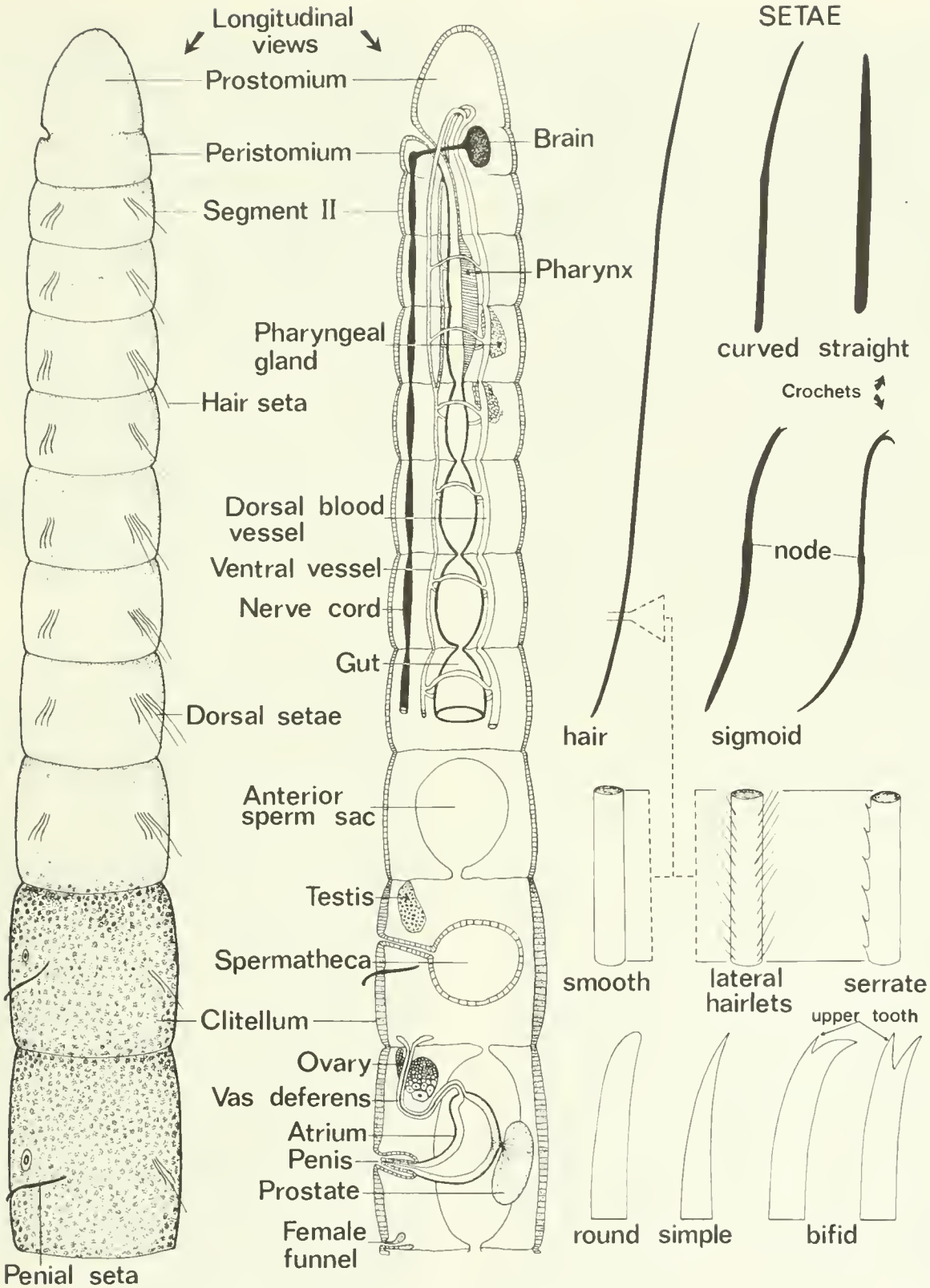


Figure 2.—Left, exterior of anterior portion of an oligochaete; middle, interior view; right, basic types of setae.

displaced anteriorly to segment V). Each spermatheca consists of an ampulla and a duct which opens to the exterior through the spermathecal pore. Sperm within the spermathecae may be in random masses, or organized into discrete, regularly oriented, usually radially symmetrical, spermatozeugmata. In the genital region of some species the ventral setae may be absent, or modified as genital (penial and spermathecal) setae. The latter can differ markedly in size or shape, or both, from the remaining body setae (somatic setae). The form of the genitalia and their segmental position are of paramount systematic importance at all taxonomic levels, especially in the microdriles; in many cases, therefore, only sexually mature individuals can be identified with certainty.

Microdriles are all small worms (usually up to 1.0 mm in diameter and 60 mm long) without a gizzard, and usually with a variable number of setae in each bundle in different body regions. Hair setae and genital setae are present in some Naididae and Tubificidae, but both are absent in Enchytraeidae: the dorsal chrochets of Naididae are usually referred to as needle setae. Most microdriles have one pair of spermathecae, and male genital ducts which are located in, or open on, the segment just posteriorly to the testes; that is, the vasa deferentia penetrate only one septum (Fig. 2). The clitellum is one cell thick, and in the smaller species it may be inconspicuous and confined to one segment. In the taxonomically important tubificid male genitalia, the vasa deferentia enter ectodermal atria, each (of the pair) consisting of a layer of inner lining cells, and an outer muscular layer covered by peritoneal epithelium. The proximal end of the atrium or atrial duct may terminate at the male pore either simply, or, more usually, as some form of modified penis which consists basically of a deep infolded ring of body wall isolating a central cylindrical organ; this, a true penis, may be surrounded by a thickened layer of cuticle known as the penis sheath. A mass of darkly staining cells, the prostate gland, whose secretions probably provide nutrients and binding fluid for the sperm mass prior to copulation, usually joins the atrium by a stalk composed of elongated processes of the gland cells. In some species, however, the prostate gland is a diffuse layer of cells surrounding the whole, or part, of the atrium, and is absent as a discrete organ in at least one species.

The Megascolecidae, which are more nearly related to the familiar lumbricid earthworms than to the previous three families, are large worms (exceeding 1.5 to 2.0 mm in diameter and 50 mm in length), usually with a gizzard and with two setae in each bundle. The important difference between the male genitalia of microdriles and megascolecids is that, whereas in microdriles the vasa deferentia pass through only one septum, in megascolecids the vasa deferentia always penetrate about six septa before opening to the exterior: in the case of the marine species, two pairs of testes occur in segments X and XI, and one pair of male openings are located on segment XVII or XVIII. Two to four pairs of spermathecal openings are present, the most posterior of which is located in or near intersegmental furrow 8/9. The clitellum is more than one cell thick and begins in the region of the thirteenth segment.

