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NOAA Technical Report NMFS Circular 440

Marine Flora and Fauna of the Northeastern United States. Turbellaria: Acoela and Nemertodermatida

Louise F. Bush

July 1981

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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U.S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, Secretary
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Terry L. Leitzell, Assistant Administrator for Fisheries

FOREWORD

This NMFS Circular is part of the subseries "Marine Flora and Fauna of the Northeastern United States," which consists 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. The manuals are published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation.

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 are deposited in the reference collections of major museums of the region.

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 is 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, includes an introduction, illustrated glossary, uniform originally illustrated keys, annotated checklist 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. Often they can serve as guides to additional information about species or groups.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R. I. Smith in 1964, and produced under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, Mass. After a sufficient number of manuals of related taxonomic groups have been published, the manuals will be revised, grouped, and issued as special volumes, which will consist of compilations for phyla or groups of phyla.

CONTENTS

Marine Flora and Fauna of the Northeastern United States. Turbellaria: Acoela and Nemertodermatida

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ABSTRACT

This manual contains an introduction to the general biology, an illustrated key to the genera, and an annotated systematic list of the orders Acoela and Nemertodermatida. The key facilitates identification of 16 families and 75 genera of Acoela and includes the 3 genera of the order Nemertodermatida. The systematic list includes 173 species which have been described from the North Atlantic, including some more southern species that might be encountered here, and gives the habitat and known distribution for each species.

INTRODUCTION

Acoel turbellarians are almost exclusively marine, and only two species, *Oligochoerus limnophilous* Ax and Dörjes, 1966 and *Limnoposthia polonica* Kolasa and Faubel, 1974, have been described from freshwater and none from any terrestrial habitat. They are common on various substrata, both intertidally and subtidally, on the continental shelf. A few are pelagic, but none have been reported to date in deep seas. Most of the work on this order, aside from the series of papers by Marcus (1950, 1952, 1954) in Brazil, has been carried out by scientists working on collections made in Europe, and new species and genera from these areas are being added even today. Relatively few species have been described from the northeast coast of the United States, but experience and materials collected thus far indicate that many, if not most, of the genera present in the eastern North Atlantic are also represented in the western North Atlantic. Therefore, in order for this publication to be most useful in the northeastern United States, I have included all known genera from the world in the key and all genera and species from the North Atlantic are included in the systematic list. The known species of the order Nemertodermatida, all of which are marine, are also from the North Atlantic.

The position of Acoela in the class Turbellaria has undergone various changes and, while almost always being recognized as a natural division, they have been ranked variously as a subclass (Graff 1904a, b), a suborder (Karling 1940, under order Archoophora), or an order (Ax 1956; Dörjes 1968a; Karling 1974). The ranking of Acoela as a separate order has the advantage of conforming to the common usage of the term "acoel" and is so used here. The separation of the order Nemertodermatida from Acoela is a more recent development as is explained below.

The subdivisions of Acoela have not been generally agreed upon. Graff (1882) recognized two families, Proporidae and Aphanostomidae (= Convolutidae). Luther (1912) retained Proporidae and Convolutidae as major subdivisions of the group based on the presence or absence of a seminal bursa, and this arrangement into two principal families was more or less followed by other workers until the series of papers by Westblad appeared (1940, 1942, 1945, 1946, 1948). Westblad in his final paper proposed the division of Acoela into three tribes: Opisthandropora-Abursalia, Proandropora-Abursalia, and Proandropora-Bursalia, with a series of families included in each tribe. As the names imply, these were based on the position of the male genital pore and on the presence or absence of the seminal bursa. Recently, Dörjes (1968a), in his comprehensive survey of Acoela, criticized Westblad's arrangement in detail and simply divided the order into 15 families, based primarily on the structure of the male organs. This avoids at least some of the problems and inconsistencies of Westblad's system and is the arrangement, with the following exceptions, which I have used in this paper. An additional family, Antroposthiidae, has been defined recently by Faubel (1976) and is included here as the 16th family. Also, it must be noted that two of Dörjes' families, Hofsteniidae and Nemertodermatidae, have been considered by some authors to deserve ranking as orders separate from Acoela; recent discussions by Ax (1961), Karling (1967, 1974), Tyler and Rieger (1977), and Faubel and Dörjes (1978) lead me to agree that certainly Nemertodermatidae do not belong in Acoela since they have a gut cavity during at least part of their life cycle and also have uniflagellate sperm which are distinctly different from those of Acoela. Specimens of *Nemertoderma* sp. taken by me in Vineyard Sound near Woods Hole, Mass., clearly show a gut space in some of the specimens. Observations on *Meara* (Westblad 1949), and on *Flagellophora* (Faubel and Dörjes 1978), which have open guts and characters close to *Nemertoderma*, also indicate that the family should be in a separate order. I concur with the proposals for an order Nemertodermatida (Westblad 1947; Karling 1940), and am placing *Nemertoderma, Meara,* and *Flagellophora* in the order Nemertodermatida. I am indicating the possibility of Hofsteniidae deserving placement in a separate order by a footnote in the key.

Although future work may be expected to add to the families, genera, and species of Acoela, publication of this key to families and known genera should be useful to workers in our area and encourage students on this side of the Atlantic to further work on the Turbellaria in general and Acoela in particular.

DIAGNOSTIC CHARACTERS OF THE ORDER ACOELA

The order Acoela, as the name implies, comprises those members of the class Turbellaria which do not have clearly

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defined, large open spaces in the body. They not only lack a body cavity, as is the case in all Platyhelminthes, but they also do not possess a digestive cavity with a lining of epithelial cells. The act of digestion is carried out in the central part of the body in a tissue which appears under the microscope as a meshwork of vacuolated cytoplasm with scattered nuclei. This central (digestive) parenchyma is surrounded by a denser tissue, the peripheral parenchyma, in which are imbedded the organs making up the hermaphroditic reproductive system of these animals. Surrounding the peripheral parenchyma, and more or less penetrating it, are several layers of muscle fibers and various epithelial gland cells. The exterior of the body is clothed by a layer of ciliated epithelial cells. The muscle fibers, epithelial gland cells, and outer epithelium form a complex that gives stiffness and preserves the shape of the animal. The German term "hautmuskelschlauch" (outer muscle sheath), often used in the literature, applies only to the layers of muscles, but the epithelium and its often in sunken nuclei and derived gland cells together with the muscle layers make a more or less interwoven unit which can be thought of as an outer body wall. The brain (cerebral ganglion) and large nerve chords lie in the peripheral parenchyma, or, in a few species, in the base of the outer epithelial layer. There are no skeletal or excretory systems. As in many marine flatworms, protonephridia are not present.

The acoels are small animals from ~0.5 to ~10.5 mm in length, mostly oval to elongate oval in shape and without striking surface features such as appendages or special markings. They tend to be more or less transparent or white or pale in color, although a few species are conspicuously colored by the presence of symbionts or special pigments. The lack of a gut cavity as well as of defined body spaces, usually the lack of conspicuous internal organs aside from those of the reproductive system, and the presence of a uniform parenchyma around the organs give them a homogenous appearance that enables the animals to be rather easily distinguished from other Turbellaria. Under low magnification, other characters are visible which aid in distinguishing acoels, namely the presence of a statocyst, the simple mouth opening without a pharynx or with a very simple tubelike one, and the arrangement of large eggs full of stored food material (Fig. 1). Location of the mouth and location and arrangement of sperm and the male copulatory complex (and of stored sperm in the female parts of some species) are useful for recognizing families and genera. Diagnostic characters which require observation with the higher powers of the microscope or recourse to the making of histological sections include details of the reproductive system, presence or absence of frontal or other glands, arrangement of muscle fibers in the outer body wall, and type of nervous system.

The presence of a statocyst is not unique to the acoels but this, together with the lack of a conspicuous pharynx and digestive tract and the presence of large egg cells, is a certain clue to their recognition. The circular clear vesicle of the statocyst with an enclosed statolith is easy to see in the anterior end of the living animal, but it is harder to find in fixed material. In sections it is found lying close to or imbedded in the anterior (cerebral) ganglion.

The mouth in acoels is difficult to see, since in most species it is simply a break in the outer epithelial layer closed by a few sphincter muscle fibers. It opens directly into the central digestive parenchyma (Fig. 2). In relatively few genera, there is a simple tube-shaped pharynx (pharynx simplex) (see Figs. 7, 8, 9, 23a, 24a)[2] which is essentially an invagination of the outer body wall layers. This lack of a specialized pharynx is characteristic of the Acoela as compared with the other orders of Turbellaria,

[2]References in the remainder of this section, unless otherwise indicated, are to the examples in the key where the structures are listed or are indicated by arrows on the figures.

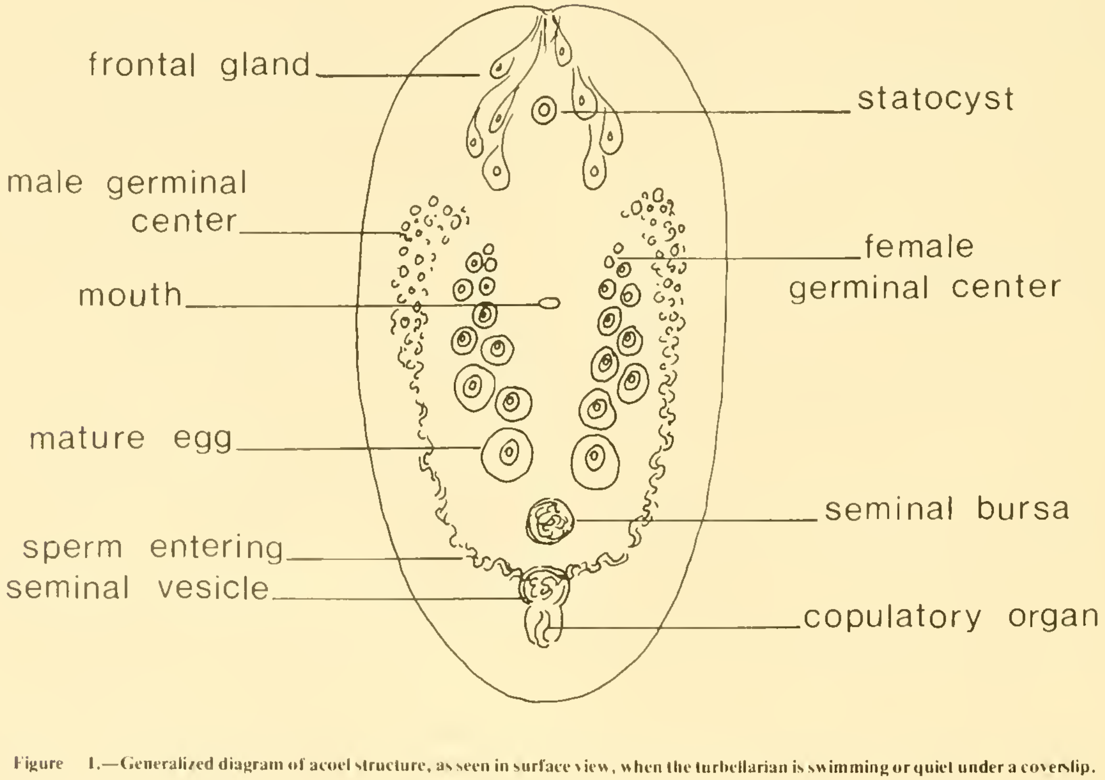


Figure 1.—Generalized diagram of acoel structure, as seen in surface view, when the turbellarian is swimming or quiet under a coverslip.

each of which is defined by a particular and usually more complex pharynx structure. The highly vacuolated central parenchyma can be seen in sections to be more or less sharply distinct from the denser peripheral parenchyma. The terms "endocytium" and "ectocytium" have been used for these two tissues since cell membranes are hard to distinguish in them. However, since some recent studies with electron microscopy have shown that many turbellarian tissues, once thought to be syncytial, are truly cellular, the use of these as general terms may be appropriate no longer. See Ax (1961) for a long discussion of this point and also Boguta and Mamkaev (1972) and Ivanov and Mamkaev (1977).

The parts of the hermaphroditic reproductive system are important in identification of genera and species. In the key, an attempt has been made to use only parts which can be determined without sections, but this is not always possible.

The female parts of an acoel may consist of only the developing and mature eggs. Thus female accessory organs may be totally lacking or there may be present an organ for storing and releasing sperm received from a partner (a seminal bursa or bursa seminalis). In a few species, a vagina is present. There are no oviducts in any of the acoels. The large size of the mature egg is due to its being entolecithal, i.e., each egg develops and stores nutritive material (yolk) in its cytoplasm. Entolecithal eggs are found in some other turbellarian orders (Archoophora), but the more usual condition in so-called higher Turbellaria (Neoophora) is for smaller ectolecithal eggs with the nutritive materials developed and stored in separate and conspicuous yolk glands. Thus the acoels lack yolk glands although in a very few species, *Hallangia proporoides, Polychoerus caudatus, Nadina pulchella,* and some species of *Oligochoerus*, a group of yolk-carrying cells near the eggs have been described. Thus, in most acoels, the eggs increase in size gradually as they mature and yolk accumulates so that a series of eggs of increasing sizes can be seen arranged conspicuously along the length of the body. The youngest stages are found in a definite area of the body (a female germinal center) that is characteristic for each species. This germinal center may be considered to be the ovary although there is no ovary wall or delimiting capsule and the center may be more or less diffuse. The term "ovary" is variously used in the literature to indicate either the germinal center or the entire mass of developing eggs. In some species, there may be a common germinal center where both eggs and sperm start their development in close proximity and then move apart as they mature (Fig. 16). The seminal bursa may be only a loosely defined vacuolated space in the parenchyma (Fig. 138) or it may be a more or less elaborate structure with epithelial or muscular walls (Figs. 29, 30). Nozzles (Figs. 42, 43) or spermatic ducts (Figs. 62, 63) or bursal appendages (Figs. 99, 100, 101) may be present. The bursa may open directly from the female pore (Figs. 69, 99), from a common genital pore (Fig. 30), or from an associated female antrum or vagina (Fig. 29). Groups of sperm associated with bursal nozzles may also be found in the parenchyma without any discernible outside connection (Figs. 46, 72a, 72b) in which case it may be postulated that sperm are stored in this way after they have been deposited either on the outside of the body or through the epidermis by hypodermic injection. However, it has been suggested also that sperm deposited in a vagina or antrum may move through the wall to form such a disconnected bursa or to lie in vacuolated spaces in the parenchyma.

The sperm develop in a male germinal center (testis) which, like the ovary, is not delimited by a definite wall. The developing stages may be arranged in a rather compact mass, may appear to be organized in follicles as in some other Turbellaria, or may be more or less scattered ("diffuse testis"). Distinctions between these types of testes and their exact definitions are not clear (see Steinböck 1966:84-85). As already noted, the male and female germinal centers may be closely associated. In most cases, however, the sperm develop dorsal to the eggs and move posteriorly in the dorsal parenchyma, since there are no sperm ducts in the male system of the acoels.

Some sort of male copulatory complex is always present although it may consist of nothing more than a space in the parenchyma where sperm accumulate close to a male genital pore (Fig. 74). Such an unwalled space in the parenchyma where sperm accumulate before ejaculation is termed a "false seminal vesicle" and such may occur not only with a simple genital pore, but also with many other types of copulatory apparatus (Figs. 80, 169, 171). A walled structure where sperm are accumulated

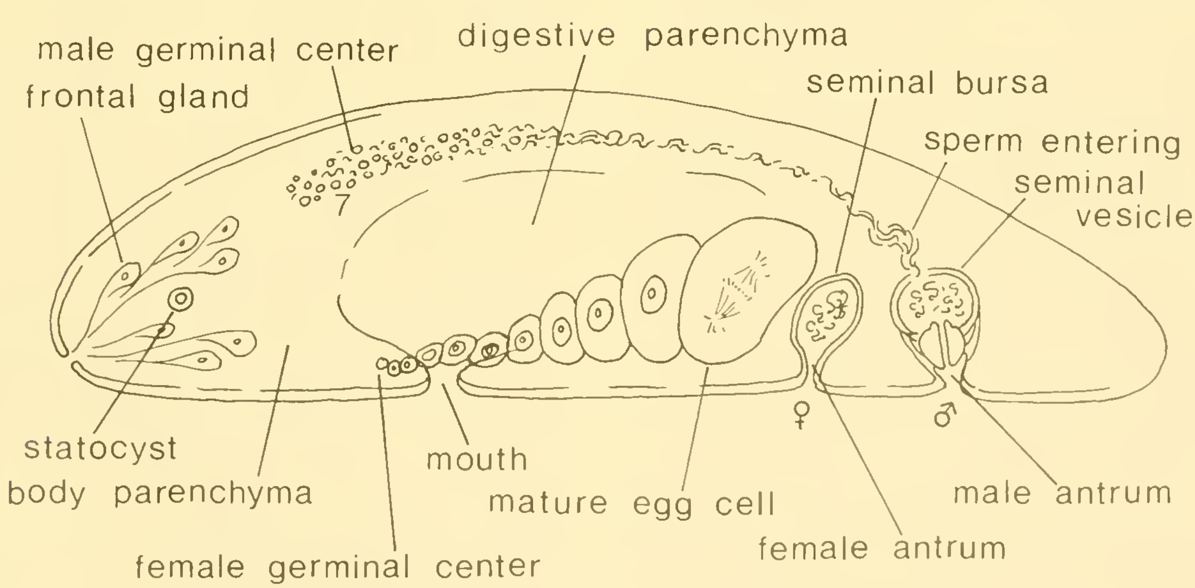


Figure 2.—Generalized diagram of acoel structures, longitudinal reconstruction.

is considered a true seminal vesicle (Figs. 18, 26a, 91); inside of this type there is usually present, besides the sperm, a granular secretion supplied by the walls of the vesicle or by associated gland cells.

Arrangements for the ejaculation of sperm in the acoels range from a simple outside opening at the end of a true or false seminal vesicle to more complex situations that include a passage to the outside (male antrum) and a well-developed penis. The penis, when present, may be composed of various arrangements of fine or coarse needles (Figs. 32b, 54, 106), may consist of a cone-shaped group of muscles (Fig. 107), or may be a glandular or muscular tube (Figs. 91, 94, 115). In some cases, it is inverted into the seminal vesicle itself when at rest and everted to the exterior when sperm are to be discharged. It may be enclosed by a penis sheath or sac which may also enclose the seminal vesicle. A special feature of some families is cuticular needles (adenodactyls) which do not make up a penis, but which are associated with the reproductive passages and which apparently have a stimulatory function (Figs. 37, 38).

The sperm of acoels are biflagellate (Hendelberg 1977) and internal fertilization is the rule, as in other Turbellaria. The arrangement of the reproductive organs suggests cross fertilization. Behavior that suggests mutual insemination has been observed a number of times and it has been shown conclusively to be the case by histological sections of animals in coitus (Hyman 1937, in *Amphiscolops langerhansi*; Westblad 1946, in *Conaperta flavibacillum*).

Asexual reproduction has been reported several times, but has been shown clearly to be a normal method only for the species *Paratomella unichaeta* (Dörjes 1966) and *Pseudohaplogonaria macnaei* (du Bois-Reymond Marcus 1957). Acoels have rather limited powers of regeneration, a characteristic which is undoubtedly associated with the lack of asexual reproduction. A summary of studies on regeneration in this order is given by Steinböck (1967) and should be referred to for its bibliography as well as for his view of the evolutionary significance of experiments in this area.

Gland cells and their secretions play an important role in the physiology of acoels judging by their large numbers and frequent occurrences. Some types of gland cells are so conspicuous as to be useful in the identification of species. Most obvious are those whose secretions are released onto the surface of the body. Rhabdites are common, and under the microscope they can be seen as small elongate bodies lying in or close to the outer epithelial layer. They are produced in the epithelium or in special epithelial cells which are sunken below the surface but which retain their connections to the surface so that the rhabdites may be extruded to the outside. Rhabdites may be scattered irregularly over the body, be present only in limited areas, or be arranged in beautiful rows running the length of the animal. Often they are colorless, but they may carry color that gives a characteristic hue to the entire animal. Rhammites are more elongated or irregular bodies lying deeper in the interior of the body.

A group of gland cells makes up the frontal gland which is characteristic of and occurs in most acoels as well as in some other turbellarians. This gland may not be conspicuous in living animals, but in stained preparations it appears as a varying number of differentially staining cells with ducts opening close together at the anterior tip of the body. In some cases, the ducts unite to form a small ampule before opening to the outside. Studies of the detailed structure of this gland suggest that it is involved in chemoreception as well as in secretion (Antonius 1970).

Other gland cells are present in association with the reproductive organs. There do not appear to be any special digestive glands, although some gland cells may be developed around the mouth or pharynx (Fig. 14). Adhesive glands in conspicuous papillae, as in some other turbellarians, are not usually present, but groups of special adhesive cilia, "haptocilia," in *Hesiolicium inops*, have been described recently (Tyler 1973; Crezée and Tyler 1976). Some cells in the parenchyma that produce pigment would be classed as gland cells.

In most species a layer of circular muscle fibers lies to the outside next to the epithelium with a layer of longitudinal fibers just inside this (Fig. 130). In the few genera where this arrangement is reversed, it is considered to be of taxonomic significance and has been used to define at least one genus (Fig. 128). There may also be a third layer of fibers arranged diagonally between, or close to the others, and sometimes there is an additional layer of circular fibers (Bush 1975). Other fibers, probably derived from these, form the sphincter around the mouth, and, in the reproductive system, muscle fibers are arranged as sphincters, retractors, protractors, and as sheets in the walls of some organs. In many acoels, muscle fibers that extend through the parenchyma from side to side are only weakly developed so that movement is restricted mostly to elongations or shortenings of the body with only a limited amount of twisting or coiling. Locomotion in these species is a characteristic gliding movement accomplished by means of the cilia on the surface. However, in some species, intraparenchymal muscles are better developed and act as retractors of the anterior or posterior ends, may be used in rolling the sides of the body ventrally as when capturing prey, or, in some interstitial species, provide more varied coiling and twisting of the body as the animals move about in spaces between the sand grains.

The nervous system of acoels has been described in relatively few species since the nerve tissue is usually not clearly differentiated in routine sections. In most acoels, however, it can be seen that there is a more or less complex cerebral ganglion lying in the parenchyma at the anterior end of the body with three to six nerve chords extending posteriorly. Some smaller nerves extend to the surface at the anterior end, to the statocyst, and to the neighborhood of the frontal gland. In a few species of acoels and in the order Nemertodermatida, all or part of the nerve tissue, instead of lying in the parenchyma inside the outer wall muscle layers, is found instead lying next to or even somewhat intermeshed with the bases of the outer epithelial cells. Such an epithelial nervous system is considered by some authors to represent a primitive situation and is, therefore, held to be of importance in plotting the evolutionary changes and relationships of the Turbellaria. For differing opinions on this point, see discussions by Ax (1961) and Karling (1974).

Sensory structures appear to be rather few and simple, but, since most of them must be represented by single cells, they are not usually identified and are probably more numerous than is realized. Observations of the reactions of living animals indicate that among the cilia there may be sensory hairs, but acoels do not have the large conspicuous sensory hairs, or the ciliated pits or grooves found in some other turbellarians. Only a few species have pigmented eye spots or pigment-cup ocelli. Electron microscopy will undoubtedly give needed information on sensory structures (e.g., the recent work by Crezée and Tyler (1976) on the caudal organ in *Hesiolicium inops*).

The life cycles of acoels have been determined mostly by inference from collection data. For more complete information, laboratory culture of the animals is required, and this has rarely been done. A recent report by Ax (1977) gave an account based on collection data for 14 species of acoels, as well as other Turbellaria, from the North Sea Island of Sylt. He concluded that in 12 of the 14 acoels there is a polyvoltine life cycle (i.e., with more than one generation per year). Also, he noted that "the polyvoltine life cycle is an important prerequisite for the immense population development of several interstitial acoels. In addition the brood size for acoels commonly consists of many eggs." Apelt (1969) cultured successfully several species of acoels through at least one generation. He followed the embryological development, and his observations agree with those of earlier workers showing that the acoels have a spiral-duet type of cleavage. He also shows the speed of development to be directly related to temperature. Almost all acoels are oviparous but Apelt mentions a few viviparous species. All have a direct type of development without larval stages. See the review by Henley (1974) for a good summary of earlier work on acoel reproduction.

DIAGNOSTIC CHARACTERS OF THE ORDER NEMERTODERMATIDA

The order Nemertodermatida includes two genera, *Nemertoderma* and *Meara*, which were originally included in the Acoela, plus a recently defined genus, *Flagellophora*, which appears to be related to the first two and which is therefore also included in this order. All these species are small forms whose general appearance and habits made it natural when they were first observed to assume they were acoels. However, the uniflagellate sperm in *Nemertoderma* and *Meara* (Tyler and Rieger 1975; Hendelberg 1977) and the presence of a gut cavity at least some time during their life history differentiate these genera from acoels. The presence of two statoliths instead of one in the statocyst makes the distinction between nemertodermatids and acoels relatively easy, the only reported cases of two statoliths in acoels being in fusion and regenerated specimens (Steinböck 1966). The known species of *Nemertoderma* and *Flagellophora* are free-living sublittoral forms; *Meara* is represented by one species from the gut or body cavity of holothurians.

The size range for nemertodermatids is from ~0.5 to ~3.0 mm. They are generally without conspicuous external features except that in *Nemertoderma bathycola* the thick outer epithelium has very large vacuoles so that under low magnification the living animal appears to have a shining outer layer. While the other known nemertodermatids are generally oval in form, *Nemertoderma rubra* is a typical interstitial form with an elongated body and a coiling, twisting type of movement.

The digestive tract is a somewhat variable cavity lined by an epithelium that includes two types of cells, amoeboid digestive cells and club-shaped gland ("körnerkolben") cells, with coarse granules in their cytoplasm. These gland cells are considered to be an important characteristic of the order. The mouth, located on the ventral side, may have slightly thickened lips as in *Meara* or an inturned short section of the epithelium as in *Nemertoderma*, but in *Flagellophora* it appears to be lacking altogether. This last genus is characterized by a flagellar organ (Fig. 181a, b) which reaches from the anterior end to the neighborhood of the gut and which may take the place of a mouth in securing food, but there is little known about the habits of this species.

As already noted, the nervous system in the Nemertodermatida is epithelial or subepithelial. A mass of nerve tissue at the anterior end just under or closely associated with the epithelium represents a cerebral center. Associated with the epithelium all over the body there is a generally diffuse nerve plexus which thins out toward the posterior end and which also shows longitudinal thickenings that probably function as longitudinal nerves. Aside from the statocyst, sense organs have not been described.

The reproductive systems in the Nemertodermatida are relatively simple and similar to those in the acoels. Testes and ovaries may be represented by a common germinal center or may be clearly separated as compact or follicular units. Female accessory organs are lacking in *Nemertoderma* and *Meara*, but in *Flagellophora* there is a large seminal bursa which opens dorsally at the center of the body. The male pore is located in the posterior end of the body, ventrally in *Flagellophora* and terminally in *Nemertoderma* and *Meara*. In *Nemertoderma* there is a long male antrum with a seminal vesicle and a mass of associated glands. In *Meara* the antrum is shorter and the seminal vesicle is smaller and without conspicuous glands. In *Flagellophora* there is a short male antrum with only a false seminal vesicle. The eggs, as in Acoela, are entolecithal but, as already noted, the sperm are uniflagellate in contrast to the biflagellate sperm of the acoels.

ECOLOGY

Little is known concerning the ecology of the acoels and even less about the nemertodermatids for whom we have only the evidence from collection records. Certainly the acoels are more common and occur in a wider variety of habitats than the nemertodermatids. As noted above, our records for the nemertodermatids are all from sublittoral habitats or, in the case of *Meara*, as entocommensals from holothurians. The acoels are common subtidally on the surface of sand or sandy mud or intertidally in rock pools and among detritus or algae in shallow water. Neither group can withstand drying and their soft bodies seem to prevent their burrowing within soft mud deposits; relatively few species have been found associated with the interstitial fauna of sandy beaches although more are being described from this habitat as it is being explored further. A few species of acoels are pelagic and some acoels have been classed as parasitic (probably commensals) since they are found on, or in the body spaces of, larger animals.

Laboratory studies which determine accurately the kind and range of factors to which these animals react await their culture in vitro. The recent work by Apelt (1969), which has been mentioned above, gives the best example of quantitative data. Observations on behavior are found scattered in the literature.

The role played by acoels in animal communities may be inferred from their food relationships as well as from the numbers present in any one area. Food items may be determined in some specimens from remains found in the digestive parenchyma. Many species of acoels seem to be predators or scavengers, much the same as other turbellarians. In spite of small size and fragile bodies acoels may be fast swimmers; I have observed *Neochildia fusca* moving very quickly to overwhelm prey such as small worms, crustaceans, and other small invertebrates. When young, members of this species are found to contain diatoms almost exclusively, but they shift to the role of active predators as they grow larger and mature. In some habitats acoels are only a small part of the biological community structure, but often they are present in enormous numbers (Ax 1977). In such cases they must play a significant role in the food web of the community.

COLLECTING AND EXAMINATION METHODS

The small size and rather fragile body structure of both the acoels and the nemertodermatids present difficulties in their collection and study. Both their fragility and small size result in most species not being recovered by general sampling techniques such as benthic nets or sledges. Relatively undisturbed samples of bottom materials, algae, or other plant materials which are brought into the laboratory and processed there give the best results. The most effective methods for processing are: 1) allowing natural concentration of the specimens at the surface of bottom samples or at the surface of the overlying water after standing, 2) washing out or sieving of specimens with or without the use of narcotic solutions, and 3) seawater ice treatment. A few of the larger or more conspicuous species (e.g., *Polychoerus caudatus*, a bright orange species) may be collected by hand from stones or shells in the intertidal zone. The seawater ice method has been shown to be superior for quantitative analysis of interstitial species (Uhlig et al. 1973).

Some species which normally live on or near the surface of the substratum tend to go downwards when disturbed and many become mixed with the substratum in spite of care in collecting. If the substratum samples or masses of algae or other plants are allowed to stand in the collecting water in the laboratory, however, many of the animals concentrate at the surface of the substratum or at the surface of the water. The length of time necessary for this to occur may vary from a few hours to a day or so. Apparently, the animals are reacting to lack of oxygen in lower layers, although change of temperature may also be involved. They may be picked up from the surface with a medicine dropper, either with or without the aid of a dissecting scope.

Washing out of specimens from the substratum may be done in several ways. Vigorous shaking of algae or other plant material in seawater will dislodge some specimens. Vigorous stirring of sand samples in seawater followed by quick decanting of the water as sand particles settle will recover many specimens since neither the acoels nor the nemertodermatids have the strongly developed adhesive organs found in some other turbellarians. For most interstitial organisms a narcotizing solution (usually 7% $MgCl_2$ in tap water) is used so that the animals may be passively washed out by stirring and decanting, by sieving, or by elutriation of the material in a separation funnel (see Hulings and Gray 1971, for an account of various methods). On replacement of the narcotizing solution the animals recover readily if they have not been left in the narcotic too long, but acoels tend to die very soon and also to break up when handled in the relaxed state. If the material is fixed and stained with a general stain, such as Rose Bengal, before washing out,this difficulty is avoided, but the process of sorting afterwards is much more difficult since most turbellarians, and especially acoels and nematodermatids, look like small oval lumps after fixation and can be easily mistaken for broken bits of tissue or for ciliates which may be about the same size.

The seawater ice method is an effective method (Uhlig et al. 1973) for recovering Turbellaria brought into the laboratory with sand or sandy mud and is being adopted by many workers who desire a quantitative analysis of such material. This method involves the use of a temperature and water salinity gradient to induce the animals to leave the substratum. A simple apparatus (Fig. 3) is set up consisting of a tube to hold the substratum samples plus seawater ice which provides a slight temperature gradient but, more importantly, results in a change from low to high salinity of the water that runs through the sample as melting occurs. The live animals collect in the dish at the bottom of the apparatus and can then be sorted and prepared for further study. The chief drawback of this method is that it is somewhat time consuming and may not be worthwhile if only a quick determination of the most prominent members of a fauna is desired.

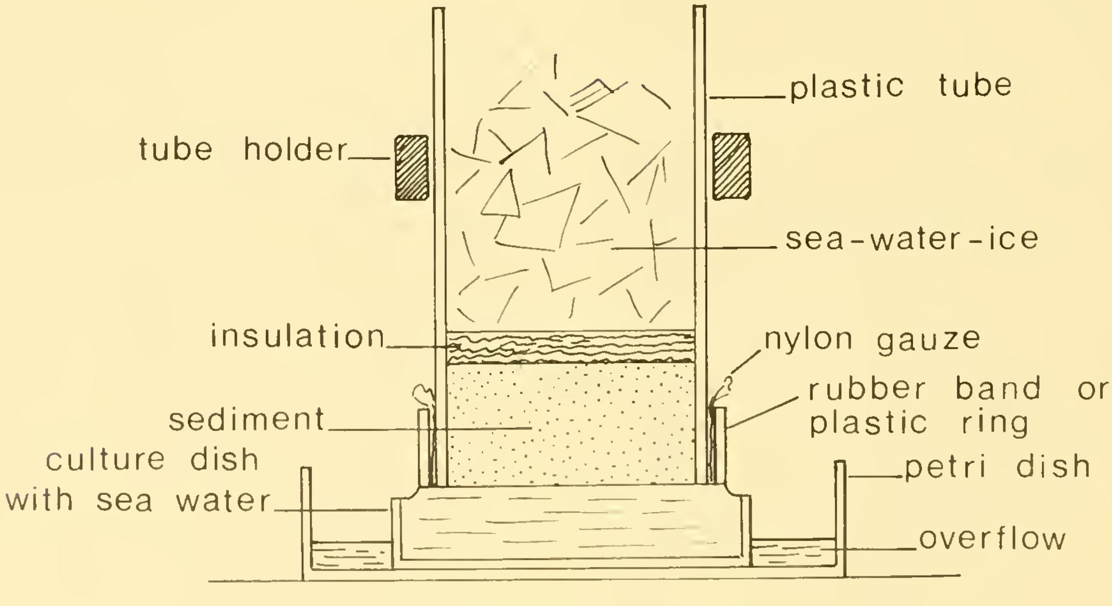


Figure 3.—Apparatus for seawater ice treatment of sediment (redrawn from Uhlig et al. 1973). Use of the insulation layer is optional.

Acoels may be kept in small dishes in the laboratory for hours, days, or even months. In plain seawater many species will live for a day or so. However, adding a bit of substratum may provide enough food for them to live much longer, and when food preferences are known they may be maintained through at least part of a life cycle. Eggs are often laid by mature adults during the first few days in dishes in the laboratory and young hatched from such a "culture" may survive for a time even without further feeding. Apelt (1969) maintained several species by supplying cultured diatoms to the animals and was thus able to study the complete life cycles.

For the easiest identification by use of the following key, it is best to begin with living animals. In some cases fixation and perhaps sectioning will be necessary after the living animals have been observed. Where only fixed material is available, whole mounts are of some help but in most cases sectioning is necessary.

Observation of living animals is done in a drop of water under a coverslip with the amount of water adjusted so that the coverslip just slightly flattens the acoel, thus holding the animal quiet and also flattening the body to achieve greater transparency. A narcotic such as $MgCl_2$ may be added to the drop of water, but the difference between achieving just strong enough a solution of the narcotic to quiet the animal and too strong a solution which kills it and causes it to disintegrate is very narrow. Such treatment is difficult to use with acoels. Flattening of the animal may also be achieved by the use of a specially built "rotocompressor" such as Heunert and Uhlig (1966) described but, so far as I am aware, these are not available commercially. The larger structures referred to in the key and many of the finer details of organs such as the seminal bursa may be observed by study of living animals with ordinary low power (100×) or high dry (430×) magnification. The use of phase contrast or interference contrast is best for studying these transparent animals, but is not essential.

