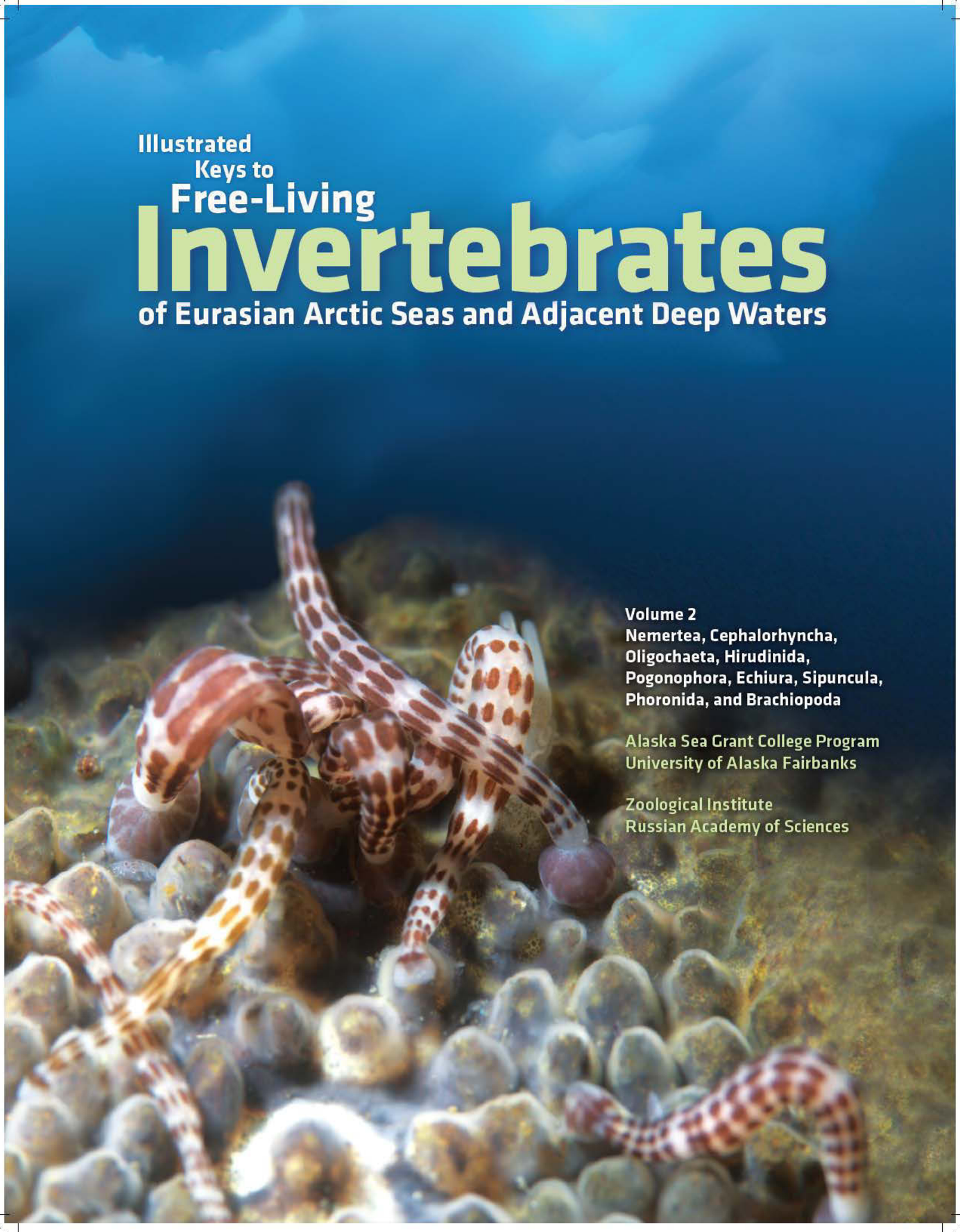
Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters



Volume 2
Nemertea, Cephalorhyncha, Oligochaeta, Hirudinida, Pogonophora, Echiura, Sipuncula, Phoronida, and Brachiopoda

Alaska Sea Grant College Program
University of Alaska Fairbanks

Zoological Institute
Russian Academy of Sciences

Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters

B.I. SIRENKO, SERIES EDITOR

Volume 2
Nemertea, Cephalorhyncha, Oligochaeta, Hirudinida, Pogonophora, Echiura, Sipuncula, Phoronida, and Brachiopoda

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Cover photo of *Heptacyclus virgatus* (Oka, 1910) (Hirudinida) by A. Ratnikov. Background under-ice photo by Elizabeth Siddon. Book and cover design by Garry Utermohle, garryou.com.

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Preface

This English translation is the second contribution in a series of volumes entitled *Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters*. This unprecedented attempt will provide the international science community with a comprehensive set of tools for marine species identification that are essential to an understanding of arctic and global biodiversity. The outstanding taxonomic expertise dedicated to these volumes is based on Russia's long history of arctic invertebrate taxonomy, as well as persistent exploration of the arctic seas and their fauna over the past century. Hundreds, if not thousands, of type specimens of arctic fauna are archived in the collections of the Zoological Institute in St. Petersburg and other major collections in museums and institutes around Russia.

Climate change, species invasions, fisheries effects, oil and gas exploration, tourism, and other major facets of the human footprint in the ocean are altering marine communities. To understand such change, biodiversity studies, from simple species inventories to functional linkages between diversity and ecosystems, have regained the prominence they deserve in the global scientific community. Within this context, the International Census of Marine Life (CoML) was launched in 2000, with its arctic component, the Arctic Ocean Diversity project (ArcOD), beginning in 2004. CoML is a global network of researchers in more than 80 nations engaged in a 10-year scientific initiative to assess and explain the diversity, distribution, and abundance of life in the oceans addressing the questions "What lived in the oceans in the past, what lives in the oceans now, and what will live in the oceans in the future?" Within this framework, ArcOD seeks to inventory biodiversity in the arctic sea ice, water column, and seafloor—from the shallow shelves to the deep basins—using a three-level approach: compilation of existing data, taxonomic identification of existing samples, and new collections focusing on taxonomic and regional gaps.

After review by an international panel of scientists, ArcOD was accepted as an official activity of the 2007-2009 International Polar Year (IPY). Thus, this book series stands as a unique and important contribution by ArcOD and the publisher, the Alaska Sea Grant College Program, to the legacy of 2007-2009 IPY.

To address biodiversity and other biological research questions in the Arctic, reliable and comprehensive identification keys are essential. ArcOD's Dr. Boris Sirenko has taken on the challenging and unparalleled task to coordinate the compilation of arctic invertebrate identification keys on a near panarctic scale. The ArcOD steering group identified this project as a major undertaking and legacy for ArcOD with the goal of facilitating, improving, and standardizing arctic taxonomy and species identification. This second key has been translated from Russian into English to make it available to a global audience. Volume 1 was published in 2009.

We are excited to facilitate the widespread distribution of this milestone in arctic diversity assessment. We thank the authors for their tireless efforts of putting the individual chapters together, Dr. Galina Buzhinskaja (Zoological Institute) for her efforts in editing this second volume, Dr. Boris Sirenko (Zoological Institute) for the grand oversight, Dr. Kenneth Coyle (University of Alaska Fairbanks) for the flawless translation, Sue Keller (Alaska Sea Grant) for the dedicated editing of the English version, and Alaska Sea Grant director Dr. David Christie for making publication possible.

Footnotes were added throughout by the ArcOD team to make the user aware of differences of opinion between chapter authors and other expert taxonomists.

—Bodil Bluhm, Rolf Gradinger, and Russ Hopcroft, Arctic Ocean Diversity Census of Marine Life project. The ArcOD project office is located at the University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Introduction

B.I. Sirenko

Despite the severe climate, the marginal seas of the Arctic Ocean sustain a fairly diverse fauna consisting of over 5000 species of free-living invertebrates. In recent years, the Arctic has attracted increasing attention. The scale of commercial development of useful minerals has been growing, not only along the shore but also on the shelf. Measures are required to minimize the anthropogenic impacts on the living resources and to preserve the unique arctic fauna. This is not possible without accurate information on the species diversity and quantitative distribution of all the characteristic fauna of the arctic seas, and this cannot be done without keys.

Until now, specialists studying the faunistic composition of arctic seas have relied on the book *Keys to the Fauna and Flora of the Northern Seas of the USSR*, edited by N.S. Gaevskaya. This source was highly regarded in its time but is now 50 years old and very outdated. It contains only about 30% of the currently known species in the northern seas of Russia. In addition, many of the species names in the book are no longer valid. For the above reasons, a new key is being generated consisting of a series of separately published volumes. The original hope was to place all ~5000 species into eight volumes, arranged according to the systematic affinities of the various groups, but this proved impractical. It was therefore decided to publish the volumes separately in the order that they are completed, but more or less maintaining the arrangement of each group according to its systematics.

This volume of the *Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters* covers groups of wormlike invertebrates composed of a small number of species: nemertines, priapulids, kinorhynchs, oligochaetes, leeches, pogonophorans, echiurans, sipunculans, phoronids, and brachiopods.

Some of the species in these groups are among the dominant or subdominant animals in the benthic communities of the arctic seas. Among those are the large sipunculan *Golfingia margaritacea*, the priapulid *Priapulus caudatus*, and others. The most species-rich of the groups, the nemertines, contains both bathyal and pelagic members, and the most widely distributed arctic species include *Poseidon (=Lineus) ruber* and *Cerebratulus marginatus*. Oligochaetes are especially abundant in shallow waters where they also commonly dominate benthic communities. Kinorhynchs are not very well studied with respect to their taxonomy and the species currently known consist of only a portion of the kinorhynch species likely inhabiting the meiobenthos. Most of the leaches in arctic seas attach to fish, crustaceans, and pycnogonids but they are also found unattached and they are therefore included in the key, which covers the free-living species. The relatively small brachiopod group occurs mainly in lower sublittoral and bathyal regions.

Compared to the previously published *List of Species of Free Living Invertebrates of the Eurasian Arctic Seas and Adjacent Deep Waters* (2001), this book presents more detailed information on both the species composition and the distributions of the species thanks to the processing of new material from the Laptev and Chukchi seas. The illustrated keys include all species actually collected from the Eurasian seas of the Arctic and adjacent deep regions of the central Arctic Basin (Fig. 1).

Each key is organized in a single format: (1) a short characterization of the group, including an explanation of the terms used in the keys; (2) individual keys for each taxonomic group from class to species; (3) a brief summary of two to three of the more important synonymies, the species' zoogeographic grouping, its typical distribution across its range, its horizontal and vertical distribution within the area covered by the key, and a brief summary of its ecology; (4) a list of the important literature sources for the group; (5) figures

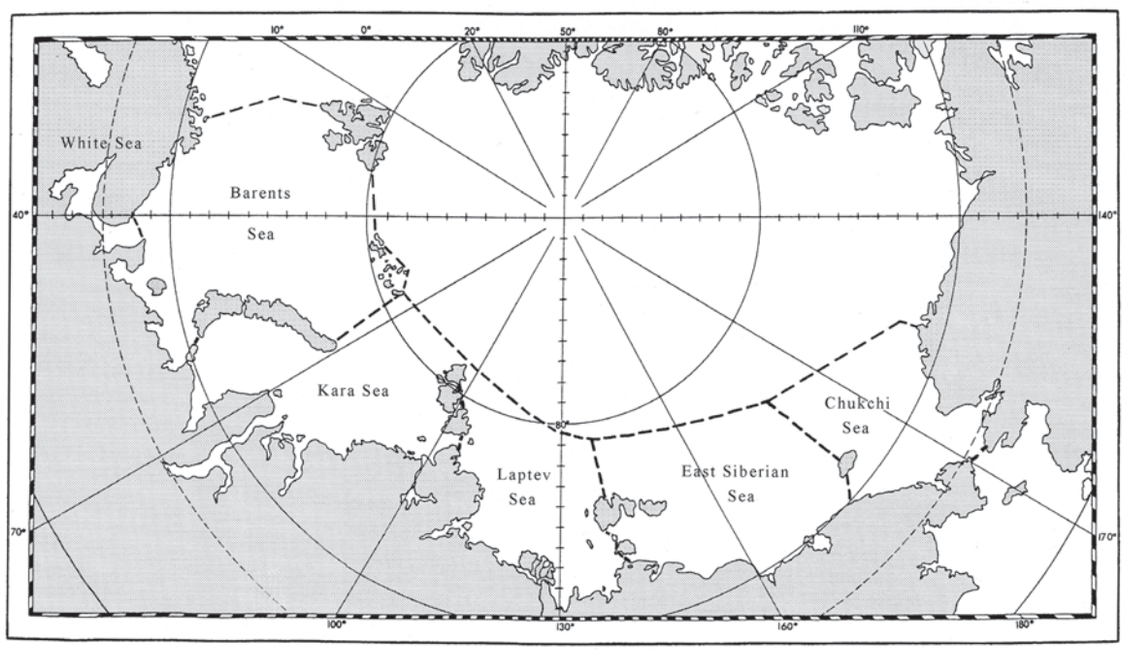

Figure 1. Map showing locations of Eurasian arctic seas and adjacent central Arctic Basin, as referenced in this volume.

and/or photographs. Each volume includes an appendix with a list of zoogeographical groups with their characteristics and a map showing the area of the species in the world's oceans.

Most taxonomists use parenthetical keys (E. Mayr, 1969, Principles of systematic zoology, McGraw-Hill, New York, 428 pp.). This format is also used in our illustrated keys. This key has the advantage that the thesis and antithesis occur next to or near one another, which facilitates comparison. With this format, it is easy to move both forward and backward following the numbers, which indicate the route moving through the various selections.

All keys were prepared by highly qualified, experienced taxonomists from a variety of scientific institutions of Russia, Ukraine, Estonia, and the U.S.A. including: Zoological Institute of the Russian Academy of Sciences (RAS), St. Petersburg, Russia, (Y.V. Mamkaev, R.V. Smirnov, G.N. Buzhinskaja); A.V. Zirmunskiy Institute of Marine Biology, Far East Division of RAS, Vladivostok, Russia (A.V. Adrianov and A.V. Chernyshev); the P.P. Shirshov Institute of Oceanology, Moscow, Russia (O.N. Zezina); the P.G. Demidov State University of Yaroslavl, Yaroslavl, Russia (V.P. Semernoy); the Institute of Biology of the Southern Seas of the Ukrainian National Academy of Sciences, Sevastopol, Ukraine (V.V. Murina); the V.N. Karazin National University of Kharkiv, Kharkiv, Ukraine (S.Y. Utevsky); Estonian University of Life Sciences, Tartu, Estonia (T. Timm); and the Institute of Marine Biology, Charleston, Oregon, U.S.A. (S.A. Maslakova).

Considering the great interest of colleagues from Europe, the U.S.A., Canada, and many other countries in the creation of similar keys, this volume has been translated and prepared for publication in the United States. This was done by Ken Coyle, Bodil Bluhm, Rolf Gradinger, and Russ Hopcroft from the University of Alaska Fairbanks, Fairbanks, Alaska, U.S.A. All sections of the key were peer-reviewed by specialists on the respective groups of animals.

I sincerely thank all authors, reviewers, and the editor of the volume, G.N. Buzhinskaja, and also the above-mentioned American colleagues.

Phylum Nemertea

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Nemerteans, called ribbon worms, are primarily marine, occurring from the littoral zone to depths of 9000 m. They are mostly free-living benthic animals, although pelagic and symbiotic species are also known. About 1200 species have been described. The body is bilaterally symmetrical, elongated to thread-like, and unsegmented. Fixed specimens (especially in alcohol) can be very contracted and sometimes disintegrate into fragments. Species of the genus *Annulonemertes* have regular, fine, transverse constrictions that may create the appearance of true segmentation (Pl. VIII, Figs. 1, 3). Body length varies from several millimeters (in some interstitial species) to 30 m (*Lineus longissimus*). The color, although variable, is often the most obvious and characteristic diagnostic feature; however, after fixation it usually changes. It is, therefore, preferable to identify the animals while they are alive. The anterior end often has a pair of lateral cephalic slits through which a pair of cerebral organs open to the outside (Pl. I, Fig. 1; Pl. IV, Fig. 8; Pl. VI, Figs. 8, 9). Many of the enoplan (armed with stylets) and some anoplan (unarmed) nemerteans have a transverse or V-shaped furrow behind the cephalic slits (Pl. VI, Fig. 8), which is often referred to as the posterior cephalic slits or furrow (or the neck furrow), although the structure is unpaired in the vast majority of species. Many heteronemerteans have a "tail" called the caudal cirrus (Pl. IV, Figs. 2, 7), which may be lost during collection or fixation (in the latter case, its presence can sometimes be ascertained by a characteristic stub near the anus).

The body wall consists of the following layers: a ciliated epithelium, a connective tissue dermis (which is often mistakenly referred to as the basal lamina in the Russian literature), and two to four layers of circular and longitudinal muscles (Pl. II, Figs. 2, 4-7). The epithelium and the dermis collectively form the epidermis. Heteronemerteans have a special subepithelial stratum, called the cutis, which contains subepithelial glands and separate dermal muscle fibers. Almost all nemerteans have a layer of diagonal muscles between the outer circular muscles and the inner longitudinal muscles, but the layer is often very thin and not discernible in cross sections. All species except the aberrant *Arhynchonemertes axi* have a long muscular proboscis that rests in a special cavity called the rhynchocoel (Pl. I); the wall of the rhynchocoel has 1-3 (usually 2) muscle layers. The proboscis of enoplan nemerteans is tripartite, with the middle region containing stylets; the stylet apparatus consists of a base with one (Monostilifera) or several (Polystilifera) central stylets and sacs with accessory stylets (Pl. VII, Fig. 5; Pl. IX, Fig. 2). The shape of the base and stylets, as well as the length ratio of base (B) to central stylet (S) are used as specific characters in monostiliferan nemerteans. The structure of the anterior region of the proboscis (the distribution of muscle layers, the number of nerves, the presence of muscle crosses) is also important for identification of some nemerteans. The proboscis is everted through a terminal or subterminal opening called the rhynchopore. The foregut and rhynchopore in the majority of enoplan nemerteans open into a short canal, the rhynchostomodeum (or rarely into a shallow epithelial depression called the atrium). Therefore, in enoplans, the proboscis everts through a shared opening with the mouth called a rhynchostome (Pl. I, Fig. 3).

The digestive system consists of three regions: the anterior (foregut), middle (midgut or intestine), and posterior (hindgut). The mouth in anoplan nemerteans is located on the ventral side of the head behind the brain, and leads into a foregut, which is not further differentiated into regions (Pl. I, Fig. 1). The intestine can be with or

without lateral diverticula. The foregut in enoplan nemerteans is differentiated into the esophagus, stomach, and pylorus (from anterior to posterior). The enoplan intestine (midgut) has a blind anterior diverticulum, called the cecum, which is located below the pylorus, and often is equipped with lateral pouches.

The brain consists of two pairs of cerebral ganglia (dorsal and ventral); the right and left ganglia are connected by a commissure above (dorsal) and below (ventral) the rhynchocoel, forming a ring around it. The ventral ganglia attenuate posteriorly, giving rise to a pair of prominent lateral nerve cords; these meet in a posterior anastomosis near the anus. Often there is also an unpaired dorsal nerve, originating from the dorsal commissure of the brain. The brain and lateral nerve cords consist of a central fibrous core (neuropile) and a peripheral ganglionic region. The sense organs may include eyes, one or three frontal organs (Pl. I, Figs. 1, 2) and a pair of subepidermal cerebral organs. These often are fused to the posterior of the dorsal ganglia in anoplan nemerteans (Pl. I, Fig. 1), whereas in enoplan nemerteans they are most commonly located anterior to the brain (Pl. I, Fig. 3), but may be next to or posterior to the brain. The cerebral organs are represented by simple epithelial pits in the paleonemertean family Tubulanidae and are entirely absent in some nemerteans. A pair of epithelial lateral organs is found laterally some distance behind the mouth in many members of the families Tubulanidae and Callineridae; they appear as small, round to oval patches of modified epithelium, often of paler color than the surrounding epithelium (Pl. III, Fig. 3). Enoplans commonly have long tactile cilia or cirri (Pl. VIII, Fig. 6). Cephalic glands are present at the anterior end, but they are discernible only on sections and squash preparations (Pl. I, Figs. 2, 3).

The circulatory system is closed; in its simplest form it consists of two lateral vessels connected at the anterior and posterior ends of the body. A dorso-median blood vessel (Pl. I, Fig. 2) normally is found between the rhynchocoel and the gut in hetero- and hoplonemerteans. Large dilations of the blood vessels in the form of blood sinuses, also referred to as lacunae, are common in anoplan nemerteans. The blood is often colorless, but is red in some species. Most nemerteans have separate sexes; the numerous sac-like gonads are situated between the lateral diverticula of the gut (Pl. I, Fig. 2). Specialized copulatory organs are absent in benthic nemerteans. Sexual dimorphism is found only in some pelagic nemerteans. The testes in males of pelagic nemerteans occur in anterior clusters, while the ovaries in females are found along the sides of the body between the lateral diverticula, as is typical for other (benthic) nemerteans.

Identification of the majority of species requires knowing the color of the living specimens, which may have a characteristic pattern of spots or bands. The color is often paler on the ventral surface than on the dorsal surface. The gut contents, gonads, and reddish brain are commonly visible through the integument, which can influence the perceived color of the specimen. The color usually disappears completely after fixation in alcohol. It is better preserved in formalin, but certainly not in all species. When live nemerteans are compressed between two microscope slides (small specimens can be mounted between a slide and a cover glass), one can determine the number and distribution of the eyes, the length of the rhynchocoel, and the structure of the proboscis and gut, and, with some experience, determine the position of the cerebral organs and the structure of the circulatory system. In some heteronemerteans, the eyes do not contain dark pigment, and are, therefore, only detectable in transmitted light. The severed head of live nemerteans can be mounted in a drop of glycerin and compressed under a glass slide supported by clay feet. The eyes and brain can remain visible in this temporary preparation for over a month. Study of the stylet armature in nemerteans requires mounting the dissected proboscis of live specimens under a coverslip in a drop of seawater or a 1:1 mixture of seawater and glycerin. Dissection is most easily accomplished by cutting the nemertean into two parts with a scalpel or a razor blade; the proboscis usually falls out from the cut. If the proboscis is large, the bulky anterior region must be separated from the stylet-bearing middle region with a razor blade, in order to compress the proboscis to a sufficient degree to examine the stylets. Nemerteans can be fixed in Bouin's solution or a 4% solution of formaldehyde made up in ambient seawater, with mandatory anesthesia in an isotonic solution of 7.5% magnesium chloride mixed 1:1 with seawater. Note

that the head of anesthetized nemerteans often loses its characteristic shape and the integument becomes less translucent. Many species undergo severe muscular contraction under the influence of magnesium chloride, often resulting in autotomy (common for anoplans, less so for enoplans); therefore one should relax the worms gradually, first by adding 7.5% magnesium chloride diluted 1:1 with seawater, followed by a change in 7.5% magnesium chloride. In some cases, it is sufficient to treat small nemerteans with a 7.5% solution of magnesium chloride for 1-2 hours, but it may be necessary to relax large nemerteans (over several centimeters in length) in the anesthetic solution in a refrigerator (4ºC) for several hours. Cutting the partially narcotized worm into two or more pieces may accelerate the process. Histological preparations of nemerteans can be prepared after fixation in 4% formaldehyde (1-2 hours for small and up to 8 hours for large nemerteans), post-fixation in Bouin's picric-formal-acetic fixative (for 2-3 days), and subsequent storage in 70% ethanol.

The cephalic slits and neck furrow are clearly visible in fixed nemerteans, but the eyes often become indistinguishable. The stylets may partially or completely dissolve after prolonged storage in formalin. Examination of the stylet armature requires clearing of the middle region of the proboscis in xylene (or similar solvent) after dehydration in an alcohol series. Detailed study of nemertean anatomy requires preparation of serial paraffin sections (7-8 μ thick) of the anterior portion of the body, subsequent staining (Mallory's trichrome and its modifications work best), and mounting in Canada balsam, Permount, or some other media suitable for microscopic examination and long-term storage. The distribution of muscle layers in the body wall, the rhynchocoel and proboscis, and also the position of the lateral nerve cords can be determined on thick cross sections of the anterior third of the body of fixed specimens cut with a razor blade. Such sections can be lightly stained with methyl green or eosin. The length of the rhynchocoel and the presence of stylet armature can be ascertained by dissecting the fixed specimens with a razor blade along the dorsal surface.

The identification keys, where possible, are based on the most accessible characters. The color and body shape are based on live specimens unless otherwise stated. The key goes straight to species for the family Lineidae, and to genus for monostiliferan nemerteans. As the modern classification of nemerteans is undergoing revision, the rank of some groups is given in quotes. The genus names of species whose generic affinity is uncertain are also given in quotes.

Key to "subclasses" (or "classes") of the nemerteans

1(2) Mouth posterior to brain, always separate from the rhynchopore. Proboscis without a middle region bearing stylets. Brain and lateral nerve cords in the body wall (composed of epidermis and muscle layers). . . . . **Anopla**

2(1) Mouth and rhynchopore often share a common terminal or subterminal opening; rarely mouth is separate, but it is always anterior to the brain. Proboscis with middle region equipped with stylets (except Malacobdella). Brain and lateral nerve cords internal to epidermis and muscle layers of the body wall. . . . . **Enopla**

"Subclass" Anopla (unarmed nemerteans)

This paraphyletic group traditionally has been divided into the Paleonemertea and the Heteronemertea. Currently the heteronemerteans and the paleonemertean families Hubrechtiidae and Hubrechtellidae are united into a single taxon (superorder or subclass), the Pilidiophora. In this key, the paleonemerteans are divided into three orders.

Key to orders of the "subclass" Anopla

1(2) Mouth at a substantial distance behind the brain. Body very thin, thread-like, pre-oral region elongated, without cephalic slits or eyes. Lateral nerve cords and brain located in the inner longitudinal muscle layer of the body wall (Pl. II, Fig. 6) . . . . . **Archinemertea, family Cephalotrichidae, *Cephalothrix linearis* (Rathke, 1799) (Pl. II, Fig. 3)**

Length to 15 cm.
Eastern Atlantic widespread boreal. White Sea, Barents Sea.
Intertidal to 5 m, beneath rocks and among algae.
White or slightly yellowish worms without any pigment spots.

2(1) Mouth immediately behind the brain. Pre-oral region not usually elongated, often with lateral slits. Brain and anterior portion of lateral nerve cords not within the inner longitudinal muscle layer.

3(6) A well-developed layer of outer longitudinal muscle is absent, or present (*Carinoma*) in foregut region only. At least the anterior-most portion of the lateral nerve cords is intra- or subepidermal (Pl. II, Figs. 2, 4, 5). Head without distinct lateral slits and eyes. Middorsal blood vessel absent.

4(5) Lateral nerve cords within or beneath the epidermis for their entire length. Cerebral organs present. Lateral organs present or absent. Body of fixed (in formalin) specimens with a broad, dark band (usually claret or brown) a short distance behind the mouth. Intestine without distinct lateral diverticula . . . . . **Tubulaniformes, family Tubulanidae**

5(4) Lateral nerve cords are beneath the epidermis anteriorly, but submerged into the inner longitudinal muscle layer posteriorly. Cerebral and lateral organs absent. Fixed specimens pale colored, without broad dark band behind the mouth. Intestine with distinct lateral diverticula . . . . **Carinomiformes, family Carinomidae, *Carinoma uschakovi* Chernyshev, 1999**

Length to 35 mm.
Barents and White seas.
Upper subtidal, on silt or silty sand.
Color of live specimens not known (in other carinomids, the color is pale, monochromatic).

6(3) Well-developed outer layer of longitudinal muscles present along entire body. Lateral nerve cords between the layers of outer longitudinal muscles and circular muscles (Pl. II, Fig. 7). Head with lateral slits (often longitudinal) and usually with eyes. Middorsal blood vessel present . . . . . **Heteronemertea**

Key to genera of the family Tubulanidae

1(2) Brain and lateral nerve cords are intraepithelial. Lateral blood vessels underneath the inner circular muscle layer. Lateral organs absent. Color of live specimens likely pale with a darker band a short distance behind the mouth . . . . . ***Carinina***

2(1) Brain and lateral nerve cords (at least their fibrous portion) between dermis and the outer layer of circular musculature. Lateral blood

vessels outside the inner layer of circular muscles. Lateral organs present or absent. Background body color orange, red, or brown.

3(4) Body often with transverse and longitudinal white bands. The ganglionic and fibrous portion of the lateral nerve cords and brain are separated from the epithelium by dermis. Lateral organs present or absent . . . . . ***Tubulanus***

4(3) Body an intense orange or red color, without white longitudinal and transverse bands. Ganglionic portion of brain and lateral nerve cords is directly beneath the epithelium; fibrous portion of lateral nerve cords is beneath the dermis. Lateral organs present . . . . . ***Protubulanus*** **Chernyshev, 1995, *Protubulanus* cf. *theeli* (Bergendal, 1902) (Pl. III, Figs. 1-3)**

Length 3-4 cm.
White Sea.
Depth 30-40 m, in mud.

Key to species of *Carinina* Hubrecht, 1885

1(2) Only upper dorsal nerve present. Cephalic blood lacuna simple . . . . . ***C. wijnhoffae*** **Kulikova, 1984 (Pl. III, Fig. 1)**

Length to 48 mm (fixed specimens).
White Sea.
Depth 20-160 m, soft sediment.

2(1) Both the upper and lower dorsal nerves present. Cephalic blood lacuna forms a net of anastomosing branches near the proboscis opening. . . . . ***Carinina*** **sp. (Pl. II, Fig. 2)**

Synonymy: *Procarinina atavia* sensu Uschakov, 1928
Length to 30 mm (fixed specimens).
Barents Sea.
Subtidal.

Key to species of *Tubulanus* Renier, 1804

1(2) Longitudinal stripes absent, only transverse white rings are present. Background color dark red, anterior margin of head white. The anterior three rings are farther apart than the subsequent rings . . . . . ***T. albocinctus*** **(Coe, 1904) (Pl. III, Fig. 5)**

Length to 30 cm.
Eastern Pacific widespread boreal. Chukchi Sea.
Upper subtidal zone.

2(1) White longitudinal stripes present.

3(4) Background color brownish-red to orange-red, with white transverse rings and three longitudinal stripes; the first transverse band is on the head. Lateral organs possibly absent . . . ***T. annulatus*** **(Montagu, 1804) (Pl. III, Fig. 6)**

Length to 75 cm
Atlantic subtropical-boreal. Reported from Chukchi Sea (North American coast), likely also occurs in the Barents Sea.

4(3) Background color dark brown, with white transverse rings and three longitudinal thin stripes; first transverse band posterior to the head. Lateral organs near the third transverse band. . ***T. capistratus*** **(Coe, 1901) (Pl. III, Fig. 4)**

Length to 100 cm.
Eastern Pacific high boreal. Chukchi Sea (North American coast).
Upper subtidal, beneath rocks.

Key to families of the order Heteronemertea

1(2) Lateral cephalic slits oblique or transverse (sometimes poorly developed), often with thin longitudinal accessory furrows on the slits. Musculature of the proboscis consists of outer longitudinal and inner circular layers; muscle crosses absent (Pl. IV, Fig. 5). One frontal organ present. Caudal cirrus absent . **Baseodiscidae, genus *Baseodiscus, Baseodiscus* sp.**

Length unknown.
White Sea.
Upper subtidal, silt.

2(1) Lateral cephalic slits longitudinal, long. Proboscis musculature consists of outer longitudinal, circular, and inner longitudinal layers, or outer circular and inner longitudinal layers; often there are two (rarely one) muscle crosses (Pl. IV, Fig. 6). Usually with three frontal organs. Caudal cirrus present or absent. . . . . **Lineidae**

Key to species of the family Lineidae

Identification of the lineid genera is an extremely complicated procedure. Therefore, the key goes straight to the species level. The key does not include the following species, whose validity is doubtful: *Lineus sainthilairi* Uschakov, 1926 and *L. marisalbi* Uschakov, 1926 (White Sea); *Cerebratulus zachsi* Uschakov, 1926 (White and Barents seas); and *C. rigidus* Isler, 1900 (Barents Sea). Earlier the species *Lineus kristinebergensis* Gering, 1912 was reported from the White Sea (Uschakov, 1926), but our examination of the specimens held at the Zoological Institute in St. Petersburg did not confirm the record.

1(2) Lateral cephalic slits very long, reach behind the mouth . . . . . ***Cerebratulus fissuralis*** **Friedrich, 1958 (Pl. IV, Fig. 8)**

Synonymy: *Cerebratulus longifissus* sensu Punnett, 1903.
Length unknown (known from fragments), width to 8 mm.
Atlantic high boreal. Barents Sea.
Depth 70 m.
Color snow white.

2(1) Lateral cephalic slits do not extend behind the mouth.

3(4) Body of fixed (in alcohol) specimens very short and wide: the ratio of the width to length is 1:2-3. . . . . ***"Cerebratulus" brevis*** **Uschakov, 1926 (Pl. V, Fig. 1)**

Length 3-4 cm (fixed specimen), body substantially flattened, edges of the body are pointed. The color of live specimens is not known. Proboscis with two layers of muscles; therefore

assignment to the genus *Cerebratulus* is provisional.
White Sea.
Depth 274 m, silt.

4(3) Body of fixed specimens is longer and narrower.

5(18) Several dark ocelli are found on each side of the head near lateral cephalic slits.

6(11) Caudal cirrus absent (in live specimens with undamaged posterior end).

7(8) Body width to 1.2 mm, coils when contracted. Body cream-colored, grayish-green, reddish, or brown. Capable of sexual (unknown for specimens from Russian seas) and asexual reproduction (by fission); development via a pilidium larva . . . ***Ramphogordius sanguineus*** **(Rathke, 1799) (=** ***Lineus sanguineus*****) (Pl. IV, Fig. 3)**

Length to 20 cm.
Bipolar. White Sea.
Intertidal, under rocks and among algae.

8(7) Body width to 3-4 mm, does not coil when contracted, but it broadens and shortens. Reproduces sexually only.

9(10) Body color red, brownish-red, violet-red, rarely yellowish-brown; sometimes with thin light transverse bands that may appear as constrictions. Egg cases 1.5-2 cm long, covered with thick, parchment-like membrane, resistant to desiccation (Pl. V, Fig. 8). Develops via encapsulated adelphophagous Desor's larvae . . . . . ***Poseidon ruber*** **(Müller, 1774) (=** ***Lineus ruber*****) (Pl. V, Figs. 4-6)**

Length to 20 cm.
Subtropical-Arctic. White, Barents, Kara, and Chukchi seas.
Intertidal to 15 m depth, under rocks, among algae and mussels.
Survives low salinity to 8 parts per thousand.

10(9) Body color green, grayish-green, brownish-green, olive, rarely dark-gray; mature specimens often with very thin light transverse and sometimes longitudinal (lateral and dorsal) bands and small whitish lateral spots indicating position of the gonopores. Egg cases 3-4 cm long, covered with a thin and soft membrane (Pl. V, Fig. 7). Develops via encapsulated lecithotrophic Desor's larva . . . . . ***Poseidon viridis*** **(Müller, 1774) (Pl. V, Fig. 8)**

Synonymies: *Lineus viridis, L. gesserensis* Dalyell, 1853; *L. desori* Schmidt, 1946.
Length to 20 cm.
Subtropical-Arctic.
Distribution and ecology similar to that of *P. ruber*, but it occurs and deposits egg cases lower on the intertidal, and is more sensitive to low salinity.
Newly hatched juveniles of both species are nearly white (unpigmented), with two eyes. One commonly sees specimens with intermediate coloration between the two species; however, the presence of hybrids has not been verified genetically.

11(6) Caudal cirrus present.

12(13) Lateral margins of the body are thin, paler than the dorsal side. Body strongly flattened. Yellowish, grayish, or rose, with small, dark (rarely orange) spots on the dorsal surface . . . . . ***Cerebratulus fuscus*** **(McIntosh, 1873-1874) (Pl. IV, Fig. 4)**

Length to 10 cm.

Atlantic subtropical-boreal. Reported from Chukchi Sea (North American coast) and White Sea.
Subtidal.

13(12) Lateral margins of the body rounded, not paler than the dorsal side. Not yellowish, grayish, or rose.

14(15) Dorsal side reddish-brown, rarely yellowish-brown, dirty green, or reddish-violet, always with white transverse bands (ventral side lighter, without bands). Head sometimes with a white spot on dorsal side. Eyes 3-12 on each side of head . . . . . ***Micrura fasciolata*** **Ehrenberg, 1828 (Pl. IV, Fig. 2)**

Length to 15 cm.
Atlantic subtropical-boreal. Barents and White seas.
Intertidal to 30 m depth; on rocky bottom and shell hash.

15(14) Primary color of dorsal side grayish-green, brownish-green, rarely reddish-purple; without transverse white bands (not to be confused with light constrictions between the body "segments," which are sometimes present in large specimens) or a white spot on the head. Specimens with greenish pigmentation often have a rose-colored or red head. Eyes 4-20 on each side of head.

16(17) Body length 2-5 cm. With four pairs of eyes. Mouth round . . . . . ***Micrura varicolor*** **Punnett, 1903**

Eastern Atlantic high boreal. Barents and White seas.
Depth 30-256 m, on rocky bottom and mixed sediments, aleurites.

17(16) Body length 6-7 cm. With 10-12 pairs of very small eyes. Mouth elongate. . . . . ***Micrura*** **sp. (Pl. V, Fig. 3)**

White Sea.
Depth 3-40 m, on silt.
Possibly a pale form of *M. fasciolata*.

18(5) Eyes either absent or lack dark pigment, or small and nearly undetectable.

19(24) Body strongly flattened, wide, with sharp, pale margins. Caudal cirrus present. Capable of swimming with undulating motion.

20(21) Body margins yellowish; cephalic slits yellowish-rose at margins. Dorsal side of body chestnut-brown . . . . . ***Cerebratulus borealis*** **(Diesing, 1845)**

Length to 10 cm (fixed specimens).
Arctic. White and Barents seas.
Depth 50-200 m.

21(20) Body margins pale (often white), but not yellow.

22(23) Dorsal side of body blackish-brown. Cephalic blood sinus does not surround the cerebral organs . . . . . ***Cerebratulus barentsi*** **Bürger, 1895 (Pl. IV, Fig. 9)**

Length to 10 cm (fixed specimens).
Arctic. White, Barents, and Kara seas, and Spitsbergen.
Depth 100-200 m. Silt with pebbles.

23(22) Dorsal side of body gray, brownish-gray, or rosy-gray. Cephalic blood sinus surrounds the cerebral organs . ***Cerebratulus marginatus*** **Renier, 1807 (Pl. VI, Figs. 1-2)**

Length to 40 cm.
Widespread boreal Arctic. White, Barents, Chukchi, and Kara seas, and Spitsbergen.
Intertidal to 220 m depth. On silty sediments.
Very small, almost undetectable eyes (1-3 on each side) may be present near the anterior end of the cephalic slits in some specimens. Likely a species group.

24(19) Body, if flattened, not wide; body margins not sharp; not capable of swimming.

25(26) Dorsal side of body uniformly colored bright reddish-rose . . . . . ***"Lineus"*** **kolaensis Uschakov, 1928**

Length to 60 cm.
Barents Sea.
Depth 258 m.
Proboscis with three muscle layers; therefore its assignment to *Lineus* is provisional.

26(25) Dorsal side of body not uniformly colored bright reddish-rose.

27(28) Body dark brown or yellowish-brown with two white or yellowish dorsal longitudinal stripes. Caudal cirrus absent . . . . . ***"Lineus" bilineatus*** **(Renier, 1804) (Pl. V; Fig. 2)**

Length to 70 cm.
Amphiboreal. White Sea
Upper subtidal, silt.
This species is different from the genera *Lineus* and *Poseidon* both morphologically and genetically; therefore it must be placed in a different genus, for which one could resurrect the name *Siphonenteron* Renier, 1847.[1]

28(27) Body without pale dorsal longitudinal stripes. Caudal cirrus present or absent.

29(30) Body about 1 mm wide, white, without caudal cirrus . . . . . ***"Cerebratulus" niveus*** **(Punnett, 1903)**

Length to 3 cm.
Eastern Atlantic high boreal. White and Barents seas.
Depth 115-225 m.

30(29) Body 2-4 mm wide, not white, caudal cirrus present.

31(32) Body purplish-brown dorsally. Anterior tip of head white, often with yellowish eyespots . . . . . ***Micrura purpurea*** **(Dalyell, 1853) (Pl. IV, Fig. 1)**

Length to 20 cm.
Atlantic widespread boreal. Barents Sea (Scandinavian coast)

[1] Editorial note: opinions by other Nemertea taxonomists differ on this statement.

and Chukchi Sea (North American coast).
Subtidal, among rocks and *Laminaria*.

32(31) Body pinkish, brownish-rose, or light brown. Anterior tip of head without yellow eyespots.

33(34) Ventral side of body with median cream or rose-colored stripe (through which the gut is visible). Head margins light colored, but not white. Subepithelial glands highly developed in the foregut. . . . . .***Micrura alaskensis*** **Coe, 1901 (Pl. IV, Fig. 7)**

Length to 50 cm.
Pacific widespread boreal. Chukchi Sea (North American coast).
Intertidal, beneath rocks.

34(33) Ventral side of body without median pale stripe. Head margins and cephalic slits white. Subepithelial glands not developed in foregut. . . . . .***Micrura lithotamnii*** **Uschakov, 1928**

Length to 16 cm.
Barents Sea.
Depth 8-10 m, on *Lithothamnion*.

Key to the subclass Enopla (= Hoplonemertea)

To facilitate identification, the family Malacobdellidae is listed separately, although it belongs to Eumonostilifera.

1(2) Stylets absent. Body with a posterior sucker. Intestine without lateral diverticula, zigzags through the body . . . . . **family Malacobdellidae,** ***Malacobdella grossa*** **(Müller, 1776) (Pl. VI, Fig. 3)**

Length to 3 cm.
Amphiboreal. White and Barents seas.
Commensal in the mantle cavity of bivalves *Arctica islandica* and *Mya truncata*.

2(1) Stylets present. Sucker absent. Intestine not as above.

3(7) Stylet armature of the polystiliferan type: several short conical stylets on an arch-shaped base (Pl. VII, Fig. 5). . . . . .**order Polystilifera**

5(6) Cerebral organs and nephridia present. Rhynchocoel with long branching lateral diverticula, rhynchocoel wall comprises interwoven muscle fibers (Pl. VI, Fig. 5). Benthic. Body wide, flattened, dorsal side of body reddish-brown . . . . . **suborder Reptantia, family Uniporidae,** ***Uniporus borealis*** **(Punnett, 1901) (Pl. VI, Fig. 4)**

Length to 58 mm.
Atlantic high boreal. Barents Sea.
Depth 200-250 m.

6(5) Cerebral organs and nephridia absent. Rhynchocoel without lateral diverticula, rhynchocoel wall comprises three separate muscle layers with occasional interlacing of muscle fibers (Pl. VII, Fig. 4). Pelagic. Body without dark pigment . . . . . **suborder Pelagica, family Dinonemertidae**

7(3) Stylet armature of monostiliferan type: a single central stylet on an elongated pear-shaped base (Pl. IX, Fig. 2) . . . . . **suborder Monostilifera**

8(9) Lateral cephalic furrows well developed, with thin secondary longitudinal furrows (poorly distinguishable in fixed material). Neck furrow often located at a considerable distance behind the brain. Eyes numerous, large. Wall of rhynchocoel comprises interwoven muscle fibers. Central stylet always longer than base. Sometimes an additional stylet present within the base . . . . . **suborder Cratenemertea, family Cratenemertidae**

9(8) Lateral cephalic furrows developed to varying degrees, without secondary longitudinal furrows. Neck furrow located immediately behind the brain or in the brain region, rarely absent. Size and number of eyes variable, sometimes absent. Wall of rhynchocoel comprises two separate muscle layers. Central stylet usually shorter or equal in length to base, rarely longer than base. Additional stylet absent inside base . . . . . **suborder Eumonostilifera**

Suborder Pelagica, Family Dinonemertidae
Key to species of the genus *Dinonemertes* Laidlaw, 1906

1(2) Rhynchopore and mouth open separately. Cecal diverticula do not appear inflated . . . . . ***D. alberti* Brinkmann, 1917, (non *Planktonemertes alberti* Joubin, 1906) (Pl. VII, Fig. 6)**

Length to 76 mm.
Atlantic Arctic bathyal. Central Arctic Basin.
Bathypelagic, deeper than 1000 m.

2(1) Rhynchopore and mouth open in a common slit-like depression (atrium). Cecal diverticula appear inflated . . . . . ***D. arctica* Korotkevitsch, 1977 (Pl. VII, Figs. 1-4)**

Length to 72 mm.
Arctic bathyal. Central Arctic Basin.
Bathypelagic.

Suborder Cratenemertea, Family Cratenemertidae
Key to species of the genus *Nipponnemertes* Crandall, 2001

1(2) Eyes form four indistinct longitudinal rows: two outer rows (along the head margins) with large eyes and two inner rows with smaller eyes. Dorsal side of body brownish-red in fixed specimens . . . . . ***N. pacifica* (Coe, 1905) (Pl. VI, Fig. 6)**

Length to 75 mm (fixed specimens).
Eastern Pacific widespread boreal. Chukchi Sea (North American coast).
Upper subtidal.

2(1) Eyes do not form longitudinal rows. Dorsal side of body brown, red, or rose-colored in live specimens . . . . . ***N. pulchra* (Johnston, 1837) (Pl. VI, Figs. 7-9)**

Length to 60 mm.
Atlantic widespread boreal. White Sea, Spitsbergen.
Upper subtidal, various sediment types.

Key to genera of the suborder Eumonostilifera (= Distromatonemertea)

1(2) Body appears "segmented." Eyes absent. . . . . **genus *Annulonemertes***

2(1) Body unsegmented.

3(4) Body divided into two regions: narrower anterior region with rhynchocoel and wider posterior region with gonads. Body pinkish in live specimens. With two eyes . . . . . **Monostilifera gen. sp. 1 (Pl. VIII, Figs. 4, 5)**

Length 4-5 mm.
White Sea.
Depth 120 m. Silt.

4(3) Body not divided into two distinct regions.

5(6) Cirri distributed all over the body. Eyes absent. Ovaries (each with a single oocyte) restricted to posterior half of body . . . . **Monostilifera gen. sp. 2 (Pl. VIII, Figs. 6, 7)**

Length 3-3.5 mm.
White Sea.
Depth 40 m. Sand.

6(5) Cirri, if present, located terminally only (on the head and posterior end of body). Eyes present or absent. Ovaries located in both the posterior and anterior halves of body.

7(18) Head with four simple, double, or compound (consisting of several ocelli) eyes (eyes can be masked by dark head pigment).

8(9) Rhynchocoel no more than ¼ of body length. Commensal with sea anemones. . . . . **genus *Cryptonemertes, C. actinophila* (Bürger, 1904) (Pl. VII, Fig. 10)**

Length to 40 mm.
Widespread boreal Arctic, circumpolar. Barents Sea and likely White Sea, Spitsbergen.
Subtidal, beneath the pedal disk of sea anemones (primarily *Stomphia*).
Color orange to reddish-brown, blood is red.

9(8) Rhynchocoel considerably longer than half the body length. Free living.

10(15) Eyes simple.

11(14) Body somewhat flattened with wider head. Cerebral organs medium to large, located very close to the brain or immediately adjacent to it. Cephalic furrows well-developed.

12(13) Blood is colorless. . . . . **genus *Tetrastemma***

13(12) Blood is red . . . . . **genus *Quasitetrastemma, Q. bicolor* (Coe, 1901) (Pl. XI, Fig. 8)**

Length to 6 cm.
Pacific high boreal. Chukchi Sea.
Intertidal and upper subtidal to 50 m depth, among algae.
Dorsal side of body from light brown to dark brown, with a median light stripe (color retained in formalin).

14(11) Body round in cross section, head same width as adjacent body or slightly narrower. Cerebral organs very small, located far in

front of brain. Cephalic furrows very short, barely distinguishable or absent . . . . . **genus *Oerstedia***

15(10) Eyes double or compound (each consisting of 2-7 ocelli, distinguishable only with the compound microscope).

16(17) Eyes double (all or some). Gonads bilobed. Base of central stylet cylindrical . . . . . **genus *Gurjanovella* (part)**

17(16) Eyes compound. Gonads sac-like. Base of central stylet pear-shaped. . . . . **genus *Nareda***

18(7) Eyes absent or more than eight.

19(24) Length of rhynchocoel from ¼ to ¾ of body length. Body narrow to thread-like; often contorted after fixation.

20(21) Dorsal surface dark green, ventral cream-colored or light green. Stylets curved, base long and very narrow . . . . . ***Emplectonema, E. gracile* (Johnston, 1837) (Pl. X, Figs. 7, 8)**

Length to 50 cm.
Amphiboreal. Chukchi Sea (North American coast).
Intertidal to 38 m depth, rocky bottom.

21(20) Body color not as above. Stylets straight, base not as above.

22(23) Length of rhynchocoel less than half the body length. Stylets smooth or with longitudinal sculpturing. Dorsal surface of body usually with pigment spots, which may be very small. . . . . **genus *Neesia***

23(22) Rhynchocoel more than half the body length. Stylets with spiral sculpturing. Dorsal surface of one color, from dark brown to cherry-brown, ventral side cream-colored or yellowish . . . . . **genus *Paranemertes, P. peregrina* Coe, 1901 (Pl. X, Figs. 1,2)**

Length to 40 cm.
Pacific widespread boreal. Chukchi Sea (North American coast).
Intertidal, rocky sediments.

24(19) Rhynchocoel reaches posterior tip of body. Body narrow to wide, often retains its shape after fixation (not contorted).

25(26) Body short, wide, and thick. Head small, ½ to ¼ of trunk width; head with characteristic pattern of six light radial stripes spreading from the tip of the head. Cephalic furrows encircle the head. Neck furrow indistinct. Color of fixed (both formalin and alcohol) individuals is bright green or grayish-green (color of live individuals is greenish-brown, olive-brown, or brown). Testes bilobed. Rhynchostome ventral . . . . . **genus *Gurjanovella***

26(25) Body slender. Head not usually narrower than trunk (if narrower, then it is not less than ⅔ trunk width); head without pattern of six radial stripes. Color of fixed and live individuals whitish, yellowish, rose, reddish, or brown. Testes sac-like. Rhynchostome subterminal. . . . . **genus *Amphiporus***

Key to species of the genus *Annulonemertes* Berg, 1985

1(2) Body length 2-3 mm, easily fragmented into separate "segments." Rhynchocoel no more than ⅓ of body length. Accessory stylet pouches 1 or 2 . . . . . ***Annulonemertes* sp. 1 (Pl. VIII, Figs. 1, 2)**

White Sea.
Depth 80-120 m. Silt.

2(1) Body length 3-8 mm, does not easily fragment. Rhynchocoel ½ to ⅔ of body length. Accessory stylets in 2 pouches . . . . . ***Annulonemertes* sp. 2 (Pl. VIII, Fig. 3)**

Barents Sea.
Intertidal, sand.

Key to species of the genus *Tetrastemma* Ehrenberg, 1928

1(2) Central stylet less than half the length of the massive conical base (ratio of the length of the base to the length of the stylet [B/S] greater than 2) . . . . . ***Tetrastemma* sp. 1 (Pl. XII, Fig. 8)**

Length to 20 mm.
White Sea.
Depth 172 m.
B/S = 3. Dorsal side reddish-brown, without spots and stripes.

2(1) B/S less than 2. Base oval or pear-shaped.

3(4) Two dark longitudinal stripes on head connect the anterior and posterior eyes; a light medial band can occur between the eyes . . . . . ***T. vermiculum* (Quatrefages, 1846) (Pl. XI, Fig. 9)**

Length to 15 mm.
Atlantic subtropical-boreal. Barents Sea.
Upper subtidal, on algae.

4(3) Head without pattern as above.

5(6) Length of the central stylet base from 160 μm (in juveniles) to 385 μm. Eyes small, difficult to distinguish. Body rose-colored. ***Tetrastemma* sp. 2 (Pl. XII, Figs. 6, 7)**

Length to 12 mm.
White Sea.
Depth 20-120 m. Silt.