Ecology

The marine Oligochaeta are essentially benthic organisms which live within, and feed on, the bottom deposits. Many species are free-burrowing animals which feed indiscriminately on the bottom deposits, while others are meiobenthic (interstitial) worms which inhabit the interstices of the substrata and feed only on the very small organic particles, or browse off material from the surfaces of the larger particles. Megascolecidae and some Naididae, Tubificidae, and Enchytraeidae are free-burrowing, and some Tubificidae, Enchytraeidae, and possibly some Naididae, are meiobenthic. The major requirements for the survival of oligochaetes in the marine environment, apart from the obvious physiological adaptions, therefore, are the availability of suitable substrata and their ability to compete successfully with other deposit feeders in a given habitat (for example, Polychaeta, Echinodermata, Mollusca, Crustacea). Despite the fact that such situations are frequent from the littoral zone to the abyssal plain, the Oligochaeta are only now being recognized as regular components of the marine benthic ecosystem; hence little specific information on their ecology is available. It is known, however, that oligochaetes assume a very important role in polluted

areas; habitats in which organic matter can accumulate and oxygen can become depleted, are often inhabitated by large populations of a few species of oligochaetes, especially Tubificidae. For example, in the San Francisco Bay system Brinkhurst and Simmons (1968) found that the Tubificidae formed up to 97.8% of the total bottom fauna in grossly polluted habitats, and concluded that "changes in abundance of certain species may yield good supporting evidence of the nature and source of pollution materials" (p. 193).

The major types of habitats in which marine or brackish water oligochaetes can be found may be summarized as follows:

1. Littoral zone.
   a. In damp sand and mud (Enchytraeidae, Tubificidae, Megascolecidae).
   b. In and under decaying seaweed (Enchytraeidae, Megascolecidae).
   c. Under stones and rocks lying on sand (Tubificidae).
   d. In or near sources of fresh water on the beach (Enchytraeidae, Tubificidae).
2. Sublittoral zone.
   a. In the sediment (Enchytraeidae, Tubificidae, Naididae).
   b. On sediment or plant surfaces (Naididae).

Collecting Methods

Marine Oligochaeta are collected by extracting fixed or living worms from the sediment or vegetable material in which they live. In the littoral zone the substrate may be collected simply by digging or scooping material into containers, or by a simple coring device. Any of the various automatic corers, dredges or grabs, or in very shallow water a fine mesh hand net, are suitable for obtaining sublittoral material. If samples can be processed immediately to extract living worms (especially for Enchytraeidae), the sediment is washed through a series of wire screens, the finest having a mesh diameter of 0.5 mm or less; all but the very small oligochaetes are retained by the latter. Material to be killed and fixed (before or after sorting) is treated as follows: animals are narcotized in 0.015% propylene phenoxetol, fixed in 10% Formalin solution for 48 hr, and stored in 85% ethanol.

Examination Procedure

The anatomy of the oligochaetes can be studied by a variety of methods; the keys have been designed so that wherever possible taxonomic characters can be observed using a minimum of manipulation or treatment. Characters used in couplets 1 to 11 can be seen by mounting fixed worms temporarily in glycerol or Amman's lactophenol (400 g carbolic acid, 400 ml lactic acid, 800 ml glycerol, 400 ml water). The latter clears tissue by maceration and is therefore not recommended when subsequent treatment may be necessary; it is, however, a useful medium for mounting large collections for routine identification (Brinkhurst, 1963). In general, external characters and cuticular structures can be examined by simple whole mounts. From couplet 12, however, internal characteristics assume increasing importance and are best examined using stained, whole, or dissected, animals. The following procedure has proven effective; worms are stained in acetic haematoxylin, washed, and transferred to acid alcohol (5 drops of hydrochloric acid per 50 ml of 70% ethanol) until they are almost completely destained (to a very light red or pink color); the animals are then "blued" in alkaline alcohol (5 drops of concentrated ammonium hydroxide per 50 ml of 10% ethanol) and dehydrated in 100% ethanol. One of two procedures may then follow: (a) the whole animal may be cleared in xylol and mounted in Canada balsam or (b) the genitalia of the worms may be dissected out using microscalpels or fine sharpened needles, and the parts cleared in xylol and mounted in Canada balsam.

Most characters used in the key can be observed on whole stained animals, but dissection may be necessary for a critical examination of the genitalia of some species. If only one or two individuals are available for identification, it is recommended that a stained whole worm, mounted temporarily in xylol (xylol is highly volatile and the fumes are inflammable and toxic, therefore great care should be exercised) should be examined briefly to decide whether any further treatment is necessary. If dissection is needed the animal is returned to 100% ethanol because xylol makes the tissues very brittle and dissection almost impossible.

If living material is available, small specimens can be examined microscopically by mounting

them in a drop of seawater, immobilizing them with gentle pressure on a cover slip, and blotting off the excess water. Larger individuals are immobilized by mounting them in a drop of gelatine solution, which is just ready to set, and placing a cover slip over the mountant using gentle pressure. Details of the alimentary canal, pharyngeal glands, and peptonephridia of the Enchytraeidae can be seen more readily in living animals.

Because most marine oligochaetes are poorly known and because many have been described only within the last 6 years, the known distribution of many species merely reflects the distribution and collecting activities of a few specialists. Therefore, the scope of this work is expanded somewhat to include species which are known from the entire east coast of North America. It is hoped that this introduction to the marine Oligochaeta will stimulate further interest in this important class and be instrumental in amassing more information on their ecology and distribution.

KEY TO THE MARINE OLIGOCHAETA OF THE EAST COAST OF NORTH AMERICA

The first five couplets of the key, which strictly apply only to those species included in this key, are designed so that immature Oligochaeta may be identified to their family; immature Naididae and Enchytraeidae can usually be identified to species but immature Tubificidae usually cannot.

1 Hair setae present. 2

1 Hair setae absent. 3

2 (*1*) Dorsal setae absent on segments II to V. Eyes usually present. Male and spermathecal pores situated on segments VI and V respectively NAIDIDAE (in part).[1] .. 9

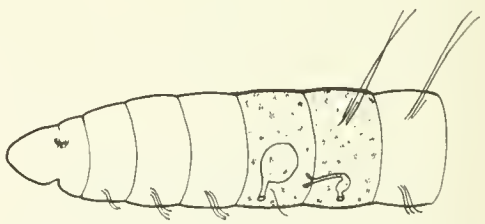


Figure 3.—Generalized naidid; lateral view, anterior segments.

2 (*1*) Dorsal setae present from segment II onwards. Eyes always absent. Male and spermathecal pores situated on segments XI and X respectively TUBIFICIDAE (in part) 12

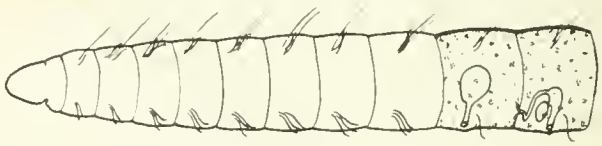


Figure 4.—Generalized tubificid; lateral view, anterior segments.

3 (*1*) Setae with bifid ends, at least in some parts of the body. Body wall generally thin, imparting fragile appearance to worm. Genital pores on segments V and VI, or X and XI. 4

3 (*1*) All setae with simple-pointed or rounded ends. Body wall generally thick, robust, imparting rigid appearance to worm. Male pores on segment XII or XVIII. 5

[1] "In part" indicates that only part of a taxon will key out at that point.