Fixing of materials for further examination may be done with any of the standard histological fixatives. The one most commonly used, especially in field work, is hot or cold Bouin's since specimens may be left in this for an indefinite period of time. Fixation with this solution, although not considered as good for cytological details, is quite satisfactory for routine identification. Animals can be picked up in a finely drawn-out medicine dropper with as little water as possible and dropped directly into the fixative. For animals as small as most species of these two orders, the fixation is almost instantaneous, and there is relatively little contraction or shrinking of the specimens. Specimens fixed in Formalin with other animals, plant material, or both may be used, but the fixation is poor and often specimens are distorted or broken.

Whole mounts may be stained in Borax Carmine which is probably best for museum specimens since it does not fade as much as many of the hematoxylins. However, I have had better differentiation with a trichrome stain (stock solution: Chromotrope 2R, 0.6 g; Fastgreen FCF, 0.3 g; phosphotungstic acid, 0.7 g; acetic acid, 1.0 ml; distilled water 100.0 ml. See Horen 1957), if it is used in a very dilute solution. For this, specimens which have been fixed in Bouin's (10-20 min) should be washed (several changes for about 1 h) in 70% alcohol. After washing they are left in the dilute stain overnight, then dehydrated and mounted. For the best whole mounts, animals should be fixed by allowing the Bouin's to flow over the animal held slightly flattened under a coverslip.

For sections, any of the standard histological methods may be used. Imbedding in paraffin and sections 6-10 μ m thick has proved satisfactory. Various stains may be used, but since the structure of acoels depends almost entirely on the structure of individual cells, the most satisfactory stains will be those which bring out as clearly as possible the nuclei and shape of cells and muscle fibers. For this the old standby, a combination of iron hematoxylin with a counterstain such as eosin or orange G, is still the most reliable. Mallory's triple stain is fairly good, but many of the stains for special tissues used in histology are not effective since acoels do not have such specialized tissues. The use of electron microscopy is producing much needed information about these animals but cannot be used primarily for identification of species.

GLOSSARY

Terms are defined here as used in this key; included are some equivalent terms common in the literature. Terminology used for reproductive organs has varied considerably in the past and definitions given here are an attempt to render in English the most recent usage of Dörjes (1968a), Antonius (1968), and other European workers.

Accessory organs Organs which aid in reproduction as accessories to the ovary and testis.

Adenodactyl A bundle of fine cuticular needles lying with inner ends in the wall of the male antrum and with points projecting into the antrum; the inner ends are associated with gland cells. Functions as a stimulatory ("reizorgan") or adhesive organ; compare "prostatoid organ."

Antrum See "female antrum," "male antrum" (in some authors "atrium" is used instead of "antrum."

Archipharynx A type of pharynx unique to the family Nadinidae; consists of a short ciliated outer section and long, funnel-shaped inner part; the wall of the outer section has muscle fibers which are extensions of those of the outer body wall; the wall of the inner section has an added inner layer of very heavy circular muscles; a sphincter muscle separates the two parts.

Atrium See "common genital atrium."

Bursal appendage An appendage on the seminal bursa; see "spermatic duct."

Bursal nozzle A cuticularized structure associated with the seminal bursa or with groups of stored sperm.

Bursal sphincter See "spermatic duct."

Bursa seminalis Same as seminal bursa.

Central parenchyma See "parenchyma."

Common genital atrium Passage leading from the exterior to both male and female reproductive organs.

Common genital pore Opening from the exterior to both female and male reproductive organs; may be associated with a common genital atrium or the male and female parts may open directly from it.

Common germinal center The site in some species where the early stages of both eggs and sperm are intermingled or lie close together.

Ductus spermaticus Same as spermatic duct.

False seminal vesicle See "seminal vesicle."

Female antrum Passage leading to the female organs which is considered to be an inpocketing of the outer body wall as indicated by an epithelial lining that is continuous with and similar to the outer epithelium.

Female accessory organs Organs in the female beside the ovary and eggs; in the acoels these consist of the seminal bursa and associated parts, but may be lacking altogether.

Female germinal center Area where the earliest stages of development of eggs are found; in the acoels it is not delimited by a capsule and is continuous with the string of eggs which move along the body as they develop; "ovary" is often used to include both the germinal center and the string of eggs.

Flagellar organ Organ consisting of several flagella in an elongated channel at the anterior end of the body in some members of the order Nemertodermatida. The flagella arise in an oval enlargement at the proximal end of the channel and may be protruded through the open end of the channel at the anterior tip of the body.

Frontal gland Group of gland cells whose ducts open at the anterior end of the body either singly or variously combined, with or without a small ampule at the outer end of the ducts.

Germinal center See "female germinal center," "male germinal center."

Haptocilia Specialized cilia with adhesive tips.

Körnerkolben cells Large club-shaped gland cells with coarse secretory granules; characteristic of the intestine of the Nemertodermatida.

Male antrum Passage leading to the male organs which is considered to be an inpocketing of the outer body wall as indicated by an epithelial lining which is continuous with and similar to the outer epithelium.

Male copulatory complex All organs involved in the transfer of sperm to a partner. This includes the penis and associated glands and ducts.

Male germinal center Area where the earliest stages of sperm development take place; not set off by a wall or capsule and may be scattered groups of cells; "testes" often used for this general area.

Nozzle See "bursal nozzle."

Outer body wall Includes the outer epithelial layer and the underlying circular, longitudinal, and, if present, oblique muscle layers plus intermingled parenchyma and gland cells.

Ovary Includes the female germinal center and the string of developing eggs; see "female germinal center."

Parenchyma The mass of generalized cells filling most of the body in acoels; peripheral parenchyma is the outer part of this mass which surrounds the body organs; the central parenchyma is the more vacuolated central part in which digestion occurrs.

Penis Glandular, muscular, or cuticularized structure which serves directly to convey sperm to the partner; a wide variety of structures are included under this term.

Penis sac Sac, not part of the wall of the penis, that surrounds the penis and may also surround the seminal vesicle and, in a few cases, the male antrum also.

Peripheral parenchyma See "parenchyma."

Pharynx simplex A simple tube that structurally is an inturned part of the outer body wall.

Prostatoid organ A thick-walled pocket containing a secretion and, sometimes, with a cuticularized point or needle at its open end; may open either into the male antrum or onto the ventral surface of the body; believed to function as a stimulatory ("reizorgan") or adhesive organ; compare "adenodactyl."

Rhabdites Oval to elongate-oval rods, secreted by, and lying in, outer epithelium or in epithelial cells sunken into the parenchyma; may be clear, semitransparent, or colored and may protrude on the surface of the body.

Rhammites Similar to rhabdites but long, sinous, or irregular in shape and always found in cells sunken into the parenchyma.

Seminal bursa Walled sac that receives and stores sperm from a partner.

Seminal vesicle Area where sperm accumulate before ejaculation; a true seminal vesicle is a walled organ associated with the male copulatory organ; a false seminal vesicle is simply a space in the parenchyma associated with the copulatory organ or the male genital pore.

Spermatic duct Duct leading from the seminal bursa; may be outside of the bursa (bursal appendage) or may be inverted inside the bursa; may be cuticularized (bursal nozzle) or may consist only of cellular and/or muscular elements; may act as a sphincter. Its evolutionary precursor appears to be only a cap of cells (see Dörjes 1968a:73-74).

Statocyst Sense organ in anterior end of body. In Acoela it is composed of a cellular vesicle which contains a lithocyte enclosing a statolith; in Nemertodermatida it is similar but contains two lithocytes, each with a statolith.

Syncytial bursa Area in the parenchyma where bundles of sperm received from a partner accumulate and which thus serves as a bursa in addition to or in the place of a seminal bursa.

Testis See "male germinal center."

True seminal vesicle See "seminal vesicle."

Vagina Passage leading to the seminal bursa whose lining epithelium and wall structure does not correspond to that of a female antrum, or where a passage is present in addition to the female antrum; this term is loosely used and not well defined.

KEY TO THE FAMILIES AND GENERA OF ACOELA AND NEMERTODERMATIDA OF THE WORLD

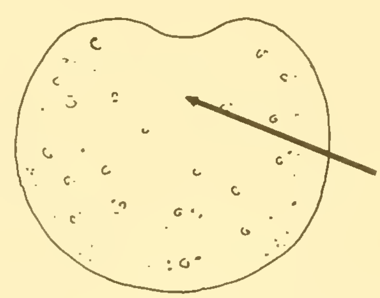
This key includes the known families and genera of the world since the acoels in the western North Atlantic are poorly known, and anyone working with material from the northeastern United States will need to start by comparing specimens with the families and genera already described from other areas. Particularly pertinent are the genera from the eastern North Atlantic since we already know that many of the same genera and some of the same species also occur here. New genera are being defined from time to time, and some appearing very recently, since the key was completed, are added by means of footnotes at appropriate places.

The arrangement of the families and parts of the key are based on Dörjes (1968a) and the debt owing to him is gratefully acknowledged, but I am responsible, of course, for the key and systematic list as here presented.

In identifying material it is most desirable to start with a study of living specimens slightly flattened under a coverslip; the identification to genus often can be made in this way. When this does not suffice, the only recourse is to fix the animals and make sections as suggested on page 7. Unfortunately, in my experience, whole mounts satisfactory for identification purposes are very difficult to attain. The inclusion of a complete diagram for at least one species in each genus will facilitate identification and the annotated systematic list of species for each genus will provide further clues. Page references in the key after each family refer to its location in the systematic list. All figures in the key have been redrawn from the original descriptions so far as possible and the type species for each genus is included in all but a few cases. Except where otherwise noted, all figures are sagittal reconstructions of the entire animal or of male and female accessory organs. Arrows on the figures indicate characters listed in the key.

1 Statocyst absent—three instances are reported where statocyst is lacking in species otherwise having the characters of Acoela: *Amphiscolops sargassi* Hyman from Bermuda; *Amphiscolops evelinae* Marcus from Brazil; *Haplodiscus piger* Weldon from the North Atlantic (Fig. 4).

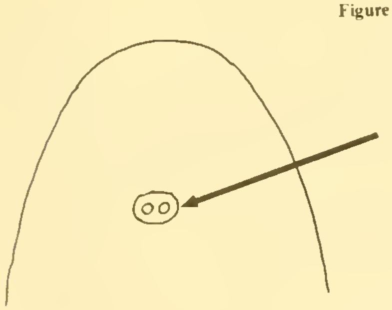
Figure 4.—*Haplodiscus piger*, dorsal view.



1 Statocyst present 2

2 (*1*) Statocyst with more than one statolith (Fig. 5) ....
.... Order NEMERTODERMATIDA 87

Figure 5.—Anterior end, dorsal view.



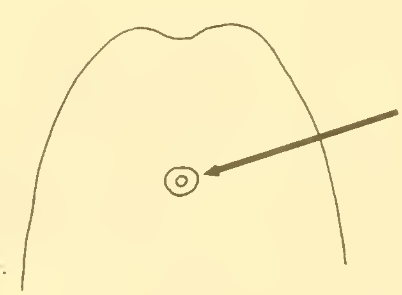


Figure 6.—Anterior end, dorsal view.

2 (*1*) Statocyst with only one statolith (Fig. 6) ....
.... Order ACOELA 3

3 (*2*) Mouth with pharynx simplex opening terminally at the posterior end of the body (Fig. 7) .... Family DIOPISTHOPORIDAE (p. 60) .....
Genus *Diopisthoporus*.

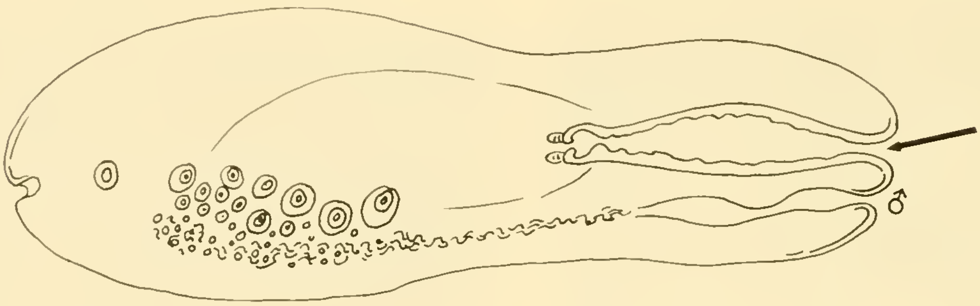


Figure 7.—*Diopisthoporus longitubus*.

3 (*2*) Mouth opening with or without a pharynx but not terminal at the posterior end of the body 4

4 (*3*) Mouth with pharynx at the anterior end or very close to front end and with male pore at posterior end of body (Fig. 8). *Archiproporus minimus* An der Lan has been placed in *Proporus* (Westblad 1945) but is now considered to deserve ranking in a separate genus (Karling 1974:8); description of this species is unclear on some points and position of the genus seems to me uncertain (Fig. 9) .... Family PROPORIDAE (p. 58) ....
Genus *Proporus*.
Genus *Archiproporus*.

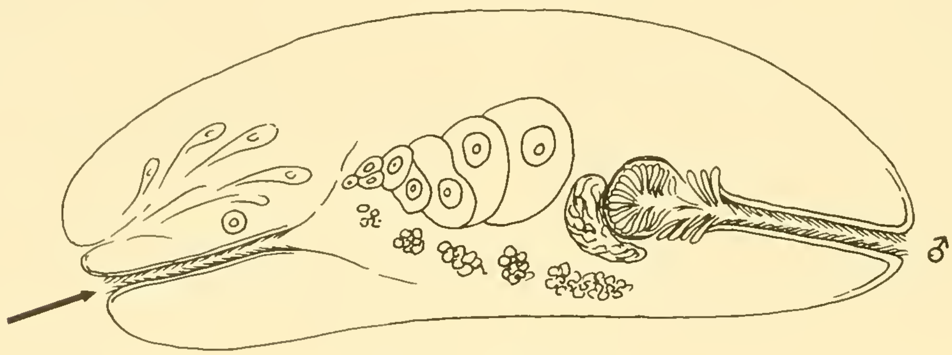


Figure 8.—*Proporus venenosus*.

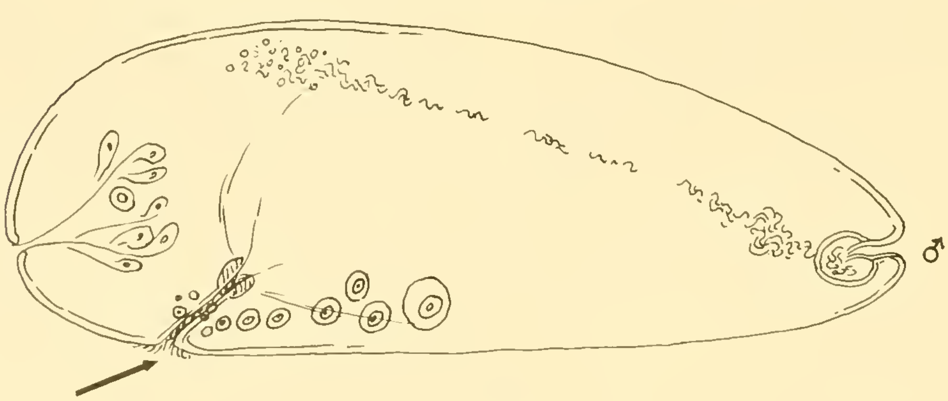


Figure 9.—*Archiproporus minimus*.

4 (*3*) Mouth opening with or without a pharynx but not terminal at anterior end of body, or, if terminal or subterminal at anterior end, then male pore not terminal at posterior end 5

5 (*4*) String of developing eggs extends behind the male copulatory organ into the posterior end of the body (Figs. 10, 11) 6

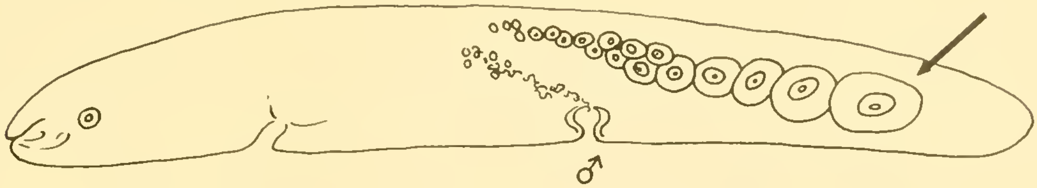


Figure 10.—Diagramatic longitudinal section.

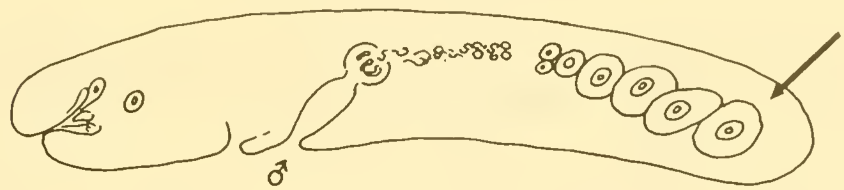


Figure 11.—Diagramatic longitudinal section.

5 (*4*) String of developing eggs ends anterior to or at the level of the male copulatory organ (Fig. 12) 13

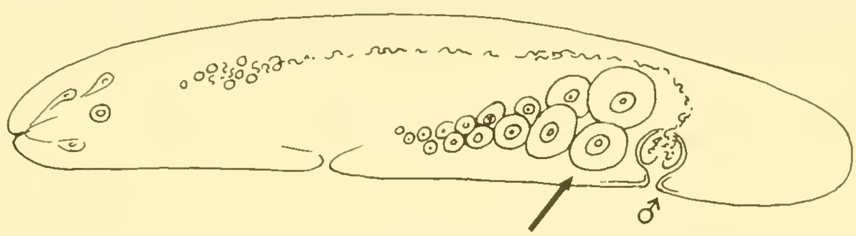


Figure 12.—Diagramatic longitudinal section.

6 (*5*) Mouth with a pharynx simplex (Fig. 13) .... Family SOLENOFILOMORPHIDAE (p. 63) 7

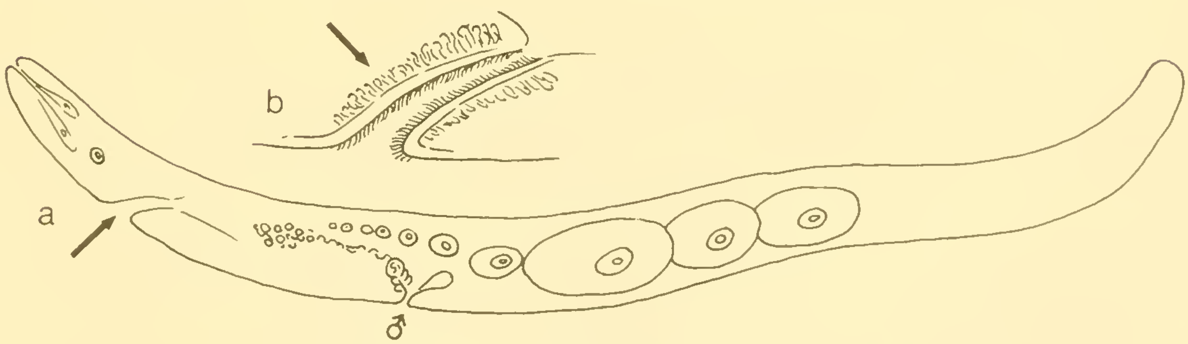


Figure 13.—*Oligofilomorpha interstitiophilum*: a-sagittal reconstruction; b-sagittal section of pharynx.

6 (*5*) Mouth without a pharynx 11

7 (*6*) Rhammites absent 8

7 (*6*) Rhammites present (see Figs. 17, 18) 10

8 (*7*) Wreath of large cells present around the mouth (Fig. 14) .... Genus *Myopea*.

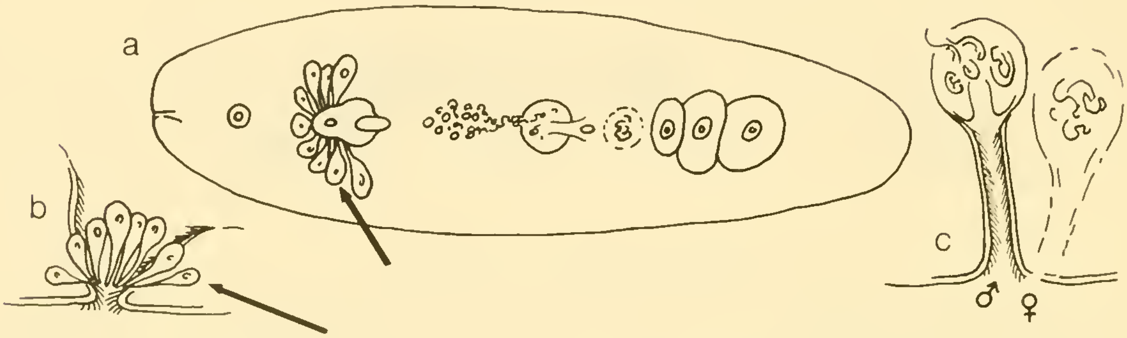


Figure 14.—*Myopea crassula*: a-dorsal view; b-section through mouth and pharynx; c-male and female accessory organs.

8 (*7*) No wreath around the mouth although glandular epithelium of the pharynx may vary in thickness 9

9 (*8*) Seminal bursa present (Fig. 15) (see also Fig. 13) .... Genus *Oligofilomorpha*.

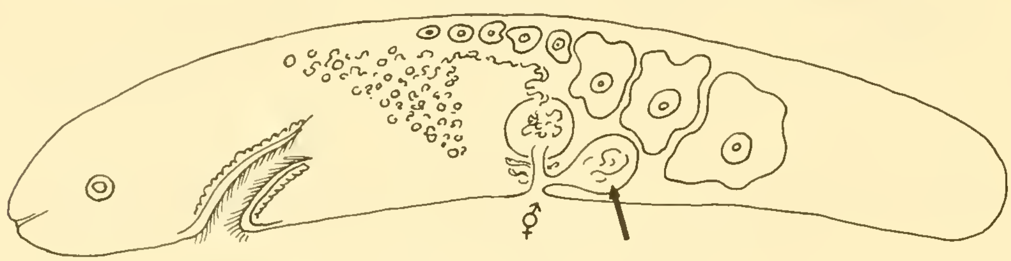


Figure 15.—*Oligofilomorpha karlingi*.

9 (*8*) Seminal bursa absent (Fig. 16) .... Genus *Solenofilomorpha*.

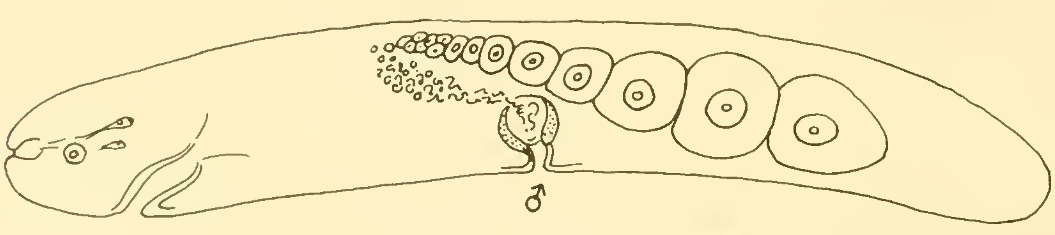


Figure 16.—*Solenofilomorpha longissima*.

10 (*7*) Rhammites scattered near the entire ventral surface but concentrated around the mouth; seminal vesicle very large so as to almost fill the body in cross section; male antrum with a network of longitudinal muscles running through it (Fig. 17) . . . . Genus *Fusantrum*.

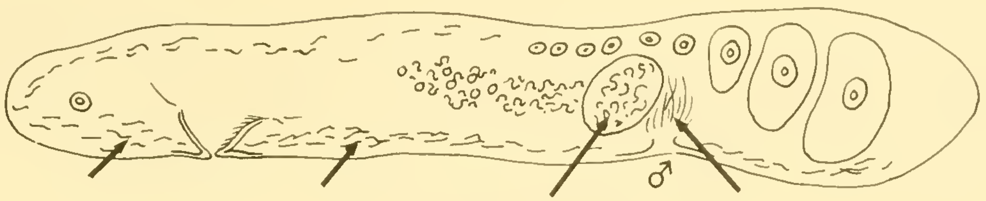


Figure 17.—*Fusantrum rhammiphorum.*

10 (*7*) Rhammites in rhammite tracts anterior to the mouth; seminal vesicle and male antrum well defined with muscle fibers in the walls (Fig. 18) . . . . Genus *Endocincta*.

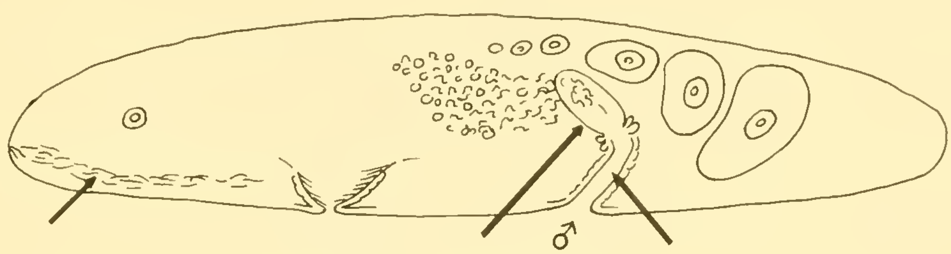


Figure 18.—*Endocincta punctata.*

11 (*6*) Male pore in anterior of body close to mouth; tubelike ciliated male antrum (Fig. 19) . . . . Family ANTIGONARIIDAE (p. 62) . . . .

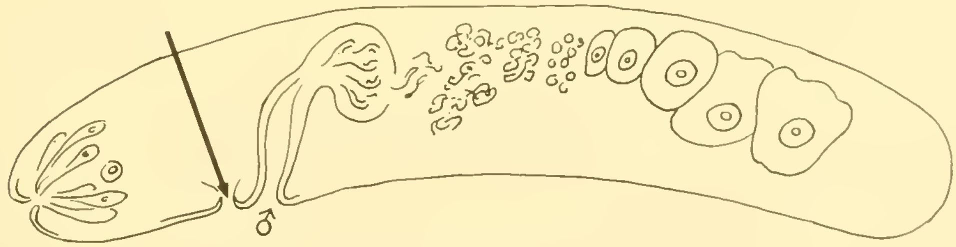


Figure 19.—*Antigonaria arenaria.*

11 (*6*) Male pore not in anterior end; male antrum absent; haptocilia present (Fig. 20) . . . . Family PARATOMELLIDAE (p. 61) 12

12 (*11*) A caudal sensory organ present (Fig. 20); no asexual reproduction .... Genus *Hesiolicium*.

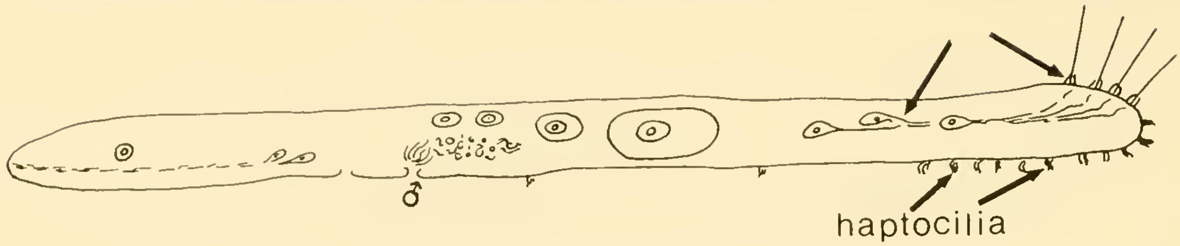


Figure 20.—*Hesiolicium inops.*

12 (*11*) Caudal sensory organ absent (Figs. 21, 22); both sexual and asexual reproduction .... Genus *Paratomella*.

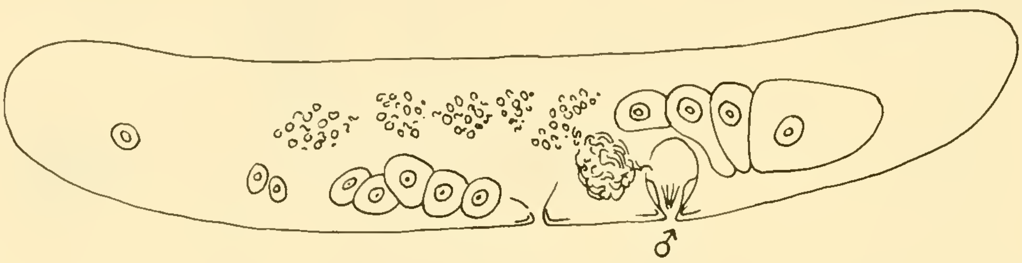


Figure 21.—*Paratomella unichaeta.*

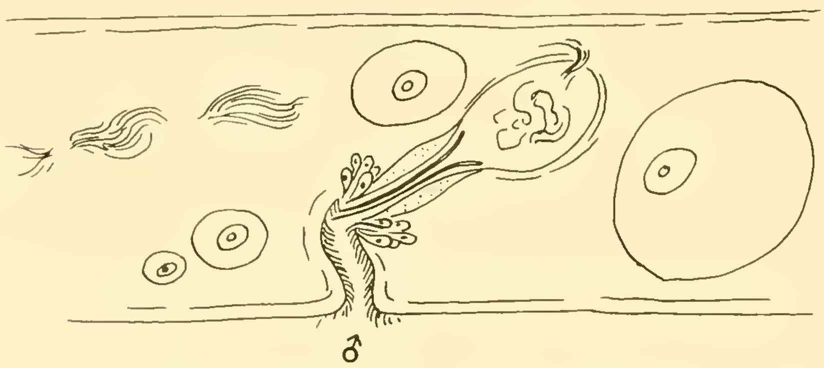


Figure 22.—*Paratomella rubra*, **sagittal section through body at level of male accessory organs.**

13 (*5*) Mouth opening at or close to the anterior end of body 14

13 (*5*) Mouth opening not close to anterior end 18

14 (*13*) Male pore close to mouth at anterior end; bursa seminalis absent .... Family HOFSTENIIDAE[3] (p. 61) 15

14 (*13*) Male pore not close to mouth; bursa seminalis present .... Family HALLANGIIDAE (p. 60) 17

[3]The Hofsteniidae are sometimes placed in an order or suborder separate from the Acoela (e.g., Karling 1940). However, until this point has been resolved by further studies, the tendency at present appears to be to retain them in the Acoela (see Steinböck 1966, for a complete review of this question).

15 (*14*) Pharynx long, tube-shaped, thick, and muscular; mouth opening subterminal at anterior end (Fig. 23) .... Genus *Hofstenia*.

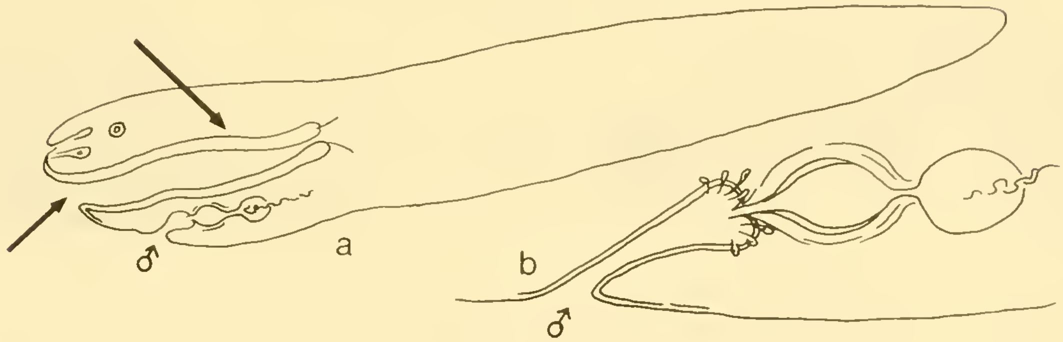


Figure 23.—*Hofstenia atroviridis*.

15 (*14*) Pharynx with only weakly muscular walls, either tube-shaped or short and globular; mouth opening ventral near anterior end 16

16 (*15*) Pharynx long (about one-fourth body length), thin and tube-shaped (Fig. 24a); seminal vesicle enclosed in a thick muscular wall which encloses also the cuticular elements of the penis (Fig. 24b). One species from the Mediterranean .... Genus *Hofsteniola*.

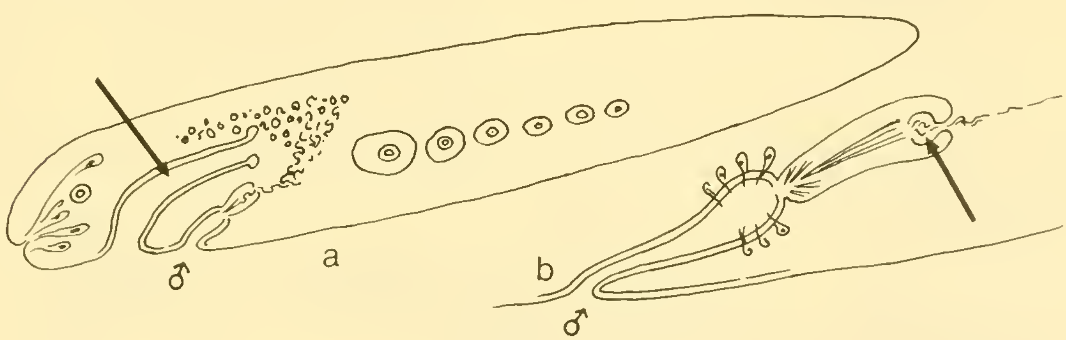
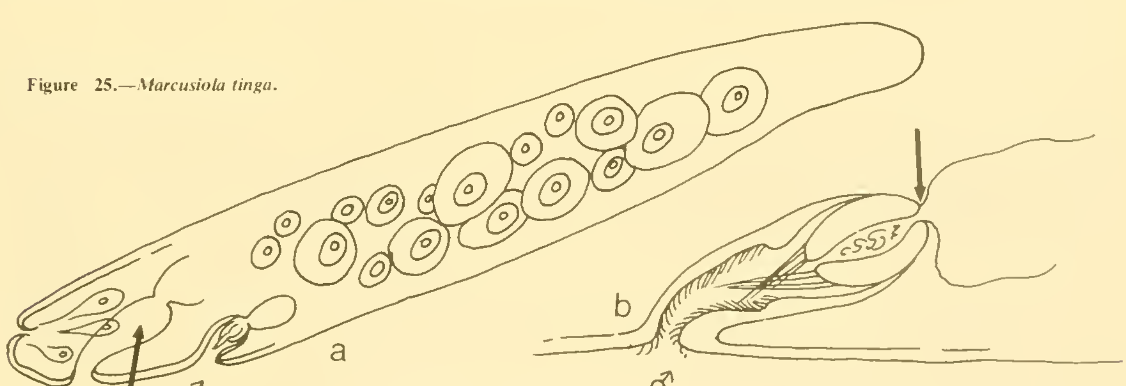


Figure 24.—*Hofsteniola pardii*.

16 (*15*) Pharynx short (about one-sixth body length), thin-walled and globular (Fig. 25a); seminal vesicle clearly separated from the bulb of the penis by a constriction (Fig. 25b). One species from Brazil .... Genus *Marcusiola*.

Figure 25.—*Marcusiola tinga*.



17 (*14*) Penis and seminal vesicle well developed (Fig. 26); free-living ....
.... Genus *Hallangia*.