6(5) Length of base not greater than 140 μm. Eyes easily distinguishable.

7(8) Body whitish, yellowish, orange, green, sometimes with brownish tones. Cephalic gland does not reach behind the brain. . . . . ***T. candidum* (Müller, 1774) s.l. (Pl. XII, Figs. 1, 2, 5)**

Length to 15 mm.
Atlantic subtropical-boreal. White and Barents seas.
Intertidal and upper subtidal, on algae.

8(7) Body pink or reddish. Cephalic gland well developed, reaches behind the brain . . . . . ***T. laminariae* Uschakov, 1928 (Pl. XII, Figs. 3, 4)**

Length to 19 mm.
Atlantic high boreal. White and Barents seas.
Intertidal and upper subtidal, on algae.

Key to species of the genus *Oerstedia* Quatrefages, 1846

1(2) Body color highly variable: brown (from yellowish to dark browns with varying shades) with a pale medial longitudinal band, with brown spots or transverse bands. Proboscis with 10 nerves. . . ***O. dorsalis*** **(Abildgaard, 1806) (Pl. XI, Figs. 1, 2)**

Length to 30 mm (often 10-15 mm).
Amphiboreal. Barents Sea, Spitsbergen.
Intertidal to 5 m depth, among algae.
One can also find a sibling species, *O. striata* Sundberg, 1988, which has the following body colors: transverse brown bands crossing longitudinal pale bands.

2(1) Body color whitish-yellow, orange to brown and brick red, lacking bands or bright spots. Sometimes the pigment is distributed unevenly, forming very small dots distinguishable only under magnification. Proboscis with 11 nerves. . . . . ***Oerstedia*** **sp. (Pl. XI, Figs. 3-7)**

Length 7-12 mm.
White Sea.
Depth 4-20 m, on red algae and Laminaria.
It is possible that this species is just a smaller form of *O. dorsalis*.

Key to species of the genus *Nareda* Stimpson, 1854

1(2) Body of single color, whitish-yellow. . . . . ***N. aberrans*** **(Coe, 1901) (Pl. VII, Fig. 11)**

Length to 12 mm.
Eastern Pacific high boreal. Chukchi Sea (North American coast).
Upper subtidal.

2(1) Dorsal side of body reddish-brown, a similar spot present on the head . . . . . ***N. superba*** **Stimpson, 1854 (Pl. VII, Figs. 7-9)**

Synonymy: *Tetrastemma albicolis* Uschakov, 1928.
Length to 30 mm.
Atlantic high boreal. Barents Sea.
Upper subtidal, on *Lithothamnion*.

Key to species of the genus *Gurjanovella* Uschakov, 1926

Apparently, the species *"Amphiporus" cordiceps* (Jensen, 1878), which was described from the coast of Norway and has been reported from the White Sea, also belongs to this genus. Based on the body color, this species does not differ from *G. littoralis* and *G. murmanica* as well as *Cyanophthalma cordiceps* (Friedrich, 1933), but since the type description does not include information about the eyes and internal structure, the systematic position of *"Amphiporus" cordiceps* remains uncertain. The dorsal diverticulum of the rhynchocoel, described for *G. littoralis* and *G. murmanica*, apparently is the result of contraction during alcohol fixation. The genus *Cyanophthalma* Norenburg, 1986, could be a junior synonym of *Gurjanovella*.

1(2) Four double-cup eyes present (some eyes may be simple or consist of three ocelli). Body color is whitish, yellowish, or orange-yellow; fluid in the rhynchocoel can be pale violet. Base of central stylet massive, cylindrical, length 240-1200 μm, B/S from 2.2 to 2.7. . . . . ***G. arctica*** **(Uschakov, 126) (Pl. IX, Figs. 1-3)**

Synonymy: *Tetrastemma arctica* Uschakov, 1926.
Length to 30 mm.
Arctic Eurasian. White, Barents, and Kara seas.
Lower intertidal to 45 m, lives on silty sand.

2(1) Eyes numerous or absent. Body olive-green or brown, with six short pale radial bands running from the end of the head to the cephalic furrows. Length of base no more than 200 μm.

3(4) Eyes present . . . . . ***G. littoralis*** **Uschakov, 1926 (Pl. IX, Figs. 4-6)**

Length to 30 mm.
White Sea.
Depth 10-40 m. Silt.

4(3) Eyes absent. . . . . ***G. murmanica*** **Uschakov, 1926 (Pl. IX, Fig. 7)**

Length to 40 mm.
Barents Sea.
Intertidal, silty sand.

Key to species of the genus *Neesia* Girard, 1893

This genus has been restored for *Emplectonema* with an anteriorly split longitudinal muscle layer (i.e., "longitudinal precerebral septum"). The morphology of the genus *Neesia* is more similar to *Paranemertes* than to *Emplectonema* s.l. It differs from *Paranemertes* by having a shorter rhynchocoel. It is possible that further studies will result in combining these two genera.

1(2) Two pouches with accessory stylets. Dorsal surface is brown or reddish-brown, pigment often in small patches. Stylets smooth . . . . . ***N. neesii*** **(Oersted, 1843) (Pl. X, Figs. 3, 4)**

Length to 60 cm.
Atlantic subtropical-boreal. Barents Sea.
Intertidal and upper subtidal, among algae and rocks.

2(1) Four pouches with accessory stylets. Dorsal surface with dark gray or violet spots. Stylets with thin longitudinal and slightly oblique sculpturing. . . . . ***N. derjugini*** **(Uschakov, 1928) (Pl. X, Figs. 5, 6)**

Length to 38 cm.
Barents Sea.
Intertidal and upper subtidal among algae.
Longitudinal precerebral septum is very poorly developed in this species.

Key to species of the genus *Amphiporus* Ehrenberg, 1831

Amphiporus bicolor Bürger, 1895, described based on preserved specimens from the Barents Sea (680 m depth), is not included in the key.

1(2) Base of central stylet 0.8-1.0 mm long, central stylet length ⅓-¼ base length . . . . . ***A. macracanthus* Coe (Pl. XIII, Fig. 4)**

Length to 25 mm (fixed specimens).
Chukchi Sea (North American coast).
Upper intertidal; gravel and rocks.

2(1) Base of central stylet less than 0.4 mm long, central stylet longer than half of base.

3(4) Eyes absent. Dorsal side of body pink, orange or, less frequently, brown . . . . . ***A. groenlandicus* Ørsted, 1843.**

Length to 12 cm.
Arctic Eurasia. White and Barents seas, Spitsbergen.
Depth 100-240 m. Silt.
Sections of a specimen from the Barents Sea (identified as *A. groenlandicus* by P.V. Uschakov) were examined and eyes were observed; therefore reports of this species in Russian waters require verification.

4(3) Eyes present.

5(12) Body narrow, width 0.8-2 mm. Dorsal side whitish, gray, yellowish, pinkish, or pale reddish; the red brain is often visible through the integument. Width of the head in live specimens often less than the maximum width of body.

6(7) Proximal part of the base broad and nearly straight. Dorsal side rose-brick-yellowish . . . . . ***A. murmanicus* Uschakov, 1928 (Pl. XII, Figs. 9, 10)**

Length to 50 mm.
Barents Sea.
Upper intertidal, on *Lithothamnion*.

7(6) Proximal part of base rounded. Dorsal side usually paler.

8(9) Eyes form four oblique rows: two outer anterior and two inner posterior. Body yellowish, whitish with rose-colored tones . . . . . ***A. imparispinosus* Griffin, 1898 (Pl. XIII, Fig. 5)**

Length to 75 mm.
Pacific widespread boreal. Chukchi Sea (North American coast).
Intertidal and upper subtidal, among rocks and algae.

9(8) Eyes not arranged as above.

10(11) Eyes in four groups of 3-16 each (2-4 eyes per group in juveniles). Neck furrow located behind the brain. Cecal diverticula do not reach brain. Body white, grayish, or rose-colored . . . . . ***A. lactifloreus* (Johnston, 1828) (Pl. XIII, Figs. 6-8)**

Length to 10 cm.
Atlantic boreal Arctic. White, Barents, and Chukchi seas.
Intertidal to 10 m depth, among rocks and algae.

11(12) Numerous eyes distributed along the dorsal head margin. Neck furrow located in the brain region. Cecal diverticula reach

brain. Body pale pink, rosy-orange, sometimes with reddish tones . . . . . ***A. dissimulans*** **Riches, 1893 (Pl. XIII, Fig. 9)**

Length to 8 cm.
Eastern Atlantic widespread boreal. Barents Sea (Scandinavian coast).
Upper subtidal, among rocks and algae.

12(5) Body width 3-10 mm. Dark red, reddish-brown, or dark brown dorsally; ventral side pale. Head narrower than adjacent body, with two pale oblique bands between the anterior and posterior groups of eyes (bands correspond to cephalic slits) and two pale spots near the posterior group of eyes. Brain reddish, but often not visible through the integument. . . . . ***A. angulatus*** **(Müller, 1774) (Pl. XIII, Figs. 1-3)**

Length to 20 cm.
Widespread boreal Arctic, circumpolar. White, Barents, Laptev, Kara, and Chukchi seas, Spitsbergen.
Intertidal to 250 m depth, on variable substrates, often silt.

Acknowledgment

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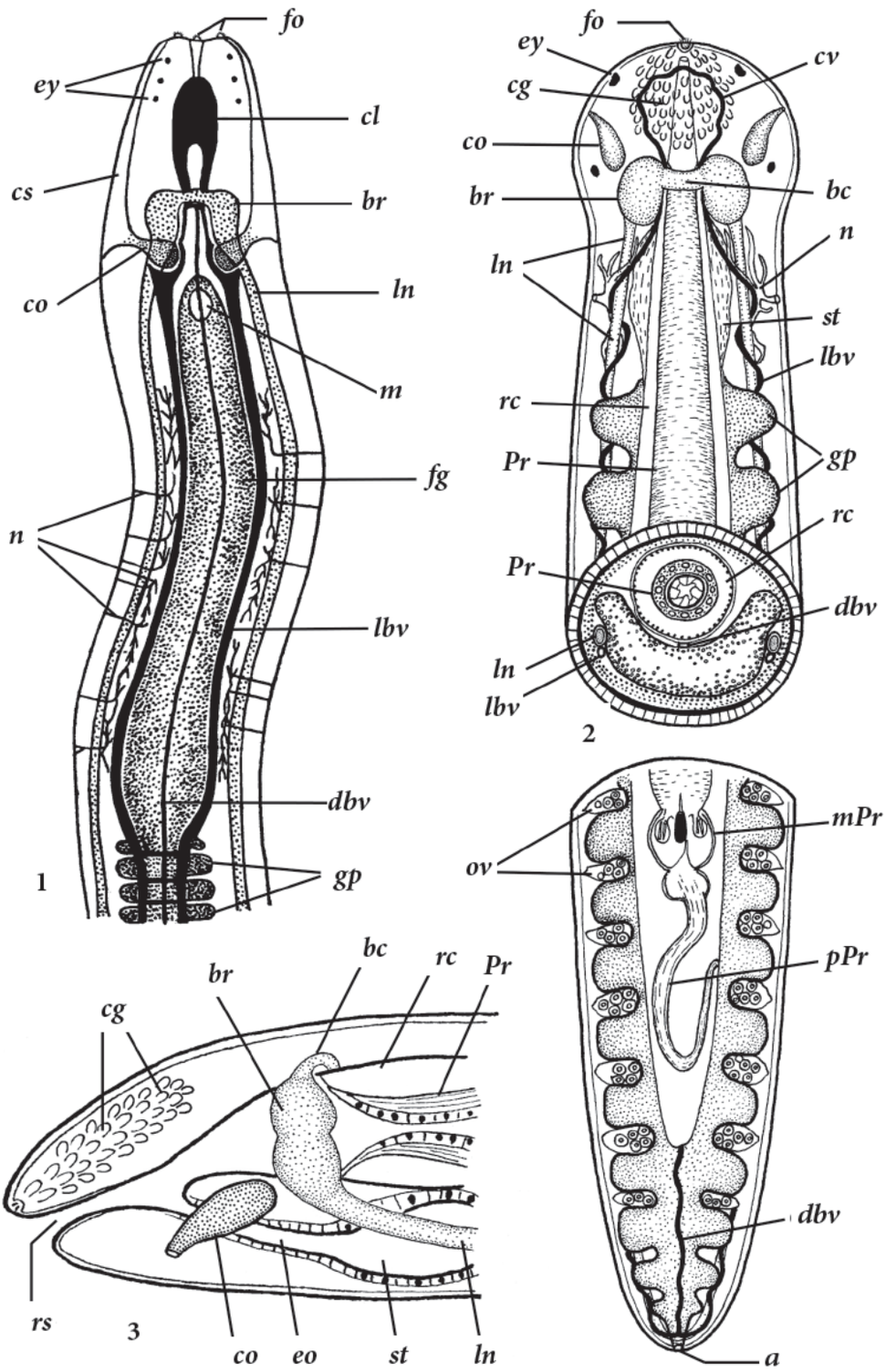

Plate I

Fig. 1 Structure of the anterior end of unarmed nemertines (*Poseidon viridis*).
Fig. 2 Structure of armed nemertines.
Fig. 3 Structure of the anterior end of body of armed nemertines, lateral view.

Abbreviations: *a*: anus. *bc*: commissure of brain. *br*: brain. *cg*: cephalic gland. *cl*: cephalic blood lacuna. *co*: cerebral organ. *cs*: cephalic slits. *cv*: cephalic blood vessel. *dbv*: dorsal blood vessel. *eo*: esophagous. *ey*: eyes. *fg*: foregut. *fo*: frontal organ. *gp*: gut pockets. *lbv*: lateral blood vessel. *ln*: lateral nerve trunk. *m*: mouth. *mPr*: mid section of proboscis. *n*: nephridia. *ov*: ovaries. *pPr*: posterior portion of proboscis. *Pr*: proboscis. *rc*: rhynchocoel. *rs*: rhynchostome. *st*: stomach.

(Fig. 1 from Ivanov et al. 1981 with modifications; all others original.)

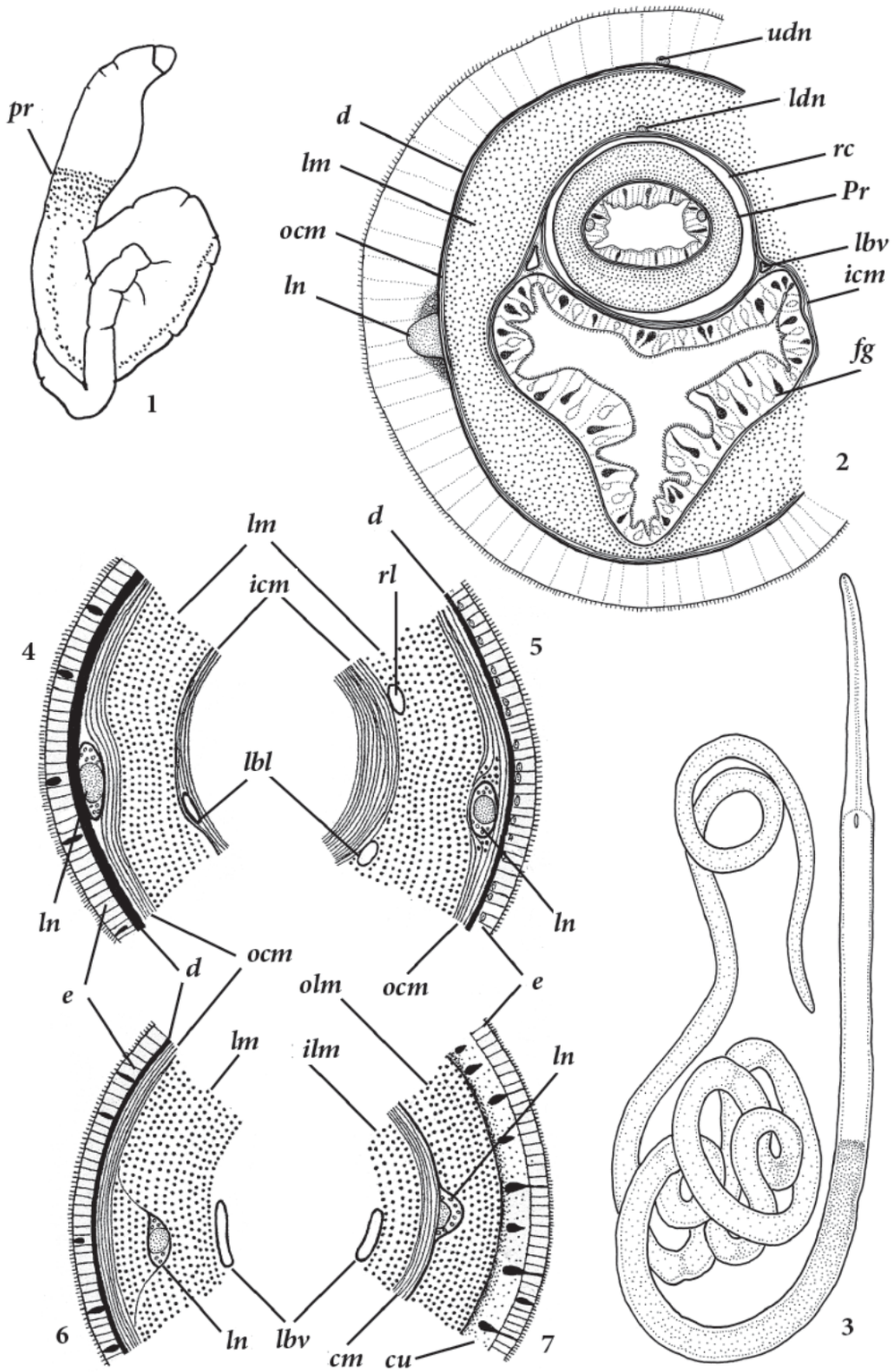

Plate II

Fig. 1 *Carinina wijnhoffae* Kulikova, 1984, fixed specimen.
Fig. 2 *Carinina* sp., cross section behind the brain.
Fig. 3 *Cephalothrix linearis* (Rathke, 1799), external view.
Figs. 4-7 Distribution of lateral nerve trunks in a cross section of *Tubulanus* (4); *Carinoma* (5); *Cephalothrix* (6); Heteronemertea (7).

Abbreviations: *cm*: circular muscle. *cu*: cutis. *d*: dermis. *e*: epithelium. *fg*: foregut. *icm*: inner circular muscle. *ilm*: inner longitudinal muscle. *lbl*: lateral blood lacuna. *lbv*: lateral blood vessel. *ldn*: lower dorsal nerve. *lm*: longitudinal muscle. *ln*: lateral nerve trunk. *ocm*: outer circular muscle. *olm*: outer longitudinal muscle. *pr*: pigment ring. *Pr*: proboscis. *rc*: rhynchocoel. *rl*: rhynchocoel lumen. *udn*: upper dorsal nerve.

(Fig. 1 from Kulikova 1984; all other figures original.)

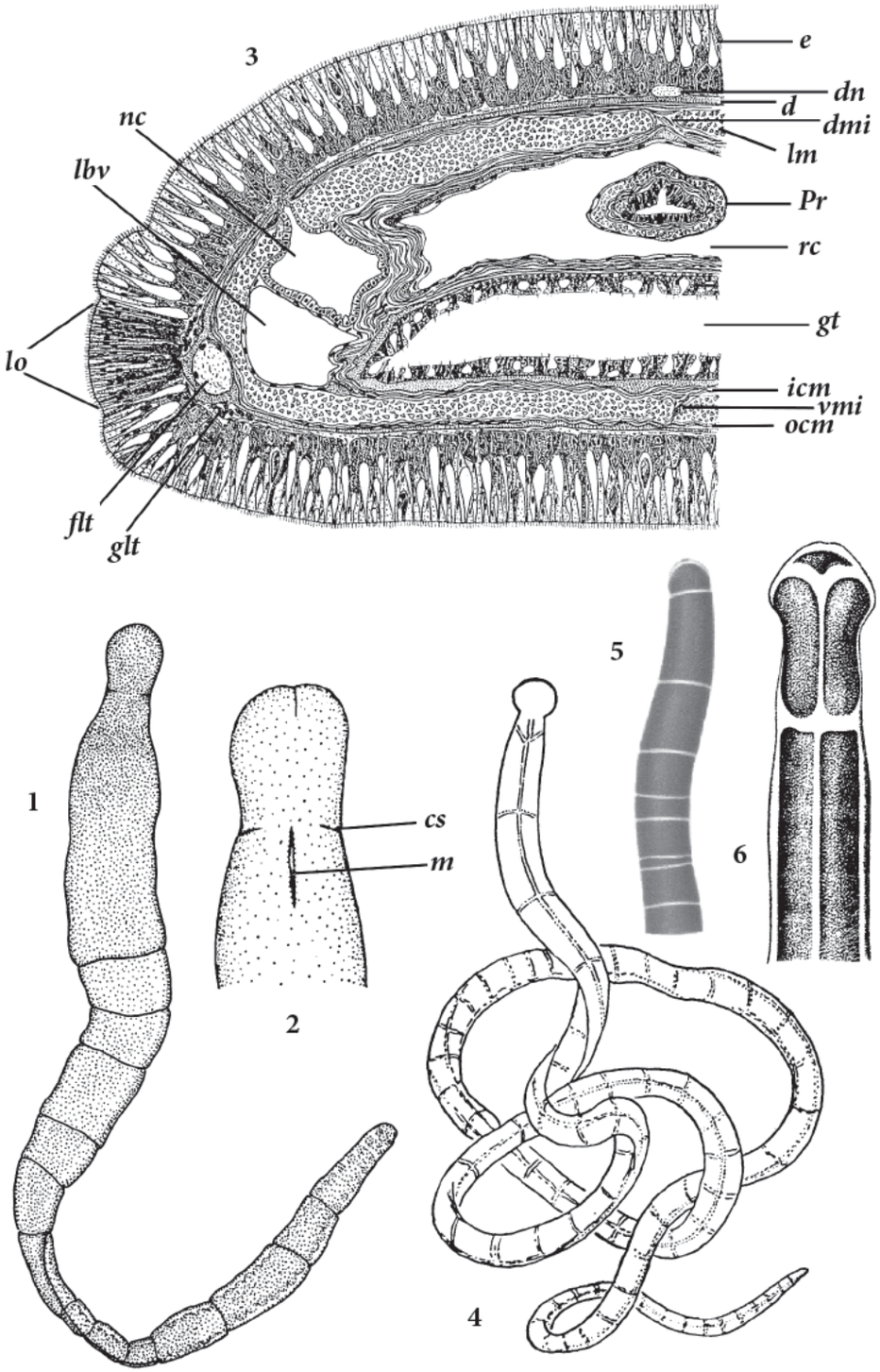

Plate III

Figs. 1-3 *Protubulanus* cf. *theeli* (Bergendal, 1902) (1: exterior view. 2: anterior end, ventral view. 3: fragment of a cross section at the lateral organs.)
Fig. 4 *Tubulanus capistratus* (Coe, 1901).
Fig. 5 *Tubulanus albocinctus* (Coe, 1904), anterior part of body, dorsal view.
Fig. 6 *Tubulanus annulatus* (Montagu, 1804), anterior part of body, dorsal view.

Abbreviations: *cs*: cephalic slits. *d*: dermis. *dmi*: dorsal muscle intersection. *dn*: dorsal nerve. *e*: outer glandular epithelium. *flt*: fibrous portion of the lateral nerve trunk. *glt*: ganglion region of the lateral nerve trunk. *gt*: gut. *icm*: inner circular muscle. *lbv*: lateral blood vessel. *lm*: longitudinal muscle. *lo*: lateral organ. *m*: mouth. *nc*: nephridia canal. *ocm*: outer circular muscle. *Pr*: proboscis. *rc*: rhynchocoel. *vmi*: ventral muscle intersection.

(Fig. 4 from Hyman 1951; Fig. 5 from Coe 1905; Fig. 6 from Joubin 1894; all others original.)

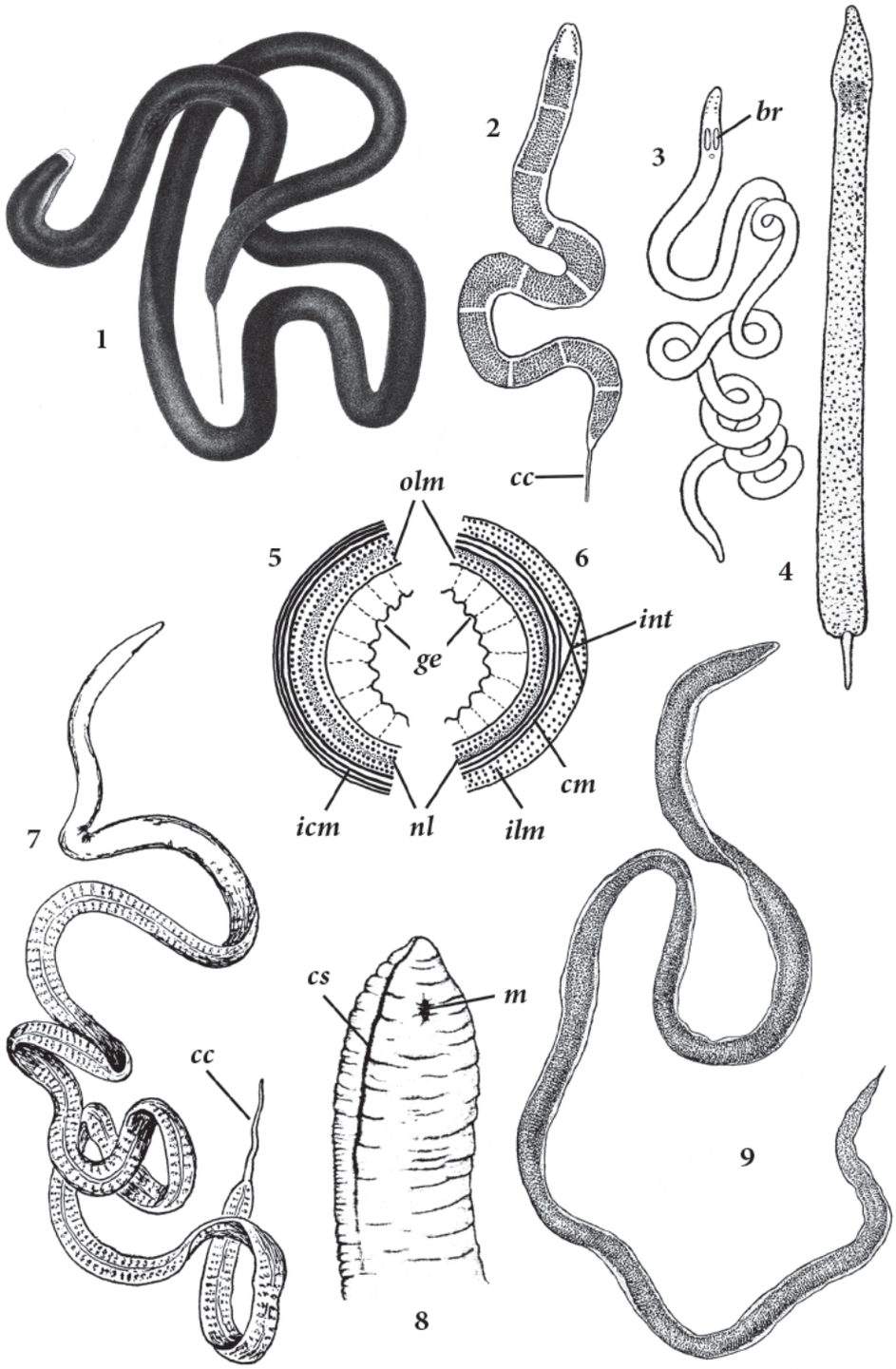

Plate IV

Fig. 1 *Micrura purpurea* (Dalyell, 1853).
Fig. 2 *Micrura fasciolata* Ehrenberg, 1828.
Fig. 3 *Ramphogordius sanguineus* (Rathke, 1799).
Fig. 4 *Cerebratulus fuscus* (McIntosh, 1873-1874).
Figs. 5, 6 Cross section of the proboscis of *Baseodiscus* (5) and *Cerebratulus* (6) in the retracted state.
Fig. 7 *Micrura alaskensis* Coe, 1901.
Fig. 8 *Cerebratulus fissuralis* Friedich, 1958, anterior end of fixed specimen, ventrolateral view.
Fig. 9 *Cerebratulus barentsi* Bürger, 1807.

Abbreviations: *br*: brain. *cc*: caudal cirrus. *cm*: circular muscle. *cs*: lateral cephalic slits. *ge*: glandular (outer) epithelium. *icm*: inner circular muscle. *ilm*: inner longitudinal muscle. *int*: intersection. *m*: mouth. *nl*: nerve layer. *olm*: outer longitudinal muscle.

(Fig. 1 from McIntosh 1873-1874; Fig. 2 from Gibson 1982 with modifications; Fig. 3 from Coe 1940; Fig. 4 from Joubin 1894; Fig. 7 from Coe 1901; Fig. 8 from Punnett 1903; Fig. 9 from Yashnov 1948; all others original.)

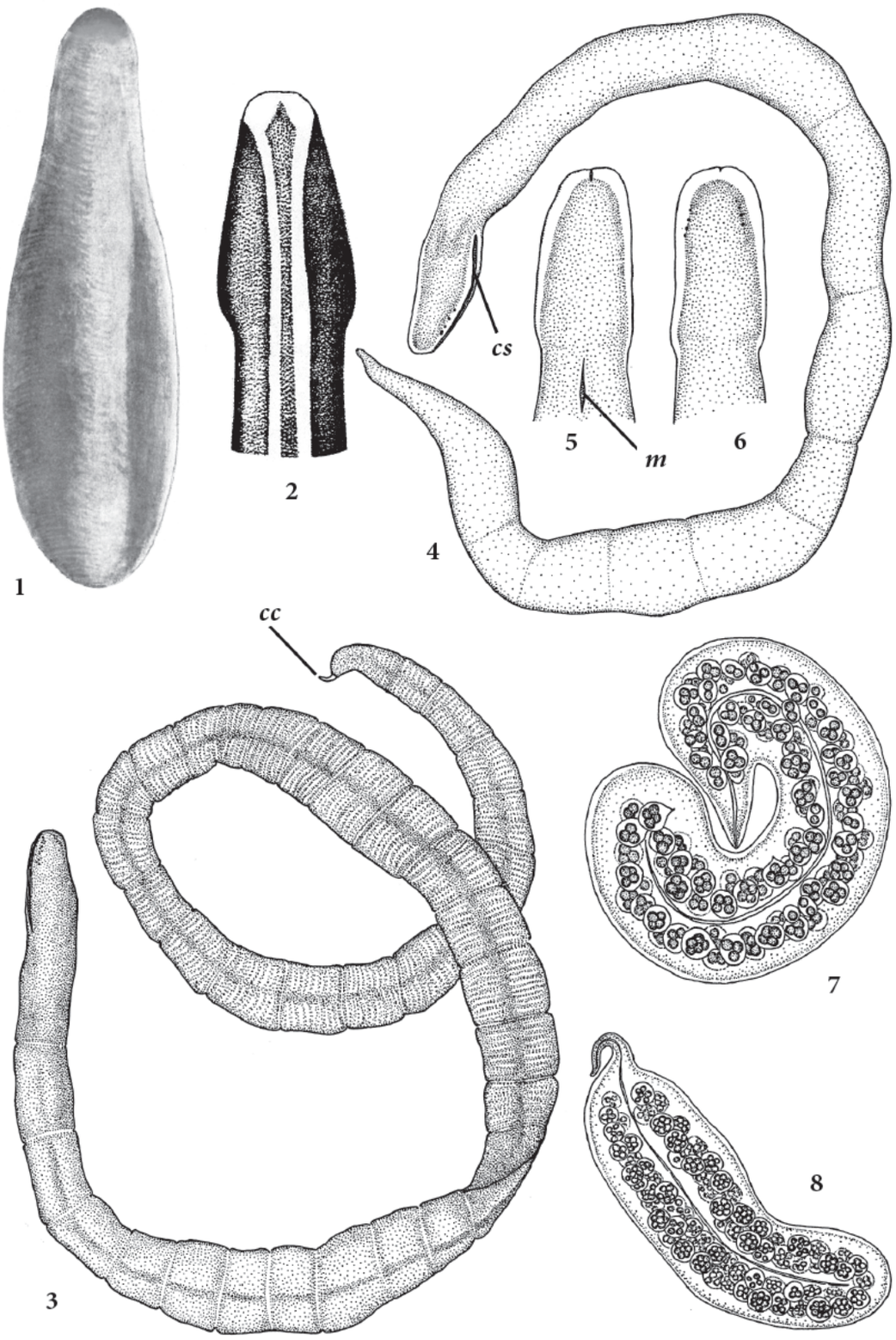

Plate V

Fig. 1 *"Cerebratulus" brevis* Uschakov, 1926 (fixed specimen).
Fig. 2 *"Lineus" bilineatus* Renier, 1804 (head, dorsal view).
Fig. 3 *Micrura* sp.
Figs. 4-6, 8 *Lineus ruber* (Müller, 1774) (4: external view. 5-6: head end from below and above. 8: egg case).
Fig. 7 *Lineus viridis* (Müller, 1774) (egg case).

Abbreviations: *cc*: caudal cirrus. *cs*: lateral cephalic slits. *m*: mouth.

(Fig. 1 from Uschakov 1928; Fig. 2 from Joubin 1894; Figs. 7, 8 from Schmidt 1951; all others original.)

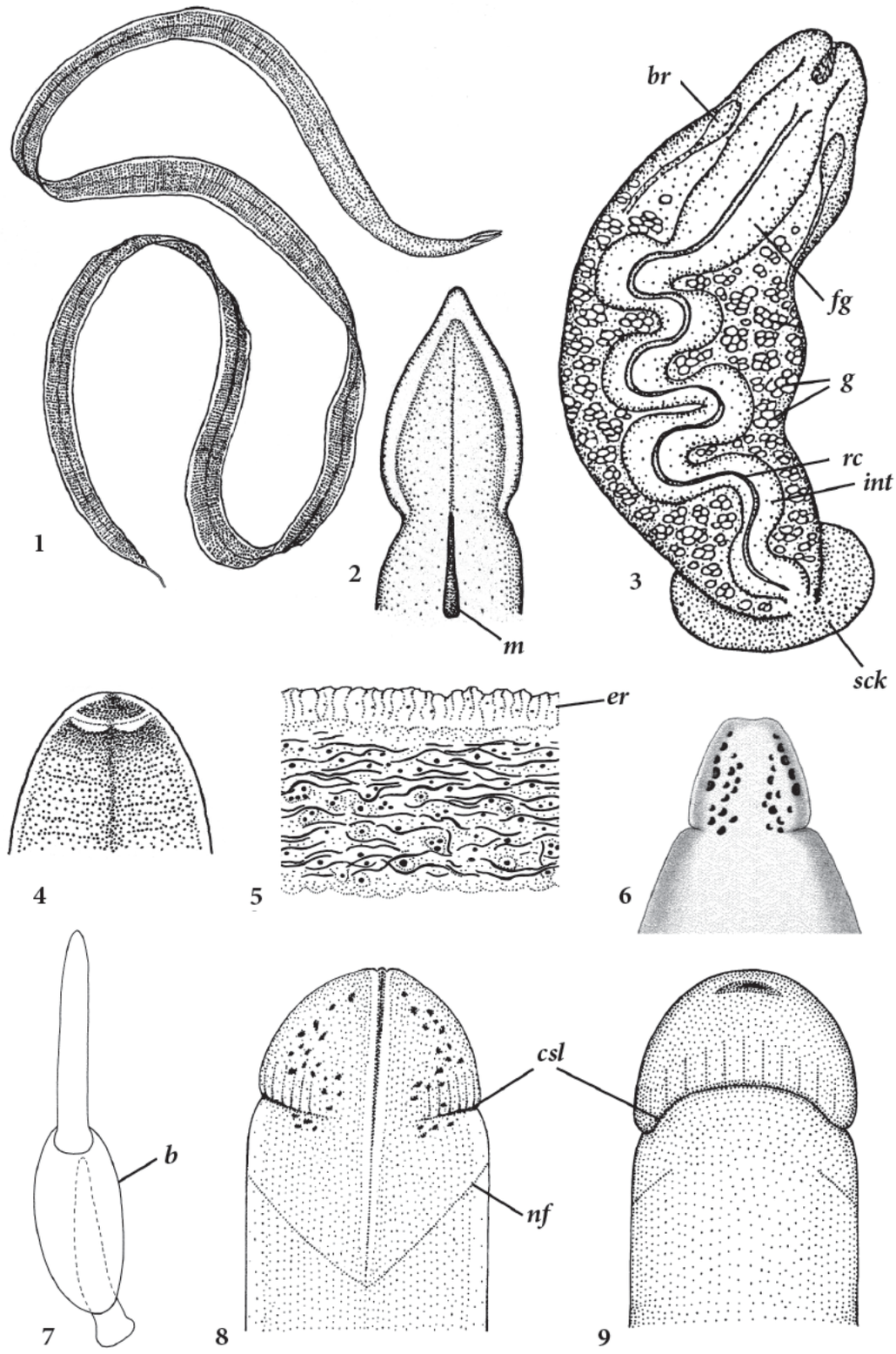

Plate VI

Figs. 1, 2 *Cerebratulus marginatus* Renier, 1804 (1: outer view. 2: head, ventral view).
Fig. 3 *Malacobdella grossa* (Müller, 1776).
Figs. 4, 5 *Uniporus borealis* (Punnett, 1901) (4: anterior end of fixed specimen, dorsal view. 5: fragment of the rhynchocoel wall in cross section).
Fig. 6 *Nipponnemertes pactfica* (Coe, 1901) (distribution of the eyes).
Figs. 7-9 *Nipponnemertes pulchra* (Johnston, 1837) (7: central stylet and base. 8, 9: head, dorsal and ventral views.)

Abbreviations: *b*: base. *br*: brain. *csl*: cephalic furrow. *er*: endothelium of rhynchocoel. *fg*: foregut. *g*: gonads. *int*: intestine. *m*: mouth. *rc*: rhynchocoel. *sck*: sucker.

(Fig. 4 from Punnett 1901; Fig. 6 from Coe 1905; Figs. 7-9 from Berg 1972a; all others original.)

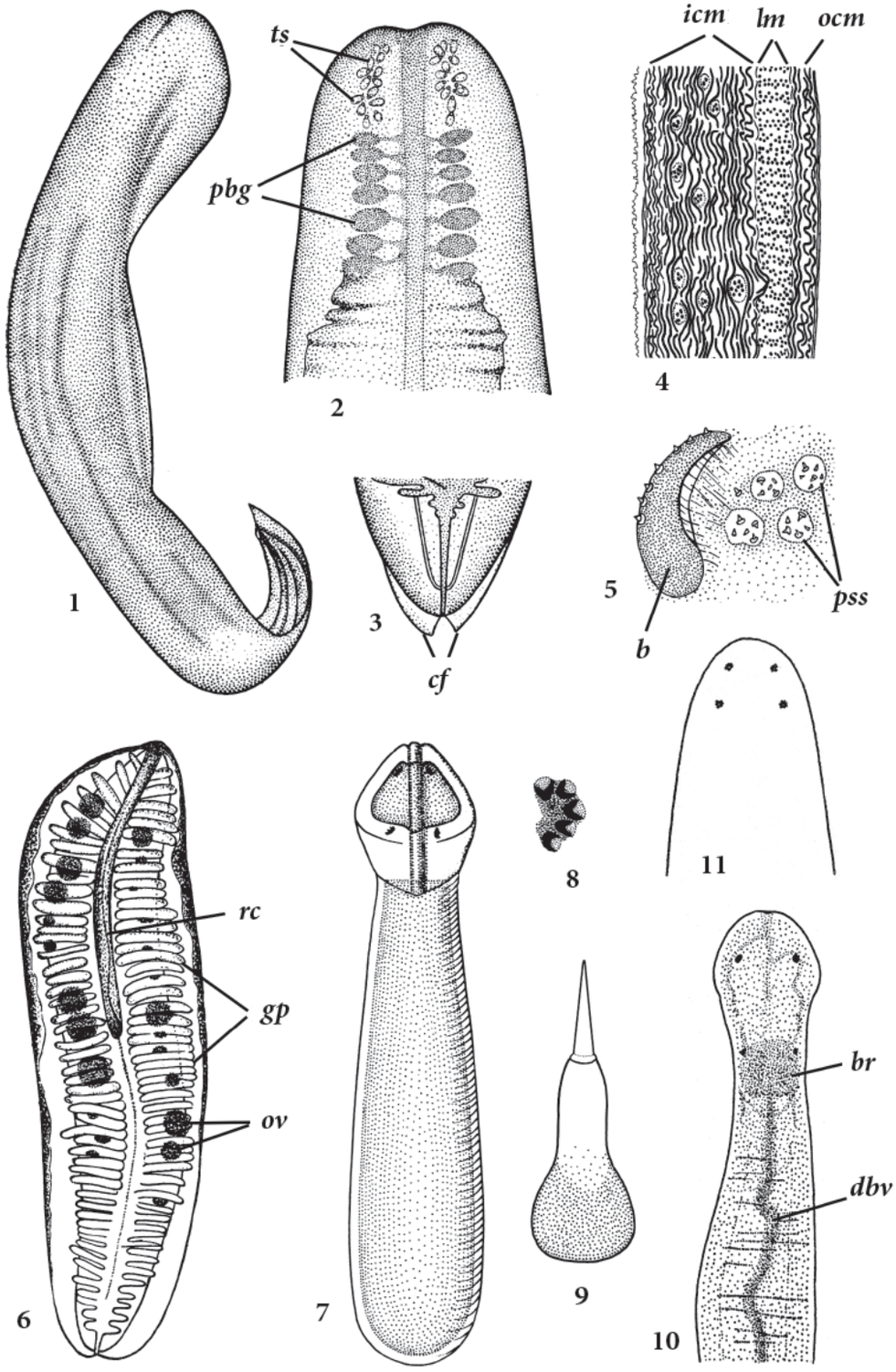

Plate VII

Figs. 1-4 *Dinonemertes arctica* Korotkevitsch, 1977 (1: fixed specimen. 2: anterior section of body. 3: posterior section of body. 4: fragment of rhynchocoel wall in cross section.)
Fig. 5 Polystiliferan armament.
Fig. 6 *Dinonemertes alberti* Brinkmann, 1917.
Figs. 7-9 *Nareda superba* Stimpson, 1854 (7: external view. 8: complex eye. 9: central stylet and base.)
Fig. 10 *Cryptonemertes actinophila* (Bürger, 1904), anterior part of body.
Fig. 11 *Nareda aberrans* (Coe, 1901), anterior part of body.

Abbreviations: *b*: base. *br*: brain. *cf*: caudal fin. *dbv*: dorsal blood vessel. *gp*: gut pockets. *icm*: inner circular muscle layer. *lm*: longitudinal muscle layer. *ocm*: outer circular muscle layer. *ov*: ovaries. *pbg*: pockets of blind gut. *pss*: pocket with stylet supply. *rc*: rhynchocoel. *ts*: testis.

(Figs. 1-3, 6 from Korotkevich 1977; Fig. 7 from Berg 1973; Fig. 10 from Gibson 1986; Fig. 11 from Coe 1901; all others original.)

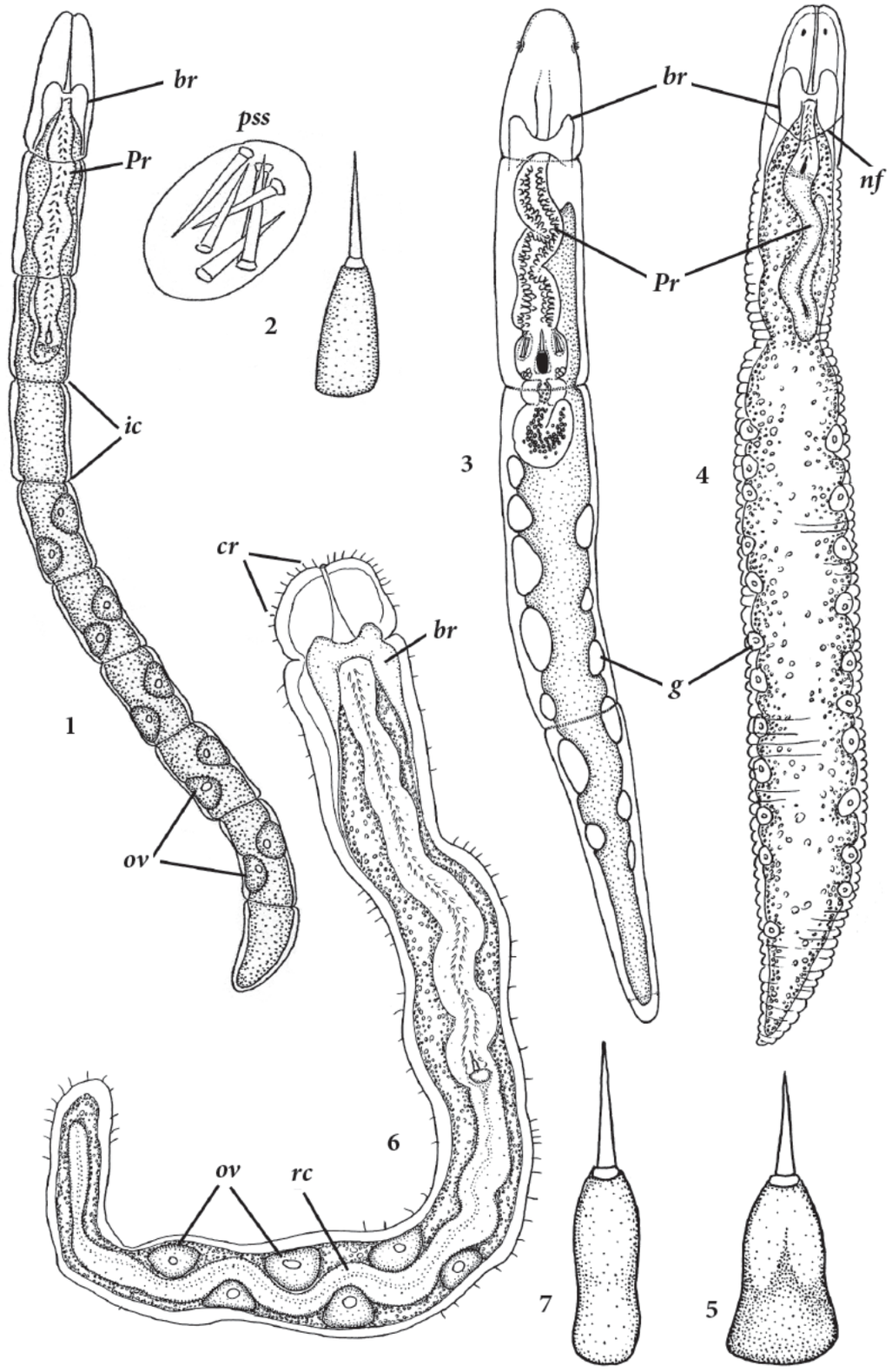

Plate VIII

Figs. 1, 2 *Annulonemertes* sp. 1 (1: outer view. 2: armament.)
Fig. 3 *Annulonemertes* sp. 2.
Figs. 4, 5 *Monostilifera* gen. sp. 1 (4: outer view. 5: central stylet and base.)
Figs. 6, 7 *Monostilifera* gen. sp. 2 (6: outer view. 7: central stylet and base.)

Abbreviations: *br*: brain. *cr*: cirrus. *g*: gonads. *ic*: "intersegmental" constriction. *nf*: neck furrow. *ov*: ovaries. *Pr*: proboscis. *pss*: pocket with stylet supply. *rc*: rhynchocoel.

(All figures original.)

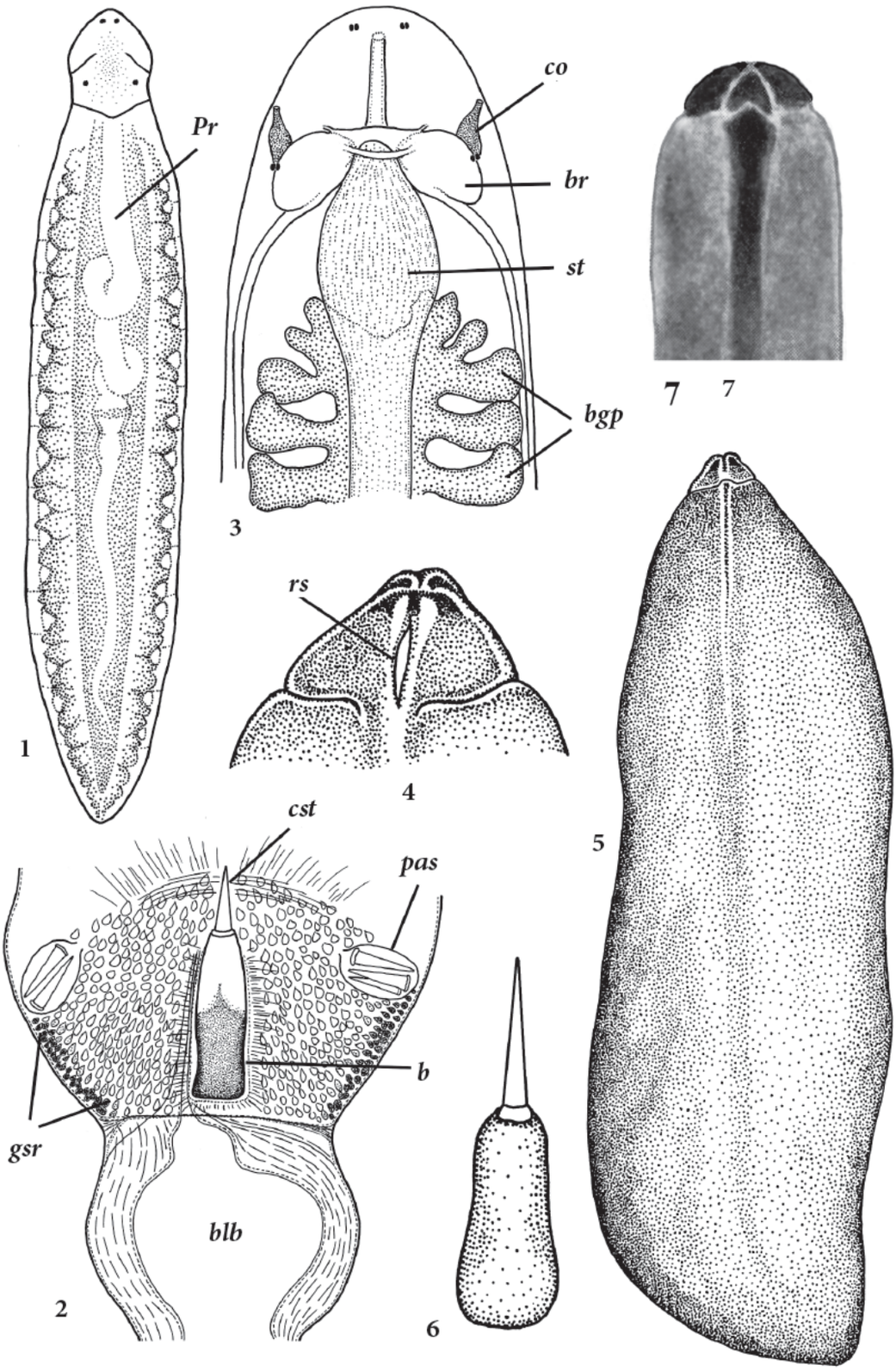

Plate IX

Figs. 1-3 *Gurjanovella arctica* (Uschakov, 1926) (1: external view. 2: mid section of proboscis. 3: anterior end of body under a cover glass, rhynchocoel not shown.)
Figs. 4-6 *Gurjanovella littoralis* Uschakov, 1926 (4: head, ventral view. 5: outer dorsal view. 6: central stylet and base.)
Figs. 7 *Gurjanovella murmanica* Uschakov, 1926 (anterior end of body.)

Abbreviations: *b*: base. *bgp*: pockets of blind gut. *blb*: bulb. *br*: brain. *co*: cerebral organ. *cst*: central stylet. *gsr*: glands of the stylet region. *pas*: pockets with accessory stylets. *Pr*: proboscis. *rs*: rhynchostome. *st*: stomach.