4 (*3*) Dorsal setae absent from segments II to IV, or totally absent. Genitalia situated in segments V and VI NAIDIDAE (in part). 6

4 (*3*) Dorsal setae present on all segments except the peristomium. Genitalia situated in segments X and XI TUBIFICIDAE (in part). 17

5 (*3*) Worms exceed 1.5 to 2.0 mm in diameter. Setae two per bundle on all segments. Male pores situated on segment XVIII. Citellum begins on segment XIII MEGASCOLECIDAE. 45

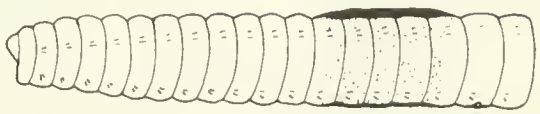


Figure 5.—Generalized megascolecid; lateral view, anterior segments.

5 (*3*) Worms usually less than 1.0 mm in diameter. Setae very rarely two per bundle in every segment and may be totally absent in some parts of the body. Clitellum begins on segment XI ENCHYTRAEIDAE 33

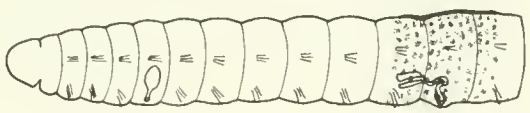


Figure 6.—Generalized enchytraeid; lateral view, anterior segments.

6 (*4*) Dorsal setae present, beginning in segment V. Ventral setal bundle of segment II fan-shaped and directed anteriorly. ..... *Paranais litoralis*

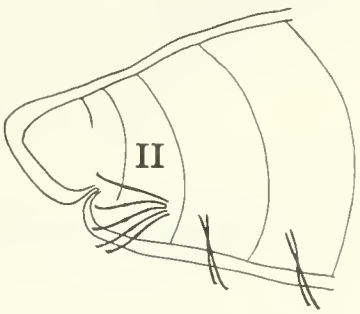


Figure 7.—Lateral view, anterior segments.

6 (*4*) Dorsal setae totally absent. Ventral setal bundle not fan-shaped. 7

7 (*6*) Worms commensal on gastropod molluscs, living in the mantle cavity and kidney. Setae with long strongly curved teeth (Fig. 8). . *Chaetogaster limnaei*

Figure 8.—Somatic seta.

7 (*6*) Worms free-living. Setae with moderately curved distal ends (Fig. 9). .. 8

Figure 9.—Somatic seta.

8 (7) Worms up to 25 mm long. Longest seta of segment II more than 200 μ long, 4.5 μ thick. Penial setae three to five per bundle. ..... *Chaetogaster diaphanus*

8 (7) Worms up to 7 mm long. Longest seta of segment II less than 165 μ long, 2 μ thick. Penial setae two per bundle. ..... *Chaetogaster cristallinus*

9 (2) Prostomium produced into long proboscis (Fig. 10) ..... *Stylaria lacustris*

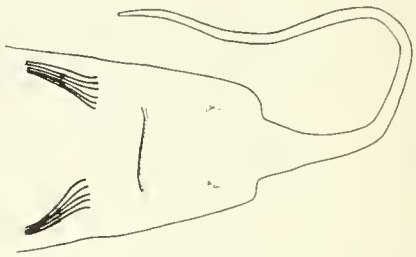


Figure 10.—Ventral view of anterior segments, showing elongate prostomium.

9 (2) Prostomium rounded. 10

10 (9) Teeth of needle setae (dorsal crochets) long and nearly parallel (Fig. 11). Upper tooth of all ventral setae about twice as long as the lower (Fig. 12) ..... *Nais elinguis*

Figure 11 (left).—Distal end of needle seta.
Figure 12 (right).—Ventral seta.

10 (9) Teeth of needle setae short, diverging (Fig. 13). Potserior ventral setae with approximately equal teeth (Fig. 14). 11

Figure 13 (left).—Needle seta.
Figure 14 (right).—Ventral seta from a posterior segment.

11 (10) Ventral setae of segments II to V with upper tooth longer than lower; setal teeth diverge at an angle less than 45° (Fig. 15). ..... *Nais variabilis*

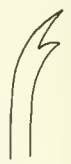
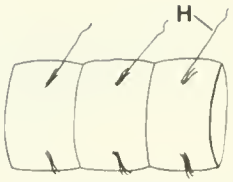


Figure 15.—Ventral seta from an anterior segment.

11 (10) Ventral setae of segments II to V similar to posterior setae, with nearly equal teeth; setal teeth diverge at an angle greater than 45° (Fig. 16). .... *Nais communis*

Figure 16.—Ventral seta from an anterior segment.

12 (*2*) Body wall smooth. Hair setae twisted distally (Fig. 17). Vasa deferentia shorter than atria; prostate gland diffuse (Fig. 18). Coelomocytes large and very numerous. .*Monopylephorus irroratus*



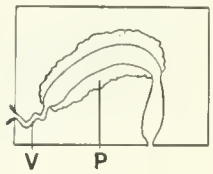
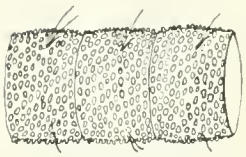
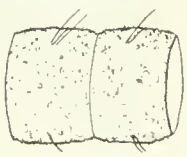


Figure 17 (top).—Lateral view of three segments from middle region of body; H, hair seta.
Figure 18 (bottom).—Diagrammatic lateral view of male genitalia (segment XI); P, prostate gland; V, vas deferens.

12 (*2*) Body wall with conspicuous papillae (Fig. 19) or with accumulations of foreign particles in ridges of epidermis (Fig. 20). Hair setae not twisted distally. Vasa deferentia longer than atria; prostate gland compact (Fig. 21). Coelomocytes absent. 13





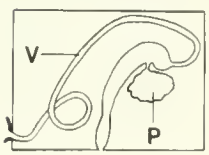


Figure 19 (top).—Lateral view of body wall, papillate forms.
Figure 20 (middle).—Lateral view of body wall, granulate forms.
Figure 21 (bottom).—Diagrammatic lateral view of male genitalia; P, prostate gland; V, vas deferens.

13 (*12*) All or some posterior dorsal setae single-pointed. 14

13 (*12*) All posterior dorsal setae (crochets) bifid. 15

14 (*13*) Body wall with large papillae. Dorsal crochets bifid with upper tooth reduced or rudimentary, or single-pointed, or both (Fig. 22). Ventral setae with upper tooth shorter than lower (Fig. 23). ....*Peloscolex benedeni* (in part)

Figure 22 (left).—Dorsal crochet.
Figure 23 (right).—Ventral seta.

14 (*13*) Body wall surrounded, at least in part, by accumulated foreign particles; papillae absent. Dorsal crochets bifid with equal teeth up to about segment VI (Fig. 24); dorsal crochets from segment VII long, single-pointed, hairlike. Ventral setae with upper tooth longer than the lower (Fig. 25). .....*Peloscolex intermedius*

Figure 24 (left).—Dorsal crochet, anterior segment.
Figure 25 (right).—Ventral seta.