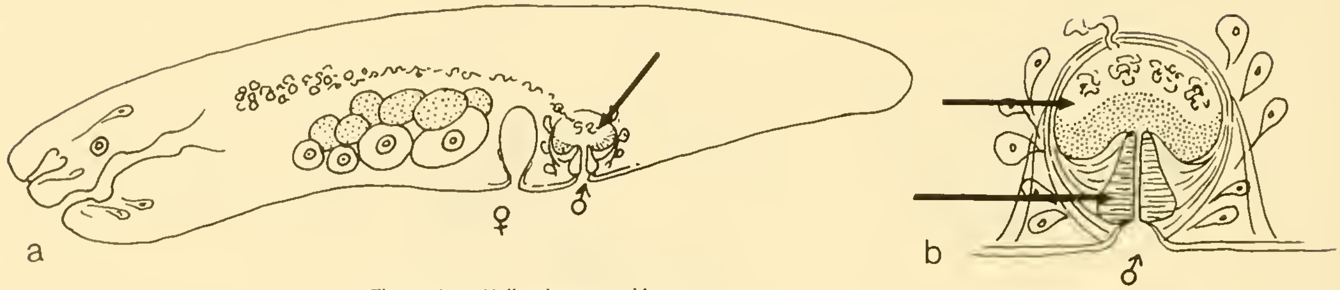


Figure 26.—*Hallangia proporoides*.

17 (*14*) Penis and seminal vesicle reduced (Fig. 27); parasitic; from the Caspian Sea ....
.... Genus *Aechmalotus*.

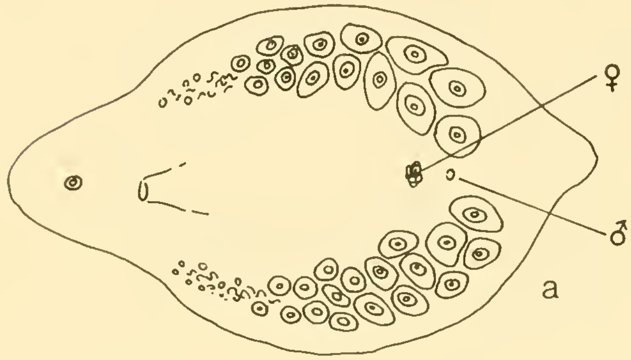


Figure 27.—*Aechmalotus pyrola*: a-dorsal view; b-cross section of copulatory organs.

18 (*13*) Mouth with archipharynx (Fig. 28)
. . . Family NADINIDAE (p. 61) ....
1 Genus *Nadina*.

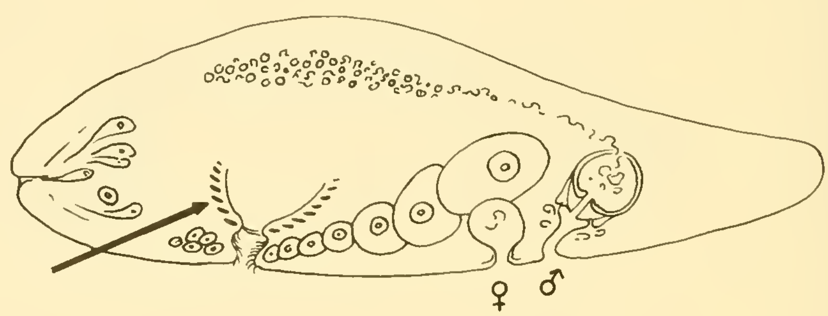


Figure 28.—*Nadina pulchella*.

18 (*13*) Mouth with pharynx simplex or without a pharynx 19

19 (*18*) Seminal bursa present, opening posterior to the male copulatory organ either through a common genital pore or through a separate female pore (Figs. 29, 30) ....
..... Family OTOCELIDIDAE (p. 61).................20

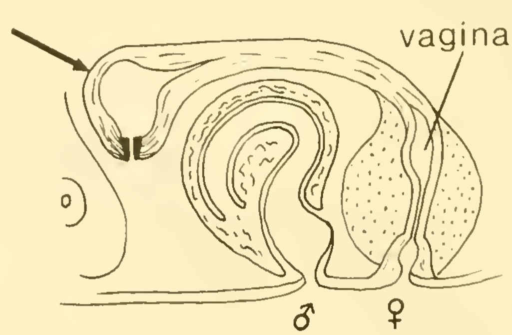


Figure 29.—*Otocelis westbladi*.

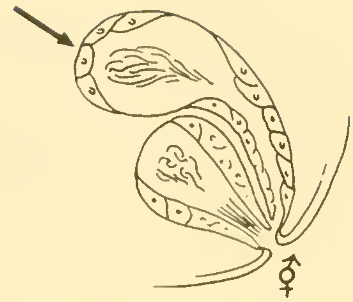


Figure 30.—*Archocelis macrorhabditis.*

19 (*18*) Seminal bursa present or absent but when present opening anterior to the male copulatory organ 25

20 (*19*) Bursal nozzles present[4] 21

20 (*19*) Bursal nozzles absent 23

21 (*20*) Testes paired and the two ovaries fused (Fig. 31a); penis muscular (Fig. 31b) .... Genus *Notocelis*.

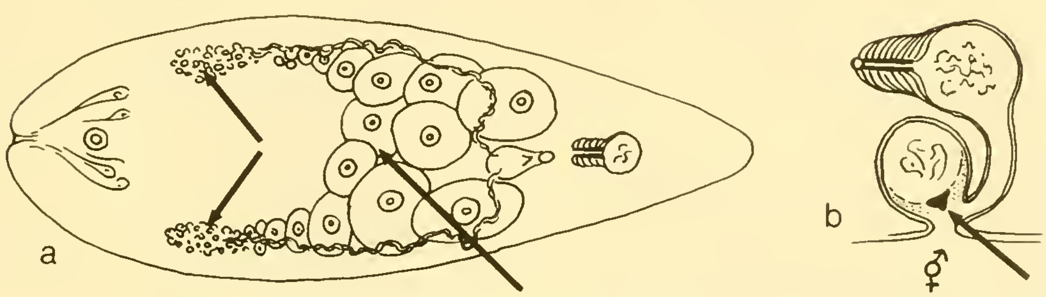


Figure 31.—*Notocelis gullmarensis*: a-dorsal view; b-sagittal reconstruction of male and female accessory organs.

21 (*20*) Testes and ovaries paired (Fig. 32a); penis muscular (Fig. 33b) or with cuticular needles (Fig. 32b) 22

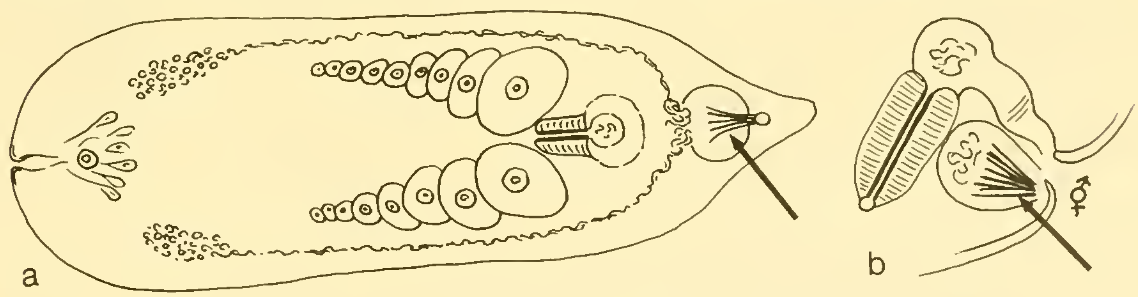


Figure 32.—*Philocelis cellata*: a-dorsal view; b-sagittal reconstruction of male and female accessory organs.

[4]Genus *Exocelis*, recently described from the Galapagos Islands, has many small nozzles, a feature which makes it easily distinguishable from the other genera of the Otocelididae. Also, the seminal bursa in this genus lies caudal to the male organ, a situation found in no other acoel.

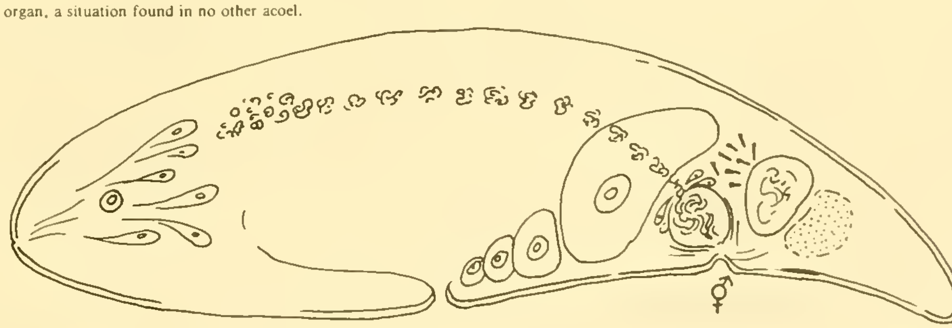


Figure 31c.—*Exocelis exopenis.*

22 (*21*) Penis with cuticular needles (Fig. 32) .... Genus *Philocelis*.

22 (*21*) Penis a muscular tube (Fig. 33) .... Genus *Otocelis*.

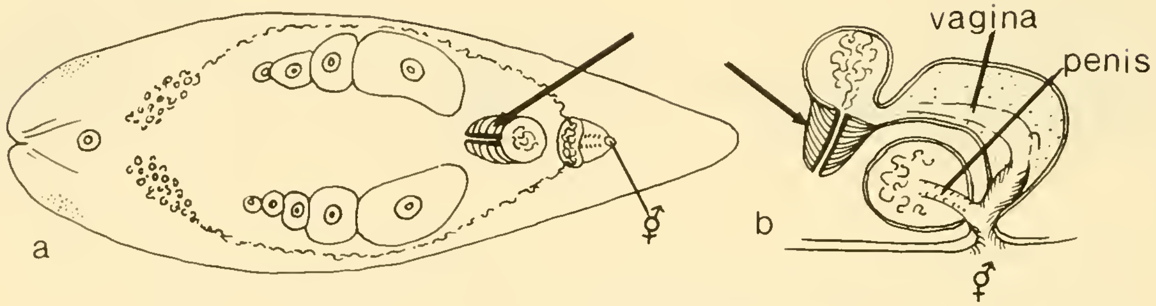


Figure 33.—*Otocelis rubropunctata*: a-dorsal view; b-sagittal reconstruction of male and female accessory organs.

23 (*20*) Ovary paired (Fig. 34a); two coiled spermatic ducts present (Fig. 34b). One species from Brazil .... Genus *Haplocelis*.

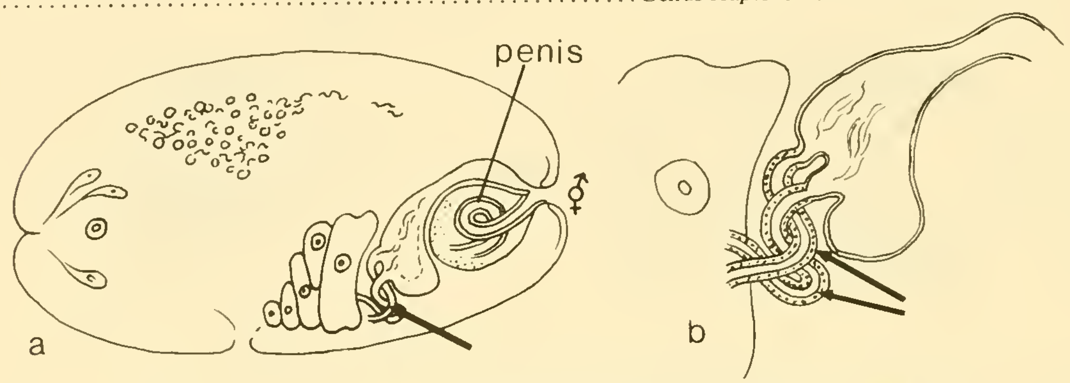


Figure 34.—*Haplocelis dichone*: a-sagittal reconstruction; b-sagittal reconstruction of seminal bursa.

23 (*20*) Ovary unpaired; spermatic duct lacking or very short 24

24 (*23*) Spermatic duct lacking; common genital pore terminal at posterior end (Fig. 35a, b) .... Genus *Archocelis*.
Genus *Parotocelis*.[5]

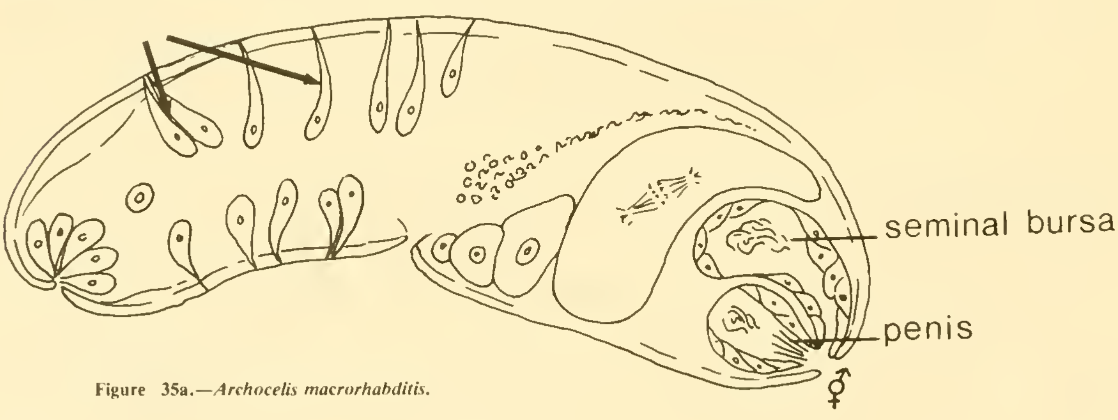
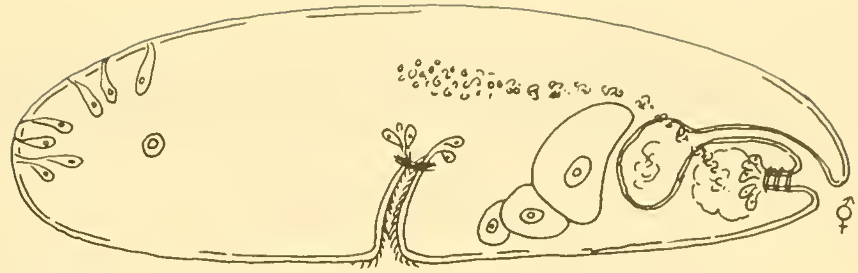


Figure 35a.—*Archocelis macrorhabditis*.

[5]Genus *Parotocelis*, recently described from the Galapagos Islands, is reported as being close to *Archocelis* and would fall here in the key. It differs from *Archocelis* in having a short ciliated male antrum and a muscular penis papilla surrounded by a crown of gland cells. In *Archocelis* a male antrum is lacking and the muscular wall of the seminal vesicle appears to serve as a penis.

Figure 35b.—*Parotocelis luteopunctata.*



24 (*23*) Spermatic duct very short; common genital pore ventral (Fig. 36) .... Genus *Haplotestis.*

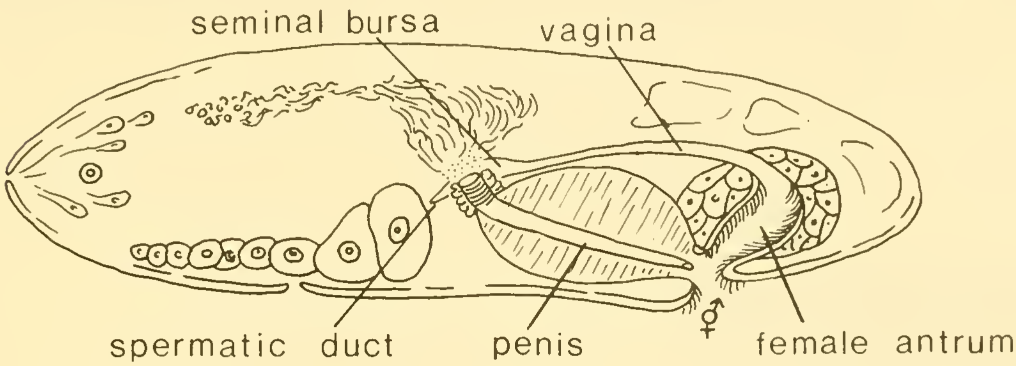


Figure 36.—*Haplotestis curvitubus.*

25 (*19*) Male antrum with adenodactyls bearing large needles and conspicuous rosettes of gland cells (Figs. 37, 38); one exception, see Genus *Paranaperus* .... Family ANAPERIDAE (p. 61) 26

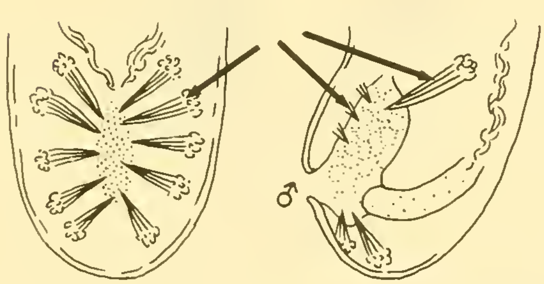


Figure 37.—*Anaperus tvaerminnensis*, dorsal and sagittal views of posterior end.

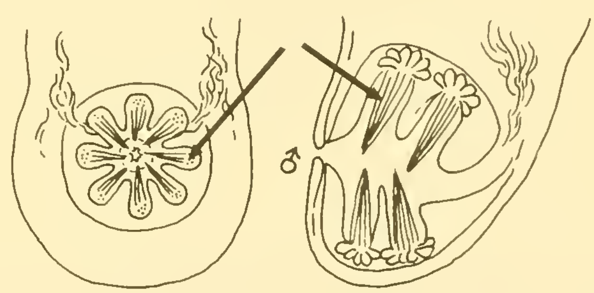
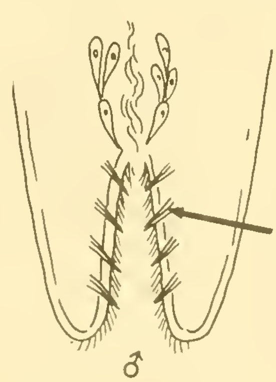


Figure 38.—*Achoerus pachycaudatus*, dorsal and sagittal views of posterior end.

25 (*19*) Male antrum without adenodactyls or with adenodactyls very small and gland cells very inconspicuous (Figs. 39, 40) 30

Figure 39.—*Kuma monogonophora*, dorsal view of posterior end.



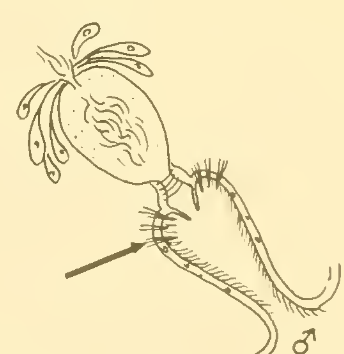


Figure 40.—*Haploposthia rubra.*

26 (*25*) Either colored rhabdites or epithelial pigment present 27

26 (*25*) Colored rhabdites and epithelial pigment lacking; adenodactyls very small. This genus is taxonomically connected to both Anaperidae and Haploposthiidae but is placed here in Anaperidae by Dörjes (1968a) (Fig. 41) .... Genus *Paranaperus*.

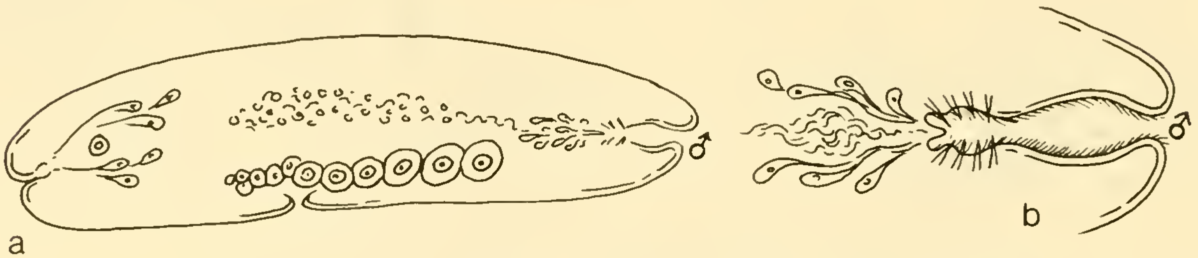


Figure 41.—*Paranaperus pellucidus*: a-sagittal reconstruction; b-dorsal view of posterior end.

27 (*26*) Seminal bursa and bursal nozzles lacking 28

27 (*26*) Either seminal bursa with a nozzle (Fig. 42) or nozzles without walled bursae (Fig. 43) present 29

Figure 42.—*Philachoerus johanni*.

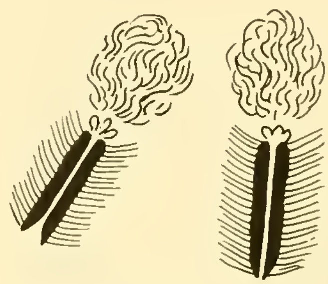


Figure 43.—*Anaperus tvaerminnensis*.

28 (*27*) Color provided by rhabdites (Fig. 44) ....
.... Genus *Achoerus*.

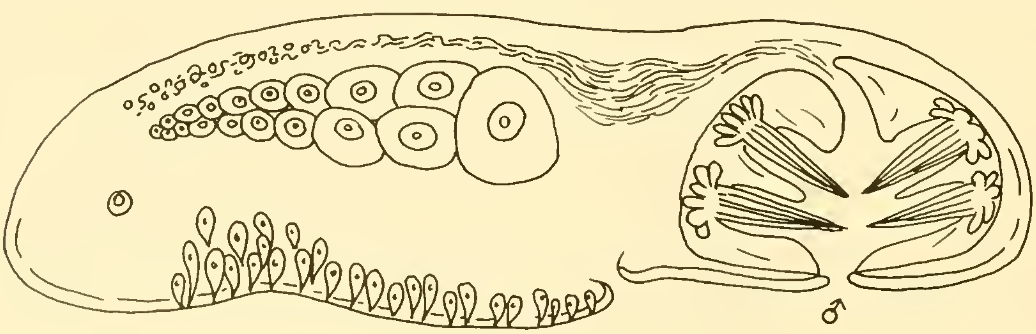


Figure 44.—*Achoerus pachycaudatus*.

28 (*27*) Color provided by epithelial pigment granules (Fig. 45). Single species from Brazil ....
.... Genus *Pseudanaperus*.

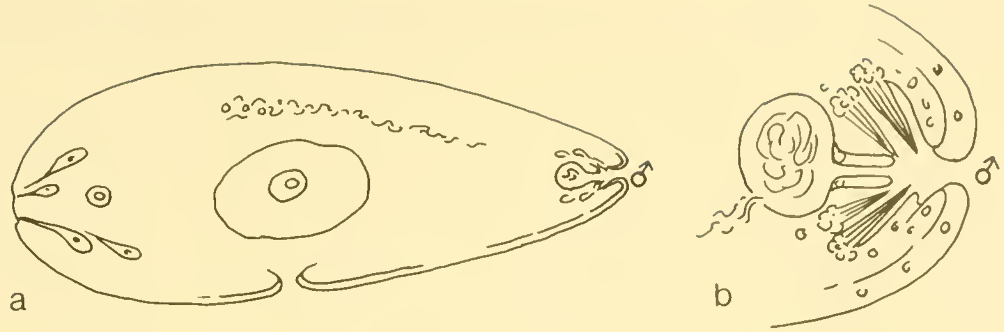


Figure 45.—*Pseudanaperus tinctus:* a-sagittal section; b-dorsal view of male accessory organs.

29 (*27*) One to many bursal nozzles present but walled seminal bursae absent (Fig. 46) .... Genus *Anaperus.*

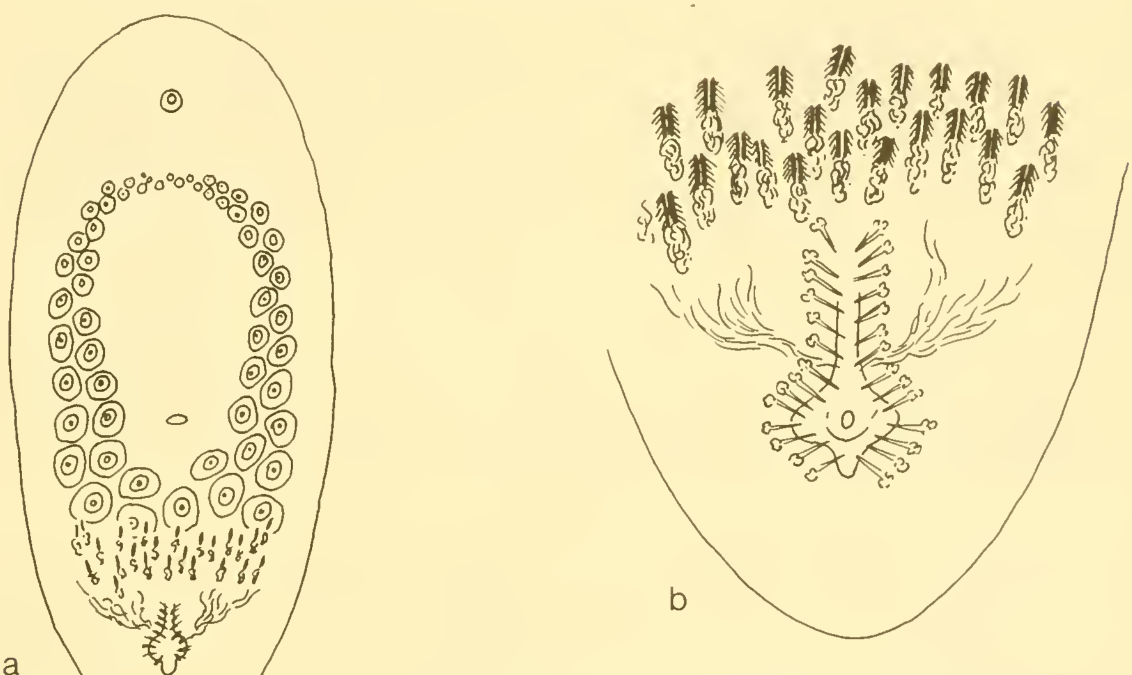


Figure 46.—*Anaperus gardineri*: a-dorsal view; b-dorsal view of male accessory organs and bursal structures.

29 (*27*) A well-developed seminal bursa with a cuticular nozzle (Fig. 47) .... Genus *Philachoerus.*

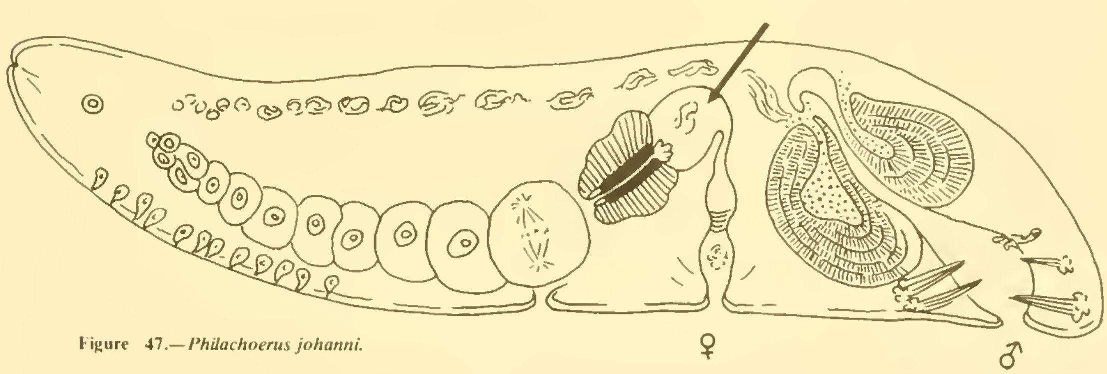


Figure 47.—*Philachoerus johanni.*

30 (*25*) Male organ simple; penis either lacking (Figs. 48, 49) or very weakly developed (Fig. 50) or its place taken by a ciliated male antrum invaginated into a sheath or sac (Fig. 51) 31

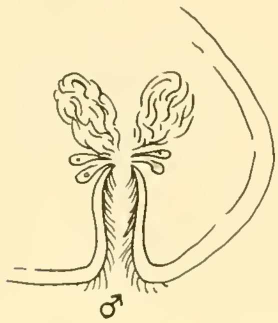


Figure 48.—*Parahaploposthia avesicula.*

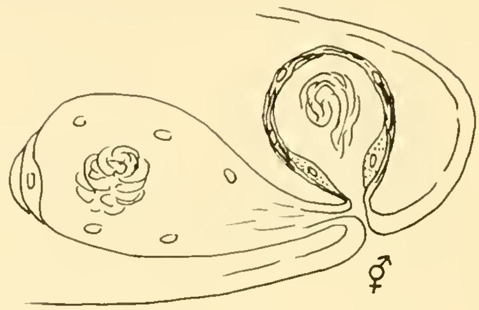


Figure 49.—*Haplogonaria simplex.*

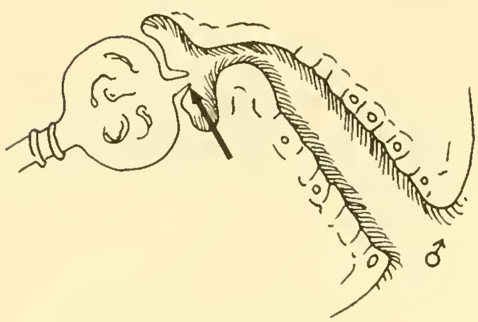


Figure 50.—*Haploposthia rubra.*

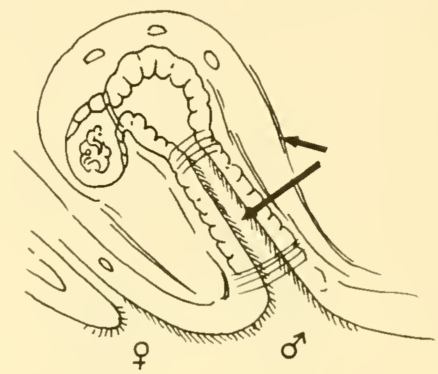


Figure 51.—*Convoluella brunea.*

30 (*25*) Male organ well developed; either a glandular cellular penial area associated with the seminal vesicle (Fig. 52) or a tube-shaped penis (Fig. 53) or a cuticularized penis stylet (Fig. 54) 46

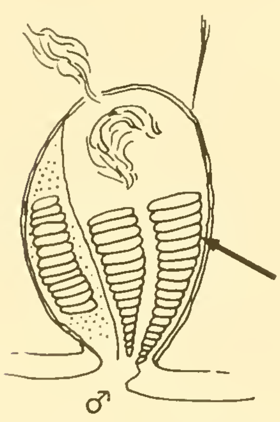


Figure 52.—*Pseudmecynostomum granulum.*

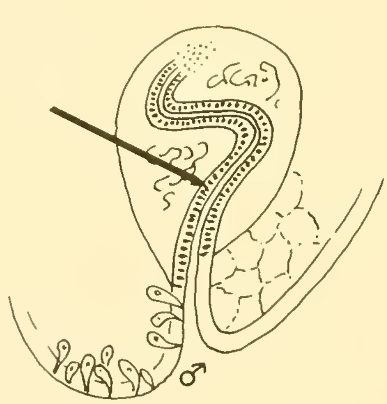


Figure 53.—*Archaphanostoma macrospiriferum.*

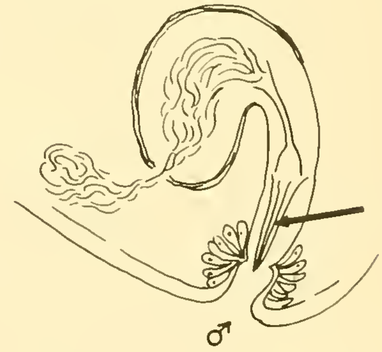


Figure 54.—*Actinoposthia haplovata.*

31 (*30*) Male organ simple; penis lacking or very weakly developed 32

31 (*30*) Male organ consists of a ciliated male antrum which is inserted at its proximal end into a sheath or sac in such a way that it opens directly from an unciliated granular vesicle with either a true or false seminal vesicle present (Fig. 55) ....
..........Family ANTROPOSTHIIDAE (p. 64) 43

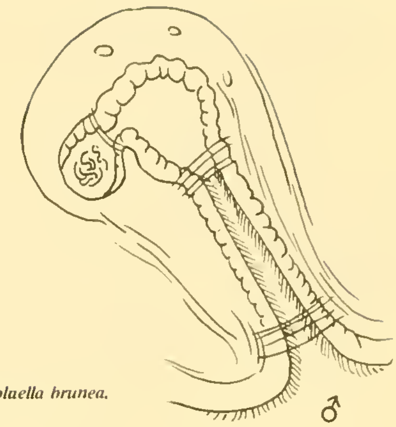


Figure 55.—*Convolaella brunea.*

32 (*31*) Male organ with a very small penis. Two species, *Haploposthia rubra* (Fig. 50) and *Haploposthia* (= *Kuma*?) *albiventer* (Fig. 86) with other characters which have placed them in the Family Haploposthiidae have very small penes. *Paranaperus pellucidus* (Fig. 41) with a very small penis and small adenodactyls appears to be taxonomically intermediate between the Family Anaperidae and the Family Haploposthiidae.

32 (*31*) Penis lacking (Figs. 56, 57, 58); often with a tube-shaped male antrum which is not inserted into a sheath or sac (Figs. 57, 58) .... Family HAPLOPOSTHIIDAE (p. 60) 33

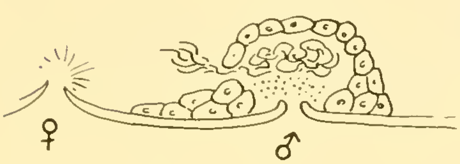


Figure 56.—*Pseudohaplogonaria vacua.*

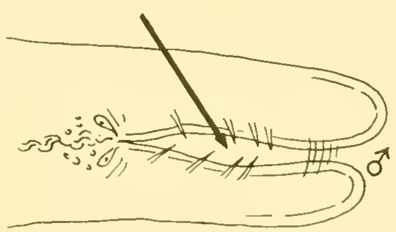


Figure 57.—*Kuma monogonophora*, dorsal view of posterior end.