(Fig. 7 from Uschakov 1928; all others original.)

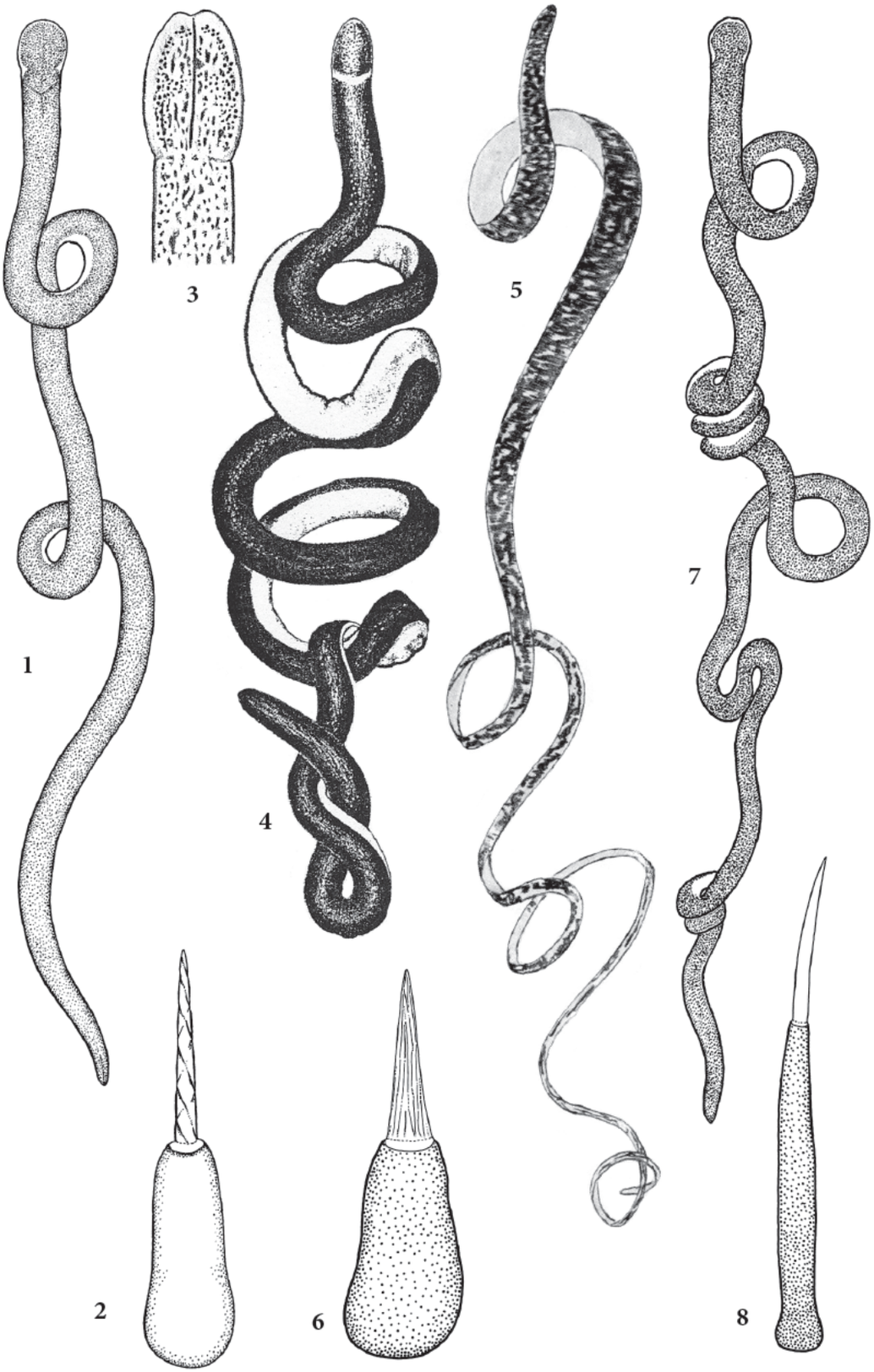

Plate X

Figs. 1, 2 *Paranemertes peregrina* Coe, 1901 (1: outer view. 2: base with central stylet.)
Figs. 3, 4 *Neesia neesii* (Oersted, 1843) (3: outer view. 4: head, dorsal view).
Figs. 5, 6 *Neesia derjugini* (Uschakov, 1928) (5: outer view. 6: base with central stylet.)
Figs. 7, 8 *Emplectonema gracile* (Johnston, 1837) (7: outer view. 8: base with central stylet.)

(Fig. 3 from Joubin 1894; Fig. 4 from McIntosh 1873-1874; Fig. 5 from Uschakov 1928; all others original.)

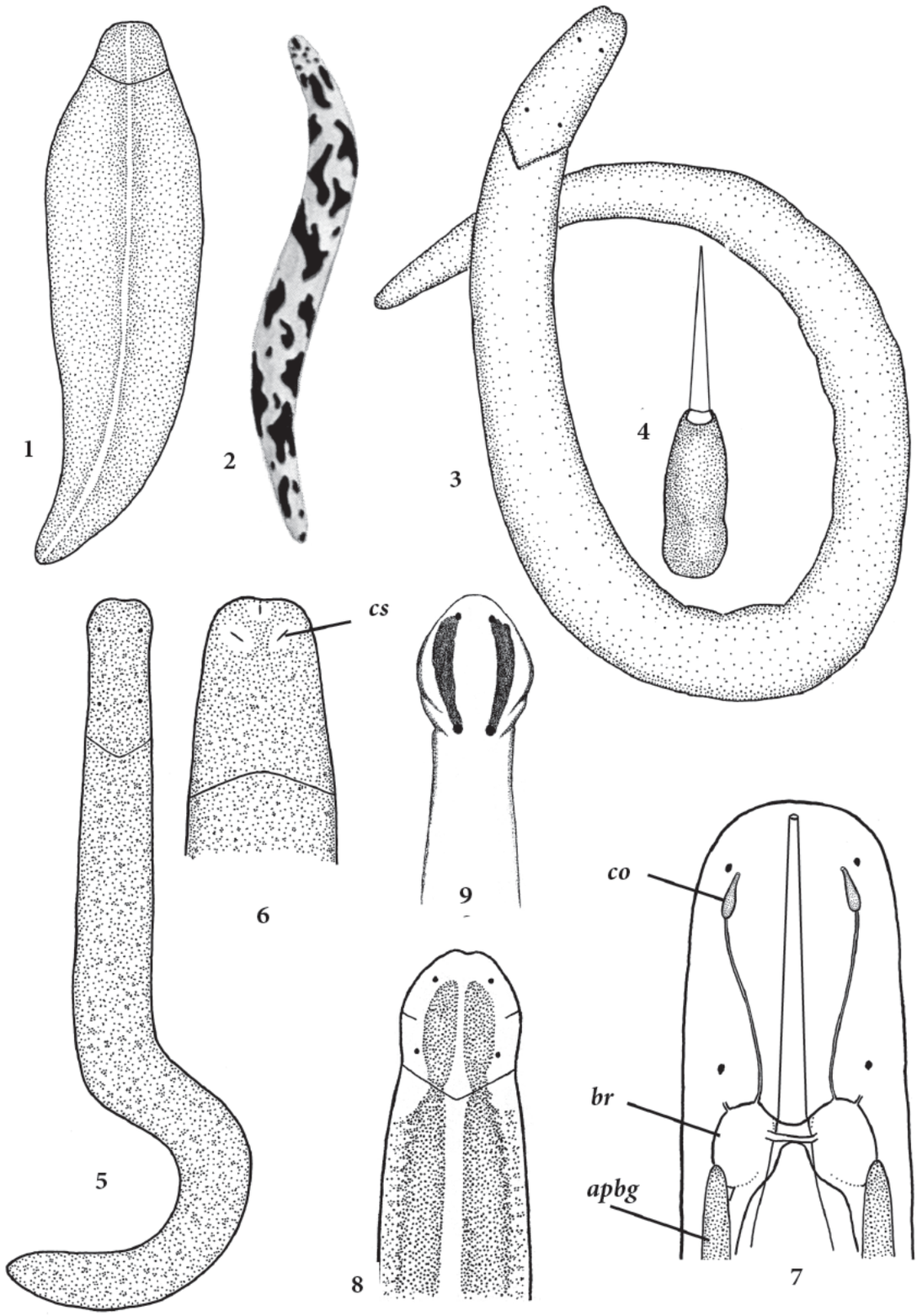

Plate XI

Figs. 1, 2 *Oerstedia dorsalis* (Abildgaard, 1806) (1: fixed specimen.)
Figs. 3-7 *Oerstedia* sp. (3, 5: external appearance. 4: base and central stylet. 6: head, ventral view. 7: anterior end of body under cover glass; proboscis not shown.)
Fig. 8 *Quasitetrastemma bicolor* (Coe, 1901) (anterior portion of body).
Fig. 9 *Tetrastemma vermiculum* (Quatrefages, 1846) (anterior portion of body).

Abbreviations: *apbg*: anterior pocket of blind gut. *br*: brain. *co*: cerebral organ. *cs*: cephalic furrows.

(Fig. 2 from Brunberg 1964; Fig. 8 from Joubin 1894; all others original.)

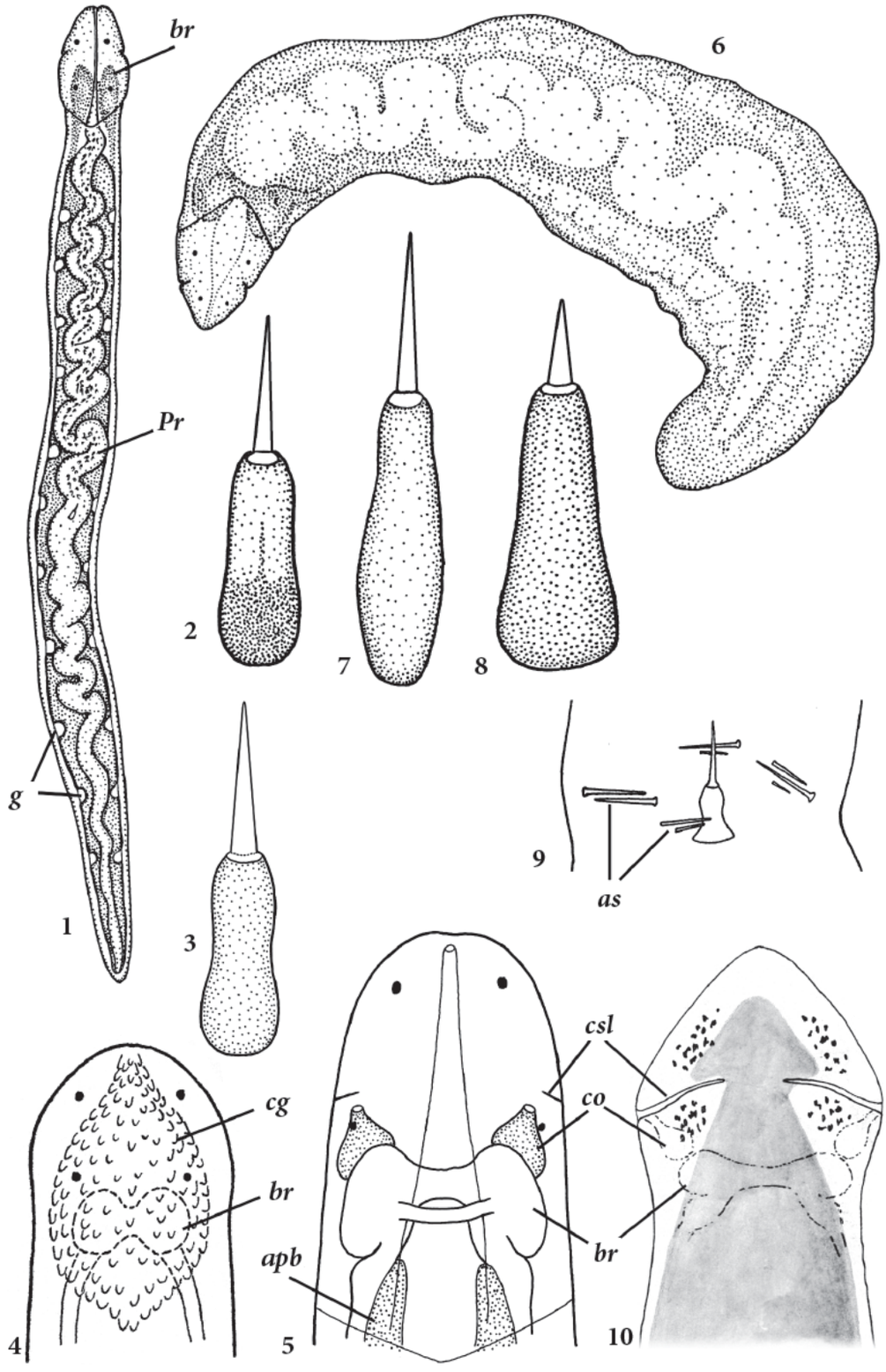

Plate XII

Figs. 1, 2, 5 *Tetrastemma candidum* (Müller, 1774) (1: outer view. 2: central stylet and base.)
Figs. 3, 4 *Tetrastemma laminariae* Uschakov, 1928 (3: central stylet and base. 4: distribution of cephalic glands.)
Figs. 6, 7 *Tetrastemma* sp. 2 (6: outer view. 7: central stylet and base).
Fig. 8 *Tetrastemma* sp. 1 (central stylet and base).
Figs. 9, 10 *Amphiporus murmanicus* Uschakov, 1928 (9: armament. 10: head end).

Abbreviations: *apb*: anterior pocket of blind gut. *as*: accessory stylets. *br*: brain. *cg*: cephalic glands. *co*: cerebral organs. *csl*: cephalic slits. *g*: gonads. *Pr*: proboscis.

(Fig. 8 from Uschakov 1926; Figs. 3, 9, 10 from Uschakov 1928; all others original.)

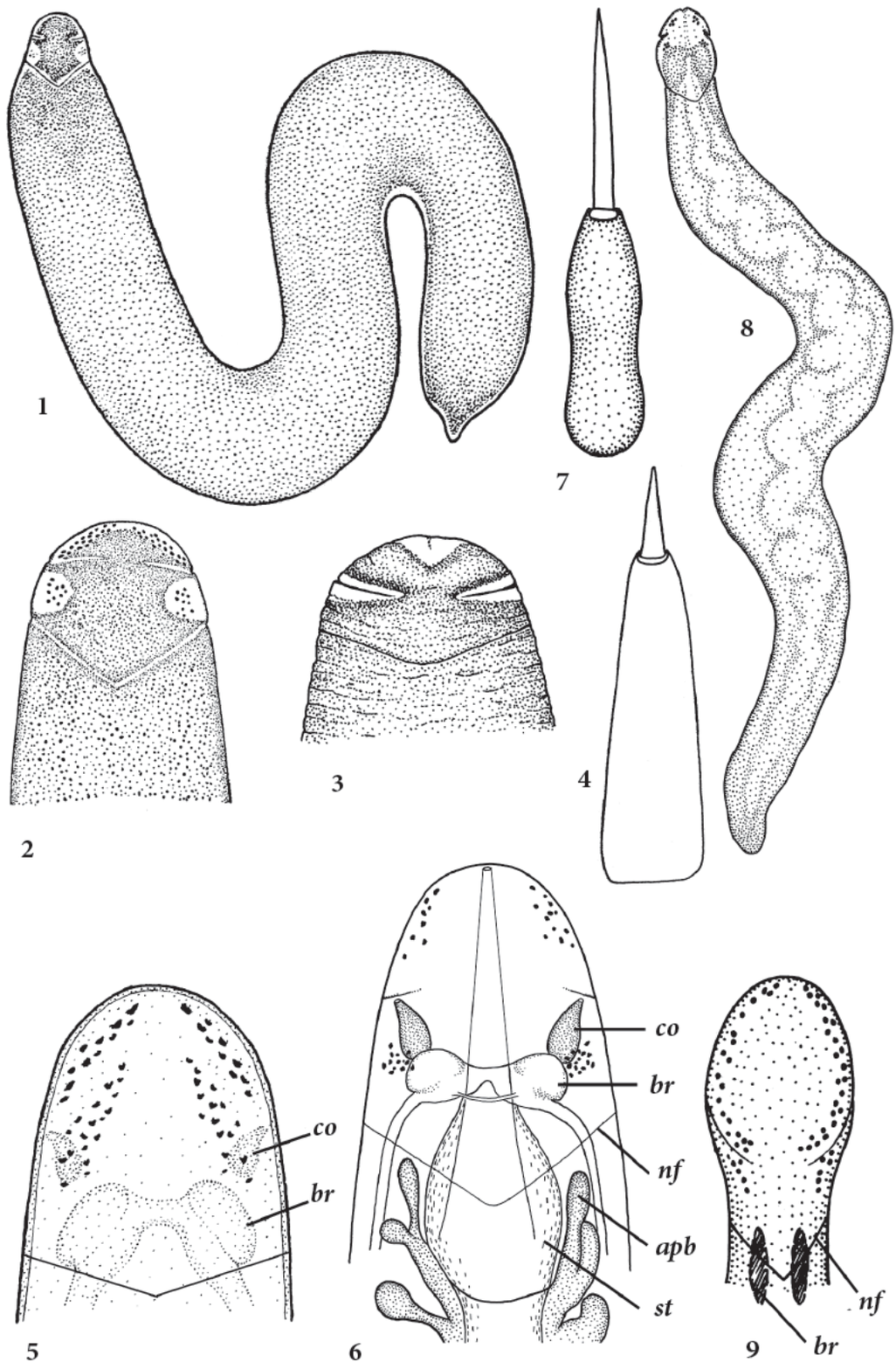

Plate XIII

Figs. 1-3 *Amphiporus angulatus* (Müller, 1774) (1: external view. 2: head end of live specimen. 3: head end of fixed specimen.)
Fig. 4 *Amphiporus macracanthus* Coe, 1905 (central stylet and base).
Fig. 5 *Amphiporus imparispinosus* Griffin, 1898 (head end).
Figs. 6-8 *Amphiporus lactifloreus* (Johnston, 1828) (6: head end, showing positions of internal organs. 7: central stylet and base. 8: external view.)
Fig. 9 *Amphiporus dissimulans* Riches, 1893 (head end).

Abbreviations: *apb*: anterior pocket of blind gut. *br*: brain. *co*: cerebral organs. *nf*: neck furrow. *st*: stomach.

(Fig. 2 from Coe 1901; Fig. 4 from Coe 1905; Fig. 9 from Berg 1972b; all others original.)

Phylum Cephalorhyncha, Class Priapulida[1]

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Priapulids are marine macrobenthic and meiobenthic worms represented by both extinct and living forms, and are widely distributed in the world oceans from littoral to abyssal (8000 m) depths. The body size of priapulids varies from 1.5 mm (*Tubiluchus*) to 40 cm (*Halicryptus higginsi*). Macrobenthic priapulids lead a burrowing lifestyle and inhabit various sediment types: silt of various consistencies, clay with a mixture of rock, gravel with a mixture of silt and clay, mixtures of silt and sand, and sandy sediments. Meiobenthic priapulids live in shell and coral sands. All adult macrobenthic priapulids are predators, while meiobenthic priapulids feed on detritus, bacteria, and algae; members of the genus *Maccabeus* feed on seston. The modern priapulid fauna comprise 20 species.

The body of the adult worm is divided into two main sections: the proboscis (including the head, introvert, and preseptum) and the trunk (including the abdomen and postseptum). Some priapulids have a tail section, consisting of one or two caudal appendages. The proboscis can be completely inverted into the trunk section, which in some priapulids is separated from the introvert by a short neck (collar). The introvert is withdrawn by contraction of a series of special retractor muscles. The introvert is extended by body cavity pressure generated by contraction of muscles in the body wall.

The anterior end of the proboscis consists of a circumoral field or oral cone. The posterior boundary of the oral cone is marked by rings of eight circumradial scalids, with nerve rings lying beneath. The oral field in macrobenthic priapulids is bounded anteriorly by rings of teeth on the extended pharynx. The central portion of the introvert in priapulids has posterior-directed sensory-locomotion appendages (scalids). The shape and position of the scalids are features used in the systematics of priapulids. Scalids are non-articulating, articulating (telescoping), and one- or two-tipped; some have sensory micro-papillae; and some are shaped like floscular papillae or have other shapes.

The collar region in macrobenthic priapulids consists of only a short band between the introvert and the trunk. The neck region in dwarf *Tubiluchus* is a separate section with a folded or lamellar cuticle and with sensory appendages (flosculi).

The trunk in macrobenthic priapulids is covered with numerous rings of folds (cuticular annuli); they vary in number from 80 to 100 in *Halicryptus* and from 40 to 50 in *Priapulus*. The annuli have variable trunk appendages in the form of glandular sensory papillae or hairlike setae. In some forms, a preanal trunk subregion can be distinguished, marked by rings of papillae or hooks and with variable warty, whorl-like, papillae-like glandular sensory appendages. The annuli are not developed in meiobenthic priapulids. The trunk of *Tubiluchus* is covered with numerous scale-like cuticular swellings—tumuli—forming longitudinal rows and rings.

The caudal appendages of dwarf priapulids often exceed the body length and they have a dense covering of scales and conical or cylindrical tumuli, among which are scattered sensory flosculi or glandular tubules. Macrobenthic priapulids have one (*Priapulus*, *Acanthopriapulus*) or two (*Priapulopsis*) caudal appendages with clusters of lateral vesicles. The shape and armament of the vesicles are taxonomic characters at the genus and species levels.

[1]Editorial note: other taxonomists label the Priapulida as a phylum and do not accept Cephalorhyncha as a phylum.

Priapulids have meiobenthic larvae, whose body is also divided into proboscis and trunk regions separated by a collar. The trunk of the larva is enclosed in a cuticular lorica consisting of longitudinal cuticular plates, whose distribution and structural features are important taxonomic characters. The collar region can contain various plates forming a closing apparatus covering the retracted proboscis within the lorica. The collar and lorica contain various glandular-sensory appendages (flosculi, microtubules, tubules) whose distribution is used as a taxonomic character.

Key to orders, families, and genera of Priapulida

1(2) Introvert conical; trunk with numerous (80-180) thin annuli covered with many hairlike spines. Caudal spines present; tail appendage absent . . . . . **order Halicrytpomorpha, family Halicryptidae, genus *Halicryptus***

2(1) Introvert cylindrical, rarely spherical; trunk with wide annuli (40-50) or lacking ringlike annuli; caudal spines absent; tail appendages always present . . . . . **order Priapulomorpha**

Key to species of the genus *Halicryptus*

1(2) Introvert about 10% of total body length; scalids both conical and in the shape of one- or two-pointed teeth. Trunk with not more than 100 annuli . . . . . ***H. spinulosus* von Siebold, 1849 (Pl. I, Fig. 1; Pl. II; Figs. 2-3)**

Length to 25 cm.
Widespread boreal Arctic circumpolar. In all seas of Arctic Ocean.
From littoral to lower sublittoral. On silt.

2(1) Introvert about 2% of total body length; scalids only conical, none are shaped like teeth; trunk usually with 120-180 annuli . . . . . ***H. higginsi* Shirley et Storch, 1999 (Pl. II, Fig. 4)**

Length to 40 cm.
Arctic. On arctic coast of Alaska.
Upper sublittoral and deeper.

Key to families, genera, and species of the order Priapulomorpha

1(2) Tail appendage lacking lateral vesicles (bare); trunk lacking annular rings; scale-like tumuli present; trunk appendages shaped like tubules; meiobenthic . . . . . **family Tubiluchidae, genus *Tubiluchus*, *T. arcticus* Adrianov et al., 1989 (Pl. I, Fig. 15)**

Length 2-6 mm (total: introvert, trunk, tail).
Atlantic boreal Arctic. Barents and White seas.
Depth 15-100 m. On shell and coarse-grain sand.

2(1) Tail appendage with lateral vesicles; trunk with annular rings; trunk appendages in shape of variable papillae; macrobenthic . . . . . **family Priapulidae**

Key to genera and species of the family Priapulidae

1(2) One tail appendage present; lateral vesicles not forming ringlike whorls . . . . . **genus *Priapulus*, *P. caudatus* Lamarck, 1816 (Pl. I, Fig. 9; Pl. II, Fig. 1)**

Length to 20 cm.
Widespread Arctic circumpolar. In all seas of Arctic Ocean.
From littoral to 3000 m. On silt.

2(1) Two tail appendages present; lateral vesicles forming ringlike whorls . . . . . **genus *Priapulopsis*, *P. bicaudatus* (Danielssen, 1868) (Pl. I, Fig. 6)**

Length to 10 cm.
Widespread boreal Arctic circumpolar. In all seas of Arctic Ocean.
Depth 7-2000 m. On silt.

Key to meiobenthic larvae of priapulids

Note: the larvae of *Halicryptus higginsi* have not yet been described.

1(4) Lorica barrel-shaped (radial), round in cross section; longitudinal plates not expressed or all plates are identical, non-sclerotic; closing apparatus from numerous collar folds or plates.

2(3) Lorica with longitudinal and transverse ridges, forming a netlike microrelief, tubules collected into a single circle in the posterior region of the lorica . . . . . **early larva of *Priapulus caudatus* Lamarck, 1816 (Pl. I, Figs. 10-11)**

Length 50-100 μm.

3(2) Lorica with well-developed longitudinal plates (20); transverse ridges absent; tubules forming several circles. . . . . **larva of *Tubiluchus arcticus* Adrianov et al., 1989 (Pl. I, Figs. 16-17)**

Length 200-300 μm.

4(1) Lorica flattened (bilateral), rectangular in cross section; sclerotic dorsal and ventral plates clearly distinguishable; closing apparatus formed from several dorsal and ventral plates or closing apparatus not expressed.

5(8) Lorica with closing apparatus composed of collar plates; each lateral sector of the lorica composed of six longitudinal plates; lorica with platelike microrelief.

6(7) Circle of sublateral tubules about ⅔ from anterior end of lorica . . . . . **mid-stage and late larva of *Priapulopsis bicaudatus* (Danielssen, 1868) (Pl. I, Figs. 7-8)**

Length 200-600 μm.

7(6) Circle of sublateral tubules about ⅘ from anterior end of lorica. . . . . **mid-stage and late larva of *Priapulus caudatus* Lamarck, 1816 (Pl. I, Figs. 12-14)**

8(5) Lorica lacking differentiated closing apparatus; each lateral sector of lorica composed of eight longitudinal plates; lorica with netlike (areolar) microrelief . . . . . **larva of *Halicryptus spinulosus* von Siebold, 1849 (Pl. I, Figs. 2-5; Pl. II, Figs. 5-7)**

Length 200-1300 μm

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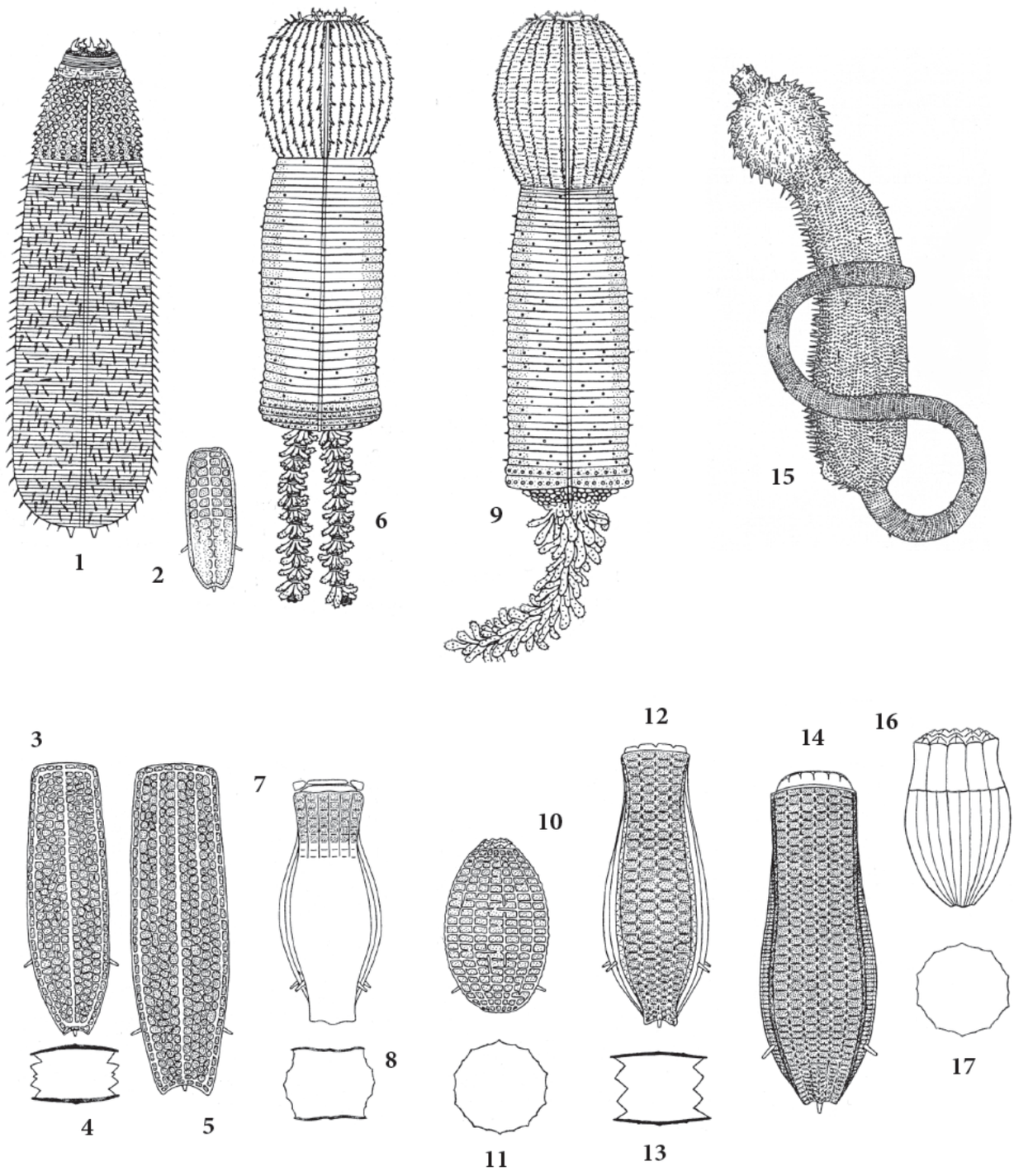

Plate I

Figs. 1-5 *Halicryptus spinulosus* von Siebold, 1849 (1: adult, ventral view. 2: lorica of early larva. 3: lorica of mid-stage larva. 4: cross section through the lorica of mid-stage larva. 5: lorica of late-stage larva).
Figs. 6-8 *Priapulopsis bicaudatus* (Danielssen, 1868) (6: adult, ventral view. 7: lorica of larva, ventral view. 8: cross section of lorica of larva.)
Figs. 9-14 *Priapulus caudatus* Lamarck, 1816 (9: adult, ventral view. 10: lorica of early barrel-shaped larva. 11: lorica, section of the early larva. 12: lorica, mid-stage larva. 13: section of the lorica of mid-stage larva. 14: lorica, late-stage larva.)
Figs. 15-17 *Tubiluchus arcticus* Adrianov et al., 1989: 15: adult male, left side. 16: lorica of larva. 17: cross section of lorica.

(Figs. 1-6, 9 from Adrianov and Malakhov 1996; Fig. 7 from Sanders and Hessler 1962; Figs. 8, 15-17 from Adrianov and Malakhov 1999; Figs. 10-14 from Higgins et al. 1993 with modifications.)

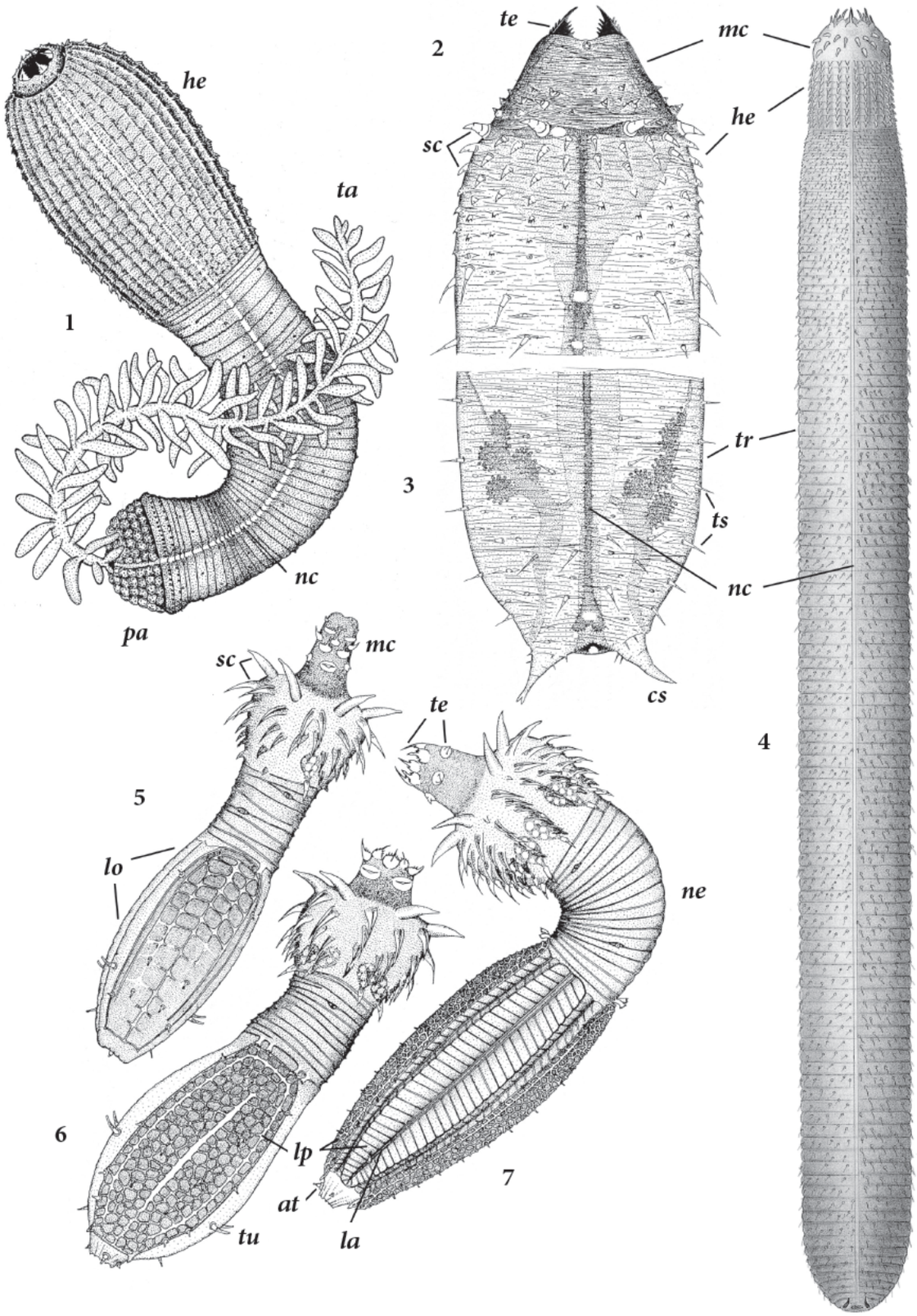

Plate II. External view of priapulids

Fig. 1 *Priapulus caudatus* Lamarck, 1816, ventral view.
Figs. 2-3 *Halicryptus spinulosus* von Siebold, 1849, ventral view. (2: anterior end. 3: posterior end.)
Fig. 4 *Halicryptus higginsi* Shirley and Storch, 1999, ventral view.
Figs. 5-7 *Halicryptus spinulosus* von Siebold, 1849 (5: early stage larvae, ventral view. 6: mid-stage larvae, dorsal view. 7: late-stage larvae, left side.)

Abbreviations: *at*: dorsal glandular tubes. *cs*: caudal spine. *he*: head. *la*: lateral commissure. *lo*: lorica. *lp*: lateral plate of lorica. *mc*: oral cone. *nc*: ventral nerve cord. *ne*: neck. *pa*: preanal section. *sc*: scalids. *ta*: caudal appendage. *te*: teeth. *tr*: trunk. *ts*: trunk spines. *tu*: tubule.

(Figs. 1-3, 5-7 from Adrianov and Malakhov 1996; Fig. 4 from Shirley and Storch 1999.)

Phylum Cephalorhyncha, Class Kinorhyncha

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One of the widely distributed groups of marine meiobenthos, kinorhynchs are observed from the poles to the tropics and at all depths from the intertidal zone to 8000 m. They occur at a wide range of salinities (from 7 to 60 parts per thousand) and temperatures (from –2 to 40°C). Kinorhynchs are seen in a variety of substrates, from semifluid silt to large shells. Their typical habitat consists of silt or silty sand with a moderate amount of organic matter, where they can reach 10,000-15,000 specimens per square meter. While there are currently about 165 valid species of kinorhynchs, they make up a small portion of the world fauna.

The size of adult kinorhynchs ranges from 200 μm to 1.2 mm not including terminal spines. The body is divided into two sections: the head (proboscis) and the trunk. The head is the first body segment and consists of a terminal oral cone and a spherical portion, having oral spines, or stylets. The head and trunk are separated by a short neck, which is covered by a series of cuticular plates, or placids, and corresponds to the second body segment. The trunk is divided into 11 segments, or zonites. The total number of segments in all kinorhynchs is 13.[1] The oral cone is retractable into the spherical part of the head. The head and neck can be withdrawn into the trunk and are called the introvert. Retraction of the oral cone and introvert is accomplished by a series of special retractor muscles. The introvert is extended by internal cavity pressure produced by dorsoventral compression of the trunk, caused by a pair of dorsoventral muscles located in each zonite.

The mouth is located at the end of the oral cone and is surrounded by nine oral stylets (the tenth is reduced), which participate in gathering food (detritus and diatoms). Scalids of the spherical portion of the introvert occur in circles, the number of which differs in different species. There can be five to eight circles of scalids and the number of scalids is different in each circle. For example, in the order Homalorhagida, genera *Pycnophyes* and *Kinorhynchus,* there are often seven circles of scalids; the number of scalids in *Pycnophyes tubuliferus* is 10, 10, 20, 10, 10, 15(13+2), and14, and in *Kinorhynchus yushini* there are 10, 10, 20, 10, 14, and 14. In the order Cyclorhagida, the most abundant species of the genus *Echinoderes*, *E. sensibilis,* has a set of scalids with the pattern 10, 10, 20, 10, 20, 6, 15(9+6), and 20(22), and the last circle consists of small rudimentary scalids (subscalids). The scalids in each circle differ in morphology. There are functionally and morphologically two main types of scalids: spinoscalids and trichoscalids.

The shape and number of the placids on the neck-closing apparatus are a fundamental systematic character for differentiating class into orders and suborders. The Homalorhagida have a bilateral closing apparatus consisting of two to four dorsal and two to four ventral placids. The Cyclorhagida have a closing apparatus with radial symmetry with a circle of 14-16 placids, or a bilateral bivalve symmetry consisting of a closed ring with deep dorsal and ventral incisions.

Zonites of the cuticularized trunk are divided into separate plates connected by flexible ligaments, which provide flexibility to the covering. The number and shape of the cuticular plates forming the trunk armor are a fundamental taxonomic character for differentiating the families and genera of kinorhynchs. The typical set of plates on the zonites consists of convex dorsal (tergal) and two ventral (sternal) plates.

The trunk segments have a variety of spines: middorsal, lateroventral, ventrolateral, lateral accessory, midterminal, laterotерminal, and laterotерminal accessory. The distribution and shape of the spines is a major systematic feature for the genera and species of kinorhynchs.

[1] Editorial note: opinions among taxonomists differ on the segment terminology. This contribution regards the trunk segments as segments 3-13, while others number the trunk segments 1-11 following Neuhaus and Higgins (2002, Integ. Comp. Biol. 42:612-632).

Kinorhynchs have separate sexes. Sexually dimorphic characters consist of copulatory spines on the terminal segment and attachment tubules on the forth segment of males. Females lack these characters and have lateroterminal accessory spines.

Key to orders, families, and genera of the class Kinorhyncha[2]

1(2) Second segment (neck) consists of 16 concentrically distributed plates (placids); trunk segments oval or like rounded triangles in cross section; segments 3 and 4 (first and second trunk segments) consist of a complete ring of cuticle; lateroventral and laterotерminal spines always present. . . . . **order Cyclorhagida, family Echinoderidae, genus *Echinoderes* (Pl. I, Figs. 1-3)**

2(1) Second segment (neck) consists of two to four dorsal and two to four ventral plates (placids); trunk segments triangular in cross section; segment 3 (first trunk segment) is always divided into a dorsal plate (tergite) and three ventral plates (sternites); only laterotерminal spines are present; lateroventral spines absent from other trunk segments. . . . . **order Homalorhagida, family Pycnophyidae, genus *Pycnophyes* (Pl. I, Figs. 4-5)**

Key to species of the genus *Echinoderes*

1(2) Middorsal spines (*ds*) on segments 6, 8, and 10; lateroventral spines (*ls*) present on segment 4. . . . . ***E. arlis* Higgins, 1966 (Pl. II, Figs. 1-5)**

Length of trunk 380-420 μm, laterotерminal spines 230-240 μm.
Arctic. East Siberian and Chukchi seas.
Depth 100-1000 m. On silt and silty sand.

2(1) Middorsal spines (*ds*) on segments 6-10; lateroventral spines absent from segment 4.

3(4) Laterotерminal spines (*lts*) at least 1.5 times greater than half of trunk length (*tl*) (*lts*/*tl* = 80-85%); posterior edge of ventral plates on segment 3 with a denticulate ridge (*dpp*) from the same cuticular elements. . . . . ***E. stockmani* Adrianov, 1999 (Pl. II, Figs. 10-12)**

Length of trunk 493 μm.
Barents Sea (Stockman oil deposit).
Silty sediments.

4(3) Laterotерminal spines (*lts*) shorter than half of trunk length (*lts*/*tl* = 17-40%); posterior edge of ventral plates on segment 3 lacking denticulate ridge, where lateral cuticular elements are almost twice as large as central elements.

5(6) Lateroventral spines (*ls*) on segments 7-11; terminal processes (*ps*) on dorsal plates (*dp*) of segment 13 lacking cleft on inner edge. . . . . ***E. tubilak* Higgins et Kristensen, 1988 (Pl. II, Figs. 6-9)**

[2] Editorial note: Undescribed or unrecorded species of known genera likely to occur in the Arctic can be identified to genus using Sørensen and Pardos (2008). Several species not included in this key are known to occur in the Arctic outside the Eurasian sector (for example listed in Higgins and Kristensen 1988).

Length of trunk 333-415 μm.
Western coast of Greenland, Greenland Sea.
Depth 9-300 m. On sandy silt and silt.

6(5) Lateroventral spines on segments 8-11; terminal processes (*ps*) on dorsal plates (*dp*) of segment 13 with a cleft on inner edge. . . . . ***E. svetlanae* Adrianov, 1999 (Pl. II, Figs 13-14)**

Length of trunk 325-343 μm.
White Sea (Kandalakshsky Bay).
Depth 15-20 m. On sand.

Key to species of the genus *Pycnophyes*

1(2) Anterior edge of dorsal plate (*dp*) on segment 3 with small dentations and four round concavities ("hollows"); middorsal processes and teeth absent from trunk segments. . . . . ***P. kielensis* Zelinka, 1928 (Pl. IV, Figs. 1-6)**

Length of trunk 450-600 μm; lateroterminal spines in females 50-80 μm and 200 μm in males.
Atlantic subtropical-boreal. Black, Mediterranean, and White seas.
Intertidal zone to 100 m depth. On silt.

2(1) Anterior edge of dorsal plate (*dp*) on segment 3 lacking rounded concavities ("hollows"); middorsal processes or teeth present on trunk segments.

3(6) Sharp dorsal teeth present; teeth on segment 12 extend beyond posterior edge of trunk; anterior lateral processes on dorsal plates of segment 3 bent inward.

4(5) Dorsal plates on segment 3 with characteristic crown-like cuticular structure; anterior edge of plate with small dentations; middorsal processes rounded on segments 3-8 and shaped like sharp teeth on segments 9-12.. . . . . ***P. arctous* Adrianov, 1999 (Pl. III, Figs. 1-6)**

Length of trunk 664-720 μm; lateroterminal spines 182-192 μm.
Arctic. Russian high Arctic, Ermak shelf.
Depth 440 m.

5(4) Dorsal plates on segment 3 lacking cuticular crown-like structures, anterior edge is even; all middorsal processes on segments 3-12 shaped like sharp teeth. . . . . ***P. chukchiensis* Higgins, 1991 (Pl. IV, Figs. 7-8)**

Length of trunk 700-720 μm; lateroterminal spines 200 μm.
Chukchi Sea.
Depth 200 m. On silt.

6(3) Sharp dorsal teeth absent; only rounded dorsal processes present (*mp*); if present, anterior lateral processes on dorsal plate of segment 3 not bent inward

7(8) Anterior-mesial thickening of the ventral pachycycli (*mtp*) present only on segment 12, they are close together at the midventral line (mva). . . . . ***P. barentsi* Adrianov, 1999 (Pl. III, Figs. 7-8)**

Length of trunk 816-824 μm; lateroterminal spines 152-164 μm.
Barents Sea.
Depth 100 m. On silt.

8(7) Anterior-mesial thickening of the ventral pachycycli (*mtp*) present also on other segments (segments 9-12 or 10-12).

9(10) Anterior edge of central ventral plate (*cvp*) of segment 3 more than half the width of posterior edge; ventral pachycycli of trunk segments with characteristic peg-and-socket articulation; ventral plates on segment 12 in females lacking lateral spots of reticulated cuticle; gonopore (*go*) in males surrounded by crown of long cuticular hairs.

10(9) Anterior edge of central ventral plate (*cvp*) of segment 3 less than half the width of posterior edge. Ventral pachycycli of the body segments lacking characteristic peg-and-socket articulation; ventral plates on segment 12 in females with lateral spots of reticulated cuticle; gonopore (*go*) in males not surrounded by crown of long cuticular hairs . . . . . ***P. galtsovae*** **Adrianov, 1999 (Pl. III, Figs. 9-12)**

Length of trunk 790-840 μm; lateral terminal spines 160-172 μm.
Barents Sea.
Depth 100 m. On silt.

11(12) Anterior-mesial thickening of the ventral pachycycli (*mtp*) of segment 12 oval; posterior edge of ventral plates on segment 12 with pair of large papillae, reaching posterior edge of ventral plates of segment 13; most of plate length on segment 13 is covered by plates . . . . . ***P. mokievskii*** **Adrianov, 1995 (Pl. IV, Figs. 15-18)**

Length of trunk 800-840 μm; lateral terminal spines 190-200 μm.
Arctic. Greenland and Barents seas.
Depth 6 m. On silt.

12(11) Anterior-mesial thickening of ventral pachycycli (*mtp*) of segment 12 almost right angled; posterior edge of ventral plates on segment 12 lacking papillae; much of plate length on segment 13 is not covered by plates of segment 12 . . . . . ***P. spitsbergensis*** **Adrianov, 1995 (Pl. IV, Figs. 9-14)**

Length of trunk 900-920 μm; lateral terminal spines 180-200 μm.
Arctic. Greenland and Barents seas.
Depth 6 m. On silt.

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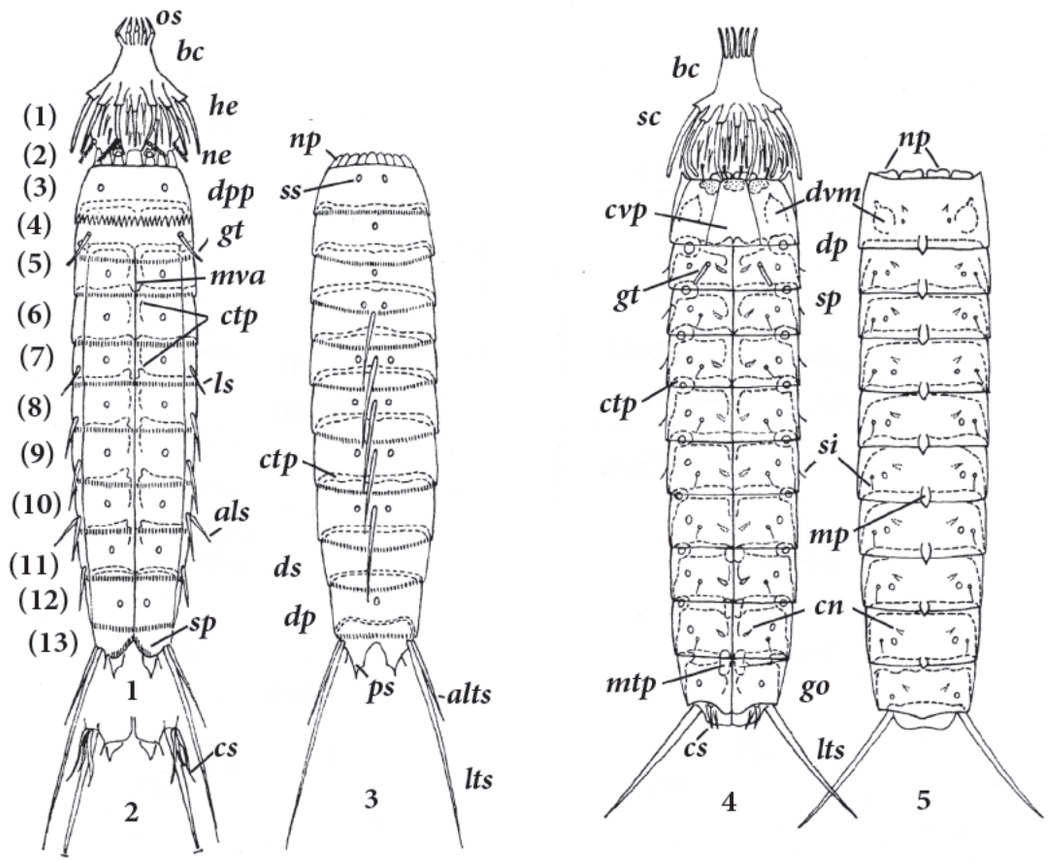

Plate I. Diagram of kinorhynch morphology.

Figs. 1-3 *Echinoderes* sp. (order Cyclorhagida, family Echinoderidae).
Figs. 4-5 *Pycnophyes* sp. (order Homalorhagida, family Pycnophyidae).
Fig. 1 Whole body with protruding introvert, female, ventral view.
Fig. 2 Posterior end of body (segments 12-13), male, ventral view.
Fig. 3 Whole animal with inverted introvert, female, dorsal view.
Fig. 4 Whole animal with protruding introvert, male, ventral view.
Fig. 5 Whole animal with inverted introvert, male, dorsal view.

Abbreviations: *als*: accessory lateral spine. *alts*: accessory laterоterminal spine. *bc*: buccal cone. *cn*: cuticular notches. *cs*: copulatory spines. *ctp*: inner cuticular thickening (pachycycli) of the plates. *cvp*: central ventral plate (central sternite). *dp*: dorsal plate (tergite). *dpp*: denticulation on the posterior edge of plates. *ds*: middorsal spine. *dvm*: impressions of the dorsoventral muscles. *go*: gonopore. *gt*: gland tubule. *he*: head. *ls*: lateroventral spine. *lts*: laterоterminal spine. *mp*: middorsal process. *mtp*: anterior-mesial thickening of the pachycycli. *mva*: midventral articulation. *ne*: neck. *np*: neck plates (placids). *os*: oral stylets. *ps*: posterior terminal process on dorsal plate of segment 13. *sc*: scalids. *si*: sensitive setae. *sp*: ventral plate (sternite). *ss*: sensory spot.

(All illustrations are original.)