15 (*13*) Body wall covered with large papillae. Posterior dorsal crochets with upper tooth shorter and thinner than the lower (Fig. 26). Anterior hair setae short and strongly bent ..... *Peloscolex dukei*

Figure 26.—Dorsal crochet.

15 (*13*) Body wall surrounded, at least in part, by accumulations of foreign particles; papillae small or absent. Posterior dorsal crochets with subequal teeth (Fig. 27, 28). Hair setae long, straight. 16

Figures 27 and 28.—Dorsal crochets.

16 (*15*) Anterior dorsal crochets with at least one distinct intermediate tooth (Fig. 29). ..... *Peloscolex nerthoides*

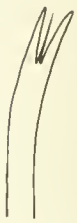


Figure 29.—Dorsal crochet.

16 (*15*) Anterior dorsal crochets without intermediate teeth (Fig. 30). .... *Peloscolex apectinatus*

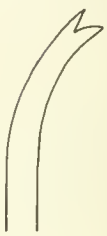


Figure 30.—Dorsal crochet.

17 (*4*) Body wall covered, at least in part, by papillae or accumulation of foreign particles, or both. Penial setae absent. 18

17 (*4*) Body wall smooth; if, rarely, some foreign particles surround body, then penial setae are present. 19

18 (*17*) Body wall with large papillae. Dorsal crochets bifid with upper tooth reduced or rudimentary or single-pointed, or both (Fig. 31). .... *Peloscolex benedeni* (in part)

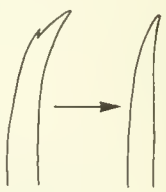


Figure 31.—Range of form of dorsal crochets.

18 (*17*) Two or more anterior segments of body wall without papillae, or body with accumulations of foreign particles on some parts. Dorsal crochets with upper tooth well developed; never rudimentary or absent (Fig. 32). .... *Peloscolex gabriellae*

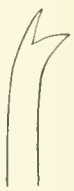


Figure 32.—Dorsal crochet.

19 (*17*) Cuticular penis sheath present. Penial setae absent. 20

19 (*17*) Cuticular penis sheath absent. Penial setae present or absent. 22

20 (*19*) Penis sheath long, cylindrical, with hooded end; over eight times longer than wide (Fig. 33). . . .. *Limnodrilus hoffmeisteri*

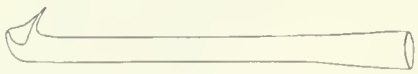


Figure 33.—Penis sheath.

20 (*19*) Penis sheath thimble-shaped to somewhat elongate; less than six times longer than wide. 21

21 (*20*) Penis sheath elongate with a cuticular hook laterally, near the distal end (Fig. 34). Anteriorly setae shallowly bifid (Fig. 35); posteriorly setae single-pointed (Fig. 36). ..... *Tubifex longipenis*

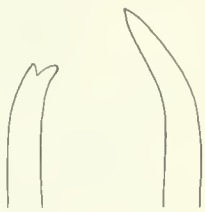


Figure 34 (top).—Penis sheath.
Figure 35 (bottom left).—Dorsal and ventral anterior setae.
Figure 36 (bottom right).—Dorsal and ventral posterior setae.

21 (*20*) Penis sheath thimble-shaped, unornamented (Fig. 37). All setae bifid (Fig. 38). ..... *Tubifex pseudogaster*

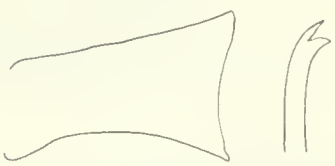


Figure 37 (left).—Penis sheath.
Figure 38 (right).—Dorsal and ventral setae.

22 (*19*) Anterior setae two per bundle, some blunt and some with trifid ends (Fig. 39). Posterior setae one per bundle, bifid with short teeth which diverge at an obtuse angle; upper tooth often reduced or rudimentary; setal node characteristically asymmetrical (Fig. 40). . . . . *Clitellio arenicolus*

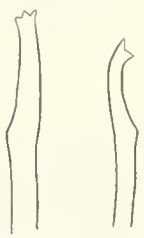


Figure 39 (left).—Anterior seta.
Figure 40 (right).—Posterior seta.

22 (*19*) Anterior setae rarely two per bundle, never with trifid ends. Posterior setae rarely one per bundle, never with teeth diverging at an obtuse angle. Setal node more or less symmetrical. 23

23 (*22*) Genital setae (penial, or spermathecal, or both) present. 24

23 (*22*) Genital setae absent. 29

24 (*23*) Somatic setae broad, bifid, with upper tooth shorter and much thinner than lower (Fig. 41). Spermathecal setae three to four per bundle, single-pointed to very faintly bifid (Fig. 42). External male pore single, median. ..... *Smithsonidrilus marinus*

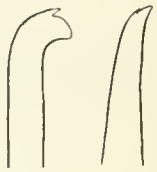


Figure 41 (left).—Somatic seta.
Figure 42 (right).—Spermathecal seta.

24 (*23*) Somatic setae not of previous form. If present, spermathecal setae not of previous form. External male pores paired, ventrolateral. 25

25 (*24*) Posterior dorsal setae one per bundle with strongly curved ends and small thin upper teeth (Fig. 43). Posterior ventral setae normal bifids, much smaller than dorsals (Fig. 44). Spermatozeugmata present. Spermathecal setae present. ..... *Isochaeta hamata*

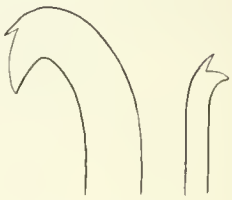


Figure 43 (left).—Dorsal seta.
Figure 44 (right).—Ventral seta.

25 (*24*) Posterior dorsal setae more than one per bundle and not of previous form. Spermatozeugmata absent. Spermathecal setae absent. 26

26 (*25*) Posterior dorsal setae single-pointed, strongly curved (Fig. 45). Penial setae of two types; each penial bundle contains one giant penial and 8 to 12 small clubbed penials with small reflexed distal tooth (Fig. 46). Two prostate glands join each pear-shaped penial bulb (Fig. 47). ..... *Adelodrilus anisosetosus*

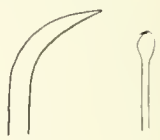
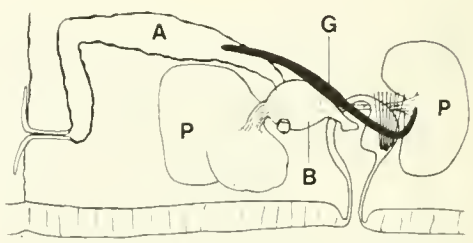


Figure 45 (top left).—Dorsal seta.
Figure 46 (top right).—Distal end of small penial seta.
Figure 47 (bottom).—Lateral view of male genitalia; A, atrium; B, penial bulb; G, giant penial setae; P, prostate gland.