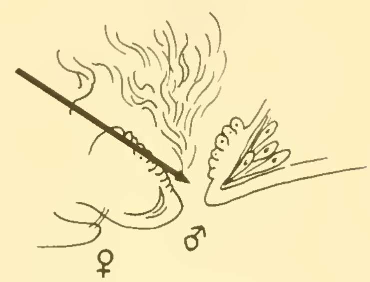


Figure 58.—*Parahaplogonaria maxima.*

33 (*32*) Seminal bursa present either with a distinct wall (Fig. 59) or as a more or less well-defined vacuolated or syncytial space in the parenchyma (Fig. 60) 34

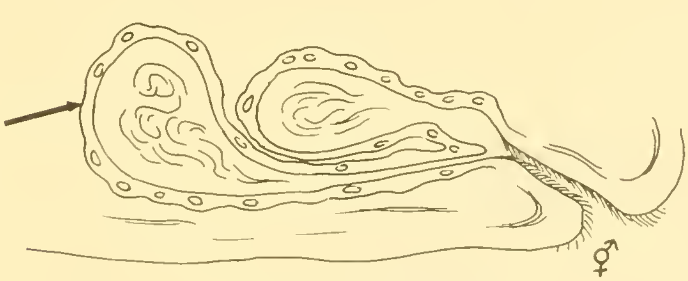


Figure 59.—*Haplogonaria elegans.*

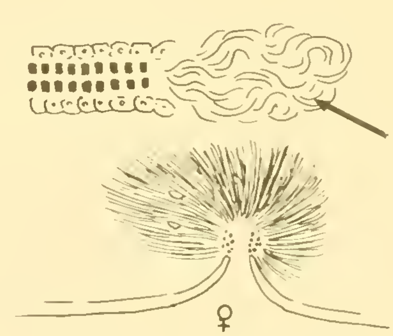


Figure 60.—*Pseudohaplogonaria vacua.*

33 (*32*) Seminal bursa lacking 38

34 (*33*) Either no cuticular nozzle on the seminal bursa (Fig. 61), or an attached (Fig. 62), or an invaginated (Fig. 63) muscular spermatic duct may be present instead 35

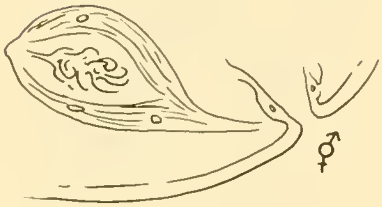


Figure 61.—*Haplogonaria glandulifera.*

Figure 62.—*Pseudokuma orphinum.*

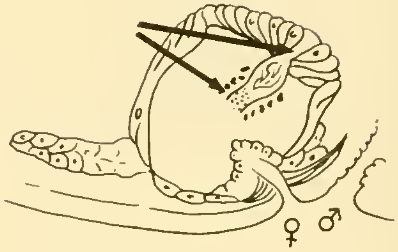


Figure 63.—*Parahaplogonaria maxima.*

34 (*33*) A cuticular nozzle present either on a seminal bursa (Fig. 64), or near the vacuolated space serving as a bursa (Fig. 65) 37

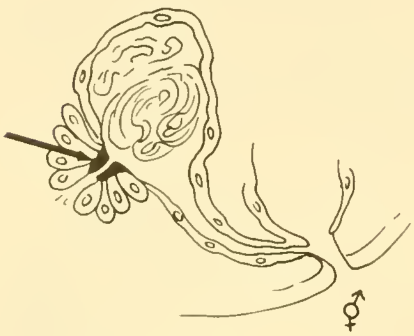


Figure 64.—*Deuterogonaria thauma.*

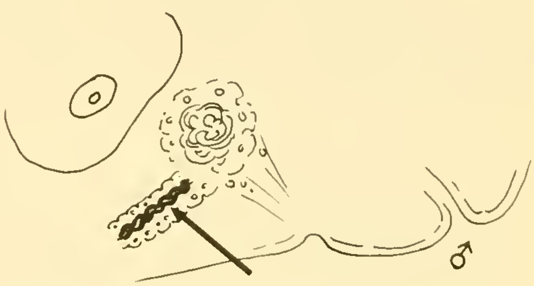


Figure 65.—*Pseudohaplogonaria stylifera.*

35 (*34*) Seminal bursa without a nozzle and without a spermatic duct (Figs. 66, 67, 68). See also Figures 59, 61 .... Genus *Haplogonaria.*

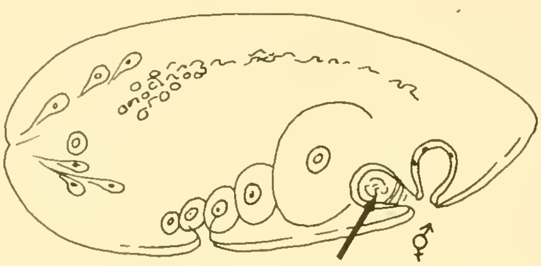


Figure 66.—*Haplogonaria minima.*

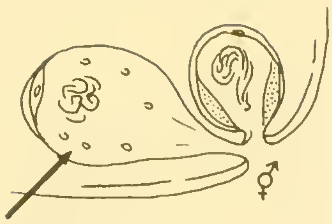


Figure 67.—*Haplogonaria simplex.*

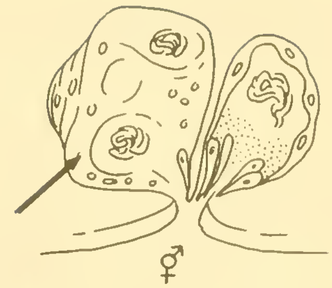


Figure 68.—*Haplogonaria macrobursalia.*

35 (*34*) Seminal bursa without a nozzle but with either an invaginated or an attached muscular spermatic duct 36

36 (*35*) Muscular spermatic duct invaginated into the seminal bursa; false seminal vesicle present close to male pore (Fig. 69) . . . . Genus *Parahaplogonaria*.

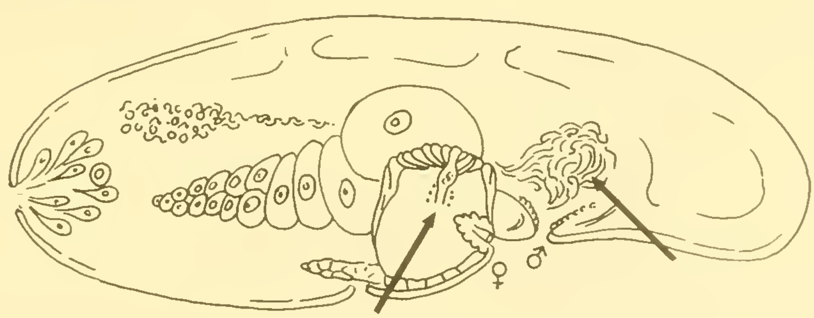


Figure 69.—*Parahaplogonaria maxima.*

36 (*35*) Muscular spermatic duct not invaginated; true seminal vesicle present. One species from Brazil (Fig. 70) . . . . Genus *Pseudokuma*.

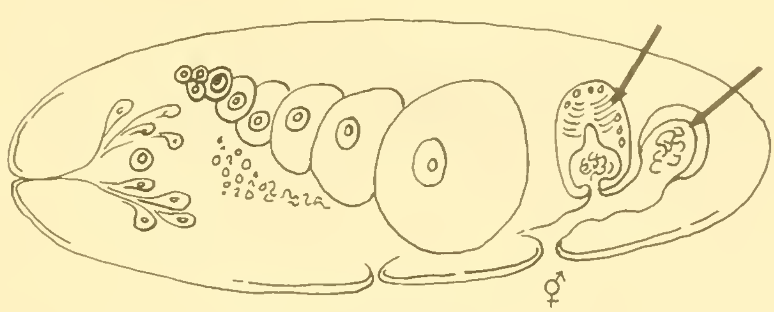


Figure 70.—*Pseudokuma orphinum.*

37 (*34*) Seminal vesicle with a separate glandular area present on one side; seminal bursa well developed with a strongly cuticularized nozzle (Fig. 71). One species from Brazil .... Genus *Deuterogonaria*.

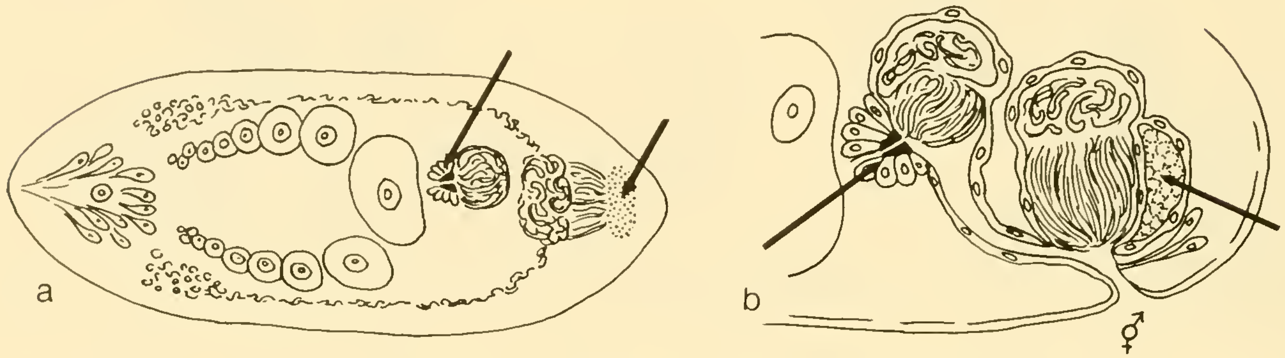


Figure 71.—*Deuterogonaria thauma*: a-dorsal view; b-sagittal reconstruction of male and female accessory organs.

37 (*34*) Seminal vesicle lacking or only weakly developed; seminal bursa weakly developed or lacking but a weakly cuticularized nozzle always present (Figs. 72, 73) .... Genus *Pseudohaplogonaria*.

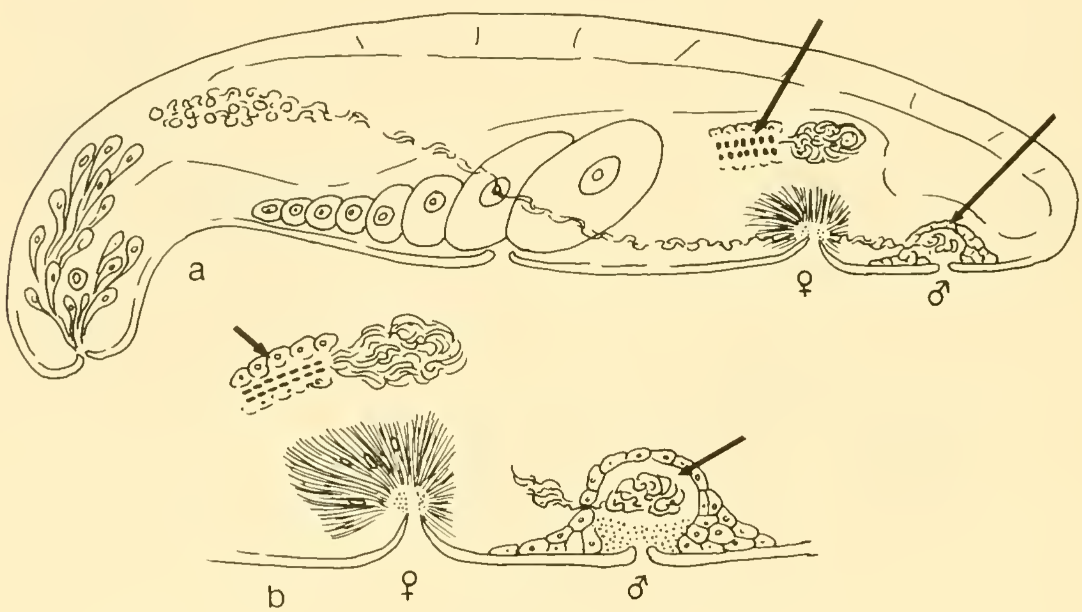


Figure 72.—*Pseudohaplogonaria vacua*.

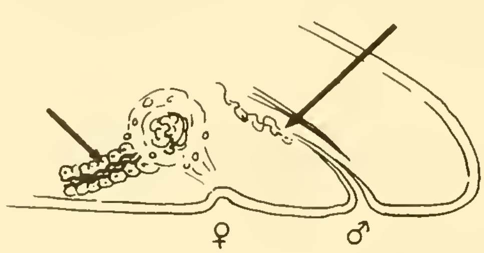


Figure 73.—*Pseudohaplogonaria stylifera*.

38 (*33*) Male antrum, penis, and seminal vesicle all lacking; a false seminal vesicle present at the posterior end of the body (Fig. 74) .... Genus *Simplicomorpha.*

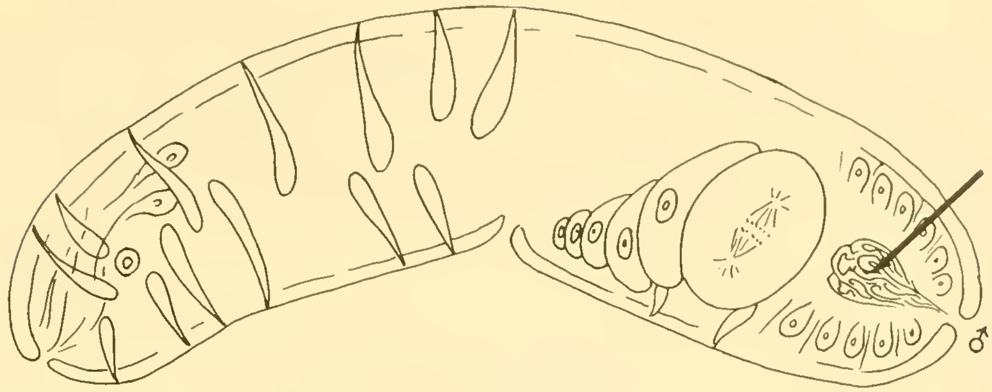


Figure 74.—*Simplicomorpha gigantorhabditis.*

38 (*33*) Male antrum present (Figs. 75, 76) 39

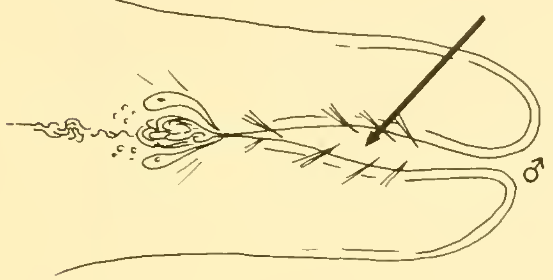


Figure 75.—*Kuma monogonophora*, dorsal view of posterior end.

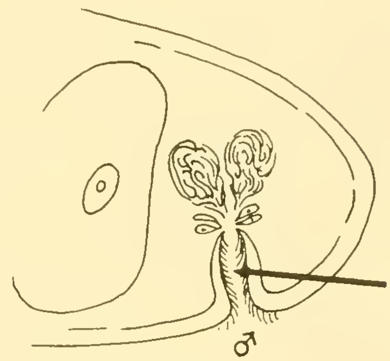


Figure 76.—*Parahaploposthia avesicula*, sagittal section of posterior end.

39 (*38*) Semiglobular caudal organ present, consisting of a ciliated inpocketing of the terminal end of the body which is surrounded by and into which open gland cells containing pear-shaped droplets of secretion (Fig. 77)...... .... Genus *Adenocauda.*

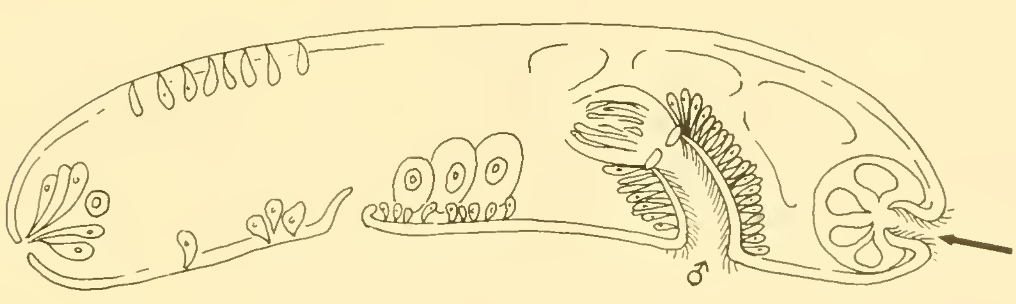


Figure 77.—*Adenocauda helgolandica.*

39 (*38*) Caudal organ lacking 40

40 (*39*) Frontal organ lacking (Figs. 78, 79) ....
.... Genus *Afronta*.

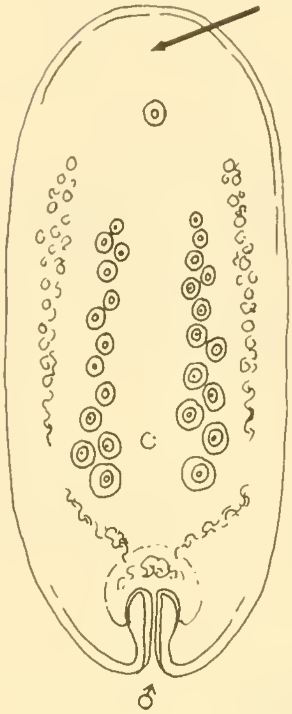


Figure 78.—*Afronta aurantiaca*, dorsal view.

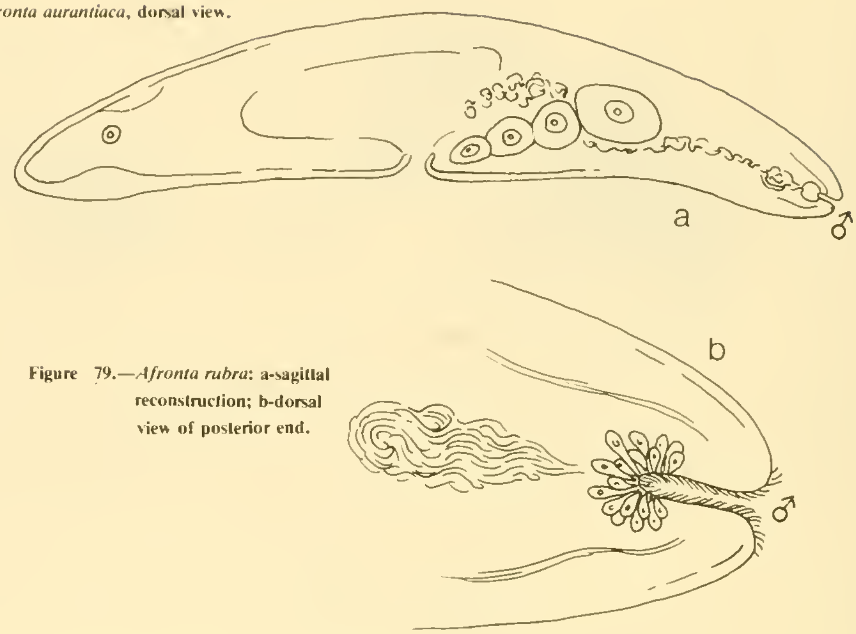


Figure 79.—*Afronta rubra*: a-sagittal reconstruction; b-dorsal view of posterior end.

40 (*39*) Frontal gland present 41

41 (*40*) A pair of false seminal vesicles present (Figs. 80, 81) ....
.... Genus *Parahaploposthia*.

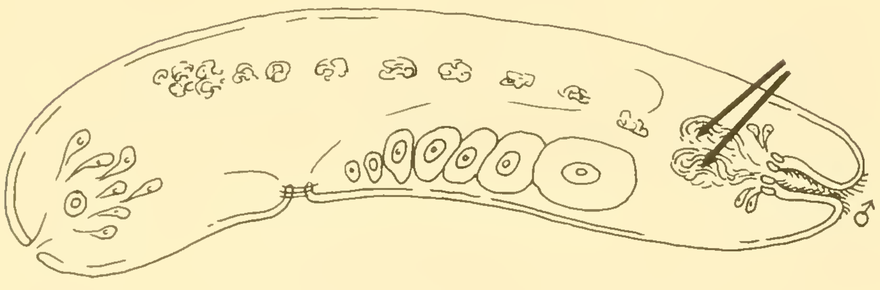
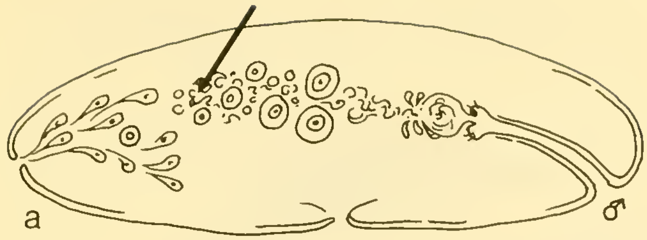


Figure 80.—*Parahaploposthia cerebroepitheliata*.

Figure 81.—*Parahaploposthia avesicula*.

41 (*40*) Either a true seminal vesicle or a single false seminal vesicle present 42

42 (*41*) Colored by rhabdites or stored body pigment; common germinal center for eggs and sperm (Figs. 82, 83) ....
.... Genus *Haploposthia*.



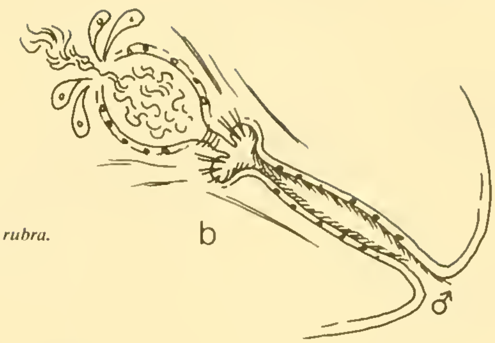


Figure 82.—*Haploposthia rubra.*

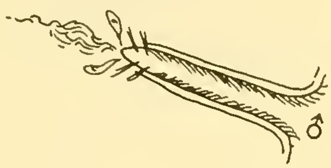


Figure 83.—*Haploposthia rubropunctata.*

42 (*41*) Colorless; separate germinal center for eggs and sperm (Figs. 84, 85, 86) ....
.... Genus *Kuma.*

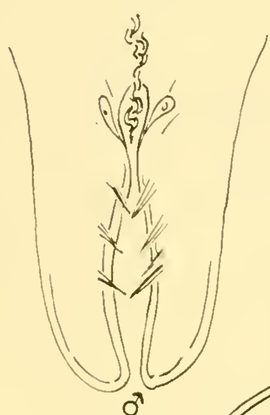


Figure 84.—*Kuma monogonophora,* dorsal view of posterior end.

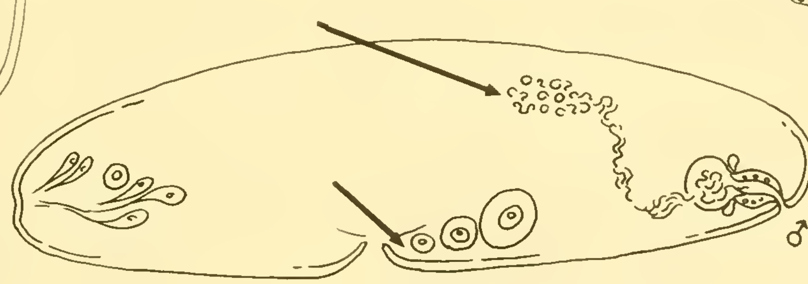
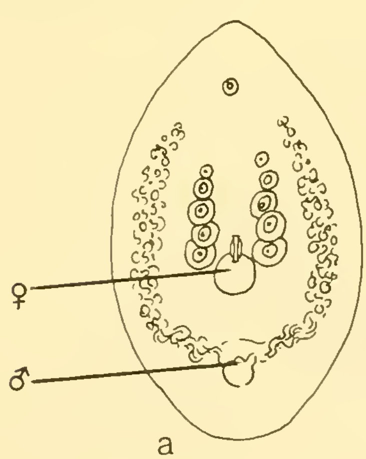


Figure 85.—*Kuma brevicauda.*

Figure 86.—*Kuma albiventer.*

43 (*31*) Prostatoid organ present at male pore; seminal bursa with a cuticularized nozzle (Fig. 87) ....
.... Genus *Adenopea.*



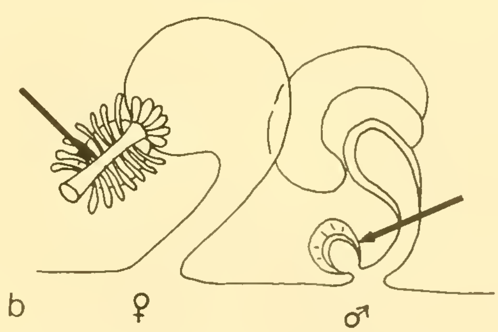


Figure 87.—*Adenopea illardatus*: a-dorsal view; b-sagittal reconstruction of accessory organs.

43 (*31*) Prostatoid organ absent; seminal bursa either lacking or, if present, without a cuticularized nozzle 44

44 (*43*) Seminal bursa lacking (Fig. 88) ....
....Genus *Unantra*.

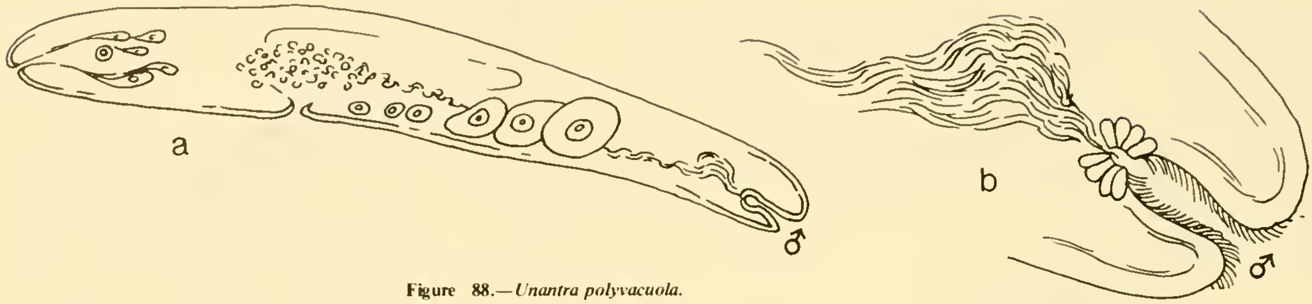


Figure 88.—*Unantra polyvacuola.*

44 (*43*) Seminal bursa present 45

45 (*44*) Seminal bursa with a cellular nozzle (Fig. 89) ....
....Genus *Antroposthia*.

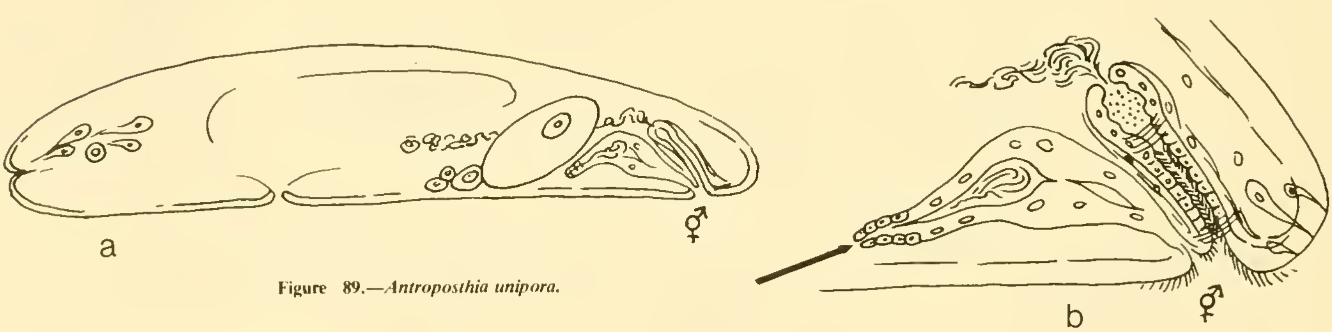


Figure 89.—*Antroposthia unipora.*

45 (*44*) Seminal bursa with a small cap of cells, rather than a nozzle (Fig. 90) ....
....Genus *Convoluella*.

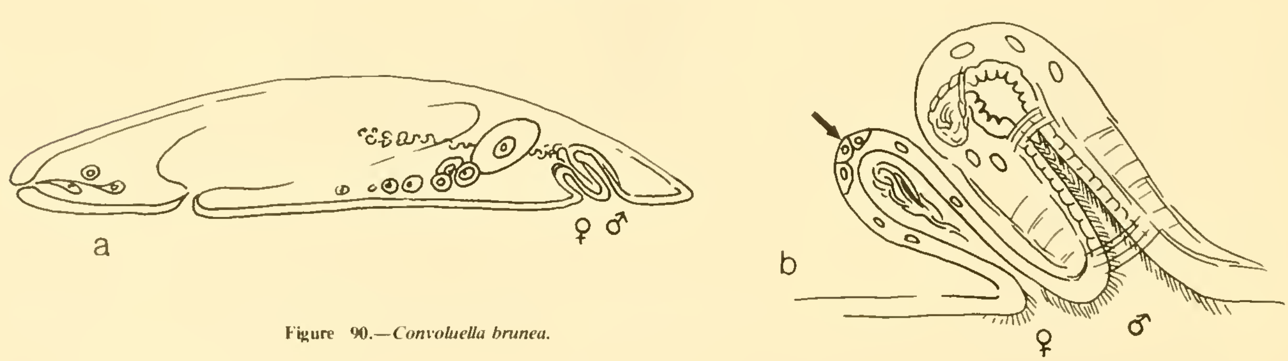


Figure 90.—*Convoluella brunea.*

46 (*30*) Copulatory organ a globular structure inside of which is a proximal seminal vesicle and a distal glandular region which serves as a penis (Figs. 91, 92) .... Family MECYNOSTOMIDAE (p. 63) 47

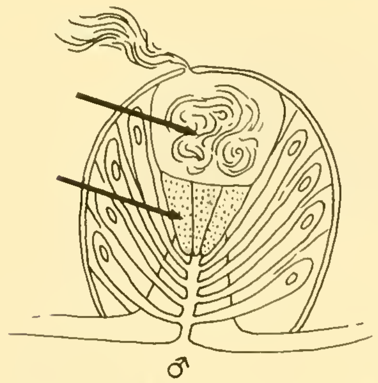


Figure 91.—*Mecynostomum haplovarium*, sagittal section.

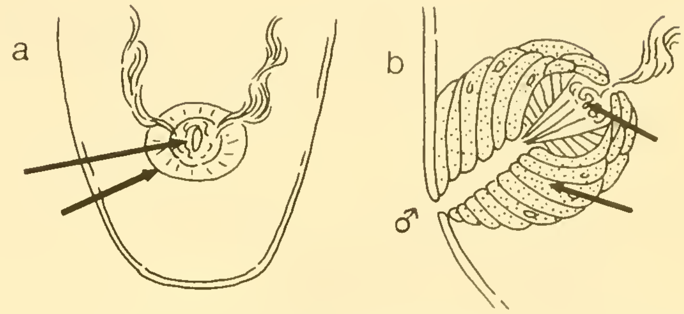


Figure 92.—*Pseudmecynostomum pelophilum*: a-dorsal view of posterior end; b-sagittal section of copulatory organ.

46 (*30*) Copulatory organ either a conical penis made up of cellular, muscular, or cuticular parts (Fig. 93), or a tube-shaped penis formed by an invagination of the body wall (Fig. 94) 52

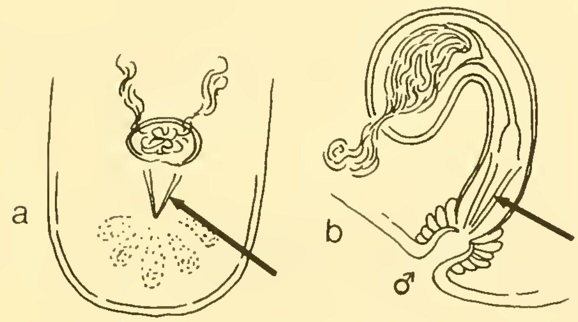


Figure 93.—*Actinoposthia haplovata*: a-dorsal view of posterior end; b-sagittal section of copulatory organ.

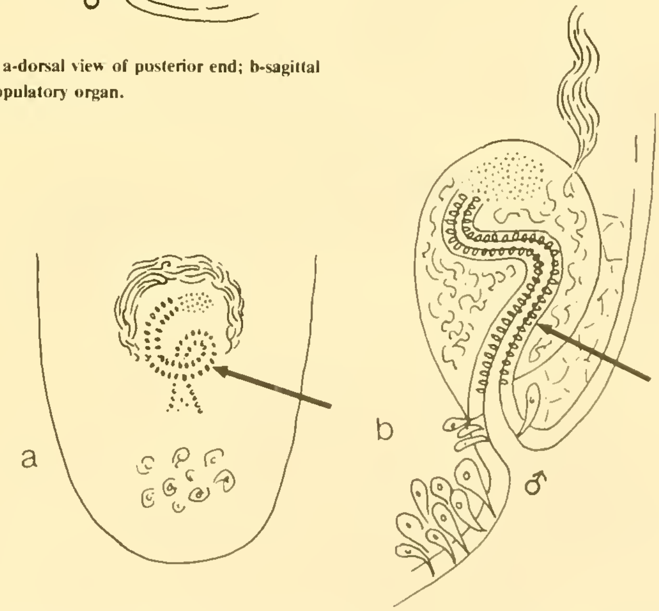


Figure 94.—*Archaphanostoma macrospiriferum*: a-dorsal view of posterior end; b-sagittal section of copulatory organ.

47 (*46*) Seminal bursa lacking (Figs. 95, 96) .... Genus *Mecynostomum.*

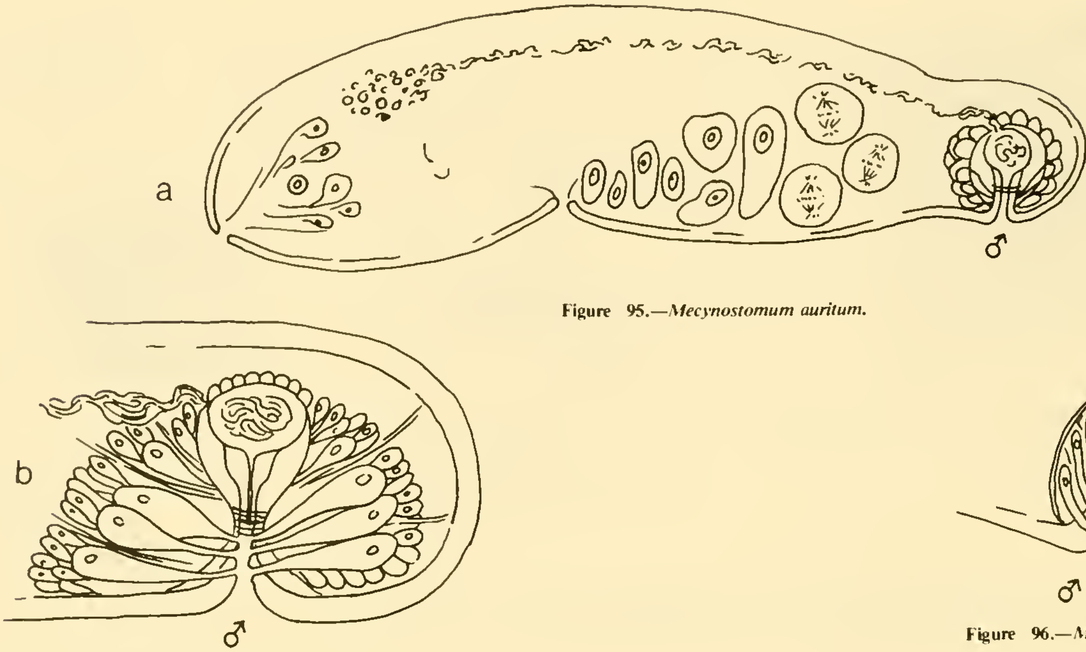


Figure 95.—*Mecynostomum auritum.*

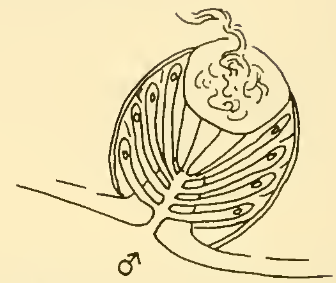


Figure 96.—*Mecynostomum haplovarium.*

47 (*46*) Seminal bursa present 48

48 (*47*) Seminal bursa lacking an appendage (Fig. 97); in *Pseudmecynostomum maritimum* the bursal wall develops a protrusion over the ripe eggs (Fig. 98)......................... Genus *Pseudmecynostomum.*

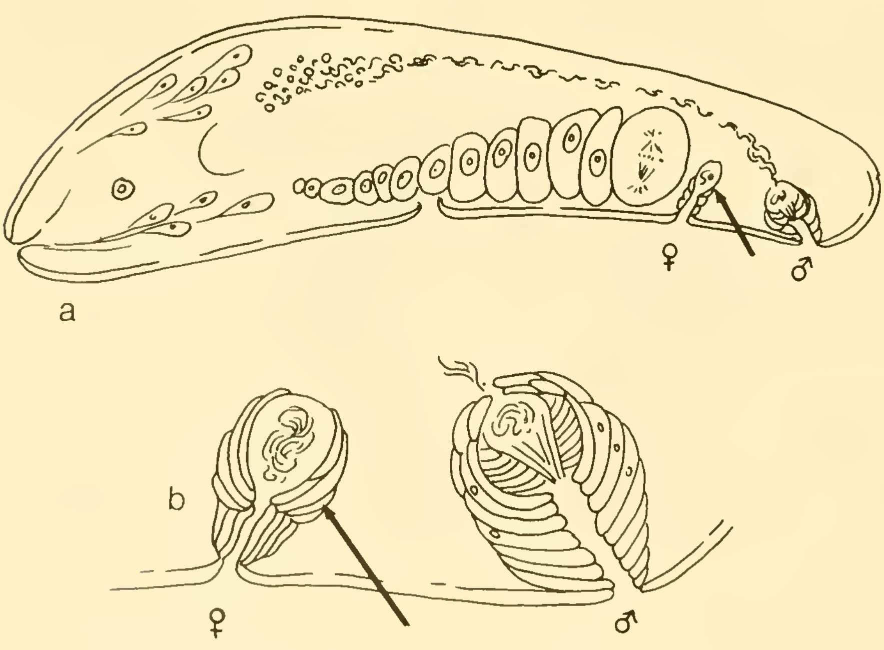


Figure 97.—*Pseudmecynostomum pelophilum.*

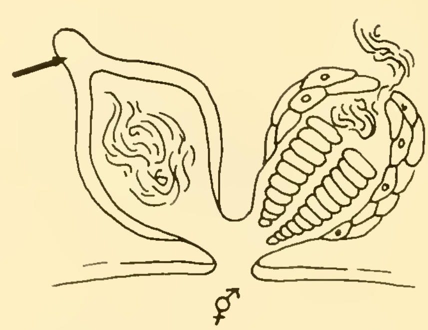


Figure 98.—*Pseudmecynostomum maritimum.*

48 (*47*) Seminal bursa with a cellular (Fig. 99), muscular (Fig. 100), or cuticular (Fig. 101) appendage 49

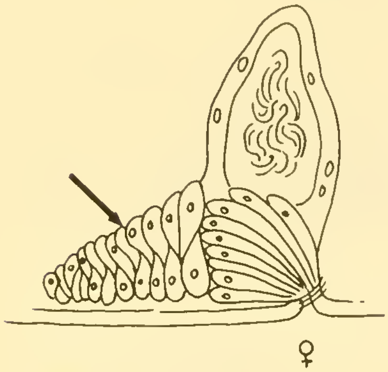


Figure 99.—*Postmecynostomum pictum.*

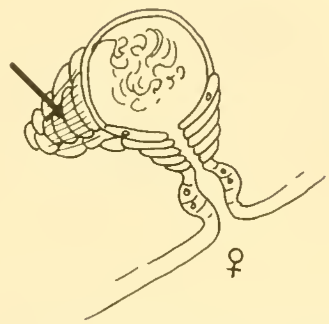


Figure 100.—*Paramecynostomum diversicolor.*

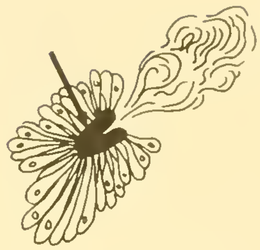


Figure 101.—*Paedomecynostomum bruneum.*

49 (*48*) Appendage cuticular 50

49 (*48*) Appendage cellular or muscular 51

50 (*49*) Seminal bursa weakly developed without a well-defined wall but with spermatic duct strongly cuticularized to form a conspicuous nozzle (Fig. 102) .... Genus *Paedomecynostomum*.