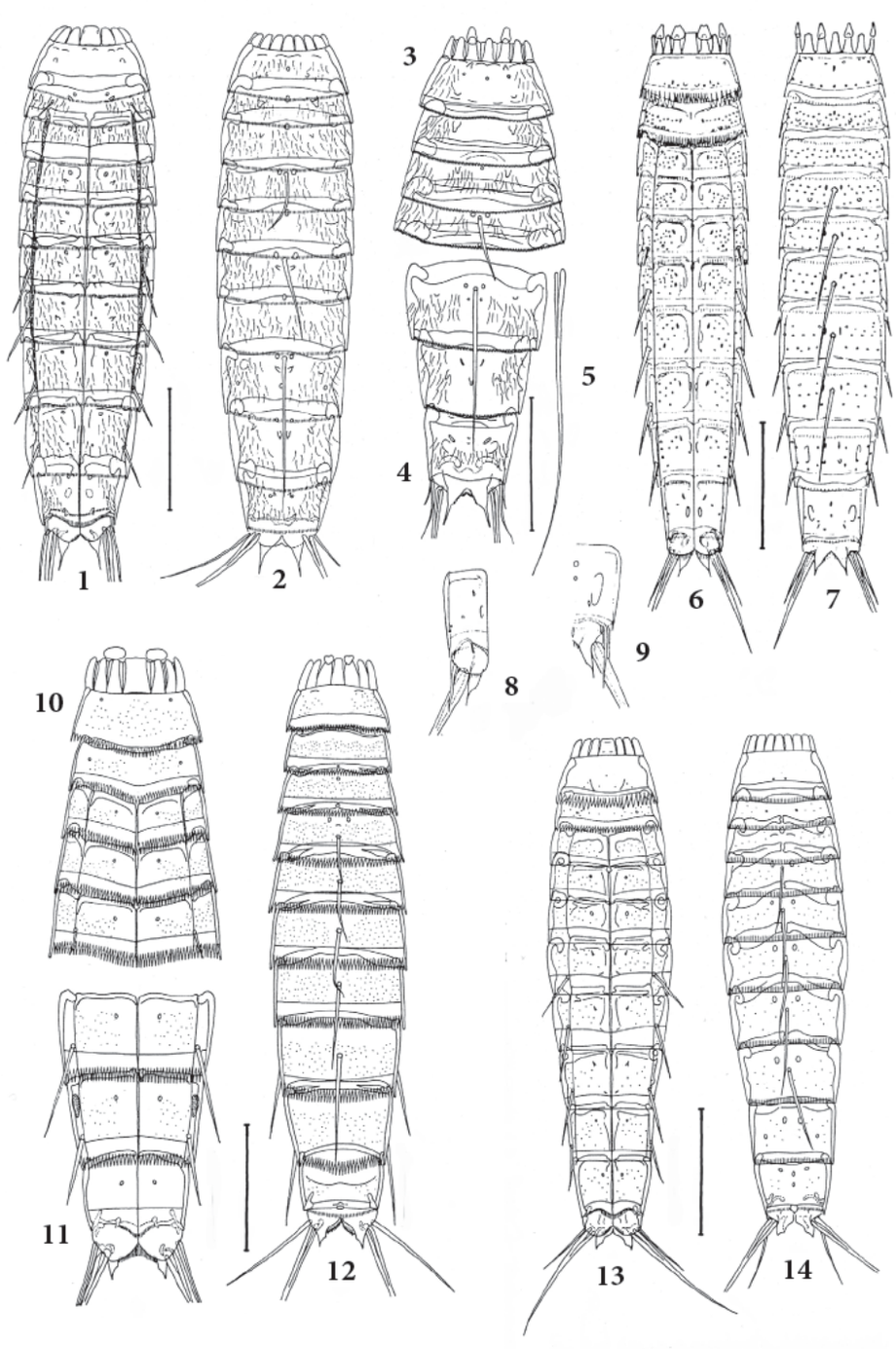

Plate II

Figs. 1-5 *Echinoderes arils* Higgins, 1966.
Figs. 6-9 *Echinoderes tubilak* Higgins et Kristensen, 1988.
Figs. 10-12 *Echinoderes stockmani* Adrianov, 1999.
Figs. 13-14 *Echinoderes svetlanae* Adrianov, 1999.

(1, 6, 13: whole animal with introverted introvert, female, ventral view. 2, 7, 12, 14: whole animal with inverted introvert; female, dorsal view. 3: anterior [2-6] segments, male, dorsal view. 4: posterior [10-13] segments, male, dorsal view. 5: laterotermínal spine. 8: left half of segments 12-13: ventral view. 9: right half of segments. 12-13: dorsal view. 10: anterior segments [2-7], female, ventral view. 11: posterior segments [10-13], female, dorsal view.)

(Figs. 1-5, 10-14 from Adrianov and Malakhov 1999, Figs. 6-9 from Higgins and Kristensen 1988.)

Scale 100 µm.

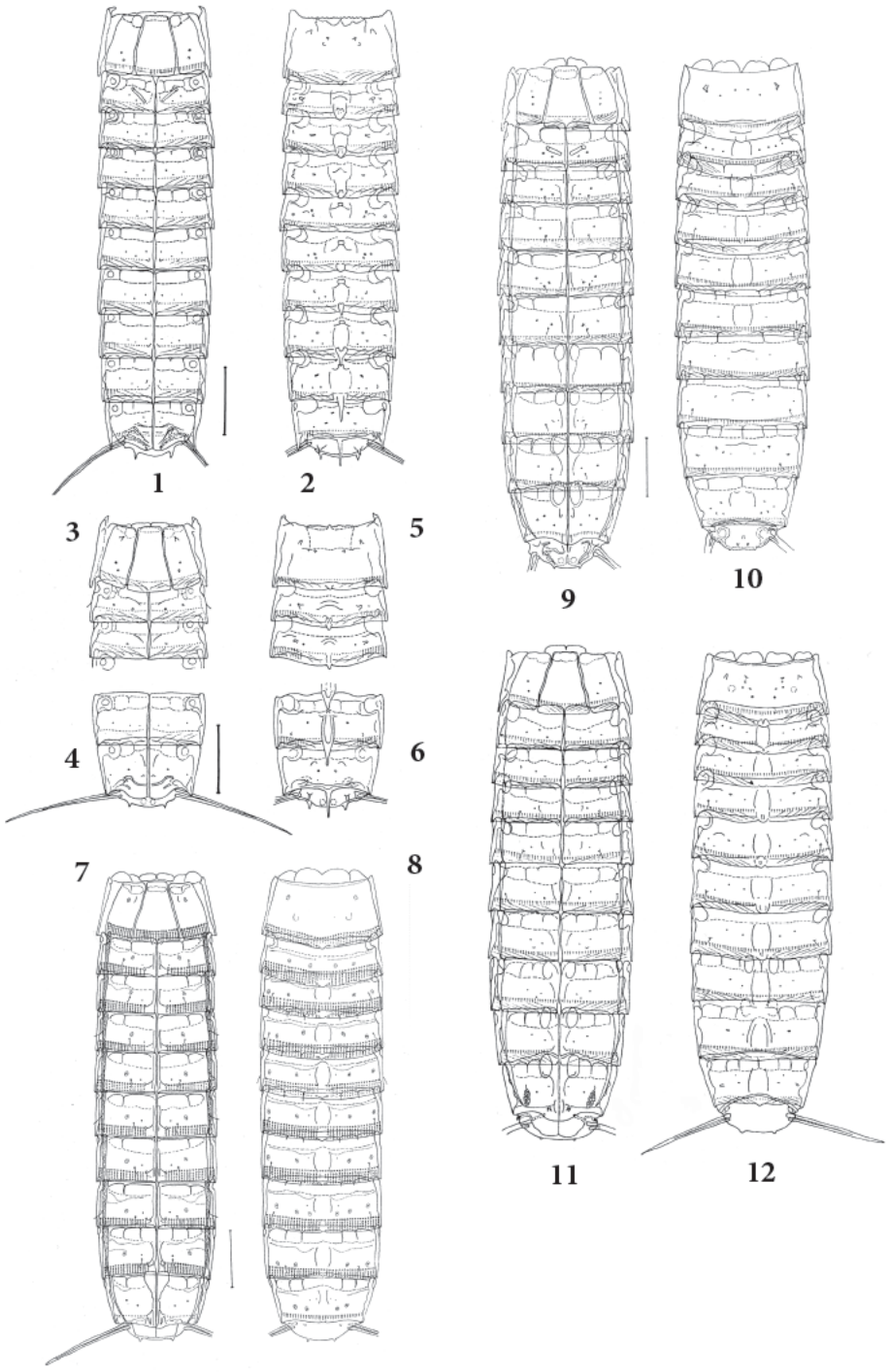

Plate III

Figs. 1-6 *Pycnophyes arctous* Adrianov, 1999.
Figs. 7-8 *Pycnophyes barentsi* Adrianov, 1999.
Figs. 9-12 *Pycnophyes galtsovae* Adrianov, 1999.

(1, 9: whole animal with inverted introvert, male, ventral side. 2, 10: whole animal with inverted introvert, male, dorsal side. 3: anterior [3-5] segments, female, ventral view. 4: posterior [11-13] segments, female, ventral view. 5: anterior [3-5] segments, female, dorsal view. 6: posterior [11-13] segments, female, dorsal view. 7,11: whole animal with inverted introvert, female, ventral view. 8, 12: whole animal with inverted introvert, female, dorsal view.)

(From Adrianov and Malakhov 1999.)

Scale 100 µm.

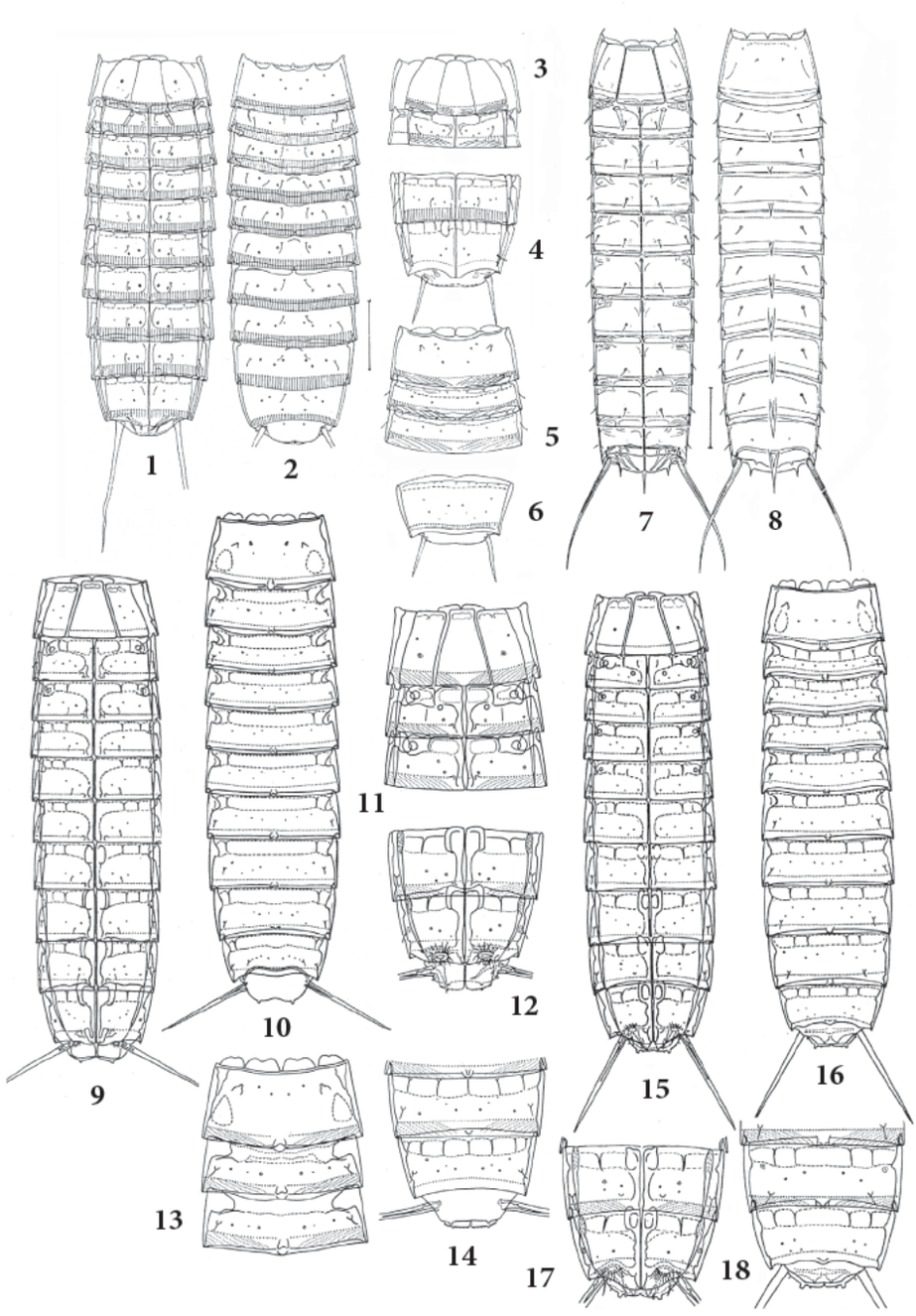

Plate IV

Figs. 1-6 *Pycnophyes kielensis* Zelinka, 1928.
Figs. 7-8 *Pycnophyes chukchiensis* Higgins, 1991.
Figs. 9-14 *Pycnophyes spitsbergensis* Adrianov, 1995.
Figs. 15-18 *Pycnophyes mokievskii* Adrianov, 1995.

(1, 7, 15: whole animal with inverted introvert, male, ventral view. 2, 8, 16: whole animal with inverted introvert, male, dorsal view. 3: anterior [2-4] segments, females, ventral view. 4: posterior [11-13] segments, female, ventral view. 5: anterior [2-5] segments, female, dorsal view. 6: posterior [12-13] segments, female, dorsal view. 9: whole animal with inverted introvert. female, ventral view. 10: whole animal with inverted introvert, female, dorsal view. 11: anterior (2-5) segments, male, ventral view. 12, 17: posterior [11-13] segments, male, ventral view. 13: anterior [2-5] segments, male, dorsal view. 14, 18: posterior [11-13] segments, males, ventral view.)

(Figs. 1-6, 9-18 from Adrianov and Malakhov 1999, Figs. 7-8 from Higgins 1991.)

Scale 100 µm.

Phylum Annelida, Class Clitellata, Subclass Oligochaeta[1]

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The oligochaete body varies from threadlike to a terete shape. The length can vary from tenths of a millimeter to tens of centimeters (aquatic), or to 2.5 m (terrestrial). For marine oligochaetes, the length usually does not exceed 30 mm. The number of segments (somites) varies from several (six to eight) to tens and hundreds. Segments are conventionally indicated by Roman numerals (I, II, III, etc.) The anterior end of the body consists of a clearly expressed or somewhat reduced head or preoral lobe (prostomium), followed by the oral (first) segment or peristomium lacking setae. The mouth is located on the ventral side between the prostomium and the first segment (when the prostomium is reduced, the mouth is more or less terminal). Several (four to eight) of the anterior segments can have some structural modifications, e.g., nephridia are absent from these segments, or setae can be different here.

Starting with the second, all segments bear four (rarely two) bundles of setae (chaetae); setae may be absent from some segments in some species, and in a few species setae may be absent altogether. The number of setae in bundles, and their distribution and shape, are important taxonomic characters. The basic forms of the setae in aquatic oligochaetes are hairlike and bifid. All other shapes can be derived from these forms: short but simple-pointed (including needle), trifid, pectinate (with intermediate denticles), fanlike, and others. The hair setae can be smooth or plumose (called serrate when denticles are on one side), thin and long, or shorter and stouter. Bifid setae are straight or, more often, S-shaped (sigmoid) and often have a medial thickening (nodulus). A distal (upper) and proximal (lower) tooth are distinguishable on the distal end of bifid setae. Ventral setae are used for gripping and crawling on the substrate while the hairlike and fanlike setae are, in all probability, for retention in the upper layer of liquid sediment. Many species also have modified, ventral genital setae, which play a role in copulation: penial setae located near the male genital pores and spermathecal setae at the spermathecal pores.

The body wall of the worms consists of an outer cuticle that varies in thickness, a single layer of epithelium, and two layers of muscles: an outer circular muscle layer and inner longitudinal. The inner side of the body wall is lined with peritoneal epithelium. There can also be diagonal muscles, dorsoventral muscles in the septa, and retractor and protractor muscles for some internal organs and setae.

The coelom in each segment consists of two coelomic cavities; in a mesentery between these cavities lie the dorsal blood vessel, digestive tube, ventral blood vessel, and ventral nerve trunk. The coelomic space of adjacent segments is separated by thin, muscular septa (dissepiments), corresponding more or less to the outer intersegmental grooves. The coelomic fluid can contain free or aggregated coelomocytes; their presence, shape, and structure serve as a systematic character.

The digestive tube consists of the following components: mouth, oral cavity, pharynx, esophagus, midgut, and hindgut. The oral cavity (in the first and second segments) has a ciliated lining. The pharynx can have a highly developed musculature and be lined with a thickened cuticle; a pharyngeal pocket and glands are

[1]Subclass Oligochaeta Grube, 1850

mostly present on the dorsal side. The esophagus starts as a narrow tube that can gradually or abruptly widen to a stomach (particularly in the family Lumbricidae) at the beginning of the midgut. Starting with a certain segment, the esophagus bears chloragogen cells on the outside and has various glands, including septal (pharyngeal) glands, with ducts leading to the pharynx; in addition, tubular "peptonephridia" or salivary glands can be attached to the very beginning of the esophagus in the family Enchytraeidae. The number and shape of these glands serve as systematic characters. The midgut (digestive region) following the esophagus is the longest and simplest section; it exhibits peristalsis due to circular and longitudinal muscles. On the outside of the midgut (like the posterior portion of the esophagus) there is a more or less thick cover of dark chloragogen cells; the inside is ciliated. The hindgut has weaker chloragogen cover but more developed internal ciliation and a web of blood vessels (or gut sinus), related to intestinal respiration in these worms.

The circulatory system is closed and often includes an intestinal sinus or a web of blood vessels. Blood flows toward the anterior in the pulsating dorsal blood vessel and from anterior to posterior in the ventral blood vessel. The dorsal blood vessel divides in the anterior end; two branches run into the cephalic lobe, then turn backward and unite to form the ventral blood vessel. The dorsal and ventral blood vessels are connected by lateral (circular) vessels; a few of the latter can have muscular dilatations that pump the blood similar to a heart. The dorsal and lateral blood vessels can have branched and unbranched blind appendages; the shape and character of those serve as taxonomic characters. In addition, there is a net of small blood vessels and capillaries surrounding the gut, and sometimes inside the body wall. The blood can be colorless or have yellow or red pigment.

Excretory organs of oligochaetes are paired metanephridia, located in most body segments but missing from several of the anterior segments. A typical nephridium is located in two adjacent segments and consists of the anteseptal (preseptal) and postseptal sections. The anteseptal section consists of a ciliated funnel opening into the body cavity of the preceding segment and a short section of the nephridial tube. The postseptal section is located in the next segment and consists of a convoluted nephridial tube of varying length forming a number of loops. The loops can lie freely in the coelomic space or can be knit together partially or completely. The distal end of a postseptal section is usually longer and less convoluted. Its terminal end can be widened to form a kind of urinary bladder. Just beyond this wider section, the nephridial duct penetrates the body wall and opens with a nephridial pore near the ventral setae.

The nervous system of oligochaetes consists of the suprapharyngeal or cephalic ganglion (brain), located in the cephalic lobe and some anterior-most segments, the circumpharyngeal nerve ring, and the ventral nerve trunk forming ganglia in the segments, linking each other with connectives. The shape of the cephalic ganglion can serve as a taxonomic character.

Oligochaetes are hermaphrodites. Their typical reproductive system consists of the following internal organs: paired gonads (testes and ovaries); gonoducts (male and female) with their accessory glands and copulatory organs, sperm and egg sacs; and spermathecae. Male ducts begin with an anteseptal funnel like the nephridia. The proximal, usually longer and thinner portion of the male duct is called the sperm duct or vas deferens. The distal, wider section of the male gonoduct where spermatozoids or spermatozeugmata accumulate before copulation is called the atrium. The most consistent glandular components of the atrium are the prostate cells, located on the outer side of the atrium. Individual cells can release their secretions directly into the atrial cavity (diffuse prostate gland) or form aggregations separate from the atrium in a common membrane with a more or less elongate stalk (compact prostate gland). The copulatory apparatus can consist of only the ejaculatory ducts, but includes penes or pseudopenes in the majority of aquatic oligochaetes (a pseudopenis differs from the penis in its lack of a penial sac). In Enchytraeidae, there are no atria and the copulatory apparatus is represented by a penial bulb consisting of muscular and glandular tissue. Female gonoducts are represented only by a funnel in the coelom and an external pore on the body surface. Various accessory

organs of the reproductive system exist such as the clitellum and other skin glands, genital setae, seminal capsules, etc. Sperm and egg sacs are saclike outgrowths of the septa, stretching for several segments anteriorly and posteriorly, where the maturing reproductive cells accumulate. The formation of spermatozeugmata is characteristic of many oligochaetes of the family Tubificidae. Spermatozeugmata are compact packages of spermatozoids in the atrium and later in spermathecae. Spermatozeugmata can be covered by a membrane (one layer or multiple layers) and can vary in shape.

There is a mutual exchange of sperm into the partner's spermatheca during copulation. The eggs are fertilized and develop in an egg cocoon secreted by the clitellum and laid in the sediment or attached to underwater plants. Development is direct.

The presence of a clitellum is characteristic of sexually mature individuals only. The clitellum is a thickened, glandular portion of epithelium on several segments, which always bears male and female genital pores in aquatic oligochaetes and enchytraeids. There are two major types of clitella: a muff-like belt surrounding the respective body segments evenly on all sides, and a saddle-shaped clitellum developed only on the dorsal and lateral sides of the animal; the clitellum can be poorly developed on the ventral side or can have a non-glandular field near the male genital pores.

In addition to sexual reproduction, many oligochaetes can undergo asexual reproduction by paratomic division including the formation of a chain of zooids, or by architomy (fragmentation).

Oligochaetes inhabit soils, and bottom sediments of the fresh, brackish, and marine waters. Some enchytraeids (members of the genera *Enchytraeus*, *Lumbricillus*, and *Marionina*) often form aggregates of thousands of individuals in the supralittoral zone, especially among algae washed up on the beach. The greatest species diversity (about 5000 species) has been found from soils and freshwater bodies. More than 800 species of oligochaetes are known from oceans, seas, and brackish environments. The relatively low species diversity in marine and brackish environments may be due to insufficient studies in these habitats. Many oligochaete species are known to be very resistant to unfavorable environmental conditions: oxygen deficiency, eutrophication, silting, chemical and bacterial contamination, etc. This resistance facilitates a wide distribution of oligochaetes on shelf seas.

At present, the list of oligochaetes in the northern seas of Russia consists of 39 species of the following families: Naididae (3), Tubificidae (9), and Enchytraeidae (27). This list is undoubtedly incomplete, due to the scarcity of focused studies of oligochaetes. Three species [*Lumbricillus muscicolus* (Stephenson, 1924), *L. reynoldsoni* Backlund, 1948, and *Marionina crymodes* (Stephenson 1922)] reported only from the Spitsbergen islands (Norway) in the Barents Sea are not included in the key due to insufficient information about them.

Key to families of the subclass Oligochaeta Grube, 1850

1(4) Setae mostly of various types, usually including bifid ones in the ventral bundles, and often also hairlike, needle, or pectinate in the dorsal bundles. Testes located in the same segment with the spermathecae; ovaries, male gonoducts, and male genital pores in the next segment.

2(3) Clitellum usually on segments V-VI or VI-VII, spermathecal pores on segments IV or V, male genital pores on segments V or VI, female genital pores in the groove between segments V and VI, or between segments VI and VII. Testes in segment IV or V, ovaries in segment V or VI. Eyes sometimes present. Small, usually transparent worms, some of them able to swim. Asexual

reproduction by paratomy with formation of chains of individuals (zooids) prevailing. . . . . **Naididae (Pl. I)**

3(2) Clitellum most often on segments XI-XII. Spermathecal pores then on segment X, male pores on segment XI, female pores in the groove between segments XI and XII. Eyes always absent. Worms often pink or red color due to the red blood. Never swimming. Asexual reproduction lacking or (seldom) in the form of architomy . . . . . **Tubificidae (Pl. I)**

4(1) Setae always uniformly simple-pointed, usually two or more per bundle. Clitellum usually on segments XII-XIII, spermathecae in segment V, with pores in the groove between segments IV and V; male genital pores on segment XII, female pores in the groove between segments XII and XIII. External duct of spermathecae opens with a spermathecal pore, and spermathecal ampullae of most Enchytraeidae connect with the esophagus either directly or via a short duct. Eyes absent. Worms predominantly white, sometimes with pink, yellow, or gray shade. Never swimming. Asexual reproduction can occur (if at all) in the form of architomy. . . . . **Enchytraeidae (Pl. I)**

Key to genera and species of the family Naididae

1(2) Dorsal setae begin on segment VI. In addition to hairlike setae, shorter needle setae with a thin, bifid, or simple tip may be present in dorsal bundles, differing markedly in shape from the sigmoid, bifid ventral setae. Eyes usually present. . . . . .**genus *Nais, N. elinguis* Müller, 1774 (Pl. II, Figs. 1-3)**

Teeth on the bifid needle setae almost parallel. Distal tooth in ventral setae of longer than proximal one by 2-2.5 times.
Length 2.2-12 mm (chain of zooids), segments 12-21 (the first zooid) or 15-40 (single, not budding specimen).
White Sea (Kandalakshsky Bay). Littoral. Salinity to 20‰.

2(1) Dorsal bundles do not begin on segment VI. All setae bifid only. Eyes absent.

3(4) Dorsal bundles begin on segment V . . . . . .**genus *Paranais, P. litoralis* (Müller, 1784) (Pl. II, Figs. 4-7)**

Ventral and dorsal setae similar but can differ slightly in size and relative length of teeth. Distal tooth in ventral setae of segment II longer than proximal, toward the back the length of teeth becomes equal.
Length 2-14 mm, segments 14-17 (the first zooid) or 13-46 (single specimen).
White Sea.
Littoral.
Salinity 5-20‰.

4(3) Dorsal bundles begin on segment III. Setae very thin, with equal, diverging teeth. . . . . **genus *Amphichaeta, A. sannio* Kallstenius, 1892 (Pl. II, Fig. 8)**

Setae on segments II and III thinner and longer than others, on segment II four setae in ventral bundles, on remaining segments usually three setae in both dorsal and ventral bundles.
Length of the first zooid 1.5 mm, segments 9.

White Sea (Kandalakshsky Bay).
Littoral.
Salinity 5-20‰.

Key to genera and species of Tubificidae Udekem, 1859

1(2) Atrium without any specialized prostate gland, tubular. Setae in ventral and dorsal bundles similar: either simple-pointed or with a thinner distal tooth . . . . . **genus *Clitellio***

2(1) One or two distinct, separate prostate glands attached to atrium.

3(6) Prostate gland discharges into proximal section of tube- or comma-shaped atrium. No modified genital setae.

4(5) Setae in dorsal bundles hairlike and pectinate or only bifid, rarely simple-pointed; ventral setae bifid or simple-pointed. Penes enclosed in chitinous sheaths, lying in large penial sacs . . . . . **genus *Tubificoides***

5(4) Dorsal bundles on segments II-III (IV) contain 2-4 pectinate setae with short intermediate denticles. Beginning with segments IV-V, dorsal setae 5-15 per bundle, with very wide (spade- or fan-shaped), longitudinally striped distal ends. Ventral setae with distinctly longer upper tooth, on anterior segments 3-6 per bundle, posteriorly 1-2 . . . . . **genus *Heterochaeta* Claparède*, H. costata* (Claparède, 1863) (Pl. IV, Figs. 5-10)**

Penial sheath short, cone-shaped, with oblique widening of distal end.
Color red in live worms.
Length 15-18 mm, segments about 40.
Barents and White seas.
Littoral.
Salinity 5-22‰.

6(3) Two prostate glands discharge into opposite ends of atrium. Large bundles of penial setae present. . . . . **genus *Thalassodrilus*, *T. prostatus* (Knöllner, 1935) (Pl. IV, Figs. 11-15)**

Setae with upper tooth shorter and thinner, 3-9 per bundle. Sexually mature individuals have 8-16 penial setae per bundle on segment XI, deeply set in body close to male genital pores in large muscular sacs; the simple, blunt distal ends of penial setae closely converge with each other. Atria pear-shaped, with thick walls. Spermathecae with short, thick duct.
Length 6-10 mm, segments 25-40.
Barents Sea.
Littoral.

Key to species of the genus *Clitellio*

1(2) Setae either simple-pointed or with a rudimentary upper tooth. Atria long, tubular, ending with penes in small penial sacs. . . . . ***C. (Clitellio) arenarius* (Müller, 1776) (Pl. II, Figs. 9-13)**

Anteriorly 2-5 bifid setae per bundle, 90-130 μm long, with rudimentary upper tooth. One single, simple-pointed seta in ventral bundles on segment X of adult animals; ventral setae absent from segment XI. Simple setae can occur also posteriorly.
Length 20-65 mm, width to 1-1.5 mm, segments 64-200.
Barents and White seas.
Littoral.

2(1) Setae uniform, all bifid, with long teeth. Atrium long, tubular, ending with thick penes in small penial sacs . . . . . ***C. (Clitelloides) orientalis*** **Finogenova, 1991 (Pl. II, Figs. 14-15)**

Anterior bundles with 3-7 bifid setae, their thinner upper tooth longer or equal in length to the lower one; setae 1-2 posteriorly, the upper tooth becoming equally long or slightly shorter. Vasa deferentia and tubular atria longer than in *C. arenarius*. Distal portion of atria tapering.
Length 31 mm, segments more than 73.
East Siberian Sea (Chaun Bay).
Depth 3 m.
On rocks and sand.

Key to species of the genus *Tubificoides*

1(8) Dorsal bundles with only bifid setae, with rudimentary upper tooth.

2(7) Body covered with epidermal papillae or glandular rings.

3(4) Whole body densely covered with epidermal papillae . . . . . ***T. benedeni*** **(Udekem, 1855) (Pl. III, Figs. 1-7)**

Synonymy: *Peloscolex benedeni.*
All setae in bundles with smaller upper tooth. Penial sheath with distinct funnel-like dilation of distal end.
Length 35-60 mm, segments 40-50.
White Sea (Kandalakshsky Bay), Barents Sea (Murmansk coast), and in the salt zone of the meromictic Lake Mogilnoye on Kildin Island.
Littoral.
Salinity 5-34.5‰.

4(3) Body surface covered with transverse glandular rings.

5(6) Penial sheaths slightly conical, with distal lateral dilation . . . . . ***T. robustocoleus*** **Finogenova, 1994 (Pl. IV, Figs. 2-4)**

Surface of body with glandular rings (up to 8 per segment) starting with segments IV-VI. Spermathecae large, sac-shaped, with long muscular duct.
Length more than 10 mm.
East Siberian Sea (Chaun Bay).

6(5) Penial sheath slightly conical, not dilated at the distal end. . . . . ***T. peveki*** **Finogenova, 1994 (Pl. IV, Fig. 1)**

Body surface with several glandular rings on each segment starting on VI. Spermathecal duct long and thin.
Length 2.5-6.0 mm (determined from fragments).
East Siberian Sea (Chaun Bay).
Depth 7 m.
On silt.

7(2) Body smooth . . . . . ***T. pseudogaster*** **(Dahl, 1960) (Pl. III, Figs. 8-9)**

Penial sheath cylindrical. Spermathecal ampullae pear-shaped, duct short, wide. Spermathecal pores in lateral line.
Length 14 mm, segments 50 or more.
Barents Sea.

8(1) Dorsal bundles on segments II-V (VI) with hairlike and bifid setae; after segments VI-VII setae are hairlike and simple-pointed. Body smooth, or with adhering foreign material on tail portion. . . . . ***T. cuspisetosus*** **Baker, 1983 (Pl. III, Fig. 10)**

Penial sheaths long, thin, somewhat widened at base. Spermathecae tube-shaped, with long duct wider at base.
Length 10-14 mm, segments 39-67.
East Siberian Sea (Chaun Bay).
Depth to 18 m.
On silt.

Key to genera and species of the family Enchytraeidae

1(8) Testes compact. Setae straight or slightly bent. Mostly white or grayish worms when alive.

2(5) Setae in more or less irregular bundles, sometimes paired.

3(4) Testes covered by a seminal vesicle. Salivary glands (peptonephridia) present. Large or small worms. . . . . **genus *Enchytraeus***

4(3) Testes free in body cavity (but see remark for *Marionina bulbosa*). Salivary glands absent. Small worms. . . . . **genus *Marionina***

5(2) Setae in strongly symmetrical, fanlike bundles.

6(7) Inner setae in a bundle equal in length or slightly shorter than the outer ones, not strongly paired; all setae equally thick and sharp-tipped. Broad, forward-directed intestinal appendages in segment VIII beside the end of esophagus . . . . . **genus *Henlea***

7(6) Setae in bundles located in symmetrical pairs, with obtuse tip; those in inner pairs always considerably shorter and thinner than the outer ones. No intestinal appendages. . . . . **genus *Fridericia, F. parathalassia*** **Schmelz, 2002 (Pl. V, Fig. 7)**

Synonymy: *Fridericia callosa* (Eisen, 1878) partim.
Setae in bundles of 4-6 on anterior segments, lacking proximal hook or with a small hook; remaining segments with setae in bundles of two. Sperm funnels 2 times longer than wide. Spermathecae with very large onion-shaped ampulla without any diverticula; duct short, with a very small gland on distal end.

Length 10-20 mm, segments 57-67.
Siberian coast, Novaya Zemlya, and White Sea (Solovetskiye Islands).

8(1) Testes deeply slit into numerous lobes and covered by a seminal vesicle. Spermathecal pore always surrounded with a rosette of glands in body cavity. Setae sigmoid or (less often) straight. Color often red or pink when alive. . . . . **genus *Lumbricillus***

Key to species of the genus *Enchytraeus*

1(2) Spermathecae with bipartite or bifurcated ampulla; the short duct densely covered with gland cells. . . . . ***E. albidus* Henle, 1837 (Pl. V, Figs 1-4)**

Setae in bundles of 2-5, almost straight but with a proximal hook, blunt-tipped.
Color white.
Length 10-35 mm, segments 46-74.
White Sea (Solovetskiye Islands, Kandalakshsky Bay), Barents Sea (Murmansk coast).
Littoral.

2(1) Spermathecae with a wide conical, forward-directed diverticulum; duct very short, without glandular cover but with small glands at the opening . . . . . ***E. kincaidi* Eisen, 1904 (Pl. V, Figs. 5-6)**

Synonymy: *Enchytraeus liefdeensis* Stephenson, 1924.
Setae in bundles of 2-3, straight but curved in basal part.
Length 10-11 mm, segments about 67.
Color whitish or yellowish.
West Spitsbergen.
Littoral.

Key to species of the genus *Henlea*

1(2) Spermathecal duct much longer than ampulla, without any glands . . . . . ***H. nasuta* (Eisen, 1878) (Pl. V, Fig. 8)**

Setae in bundles of 3-8. Dorsal vessel arising in segment VIII. One pair of intestinal diverticula in segment VIII. Pear-shaped spermathecal ampulla not sharply delineated from the duct.
Color yellowish gray.
Length 15-30 mm, segments 50-62.
White Sea (Solovetskiye Islands).
Littoral.
Amphibiotic species.

2(1) Spermathecal duct shorter than or equal in length to ampulla, glands near spermathecal pore present . . . . . ***H. ochracea* (Eisen, 1878) augm. Welch, 1919 (Pl. V, Figs. 9-11)**

Setae in bundles of 2-6. Dorsal vessel arising in segment IX. One pair of intestinal diverticula in segment VIII. Spermathecal ampulla spindle-shaped, its transition into the duct gradual.
Color white or light yellowish.
Length 15-25 mm, segments 51-60.

White Sea (Solovetskiye Islands), arctic coast of Canada.
Littoral.
Amphibiotic species.

Key to species of the genus *Lumbricillus*

1(6) Setae paired or 2-3 per bundle, straight or slightly sigmoid.

2(3) Setae always 2 per bundle, straight with a proximal curve, of variable thickness. . . . . ***L. dubius*** **Stephenson, 1911 (Pl. VII, Fig. 5)**

Sperm funnels about four times longer than wide. Spermathecae with small sac-shaped or spindle-shaped ampulla and longer, thick-walled duct.
Color whitish.
Length 7-12 mm, segments 44-47.
White Sea (Kandalakshsky Bay).
Littoral.

3(2) Setae 2-3 per bundle, straight or slightly sigmoid.

4(5) Sperm funnels very long, about 15 times longer than wide . . . . . ***L. arenarius*** **(Michaelsen, 1889) (Pl. VI, Fig. 10)**

Spermathecae with roundish ampulla hardly set off from the thick-walled duct, inner canal of duct lined with hyaline cells in its proximal half. Setae 2-3 per bundle, straight or slightly sigmoid.
Color reddish.
Length to 15 mm, segments 36-43.
Barents Sea.
Littoral.

5(4) Sperm funnels very short, about 1.5 times longer than wide . . . . . ***L. bulowi*** **Nielsen et Christensen, 1959 (Pl. VI, Figs. 11-12)**

Ampulla of spermathecae not clearly distinct from duct. Duct up to 5-6 times longer than ampulla, widening proximally due to thickening of its wall, without hyaline lining. Setae 2-3 per bundle, almost straight.
Color reddish.
Length to 12 mm, segments 32-40.
Barents Sea.
Littoral.

6(1) Setae more than 3 per bundle, at least in the anterior-most bundles; more or less sigmoid.

7(10) Spermathecal duct covered with glands (including the gland rosette at the pore).

8(9) Sperm funnels ovoid, only 1.5 times longer than wide . . . . . ***L. semifuscus*** **(Claparède, 1861) (Pl. VIII, Figs. 1-2)**

Testes triangular, indistinctly lobed. Spermathecae with sac-shaped or globular ampulla and a longer duct, wall of duct covered with small glands. Setae 2-8 per bundle, sigmoid.

Color red but anteriorly whitish.
Length 5-25 mm, segments 23-45.
White and Barents seas (Kola Peninsula).
Littoral.
On different sediments.

9(8) Sperm funnels 2-7 times longer than wide . . . . . .***L. pagenstecheri*** **(Ratzel, 1869) (Pl. VI, Figs. 5-7)**

Testes deeply cleft into numerous lobes. Spermathecae with roundish ampulla clearly distinct from duct, duct covered with thick layer of tall glandular cells. Setae straight or slightly sigmoid, 4-7 per bundle anteriorly.
Color yellowish to light brown but with red blood.
Length 14-18 mm, segments 41-51.
Barents Sea (Kola Peninsula) and Spitsbergen.

10(7) Spermathecal duct not glandular (except for the terminal rosette of glands), sometimes very short or lacking.

11(16) Sperm funnels tubular, 3-12 times longer than wide.

12(13) Spermathecae consisting of a spindle-shaped ampulla and short duct. . . . . ***L. viridis*** **Stephenson 1911 (Pl. VII, Fig. 6)**

Sperm funnels 6-8 times longer than wide. Setae straight or slightly sigmoid, 3-9 per bundle.
Color green due to green intestine.
Length 20-25 mm, segments 40-50.
White Sea.

13(12) Spermathecae ductless, the ampulla opening immediately into external pore among a broad rosette of glands.

14(15) Spermathecal ampulla simple, spindle-shaped. . . . . ***L. rivalis*** **Levinsen, 1883 (Pl. VI, Figs. 8-9)**

Sperm funnels about 10 times longer than wide. Setae sigmoid, 5-12 per bundle.
Color red.
Length 20-35 mm, segments 50-60.
White and Barents seas (Kola Peninsula).
Littoral.
On decomposing masses of marine algae.

15(14) Spermathecal ampulla bipartite: the ectal portion thick-walled, the ental portion thin-walled and containing sperm. . . . ***L. lineatus*** **(Müller, 1774) (Pl. VI, Figs. 1-4)**

A complex taxon including several polyploid, parthenogenetic forms. Sperm funnels 3-5 times longer than wide. Setae sigmoid, 4-8 per bundle anteriorly but 2-4 in posterior segments.
Color reddish.
Length 5-20 mm, segments 35-58.
Barents Sea (Kola Peninsula).

16(11) Sperm funnels shorter, 1.5-3.5 times longer than wide.

17(24) Spermathecal ampullae connect with esophagus ventrally side by side, or with a common pore or a common ental duct; the short ectal ducts entirely hidden among the rosette of glands.

18(21) Distal end of spermathecal duct heavily muscular.

19(20) Distal end of the spermathecal duct bulged, muscular, bulbous . . . . . .***L. rubidus*** **Finogenova et Strelzov, 1978 (Pl. VII, Figs. 11-15)**

Sperm funnels 1.2-1.5 times longer than wide. Spermathecal ampullae sac- or spindle-shaped, connecting with esophagus ventrally side by side. Setae slightly sigmoid, 1-9 per bundle.
Color reddish-brown.
Length 3-11 mm, segments 28-48.
Barents Sea (Murmansk coast).
Littoral.
On sand or silty sand.

20(19) Distal end of spermathecae not bulged. . . . . ***L. murmanicus*** **Finogenova et Strelzov, 1978 (Pl. VII, Figs. 7-10)**

Sperm funnels 1.5-3.5 times longer than wide. Spermathecal ampullae tubular, wider and much longer than the ectal duct, connecting with esophagus with a common pore. The duct is short, with thick muscular walls. Setae sigmoid, 2-9 per bundle.
Color greenish brown, in forebody pink.
Length 4.7-7 mm, segments 27-37.
Barents Sea (Murmansk coast, Dalniye-Zelentsy Bay).
Littoral.

21(18) Distal end of spermathecal duct thin-walled.

22(23) Spermathecal ampullae connected with esophagus, from the ventral side, with a short common ental duct. Smaller worms (length 6-7.5 mm, segments 26-34) but with more numerous setae (8-13 per bundle, sigmoid) . . . . . ***L. pseudominutus*** **Timm, 1988 (Pl. VIII, Figs. 3-6)**

Sperm funnels two or more times longer than wide. Spermathecal ampulla spindle-shaped, thick-walled; narrow duct not distinctly separated from the ampulla.
White Sea.
Littoral.

23(22) Spermathecal ampullae connected with esophagus, ventrolaterally, side by side. Larger worms (length 12-15 mm, segments 42-48) but with smaller number of setae (3-6 per bundle, sigmoid). . . . . .***L.*** **cf.** ***helgolandicus*** **Michaelsen, 1934 sensu Nielsen et Christensen, 1959 (Pl. VII, Fig. 4)**

Sperm funnels 2-3 times longer than wide. Spermathecal ampulla oval or spindle-shaped, not distinctly separated from duct. The gland rosette at spermathecal pore hides most of the external duct.
Color whitish.
White Sea.

24(17) Spermathecal ampulla connects with esophagus laterally or dorsolaterally, with separate pore or ental duct.

25(26) Spermatheca sac-shaped, short and wide, not separated from ampulla and duct; the ental end of ampulla joining esophagus with a broad pore . . . . . ***L. immoderatus*** **Finogenova, 1988 (Pl. VIII, Figs. 9-10)**

Sperm funnels large, 2.5-3 times longer than wide. Setae very slightly sigmoid, 3-5 per bundle.
Length 5.5-6 mm, segments 31-32.
White Sea.
Littoral.

26(25) Spermathecae consist of an ampulla and duct; ental pore narrow.

27(28) Spermathecae tubular, with gradual transition from ampulla to duct; distal portion of duct with chitinous lining and filled with secretion. . . . . ***L. horridus*** **Finogenova, 1988 (Pl. VIII, Figs. 7-8)**

Sperm funnels 2.2 times longer than wide. Setae sigmoid, 3-9 per bundle.
Length 3.8-4 mm, segments 26-29.
White Sea (Kandalakshsky Bay).

28(27) Spermathecal duct without chitinous lining.

29(30) Spermathecae with roundish ampulla; duct 5-6 times longer than ampulla, proximally dilating ("trumpet-shaped" in original description). . . . . ***L. tuba*** **Stephenson, 1911 (Pl. VII, Fig. 1)**

Sperm funnels 1.5 times longer than wide. Setae slightly sigmoid, 2-6 per bundle.
Color whitish or pale pink.
Length about 12 mm, segments 33-41.
East Siberian Sea.

30(29) Spermathecae with very short, thin duct and longer, proximally narrowing ampulla . . . . . ***L.* cf. *kaloensis*** **Nielsen et Christensen 1959 (Pl. VII, Figs. 2-3)**

Sperm funnels 2-3 times longer than wide. Setae sigmoid, 3-7 per bundle.
Color whitish or reddish.
Length about 12 mm, segments about 36.
Barents Sea.
Littoral.
On sand and among rocks.

Key to species of the genus *Marionina*

1(4) Ventral and dorsal bundles of setae present.

2(3) Setae with hook-shaped proximal end. . . . . ***M.* cf. *spicula*** **(Leuckart, 1847) (Pl. IX, Figs. 1-4)**

Setae straight, 2-6 per bundle.
Color whitish.
Length 4-5 mm, segments 27-30.
Barents Sea.
Littoral.

3(2) Setae straight, with slightly bent proximal end. . . . . ***M. bulbosa*** **Finogenova, 1994 (Pl. IX, Figs. 7-9)**

Testes small and compact but with slightly lobate ends, in seminal vesicle. Sperm funnels 10-13 times longer than wide. Penial bulbs very large in comparison with the worm itself, 130 µm long and 90 µm wide. Spermathecae with roundish or sac-shaped ampulla sharply separated from the duct consisting of tall cells; the duct is covered with separate gland cells becoming taller at the spermathecal pore. Setae 3 per bundle anteriorly, 2 per bundle posteriorly.
Length 4.5-5.5 mm. Segments 40.
East Siberian Sea (Chaun Bay). Depth 3 m. On coarse sand.

Remark: Because of the presence of a seminal vesicle, the partially lobate structure of the testes, and large gland cells surrounding the spermathecal pore, this species may well belong either to *Enchytraeus* or *Lumbricillus*. The authors hesitate to establish its exact generic position.

4(1) Dorsal setae absent, replaced by tubercles. . . . . ***M. subterranea*** **(Knöllner, 1935) (Pl. IX, Figs. 5-6)**

Ventral setae straight with proximal hook, mostly 2 (seldom 1) per bundle.
Length 2-6 mm, segments 22-29, most often 26.
Color white.
White and Barents seas (Kola Peninsula).

Abbreviations on figures

a, *at*: atrial ampulla, atrium. *e*: eye. *es*: esophagus. *ff*: female funnel. *glsp*: glandular portion of spermatheca. *mf*: male funnel (sperm funnel). *ov*: ovary. *p*: penis. *pb*: penial bulb. *pr*: prostate gland. *psc*: penial sac. *psh*: penial sheath. *psp*: spermathecal pore. *sp* (*spa*): spermatheca (spermathecal ampulla). *spb*: spermathecal bulb. *spd*: spermathecal duct. *spv*: spermathecal vestibulum. *ss*: spermatozeugma. *t*: testis. *vch*: ventral setae. *vd*: vas deferens (sperm duct). ♂: male pore. ♀: female pore. Segment numbers and furrows between segments are denoted by Roman numerals, dissepiments with Arabic numerals.

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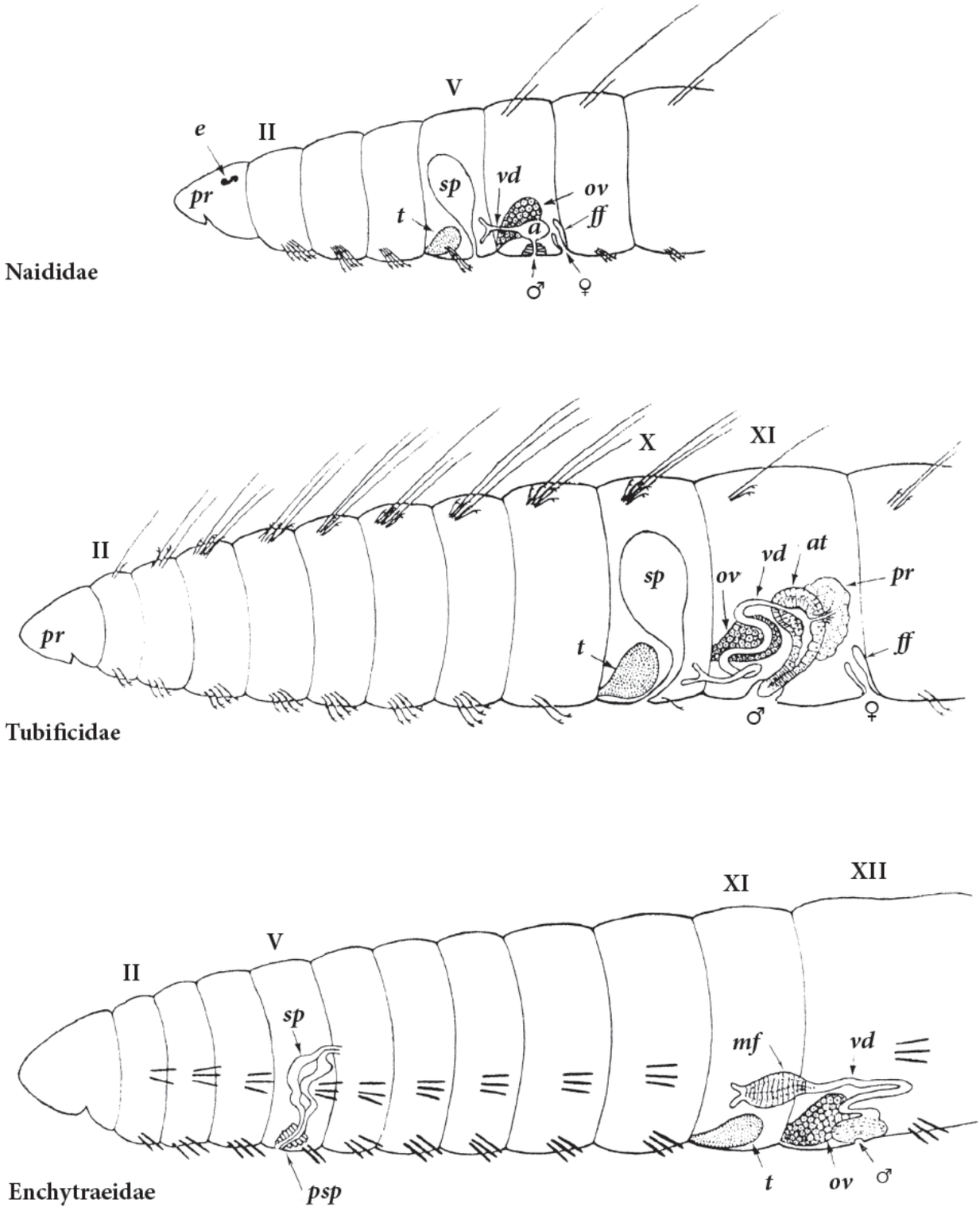

Plate I. General structure of the reproductive system of Naididae, Tubificidae, and Enchytraeidae.

(From Brinkhurst and Marchese 1989.)