26 (*25*) Posterior dorsal setae not as Figure 45. Penial setae of one type; penials approximately the same size as the somatic setae. Two prostate glands attached to each atrium. 27

27 (*26*) Penial setae two to three per bundle, strongly curved distally (Fig. 48). Atria about five times longer than wide (Fig. 49). ..... *Phallodrilus obscurus*

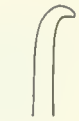
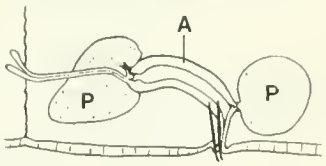


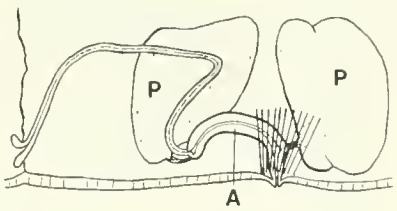
Figure 48 (top).—Penial seta.
Figure 49 (bottom).—Lateral view of male genitalia; A, atrium; P, prostate gland.



27 (*26*) Penial setae 7 to 13 per bundle; hooked or simple-pointed distally. Atria not of above form. 28

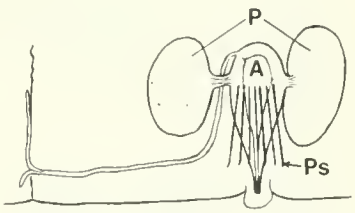
28 (*27*) Penial setae 10 to 13 per bundle; hooked distally (Fig. 50). All somatic setae bifid. Atria about eight times longer than it is wide (Fig. 51). ..... *Phallodrilus coeloprostatus*

Figure 50 (top).—Penial seta.
Figure 51 (bottom).—Lateral view of male genitalia; A, atrium; P, prostate.



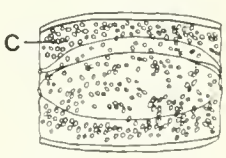
28 (*27*) Penial setae 7 to 10 per bundle, simple-pointed distally (Fig. 52). Posterior somatic setae simple-pointed. Atria small, pear-shaped, erect (Fig. 53). ..... *Phallodrilus parviatriatus*

Figure 52 (top).—Penial seta.
Figure 53 (bottom).—Lateral view of male genitalia; A, atrium; P, prostate; Ps, penial setae.



29 (*23*) Coelomocytes large and very numerous (Fig. 54). Prostate gland diffuse 30

Figure 54.—Anterior segment; C, coelomocytes.



29 (*23*) Coelomocytes absent, or small and few in number. Prostate gland compact, or absent. 31

30 (*29*) Length 8 to 15 mm. Spermatheca single, opening midventrally (Fig. 55). Penis absent. . . . . *Monopylephorus parvus*

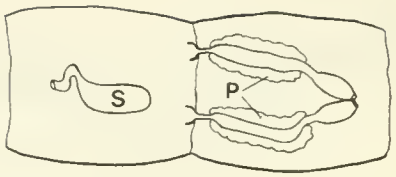


Figure 55.—Dorsal view of genitalia, segments X and XI; S, spermatheca; P, prostate.

30 (*29*) Length 25 to 46 mm. Spermathecae paired, opening medially to line of ventral setae (Fig. 56). Large penis present. . . . *Monopylephorus rubroniveus*

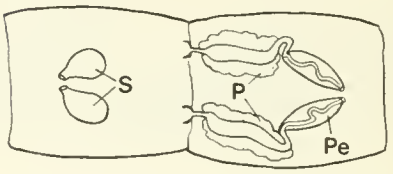


Figure 56.—Dorsal view of genitalia, segments X and XI; S, spermathecae; Pe, penis; P, prostate.

31 (*29*) Spermatheca single, opening middorsally (Fig. 57). Each atrium with two prostate glands. . . . . *Phallodrilus monospermathecus*

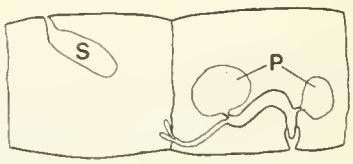
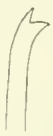


Figure 57.—Lateral view of genitalia, segments X and XI; S, spermatheca; P, prostate.

31 (*29*) Spermathecae paired; open ventrolaterally. Each atrium with no, or one, prostate gland. 32



32 (*31*) Length about 10 mm. Setae bifid with subequal teeth (Fig. 58). Atria short, cylindrical, reflexed distally, each with a compact prostate gland (Fig. 59). Male and spermathecal pores in common midventral bursae. . . . . *Limnodriloides medioporus*

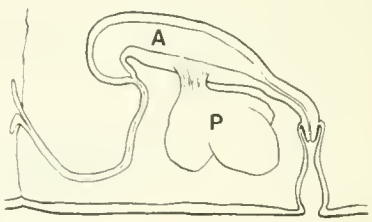
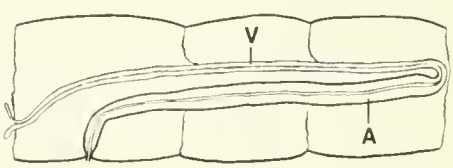


Figure 58 (top).—Seta.
Figure 59 (bottom).—Lateral view of male genitalia; A, atrium; P, prostate.

32 (*31*) Length 30 to 65 mm. Setae bifid with upper tooth small, rudimentary or absent (Fig. 60). Atria very long, cylindrical, without an external prostate gland (Fig. 61). Male and spermathecal pores ventrolateral. . . . . *Clitellio arenarius*

Figure 60 (top).—Seta.
Figure 61 (bottom).—Lateral view of male genitalia; A, atrium; V, vas deferens.



33 (*5*) Dorsal and ventral setae absent from all segments. Coelomocytes in posterior segments large, opaque, white flat discs (Fig. 62). ..... *Marionina achaeta*

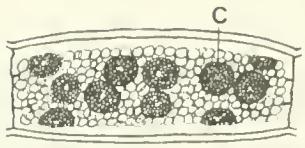


Figure 62.—Lateral view of segment from middle region of body; C, coelomocyte.

33 (*5*) Dorsal, or ventral, or both, setae present on all, or some segments. Coelomocytes not of the above form. 34

34 (*33*) Dorsal setae absent from all segments. 35

34 (*33*) Dorsal setae present on all, or some, segments. 38

35 (*34*) Whenever present, ventral setae one per bundle. 36

35 (*34*) Whenever present, ventral setae two per bundle. 37

36 (*35*) Ventral setae present on all segments. Proximal ends of setae hook-shaped (Fig. 63). Pharyngeal glands united dorsally (Fig. 64). .... *Lumbricillus codensis*

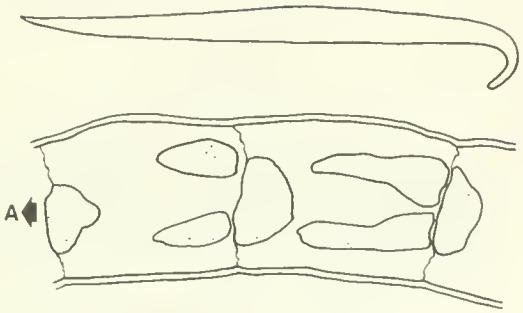


Figure 63 (top).—Ventral seta.
Figure 64 (bottom).—Dorsal view of segments V, VI, and 1/2 VII; A, anterior direction. (Stippled areas in this, and Fig. 66 to 70, are pharyngeal glands.)