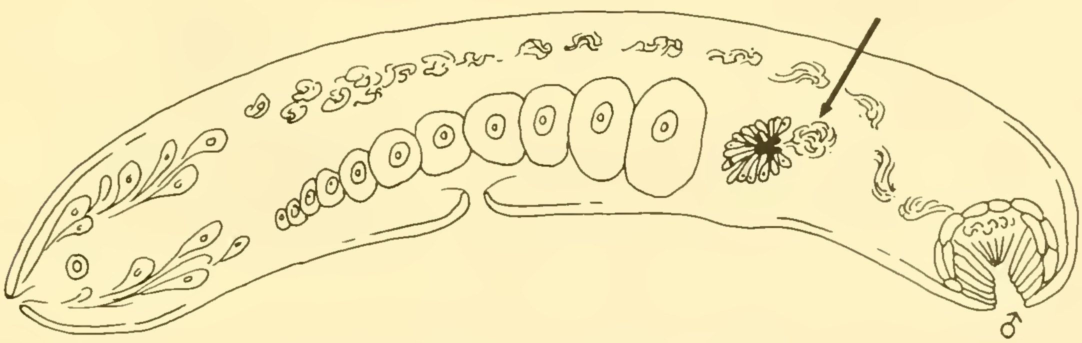


Figure 102.—*Paedomecynostomum bruneum.*

50 (*49*) Seminal bursa well developed with an appendage formed of matrix cells whose inner ends are weakly cuticularized to form a weak nozzle (Fig. 103)................. Genus *Philomecynostomum*.

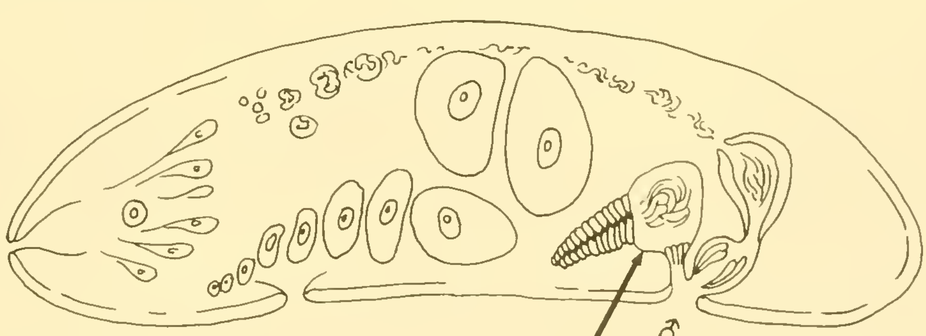
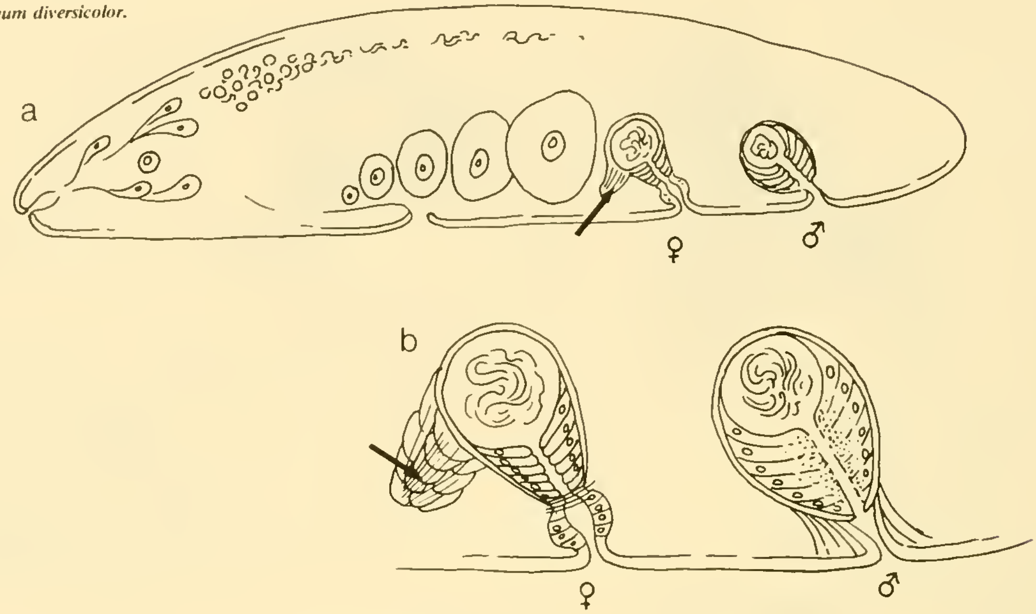


Figure 103.—*Philomecynostomum lapillum.*

51 (*49*) Appendage of bursa muscular; rhabdites present; variegated coloring from dissolved pigment and yellow to brown granules (Fig. 104) .... Genus *Paramecynostomum*.

Figure 104.—*Paramecynostomum diversicolor.*



51 (*49*) Appendage of bursa cellular; rhabdites absent; no dissolved or granular pigment (Fig. 105) .... Genus *Postmecynostomum*.
Genus *Limnoposthia*.[6]

Figure 105a.—*Postmecynostomum pictum.*

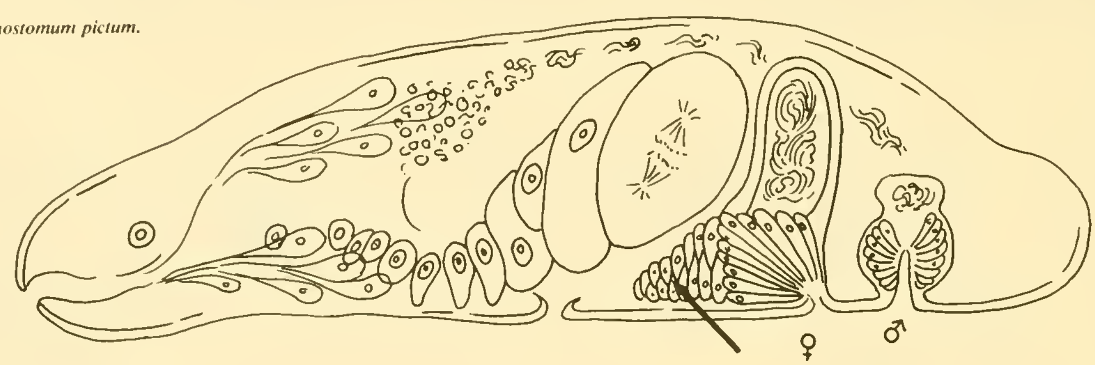
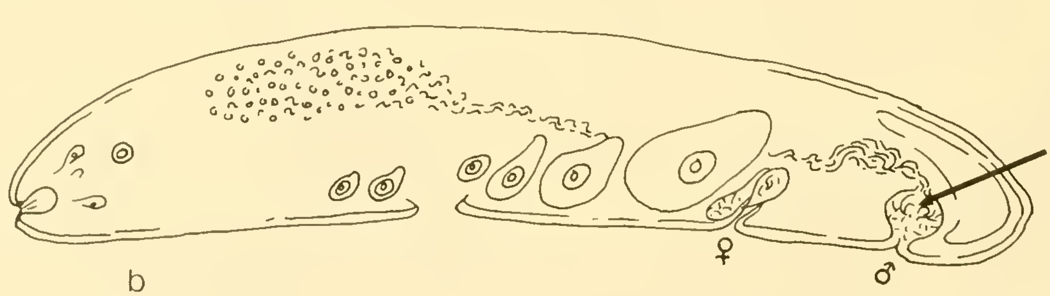


Figure 105b.—*Limnoposthia polonica*. **(See next page and text footnote 6.)**



[6]The genus *Limnoposthia* (Kolasa and Faubel 1974) was placed tentatively by the authors close to *Convoluta*, but it seems to me the illustrations and descriptions of the penial structures would lead a user of this key to a position close to *Postmecynostromum*. The structure of the penis in the illustration of *Limnoposthia polonica* suggests the glandular penis of *Postmecynostomum* and the part labeled "vas deferens" may correspond to the enclosed seminal vesicle of the Mecynostomidae. Study of actual specimens is needed to clear up this point. From freshwater lake in Poland.

Figure 105c,d.—*Limnoposthia polonica.*

52 (*46*) Copulatory organ with a cone-shaped penis built up of cuticular (Fig. 106), or muscular (Fig. 107 elements and never invaginated into a seminal vesicle .... Family CHILDIIDAE (p. 62) 53

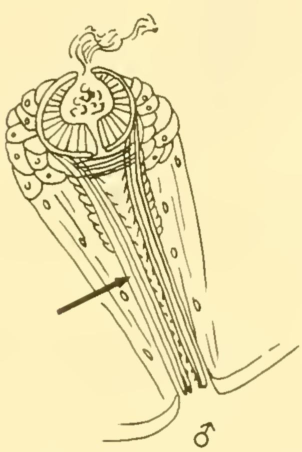


Figure 106.—*Paraphanostoma macroposthium.*

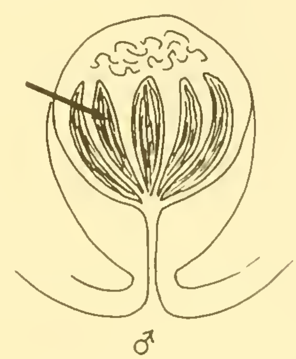


Figure 107.—*Paraproporus diovatus.*

52 (*46*) Copulatory organ with a tube-shaped, muscular and often glandular penis. This may be simply a direct invagination of the body wall without a male antrum or true seminal vesicle (Fig. 108), or it may be combined with either one or both of a male antrum or a seminal vesicle. It is often invaginated into or surrounded by the seminal vesicle (Fig. 109) or a penis sac (Fig. 110) .... Family CONVOLUTIDAE (p. 58) 63

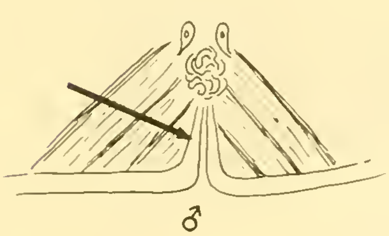


Figure 108.—*Proconvoluta primitiva.*

Figure 109.—*Pseudaphanostoma psammophilum.*

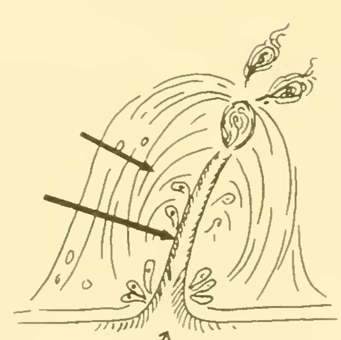


Figure 110.—*Haplodiscus bocki.*

53 (*52*) Seminal bursa lacking; a syncytial area in the parenchyma, which serves as a bursa, may be present 54

53 (*52*) Seminal bursa present 58

54 (*53*) Two copulatory organs present (Fig. 111) . . . . Genus *Childia.*

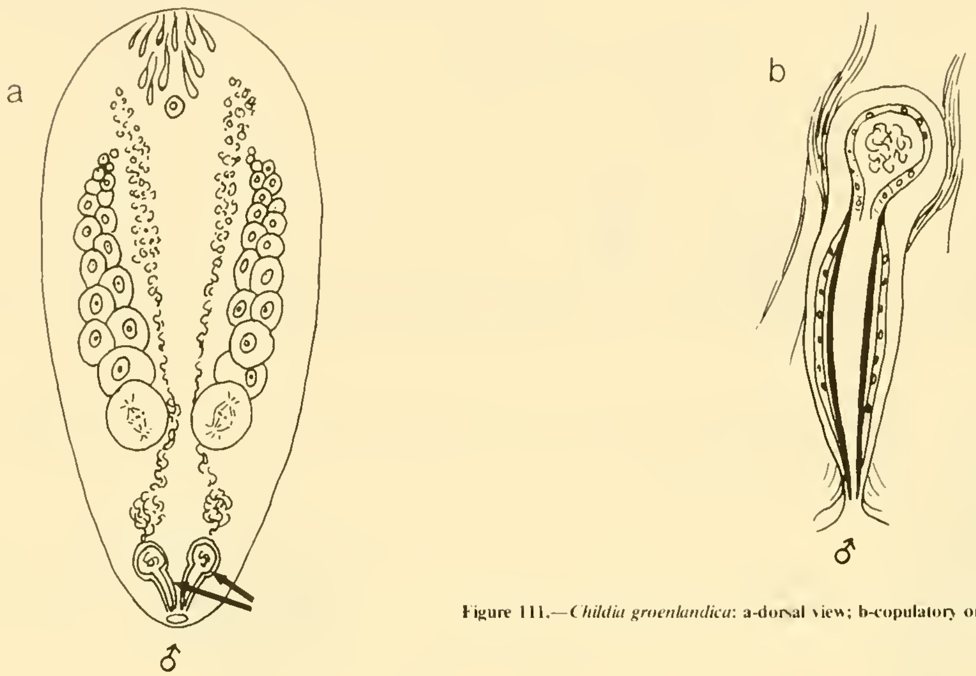


Figure 111.—*Childia groenlandica*: a-dorsal view; b-copulatory organ.

54 (*53*) A single copulatory organ 55

55 (*54*) A rosette of muscles, fine cuticular needles or glands at the distal end of the seminal vesicle appears like a penis but may serve as a stimulatory organ (Figs. 112, 113) . . . . Genus *Paraproporus.*

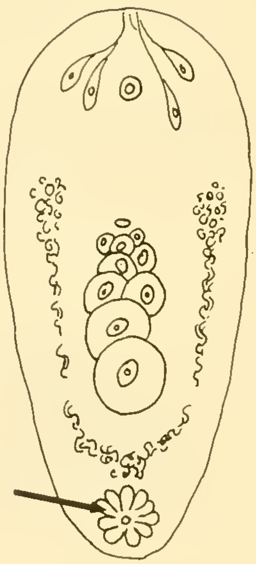


Figure 112.—*Paraproporus rubescens.*

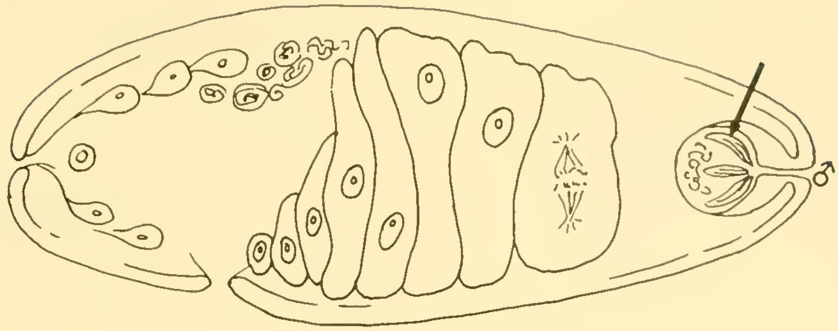


Figure 113.—*Paraproporus diovatus.*

55 (*54*) Copulatory organ not a rosettelike arrangement; penis with strongly cuticularized needles (Fig. 114), muscle layers in its wall (Fig. 115), or a cuticularized papilla surrounded by matrix cells (Fig. 116) 56

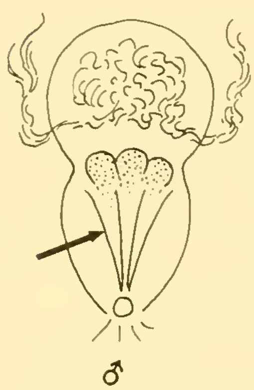


Figure 114.—*Actinoposthia longa.*

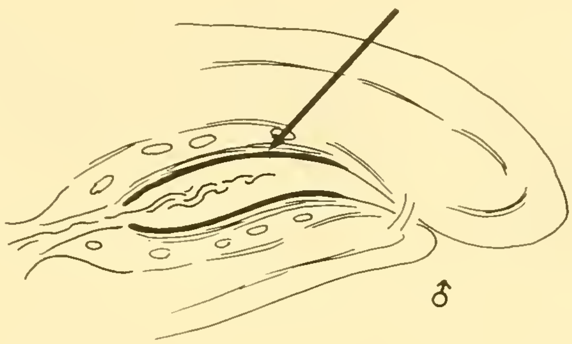


Figure 115.—*Actinoposthia pigmentea.*

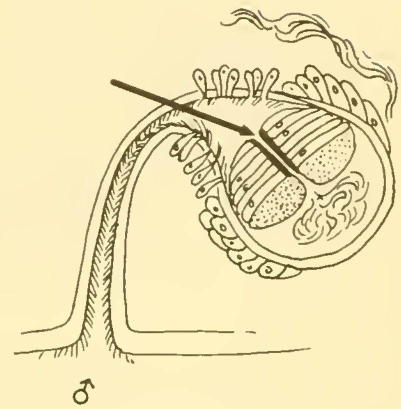


Figure 116.—*Atriofronta polyvacuola.*

56 (*55*) Male antrum long, tube-shaped and ciliated; penis a thin cuticularized tube clothed in matrix cells (Fig. 117) . . . . Genus *Atriofronta.*

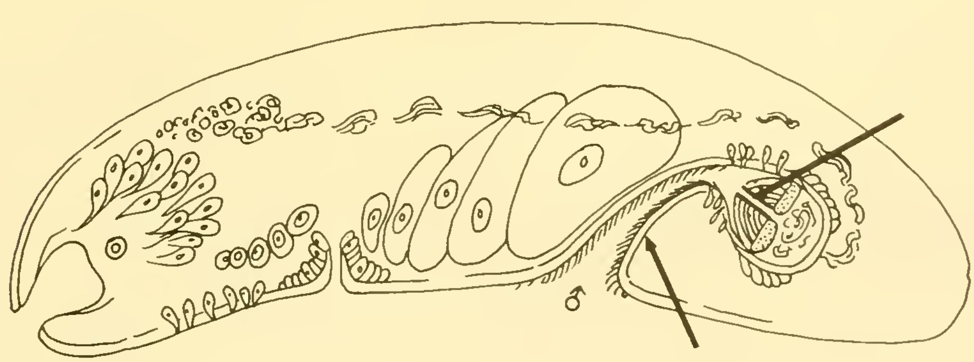


Figure 117.—*Atriofronta polyvacuola.*

56 (*55*) Male antrum short; penis with cuticularized stylet needles or muscle layers in its wall 57

57 (*56*) Seminal vesicle present; large cyanophile gland cells absent (Figs. 118, 119, 120, 121) .... Genus *Actinoposthia*.

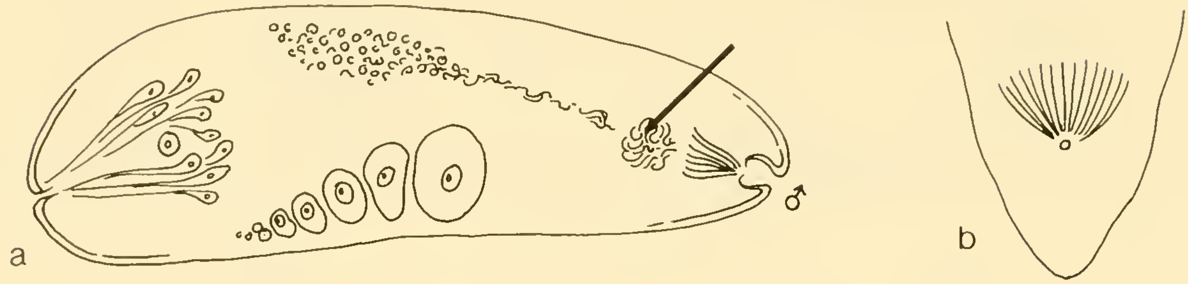


Figure 118.—*Actinoposthia caudata*: a-sagittal reconstruction; b-dorsal view of posterior end.

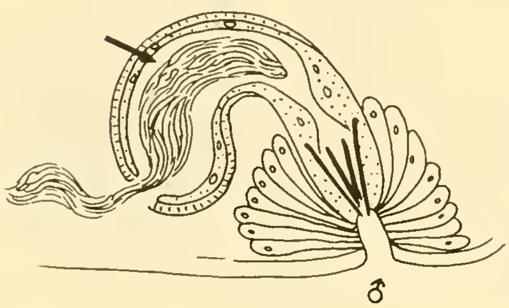


Figure 119.—*Actinoposthia haplovata.*

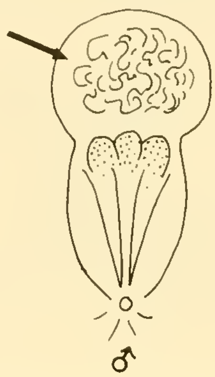


Figure 120.—*Actinoposthia longa*, dorsal view.

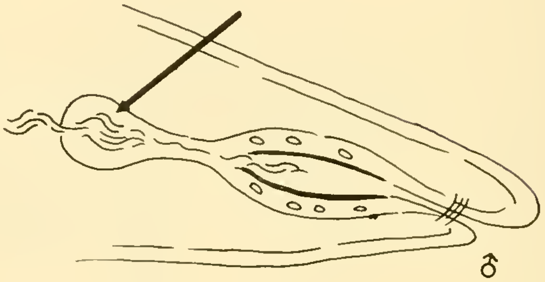


Figure 121.—*Actinoposthia pigmentea.*

57 (*56*) Seminal vesicle lacking; large cyanophile gland cells surround the copulatory apparatus (Fig. 122) .... Genus *Microposthia*.

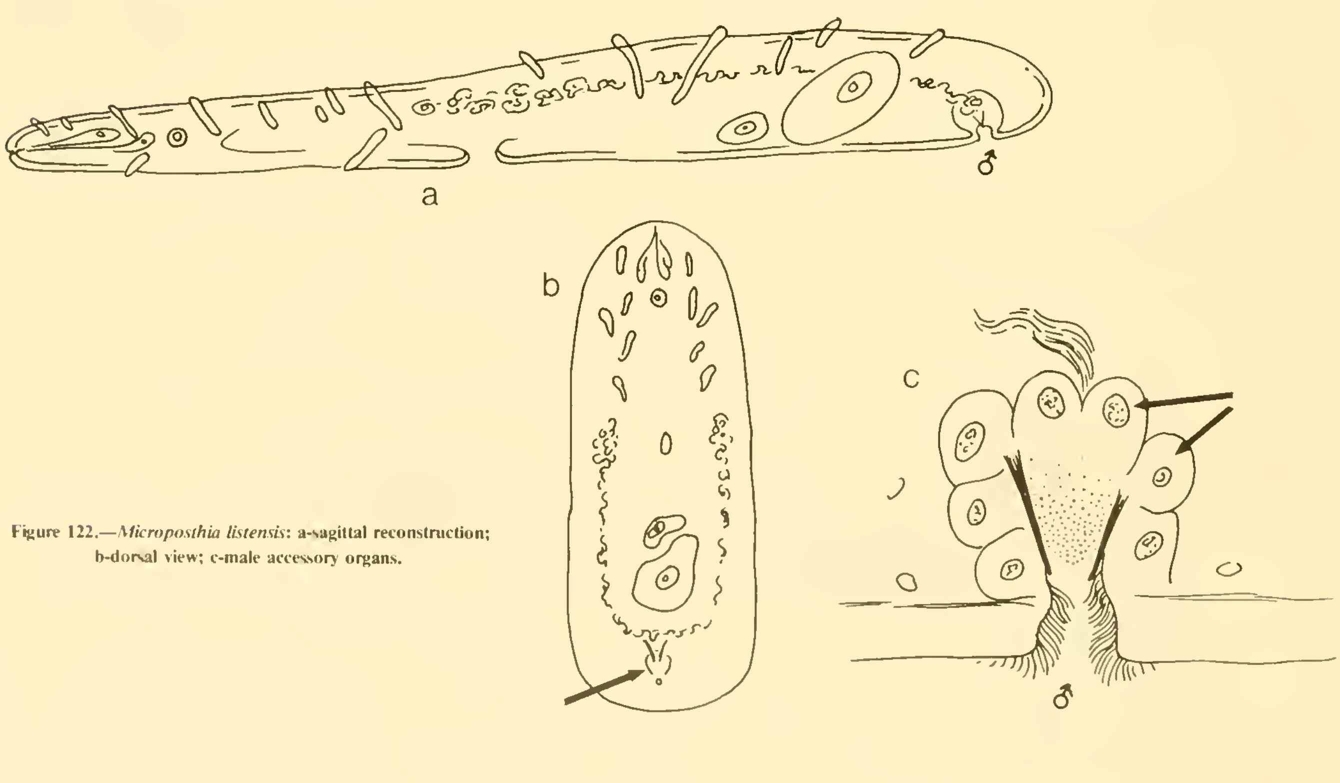


Figure 122.—*Microposthia listensis*: a-sagittal reconstruction; b-dorsal view; c-male accessory organs.

58 (*53*) Seminal bursa with a cuticularized nozzle (Fig. 123) 59

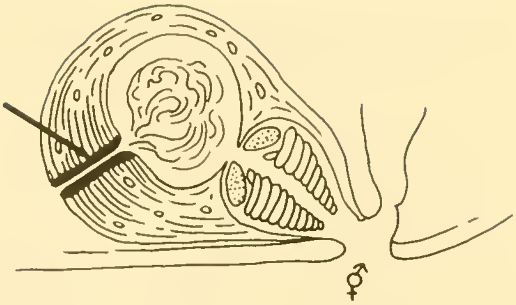


Figure 123.—*Philactinoposthia saliens.*

58 (*53*) Seminal bursa lacking a cuticularized nozzle 60

59 (*58*) Four copulatory organs present (Fig. 124) . . . . Genus *Tetraposthia.*

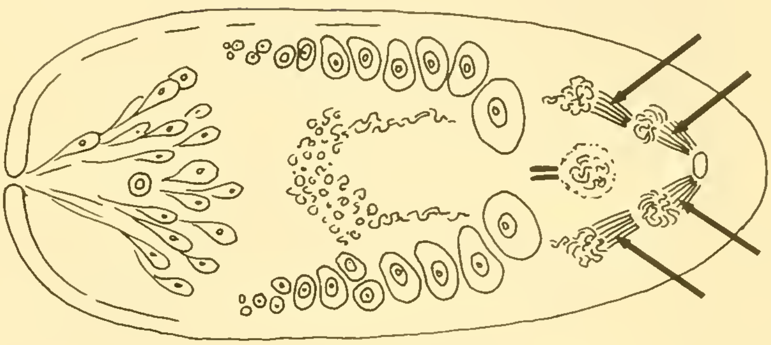


Figure 124.—*Tetraposthia colymbetis.*

59 (*58*) A single copulatory organ present (Figs. 125, 126) . . . . Genus *Philactinoposthia.*
Genus *Monoposthia.*[7]

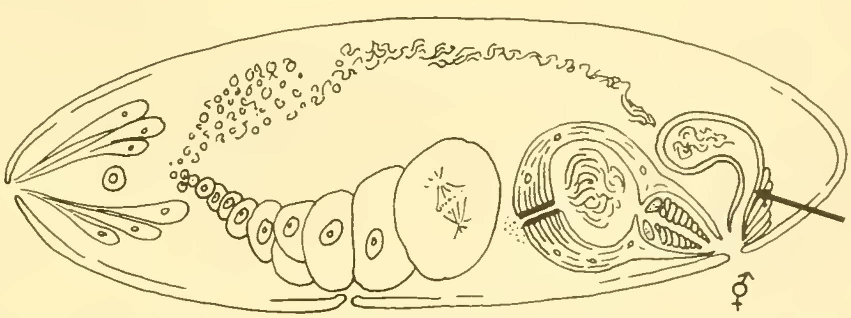


Figure 125a.—*Philactinoposthia saliens.*

Figure 125b.—*Monoposthia pseadovesicula.* (See text footnote 7.)

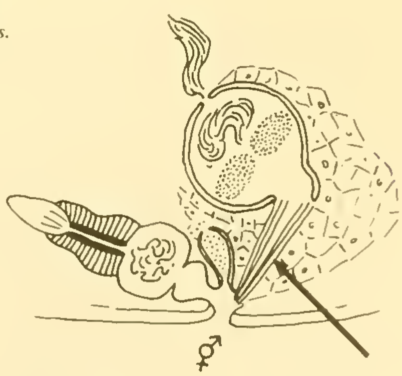


Figure 126.—*Philactinoposthia adenogonaria.*

[7]Genus *Monoposthia*, recently described from the Galapagos Islands, is close to the genus *Philactinoposthia* but lacks a true seminal vesicle, such as is present in *Philactinoposthia*.

60 (*58*) Outer body wall muscle layers consist of outer longitudinal and inner circular layers (Fig. 128); frontal gland very small or lacking (Figs. 127, 129) . . . . Genus *Paraphanostoma*

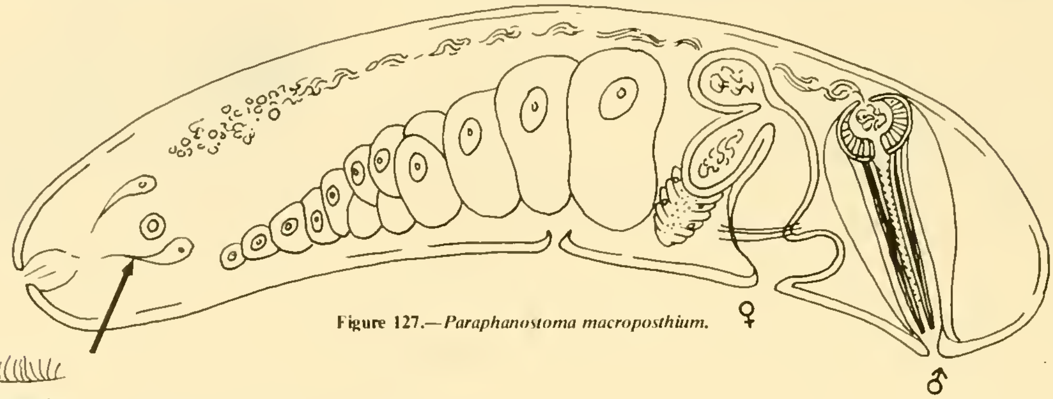


Figure 127.—*Paraphanostoma macroposthium.*

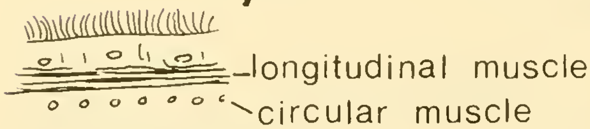


Figure 128.—Longitudinal section of body wall.

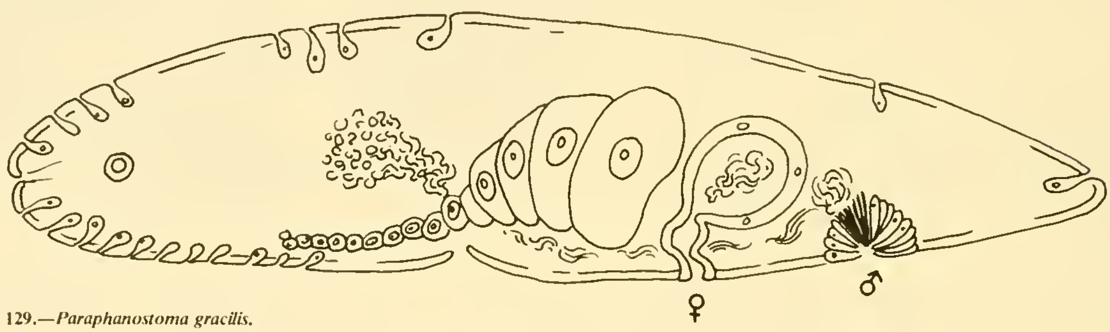


Figure 129.—*Paraphanostoma gracilis.*

60 (*58*) Outer body wall muscle layers with outer circular and inner longitudinal fibers (Fig. 130); frontal gland well developed 61

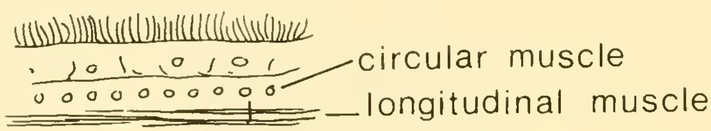


Figure 130.—Longitudinal section of body wall.