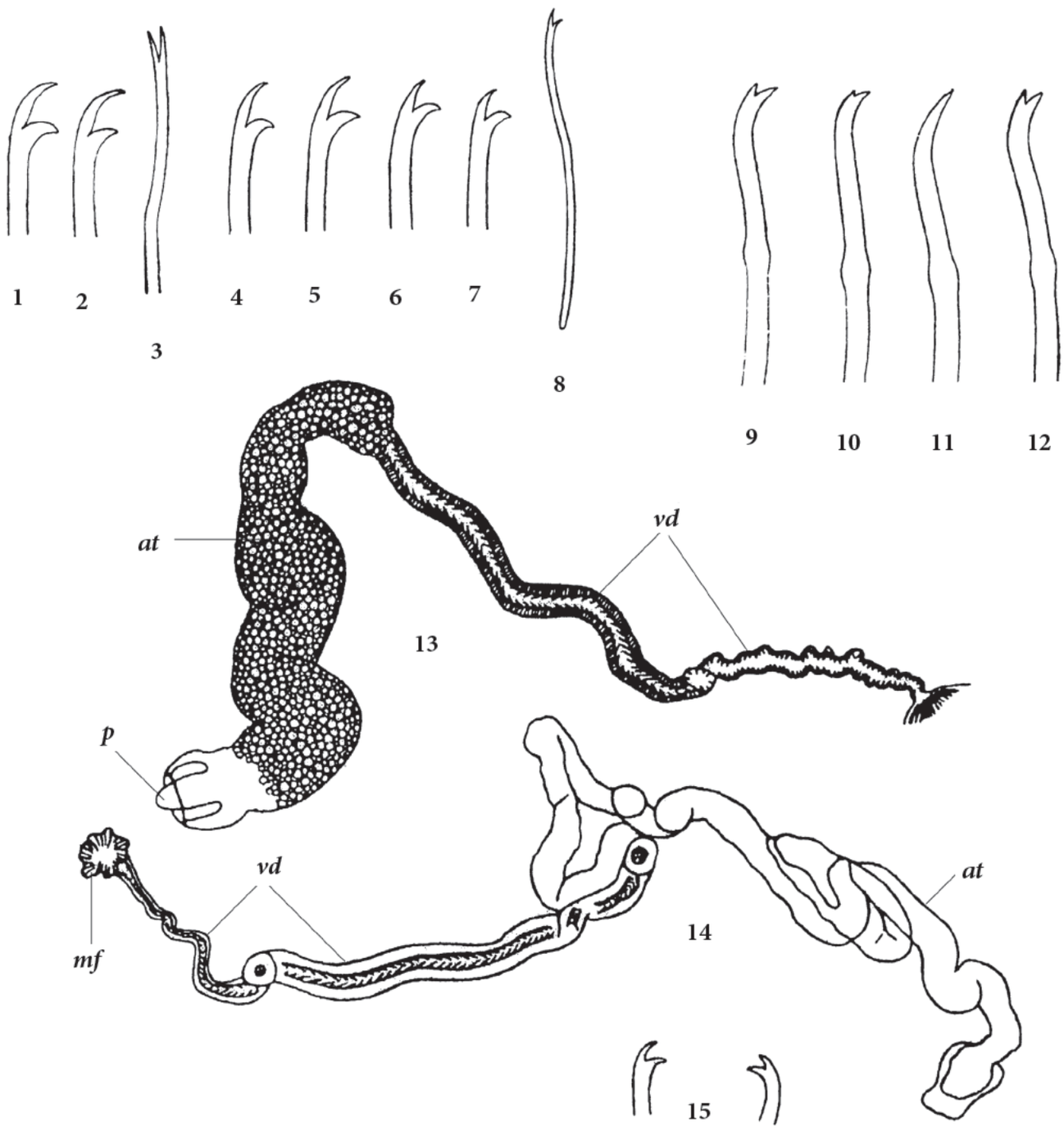

Plate II

Figs. 1-3 *Nais elinguis* Müller, 1774 (1: ventral setae of segment II. 2: ventral seta of midbody. 3: needle seta of dorsal bundle.)
Figs. 4-7 *Paranais litoralis* (Müller, 1784) (4: ventral seta of segment II. 5: ventral seta of segment III. 6: ventral seta of posterior portion of body. 7: dorsal seta from midbody.)
Fig. 8. *Amphichaeta sannio* Kallstenius, 1892 (seta.)
Figs. 9-13 *Clitellio (Clitellio) arenarius* (Müller, 1776) (9,10: ventral setae of segment V. 11: ventral setae of segment XII. 12: dorsal seta of segment V. 13: male gonoduct.)
Figs. 14-15 *Clitellio (Clitelloides) orientalis* Finogenova, 1991 (14: male gonoduct. 15: setae from segments VI and IX.)

(Figs. 1-8 from Sperber 1948; Figs. 9-12 from Chekanovskaya 1962; Figs. 13-15 from Finogenova 1991.)

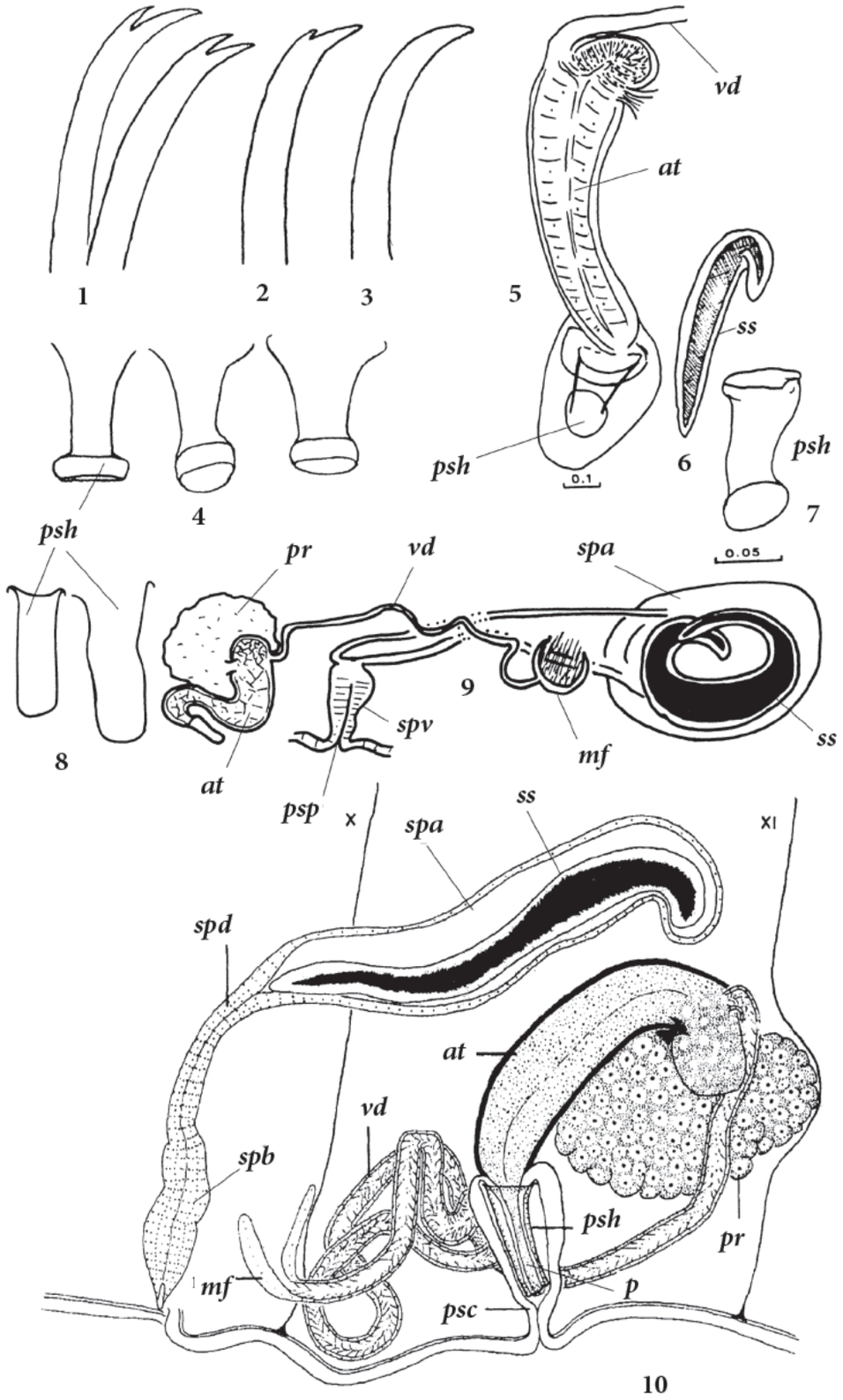

Plate III

Figs. 1-7 *Tubificoides benedii* (Udekem, 1855) (1: setae of a bundle on anterior segments. 2: seta from midbody. 3: seta from a posterior segment. 4: penialsheaths. 5: male gonoduct. 6: spermatozeugma. 7: penial sheath.)
Figs. 8-9 *Tubificoides pseudogaster* (Dahl, 1960) (8: penial sheath. 9: male gonoduct and spermatheca.)
Fig. 10 *Tubificoides cuspisetosus* Baker, 1983. (spermatheca and male gonoduct.)

(Figs. 1-4 original; Figs. 5-7 from Brinkhurst 1985; Figs. 8-9 from Brinkhurst 1986; Fig. 10 from Baker 1983.)

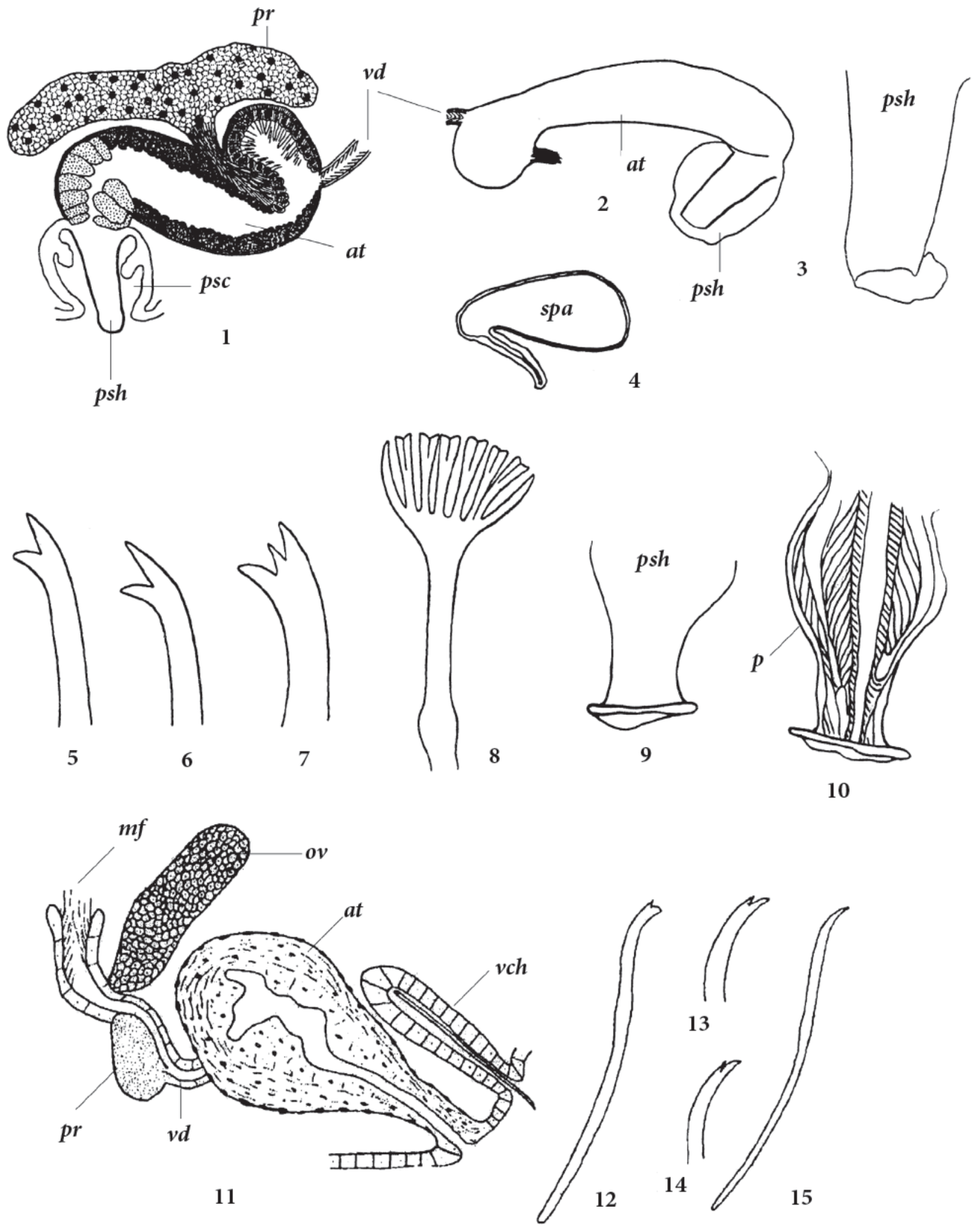

Plate IV

Fig. 1 *Tubificoides peveki* Finogenova, 1994 (male gonoduct.)
Figs. 2-4 *Tubificoides robustocoleus* Finogenova, 1994. (2: male gonoduct. 3: penial sheath. 4: spermatheca.)
Figs. 5-10 *Heterochaeta costata* Claparède, 1863. (5: ventral seta from segment II. 6: ventral seta from a posterior segment. 7: dorsal seta from segment IV 8: dorsal seta from segment V [fanlike]. 9: penial sheath. 10: extruded penis with penial sheath.)
Figs. 11-15 *Thalassodrilus prostatus* (Knöllner, 1935) (11: male gonoduct. 12: ventral seta. 13: dorsal seta from anterior segments. 14: dorsal seta from midbody. 15: dorsal seta from a posterior segment.)

(Figs. 1-4 from Finogenova 1994; Figs. 5-8 from Chekanovskaya 1962; Figs. 9-10 original; Figs. 11-15 from Brinkhurst 1971.)

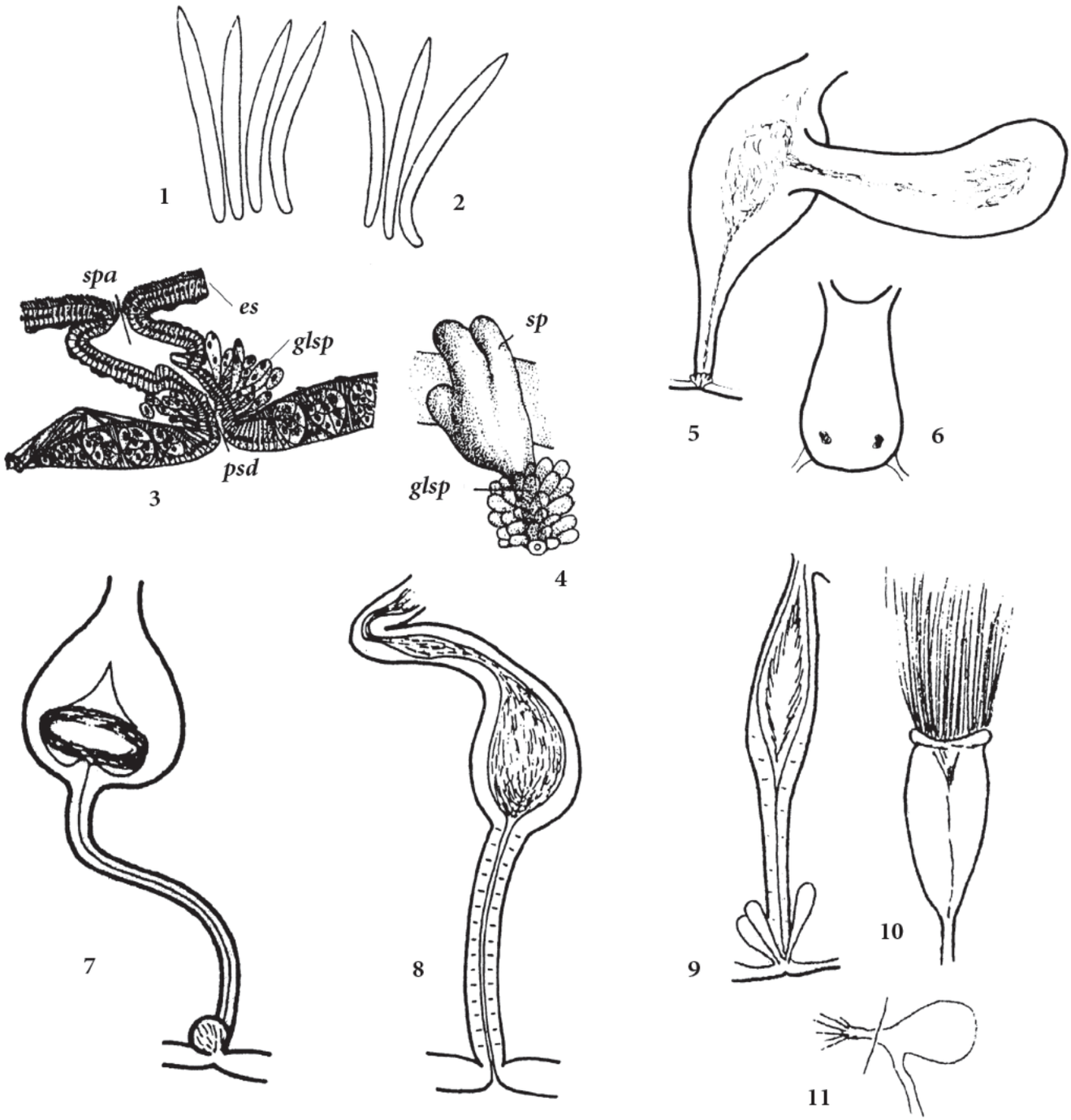

Plate V

Figs. 1-4 *Enchytraeus albidus* Henle, 1837 (1: ventral setae from segment VI. 2: ventral setae from a posterior segment. 3,4: spermatheca in longitudinal section and from surface.)
Figs. 5-6 *Enchytraeus kincaidi* Eisen, 1904 (5: spermatheca. 6: brain.)
Fig. 7 *Fridericia parathalassia* Schmelz, 2002 (spermatheca.)
Fig. 8 *Henlea nasuta* (Eisen, 1878) (spermatheca.)
Figs. 9-11 *Henlea ochracea* (Eisen, 1878) (9: spermatheca. 10: sperm funnel. 11: nephridium.)

(Figs. 1-4 from Chekanovskaya 1962; Figs. 5-6 from Nurminen 1965; Figs. 7-8 from Nielsen and Christensen 1959; Figs. 9-11 from Nurminen 1973.)

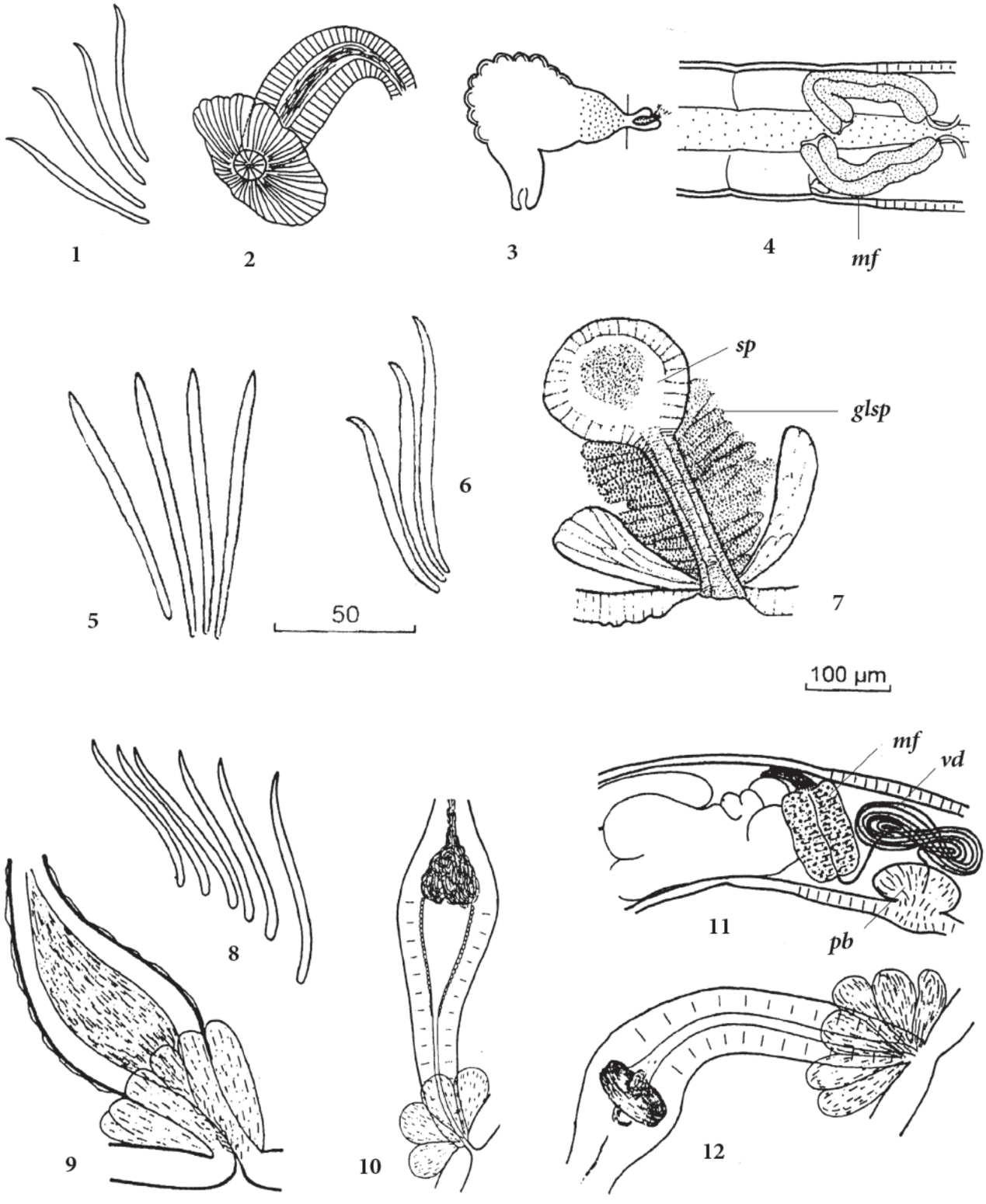

Plate VI

Figs. 1-4 *Lumbricillus lineatus* Müller, 1774 (1: setal bundle from anterior segments. 2: spermatheca. 3: nephridium. 4: proximal section of male gonoducts.)
Figs. 5-7 *Lumbricillus pagenstecheri* (Ratzel, 1869) (5: setal bundle from anterior segments. 6: setal bundle from a posterior segment. 7: spermatheca.)
Figs. 8-9 *Lumbricillus rivalis* Levinsen, 1883, augm. Ditlevsen, 1904 (8: setal bundle from anterior segments. 9: spermatheca.)
Fig. 10 *Lumbricillus arenarius* (Michaelsen, 1889) (spermatheca.)
Figs. 11-12 *Lumbricillus bulowi* Nielsen and Christensen, 1959 (11: male gonoduct. 12: spermatheca.)

(Figs. 1-2 from Timm 1999; Figs. 3-4 from Nielsen and Christensen 1959; Figs. 5-7 from Timm 2005; Figs. 8-12 from Nielsen and Christensen 1959.)

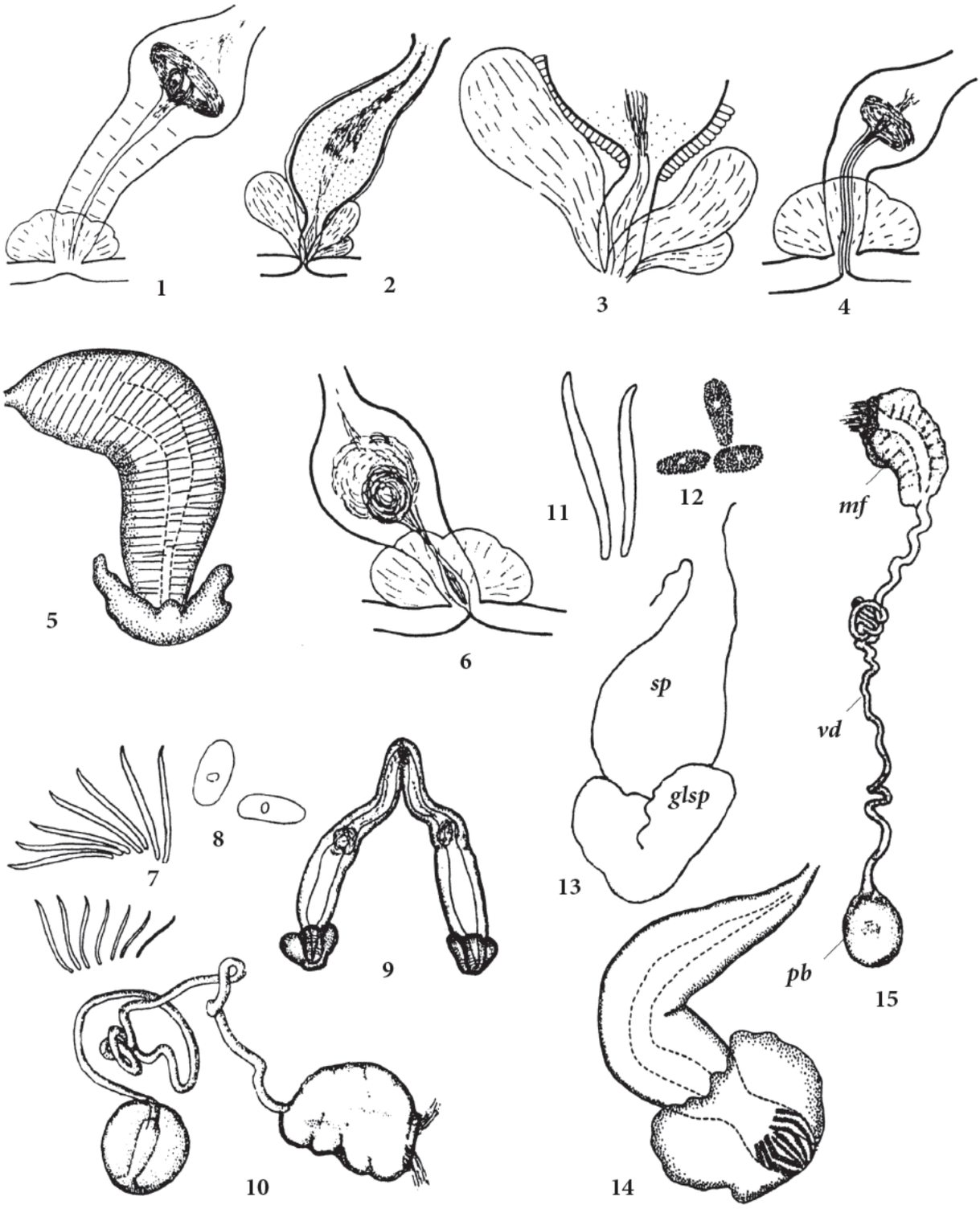

Plate VII

Fig. 1 *Lumbricillus tuba* Stephenson, 1911 (spermatheca.)
Figs. 2-3 *Lumbricillus* cf. *kaloensis* Nielsen et Christensen, 1959 (2: spermatheca. 3: distal portion of spermatheca.)
Fig. 4 *Lumbricillus* cf. *helgolandicus* (Michaelsen, 1959) (spermatheca.)
Fig. 5 *Lumbricillus dubius* Stephenson, 1911 (spermatheca.)
Fig. 6 *Lumbricillus viridis* Stephenson, 1911 (spermatheca.)
Figs. 7-10 *Lumbricillus murmanicus* Finogenova et Strelzov, 1978 (7: setal bundles [above from VI, below from XV segment]. 8. Coelomocytes. 9: spermathecae. 10: male gonoduct.)
Figs. 11-15 *Lumbricillus rubidus* Finogenova et Strelzov, 1978 (11: setae. 12: coelomocytes. 13,14: spermatheca. 15: male gonoduct.)

(Figs. 1-4 from Nielsen and Christensen 1959; Fig. 5 from Finogenova and Timm 1988; Fig. 6 from Nielsen and Christensen 1959; Figs. 7-15 from Finogenova and Strelzov 1978.)

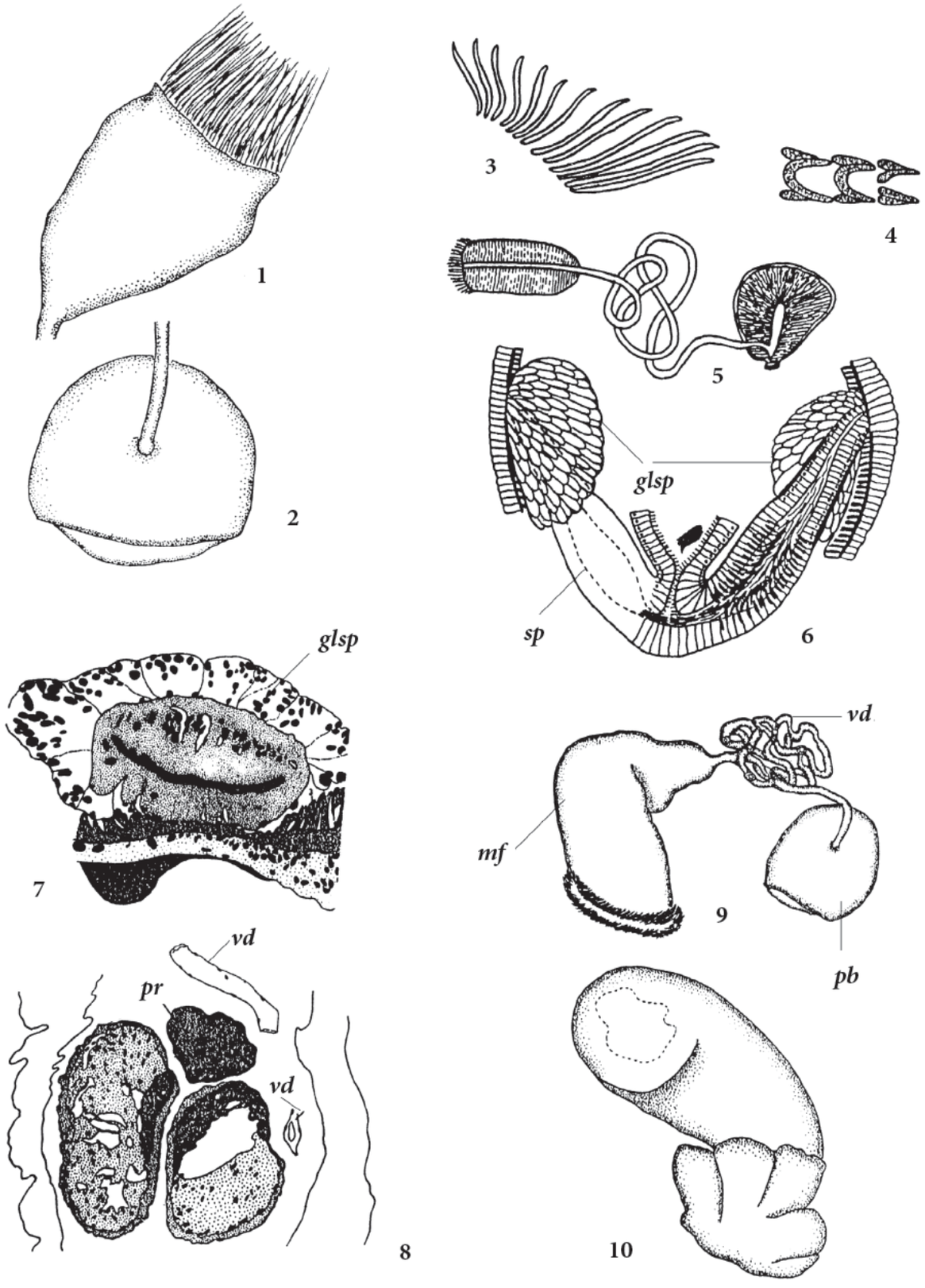

Plate VIII

Figs. 1-2 *Lumbricillus semifuscus* (Claparède, 1861 augm. Stephenson, 1911 (1: sperm funnel. 2: penial bulb.)
Figs. 3-6 *Lumbricillus pseudominutus* Timm, 1988 (3: bundle of ventral setae from segment X. 4: septal glands [schematic]. 5: male gonoduct [reconstruction]. 6: spermatheca and its connection to the esophagus [reconstruction].)
Figs. 7-8 *Lumbricillus horridus* Finogenova, 1988 (7: distal portion of the spermatheca [cross section]. 8: penial bulb [cross section].)
Figs. 9-10 *Lumbricillus immoderatus* Finogenova, 1988 (9: male gonoduct. 10: spermatheca.)

(Figs. 1-10 from Finogenova and Timm 1988.)

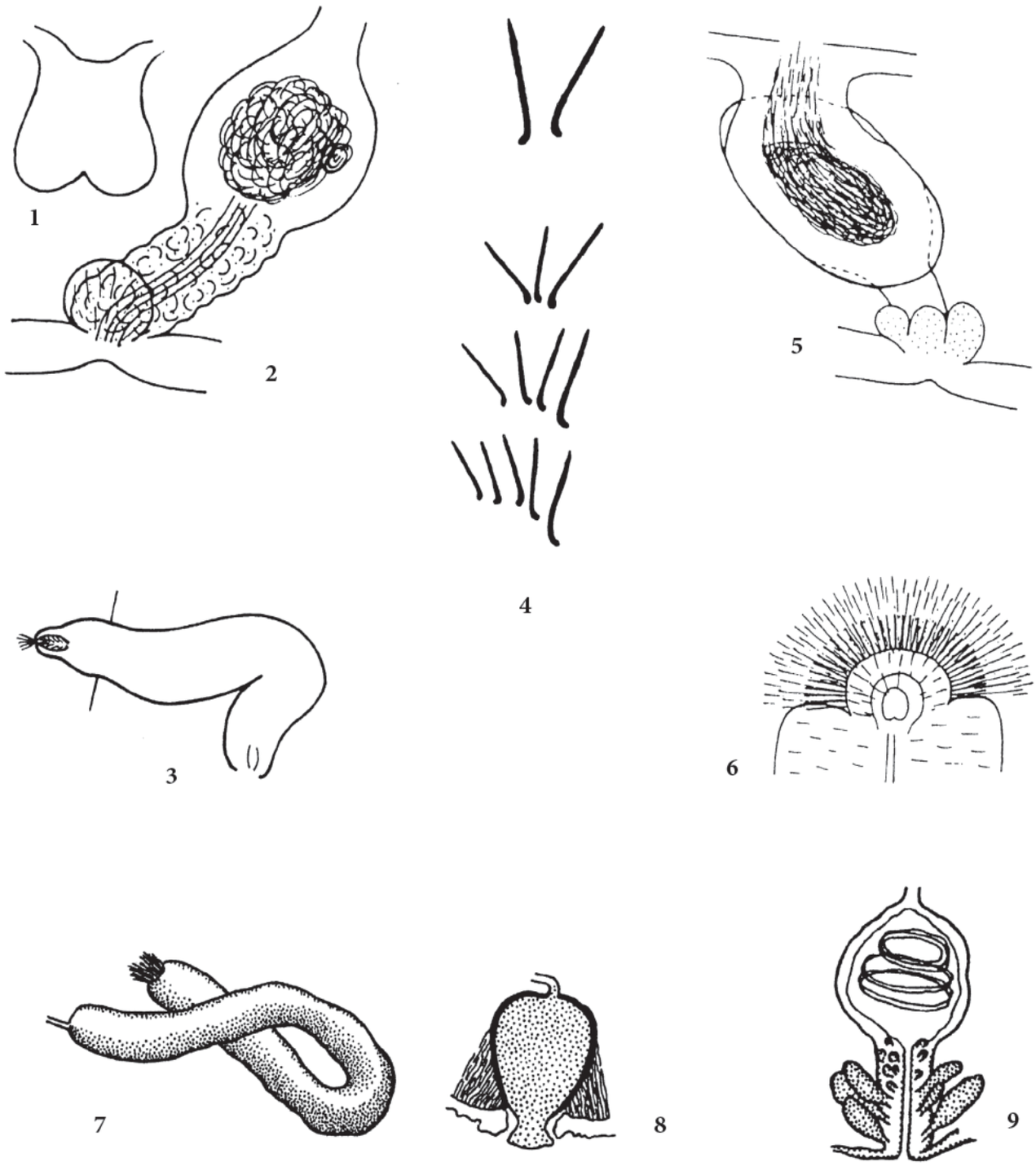

Plate IX

Figs. 1-4 *Marionina* cf. *spicula* (Leuckart, 1847) (1: brain. 2: spermatheca. 3: nephridium. 4: setae.)
Figs. 5-6 *Marionina subterranea* (Knöllner, 1935) (5: spermatheca. 6: preseptal portion of the sperm funnel.)
Figs. 7-9 *Marionina bulbosa* Finogenova, 1994 (7: sperm funnel. 8: penial bulb. 9: spermatheca.)

(Figs. 1-6 from Nielsen and Christensen 1959; Figs. 7-9 from Finogenova 1994.)

Phylum Annelida, Class Clitellata, Order Hirudinida[1]

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Leeches are freshwater, marine, and terrestrial annelids. According to traditional classifications, leeches (Hirudinea) and the related group Oligochaeta are classes in the subphylum Clitellata, belonging to the phylum Annelida. Recent phylogenetic analyses have revealed that the class Oligochaeta is paraphyletic. While leeches, branchiobdellidans, and acanthobdellidans are a monophyletic group, each of these three taxa in turn is a monophyletic group, and all of them are an advanced group of oligochaetes. It was therefore recommended that leeches, branchiobdellidans, and *Acanthobdella peledina* would be considered as orders named Hirudinida, Branchiobdellida, and Acanthobdellida respectively, and that Clitellata would be synonymized with Oligochaeta (Siddall et al. 2001). In this work we retain the viewpoint that the class name Clitellata is preferred, since this group comprises all annelids with a clitellum.

Characteristic features of leeches have been determined by the transition of their ancestors to temporary external parasitism on larger animals. Leeches are either predators consuming macroinvertebrates, or ectoparasitic sanguivores feeding mostly on vertebrates. Marine leeches belong primarily to the family Piscicolidae; they are ectoparasitic on fishes with very few species presumably parasitizing crustaceans. Leeches of the family Ozobranchidae are seen on sea turtles in tropical seas. There are about 680 total species of leeches (Sket and Trontelj 2008), including about 150 species of Piscicolidae. Piscicolids are most abundant in boreal and notal waters, and occur at depths of 1.5 to 2400 m.

The size of leeches is quite variable: small leeches reach lengths of 30 mm, medium size is 30-60 mm, and large leeches are greater than 60 mm. Some piscicolids (*Megaliobdella szidati* Meyer and Burreson, 1990) even reach 340 mm in length. The body shape varies from cylindrical to leaflike. The body consists of 34 post-oral segments (somites) and a non-segmental prostomium. Secondary external annulation obscures the original external segmentation. Segments with the largest number of annuli (complete segments) occur in the middle of the body. The segments at both ends are modified to form suckers. The anterior sucker is usually smaller than the posterior sucker. The mouth pore is located either at the anterior edge of the anterior sucker, or not far from its center. The anus opens on the dorsal side of the body, anterior to the posterior sucker. Eyes are often present on the anterior end of the body. Segmental ocelli can be distributed along the sides of the body; eyelike spots on the posterior sucker also apparently have a sensory function. Annuli on the tenth to twelfth segments are frequently thickened and swollen by glands that secrete the cocoon. These segments form a clitellum. Midventrally, the clitellum bears a single male gonopore anterior to a single female gonopore. The male gonopore is larger and more easily seen than the female one. In some piscicolid leeches there is a specialized region called the copulatory area, located on the ventral surface of the clitellum, for the reception of spermatophores. The clitellar and preclitellar regions form the trachelosome; the rest of the body posterior to the trachelosome is called the urosome. The body surface is smooth or with papillae and tubercles having a sensory function.

The body wall consists of the thin cuticle, the epidermis, the connective-tissue dermis, and circular, oblique, and longitudinal muscles. There are also dorsoventral muscle strands. The epithelial layer is rich in glands.

The central nervous system includes the suprapharyngeal ganglion, the subpharyngeal ganglion, the ventral nerve cord, and the posterior mass consisting of seven ganglia.

The rhynchobdellid leeches (Rhynchobdellida) have an eversible muscular proboscis. The arhynchobdellid leeches (Arhynchobdellida), which lack the proboscis, are characterized by the presence of a muscular

[1]Class Clitellata Michaelsen, 1919, order Hirudinida Lamarck, 1818

sucking pharynx, with or without jaws. The pharynx (or proboscis) opens into a narrow tube, the esophagus, which has a pair of diverticula in some rhynchobdellids. The esophagus leads to the crop, which can be a straight tube but often has lateral ceca. The last pair of the ceca (posterior crop ceca) is usually larger than the others; in the majority of piscicolids they are fused together. The intestine is usually a simple tube or, as in rhynchobdellids, it has four pairs of lateral diverticula. The intestine opens into the short straight rectum leading to the anus.

All leeches are hermaphrodites. The gonads are located in coelomic sacs; these structures are called testisacs and ovisacs (testes and ovaries). The testisacs are located posterior to the thirteenth segment and are usually paired spherical structures located intersegmentally. A short vas efferens connects each testisac to a vas deferens, which runs anteriorly on each side of the body. Each vas deferens widens or becomes greatly coiled (in this case it is called the epididymis) anterior to the first pair of testisacs, thus forming a seminal reservoir, which runs into a thick-walled ejaculatory bulb. The pair of ejaculatory bulbs enters the atrial cornua, which are attached to the common atrium. The atrium has gland cells that may form accessory glands on its outer surface. The atrial cavity leads to the bursa, which opens to the outside via the male gonopore. The atrium in many arhynchobdellid leeches (Arhynchobdellida) is modified to form an eversible penis. The female reproductive system consists of one pair of ovisacs, which are either small spherical organs or elongate tubes. The oviducts extend from the ovaries and converge to form the vagina leading to the female gonopore. In many piscicolids, a specialized tissue called the conductive tissue acts as a pathway for sperm moving to the ovisacs. Fertilization is internal. The eggs are laid in cocoons.

In leeches, the coelomic cavity is invaded by connective tissue (parenchyma) to form a system of interconnecting channels (lacunae), called the coelomic (lacunar) system. Rhynchobdellid leeches possess a blood vascular system. In arhynchobdellid leeches, the true blood vascular system is completely lost and the coelomic system performs its function. The coelomic system, in piscicolids, frequently consists of a dorsal sinus, a ventral lacuna, lacunae of testisacs, and two lateral lacunae. The lateral lacunae may be connected to the dorsal lacuna by means of segmental transverse lacunae. The ventral lacuna in each segment may be connected to the dorsal lacuna by communicating lacunae (main communications). Accessory communications connect testicular and dorsal lacunae. Some species of piscicolid leeches have one or two pairs of lateral pulsatile vesicles per urosomal segment for circulating coelomic fluid. The pulsatile vesicles are clearly visible from the outside in representatives of the subfamily Piscicolinae.

The excretory system of leeches includes up to 17 pairs of modified metanephridia. Most piscicolid leeches have lost ciliated funnels; their nephridial tubules are interconnected to form an anastomosing network called the plectonephridium.

According to the traditional classification, the class Hirudinea is divided into two subclasses, Archihirudinea and the Euhirudinea. Archihirudineans retain setae (chaetae) on the anterior part of the body; setae are absent in euhirudineans. However, this classification does not consider the fact that the group most closely related to euhirudineans is crayfish leeches (Branchiobdellida) (Siddall et al. 2001), which earlier were not thought to belong to the class Hirudinea, but were considered a specialized group within the class Oligochaeta. True leeches (Euhirudinea) are often divided into two orders: Rhynchobdellida and Arhynchobdellida. Rhynchobdellid leeches have a proboscis while arhynchobdellids have a pharynx. However, it was recently found that rhynchobdellids are a paraphyletic group, and the proboscis is a primitive feature characteristic of true leeches as a whole and has been lost in arhynchobdellids (Trontelj et al. 1999). Leeches of the Arctic Ocean belong exclusively to the family Piscicolidae, which has been assigned to the order Rhynchobdellida. Since the Rhynchobdellida are not a monophyletic group, and Hirudinida should be considered an order, it is suggested that the above division into orders should be rejected. Moreover, the traditional division of the family Piscicolidae into three subfamilies (Platybdellinae, Pontobdellinae, and Piscicolinae) is also incompatible with recent phylogenetic analyses as the subfamilies have been found not to be natural groups (Williams and Burreson 2006, Utevsky et al. 2007).

Family Piscicolidae Johnston, 1865

The suckers are more or less distinct from the body. Characteristic features for many species include the fusion of posterior crop ceca, the presence of conductive tissue and a copulatory area, and plectonephridia. The structure of the coelomic system varies from a simple state to a complex system of channels connected with pulsatile vesicles. The cocoon has a dense envelope and is attached to the substrate. The embryos are albuminotrophic (they feed on the contents of their own cocoons). Piscicolid geographical distribution, biology, and taxonomy are studied in a number of works including articles by Epstein (1961, 1967), Khan and Meyer (1976), Meyer and Khan (1979), Sawyer (1986), Utevsky and Trontelj (2004), Karlsbakk (2005), and other publications.

Key to genera and species of the family Piscicolidae

1(6) Body surface with numerous small or large papillae. One or two pairs of pulsatile vesicles per segment. Six pairs of testisacs present.

2(3) Large papillae present on body surface. Complete segment four-annulate . . . . . **genus *Pontobdella*, *P. muricata* (Linnaeus, 1758) (Pl. III)**

Length 190 mm.
Atlantic subtropical-boreal. Southwestern Greenland, Mediterranean and North seas, Spitsbergen.
Parasitic on skates (*Raja* spp.)

3(2) All papillae small. Complete segment 14-annulate.

4(5) Papillae well developed only on dorsal side of body, where they form six longitudinal rows. One pair of tubercles located near female gonopore. Posterior sucker barely distinguishable from urosome. Two pairs of pulsatile vesicles (not distinguishable from outside) per segment. Ejaculatory bulb not long, not convoluted in loops . . . . . **genus *Oxytonostoma*, *O. typica* Malm, 1863 (Pl. IV, V)**

Length 32 mm.
Atlantic boreal Arctic. Barents and Kara seas, Beaufort Sea, from Massachusetts (USA) to Bay of Fundy. No records from Russian northern seas to east of Kara Sea.
On skates (*Raja* spp.).

5(4) Papillae developed equally on dorsum and ventrum, arranged in 12 longitudinal rows. Tubercles near female gonopore absent. Posterior sucker clearly distinguishable from urosome. One pair of conspicuous external pulsatile vesicles per segment. Ejaculatory bulbs long, convoluted in loops . . . . . **genus *Johanssonia***

6(1) Body surface smooth or with one pair of longitudinal lateral rows of tubercles on urosome or with small tubercles on dorsal surface of three or four last annuli of urosome. Pulsatile vesicles present or absent. Five or six pairs of testisacs present.

7(10) Two longitudinal lateral rows of tubercles on urosome or small dorsal tubercles on last annuli of urosome. Three pairs of eyes and segmental ocelli present, eyelike spots present on posterior sucker. Coelomic system reduced, lateral lacunae and pulsatile vesicles absent. Five pairs of testisacs present.

8(9) Small dorsal tubercles on last three or four annuli of urosome. Body basically lacking pigment patterns. Copulation area on clitellum absent . . . . . ***"Platybdella" olriki* Malm, 1863 (Pl. III)**

Length 11 mm.
Amphiboreal. Western Greenland, Newfoundland, Spitsbergen, eastern Kamchatka, Shikotan and Iturup islands.
On crustaceans (*Hyas* spp., *Sclerocrangon boreas*); on fishes (*Hippoglossus hippoglossus*, *Pleuronectes americanus*, *Lycodes reticulatus*).
Taxonomic remark: internal characters of this species are not studied properly and its generic affiliation is doubtful.

9(8) Small tubercles on last annuli of urosome absent. Segmentally arranged lateral tubercles on urosome present. Body with distinct brown transverse bands and thin longitudinal pigment stripes. Copulatory area on clitellum present. . **genus *Crangonobdella*, *C. fabricii* (Malm, 1863) (Pl. VI, VII)**

Length 20 mm.
Boreal Arctic. Greenland, Barents, and Kara seas, Point Barrow, Bering Strait, Bering Sea and Sea of Okhotsk, northern Sea of Japan.
On shrimp (*Sclerocrangon boreas*) and sculpins (*Myoxocephalus* spp.).

10(7) Body surface completely smooth, papillae and tubercles absent. Externally visible pulsatile vesicles present or absent. Eyes, segmental ocelli, and eyelike spots present or absent. Lateral lacunae present or absent. Five or six pairs of testisacs present.

11(12) Eleven pairs of vesicles on urosome, clearly visible from outside. Eyes, segmental ocelli, and eyelike spots absent. Six pairs of testisacs present. . . . . **genus *Calliobdella*, *C. nodulifera* (Malm, 1863)**

Length 20 mm.
Atlantic high boreal. Barents Sea, coastal waters of Norway, North Sea, Faroe Islands, Iceland, Newfoundland.
Recorded from various fish species, mostly gadids.
In *Calliobdella nodulifera*, ejaculatory bulbs are short, not convoluted in loops, in contrast to species of the genus *Johanssonia*, which also have pulsatile vesicles.

12(11) Externally visible pulsatile vesicles absent.

13(14) Anterior and posterior suckers folded along medial line like a clamshell. Mouth pore at anterior margin of sucker. Six pairs of testisacs present . . . . . **genus *Notostomum*, *N. laeve* Levinsen, 1882 (Pl. VIII)**

Length 132 mm.
Arctic circumpolar, Barents, Kara, and Laptev seas and East Siberian Sea, Canadian Arctic.
Depth 1.5-280 m. On silty sediments, silt with sand and rock.
Usually free-living, occasionally on fishes (*Reinhardtius hippoglossoides*, *Somniosus microcephalus*, *Cetorhinus maximus*, *Lycodes luetkeni*).

14(13) Anterior and posterior suckers not folded along medial line. Mouth pore not at anterior margin of sucker. Five pairs of testisacs present.

15(16) Anterior sucker bell-shaped, with annular membrane on its inner surface, attached to trachelosome by deep nuchal constriction. Seminal receptacle pore on clitellum . . . **genus *Mysidobdella*, *M. borealis* (Johansson, 1898) (Pl. IX)**

Length 15 mm.
Atlantic widespread boreal Arctic. New Jersey (USA), Bay of Fundy, Greenland, Bay of Biscay, Spitsbergen, White and Kara seas, Aleutian Islands (latter needs verification).
Depth 15-25 m. On mysids (*Mysis* spp.).

16(15) Anterior sucker not bell-shaped, deep nuchal constriction absent. Annular membrane absent. Seminal receptacle on clitellum absent.

17(20) Eyes and segmental ocelli present, posterior sucker with eyelike spots. Body strongly or weakly pigmented. Lateral lacunae present.

18(19) Anterior sucker clearly distinct from trachelosome. Body well pigmented. . . . . **genus *Heptacyclus***

19(18) Anterior sucker small, slightly distinct from trachelosome. Body weakly pigmented. . . . . **genus *Oceanobdella***

20(17) Eyes, segmental ocelli, and eyelike spots absent. Body lacking pigmented patterns. Coelomic system reduced, lateral lacunae absent . . . . . **genus *Platybdella*, *P. anarrhichae* (Diesing, 1859) (Pl. X, XI)**

Length 40 mm.
Atlantic high boreal. White, Barents, Norwegian, and North seas, Faroe Islands, Iceland, Maine (USA), Newfoundland, Baffin Island.
In the gill chamber of wolffishes (*Anarhichas* spp.).

Key to species of the genus *Johanssonia*

1(2) Anterior sucker relatively large, exceeding maximum body width by 1.2 times. Posterior sucker relatively small, exceeding body width at the attachment site by 1.5 times and 1.1 times wider than anterior sucker. Papillae on body well developed. Crop ceca sharply separated, four-chambered . . . . . ***J. arctica* (Johansson, 1898) (Pl. XII, XIII)**

Length 26 mm.
Widespread high boreal Arctic, circumpolar. Barents, Kara, Laptev, East Siberian seas and Sea of Okhotsk, Greenland, Newfoundland, Canadian Arctic.
Depth 2-231 m. On rock and silt. Free or attached to crustaceans (*Chionoecetes opilio, Hyas* spp., *Paralithodes camtschaticus* [in Barents Sea], *Colossendeis proboscidea*, *Nymphon stroemi*) and on fishes (*Hippoglossoides platessoides*, *Gadus morhua*).

2(1) Anterior sucker relatively small, about 0.8 of maximum body width. Posterior sucker relatively large, 2.1 times width of body at attachment site and 1.6 times width of anterior sucker. Papillae on body weakly developed. Crop ceca not sharply separated, smooth, not chambered, diamond-shaped . . . . . ***J. kolaensis* Selensky, 1914 (Pl. XIV, XV)**

Length 20 mm.
Atlantic. Barents Sea.
Depth 110-170 m. On wolffishes (*Anarhichas* spp.).

Key to species of the genus *Heptacyclus*

1(4) Body with distinct longitudinal reddish-brown stripes, solid or fragmented. Anterior sucker with one transverse pigment band. Radial pigment bands on posterior sucker do not run from center of sucker. Body lacks minute brown dots.