36 (*35*) Ventral setae absent from about the first 15 segments. Proximal ends of setae broad, spatulate (Fig. 65). Pharyngeal glands not united dorsally (Fig. 66). ...*Hemigrania postclitellochaeta*

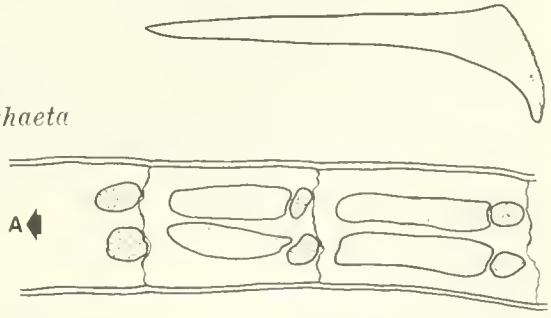


Figure 65 (top).—Ventral seta.
Figure 66 (bottom).—Dorsal view of pharyngeal glands; A, anterior direction.

37 (*35*) Ventral setae present on all segments. With three pharyngeal glands, all united dorsally (Fig. 67). ... .*Marionina subterranea*

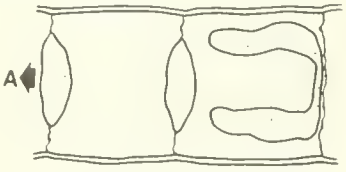


Figure 67.—Dorsal view of pharyngeal glands; A, anterior direction.

37 (*35*) Ventral setae present on segments II to VI, but are absent thereafter. With two pharyngeal glands, both united dorsally (Fig. 68). .....*Marionina preclitellochaeta*

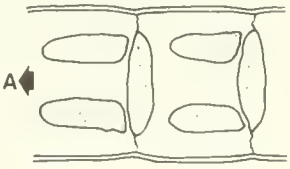


Figure 68.—Dorsal view of pharyngeal glands; A, anterior direction.

38 (*34*) One or two setae per bundle. Dorsal setae absent from segment II at least. 39

38 (*34*) Two to nine setae per bundle (very rarely one). Dorsal setae present on all segments. 40

39 (*38*) Dorsal and ventral setae two per bundle; dorsal setae of segment II, and sometimes III, absent. Posterior pharyngeal glands not united dorsally (Fig. 69). ....*Marionina southerni*

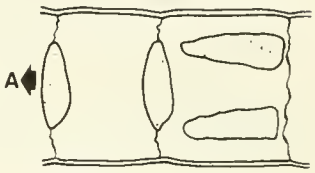


Figure 69.—Dorsal view of pharyngeal glands; A, anterior direction.

39 (*38*) Dorsal and ventral setae two per bundle on segments III to V; dorsals absent on segments II and VII to XVI; all setae one per bundle from segment XVII. Posterior pharyngeal glands united dorsally (Fig. 70). ....*Marionina welchi*

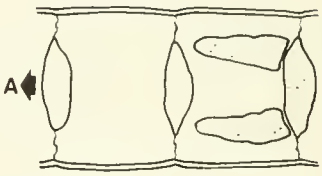


Figure 70.—Dorsal view of pharyngeal glands; A, anterior direction.

40 (*38*) Peptonephridia (P) present (seen best in living specimens) (Fig. 71). Fifteen to 35 mm long. Forty-six to 65 segments. 41

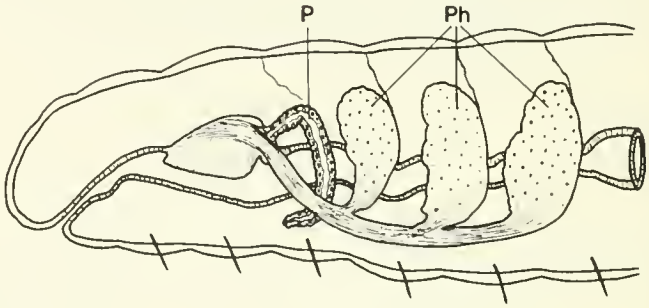


Figure 71.—Lateral view of anterior segments; P, peptonephridium; Ph, pharyngeal glands.

40 (*38*) Peptonephridia absent. Four to 15 mm long. Twenty-six to 50 segments. 42

41 (*40*) Spermathecal duct covered by a dense layer of gland cells (Fig. 72). Twenty to 35 mm long. Two to five setae per bundle posteriorly. .....*Enchytraeus albidus*

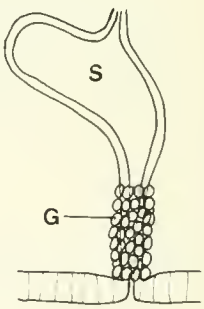


Figure 72.—Lateral view of spermatheca; S, ampulla; G, gland cells.

41 (*40*) Spermathecal duct devoid of glandular cells except for a ring of glands round the spermathecal opening (Fig. 73). Fifteen to 20 mm long. One or two setae per bundle posteriorly. .... *Enchytraeus capitatus*

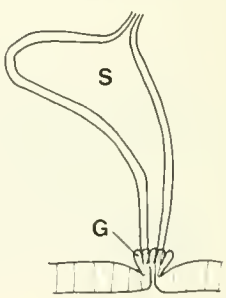


Figure 73.—Lateral view of spermatheca; S, ampulla; G, gland cells.

42 (*40*) Setae distinctly sigmoid. 43

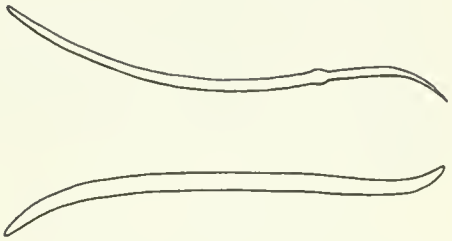
42 (*40*) Setae straight or curved at one end. 44

43 (*42*) Setae with a distinct node (Fig. 74). Twenty-six to 28 segments. ....*Cernosvitoviella immota*

Figure 74.—Seta.

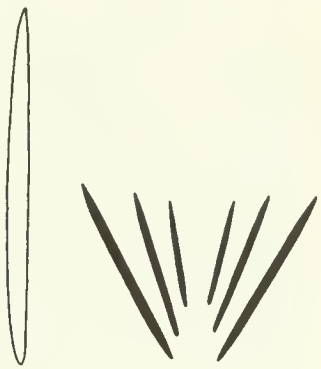
43 (*42*) Setae without a node (Fig. 75). Thirty-eight to 42 segments. .....*Lumbricillus lineatus*

Figure 75.—Seta.