61 (*60*) Seminal bursa without a spermatic duct (Fig. 131) . . . . Genus *Pseudactinoposthia.*

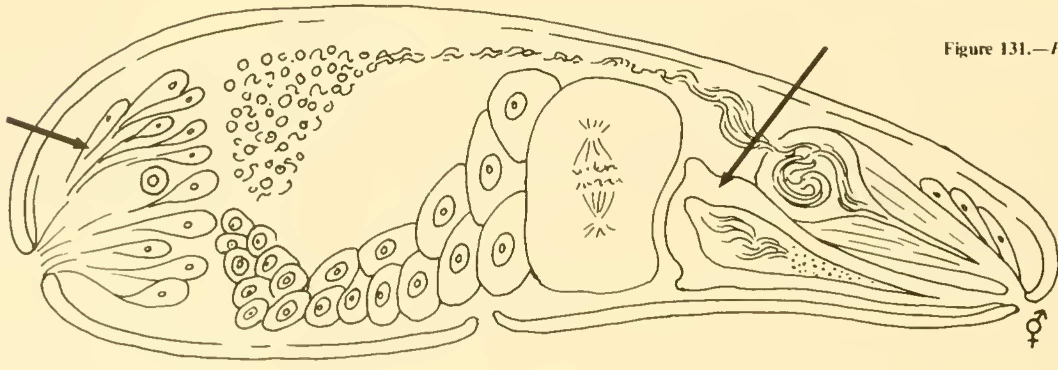


Figure 131.—*Pseudactinoposthia saltans.*

61 (*60*) Seminal bursa with a cellular (Fig. 132) or muscular (Fig. 133) spermatic duct 62

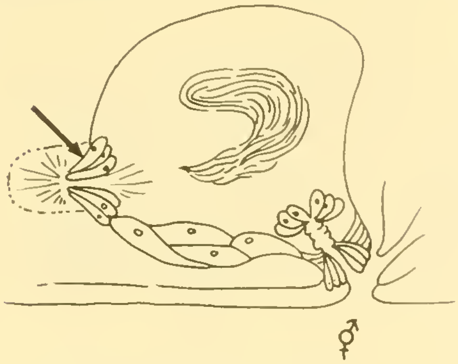


Figure 132.—*Archactinoposthia pelophila.*

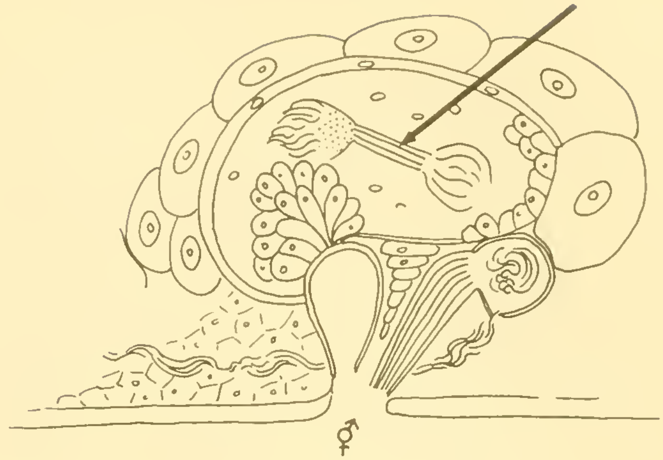


Figure 133.—*Pelophila pachymorpha.*

62 (*61*) Spermatic duct muscular, invaginated into the seminal bursa and directed posteriorly (Figs. 134, 135) . . . .
. . . . Genus *Pelophila.*

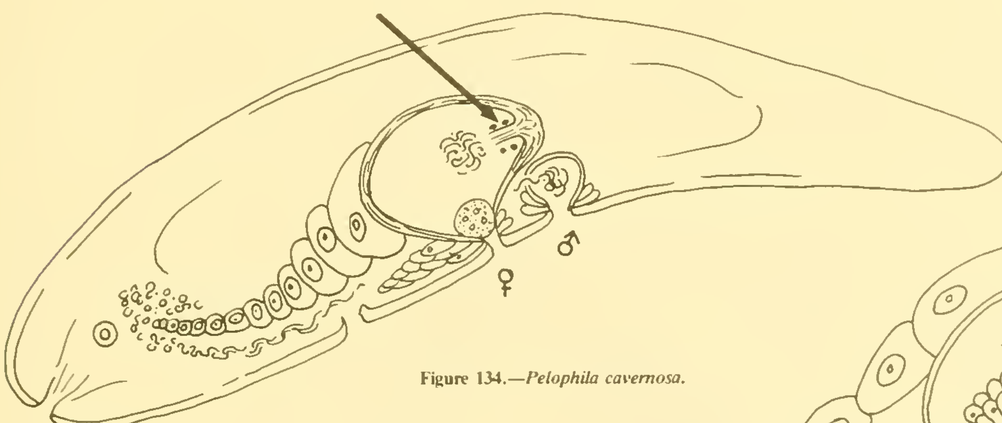


Figure 134.—*Pelophila cavernosa.*

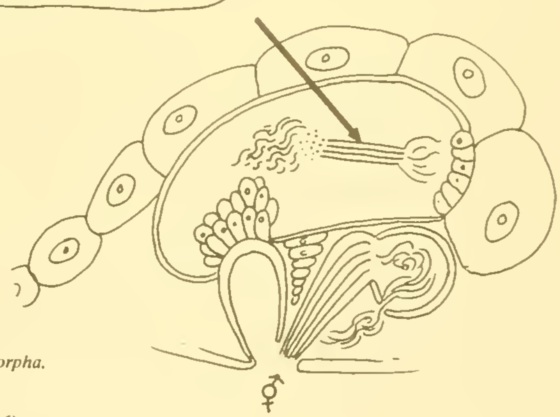
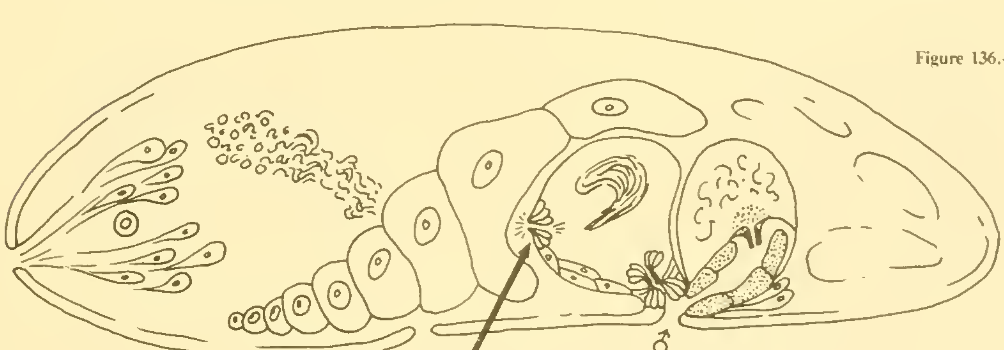


Figure 135.—*Pelophila pachymorpha.*

62 (*61*) Spermatic duct cellular, not invaginated, directed anteriorly (Fig. 136) . . . .
. . . . Genus *Archactinoposthia.*

Figure 136.—*Archactinoposthia pelophila.*



63 (*52*) Seminal bursa present as either a definite walled structure (Fig. 137), or as a network of syncytial tissue in the parenchyma (Fig. 138) 64

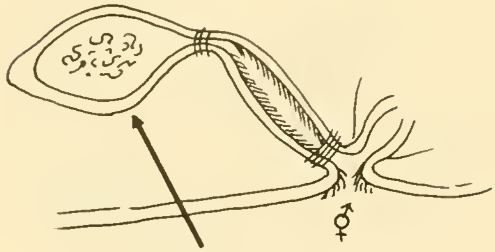


Figure 137.—*Bursosaphia baltalimaniaformis.*

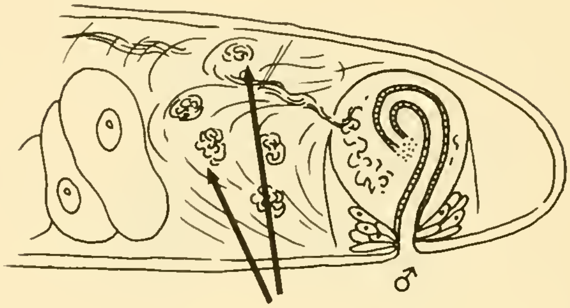


Figure 138.—*Archaphanostoma histobursalium.*

63 (*52*) Seminal bursa lacking 79

64 (*63*) Seminal bursa an extensive syncytial area in the posterior end of the body with bundles of sperm scattered therein (Figs. 139, 140, 141) .... Genus *Archaphanostoma.*

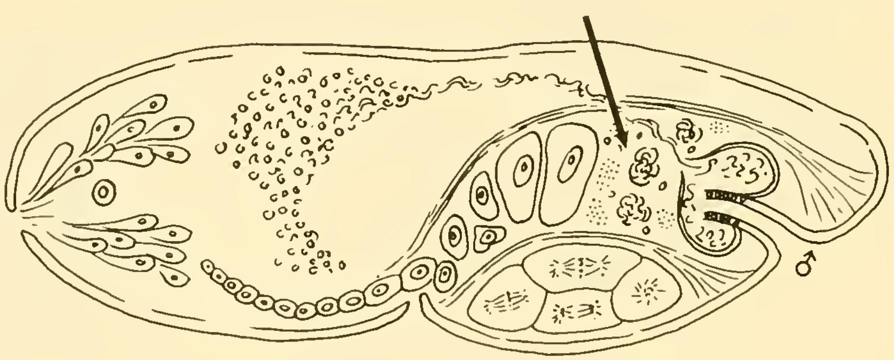


Figure 139.—*Archaphanostoma agile.*

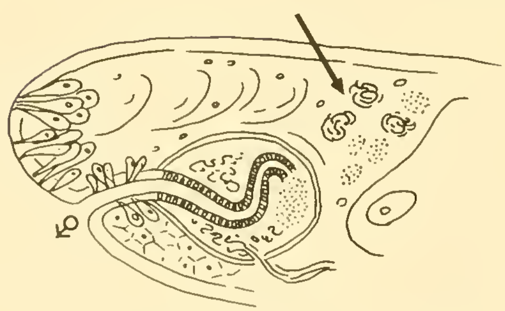


Figure 140.—*Archaphanostoma macrospiriferum.*

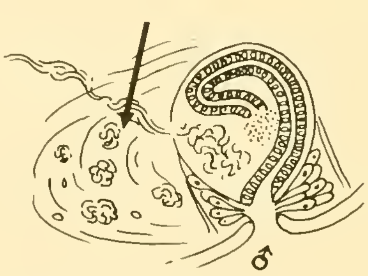


Figure 141.—*Archaphanostoma histobursalium.*

64 (*63*) Seminal bursa a definite walled structure 65

65 (*64*) Plate-shaped, planktonic (Fig. 142). Until Dörjes (1970) described *Haplodiscus bocki*, members of this genus had been reported to lack a seminal bursa, so this genus is retained under both headings in this key (see 79 (*63*), Fig. 168) .... Genus *Haplodiscus*.

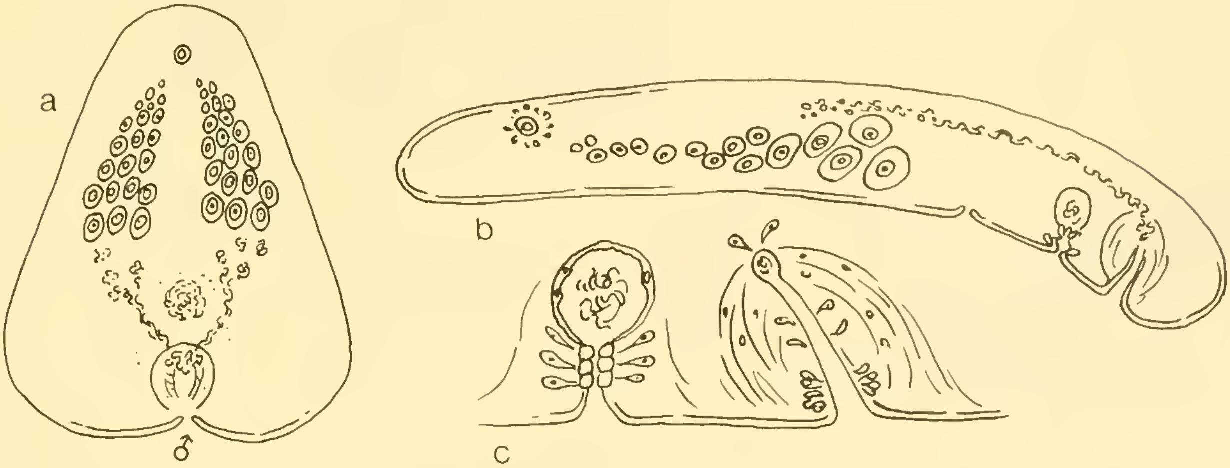
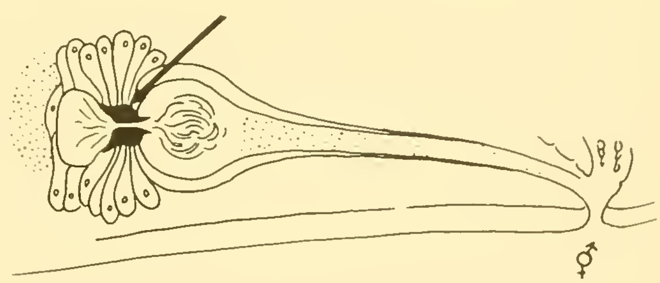


Figure 142.—*Haplodiscus bocki*: a-dorsal view; b-sagittal reconstruction; c-sagittal reconstruction of male and female accessory organs.

65 (*64*) More or less elongated in shape, benthic 66

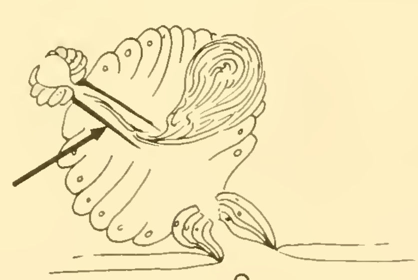
66 (*65*) Cuticularized nozzle present as an appendage on the seminal bursa (Fig. 143) 67

Figure 143.—*Conaperta norwegica*.



66 (*65*) Cuticularized nozzle absent; spermatic duct invaginated into the seminal bursa may be cuticularized (Fig. 144) 73

Figure 144.—*Postaphanostoma atriomagnum*.



67 (*66*) One bursal nozzle or a spermatic duct present 68

67 (*66*) Two to many bursal nozzles present 70

68 (*67*) Male and female genital pores separate 69

68 (*67*) Common genital pore present (Figs.145, 146)..
....Genus *Conaperta.*

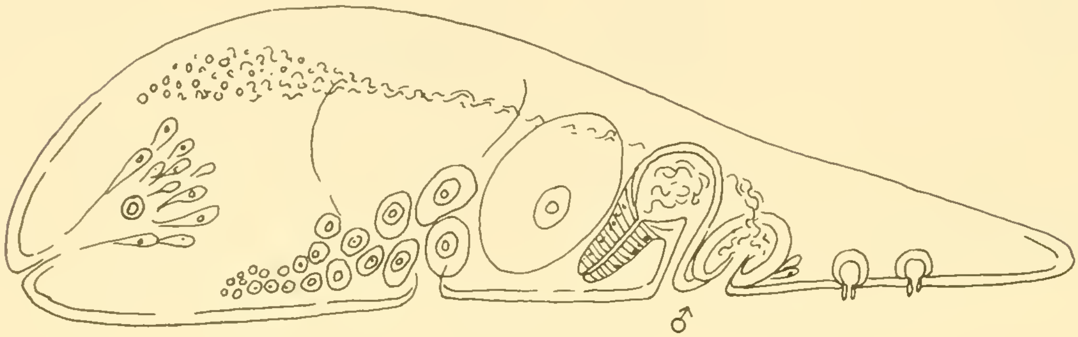
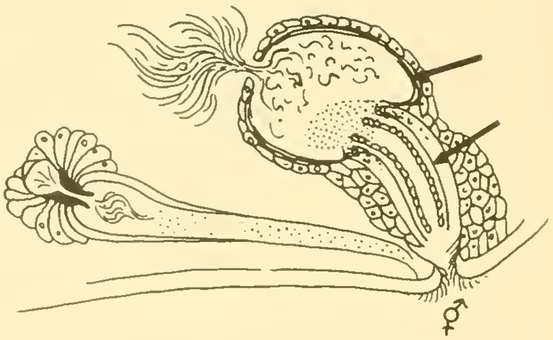


Figure 145.—*Conaperta thela.*

Figure 146.—*Conaperta norwegica.*



69 (*68*) Tube-shaped penis surrounded by a muscular seminal vesicle; bursal nozzle present (Fig. 147) ....
....Genus *Convoluta.*

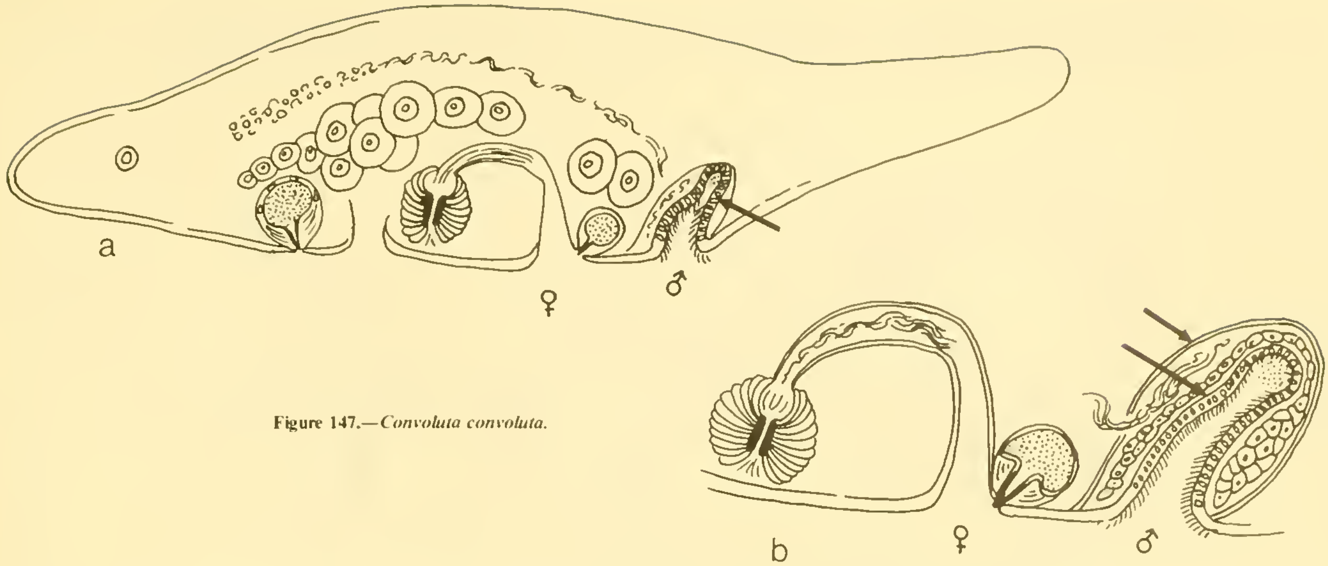


Figure 147.—*Convoluta convoluta.*

69 (*68*) Small tube-shaped penis with a false seminal vesicle attached at proximal end; cellular spermatic duct present. From Red Sea (Fig. 148) .... Genus *Brachypea.*

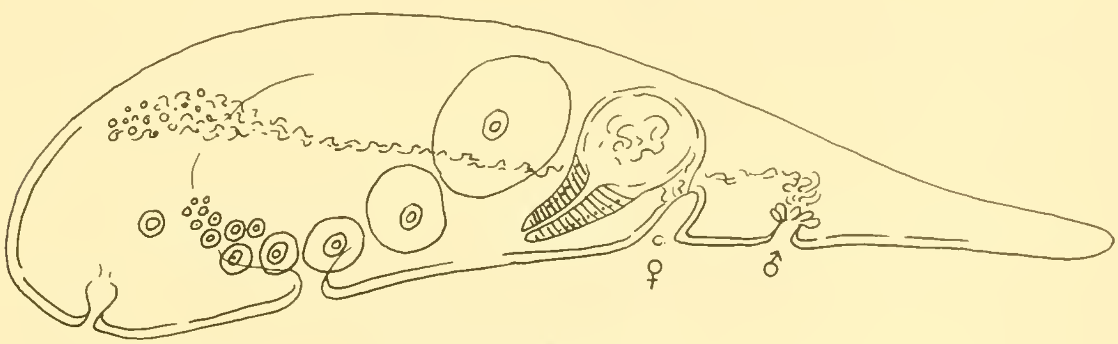
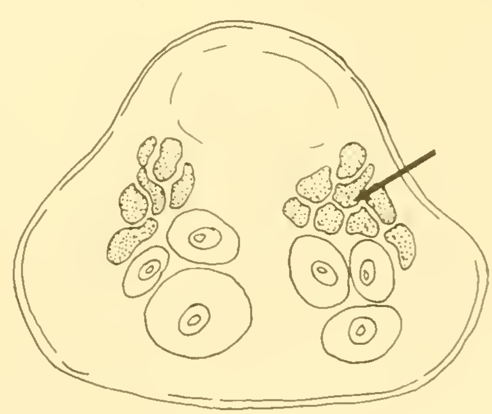


Figure 148.—*Brachypea kenoma.*

70 (*67*) Special yolk-carrying cells absent; yolk deposited in the eggs 72

70 (*67*) Developing eggs in one layer toward the ventral side of the body with a layer of special yolk-carrying cells (yolk-glandlike layer) dorsal or dorsolateral to the eggs (Fig. 149) 71

Figure 149.—*Polychoerus*, cross section.



71 (*70*) Body teardrop-shaped with pointed posterior end; two to eight pairs of prostatoid organs present (Fig. 150). One freshwater and several marine species from Caspian Sea region .... Genus *Oligochoerus*.

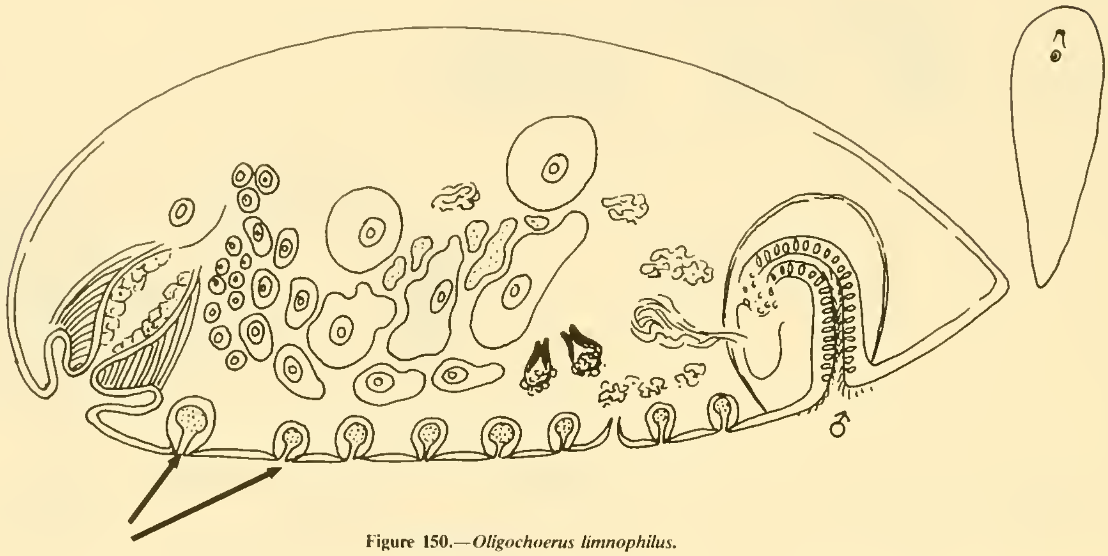


Figure 150.—*Oligochoerus limnophilus*.

71 (*70*) Body deeply notched at posterior end with one to three thin tails in the notch; prostatoid organs lacking (Fig. 151) .... Genus *Polychoerus*.

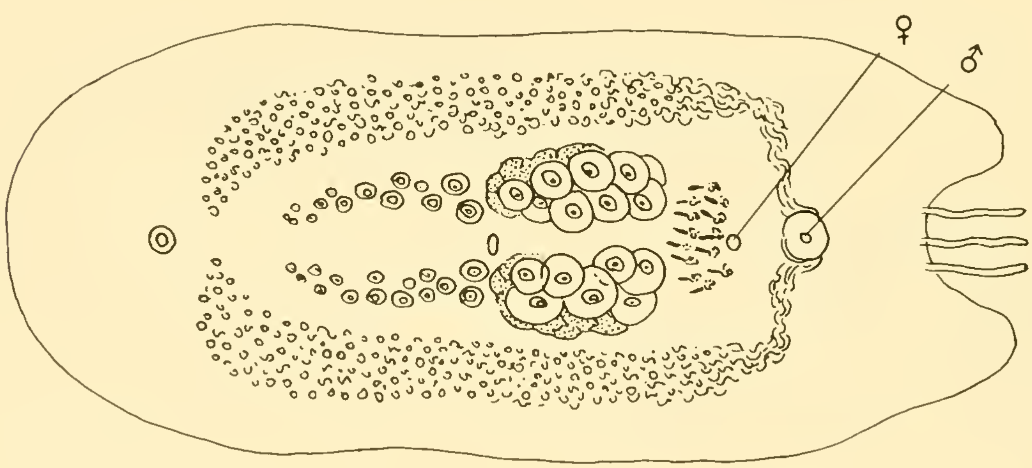


Figure 151.—*Polychoerus caudatus*, dorsal view.

72 (*70*) Separate genital pores; colored by the presence of symbionts or pigment; seminal bursa with two, more or less curved or spiraled nozzles (Figs. 152, 153, 154) .... Genus *Amphiscolops*.

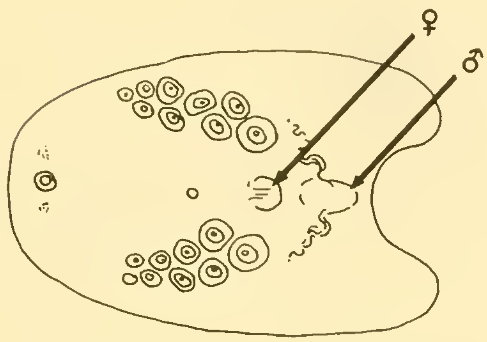


Figure 152.—*Amphiscolops langerhansi*, dorsal view.

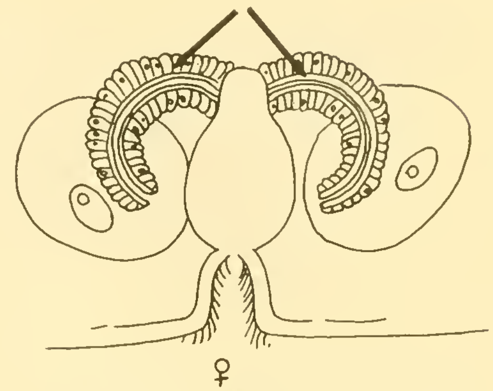


Figure 153.—*Amphiscolops cinereus*, seminal bursa.

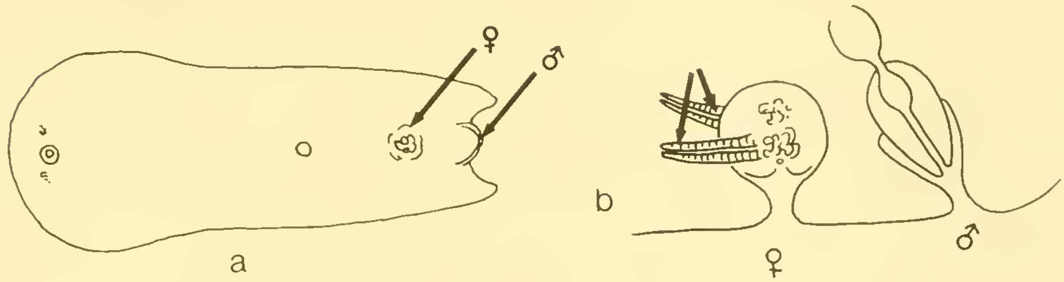


Figure 154.—*Amphiscolops bermudensis*: a-dorsal view; b-sagittal reconstruction of male and female accessory organs.

72 (*70*) Common genital pore; white, or colored only by the presence of food products; seminal bursa with two or more short cone-shaped nozzles. From the Pacific coasts of the United States and U.S.S.R. (Fig. 155) ... . Genus *Diatomovora*.

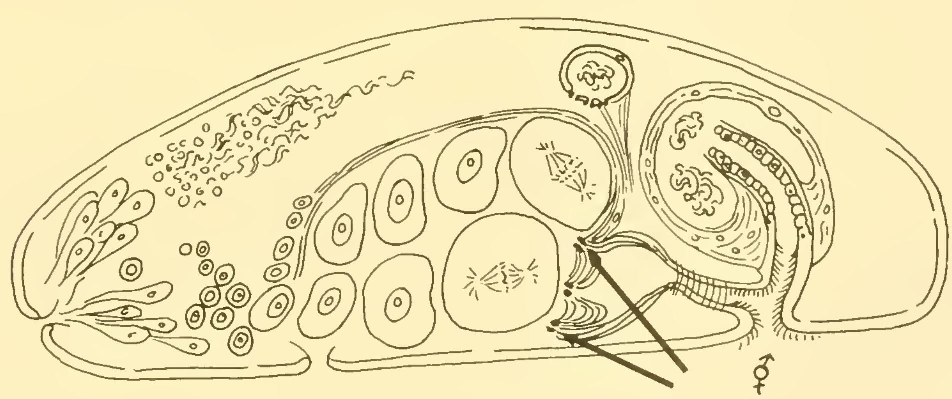


Figure 155.—*Diatomovora amoena*.

73 (*66*) Seminal bursa without a projecting external appendage, but a flattened cap of a few cells (Fig. 156) or an invaginated spermatic duct (Fig. 157) may be present 74

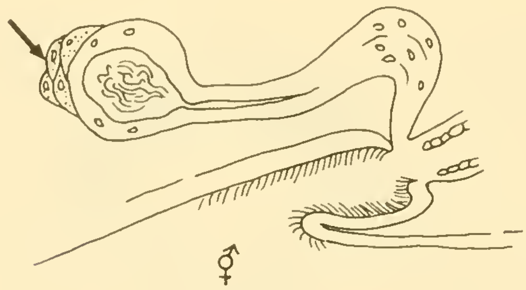


Figure 156.—*Praeconvoluta karinae.*

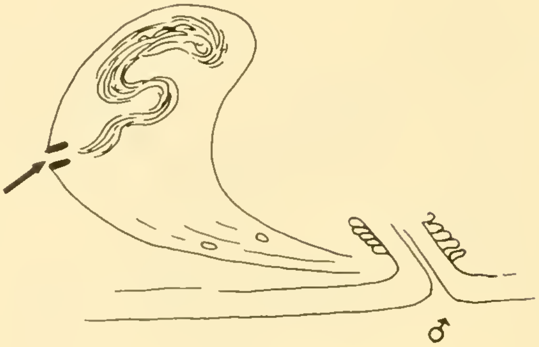


Figure 157.—*Postaphanostoma filum.*

73 (*66*) Seminal bursa with a definite external cellular or muscular (but not cuticularized) appendage (Fig. 158) 77

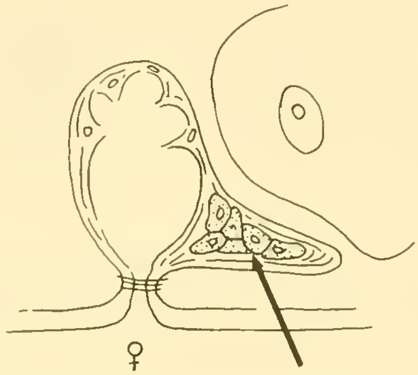
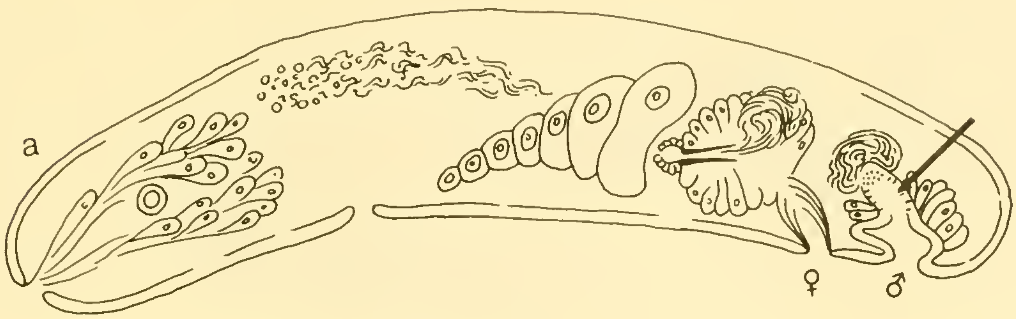


Figure 158.—*Proaphanostoma tenaissima.*

74 (*73*) True seminal vesicle lacking 75

74 (*73*) True seminal vesicle present 76

75 (*74*) Small rhabdites present, arranged in rows; female germinal center and string of eggs unpaired; penis a simple, tube-shaped invagination of the outer body wall (Figs. 159, 160). .... Genus *Postaphanostoma*.



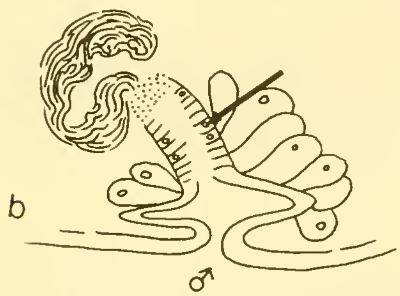


Figure 159.—*Postaphanostoma atriomagnum.*

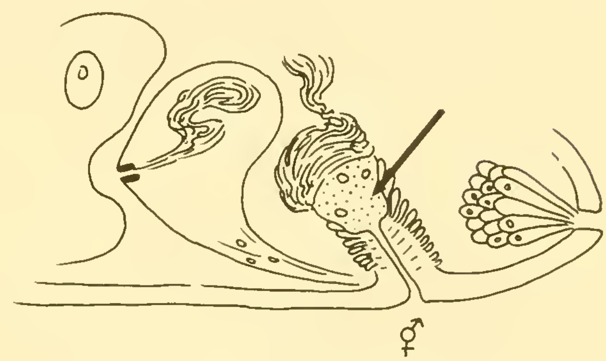


Figure 160.—*Postaphanostoma filum.*

75 (*74*) Rabdites lacking; female germinal center and string of eggs paired; penis very glandular and invaginated into a muscular penis sac (Fig. 161) .... Genus *Praeconvoluta*.

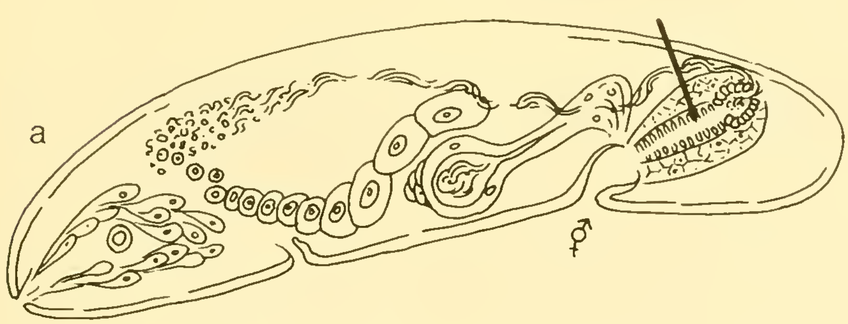
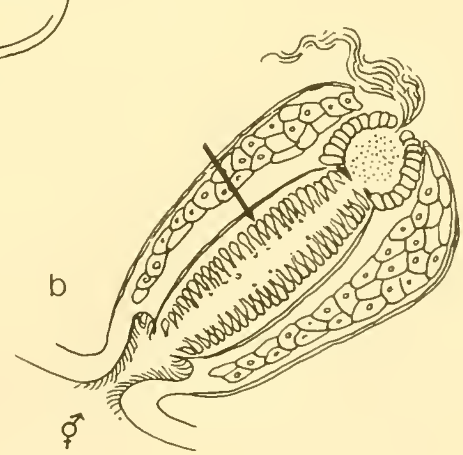


Figure 161.—*Praeconvoluta karinae.*



76 (*74*) Seminal bursa opens from a long, tubelike ciliated female antrum and is surrounded by a mass of netlike tissue (a bursal tissue), but with no appendage (Fig. 162) .... Genus *Bursosaphia*.