2(3) Body to 60 mm long. Complete segment consisting of 13-14 annuli . . . . . ***H. virgatus*** **(Oka, 1910) (Pl. XVI, XVII)**

Length 60 mm.
Pacific widespread boreal. Chukchi Sea, North Pacific Ocean from Sea of Japan and Kodiak Island to Bering Strait.
Depth 30-134 m. On sculpins (*Myoxocephalus* spp.).

3(2) Body to 35 mm long. Complete segment 6-annulate. . . . . ***H. scorpii*** **(Malm, 1863) (Pl. XVIII)**

Length 35 mm.
Atlantic high boreal. Barents Sea. In the North Atlantic from New England (USA) and Newfoundland to Greenland, Faroe Islands, and North Sea.
On sculpins (*Myoxocephalus* spp.).

4(1) Dorsum uniform brown (sometimes reddish), sometimes with faint middorsal or paramarginal longitudinal stripes. Anterior sucker with two transverse pigment bands dorsally. Posterior sucker with pigment bands radiating from center of sucker. Body with evenly scattered minute brown dots, evident even in preservative-bleached specimens. . . . . ***H. brunneus*** **(Johansson, 1896) (Pl. XVIII)**

Length 35 mm.
High boreal Arctic. New Hampshire (USA), Bay of Fundy, Newfoundland, Greenland, North, Barents, and White seas, eastern Kamchatka, Aleutian Islands.
On sculpins (*Myoxocephalus* spp.).

Key to species of the genus *Oceanobdella*

1(2) Body weakly pigmented (segmental transverse bands and radial bands on posterior sucker present) or pigment completely absent . . . . . ***O. alba*** **(Epstein and S.Y. Utevsky, 1996) (Pl. XIX, XX)**

Length 38 mm.
Western Pacific boreal. Southern Chukchi Sea, North Pacific from Sea of Japan to Bering Sea.
Depth 30-185 m. On greenlings (*Hexagrammos lagocephalus, Pleurogrammus azonus, P. monopterygius*); on sculpin (*Myoxocephalus verrucosus*).

2(1) Body without significant pigmentation. Dark x-shaped pattern present on anterior sucker and adjacent annuli of trachelosome; wedge-shaped patch of pigment on posterior sucker . . ***O. microstoma*** **(Johansson, 1896) (Pl. XVIII)**

Length 25 mm.
Atlantic high boreal. Barents Sea, North Atlantic from New England to the North Sea.
On sculpins (*Myoxocephalus* spp.).

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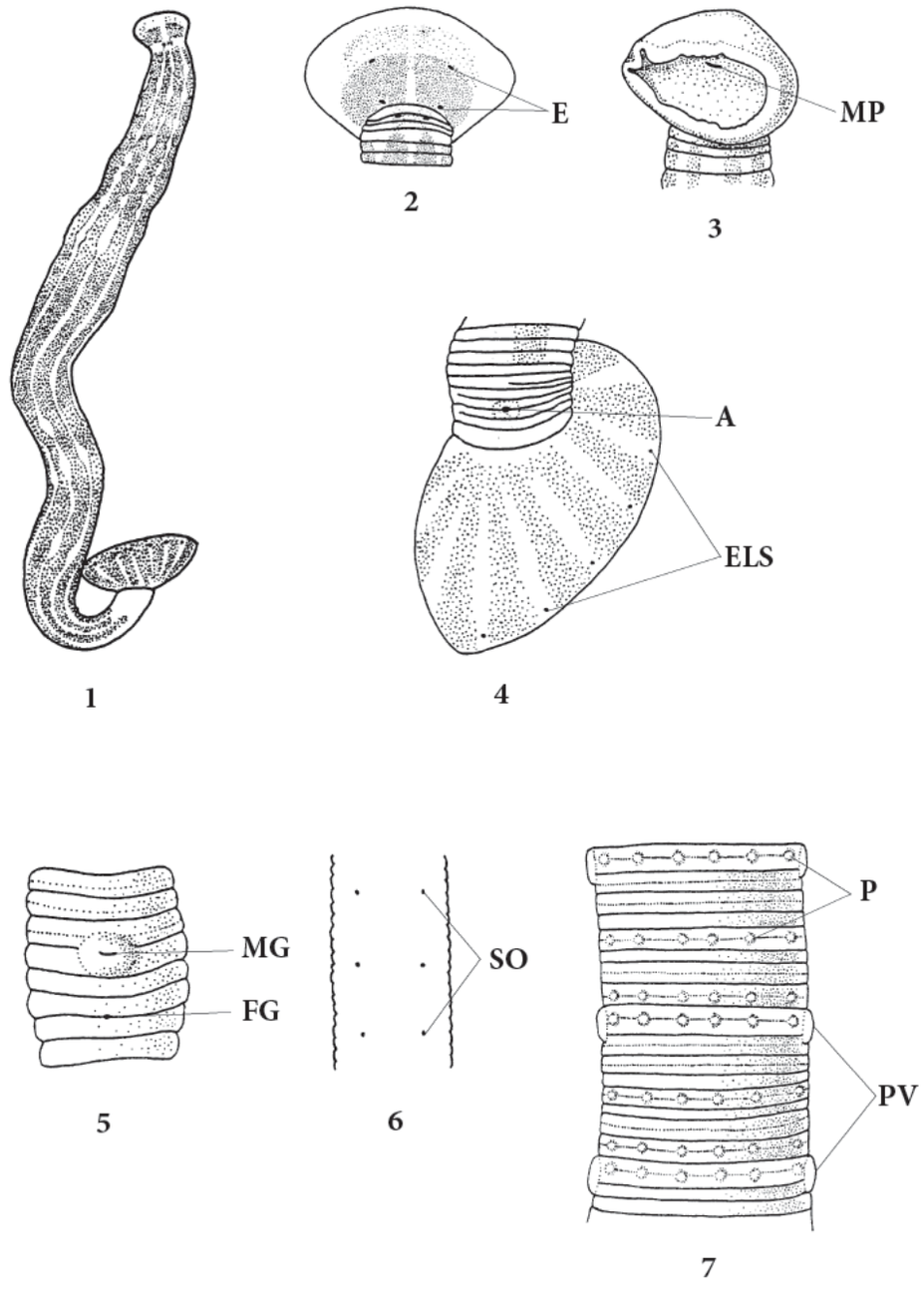

Plate I. External characters of leeches of the family Piscicolidae.

Fig. 1 Dorsal view (*Heptacyclus virgatus*).
Fig. 2 Anterior sucker, dorsal view (*Heptacyclus virgatus*).
Fig. 3 Anterior sucker, ventral view (*Heptacyclus virgatus*).
Fig. 4 Posterior sucker, dorsal view (*Heptacyclus virgatus*).
Fig. 5 Clitellum, ventral view (*Heptacyclus virgatus*).
Fig. 6 Three adjacent segments from mid-body region (*Oceanobdella microstoma*), dorsal view.
Fig. 7 Segment from crop region, dorsal view (*Johanssonia kolaensis*).

Abbreviations: A: anus. E: eye. ELS: eye-like spots. FG: female gonopore. MG: male gonopore. MP: mouth pore. P: papillae. PV: pulsatile vesicles. SO: segmental ocelli.

(Fig. 6 by permission from Appy and Dadswell 1981, illustrations by Teresa D. Appy; Figs. 1-5, 7 are original.)

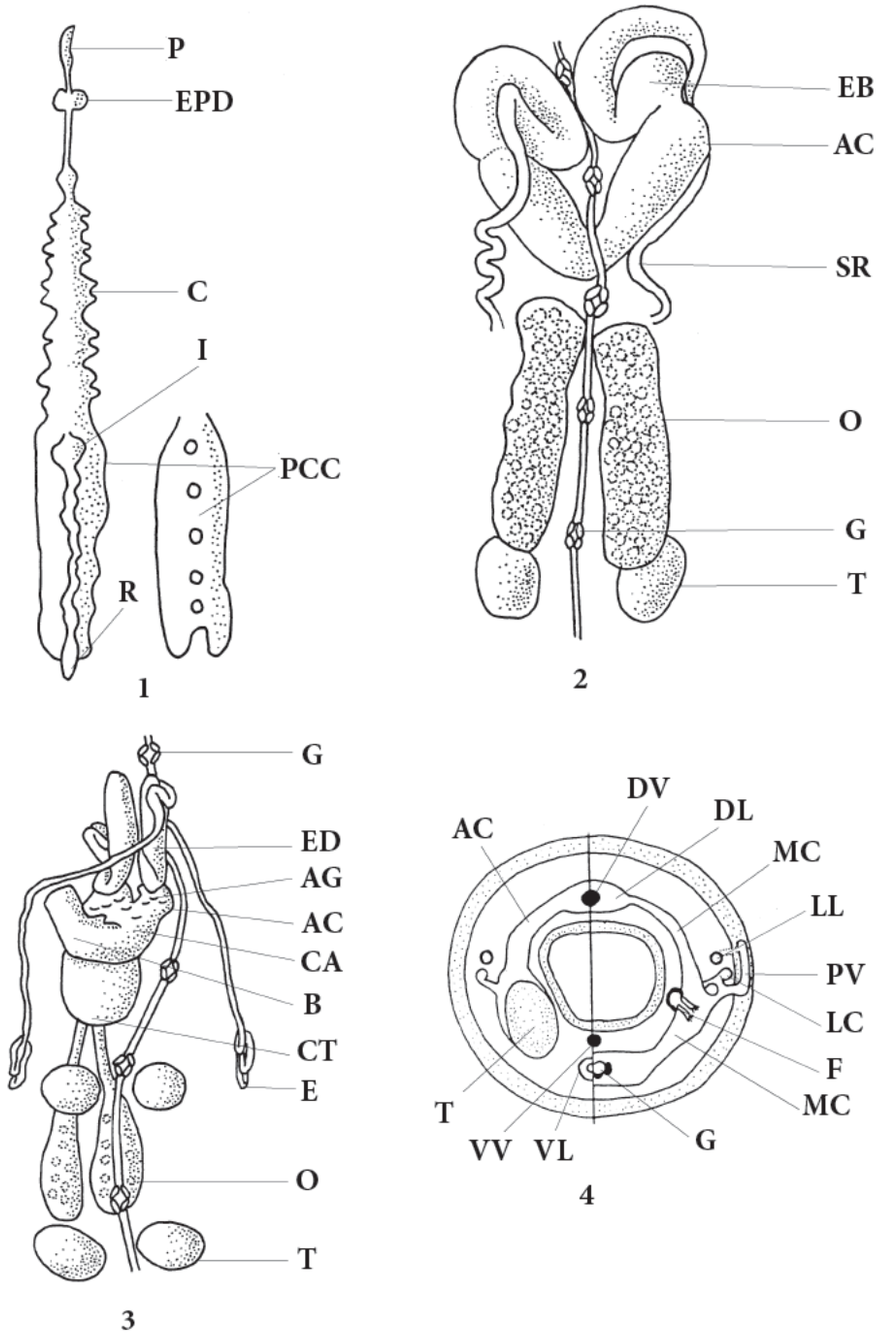

Plate II. Internal characters of leeches of the family Piscicolidae.

Fig. 1 Digestive system (*Crangonobdella fabricii*), dorsal view.
Fig. 2 Reproductive system (*Platybdella anarrhichae*), dorsal view.
Fig. 3 Reproductive system (*Johanssonia arctica*), dorsal view.
Fig. 4 Coelomic system (*Johanssonia* sp.), transverse section.

Abbreviations: AC: atrial cornu (Figs. 2, 3). AC: accessory communication (Fig. 4). AG: accessory gland. B: bursa. C: crop. CA: common atrium. CT: conductive tissue. DL: dorsal lacuna. DV: dorsal vessel. E: epididymis. EB: ejaculatory bulb. ED: ejaculatory duct. EPD: esophageal diverticulum. F: nephridial funnel. G: ganglion. I: intestine. LC: lateral canal. LL: lateral lacuna. MC: main communication. O: ovisac. P: proboscis. PCC: posterior crop ceca. PV: pulsatile vesicle. R: rectum. SR: seminal reservoir. T: testisac. VL: lateral lacuna. VV: ventral vessel.

(Figs. 1-4 are original.)

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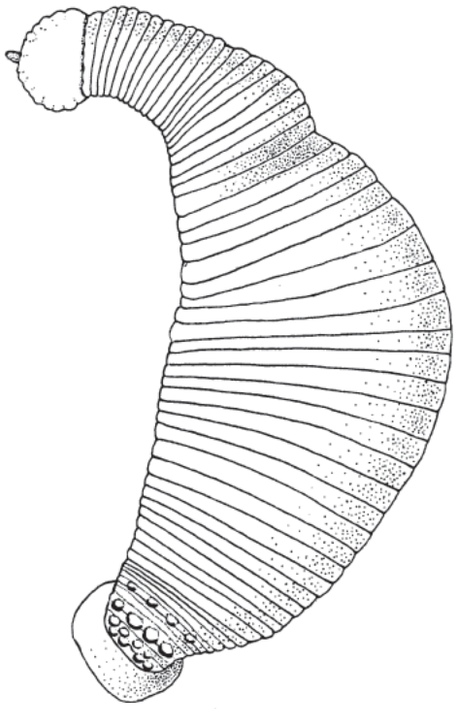

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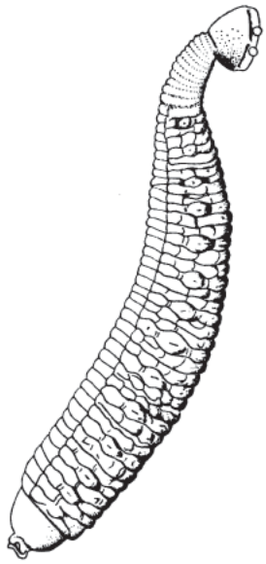

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Plate III. *Pontobdella muricata* (Linnaeus, 1758) and *"Platybdella" olriki* Malm, 1863.

Fig. 1 *Pontobdella muricata*, characteristic resting position.
Fig. 2 *Pontobdella muricata*, entire view, posterior sucker very truncated.
Fig. 3 *"Platybdella" olriki*, dorsal view.

(Figs. 1-2 from Mann 1962; Fig. 3 is original.)

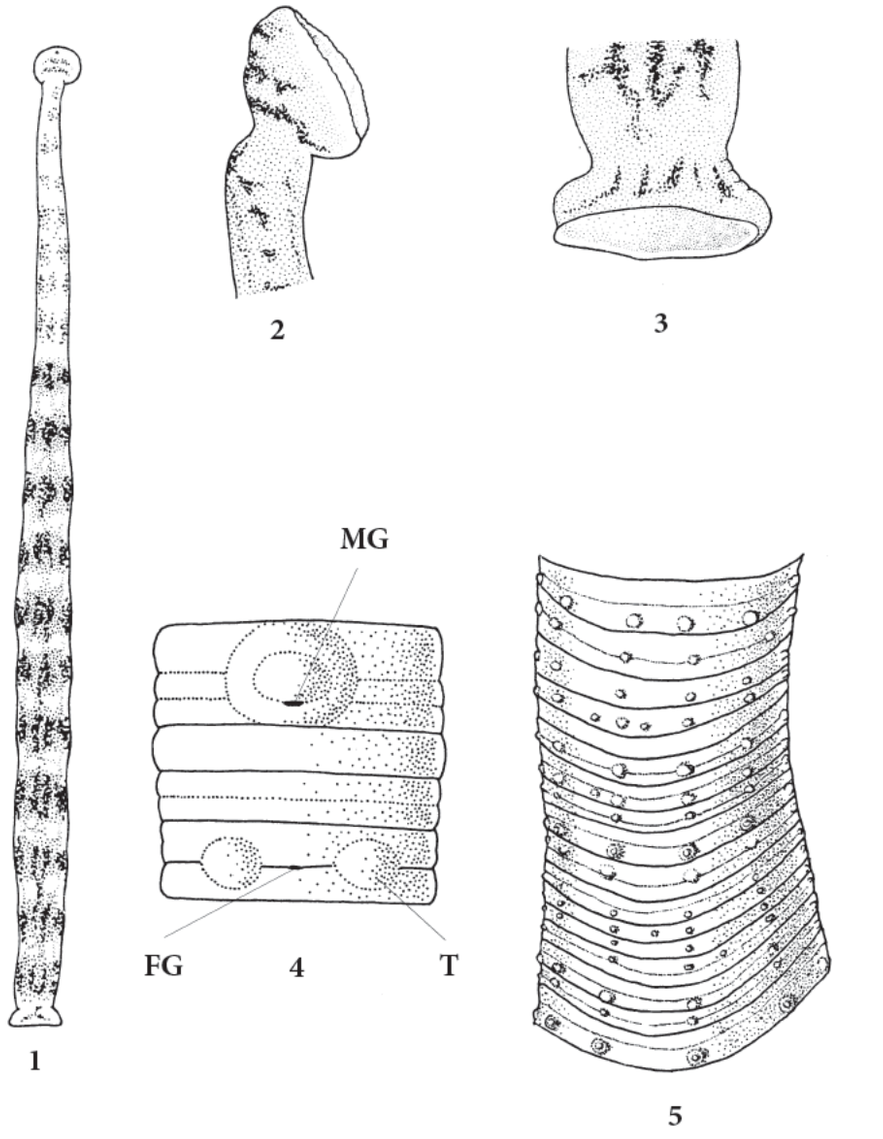


Plate IV. *Oxytonostoma typica* Malm, 1863, external characters.

Fig. 1 Entire specimen, dorsal view.
Fig. 2 Anterior sucker, lateral view.
Fig. 3 Posterior sucker, lateral view.
Fig. 4 Clitellum, ventral view.
Fig. 5 Segment from crop region, dorsal view.

Abbreviations: FG: female gonopore. MG: male gonopore. T: tubercle.

(Figs. 1-3 by permission from Appy and Dadswell 1981, illustrations by Teresa D. Appy; Figs. 4-5 are original.)

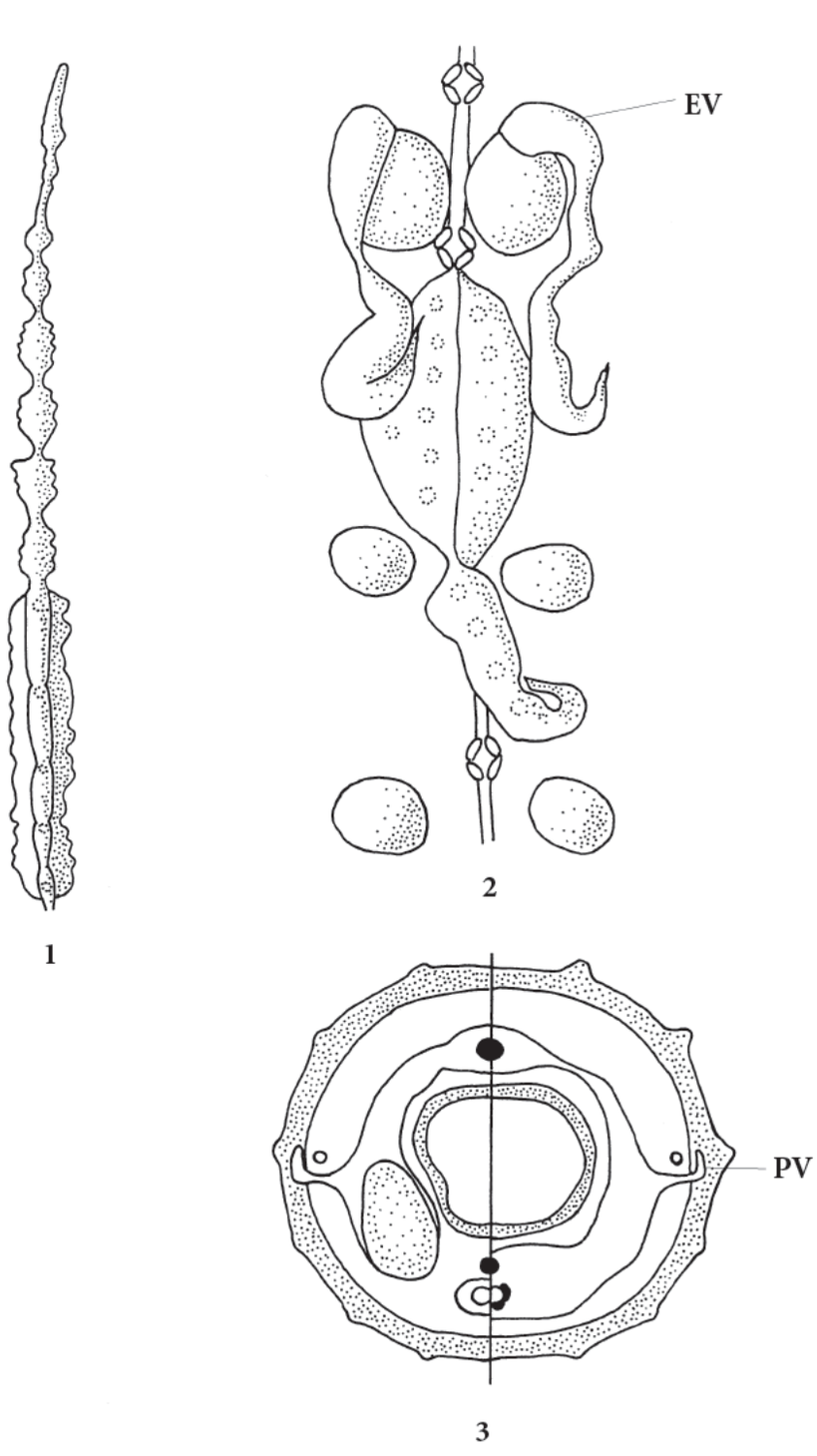


Plate V. *Oxytonostoma typica* Malm, 1863, internal characters.

Fig. 1 Digestive system, dorsal view.
Fig. 2 Reproductive system, dorsal view.
Fig. 3 Coelomic system.

Abbreviations: EB: ejaculatory bulb. PV: pulsatile vesicle.

(Figs. 1-2 are original; Fig. 3 from Selensky 1915.)

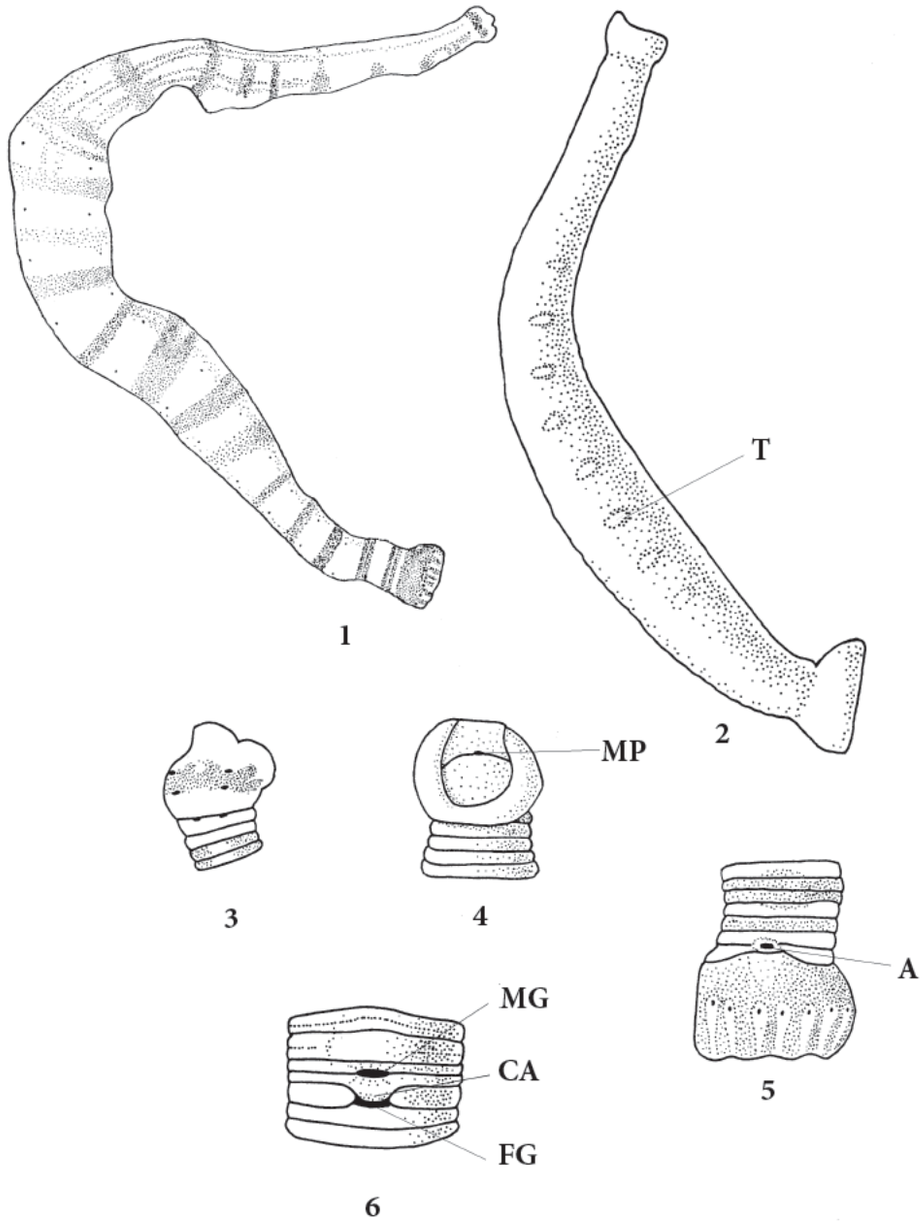


Plate VI. *Crangonobdella fabricii* (Malm, 1863), external characters.

Fig. 1 Entire specimen, dorsal view.
Fig. 2 Entire specimen, lateral view.
Fig. 3 Anterior sucker, dorsal view.
Fig. 4 Anterior sucker, ventral view.
Fig. 5 Posterior sucker, dorsal view.
Fig. 6 Clitellum, ventral view.

Abbreviations: A: anus. CA: copulatory area. FG: female gonopore. MG: male gonopore. MP: mouth pore. T: tubercle.

(Figs. 1-6 are original.)

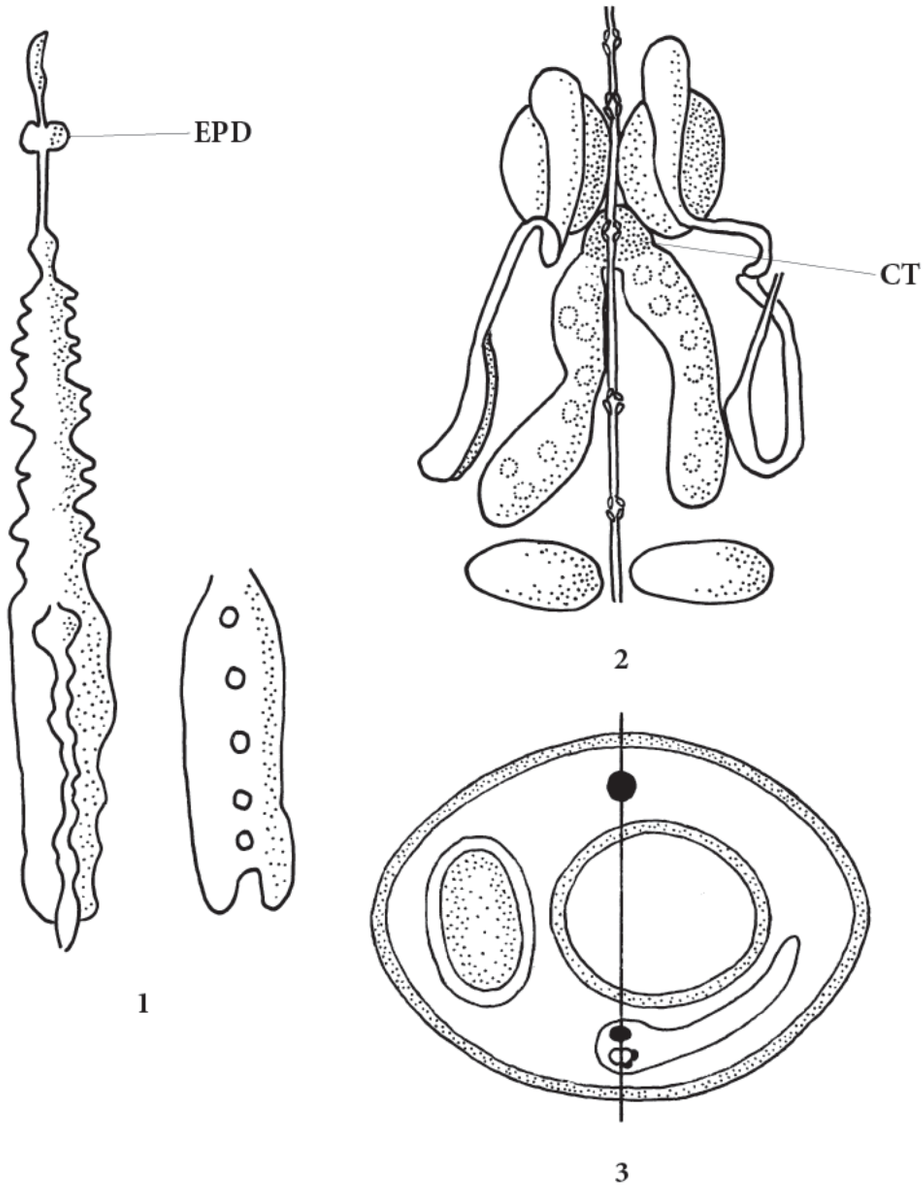


Plate VII. *Crangonobdella fabricii* (Malm, 1863), internal characters.

Fig. 1 Digestive system, dorsal view.
Fig. 2 Reproductive system; dorsal view.
Fig. 3 Coelomic system.

Abbreviations: CT: conductive tissue. EPD: esophageal diverticulum.

(Figs. 1-3 are original.)

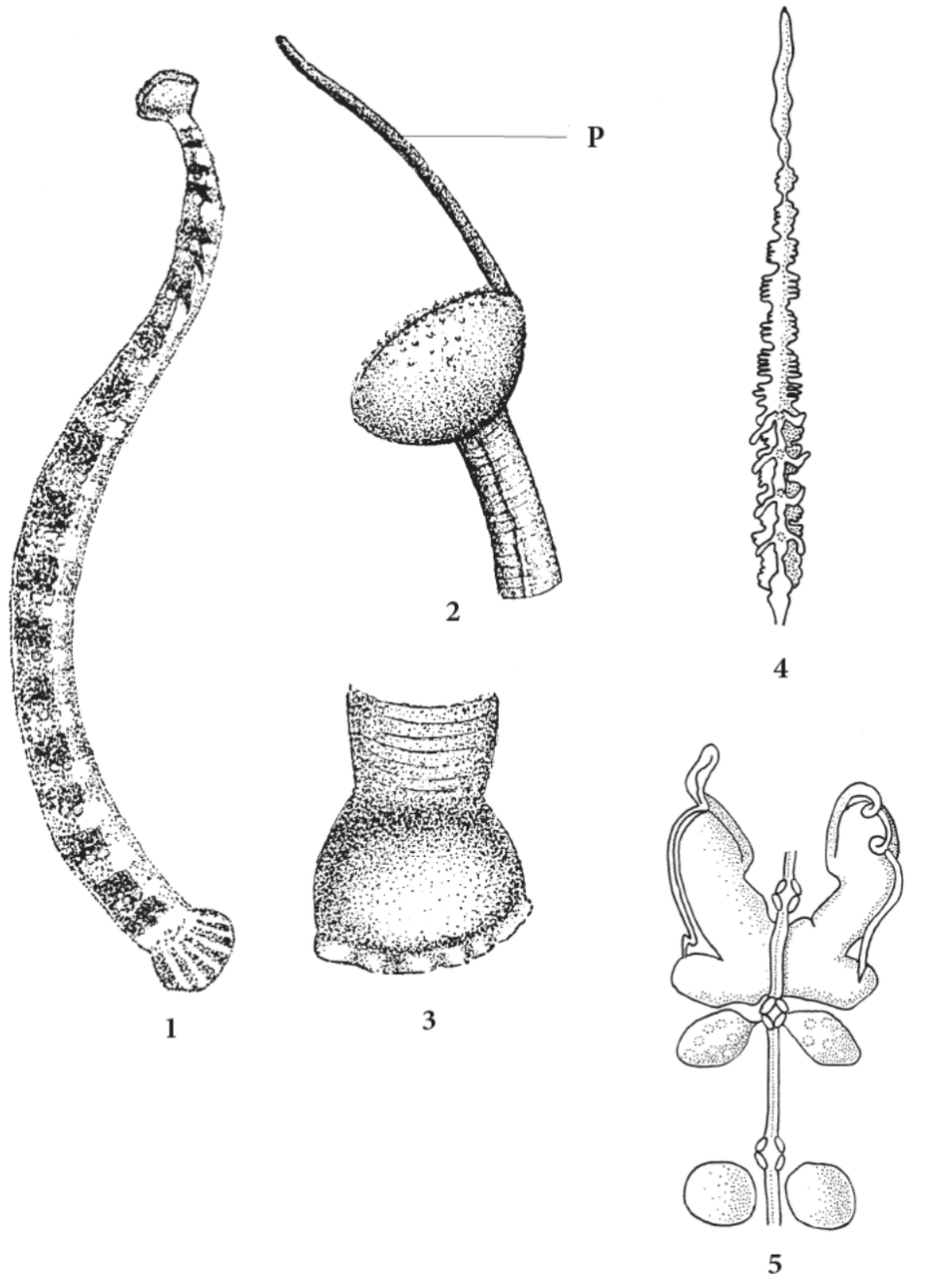


Plate VIII. ***Notostomum laeve*** **Levinsen, 1882**

Fig. 1 Entire specimen, lateral view.
Fig. 2 Anterior sucker, lateral view.
Fig. 3 Posterior sucker, lateral view.
Fig. 4 Digestive system, dorsal view.
Fig. 5 Reproductive system, dorsal view.

Abbreviation: P: proboscis.

(Figs. 1, 4, 5 are original; Figs. 2, 3 from Vasilyev 1935.)

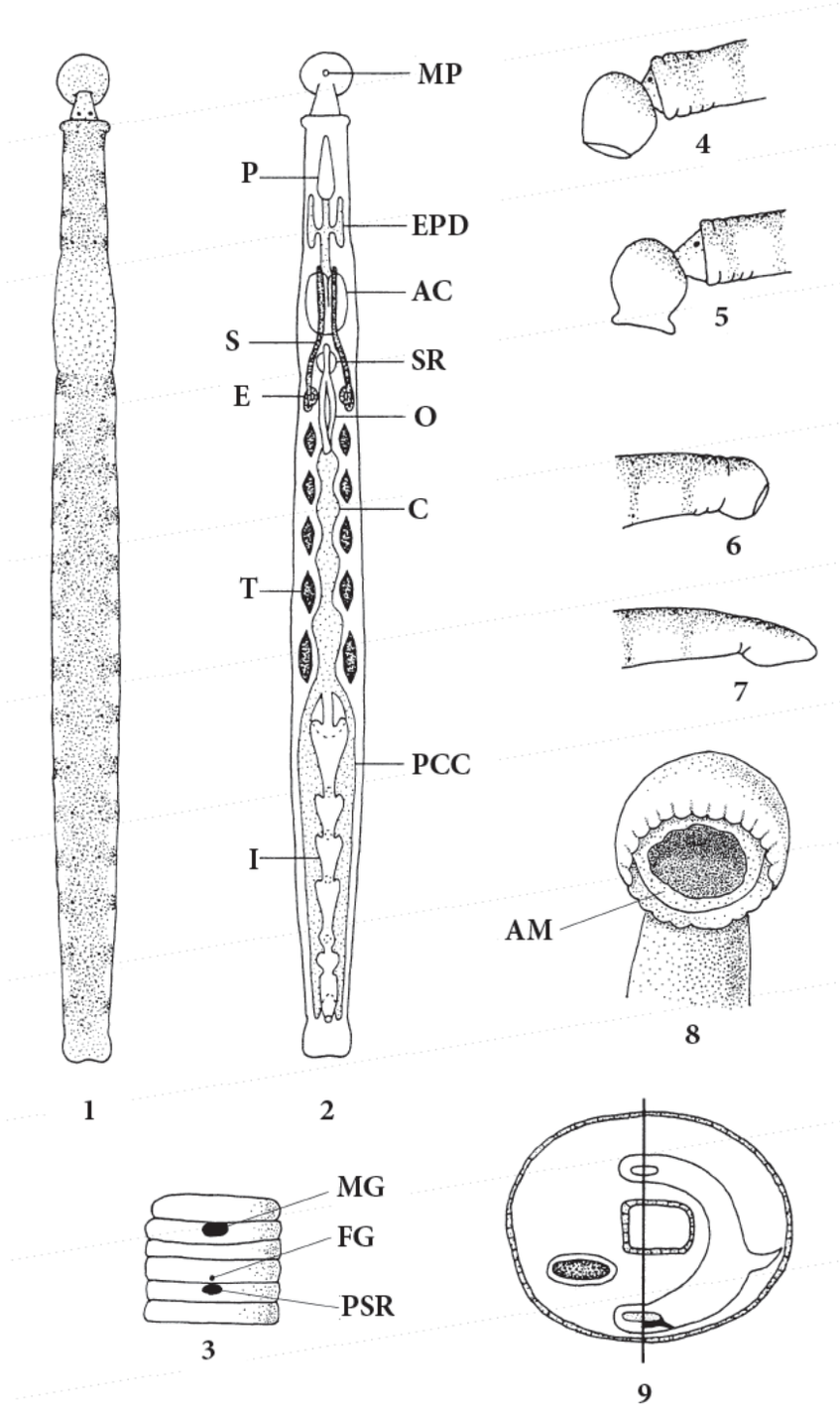


Plate IX. ***Mysidobdella borealis*** **(Johansson, 1898)**

Fig. 1 Entire specimen, dorsal view.
Fig. 2 Reconstruction of digestive and reproductive systems.
Fig. 3 Clitellum, ventral view.
Fig. 4 Anterior sucker after fixation, lateral view.
Fig. 5 Anterior sucker in living specimen, lateral view.
Fig. 6 Posterior sucker after fixation, lateral view.
Fig. 7 Posterior sucker of live specimen, lateral view.
Fig. 8 Anterior sucker, ventral view.
Fig. 9 Coelomic system.

Abbreviations: AC: atrial cornu. AM: annular membrane. C: crop. E: epididymis. EPD: esophageal diverticulum. FG: female gonopore. I: intestine. MG: male gonopore. MP: mouth pore. O: ovisac. P: proboscis. PCC: posterior crop ceca. PSR: pore of seminal receptacle. S: seminal reservoir. SR: seminal receptacle. T: testisac.

(Figs. 1-2, 4-7, 9 by permission from Burreson and Allen 1978; Figs. 3, 8 are original.)

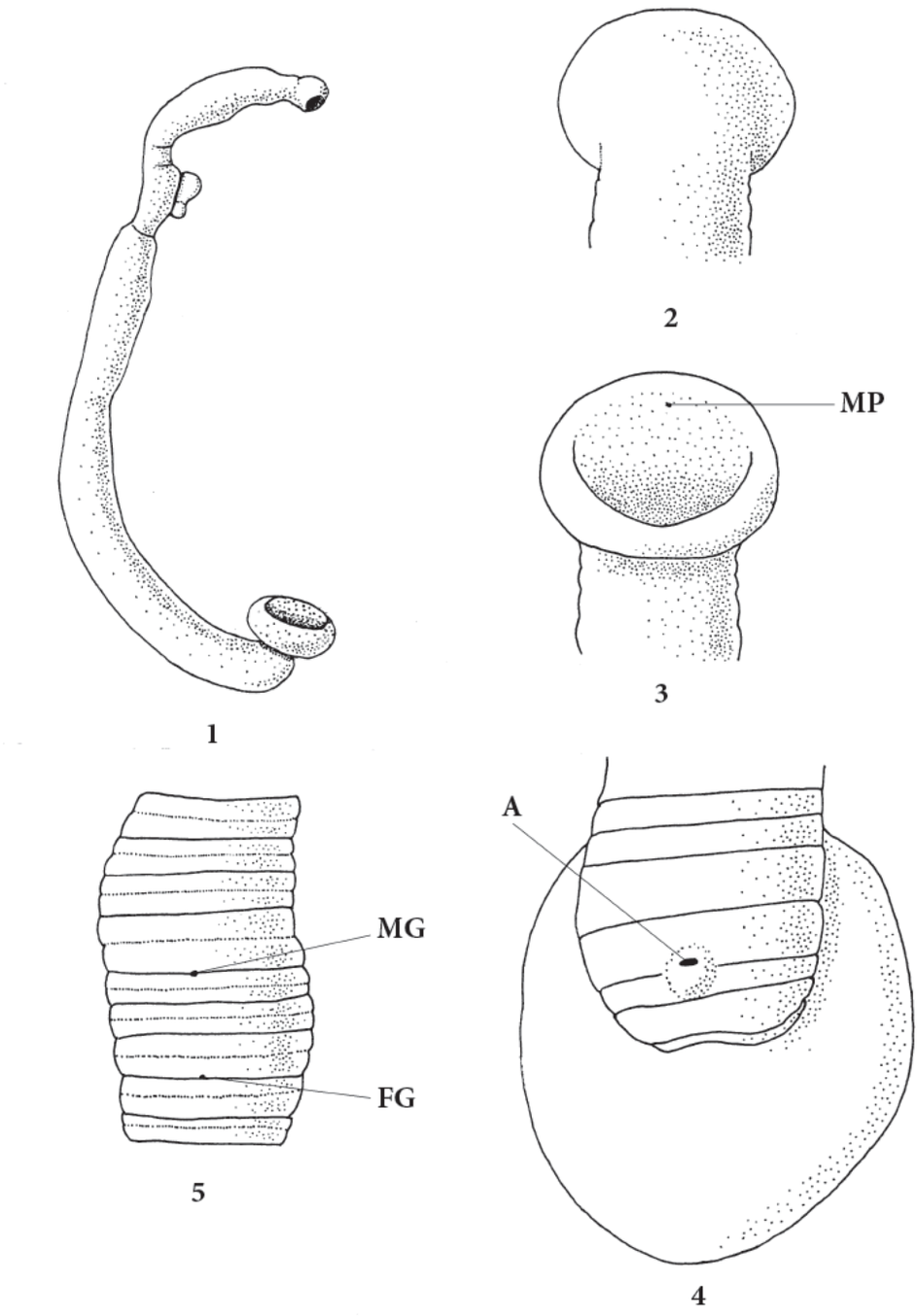
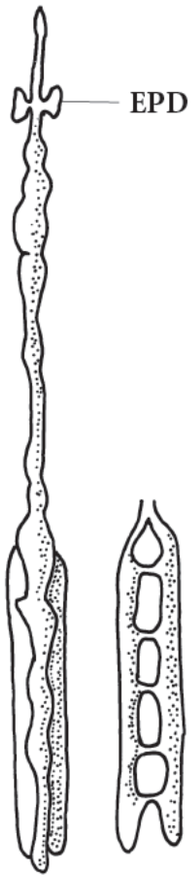


Plate X. *Platybdella anarrhichae* (Diesing, 1859), external characters.

Fig. 1 Entire specimen, lateral view.
Fig. 2 Anterior sucker, dorsal view.
Fig. 3 Anterior sucker, ventral view.
Fig. 4 Posterior sucker, dorsal view.
Fig. 5 Clitellum, ventral view.

Abbreviations: *A*: anus. *FG*: female gonopore. *MG*: male gonopore. *MP*: mouth pore.

(Figs. 1-5 are original.)



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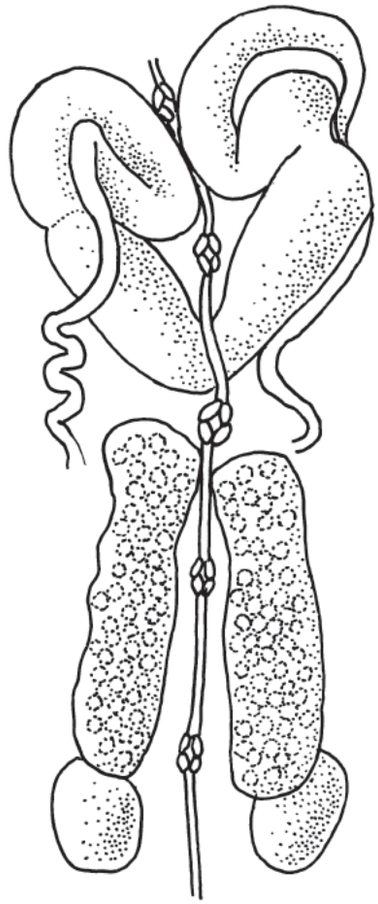

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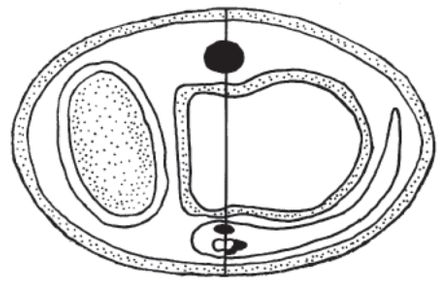

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Plate XI. ***Platybdella anarrhichae*** **(Diesing, 1859), internal characters.**

Fig. 1 Digestive system, dorsal view.
Fig. 2 Reproductive system, dorsal view.
Fig. 3 Coelomic system.

Abbreviation: EPD: esophageal diverticulum.

(Figs. 1-3 are original.)

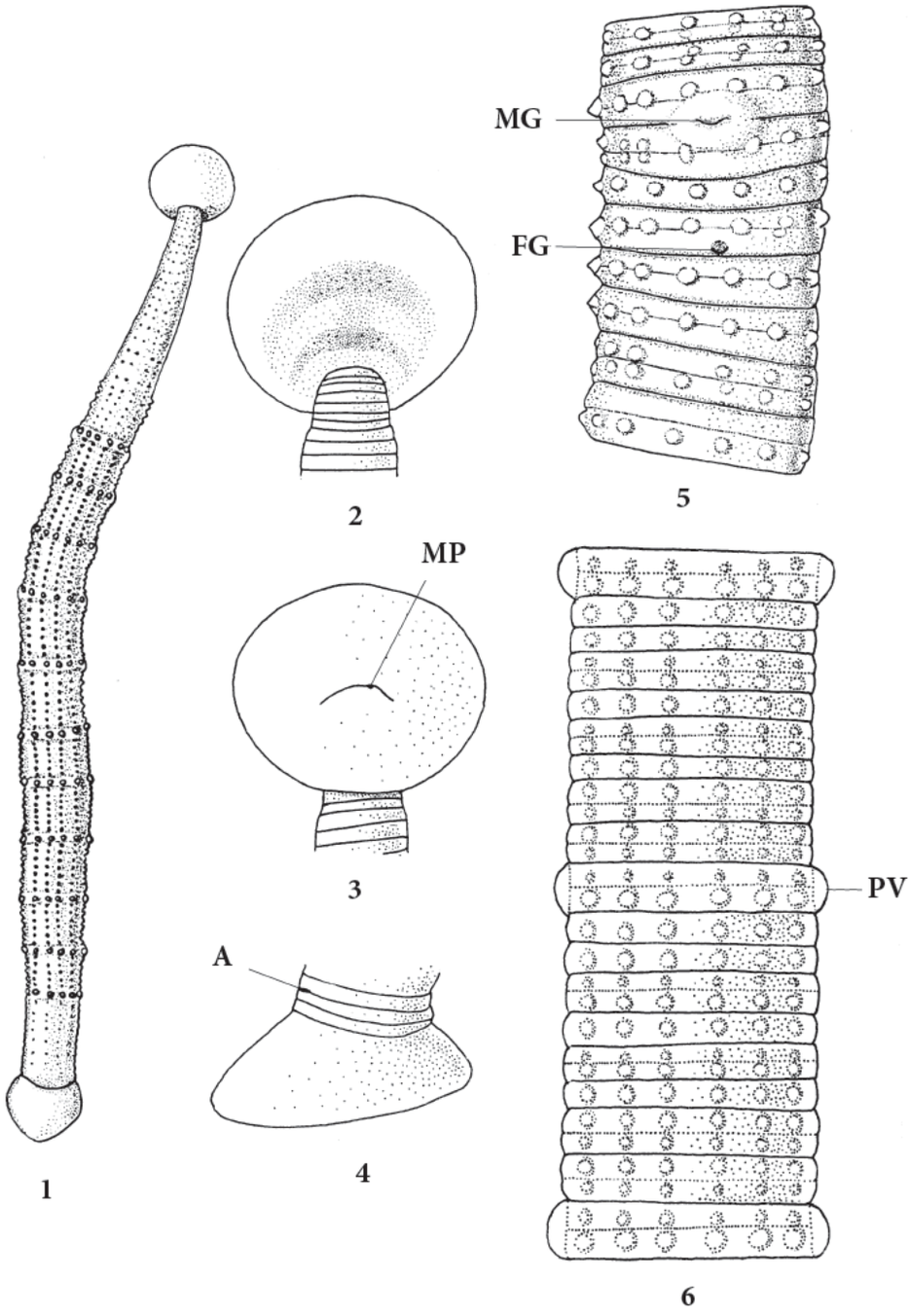


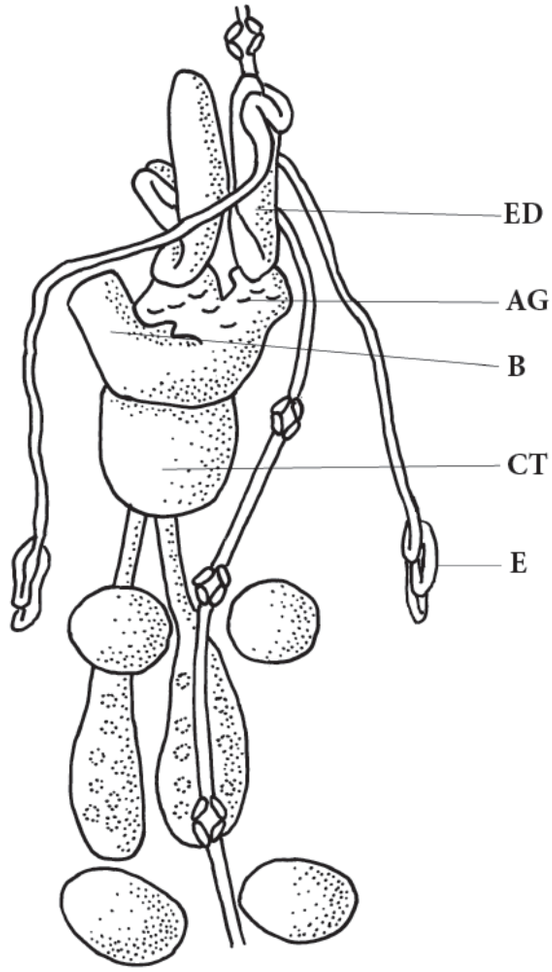
Plate XII. ***Johanssonia arctica*** **(Johansson, 1898), external characters.**

Fig. 1 Entire specimen, dorsal view.
Fig. 2 Anterior sucker, dorsal view.
Fig. 3 Anterior sucker, ventral view.
Fig. 4 Posterior sucker, lateral view.
Fig. 5 Clitellum, ventral view.
Fig. 6 Segment from crop region.

Abbreviations: A: anus. FG: female gonopore. MG: male gonopore. MP: mouth pore. PV: pulsatile vesicle.

(Figs. 1-6 are original.)

1



2

Plate XIII. *Johanssonia arctica* (Johansson, 1898), internal characters.

Fig. 1 Digestive system, dorsal view.
Fig. 2 Reproductive system, dorsal view.

Abbreviations: AG: accessory gland. B: bursa. CT: conductive tissue. E: epididymis. ED: ejaculatory duct.

(Figs. 1-2 are original.)