44 (*42*) Setae straight (Fig. 76). Setal bundle fan-shaped, with setae decreasing in size towards center of bundle (Fig. 77). Gut diverticulae present in segment VIII (best seen in living material). Thirty-nine to 50 segments. ....*Henlea ventriculosa*

Figure 76 (left).—Seta.
Figure 77 (right).—One setal bundle.

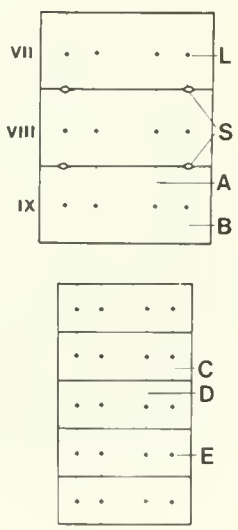


44 (*42*) Setae curved distally (Fig. 78). Setal bundles not of above form. No gut diverticulae. Twenty seven to 30 segments. .....*Marionina spicula*

Figure 78.—Seta.

45 (*5*) Mature worms up to 72 mm long, 3 mm diameter. Small spermathecal pores located in line with, or slightly lateral to, the lateralmost setae of the ventral bundles (Fig. 79). Dorsal setae in posterior segments in regular ranks (Fig. 80). Transverse genital marking present on ventral surface between segments XIX and XX. *Pontodrilus bermudensis*

Figure 79 (top).—Ventral view of segments VII to IX; A, B, lines of ventral setae; B, lateralmost; L, seta; S, spermathecal pores.
Figure 80 (bottom).—Dorsal view of some posterior segments; C, D, lines of dorsal setae; E, seta.



45 (*5*) Mature worms up to 180 mm long, 4 mm diameter. Small spermathecal pores located medial to (never in line with) the lateralmost setae of the ventral bundles (Fig. 81). Dorsal setae in posterior segments irregular, not in orderly ranks (Fig. 82). No transverse genital marking on segment XIX or XX. ..... *Pontodrilus gracilis*

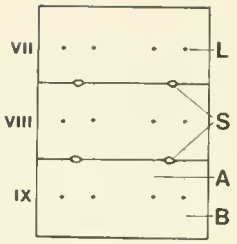


Figure 81 (top).—Ventral view of segments VII to IX; A, B, lines of ventral setae; B, lateralmost; L, seta; S, spermathecal pores.

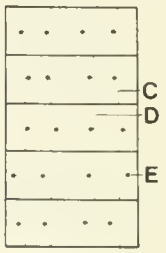


Figure 82 (bottom).—Dorsal view of some posterior segments; C, D, theoretical lines of dorsal setae; E, seta.

ANNOTATED SYSTEMATIC LIST

The following check list of Oligochaeta is arranged systematically in families, with genera arranged alphabetically under their family and species under their genus. Notes on habitat, ecology, life histories, and distribution in eastern North America are given where known. References to important papers are cited under families when applicable (monographs), and individual species (systematics, ecology, and distribution). References to species are cited at the end of the annotation on each species.

Class OLIGOCHAETA

Family NAIDIDAE. Asexual reproduction, by means of fission, occurs commonly in this family. References: Sperber (1948), Brinkhurst and Jamieson (1971).

Chaetogaster cristallinus Vejdovsky, 1883. Pennsylvania. Found in brackish water. Five segments are formed anteriorly on fission. (Brinkhurst, 1964.)

Chaetogaster diaphanus (Gruithuisen, 1828). Massachusetts to Georgia. Brackish water. Predatory on smaller worms. Five segments formed anteriorly on fission. (Brinkhurst, 1964.)

Chaetogaster limnaei von Baer, 1827. New England, but probably a cosmopolitan species. Brackish water. Commensal on pulmonate molluscs, living sometimes in the kidney but usually in the mantle cavity; feed on cercariae. (Brinkhurst, 1964.)

Nais communis Piguet, 1906. Massachusetts to Georgia(?). Brackish water. Five segments formed anteriorly on fission. (Brinkhurst, 1964.)

Nais elinguis Müller, 1773. Massachusetts to Pennsylvania, but probably a cosmopolitan species. Brackish water. Among floating seaweed. Swims actively. Five segments formed anteriorly on fission. (Brinkhurst, 1964; Lasserre, 1966.)

Nais variabilis Piguet, 1906. Connecticut to Georgia(?). Brackish water. Swims actively with spiral movements. Five segments formed anteriorly on fission. (Brinkhurst, 1964.)

Paranais litoralis (Müller, 1784). Nova Scotia to New Jersey. Brackish water and marine. Intertidal and subtidal to 7 m. In sand, in sheltered localities. Four segments formed anteriorly on fission. (Brinkhurst, 1964; Lasserre, 1966.)

Stylaria lacustris (Linnaeus, 1767). Pennsylvania and New Jersey, but probably a cosmopolitan species. Brackish water. Probably among vegetation. Swims actively.

Five segments formed anteriorly on fission. (Brinkhurst, 1964.)

Family TUBIFICIDAE. References: Brinkhurst, 1963; Brinkhurst and Jamieson, 1971.

Adelodrilus anisosetosus Cook, 1969. Cape Cod Bay, Mass. Subtidal, 10 to 21 m depth. In coarse sands. (Cook, 1971.)

Clitellio arenarius (Müller, 1776). Nova Scotia to Maryland, but probably a cosmopolitan species. Intertidal. In sand and gravel, often under stones and rocks. (Moore, 1905; Brinkhurst, 1965.)

Clitellio arenicolus (Pierantoni, 1902). North Carolina and Florida. Subtidal, 5 to 130 m depth. (Brinkhurst, 1966.)

Isochaeta hamata (Moore, 1905). Acushnet River, New Bedford, Mass. Brackish water. Intertidal, under stones. (Moore, 1905.)

Limnodriloides medioporus Cook, 1969. Massachusetts. Subtidal, 7 to 97 m depth. In fine sands and silt. (Cook, 1971.)

Limnodrilus hoffmeisteri Claparède, 1862. Massachusetts to Maryland, but probably cosmopolitan. A predominantly freshwater species sometimes found in brackish water. (Moore, 1905.)

Monopylephorus irroratus (Verrill, 1873). Massachusetts. Brackish water; intertidal freshwater seepages, often with decaying vegetable matter. (Moore, 1905; Brinkhurst, 1965.)

Monopylephorus parvus Ditlevsen, 1904. Massachusetts. Brackish water and marine. Intertidal, beneath stones, to about 7 m depth. (Moore, 1905.)

Monopylephorus rubroniveus Levinsen, 1883. Massachusetts. Brackish water and marine. Intertidal, just beneath surface; often associated with decaying vegetable matter or freshwater seepages. (Moore, 1905.)

Peloscolex apectinatus Brinkhurst, 1965. Nova Scotia and Massachusetts. Subtidal, to 21 m depth. In sand. (Brinkhurst, 1965; Cook, 1971.)

Peloscolex benedeni (Udekem, 1855). Nova Scotia to Connecticut, probably a cosmopolitan species. Brackish water and marine. Intertidal, near high water line, to 18 m depth. In gravel and sand, often beneath stones in intertidal zone. (Moore, 1905; Brinkhurst, 1965; Cook, 1971.)