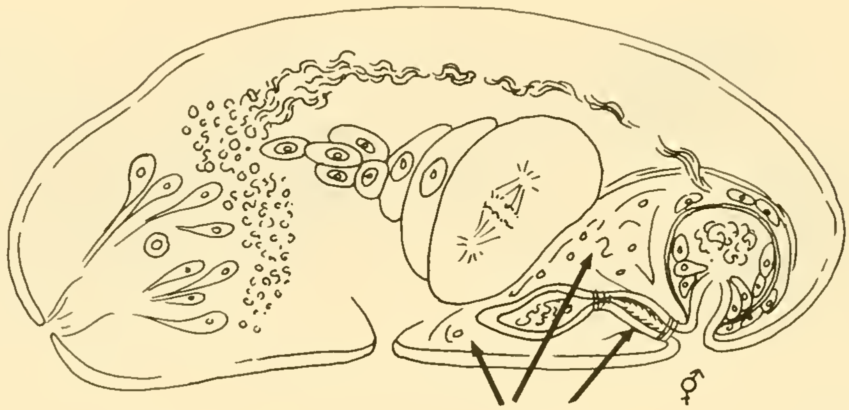


Figure 162.—*Bursosaphia baltalimaniaformis.*

76 (*74*) Seminal bursa opens almost directly from the exterior without any or with an extremely short female antrum; no appendage and no bursal tissue present but there may be an invaginated spermatic duct (Figs. 163, 164) .... Genus *Praeaphanostoma*.

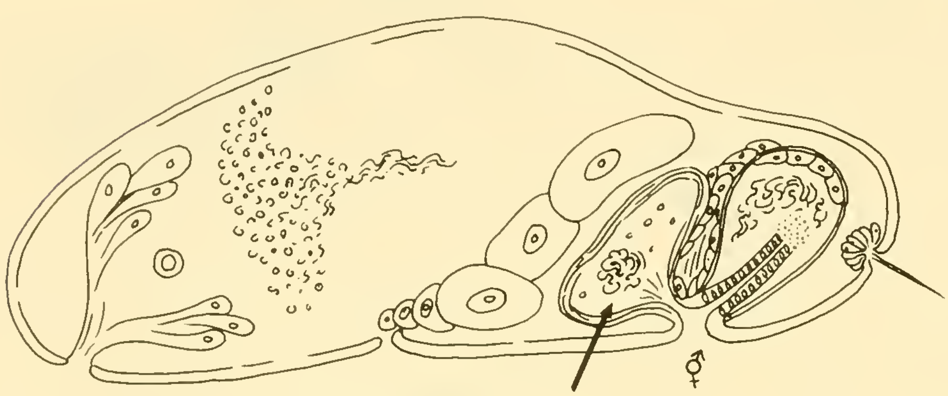


Figure 163.—*Praephanostoma chaetocaudatum.*

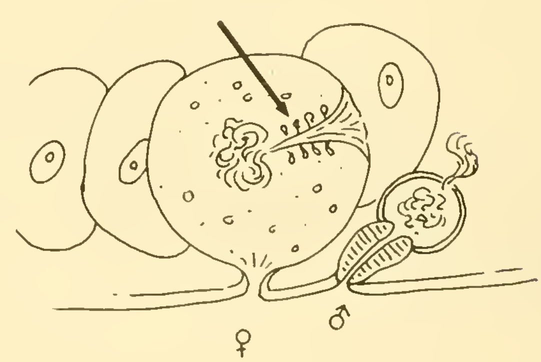
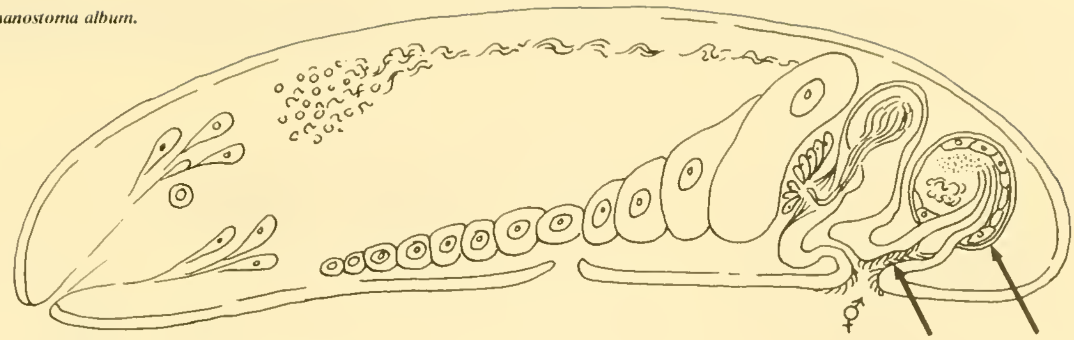


Figure 164.—*Praeaphanostoma lutheri.*

77 (*73*) Rhabdites present, arranged in irregular rows; seminal vesicle and ciliated male antrum present (Fig. 165) .... Genus *Aphanostoma*.

Figure 165.—*Aphanostoma album.*



77 (*73*) Rhabdites absent; male antrum lacking; seminal vesicle present or absent 78

78 (*77*) Seminal vesicle absent; penis a simple invagination of outer wall layers with a ball of sperm at the proximal end that is surrounded by a parenchymal net with a few muscle fibers and gland cells (Fig. 166) ....Genus *Proconvoluta.*

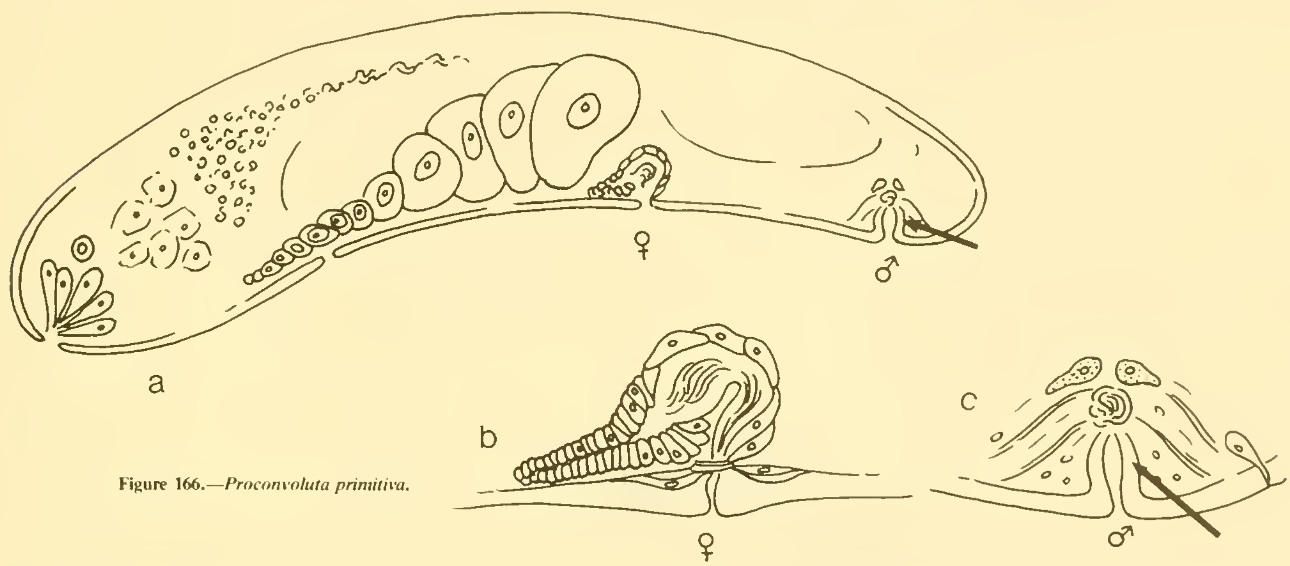


Figure 166.—*Proconvoluta primitiva.*

78 (*77*) Seminal vesicle present; penis a tubelike invagination which is further invaginated into the seminal vesicle (Fig. 167) ....Genus *Proaphanostoma.*

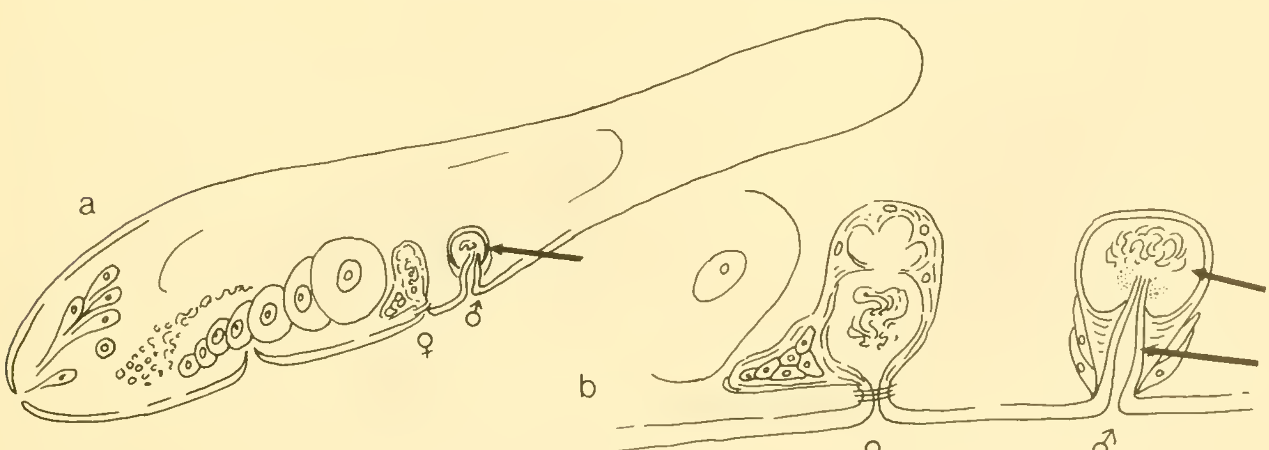


Figure 167.—*Proaphanostoma tenuissima.*

79 (*63*) Plate-shaped; planktonic (Fig. 168); until Dörjes (1970) described *Haplodiscus bocki*, the members of this genus had none of them been reported as having a seminal bursa, so the genus is retained under both headings in this key (see 65 (*64*), Fig. 142) .... Genus *Haplodiscus*.

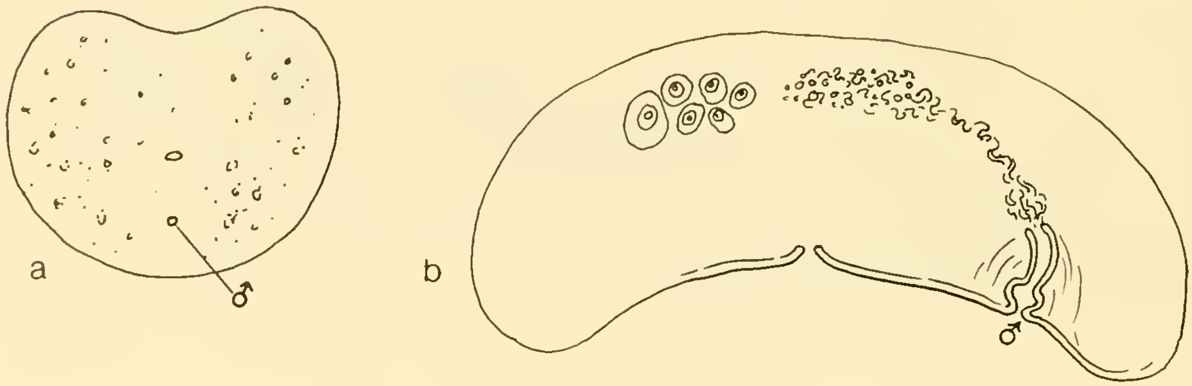


Figure 168.—*Haplodiscus piger*: a-dorsal view; b-sagittal reconstruction.

79 (*63*) Not broad and flattened but more or less elongated in shape or oval; benthic 80

80 (*79*) False seminal vesicle present (Fig. 169) 81

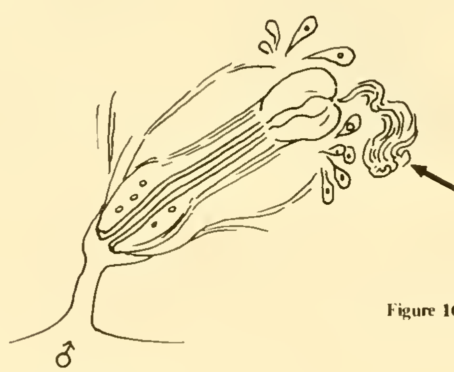


Figure 169.—*Rimicola glacialis*.

80 (*79*) True semnal vesicle present (Fig. 170) 82

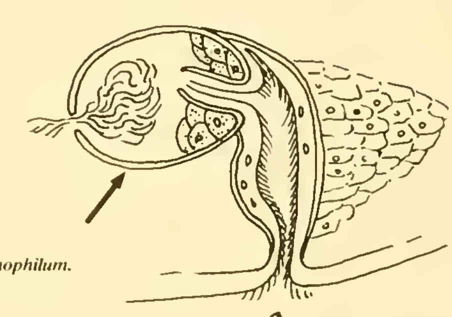


Figure 170.—*Pseudaphanostoma psammophilum*.

81 (*80*) Male antrum lacking; a glandular organ opens at the male pore and close to this at the posterior side of the penis there is a false seminal vesicle (Fig. 171) . . . . Genus *Pseudoposthia*.

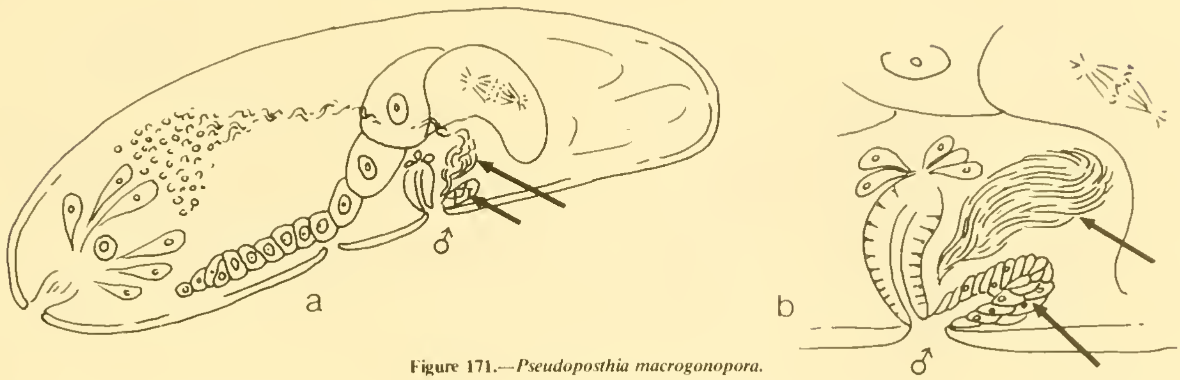


Figure 171.—*Pseudoposthia macrogonopora.*

81 (*80*) A short male antrum present; copulatory organ without a glandular organ and with the false seminal vesicle at the proximal end of the penis (Fig. 172) . . . . Genus *Rimicola*.

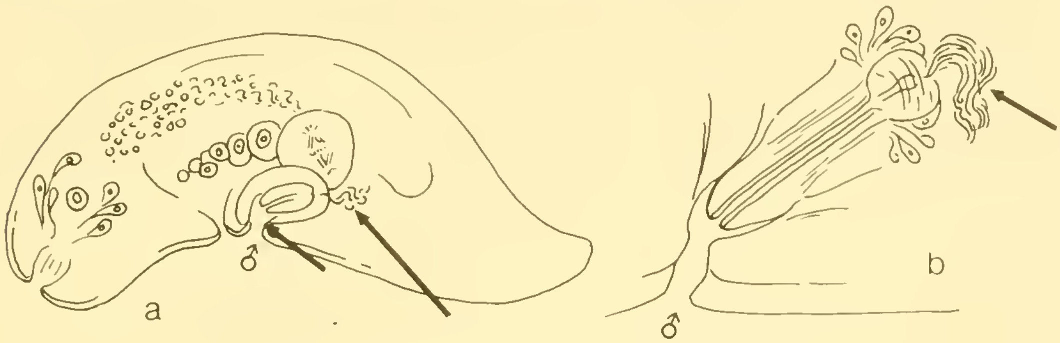


Figure 172.—*Rimicola glacialis.*

82 (*80*) Male antrum lacking (Fig. 173); parasitic. Compare *Faerlea*, 84 (*83*) . . . . Genus *Avagina*.

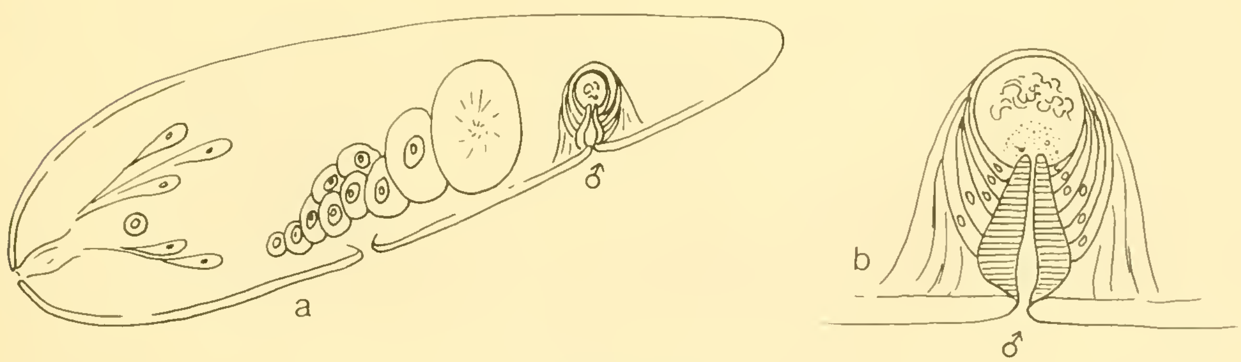


Figure 173.—*Avagina incola.*

82 (*80*) Male antrum present, although it may be very short 83

83 (*82*) Two copulatory apparatuses present (Fig. 174) .... Genus *Neochildia*.

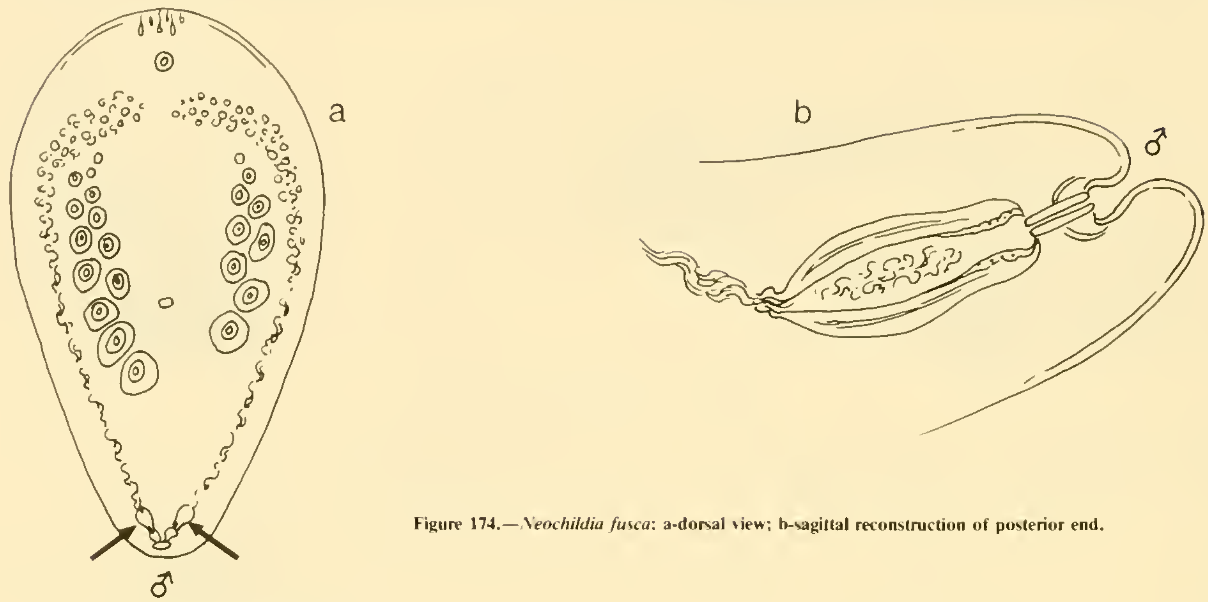


Figure 174.—*Neochildia fusca*: a-dorsal view; b-sagittal reconstruction of posterior end.

83 (*82*) One copulatory apparatus present 84

84 (*83*) Male antrum very short (Fig. 175). Compare with *Avagina* 82 (*80*), which was originally (Westblad 1945) separated from *Faerlea* on the basis of the latter being free-living. Description of a parasitic species in *Faerlea* by Dörjes in 1972, leaves only the slight differences in the male antra to distinguish these genera. They may need to be combined. .... Genus *Faerlea*.

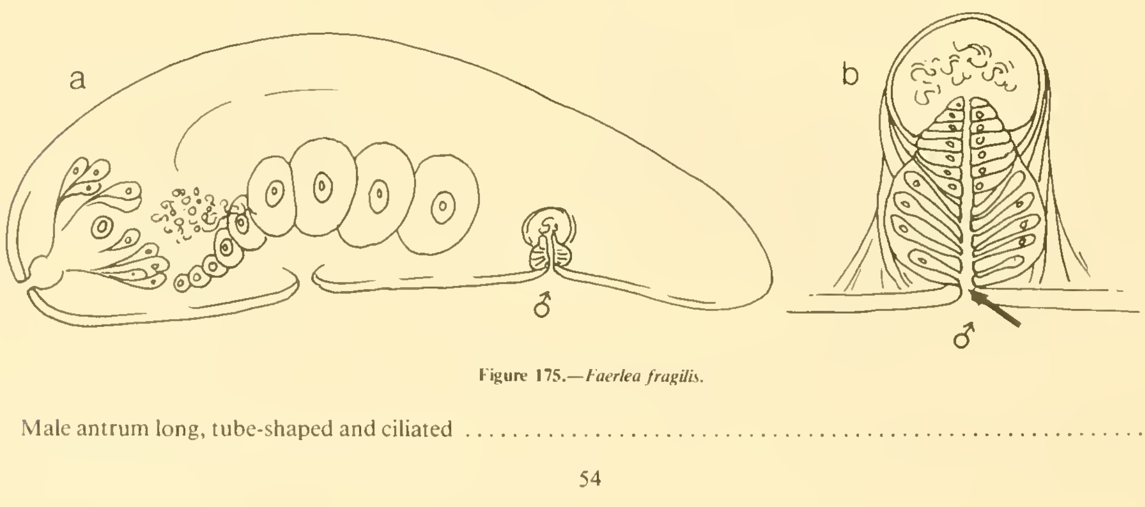


Figure 175.—*Faerlea fragilis*.

84 (*83*) Male antrum long, tube-shaped and ciliated 85

85 (*84*) Penis and male antrum without a clear line demarking one from the other (Fig. 176); from the Caspian Sea . . . . Genus *Baltalimania.*

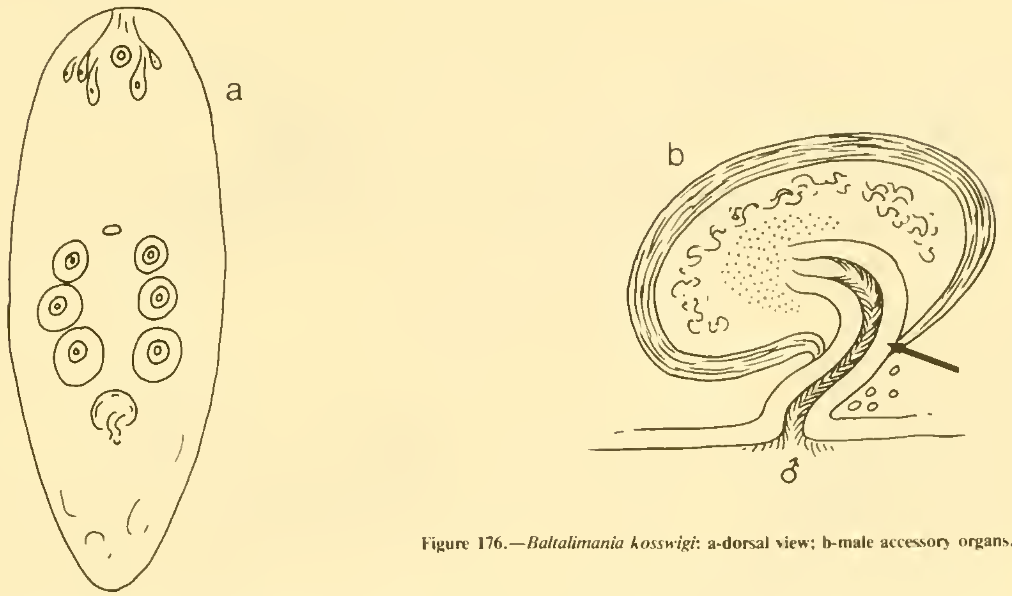


Figure 176.—*Baltalimania kosswigi*: a-dorsal view; b-male accessory organs.

85 (*84*) Penis and male antrum with a clear line distinguishing one from the other 86

86 (*85*) Colored rhabdites present as well as other pigment; a tube-shaped organ present at the anterior end as well as a frontal gland (Fig. 177). From Sakhalin Island, Pacific coast of U.S.S.R . . . . Genus *Oxyposthia.*

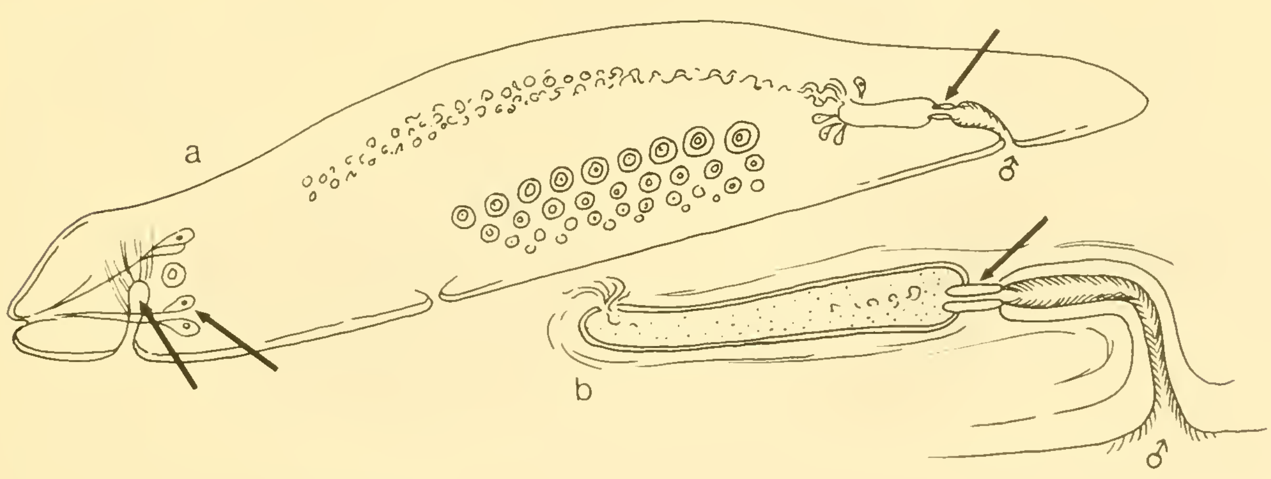


Figure 177.—*Oxyposthia praedator.*

86 (*85*) Colored rhabdites lacking, but small uncolored rhabdites in rows; tube-shaped organ lacking; frontal gland present (Figs. 178, 179, 180) . . . . Genus *Pseudaphanostoma.*

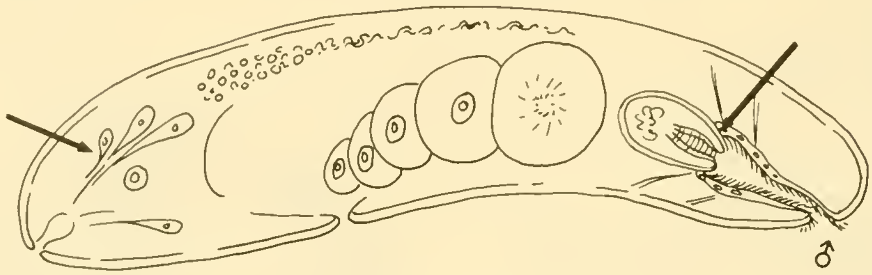


Figure 178.—*Pseudaphanostoma variabilis.*

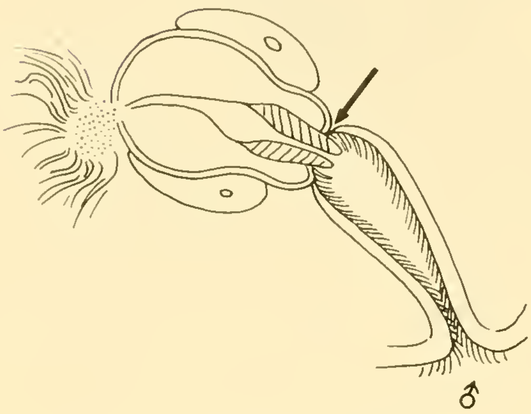


Figure 179.—*Pseudaphanostoma pelophilum.*

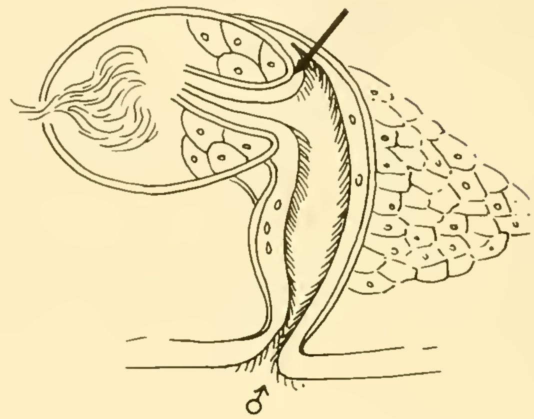


Figure 180.—*Pseudaphanostoma psammophilum.*

87 (*2*) Flagellar organ present; mouth opening absent (Fig. 181) . . . . Genus *Flagellophora.*

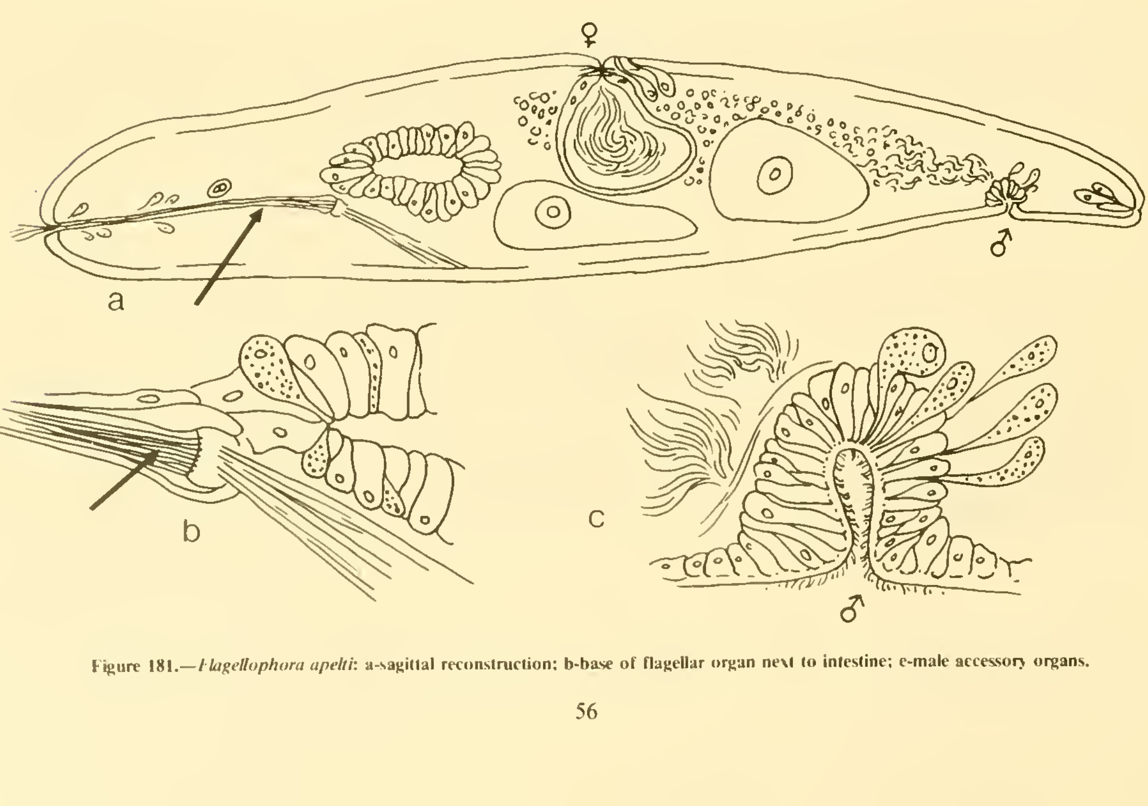


Figure 181.—*Flagellophora apelti*: a-sagittal reconstruction; b-base of flagellar organ next to intestine; c-male accessory organs.

87 (*2*) Flagellar organ absent; mouth opening present 88

88 (*87*) Frontal gland absent; ovary and testes folicular; male antrum with a side pocket but no gland cells around base of the seminal vesicle (Fig. 182); commensal in holothurians. ....Genus *Meara*.

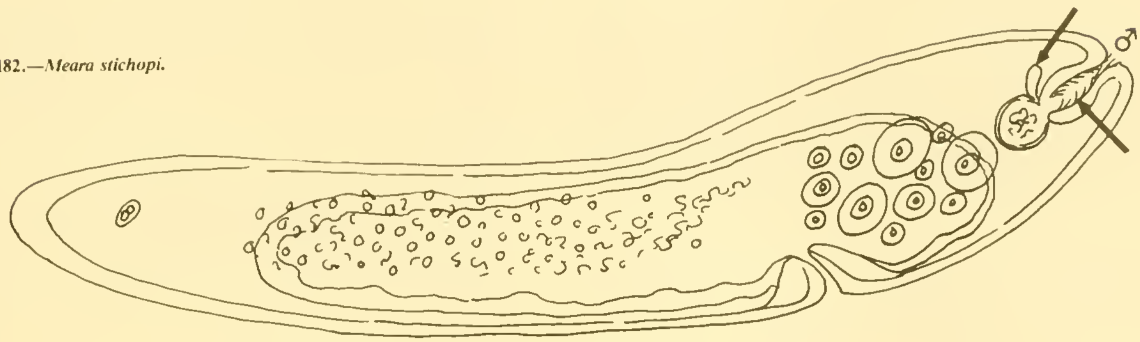


Figure 182.—*Meara stichopi.*

88 (*87*) Frontal gland well developed; compact testes and compact ovary; male antrum with many large gland cells around base of the seminal vesicle (Figs. 183, 184); free-living ....Genus *Nemertoderma*.