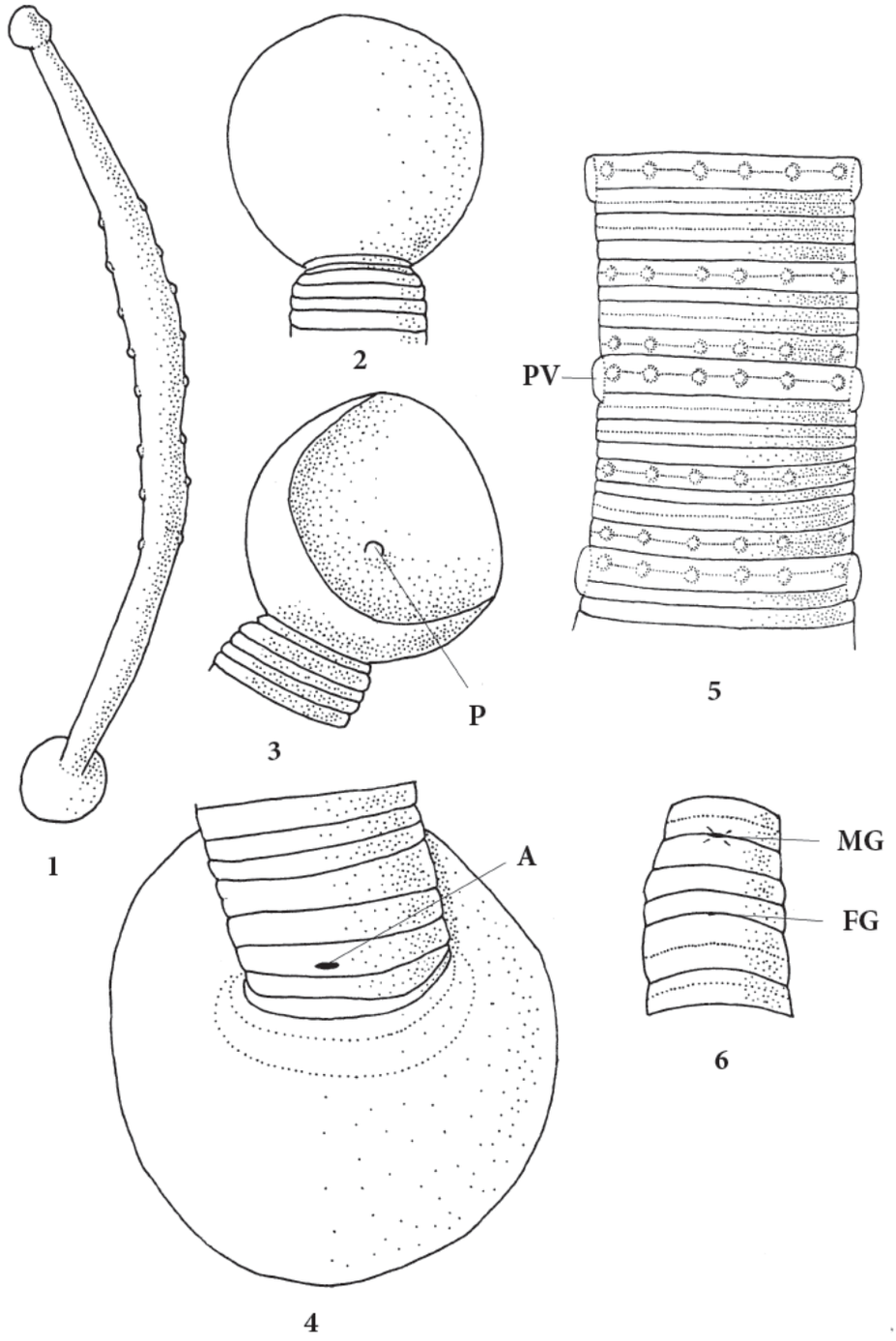


Plate XIV. *Johanssonia kolaensis* Selensky, 1914, external characters.

Fig. 1 Entire specimen, dorsal view.
Fig. 2 Anterior sucker, dorsal view.
Fig. 3 Anterior sucker, lateral view.
Fig. 4 Posterior sucker, dorsal view.
Fig. 5 Segment from crop region, dorsal view.
Fig. 6 Clitellum, ventral view.

Abbreviations: A: anus. FG: female gonopore. MG: male gonopore. P: proboscis. PV: pulsatile vesicle.

(Figs. 1-6 are original.)

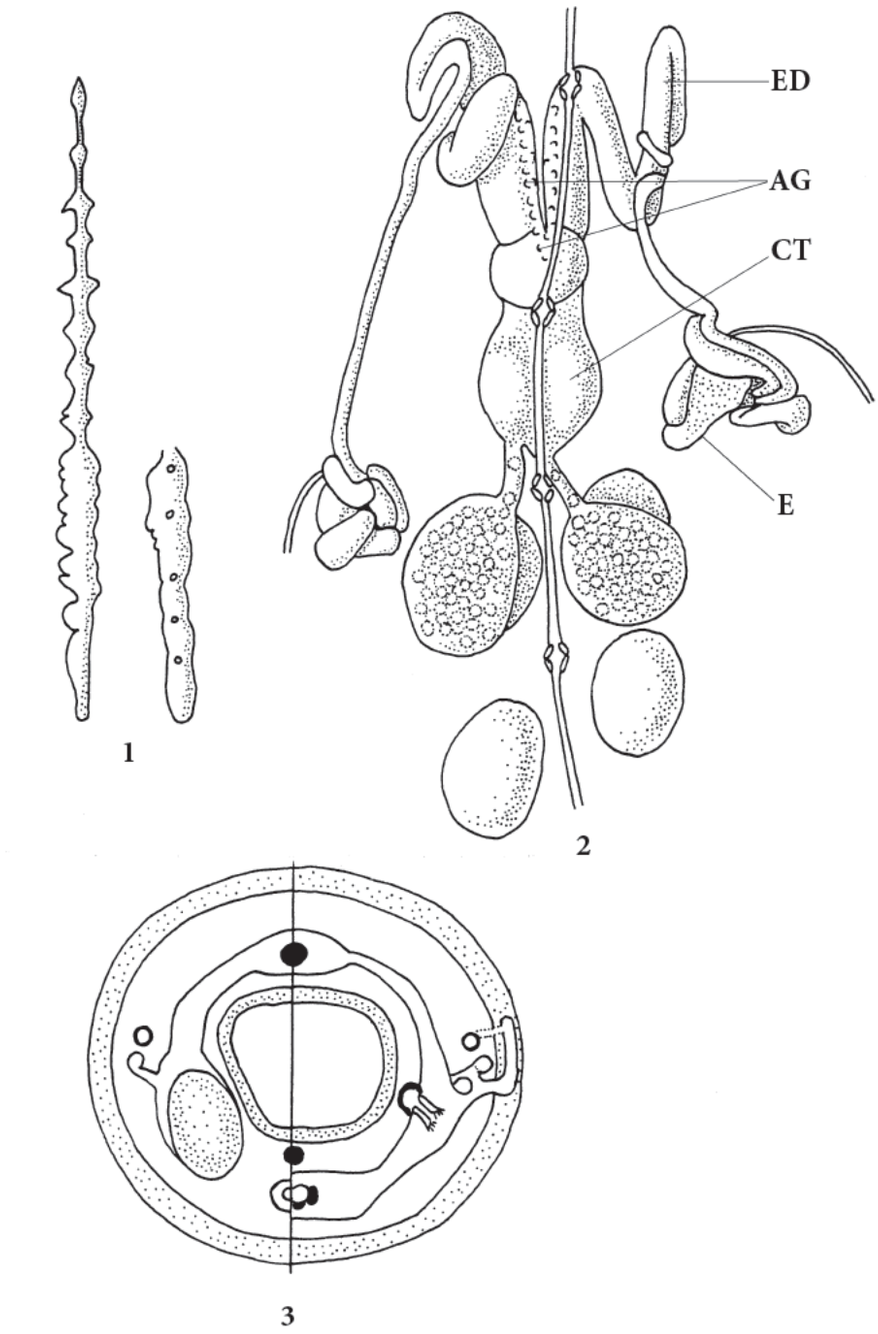


Plate XV. *Johanssonia kolaensis* Selensky, 1914, internal characters.

Fig. 1 Digestive system, dorsal view.
Fig. 2 Reproductive system, dorsal view.
Fig. 3 Coelomic system.

Abbreviations: AG: accessory gland. CT: conductive tissue. E: epididymis. ED: ejaculatory duct.

(Figs. 1-2 are original; Fig. 3 from Selensky 1915.)

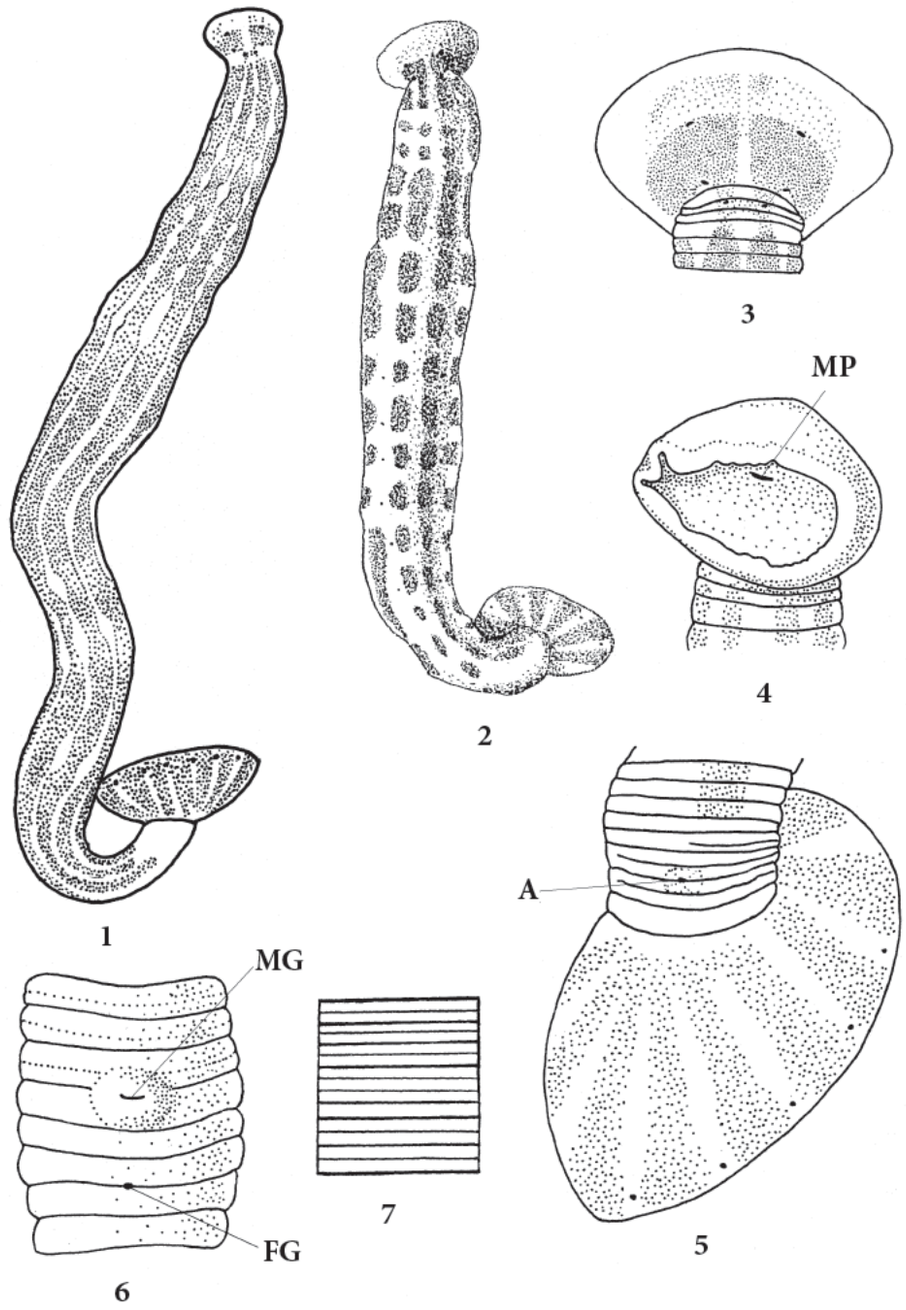


Plate XVI. *Hepacyclus virgatus* (Oka, 1910), external characters.

Fig. 1 Entire specimen, dorsal view, adult.
Fig. 2 Entire specimen, dorsal view, juvenile.
Fig. 3 Anterior sucker, dorsal view.
Fig. 4 Anterior sucker, lateral view.
Fig. 5 Posterior sucker, dorsal view.
Fig. 6 Clitellum, ventral view.
Fig. 7 Segment from crop region, diagrammatic view.

Abbreviations: A: anus. FG: female gonopore. MG: male gonopore. MP: mouth pore.

(Figs. 1-6 are original; Fig. 7 from Vasilyev 1939.)

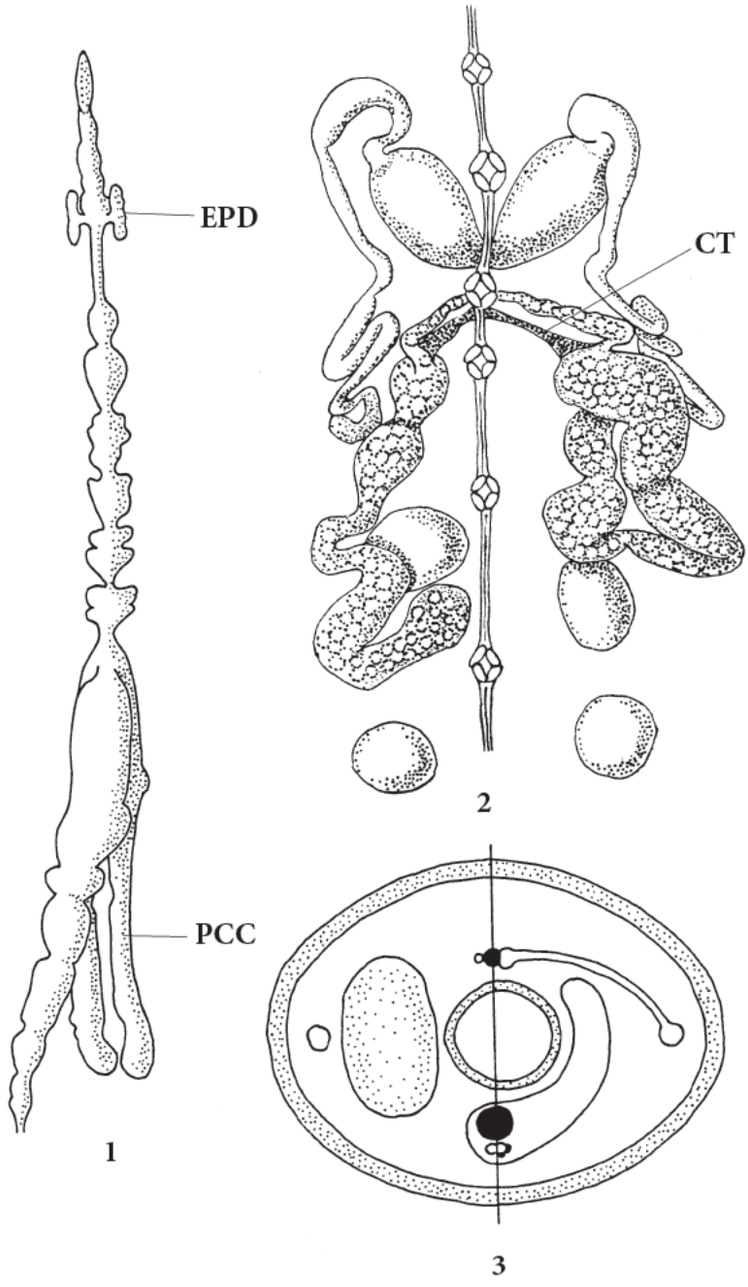


Plate XVII. *Heptacyclus virgatus* (Oka, 1910), internal characters.

Fig. 1 Digestive system.
Fig. 2 Reproductive system, dorsal view.
Fig. 3 Coelomic system.

Abbreviations: CT: conductive tissue. EPD: esophageal diverticulum. PCC: posterior crop cecum.

(Figs. 1-3 are original.)

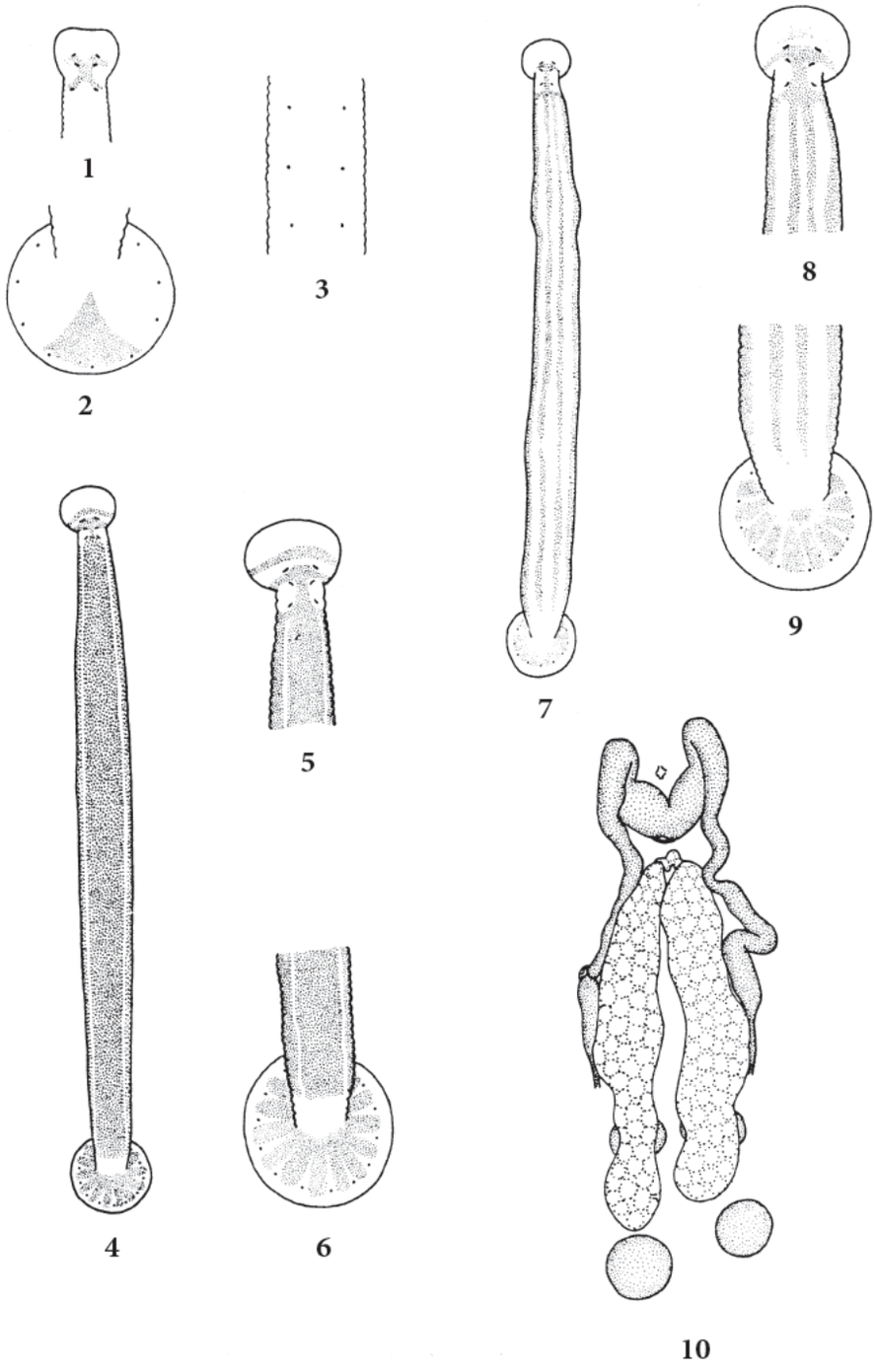


Plate XVIII. *Oceanobdella microsotoma* (Johansson, 1896), *Heptacyclus brunneus* (Johansson, 1896) and *Heptacyclus scorpii* (Malm, 1863).

Figs. 1-3 *Oceanobdella microstoma* (1: anterior sucker, dorsal view. 2: posterior sucker, dorsal view. 3: three adjacent segments of mid-body region, dorsal view.)
Figs. 4-6 *Heptacyclus brunneus* (4: entire specimen, dorsal view. 5: anterior sucker, dorsal view. 6: posterior sucker, dorsal view.)
Figs. 7-10 *Heptacyclus scorpii* (7: entire specimen, dorsal view. 8: anterior sucker, dorsal view. 9: posterior sucker, dorsal view. 10: reproductive system, dorsal view.)

(Figs. 1-10 by permission from Appy and Dadswell 1981, illustrated by Teresa D. Appy.)

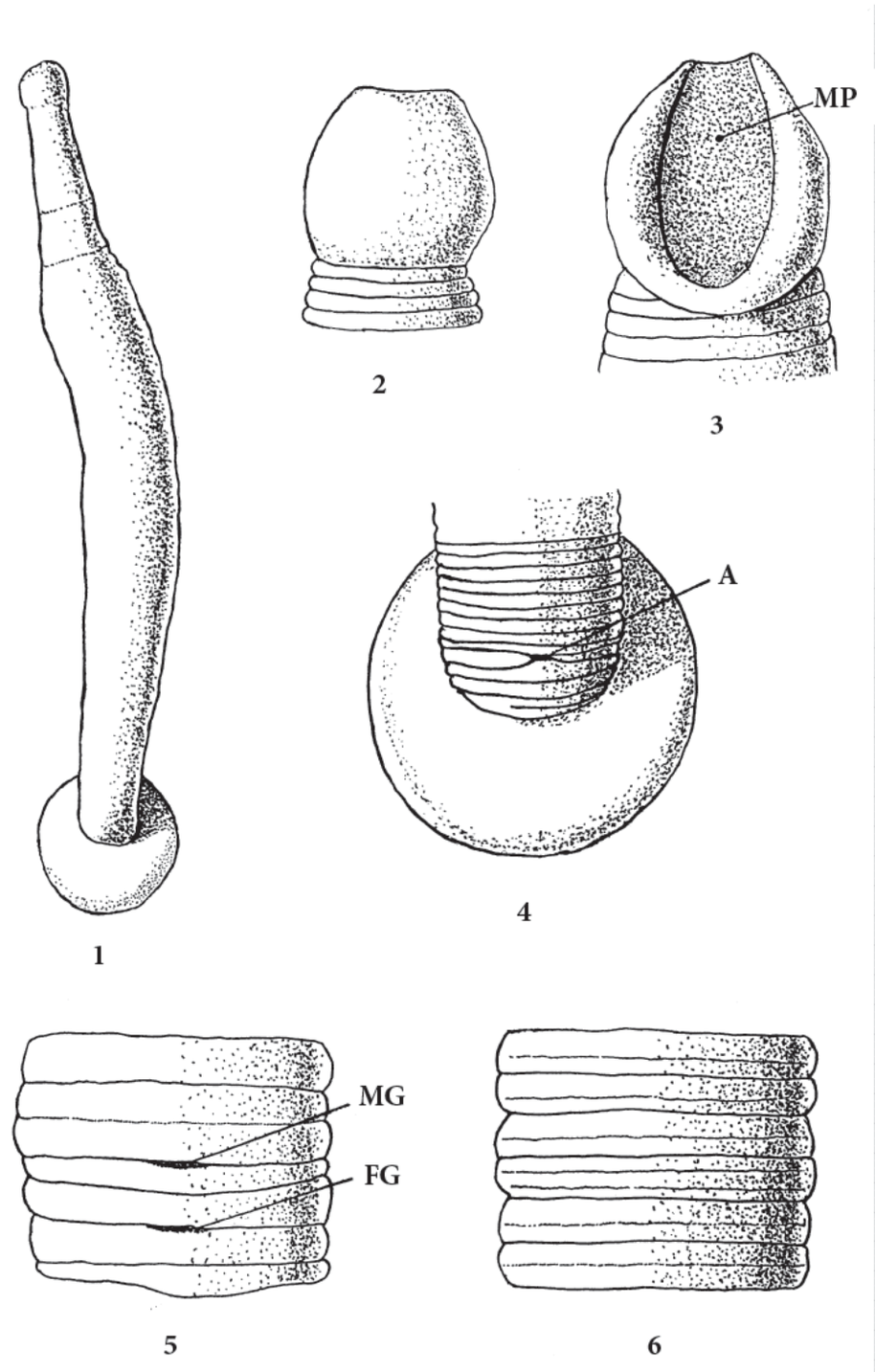


Plate XIX. ***Oceanobdella alba*** **(Epstein et S.Y. Utevsky, 1996), external characters (preservative-bleached specimen).**

Fig. 1 Entire specimen, dorsal view.
Fig. 2 Anterior sucker, dorsal view.
Fig. 3 Anterior sucker, ventral view.
Fig. 4 Posterior sucker, dorsal view.
Fig. 5 Clitellum, ventral view.
Fig. 6 Segment from crop region, dorsal view.

Abbreviations: A: anus. FG: female gonopore. MG: male gonopore. MP: mouth pore.

(Figs. 1-6 from Epstein and Utevsky 1996.)

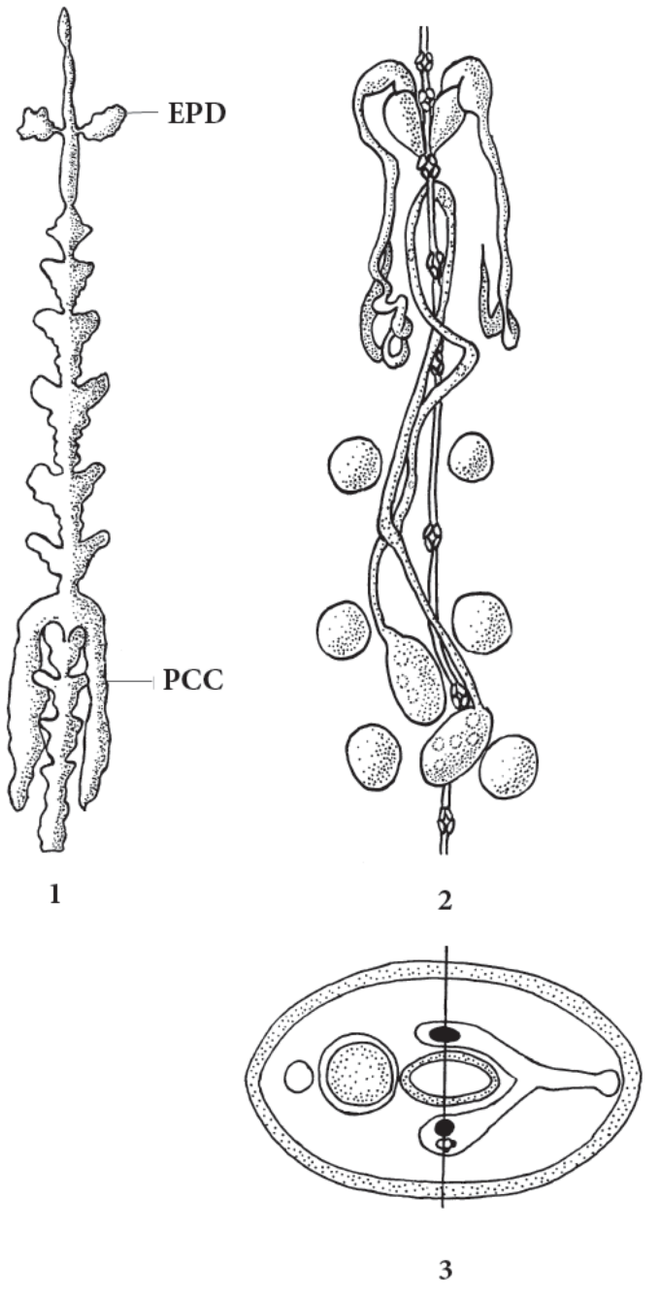


Plate XX. *Oceanobdella alba* (Epstein et S.Y. Utevsky, 1996), internal characters.

Fig. 1 Digestive system, dorsal view.
Fig. 2 Reproductive system, dorsal view.
Fig. 3 Coelomic system.

Abbreviations: EPD: esophageal diverticulum. PCC: posterior crop cecum.

(Figs. 1-3 from Epstein and Utevsky 1996.)

Phylum Annelida, Class Pogonophora

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The Pogonophora are sedentary marine worms that lack an intestine. They live in tubes made from protein and chitin, which they secrete. Pogonophora occur in all oceans and many of the marginal seas at depths from 22 to more that 8000 m. They generally prefer cold waters. About 80% of the species occur at depths between 200 and 4000 m. Pogonophora live primarily on soft silty bottoms, especially in reducing sediments, burrowing deeply (subclass Frenulata). Some prefer to live in decaying organic matter, or sediments rich in methane and sulfide (subclass Monilifera), others in warmer hydrothermal vent conditions or cold seeps (subclass Vestimentifera). There are currently about 170 species of Pogonophora, 90% of which belong to the subclass Frenulata. Pogonophora get their energy primarily from chemoautotrophic methane- or sulfur-oxidizing bacteria, living endosymbiotically in a specialized organ called the trophosome. They also get some nourishment from dissolved organic matter in the sediment pore water.

The body is bilaterally symmetrical, remarkably long (the length exceeds the width by hundreds of times), and it has several segments and sections. Pogonophorans are polymerous. The first segment consists of the cephalic lobe (or prostomium) and tentacles (palpi) with a coelomic canal; there can be one to several hundred of such tentacles. The tentacles often have pinnules, which consist of outgrowths of individual epidermal cells (in frenulates) or they are formed of many cells (in vestimentiferans). The bridle (a thickened area of the cuticle found in frenulates), a row of cuticular plates (plaques, found in moniliferans), or vestimental wings (in vestimentiferans) occur on segment two. The coelomic space of this and subsequent segments is filled with numerous multicellular glands. The cephalic lobe and segments one and two make up the anterior section (so-called forepart), which is often demarcated from the rest of the body by a transverse constriction.

A large portion of the body consists of segment three, the trunk or metasome. In Frenulata this segment has a complex regional morphology. The anteriormost "metameric" section of the preannular region is characterized by more or less regular paired papillae or dorsal ridges with a groove between them and a ciliated band (the neurotroch) on the ventral side. Following this, the nonmetameric part of the preannular region is covered with irregularly distributed papillae. The zone of thickened papillae is a peculiar portion of the posterior preannular nonmetameric region, present in many frenulates. It is characterized by a longitudinal row of regular papillae on the dorsal side and a ciliated band on the ventral side. The girdles, or annuli, are transverse rows of short bristles (setae or chaetae) developed from the primary set of segmental setae, visible in early larvae. The trunk of moniliferans and vestimentiferans is covered with scattered papillae, and is equivalent to the nonmetameric preannular region of frenulates. Girdles are present at the posterior end in moniliferans. A postannular region of the trunk is present only in Frenulata and is characterized by great length and a variety of metameric papillae and glandular regions of the epidermis. The body of all pogonophores ends with an opisthosoma, consisting of several (to several tens) of segments, and a posterior zone of growth (the pygidium), which can be simple or surrounded by one or two lobes. The segments have a set of setae (two groups dorsolaterally and two ventrolaterally) that are more numerous in moniliferans and vestimentiferans than in frenulates. The setae of the opisthosoma and annuli can differ morphologically. Those on the annuli have broad dentate heads in frenulates; the denticles on their heads are arranged in two groups, directed anteriorly and posteriorly. Between these groups there is often a noticeable intermediate zone lacking denticles. On the opisthosoma of frenulates the setae are rod- or club-shaped, while in moniliferans and vestimentiferans they are more like frenulate girdle setae.

Pogonophora have separate sexes (with the exception of one species), but external differences between males and females are not obvious in frenulates or moniliferans. Vestimentiferans have external genital grooves, showing differences between males and females. The sperm are packed into true spermatophores (subclass Frenulata) or sperm masses (spermatozeugmata) (subclass Vestimentifera, some species) or are free (subclasses Monilifera and some Vestimentifera). The spermatophores often have a variety of processes (wings, threads, etc.). The oocytes (eggs) are exuded into the space between the body and the tube wall, and are transported by means of the ciliary band to the anterior of the tube where they are either released into the water or undergo initial stages of embryonic development to the point of forming trochophore-like lecithotrophic larvae or even juveniles. Fertilization may be internal or external. The release of small eggs is characteristic of vestimentiferans and moniliferans, and also the order Thecanephria of Frenulata. Brooding of embryos in the tube is known in some members of the order Athecanephria of Frenulata. Planktotrophic trochophores and crawling, feeding larval (juvenile) stages are known in Vestimentifera. Larvae are not known in the Monilifera and Thecanephria. Pogonophora with different development types have different reproductive strategies with corresponding features of the female gametes. Large, elongate, yolky eggs in low numbers are characteristic of some Athecanephria; for all other groups of Pogonophora, the eggs are small, round, numerous, and less yolky.

Pogonophora have a protonephridium-type excretory system. The excretory pores are located at the anterior part of the body on the dorsal or ventrolateral sides.

The circulatory system is closed with a dorsal heart, sometimes enclosed in a coelomic sac (a pericardium); a cardiac body is often present in the medial blood vessels.

The tubes of Frenulata are nearly cylindrical and straight or curved and are normally not branched; they are rarely closed at the anterior or posterior ends and often have some kind of ornamentation. Most often one observes ringed tubes, more rarely ringed-segmented or segmented tubes. The rings are the areas composed of the densest and darkest colored material; the segments are the result of episodic growth and are limited by narrow encircling constrictions, wrinkles, or overlaps, sometimes with funnel-like edges, repeated at even intervals. The anterior ends of the tubes are often soft and filmy, sometimes in the form of rigid funnels. The tubes of Monilifera lack rings or segments; their shape is often very convoluted and their surface finely wrinkled. The tubes of vestimentiferans are segmented and funneled anteriorly; they are non-ringed, of tough construction, and usually closed at the very narrow posterior end, at least in the early stages of growth.

Key to subclasses of the class Pogonophora

Abbreviations: D_o = largest egg diameter; D_f = diameter of the forepart near the bridle; D_t = tube diameter at the anterior end; L_{cl} = length of the cephalic lobe; L_f = length of the forepart.

1 (2) Frenulum present, consisting of a pair of cuticular ridges encircling the anterior region of the forepart of the body (see Pl. III, Figs. 1-3); trunk (third segment) has a preannular region, girdle region, and postannular region. . . . . **Frenulata**

2(1) Frenulum absent, trunk lacks a postannular region, the girdles are either absent or immediately anterior to the opisthosoma.

3(4) A ring of small cuticular plaques encircles the anterior region of the forepart of the body (see Pl. I, Figs. 1-2). . . . . **Monilifera, order Sclerolinida, family Sclerolinidae, genus *Archeolinum*, *A. contortum* (Smirnov, 2000) (Pl. I)**

D_t 0.2-0.39 mm. D_f 0.13-0.24 mm.
Arctic. Laptev Sea and Arctic Basin to northeast of Spitsbergen.
Depth 311-2166 m. Bathyal-abyssal, on silty sediments.

4(3) Two lateral vestimental folds cover the anterior part of the body, with many cuticular plaques on the epidermis. . . **Vestimentifera (not known to occur in the Arctic)**

Key to orders of the subclass Frenulata

1(2) Postannular region bears more or less metameric transverse rows of adhesive cuticular plaques and lacks ventral glandular patches. Spermatophores are leaf-shaped. Tentacles 2-many . . . . . **Thecanephria, family Polybrachiidae, genus *Polybrachia*, *P. gorbunovi* (Ivanov, 1949) (Pl. II)**

D_t ~ 0.5 mm. D_f 0.27-0.29 mm.
Arctic abyssal. Arctic Basin, Sadko Trench.
Depth 3700-3800 m. Silty sediments.

2(1) Postannular region bears more or less metameric ventral glandular patches of epidermis (ventral shields), each opposed by a small number of dorsal papillae. Spermatophores are spindle shaped. Tentacles 1-12 . . . . . **Athecanephia**

Key to families of the order Athecanephria

1(2) Two or more rows of multicellular coelomic glands extend 2 mm or more from start of trunk on each side of dorsal furrow. If glands distributed in two rows, then two or more tentacles present . . . . . **Oligobrachiidae**

2(1) One, rarely two, rows of multicellular coelomic glands on each side of dorsal furrow. If two rows present, then one tentacle present and rows extend less than 2 mm from start of trunk. . . . . **Siboglinidae, genus *Siboglinum***

Key to genera of the family Oligobrachiidae

1(4) Two or more tentacles present.

2(3) Tentacles always two. Multicellular coelomic glands in forepart very distinct in transmitted light. Spermatophores lack wings . . . . . ***Nereilinum***

3(2) Often more than two tentacles present. Multicellular coelomic glands in forepart not visible in transmitted light. Spermatophores with pair of wings . . . . . ***Oligobrachia, O. haakonmosbiensis* (Smirnov, 2000) (Pl. III)**

Dt 0.45-0.83 mm. Df 0.45-0.7 mm.
Arctic. Laptev Sea and Arctic Basin to northeast of Spitsbergen.
Depth 100-2166 m. Silty bottoms.

4(1) One tentacle present. . . . . ***Polarsternium, P. rugellosum* (Smirnov, 1999) (Pl. IV)**

D_t 0.3-0.5 mm. D_f 0.3-0.37 mm.
Arctic Ocean, Laptev Sea.
Depth 100-556 m. Silty sediments.

Key to species of the genus *Nereilinum*

1(2) Bridle and glandular band beneath it interrupted on dorsal and ventral sides of body. Tentacles with rings of thickened cuticle. Three girdles of setae present. Spermatophores ~140 μm long. Tube segmented in posterior region, Dt 0.35-0.45 mm. ***N. squamosum* (Smirnov, 1999) (Pl. V)**

D_t 0.35-0.45 mm. D_f 0.29-0.35 mm.
Arctic. Laptev Sea and Arctic Basin to northeast of Spitsbergen.
Depth 243-603 m. Bathyal-abyssal, on silty sediments.

2(1) Bridle and glandular band beneath, interrupted only on ventral side of body. Tentacles lack areas with thickened cuticle. Two girdles of setae present. Spermatophores ~100 μm long. Tube not segmented, D_t 0.21-0.28 mm . . . . . ***N. murmanicum*** **(Ivanov, 1961) (Pl. VI)**

D_t 0.21-0.28 mm. D_f 0.15-0.32 mm.
Atlantic high boreal Arctic. Barents Sea.
Depth 170-325 m. On silty sediments.

Key to species of the genus Siboglinum

1(2) Pinnules present. Cephalic lobe long (L_{cl}/D_f ~1.81). Multicellular coelomic glands in second segment distributed in numerous rows. First setal girdle interrupted on ventral side only. Setae in girdles distributed in single rows. Tube segmented in anterior and mid regions, with 5-9 rings per segment . . . . . ***S. ekmani*** **(Jägersten, 1956) (Pl. VII)**

D_t 0.11-0.17 mm. D_f 0.1-0.15 mm.
Northeast and northwest Atlantic 350 to >2000 m. Arctic Basin to northeast of Spitsbergen.
Depth 2090-2166 m. Bathyal-abyssal, on silty sediments.

2(1) Pinnules absent. Cephalic lobe short (L_{cl}/D_r ~ 1). Multicellular glands in second segment distributed in two rows. First girdle of setae interrupted only dorsally. Setae in girdles form two to four rows. Tube not segmented.

3(4) Tentacle attached to left of body medial line. L_f/D_f 4.5-5, D_f 0.13-0.16 mm. Post-tentacular furrow present. Setal girdles distributed in pattern of 2+1; third girdle separated from two anterior girdles by 0.60-0.64 mm; second girdle interrupted only ventrally. Intermediate zone on heads of setae very broad (12-21% of head length); area of anterior group of denticles about the same as area of posterior group. Tube rings brown or yellow. . . . . ***S. hyperboreum*** **(Ivanov, 1960) (Pl. VIII)**

D_t 0.13-0.32 mm. D_f 0.13-0.16 mm.
Arctic. Laptev Sea and Arctic Basin to southeast of Spitsbergen.
Depth 55-2166 m. On silty sediments.

4(3) Tentacle attached medially. L_f/D_f 7, D_f 0.2-0.22 mm. Post-tentacular furrow absent. Setal girdles distributed in pattern of 1+2; first girdle ~0.5 mm distance from group of two posterior girdles; second girdle interrupted only dorsally. Intermediate zone on head of setae narrow (~ 3% of head length); anterior group of denticles occupies about ⅓ of head length. Tube rings colorless . . . . . ***S. norvegicum*** **(Ivanov, 1960) (Pl. IX)**

D_t 0.13-0.25 mm. D_f 0.20-0.22 mm.
Atlantic Arctic. Arctic Basin to northeast of Spitsbergen.
Depth 2090-2166 m. Bathyal abyssal, on silty sediments.

Key to species of Pogonophora using empty tubes

1(4) Anterior portion of tube segmented.

2(3) Walls of tube thick, with multiple layers. Segmented part of tube dark brown or black, lacking rings; segments with collars. D_t ~ 0.5 mm. . . . . ***Polybrachia gorbunovi*** **(Ivanov, 1949) (Pl. II)**

3(2) Walls of tube thin, with a single layer. Segmented portion of tube with yellowish-brown rings; segments lacking collars. D_t 0.11-0.17 mm . . . . . ***Siboglinum ekmani*** **(Jägersten, 1956) (Pl. VII)**

4(1) Tube, if segmented, is segmented only in most posterior region.

5(16) Tube straight; at least posterior part is ringed. D_t 0.13-0.83 mm.

6(7) Rings colorless. D_t 0.13-0.25 mm . . . . . ***Siboglinum norvegicum*** **(Ivanov, 1960) (Pl. IX)**

7(6) Rings in mid part of tube yellow to almost black. D_t 0.13-0.83 mm.

8(15) Rings more or less regular, with even edges, long (not less than ⅔ diameter of tube), nearly lacking in fibers. D_t 0.24-0.83 mm.

9(10) Rings in midsection of tube dark brown or black, almost opaque. Anterior membranous, unringed part of tube 2-5 mm long. Posterior part of tube with longitudinal ribs on surface. D_t 0.45-0.83 mm. . . . . ***Oligobrachia haakonmosbiensis*** **(Smirnov, 2000) (Pl. III)**

10(9) Rings in midsection of tube yellow or brown, translucent. Anterior membranous, unringed portion no less than 15 mm long. Tube surface without longitudinal ribs. D_t 0.24-0.5 mm.

11(14) Tube thin-walled. Rings yellow, elongate (about equal to tube diameter), very regular. Intervals between rings concave on a substantial portion of tube. D_t 0.21-0.45 mm.

12(13) Tube segmented in posterior section. D_t 0.32-0.45 mm . . . . . ***Nereilinum squamosum*** **(Smirnov, 1999) (Pl. V)**

13(12) Tube lacking segments. D_t 0.21-0.28 mm . . . . . ***Nereilinum murmanicum*** **(Ivanov, 1961) (Pl. VI)**

14(11) Tube thick-walled. Rings yellow to brown, short (about ⅔ tube diameter). Rings in posterior part of tube somewhat irregular (anastomotic), intervals between rings convex. D_t 0.3-0.5 mm. . . . . ***Polarsternium rugellosum*** **(Smirnov, 1999) (Pl. IV)**

15(8) Rings over most of tube irregular (anastomotic with uneven edges), very fibrous, length ½ to ⅔ tube diameter. D_t 0.13-0.32 m. . . . . ***Siboglinum hyperboreum*** **(Ivanov, 1960) (Pl. VIII)**

16(5) Tube without rings, very strongly twisted. D_t 0.2-0.39 mm . . . . . ***Archeolinum contortum*** **(Smirnov, 2000) (Pl. I)**

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Addendum

(Eve C. Southward, reviewer of the Pogonophora keys)

Eleven species of Pogonophora are included in these keys. Other species will probably be discovered in the future. Two known species are likely to occur in the region: *Oligobrachia webbi* (Brattegard, 1966), known from near Tromsø at 270 m depth, and *Siboglinum brevicephalum* (Flügel, 1990), known from 67°46N 06°01E, 1274 m depth, in the Norwegian Sea. In addition, *Galathealinum arcticum* (Southward, 1962), is known from the Mackenzie Delta region in the Canadian Arctic. The Bering Sea is rich in frenulate pogonophore species (Ivanov 1960, 1963), some of which might occur north of the Bering Strait.

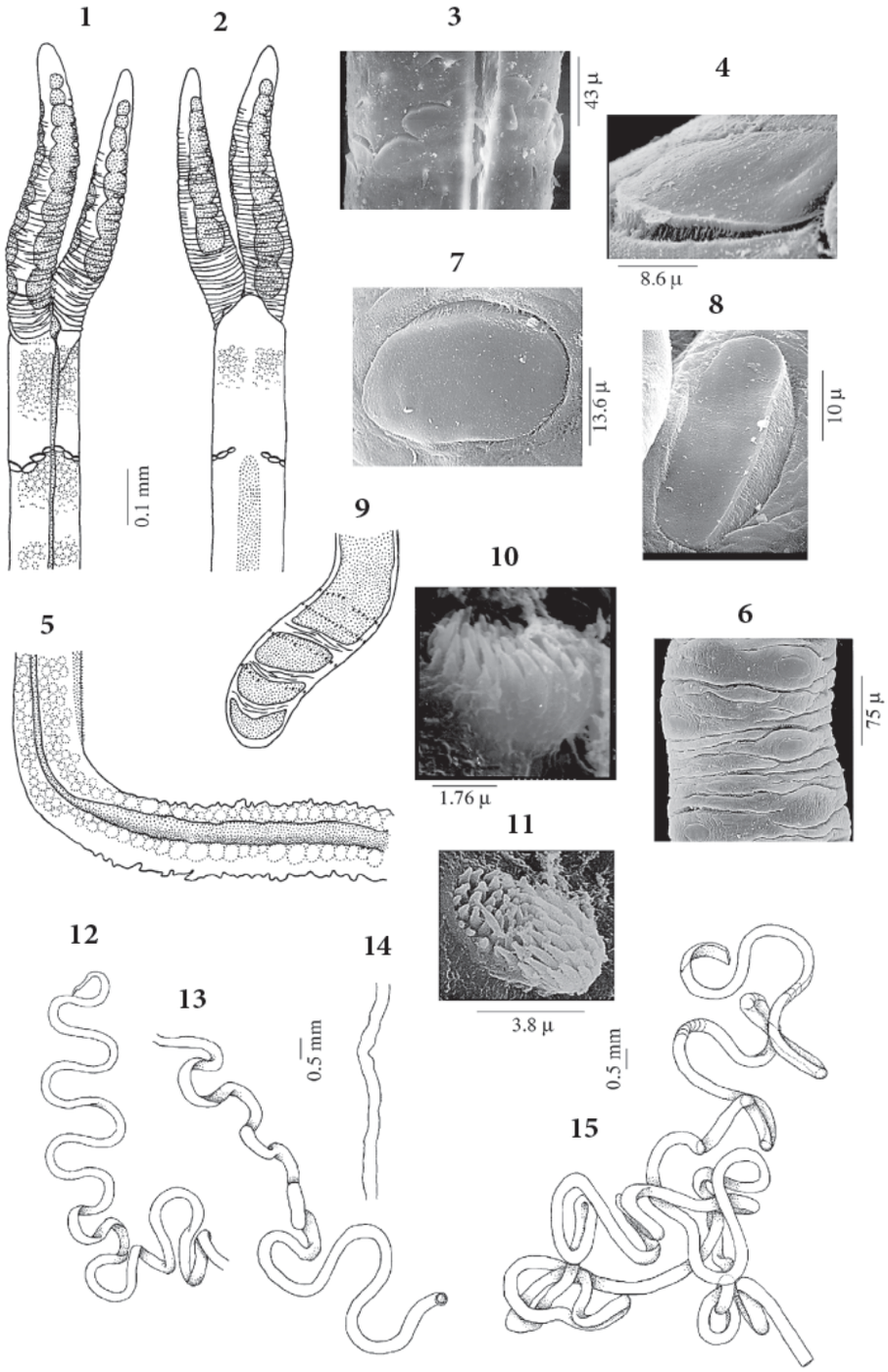

Plate I

Figs. 1-15 *Archeolinum contortum* (Smirnov, 2000)

(1: anterior end of animal with tentacles, dorsal view. 2: same, ventral view. 3: region near bridle, dorsal view. 4: cuticular plaque of bridle. 5: transitional zone between metameric and non-metameric regions of trunk, dorsolateral view. 6: region of trunk in front of the annuli and opisthosoma with groups of papillae, dorsal view. 7, 8: cuticular plaques from non-metameric region. 9: opisthosoma. 10: seta on the opisthosoma, lateral view. 11: same, viewed from above. 12-14: successive sections of weakly twisted tubes. 15: view of entire tube, very twisted.)

(Figs. 1-15 from Smirnov 2000.)

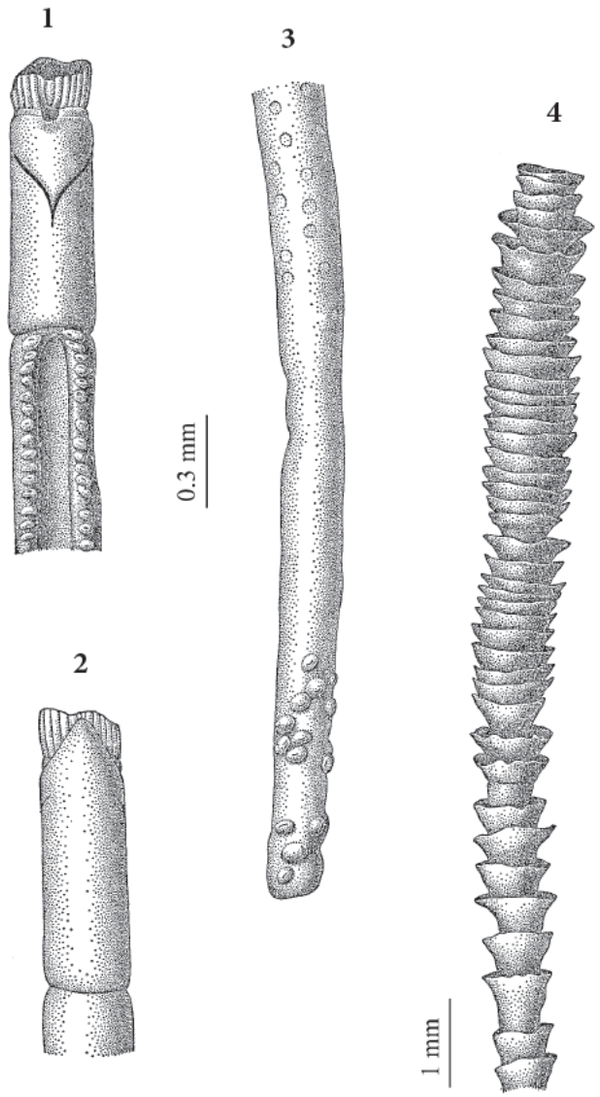

Plate II

Figs. 1-4 *Polybrachia gorbunovi* (Ivanov, 1949)

(1: forepart and anterior section of metameric region of trunk, dorsal view. 2: same, ventral view. 3: non-metameric section and thickened area, dorsal view. 4: anterior part of tube.)

(Figs. 1-4 from Ivanov 1949.)