Peloscolex dukei Cook, 1970. North Carolina. Subtidal, 19 to 200 m depth. In sand and shell fragments. (Cook, 1970a.)

Peloscolex gabriellae Marcus, 1950. Massachusetts, but probably amphi-American. A very broadly defined and problematical species of uncertain specific limits; as it is presently defined the species is found from the low water line to abyssal depths, and in brackish water. In sand. (Cook, 1970b.)

Peloscolex intermedius Cook, 1969. Massachusetts. Subtidal, 7 to 300 m depth. In very fine sands and silt. (Cook, 1971.)

Peloscolex nerthoides Brinkhurst, 1965. Massachusetts. Subtidal, to 42 m depth. In very coarse sand. Also found in brackish water on the west coast. (Cook, 1971.)

Phallodrilus coeloprostatus Cook, 1969. Cape Cod Bay, Mass. Subtidal, to 51 m depth. In sand. Mature individuals have been found in all seasons of the year. (Cook, 1971.)

Phallodrilus monospermathecus (Knöllner, 1935). Massachusetts, but possibly a cosmopolitan species. Brackish water. Intertidal, in sandy beaches, especially in or near freshwater seepages (personal observations.)

Phallodrilus obscurus Cook, 1969. Cape Cod Bay, Mass. Subtidal, to 8.5 m depth. In sand. Mature individuals found in November only. (Cook, 1971.)

Phallodrilus parviatriatus Cook, 1971. Cape Cod Bay, Mass. Subtidal, to 18 m depth. In sand. Mature individuals found in January and June. (Cook, 1971.)

Smithsonidrilus marinus Brinkhurst, 1966. North Carolina and Florida. Subtidal, to 130 m. (Brinkhurst, 1966.)

Tubifex longipenis Brinkhurst, 1965. Maine and Massachusetts. Subtidal, 6 to 51 m depth. In sand and coarse sand. In densities up to 2300 per square meter. Mature individuals found in August and September only; cocoons probably overwinter and hatch the following spring. (Cook, 1971.)

Tubifex pseudogaster (Dahl, 1960). Nova Scotia to Massachusetts. Brackish water. (Brinkhurst, 1965.)

Family ENCHYTRAEIDAE. Reference: Nielsen and Christensen, 1959.

Cernosvitoviella immota (Knöllner, 1935). Massachusetts. In salt marshes, above high tide line. (Lasserre, 1971.)

Enchytraeus albidus Henle, 1837. Maine to North Carolina, but probably a cosmopolitan species. A very tolerant species whose marine habitat is usually decaying seaweed, or under stones, near the high tide line. Also inhabits salt marshes, compost heaps, sewage beds and effluents. (Moore, 1905; Welch, 1917; Lasserre, 1971.)

Enchytraeus capitatus Bülow, 1957. Massachusetts and North Carolina. In seaweed deposits, and meiobenthic on the upper shore of sandy beaches. (Lasserre, 1971.)

Hemigrania postclitellochaeta (Knöllner, 1935). Massachusetts and North Carolina. Subtidal, 6 to about 70 m depth. In coarse sand. (Lasserre, 1971.)

Henlea ventriculosa (Udekem, 1854). Massachusetts and North Carolina. Above high tide line, in salt marshes. (Lasserre, 1971.)

Lumbricillus eodensis Lasserre, 1971. Cape Cod Bay, Mass. Subtidal, 6 to 16 m depth. In sand. (Lasserre, 1971.)

Lumbricillus lineatus (Müller, 1774). Maine to Massachusetts. Upper littoral zone. In salt marshes and seaweed deposits. (Moore, 1905; Welch, 1917; Lasserre, 1971.)

Marionina achaeta Lasserre, 1964. Massachusetts and North Carolina. Intertidal; meiobenthic, on upper shore and at ground water level on lower shore. (Lasserre, 1971.)

Marionina preclitellochaeta Nielsen and Christensen, 1963. Massachusetts and North Carolina. Intertidal; meiobenthic in sand at ground water level on middle to lower shore. (Lasserre, 1971.)

Marionina southerni (Cernosvitov, 1937). Massachusetts and North Carolina. Intertidal. In seaweed deposits. (Lasserre, 1971.)

Marionina spicula (Leuckart, 1847). Massachusetts and North Carolina. Intertidal. Meiobenthic in sand, and in seaweed deposits. (Lasserre, 1971.)

Marionina subterranea (Knöllner, 1935). Massachusetts and North Carolina. Lower intertidal. Meiobenthic in sand at ground water level. (Lasserre, 1971.)

Marionina welchi Lasserre, 1971. Cape Cod Bay, Mass. Subtidal, to about 15 m depth. In sand. (Lasserre, 1971.)

Family MEGASCOLECIDAE.

Pontodrilus bermudensis Beddard, 1891. Virginia. Above high tide line, and intertidal, on sandy beaches and under decaying seaweed. The record of this species is cited in Wass (1965) and is apparently based on specimens identified by J. P. Moore prior to 1931; it is possible that these are referable to *P. gracilis*. Both species are keyed out, however, for the sake of completeness.

Pontodrilus gracilis Gates, 1943. Florida and Beaufort, N.C. (latter record based on a personal communication by E. C. Haff, University of Georgia). Intertidal, on sandy beaches; also banks of rivers where water is brackish. (Gates, 1943.)

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INDEX TO SCIENTIFIC NAMES

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The Board established the format for the "Marine Flora and Fauna of the Northeastern United States," invites systematists to collaborate in the preparation of manuals, reviews manuscripts, and advises the Scientific Editor of the National Marine Fisheries Service.

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COORDINATOR'S COMMENTS

Publication of the "Marine Flora and Fauna of the Northeastern United States" is most timely in view of the growing universal emphasis on environmental work and the urgent need for more precise and complete identification of coastal organisms than has been available. It is mandatory, wherever possible, that organisms be identified accurately to species. Accurate scientific names unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and make possible prediction of attributes of organisms that have been inadequately studied.

The present manual, "Annelida: Oligochaeta" covers the east coast of North America. Dr. David G. Cook began his systematic study of the oligochaete fauna of the east coast in September 1967, when he commenced a 2-year postdoctoral fellowship in the Systematics-Ecology Program sponsored first by the Ford Foundation and later by the National Science Foundation. During this period he prepared a number of manuscripts on this little known group. These have since been published and provided the background for the preparation of this manual. Dr. Ralph O. Brinkhurst, a specialist on the microdrile oligochaetes of the world, carried out his study of the New England aquatic oligochaetes during the summer of 1967 and 1968 as a visiting investigator in the Systematics-Ecology Program under the support of the Ford Foundation and the National Science Foundation.

Manuals are available for purchase from the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402. The manual so far published in the series and its cost per copy is listed below.

COOK, DAVID G., and RALPH O. BRINKHURST. Marine flora and fauna of the Northeastern United States. Annelida: Oligochaeta $0.35

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