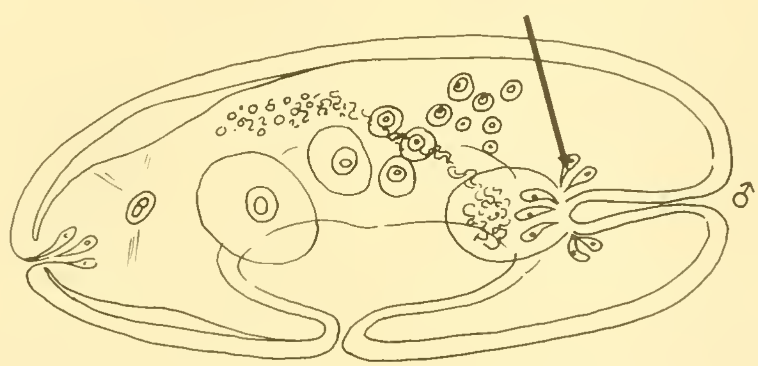


Figure 183.—*Nemertoderma bathycola.*

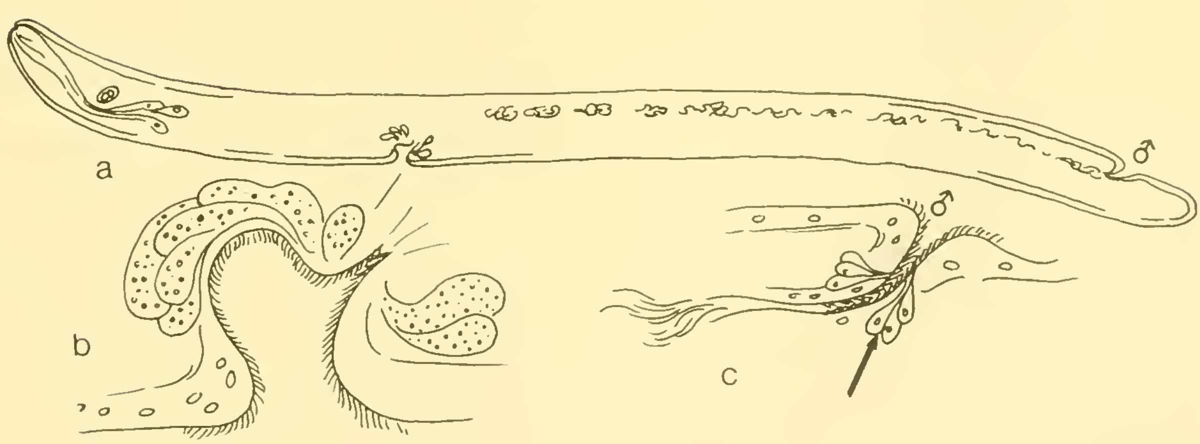


Figure 184.—*Nemertoderma rubra*: a-sagittal reconstruction; b-sagittal section through pharynx; c-sagittal section of male accessory organs.

ANNOTATED SYSTEMATIC LIST OF NORTH ATLANTIC GENERA AND SPECIES OF ACOELA AND NEMERTODERMATIDA

Species listed here include: 1) species reported in the literature or collected by the author in the area, and 2) genera and species that may be expected in this area because of their occurrence in the North Sea, the North Atlantic Ocean, or adjacent areas. Since the fauna here is as yet poorly described, it is felt to be most useful to include as many of the species and genera likely to be encountered as possible. Synonyms likely to be encountered in the literature are also included. Most of the doubtful species I have omitted altogether.

The list is arranged systematically in families as in Dörjes (1968a) with the new family Antroposthiidae Faubel added at the end. Genera are arranged alphabetically within the families and species alphabetically within the genera. Geographic distribution and habitat are indicated for each species. Asterisks indicate species for which I have records or which have been reported in the literature from the northeast coast of North America.

Order ACOELA

Family PROPORIDAE Graff, 1852

Genus *Archiproporus* An der Lan, 1936

Archiproporus minimus = *Proporus minimus* according to Westblad (1945), but see comment under 4 (*3*) in key.

Genus *Proporus* O. Schmidt, 1882

Proporus brochii Westblad, 1945. Sweden, Norway. 100-150 m.

Proporus lonchitis Dörjes, 1971. Norway. 50-200 m.

Proporus minimus (An der Lan, 1936). Norway, Greenland. 200-300 m.

Proporus rubropunctatus O. Schmidt, 1852 = *Otocelis rubropunctata*.

Proporus venenosus (O. Schmidt, 1852). British Isles, Mediterranean Sea, Black Sea. Subtidal. Includes subspecies: *P. v. venenosus* Graff, 1904, *P. v. violaceus* Graff, 1882, and *P. v. viridiflavus* Riedl, 1959.

Genus *Schizoporus* O. Schmidt, 1852

Only one species *S. venenosus* = *Proporus venenosus*.

Family CONVOLUTIDAE Graff, 1904

Genus *Adenopea* moved to Family ANTROPOSTHIIDAE

Genus *Amphichoerus* Graff, 1891 = *Amphiscolops*

Genus *Amphiscolops* Graff, 1904

Amphiscolops bermudensis Hyman, 1939. Bermuda. On seaweeds.

Amphiscolops cinereus (Graff, 1874). North Atlantic, Mediterranean Sea. On algae.

**Amphiscolops gardineri* Graff, 1910. Graff listed this in his first report on American Turbellaria, but later (1911) erected the new genus *Anaperus* for it.

Amphiscolops langerhansi (Graff, 1882). North Atlantic, Mediterranean. Tide pools, rocky shores. A species identified as this (?) was collected on algae at Virginia Key, Fla.

Amphiscolops sargassi Hyman, 1939. Bermuda, Brazil. On seaweeds.

Amphiscolops virescens Ørsted, 1845 = *Aphanostoma virescens*.

Genus *Aphanostoma* Ørsted, 1845

Many species assigned to this genus have been shuffled back and forth several times. I have followed Dörjes (1968a) as to their disposition in the following list.

Aphanostoma album Dörjes, 1968. North Sea. From muddy sand.

*?*Aphanostoma aurantiacum* Verrill, 1892. Newport, R.I. Listed as a doubtful species by various authors and not definitely identified since.

Aphanostoma auritum (M. S. Schultze, 1851) = *Mecynostomum auritum*.

Aphanostoma caudatum (An der Lan, 1936) = *Actinoposthia caudata*.

Aphanostoma divaceum Verrill, 1892. Listed by Dörjes (1968a) as a doubtful species. Probably a typographical error on *A. olivaceum*.

**Aphanostoma diversicolor* Ørsted, 1845 = *Paramecynostomum diversicolor*.

Aphanostoma elegans Jensen, 1878. Northern Europe. On algae.

Aphanostoma lutheri Westblad, 1946 = *Pelophila lutheri*.

Aphanostoma macrobursalis Westblad, 1946 = *Pseudmecynostomum macrobursalium*.

Aphanostoma macrospiriferum Westblad, 1946 = *Archaphanostoma macrospiriferum*.

Aphanostoma minimum Westblad, 1946 = *Haplogonaria minima*.

*?*Aphanostoma olivaceum* Verrill, 1892. Provincetown, Mass. Listed as a doubtful species by Graff (1911) and not reported since. Not found in my collections made there.

Aphanostoma rhomboides Jensen, 1878. Some references to this are really to *Archaphanostoma agile* (see Dörjes 1968a: 85, 157).

Aphanostoma rubropunctata (O. Schmidt, 1852) = *Otocelis rubropunctata*.

Aphanostoma tenuissimum Westblad, 1946 = *Proaphanostoma tenuissima*.

Aphanostoma virescens (Ørsted, 1845). North Atlantic from White Sea to Greenland.

Genus *Archaphanostoma* Dörjes, 1968

Archaphanostoma agile (Jensen, 1878). North Sea, North Atlantic to Greenland. Common in tide pools and in intertidal zone.

Archaphanostoma histobursalium Dörjes, 1968. North Sea. From muddy sand.

Archaphanostoma macrospiriferum (Westblad, 1946). North Sea. On soft bottom, 15-30 m.

Genus *Avagina* Leiper, 1902

Avagina aurita Meixner = *Mecynostomum auritum.*
Avagina glandulifera Westblad, 1953. North Sea in gut of *Spatangus purpureus.*
Avagina incola Leiper, 1902. British Isles and North Sea in gut of *Echinocardium.*
Avagina sublitoralis Faubel, 1976. North Sea. Subtidal in coarse sand.
Avagina tenuissima (Westblad, 1946). Dörjes (1968a) lists this here but later (1972) moves to his new genus *Proaphanostoma.*

Genus *Baltalimania* Ax, 1959

Baltalimania agile (Jensen, 1878) = *Archaphanostoma agile.*
Baltalimania macrospiriferum (Westblad, 1946) = *Archaphanostoma macrospiriferum.*

Genus *Bursosaphia* Dörjes, 1968

Bursosaphia baltalimaniaformis Dörjes, 1968. North Sea. From shelly sand under algae or in *Mytilus* colonies.

Genus *Conaperta* Antonius, 1968

Conaperta flavibacillum (Jensen, 1878). European Arctic and Atlantic coasts, Canary Islands, Black Sea, Mediterranean. On algae.
Conaperta norwegica (Westblad, 1946). Norway. 10-50 m.
Conaperta variomorpha (Dörjes, 1968). North Sea. From fine sand or clay, 6-11 m.

Genus *Convoluta* Ørsted, 1845

The number of species in this genus is very large and many placed here in the past have since been removed to other genera. I have followed Dörjes (1968a) as to disposition of these.

Convoluta cinereus Graff, 1874 = *Amphiscolops cinereus.*
Convoluta convoluta (Abildgaard, 1806). European Arctic and Atlantic coasts, North Sea, Canary Islands, Mediterranean, Black Sea. On algae. Common.
Convoluta diploposthia Steinböck, 1931 = *Anaperus rubellus.*
Convoluta flavibacillum Jensen, 1878 = *Conaperta flavibacillum.*
Convoluta groenlandica Levinsen, 1879 = *Childia groenlandica.*
Convoluta helgolandica Dörjes, 1968. North Sea. In fine sand.
Convoluta karlingi Westblad, 1946 = *Philocelis karlingi.*
Convoluta langerhansi Graff, 1882 = *Amphiscolops langerhansi.*
Convoluta lutheri Westblad, 1946 = *Pelophila lutheri.*
Convoluta macroposthia Steinböck, 1931 = *Paraphanostoma macroposthium.*
Convoluta norwegica Westblad, 1946 = *Conaperta norwegica.*
Convoluta paradoxa Ørsted, 1845 = *Convoluta convoluta.*
Convoluta pusilla Westblad, 1946 = *Philactinoposthia pusilla.*
Convoluta rhammifera Westblad, 1946 = *Philactinoposthia rhammifera.*
Convoluta roscoffensis Graff, 1904. Dörjes (1968a) says this is a species whose definition is uncertain; there are many references in the literature and many reports on experiments with animals identified as this species.
Convoluta saliens Graff, 1882 = *Philactinoposthia saliens.*
Convoluta stylifera Westblad, 1946 = *Philactinoposthia stylifera.*
Convoluta sutcliffei Hanson, 1961 = *Pseudohaplogonaria sutcliffei.*
Convoluta variomorpha Dörjes, 1968 = *Conaperta variomorpha.*
Convoluta viridipunctata Westblad, 1946 = *Pseudohaplogonaria viridipunctata.*

Genus *Faerlea* Westblad, 1945

Faerlea echinocardii Dörjes, 1972. Norway. In gut of *Echinocardium flavescens.*
Faerlea fragilis Westblad, 1945. North Sea. 30-50 m.
Faerlea glomerata Westblad, 1945. North Sea. 40 m.

Genus *Haplodiscus* Weldon, 1889

Haplodiscus piger Weldon, 1889. Pelagic. Bahamas.
Haplodiscus weldoni Böhmig, 1895. Pelagic. Sargasso Sea.

Genus *Neochildia* Bush, 1975

**Neochildia fusca* Bush, 1975. North Carolina to Maine. In or on sand or muddy sand along marsh streams or in estuaries.

Genus *Polychoerus* Mark, 1892

**Polychoerus caudatus* Mark, 1892. Formerly common from New Jersey to Maine (Verrill 1892). Now rare but has been collected on empty scallop shells (1-2 m) in Great Bay near Wauwinet, Mass., and once in bottom sand sample (5 m) at Menemsha, Mass. This beautiful orange species has been used at Woods Hole in experimental studies (Child 1907; Keil 1929).

Genus *Postaphanostoma* Dörjes, 1968

Postaphanostoma atriomagnum Dörjes, 1968. North Sea. In sand without mud or detritus, 3-18 m.
Postaphanostoma filum Dörjes, 1968. North Sea. Common interstitial form in various sands, 7-18 m.
Postaphanostoma glandulosum Dörjes, 1968. North Sea. From gravel deposits.

Genus *Praeaphanostoma* Dörjes, 1968

Praeaphanostoma brevifrons Dörjes, 1968. North Sea. From very fine sand, 5 m.
Praeaphanostoma chaetocaudatum Dörjes, 1968. North Sea. From coarse sand in shallow water.
Praeaphanostoma longum Dörjes, 1968. North Sea. In fine sand, 6 m.
Praeaphanostoma lutheri (Westblad, 1946) = *Pelophila lutheri*
Praeaphanostoma rubrum Dörjes, 1968. North Sea. In fine sand, 5 m.

Genus *Praeconvoluta* Dörjes, 1968

Praeconvoluta karinae Dörjes, 1968. North Sea. In gravel and rock pools, 1-2 m.
Praeconvoluta minor Faubel, 1974. North sea. From beach sand.
Praeconvoluta schmidti Faubel, 1977. Norway. From beach sand.

Genus *Proaphanostoma* Dörjes, 1972

Proaphanostoma tenuissima (Westblad, 1946). North Sea. 30 m.
Proaphanostoma viridis An der Lan, 1936 = *Haploposthia viridis.*

Genus *Proconvoluta* Dörjes, 1968

Proconvoluta primitiva Dörjes, 1968. North Sea. From detritus zone in shallow water.

Genus *Pseudaphanostoma* Westblad, 1946

Pseudaphonostoma brevicaudatum Dörjes, 1968. North Sea In muddy sand, shallow water.
Pseudaphanostoma pelophilum Dörjes, 1968. North Sea. In muddy sand, often with *Zostera* or *Mytilus.*
Pseudaphanostoma psammophilum Dörjes, 1968. North Sea In sand of the swash zone and sublittorally in unstable sand areas.
Pseudaphanostoma variabilis Westblad, 1946. North Sea. From clay with sand, 10-20 m.

Genus *Pseudoposthia* Westblad, 1946

Pseudoposthia macrogonopora Westblad, 1946. North Sea. From clay with sand.

Family NEMERTODERMATIDAE Steinböck, 1930

See under Order NEMERTODERMATIDA at end.

Family DIOPISTHOPORIDAE Westblad, 1940

Genus *Diopisthoporus* Westblad, 1940

Diopisthoporus brachypharyngeus Dörjes, 1968. North Sea From fine sand, 5-8 m.
Diopisthoporus longitubus Westblad, 1940. North Sea, Adriatic. From soft bottom to 360 m.
Diopisthoporus psammophilus Dörjes, 1968. North Sea. From fine sand, 5 m.

Family HALLANGIIDAE Westblad, 1948

Genus *Hallangia* Westblad, 1946

Hallangia proporoides Westblad, 1946. European Atlantic. From soft bottom to 100 m.

Family HAPLOPOSTHIIDAE Westblad, 1948

Genus *Adenocauda* Dörjes, 1968

Adenocauda helgolandica Dörjes 1968. North Sea. In fine sand, 5 m.

Genus *Afronta* Hyman, 1944

**Afronta aurantiaca* Hyman, 1944. Maine coast. Dredged in surface mud, 30 ft.
Afronta rubra Faubel, 1976. North Sea. From surf zone.

Genus *Haplogonaria* Dörjes, 1968

Haplogonaria elegans Faubel, 1976. North Sea. From sandy shallows.
Haplogonaria glandulifera Dörjes, 1968. North Sea. In fine sand, 5 m.
Haplogonaria macrobursalia Dörjes, 1968. North Sea. Surface layers of coarse sediments, 2-6 m.
Haplogonaria minima (Westblad, 1946). North Sea, Mediterranean. From soft bottom, 16-150 m.
Haplogonaria psammalia Faubel, 1974. North Sea. In beach sand.
Haplogonaria simplex Dörjes, 1968. North Sea. From coarse sand, 32 m.
Haplogonaria sinubursalia Dörjes, 1968. North Sea. From fine sand, 5-8 m.
Haplogonaria syltensis Dörjes, 1968. North Sea. From various sands to 15 m.
Haplogonaria viridis Dörjes, 1968. North Sea. From sandy mud, 5-8 m.

Genus *Haploposthia* An der Lan, 1936

Haploposthia brunea An der Lan, 1936. Greenland. From muddy bottoms, to 180 m.
Haploposthia monogonophora Westblad, 1946 = *Kuma monogonophora.*
Haploposthia rubra (An der Lan, 1936). North Sea, Greenland, Adriatic. From soft bottom to 180 m.
Haploposthia rubropunctata Westblad, 1945. North Sea, Adriatic. To 100 m.
Haploposthia viridis (An der Lan, 1936) = *Kuma viridis.*

Genus *Kuma* Marcus, 1950

Kuma monogonophora (Westblad, 1946). North Sea. 30-40 m.
Kuma viridis (An der Lan, 1936). Greenland, North Sea, Adriatic. From soft bottom, 30-250 m.

Genus *Parahaplogonaria* Dörjes, 1968

Parahaplogonaria maxima Dörjes, 1968. North Sea. From clay-mud in deep channel, 42 m.

Genus *Parahaploposthia* Dörjes, 1968

Parahaploposthia avesicula Dörjes, 1968. North Sea. In fine sand, 5 m.

Parahaploposthia brunea Faubel, 1976. North Sea. From sublittoral coarse sand.
Parahaploposthia cerebroepitheliata Dörjes, 1968. North Sea. From sand and muddy sand, 5-8 m.

Genus *Pseudohaplogonaria* Dörjes, 1968

Pseudohaplogonaria stylifera (Westblad, 1946) = *Philactinoposthia stylifera.*
Pseudohaplogonaria sutcliffei (Hanson, 1961). Bermuda. On seaweeds and sargassum.
Pseudohaplogonaria vacua Dörjes, 1968. North Sea. In fine gravel and mud.
Pseudohaplogonaria viridipunctata (Westblad, 1946). North Sea, Mediterranean, Adriatic. From soft bottoms, 5-40 m.

Genus *Simplicomorpha* Dörjes, 1968

Simplicomorpha gigantorhabditis Dörjes, 1968. North Sea. In coarse sand below swash zone.

Family OTOCELIDIDAE Westblad, 1948

Genus *Archocelis* Dörjes, 1968

Archocelis macrorhabditis Dörjes, 1968. North Sea. On shells and mud, 5 m.

Genus *Haplotestis* Dörjes, 1968

Haplotestis curvitubus Dörjes, 1968. North Sea. From coarse sand, 32 m.

Genus *Notocelis* Dörjes, 1968

Notocelis gullmarensis (Westblad, 1946). North Sea, Mediterranean. From coarse gravel with shells, shallow water.

Genus *Otocelis* Diesing, 1862

Otocelis rubropunctata (O. Schmidt, 1852). Mediterranean, Black Sea. Northern records of this are a separate species, *Otocelis westbladi*, according to Ax (1959). In detritus-rich fine sand.
Otocelis westbladi Ax, 1959. North Sea. From mud, 5-20 m.

Genus *Philocelis* Dörjes, 1968

Philocelis cellata Dörjes, 1968. North Sea. From detritus-rich sand, 2-6 m.
Philocelis karlingi (Westblad, 1946). North Sea, Baltic. In course sand, 2–6 m.

Family HOFSTENIIDAE Bock, 1923

Genus *Hofstenia* Bock, 1923

Hofstenia giselae Steinböck, 1966. Bimini. On *Thalassia.*
Hofstenia miami Correa, 1960. Florida and Curacao. On algae.

Family PARATOMELLIDAE Dörjes, 1968

Genus *Hesiolicium* Crezée and Tyler, 1976

Hesiolicium inops Crezée and Tyler, 1976. New River, N.C. In seawater.

Genus *Paratomella* Dörjes, 1966

**Paratomella rubra* Rieger and Ott, 1971. North Carolina, Mediterranean. In clean sand in shallow water.
Paratomella unichaeta Dörjes, 1966. North Sea. Clean sand and gravel, 3-5 m.

Family NADINIDAE Dörjes, 1968

One genus and one species only. Genus *Nadina*[8] Uljanin, 1870. Mediterranean.

Family ANAPERIDAE Dörjes, 1968

Genus *Achoerus* Beklemischev, 1914

Achoerus pachycaudatus Dörjes, 1968. North Sea. Shallow water, soft bottom.

Genus *Anaperus* Graff, 1911

Anaperus balticus Meixner, 1938 = *Anaperus tvaerminnensis.*
**Anaperus gardineri* Graff, 1911. Woods Hole, Mass. Sandy mud or mud, subtidal.
Anaperus rubellus Westblad, 1945. North Atlantic, Mediterranean. From soft bottom, 15-100 m.
Anaperus tvaerminnensis (Luther, 1912). North Sea to Iceland. From sand and mud to 36 m.

Genus *Palmenia* Luther, 1912

Palmenia baltica Meixner, 1938 = *Anaperus tvaerminnensis.*
Palmenia tvaerminnensis Luther, 1912 = *Anaperus tvaerminnensis.*

Genus *Palmeniola* Forsius, 1925

Palmeniola baltica Meixner, 1938 = *Anaperus tvaerminnensis.*
Palmeniola tvaerminnensis Forsius, 1925 = *Anaperus tvaerminnensis.*

Genus *Paranaperus* Westblad, 1942

Paranaperus pellucidus Westblad, 1942. North Sea, Adriatic. From soft bottom, 20-150 m.

Genus *Philachoerus* Dörjes, 1968

Philachoerus johanni Dörjes, 1968. North Sea. On surface of mud.

[8] *Myostomella* Riedl, 1954, is a synonym of this genus.

Family ANTIGONARIIDAE Dörjes, 1968

Genus *Antigonaria* Dörjes, 1968

Antigonaria arenaria Dörjes, 1968. North Sea. From fine sand, 5 m.

Family CHILDIIDAE Dörjes, 1968

Genus *Actinoposthia* An der Lan, 1936

Actinoposthia biaculeata Faubel, 1974. North Sea. From coarse sand in swash zone, 6-9 m.
Actinoposthia caudata An der Lan, 1936. Greenland. 180-300 m.
Actinoposthia haplovata Dörjes, 1968. North Sea. From fine sand, 5 m.
Actinoposthia longa Faubel, 1976. North Sea. In beach sand.
Actinoposthia pigmentea Faubel, 1976. North Sea. From sandy shallows or in sand to 10 cm.

Genus *Adeloposthia* An der Lan, 1936

One species *A. elegans* = *Parapropors elegans.* An der Lan listed this as a species of "uncertain position" and Dörjes (1968a) moved it into *Paraproporus.*

Genus *Archactinoposthia* Dörjes, 1968[9]

Archactinoposthia pelophila Dörjes, 1968. North Sea. Clay and sand, 5 m.

Genus *Atriofronta* Dörjes, 1968

Atriofronta polyvacuola Dörjes, 1968. Fine to coarse sand, to 5 m.

Genus *Childia*, 1910

Childia baltica Luther, 1912 = *Childia groenlandica.*
**Childia groenlandica* (Levinson, 1879). North Atlantic, South Atlantic (Brazil), East and West coasts of the United States, Mediterranean. Mud, algae, plankton, to 80 m.
Childia pansa Marcus, 1950 = *Childia groenlandica.*
**Childia spinosa* Graff, 1911 = *Childia groenlandica.*

Genus *Microposthia* Faubel, 1974

Microposthia listensis Faubel, 1974. North Sea. In sandy beach.

Genus *Paraphanostoma* Steinböck, 1931

Paraphanostoma brachyposthium Westblad, 1942. North Sea. Common in dredge hauls. From muddy bottom, to 360 m.

[9]In his key and definition of genera, Dörjes (1968a) lists a genus *Proactinoposthia* and a species *Proactinoposthia pelophila*, but description of a species *Archactinoposthia pelophila* is placed in position for this genus (p. 335) and it is so listed in Dörjes' (1968b) article on the ecology of the acoels.

Paraphanostoma crassum Westblad, 1942. North Sea, Adriatic. From soft bottom, 10-130 m.
Paraphanostoma cycloposthium Westblad, 1942. North Sea, Adriatic. From soft bottom, to 250 m.
Paraphanostoma dubium Westblad, 1942. North Sea to Iceland, Adriatic. From clay, 30-700 m.
Paraphanostoma gracilis Westblad, 1945. North Sea. From clay and sand, 5-60 m.
Paraphanostoma macroposthium Steinböck, 1931. North Atlantic to Iceland, Adriatic. Mostly from soft bottom, to 22 m.
Paraphanostoma submaculatum Westblad, 1942. North Sea, Adriatic. From soft bottom, 5-180 m.
Paraphanostoma trianguliferm Westblad, 1942. North Sea. From mud, sand, and shell gravel, 25-400 m.

Genus *Paraproporus* Westblad, 1945

Paraproporus diovatus Dörjes, 1968. North Sea. In fine mud.
Paraproporus elegans (An der Lan, 1936). Greenland, Iceland.
Paraproporus rosettiformis Faubel, 1974. North Sea. In medium to fine sand in shallow water.
Paraproporus rubescens Westblad, 1945. North Sea, Adriatic. From mud, 5-20 m.

Genus *Pelophila* Dörjes, 1968

Pelophila cavernosa Dörjes, 1968 = *Pelophila lutheri.*
Pelophila lutheri (Westblad, 1946). North Sea to Iceland, Mediterranean. From clay or mud, to 120 m.
Pelophyla pachymorpha Dörjes, 1968. North Sea. In coarse gravel.

Genus *Philactinoposthia* Dörjes, 1968

Philactinoposthia adenogonaria Dörjes, 1968. North Sea. From mud, 8 m.
Philactinoposthia diploposthia Dörjes, 1968. North Sea. Fine sand with some detritus, 5 m.
Philactinoposthia helgolandica Dörjes, 1968. North Sea. From coarse sand, 33 m.
Philactinoposthia pusilla (Westblad, 1946). North Sea. From sand and clay, 10-20 m.
Philactinoposthia rhammifera (Westblad, 1946). North Sea to Iceland. Occurs sporadically, 15-20 m.
Philactinoposthia saliens (Graff, 1882). North Sea, Mediterranean. From sand and mud, mostly shallow water.
Philactinoposthia stylifera (Westblad, 1946). North Sea. From clay with sand, 10-20 m.
Philactinoposthia viridis Dörjes, 1968. North Sea. From growth on an old shipwreck.
Philactinoposthia viridorhabditis Dörjes, 1968. North Sea. From fine sand.

Genus *Proactinoposthia* Dörjes, 1968

Proactinoposthia pelophila Dörjes, 1968 = *Archactinoposthia pelophila.*

Genus *Pseudactinoposthia* Dörjes, 1968

Pseudactinoposthia granaria Dörjes, 1968. North Sea. From fine sand, 8 m.

Pseudactinoposthia saltans Dörjes, 1968. North Sea. In growth on side of a boat.

Genus *Tetraposthia* An der Lan, 1936

Tetraposthia colymbetis An der Lan, 1936. Greenland. Poorly known.

Family MECYNOSTOMIDAE Dörjes, 1968

Genus *Mecynostomum* Van Beneden, 1870

Mecynostomum agile Jensen, 1878 = *Archaphanostoma agile.*

Mecynostomum auritum (Schultze, 1851). North Sea, Mediterranean, Black Sea, salt spring in Germany. From sand and mud in shallow water. Past records of this species may actually involve the following: 1) *M. auritum* without a bursa and 2) these species with a bursa: *M. auritum* forma *typica* changed to *Pseudmecynostomum westbladi* Dörjes 1968; *M. auritum* forma *flavescens* changed to *Pseudmecynostomum flavescens* (Westblad 1946); and *M. auritum* forma *glandulosum* changed to *Postmecynostomum glandulosum* (Westblad 1946) (see Dörjes 1968a:116; Dörjes and Karling 1975:181).

Mecynostomum bathycolum Westblad, 1948 = *Pseudmecynostomum bathycolum.*

Mecynostomum haplovarium Dörjes, 1968. North Sea. From detritus-rich or muddy sand, shallow water.

Mecynostomum lutheri (Westblad, 1946) = *Pelophila lutheri.*

Mecynostomum macrobursalis (Westblad, 1946) = *Pseudmecynostomum macrobursalium.*

Mecynostomum macrospiriferum (Westblad, 1946) = *Archaphanostoma macrospiriferum.*

Mecynostomum minimum Westblad, 1946 = *Haplogonaria minima.*

Mecynostomum predatum Faubel, 1976. North Sea. In beach sand.

Mecynostomum tenuissimum Westblad, 1946 = *Proaphanostoma tenuissima.*

Genus *Paedomecynostomum* Dörjes, 1968

Paedomecynostomum bruneum Dörjes, 1968. North Sea. From sand with detritus, or muddy sand, shallow water to 10 m.

Genus *Paramecynostomum* Dörjes, 1968

**Paramecynostomum diversicolor* (Ørsted, 1845). North Atlantic, Mediterranean, Black Sea, Massachusetts, Rhode Island. Algae, mud, and sand in shallow water.

Genus *Philomecynostomum* Dörjes, 1968

Philomecynostomum lapillum Dörjes, 1968. North Sea. Detritus-rich sand, shallow water.

Genus *Postmecynostomum* Dörjes, 1968

Postmecynostomum glandulosum (Westblad, 1946). North Sea. From sand with mud, 5-20 m.

Postmecynostomum pictum Dörjes, 1968. North Sea. On mud or algae in *Mytilus* colonies, to 5 m.

Genus *Pseudmecynostomum* Dörjes, 1968

Pseudmecynostomum bathycolum (Westblad, 1948). North Sea. From soft bottom, 70-90 m.

Pseudmecynostomum boreale Faubel, 1977. North Sea. From detritus-rich, muddy sand.

Pseudmecynostomum bruneofilum Faubel, 1974. North Sea. In shallow water in sand down to 10 cm.

Pseudmecynostomum bruneum Dörjes, 1968. North Sea. Mixed sand, gravel, mud.

Pseudmecynostomum flavescens Dörjes, 1968. North Sea. From sand and muddy sand, to 30 m.

Pseudmecynostomum fragilis Dörjes, 1968. North Sea. From fine sand, 5-8 m.

Pseudmecynostomum granulum Dörjes, 1968. North Sea. Dredged, on algae.

Pseudmecynostomum juistensis Dörjes, 1968. North Sea. On mud, intertidal.

Pseudmecynostomum macrobursalium (Westblad, 1946). North Sea. From clay, 25-35 m.

Pseudmecynostomum maritimum Dörjes, 1968. North Sea. From coarse gravel, 8 m.

Pseudmecynostomum papillosum Faubel, 1974. North Sea. Shallow sand area.

Pseudmecynostomum pelophilum Dörjes, 1968. North Sea. Salt meadow ditch on mud.

Pseudmecynostomum westbladi Dörjes, 1968. North Sea. From mud or sand, to 10 m.

Family SOLENOFILOMORPHIDAE Dörjes, 1968

Genus *Endocincta* Crezée, 1975

**Endocincta punctata* Crezée, 1975. North Carolina. In sand flats.

Genus *Fusantrum* Crezée, 1975

**Fusantrum rhammiphorum* Crezée, 1975. North Carolina. In sand.

Genus *Myopea* Crezée, 1975

**Myopea crassula* Crezée, 1975. North Carolina. In sandy and muddy flats.

**Myopea latafaucium* Crezée, 1975. North Carolina. From sand flats.

Genus *Oligofilomorpha* Dörjes, 1968

Oligofilomorpha interstitiophilum Faubel, 1974. North Sea. From sand flats.

Oligofilomorpha karlingi Dörjes, 1971. North Sea. From muddy sand, 8 m.

Genus *Solenofilomorpha* Dörjes, 1968

Solenofilomorpha longissima Dörjes, 1968. North Sea. From muddy sand, 5 m.

Family ANTROPOSTHIIDAE Faubel, 1976

Genus *Adenopea* Antonius, 1968

Adenopea illardatus (Löhner and Micoletzky, 1911). Pelagic in Mediterranean.

Genus *Antroposthia* Faubel, 1974

Antroposthia axi Faubel, 1974. North Sea. In coarse sand.
Antroposthia unipora Faubel, 1974. North Sea. In beach sand.

Genus *Convoluella* Faubel, 1974

Convoluella brunea Faubel, 1974. North Sea. In shallow water to 10 cm in sand.

Genus *Unantra* Faubel, 1976

Unantra polyvacuola Faubel, 1976. North Sea. In sublittoral coarse sand.

Order NEMERTODERMATIDA Karling, 1940

Family NEMERTODERMATIDAE Steinböck, 1930

Genus *Flagellophora* Faubel and Dörjes, 1978

Flagellophora apelti Faubel and Dörjes, 1978. North Sea. From coarse sand and shell gravel, sublittoral.

Genus *Meara* Westblad, 1949

Meara stichopi Westblad, 1949. North Sea. In intestine and body cavity of holothurians.

Genus *Nemertoderma* Steinböck, 1930

**Nemertoderma bathycola*, Steinböck, 1930. North Atlantic to Greenland, North Sea, Mediterranean; Buzzards Bay and Vineyard Sound, Mass. Subtidal. Four geographic varities of this species have been designated (Dörjes 1968; Riedl 1960). Variety in our area may be different.
Nemertoderma rubra Faubel, 1976. North Sea. From coarse sand.
Nemertoderma sp. A, B. D. Reported by Tyler and Rieger (1977) from North Carolina.

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SYSTEMATIC INDEX

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ACKNOWLEDGMENTS

Preparation of the "Marine Flora and Fauna of the Northeastern United States" is being coordinated by the following Board:

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The Board, which 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.

Gratitude is expressed to Melbourne R. Carriker and to members of the Systematics-Ecology Program and the Marine Biological Laboratory at Woods Hole, who provided assistance, laboratory space, and library facilities for the study of Turbellaria. Drew University also provided funds, supplies, and the use of a small laboratory on the campus. Suggestions and critical reviews by a number of persons have been very helpful and are acknowledged here with gratitude. Grace Beach, Eva Montiero, and Susan Wier were most patient in typing and proofreading the manuscript.

COORDINATING EDITOR'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, where 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 often make possible prediction of attributes of organisms that have been inadequately studied.

Louise Bush has degrees in Zoology and Entomology and was teaching Invertebrate Zoology at Drew University when an NSF Science Faculty Fellowship and a sabbatical leave from Drew University provided her a year of study in marine biology in Florida and at Woods Hole, Mass. Her interest in Turbellaria began at this time and has continued with summer work at the Marine Biological Laboratory and at the Cornell University of New Hampshire Marine Laboratory on Appledore Island, Maine. Professor Emeritus of Zoology at Drew, she continues her work with Turbellaria and serves as assistant curator in the George M. Gray Museum at the Marine Biological Laboratory in Woods Hole.

Preparation of this manual was supported in part by a grant from the Environmental Protection Agency to the Editorial Board of the "Marine Flora and Fauna of the Northeastern United States." Work on the "Marine Flora and Fauna of the Northeastern United States" by the Coordinating Editor is supported by the College of Marine Studies, University of Delaware.

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