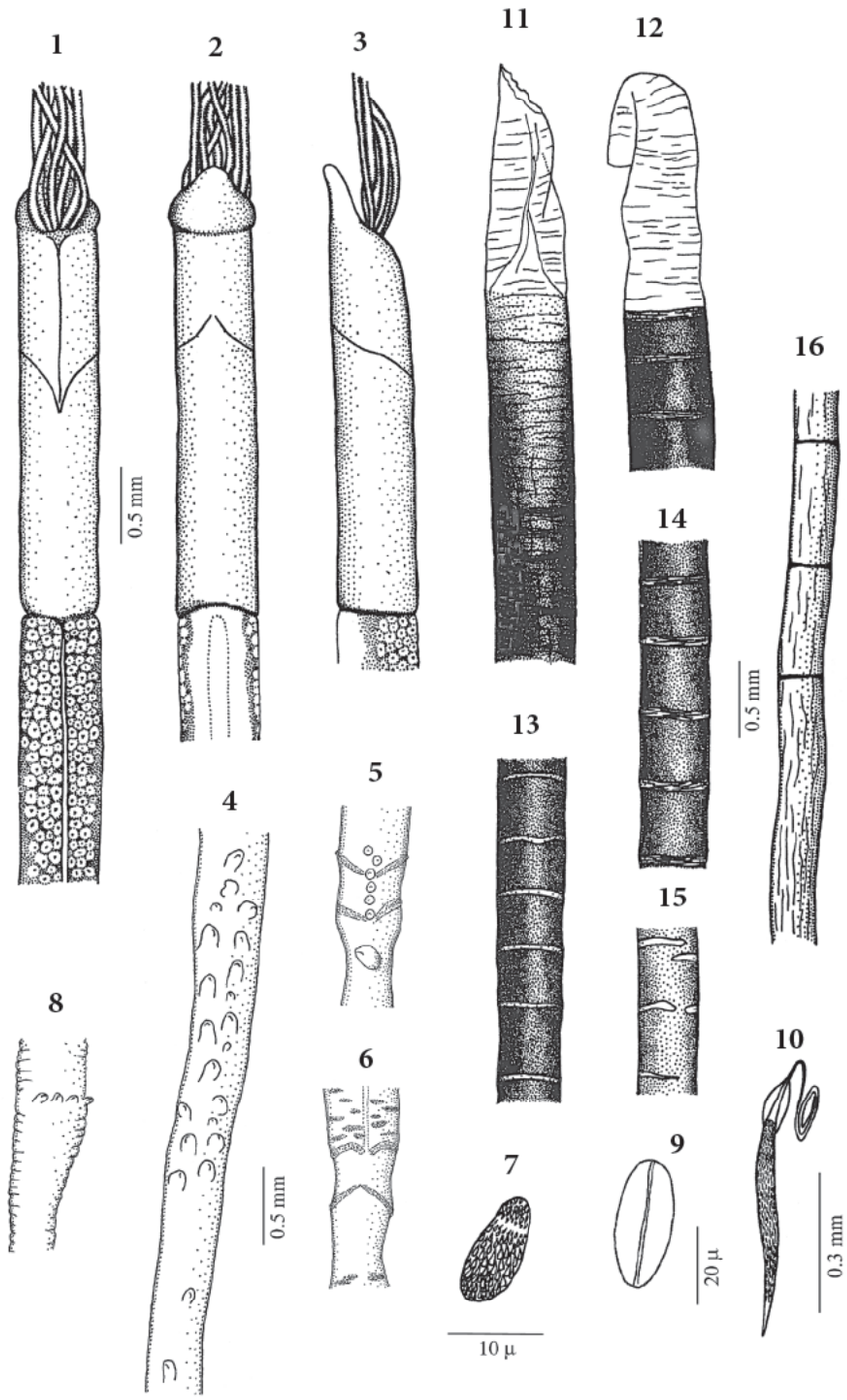

Plate III

Figs. 1-16 *Oligobrachia haakonmosbiensis* (Smirnov, 2000)

(1: forepart, tentacles and anterior part of trunk, dorsal view. 2: same, ventral view. 3: same, lateral view. 4: thickened area, dorsal view. 5: annuli, dorsal view. 6: annuli, ventral view. 7: head of setae of annulus. 8: post-annular metamere, dorsolateral view. 9: cuticular plaque from post-annular section. 10: spermatophore. 11, 12: variants in structure of anterior end of tube. 13-16: successive sections of tube.)

(Figs. 1-16 from Smirnov 2000, with modifications and additions.)

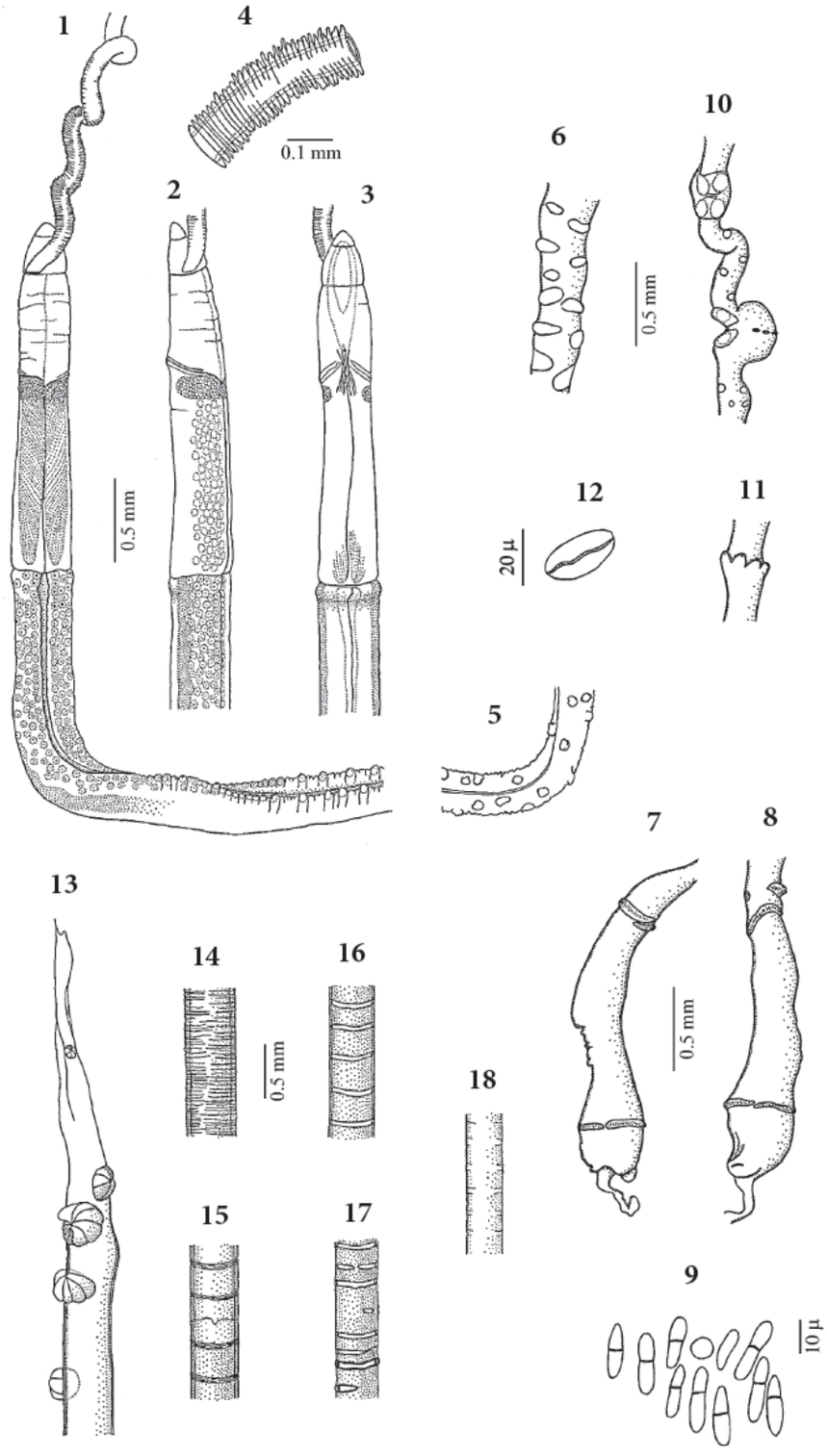

Plate IV

Figs. 1-18 *Polarsternium rugellosum* (Smirnov, 1999)

(1: forepart, tentacle, metameric section and anterior non-metameric section of trunk, dorsolateral view. 2: forepart and anterior part of metameric section, dorsal view. 3: same, ventral view. 4: portion of tentacle. 5: posterior section of non-metameric region, dorsal view. 6: thickened zone, dorsal view. 7: annular region, ventral view. 8: annular region, dorsal view. 9: portion of girdle [annulus]. 10: posterior part of post-annular section, ventral view. 11: same, proximal section. 12: cuticular plaques from post-annular section. 13-18: successive sections of tube.)

(Figs. 1-18 from Smirnov 1999, with additions.)

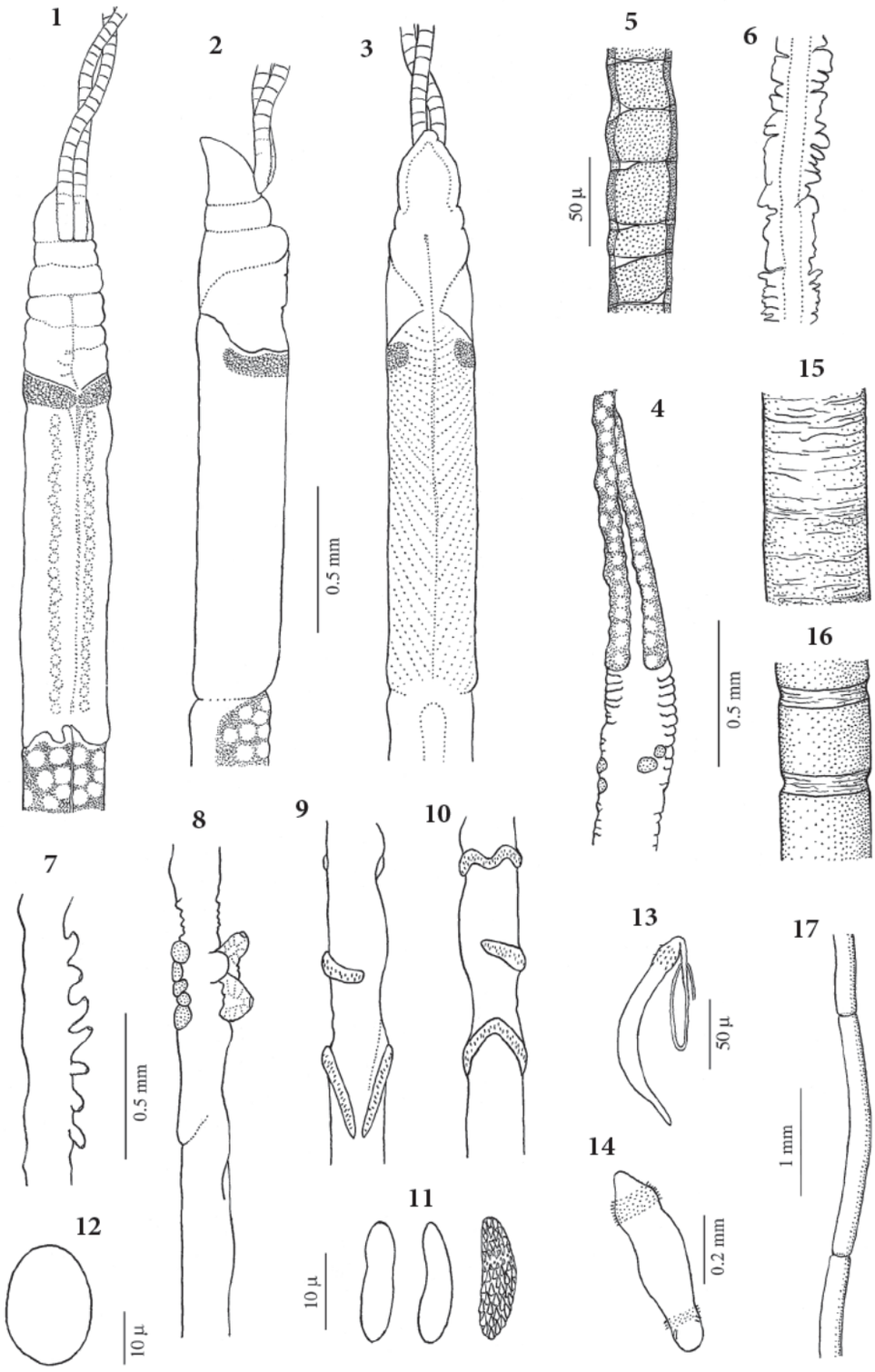

Plate V

1-17. *Neretinum squamosum* (Smirnov, 1999)

(1: forepart, tentacles and anterior part of body, dorsal view. 2: same, lateral view. 3: same, ventral view. 4: transitional region between metameric and non-metameric section of trunk, dorsal view. 5: proximal portion of tentacle. 6: tentacle, distal portion. 7: thickened section, lateral view. 8: post-annular metamere, lateral view. 9: girdle region, dorsal view. 10: girdle region, ventral view. 11: portion of girdle [annulus]. 12: cuticular plaque from post-annular section. 13: spermatophore. 14: larva. 15: membranous anterior end of tube. 16: middle region of tube. 17: posterior section of tube.)

(Figs. 1-17 from Smirnov 1999.)

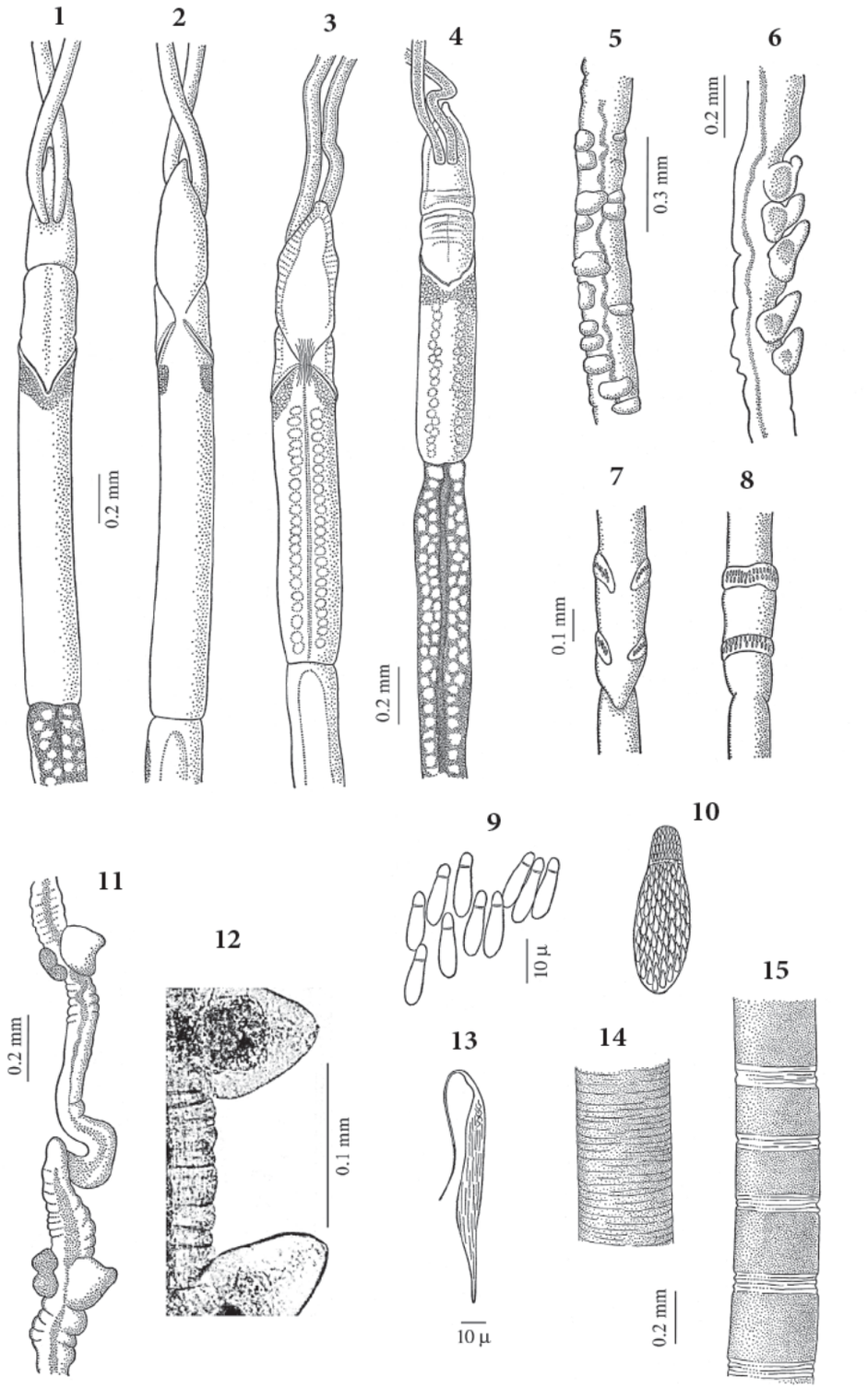

Plate VI

Figs. 1-15 *Nereiltnum murmanicum* (Ivanov, 1961)

(1, 4: forepart, tentacles, and anterior portion of trunk, dorsal view. 2, 3: same, ventral view. 5: non-metameric region of trunk, dorsal view. 6: thickened region, lateral view. 7: girdle [annulus], dorsal view. 8: girdle [annulus], ventral view. 9: section of girdle [annulus]. 10: head of seta in girdle. 11: post-annular section, lateral. 12: post-annular papilla with cuticular plaque. 13: spermatophore. 14: anterior membranous end of tube. 15: middle section of tube.)

(Figs. 1-11, 13-15 from Ivanov 1961; Fig. 12 from Flügel 1990.)

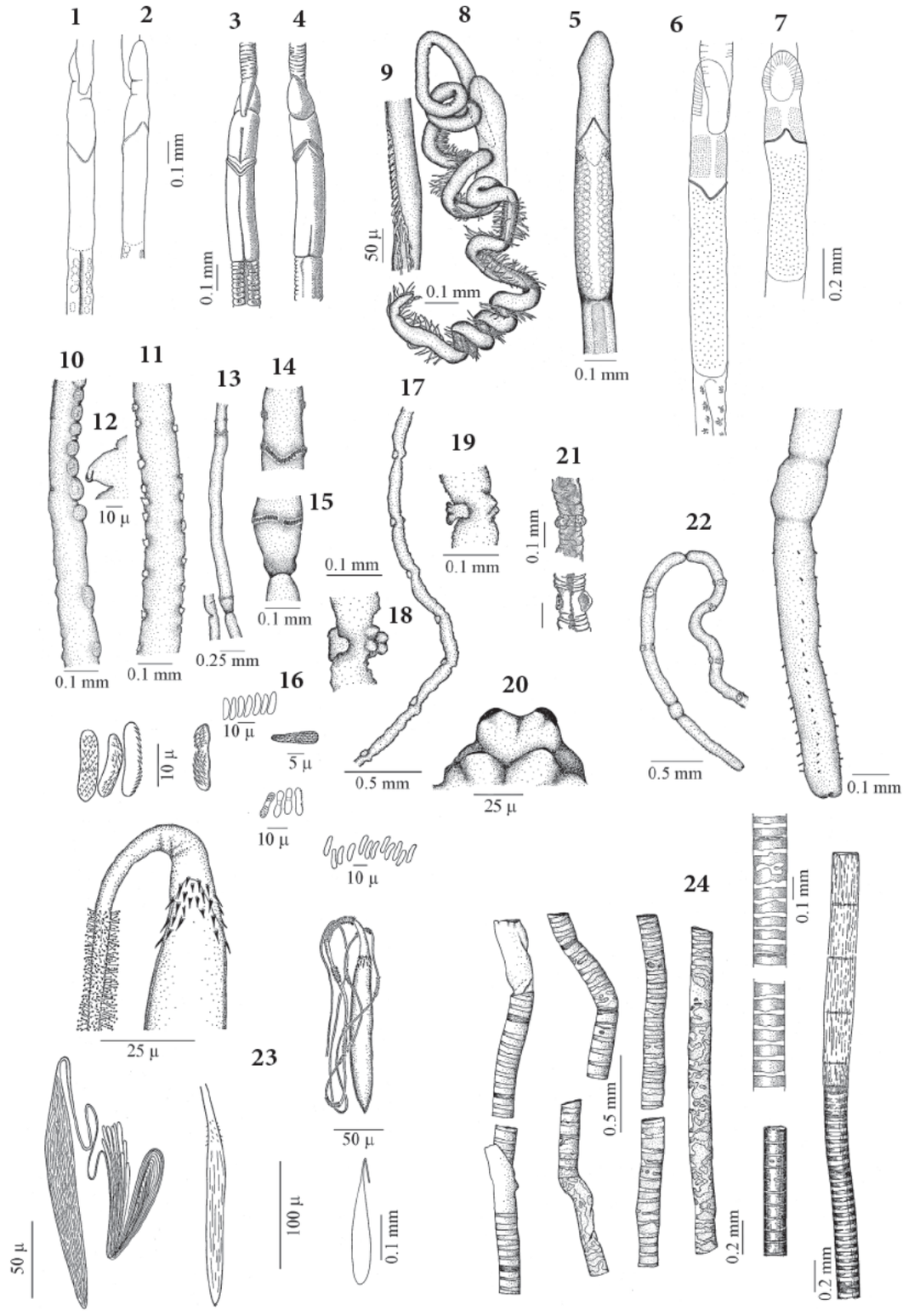

Plate VII

Figs. 1-24 *Siboglinum ekmani* (Jägersten, 1956)

(1, 3, 6: forepart, dorsal view. 2, 4, 5, 7: forepart, ventral view. 8: cephalic lobe, ventral view and tentacle with pinnules. 9: tentacle with pinnules. 10: boundary between metameric and non-metameric sections of trunk, lateral view. 11: non-metameric section, dorsal view. 12: papilla from non-metameric region. 13: region of girdle [ventral] and third girdle, lateral. 14: two anterior girdles, ventral view. 15: third girdle, ventral view. 16: section of girdle and head of seta from girdle. 17: post-annular section, lateral view. 18, 19: post-annular metameres, lateral view. 20: postannular papilla. 21: post-annular metamere of another specimen, dorsal and ventral view. 22: distal part of post-annular section and opisthosoma, lateral view. 23: variations in structure of spermatophores and its armament in different individuals. 24: various sections of the tube.)

(Figs. 1, 2, 16, 24 from Southward 1972; Figs. 3, 4, 21, 23, 24 from Ivanov 1960; Figs. 5, 8-20, 22, 24 from Webb 1964; Figs. 6, 7, 23 from Southward and Brattegard 1968; Fig. 23 from Webb 1963; Fig. 24 from Jägersten 1956.)

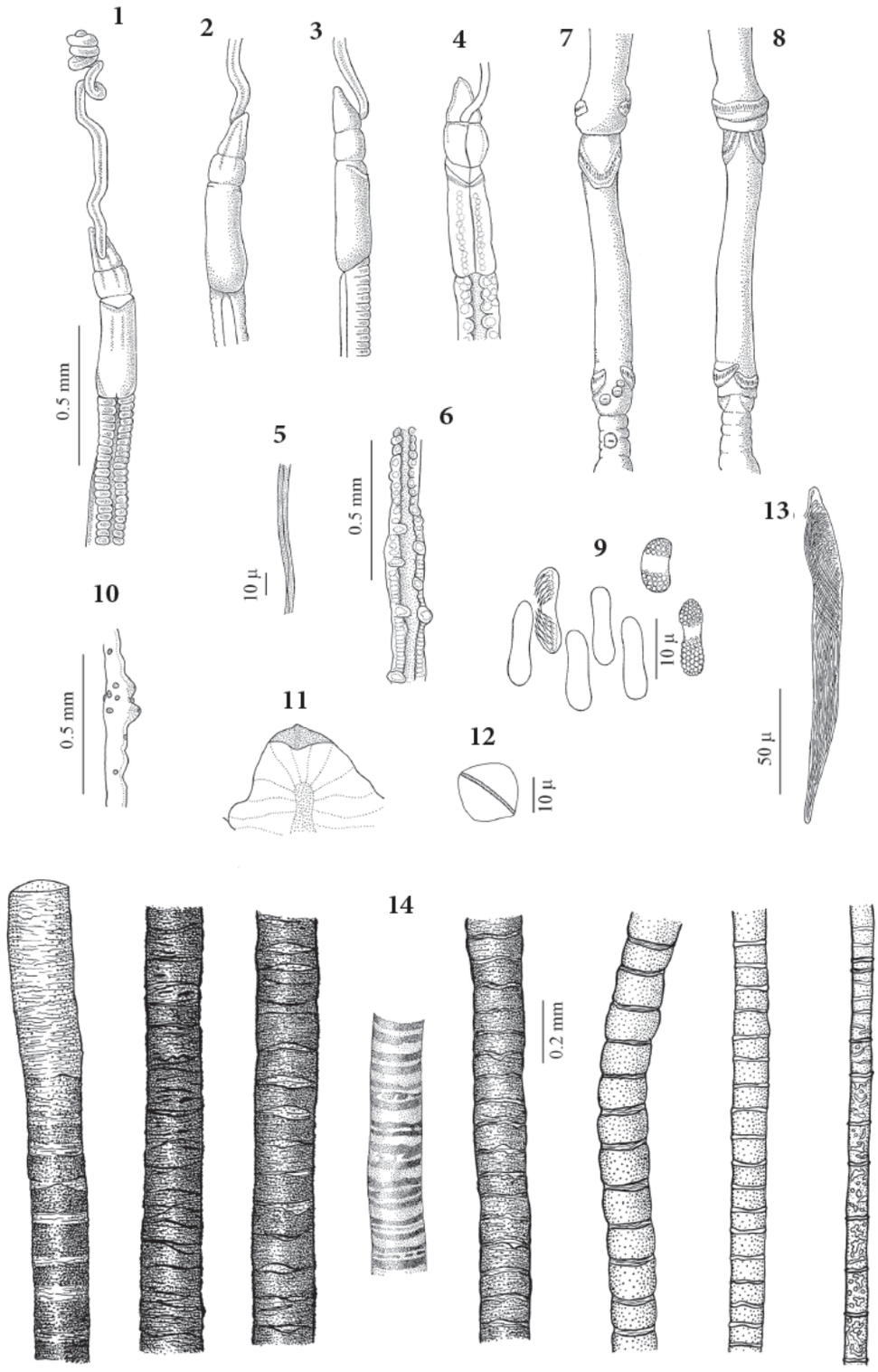

Plate VIII

Figs. 1-14 *Stboglinum hyperboreum* (Ivanov, 1960)

(1, 4: forepart, tentacle, and anterior region of trunk, dorsal view. 2: same, ventral view. 3: same, lateral view. 5: section of bridle. 6: transition zone between metameric and non-metameric section of trunk, dorsal view. 7: annular region, dorsal view. 8: annular region, ventral view. 9: portion of annulus. 10: post-annular metamere, lateral view. 11: post-annular papilla. 12: cuticular plaque from post-annular papilla. 13: spermatophore. 14: successive sections of the tube.)

(Figs. 1-3, 5, 7-9, 13, 14 from Ivanov 1960; Figs. 4, 6, 10-12, 14 from Smirnov 1999.)

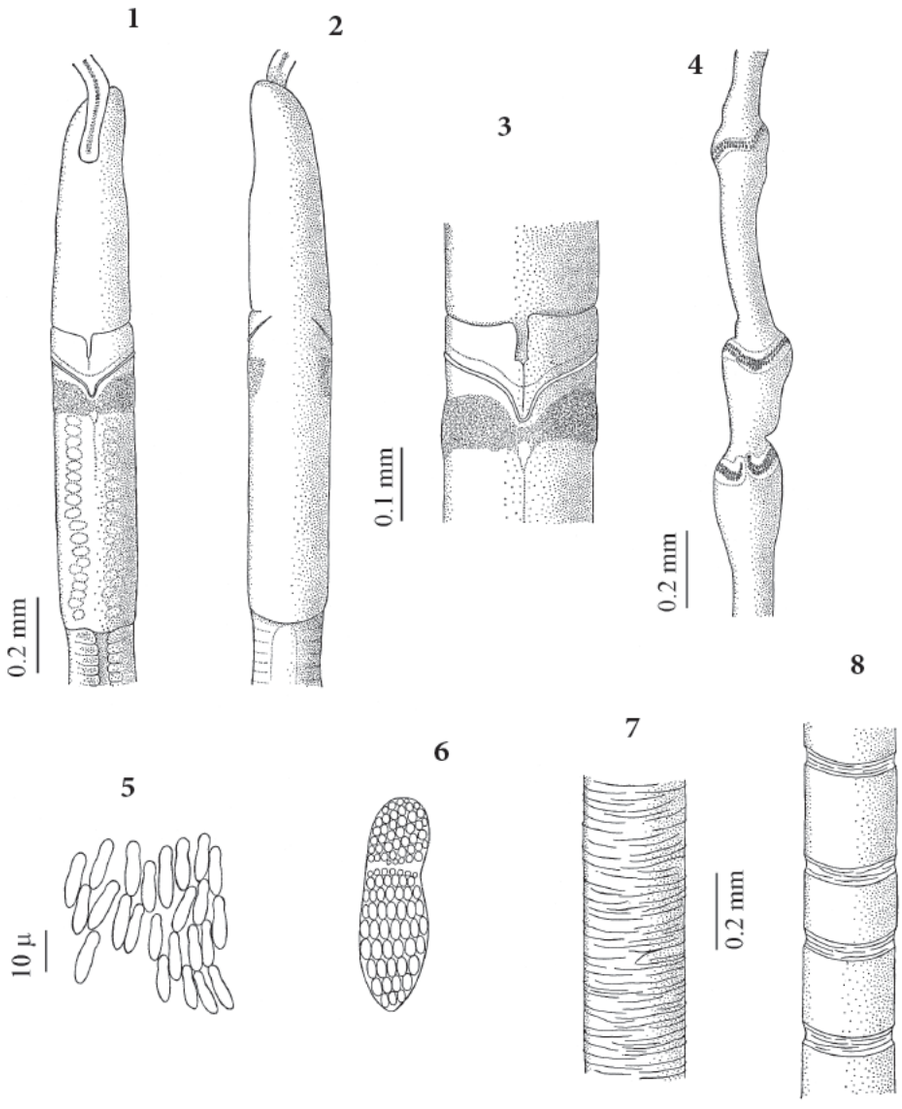

Plate IX

Figs. 1-8 *Siboglinum norvegicum* (Ivanov, 1960)

(1: forepart, dorsal view. 2: forepart, ventral view. 3: bridle region, dorsal view. 4: girdle region, dorsal view. 5: portion of annulus. 6: head of seta from annulus. 7: anterior section of tube. 8: middle section of tube.)

(Figs. 1-8 from Ivanov 1960.)

Phylum Echiura

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The phylum Echiura refers to marine animals, with the exception of a few species inhabiting brackish waters. Echiurans (about 160 species) are characterized by a broad geographic and depth distribution. They inhabit tropical, temperate, and polar waters, and are seen from the littoral zone to the ultra-abyssal zone, reaching depths of 10,000 m.

Some species reach large sizes, to 300 mm. These soft-bodied animals prefer sheltered areas, where they live in burrows. Some species make U-shaped burrows in sand or mud, while others use burrows made by other animals. With rare exceptions echiurans are deposit-feeders. They collect sand, mud, detritus, etc., using a long scoop-shaped, spade-shaped, or spoon-shaped proboscis. Echiurans are eaten by some fishes, particularly flatfishes, as well as by walruses and seals (Gay 1854, Zachs 1933, Murina and Chernyshev 2008). Some species are used as bait in Japan and Korea.

Echiurans are non-segmented, bilaterally symmetrical coelomates. The body (trunk) of echiurans is muscular, sac-like, cylindrical, or in some species ribbon-shaped. The muscular proboscis (cephalic lobe) that is usually capable of great extension, is located on the anterior end of the body near the mouth. In some species of the family Bonellidae, the anterior portion of the proboscis is divided, forming two short or long arms (Pl. I, Fig. 1). In contrast to the sipunculans, the proboscis is never withdrawn into the body. A ciliated groove is usually present on the ventral surface of the proboscis. Many echiurans have a pair of hooklike structures on the ventral surface of the body behind the mouth (ventral setae). One or two rings of anal setae are present on the posterior region of the body of some genera (Pl. 2, Fig. 1). The long digestive tract has numerous pleats and coils in the body cavity. The digestive tract consists of a foregut that is divided into a pharynx, esophagus, gizzard (a short muscular section of the foregut), and stomach or crop; a midgut; and a hindgut (cloaca). A siphon or tube is associated with the midgut for a considerable part of its length. The main organ of excretion is a pair of anal vesicles, which discharge their products into the cloaca. The anal vesicles can be shaped like blind sacs or bladders, bushy, or treelike, sometimes with dendroid outgrowths (Pl. I, Fig. 3; Pl. II, Figs. 2, 3). Their surface usually bears numerous ciliated funnels. The shape of the anal vesicles is an important taxonomic character. The anus is located at the posterior end of the body. The body cavity contains from one genital nephridium to several hundred genital nephridia. The outside opening of the nephridium is called a nephridiopore; farther inside is the nephrostome. The nephridia serve as temporary reservoirs for storage and discharge of eggs and sperm. The closed circulatory system consists of dorsal, ventral, and neuro-intestinal blood vessels. The nervous system lacks ganglia. A ventral nerve cord and pharyngeal nerve ring are present. Gonads are diffuse and occur in a mesentery over the ventral nerve cord or near the cloaca.

The animals are dioecious. There are no differences between males and females in species of the families Echiuridae and Urechidae; fertilization is external. Species of the family Bonellidae are characterized by very distinct sexual dimorphism. The females are large, and dwarf planarian-like males occur on or in the body cavity of the females; fertilization is internal in the nephridia. The eggs undergo spiral cleavage, forming pelagic trochophore larvae.

The phyletic status of the group was established by Newby (1940) and was accepted by many zoologists. However, some authors argue that echiurans definitely are annelids with completely reduced segmentation. Molecular investigations also indicate that echiurans are related to annelids (see “systematic position” in

Murina and Chernyshev 2008). According to the classification of Nishikawa (2002), the phylum Echiura includes two orders: the order Echiuroinea Bock, 1942, with two families (Echiuridae and Bonellidae) and the order Xenopneusta Fisher, 1946, with one family (Urechidae). Only two species in the order Echiuroinea are found in the Arctic.

Key to orders of the phylum Echiura

1(2) Posterior thin-walled portion of gut is widened and serves as a respiratory organ; cloaca functions as pump. Proboscis short, reduced to slightly pointed conical lobe, never breaking off during fixation. Ventral and anal setae present . . . . . **Xenopneusta**

2(1) Posterior portion of gut not modified into a respiratory organ; cloaca not modified. Proboscis normally developed, may break off during fixation. Ventral and anal setae present or absent . . . . . **Echiuroinea**

Key to families, genera, and species of the order Echiuroinea

1(2) Species with marked sexual dimorphism. Proboscis of females simple or divided; one to three nephridia present; usually two ventral setae present, or they are absent; anal setae absent; anal vesicles usually branched. Male usually small, degenerate, and parasitic on or in female. . . . . **Bonellidae, genus *Hamingia, H. arctica* (Danielssen et Koren, 1881) (Pl. I)**

Female: Proboscis long and deeply forked at the tip; ventral setae absent; anal vesicles branched; two nephridia present; nephrostome placed basally. Male: Surface ciliated; ventral setae present.

Length to 120 mm.
Bipolar. Barents Sea (Murmansk coast), Laptev Sea, Chukchi Sea, Point Barrow.
Depth 65-8035 m.
Eurybathic, on silty sediments.

2(1) Species without sexual dimorphism. Proboscis not divided; nephridia usually paired (one to three pairs) or unpaired and numerous; one pair of ventral setae present; anal setae present (genus *Echiurus*) or absent; anal vesicles usually elongate or swollen sacs, lacking branching . . . . . **Echiuridae, genus *Echiurus, E. echiurus echiurus* (Pallas, 1767) (Pl. II)**

Trunk with rings of papillae: 21-23 rings of large papillae alternate with 4-5 rings of small papillae. Proboscis with large papilla on its base. Two goldish ventral setae, curved and flattened. Two rings of anal setae. Two pairs of nephridia. Anal vesicles long tubes with many funnels.

Length to 150 mm.
Bipolar. Barents Sea (Kola Bay), Chukchi Sea.
Usually sublittoral on silty sand with gravel, aleurites, or sandy silts.

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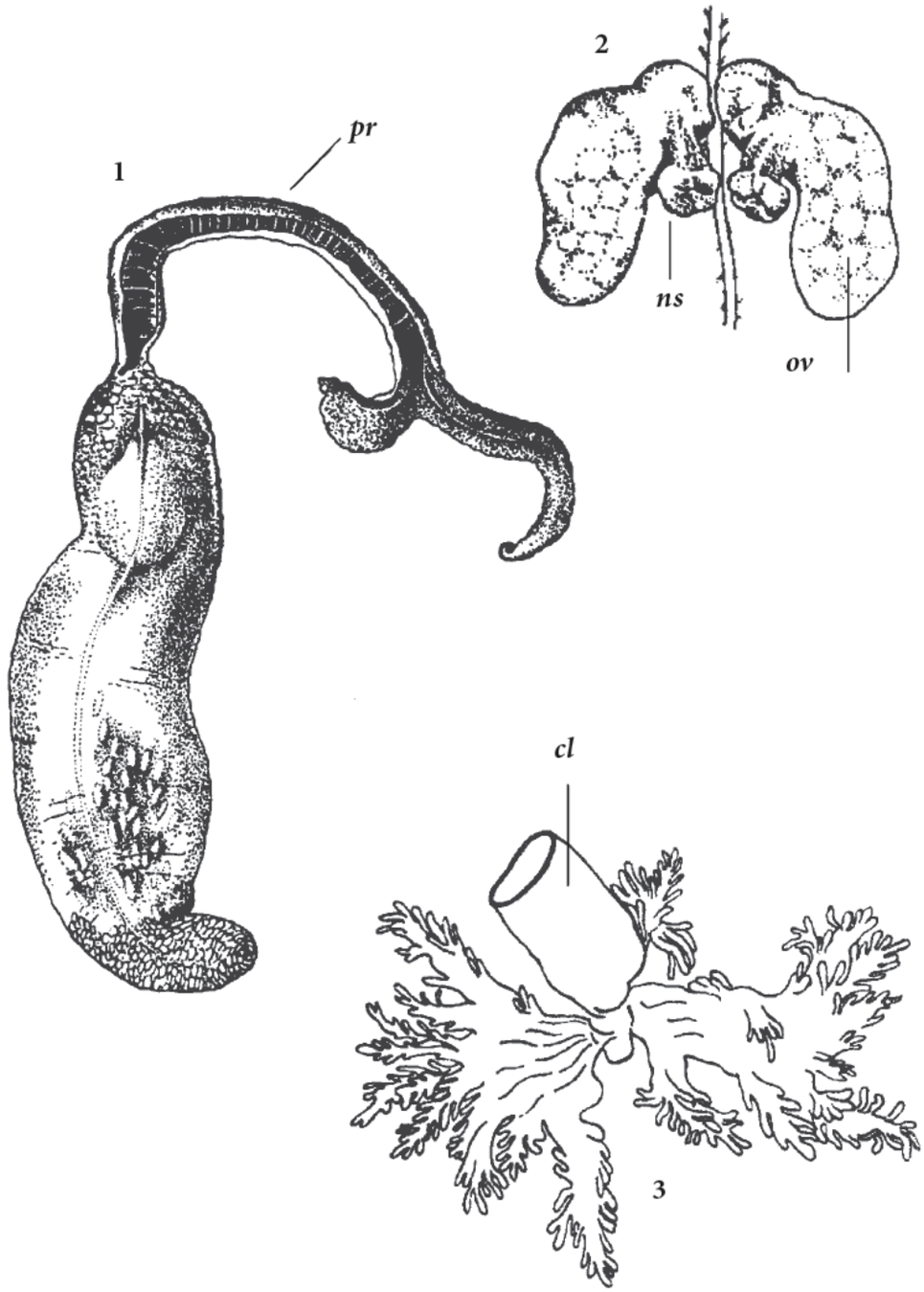

Plate I. ***Hamingia arctica*** **Danielssen et Koren, 1881.**

Fig. 1 Entire animal, ventral view of female; *pr*: proboscis.
Fig. 2 Nephridia, showing basal nephrostome and eggs. *ns*: nephrostoma. *ov*: eggs.
Fig. 3 Anal vesicles. *cl*: cloaca.

(Figs. 1-3 from Wesenberg-Lund 1934, 1937.)

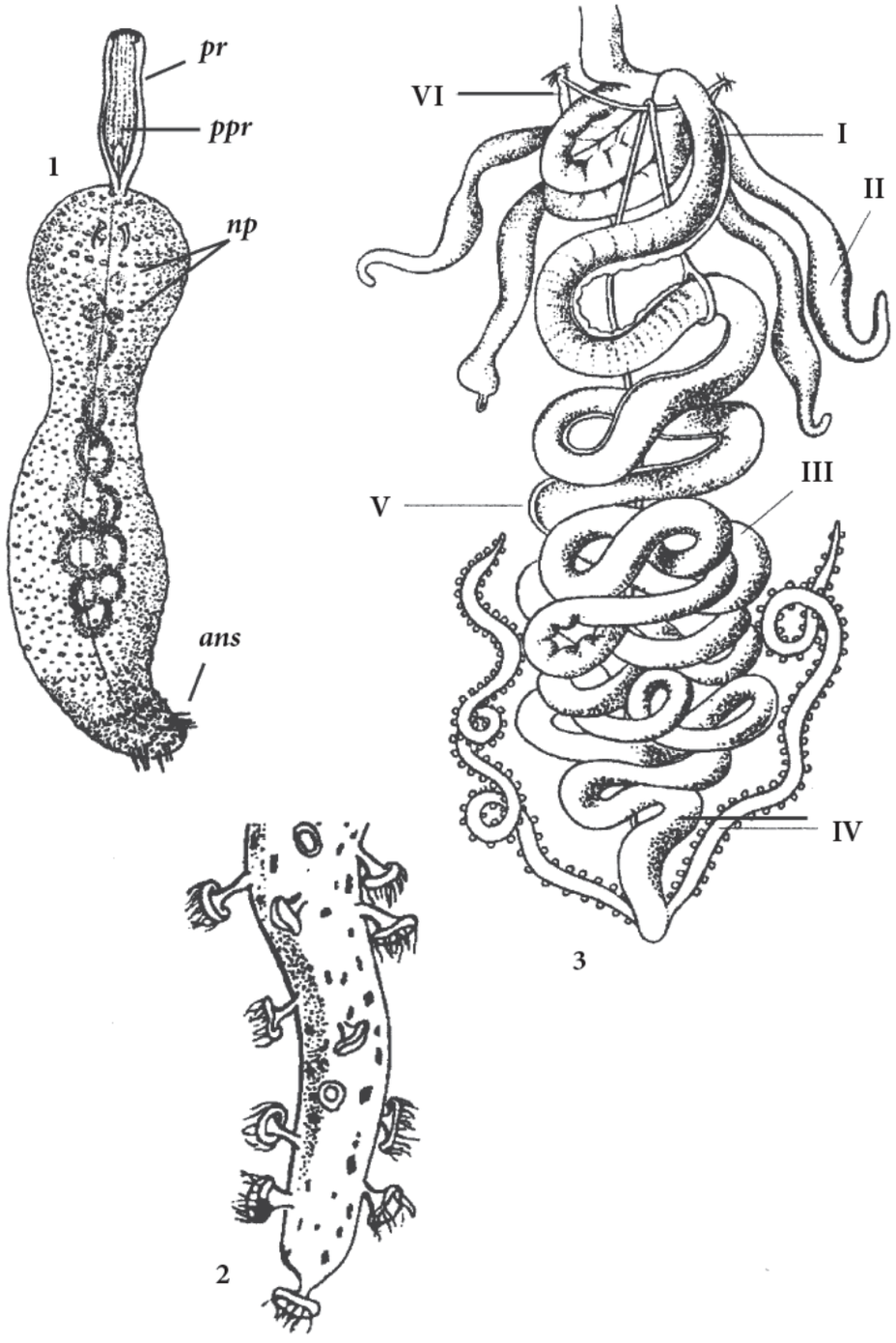

Plate II. ***Echiurus echiurus echiurus*** **(Pallas, 1767).**

Fig. 1 Entire animal, ventral view. *ans*: anal setae. *np*: nephridiopores. *ppr*: papilla of proboscis. *pr*: proboscis.
Fig. 2 Anterior part of anal vesicle.
Fig. 3 Part of dissected specimen. I: dorsal vessel. II: nephridium. III: coils of intestine. IV: anal vesicles. V: siphon. VI: ventral setae.

(Figs. 1-3 from Greef 1879.)

Phylum Sipuncula

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Sipunculans are exclusively marine benthic animals. They inhabit primarily tropical and subtropical waters at all depths from the littoral to 7000 m. They are eaten by actinians, mollusks, crabs, and sea stars, and are an important component in the diets of some benthic feeding fish, including commercially important fish as cod, plaice, and haddock. *Golfingia margaritacea* forms large populations, which can reach a biomass of 65 g per m^2 and 132 g per m^2 (more than 50% of the total benthic biomass) in the central Barents Sea and northwestern Chukchi Sea, respectively. Human consumption of large species (length 200-300 mm) of the genera *Sipunculus*, *Siphonosoma*, and *Phascolosoma* is reported from China, Japan, and the Indo-Malaysian archipelago.

With rare exceptions, sipunculans are detritus feeders. The exception consists of seston feeders of the genus *Themiste*, which have a well developed crown of tentacles. Sipunculans inhabit sediments of various types, primarily silt and sand. Some species find refuge in dead corals or use empty mollusk shells, polychaete tubes, and foraminiferan shells as habitat. Although soft-bodied, sipunculans are able to bore into hard rock, thus playing an important role in the destruction of limestone and coral reefs. The phylum includes two classes, six families, 17 genera, 166 species, and 18 subspecies (Cutler 1994). Sipunculans reported from the Arctic Ocean belong to one class, the Sipunculidea.

Sipunculans are non-segmented, coelomate, protostome worms. The body usually consists of a sac-like or cylindrical trunk and an introvert (or proboscis) that can be markedly extended. The mouth is located on the anterior end of the introvert, and it is usually completely or partly surrounded by tentacles of different shapes. The tentacular system in a few species may be reduced to a few lobes, or may be absent and replaced by an oral disk. Hooks or spines can be present on the anterior end of the introvert. The skin of the introvert and body may have papillae or tubercles. The introvert can be withdrawn into the body using one to four retractor muscles (two ventral and two dorsal). Retractor muscles in some species may be attached to longitudinal muscles by one or several roots. On the trunk of most *Phascolion* species there is a zone of papillae with hardened horny rims, which serve to anchor the worm in the shell of mollusks or in the tube of polychaetes. The digestive system consists of an esophagus, a spiraling midgut, and a rectum with circular muscles. The anus is located in the anterior section of the trunk near the base of the introvert. A pair of simple, saclike nephridia lie in the body cavity and exit via nephridial pores near the anus. Some genera have only one nephridium. A pair of cerebral ganglia form the brain, which connects to the ventral nerve cord via circum-enteric connectives.

Sipunculans are dioecious, but lack sexual dimorphism. The gonads develop near the base of the ventral retractor muscles. Asexual reproduction has been described in two species and hermaphroditism in one species (*Nephasoma minutum*, synonym *N. diaphanes*). Development is variable: direct (without larvae); with trochophore larvae, which transform into a lecithotrophic pelagosphere; and development with trochophores followed by a planktotrophic pelagosphere.

Key to families of the class Sipunculidea

1(2) One nephridium present . . . . . **Phascolionidae**

2(1) Two nephridia present . . . . . **Golfingiidae**

Key to genera of the family Golfingiidae

1(2) Four introvert retractor muscles present . . . . . **genus *Golfingia***

2(1) Two introvert retractor muscles present . . . . . **genus *Nephasoma***

Key to species of the genus *Golfingia*

1(2) Hooks absent from the introvert . . . . . ***G. margaritacea* (Sars, 1851) (Pl. I)**

Length to 60 mm, sometimes to 150 mm.

Panoceanic. In all arctic seas.
Usually littoral and upper sublittoral, rare in abyssal depths.
Eurybathic, on varying sediment types.

2(1) Hooks present on the introvert.

3(4) Hooks distributed in rings . . . . . ***G. elongata* (Keferstein, 1863) (Pl. II)**

Length to 90 mm.
Barents and Chukchi seas.
Usually sublittoral, on sand, shells, and gravel.

4(3) Hooks randomly scattered on introvert. . . . . ***G. vulgaris vulgaris* (de Blainville, 1827) (Pl. III)**

Length to 50 mm.
In all arctic seas and central Arctic Basin.
Abyssal depths below 5000 m. Eurybathic on sand and silty sand.

Key to species of the genus *Nephasoma*

1(2) Posterior end of the body drawn out into a caudal appendage. Large bladder-like papillae cover body anterior to the caudal appendage . . . . . ***N. flagriferum* (Selenka, 1885) (Pl. VII, Figs. 1, 2)**

Length to 85 mm.
Panoceanic. Barents Sea.
On silty sediments.

2(1) Posterior end of body lacking a caudal appendage; bladder-like papillae absent.

3(4) Hooks on the introvert absent. Wall of the trunk rough with transverse furrows. . . . . ***N. eremita* (Sars, 1851) (Pl. VI)**

Length to 60 mm.
Possibly bipolar. Barents, Kara, and Chukchi seas.
Sublittoral, upper bathyal. On sediments predominantly made of sand.

4(3) Hooks on introvert present. Body wall smooth.

5(6) Hooks distributed in more or less distinct rings, tentacles well developed . . . . . ***N. abyssorum abyssorum* (Koren et Danielssen, 1875) (Pl. IV)**

Length to 30 mm.
Boreal Arctic. Central Arctic Basin and all marginal arctic seas except the East Siberian Sea.
Sublittoral to upper bathyal, rarely abyssal below 5000 m depth. On silty sediments.

6(5) Hooks randomly scattered, tentacles reduced to several lobes.

7(8) Body rod-shaped, length usually exceeds width by not more than 8 times; body wall not transparent . . . . . ***N. minutum* Keferstein, 1862 (Pl. V)**

Synonymy: *N. diaphanes* (Gerould, 1913) (see Murina and Sørensen 2004).
Length to 15 mm.
Panoceanic. Central Arctic Basin and all seas of the Arctic Ocean except the East Siberian Sea.
Eurybathic, on soft sediments, silt, or clay.

8(7) Body thread-like, length exceeds width by 9-30 times; body wall semitransparent . . . . . ***N. lilljeborgi* (Danielssen et Koren, 1880) (Pl. VII, Figs. 3-7)**

Synonymy: *N. glacialis* (Koren et Danielssen, 1881).
Length to 30 mm.
Boreal Arctic. In all marginal seas of the Arctic Ocean and the central Arctic Basin, Baffin Bay.
Eurybathic, predominantly in the sublittoral and bathyal zones on silty sediments. In the Chukchi Sea it is found in tubes of polychaetes of the genus *Spiochaetopterus.*

Key to genera of the family Phascolionidae

1(2) Anus usually at the anterior end of the trunk; epidermal attachment papillae usually present; one or two retractor muscles of the introvert with two or four roots; hooks often present . . . . . ***Phascolion***

2(1) Anus located at the distal half of the introvert; epidermal attachment papillae absent; retractor muscle for the introvert in the shape of a single column, lacking distention into separate roots; hooks absent . . . . . ***Onchensoma***

Key to subgenera and species of the genus *Phascolion*

1(2) Ventral retractor muscle much thicker than dorsal; broad dark zone of papillae present in posterior half of trunk; horny protein layer of attached papillae well developed. . . . . ***P.* (*Phascolion*) Théel, 1875. *P.* (*Phascolion*) *strombus strombus* (Montagu, 1804) (Pl. VIII)**

Length 30 mm.
Panoceanic. Arctic circumpolar, in all arctic seas and in central Arctic Basin.
Usually sublittoral on sediments with a predominance of sand. Inhabits polychaete tubes and foraminiferan and mollusk shells.

2(1) Dorsal and ventral retractor muscles for introvert of the same size; no dark band of attached papillae; horny protein layer of attached papillae weakly developed or absent. . . ***P.* (*Isomya*) E. Cutler et N. Cutler, 1985. *P.* (*Isomya*) *tuberculosum* Théel, 1875 (Pl. IX)**

Length to 30 mm.
Boreal Arctic. Reported from the Barents Sea.
Predominantly sublittoral on sandy sediments, often in the shells of scaphopods.

Key to species of the genus *Onchnesoma*

1(2) Introvert with 6-10 tentacles. Entire trunk covered with large scale-like papillae . . . . . ***O. squamatum squamatum* (Koren et Danielssen, 1875) (Pl. X)**

Length to 10 mm.
Atlantic high boreal. Reported from the southwestern Barents Sea.
Sublittoral on sediments of various types.

2(1) Oral disk present, tentacles absent. Large scale-like papillae absent . . . . . ***O. steenstrupii steenstrupii* Koren et Danielssen, 1875 (Pl. XI)**

Length to 5 mm.
Panoceanic. Southwestern Barents Sea.
Usually sublittoral and upper bathyal, rarely 2100-3000 m.
On silt, sand, and shell sediments.

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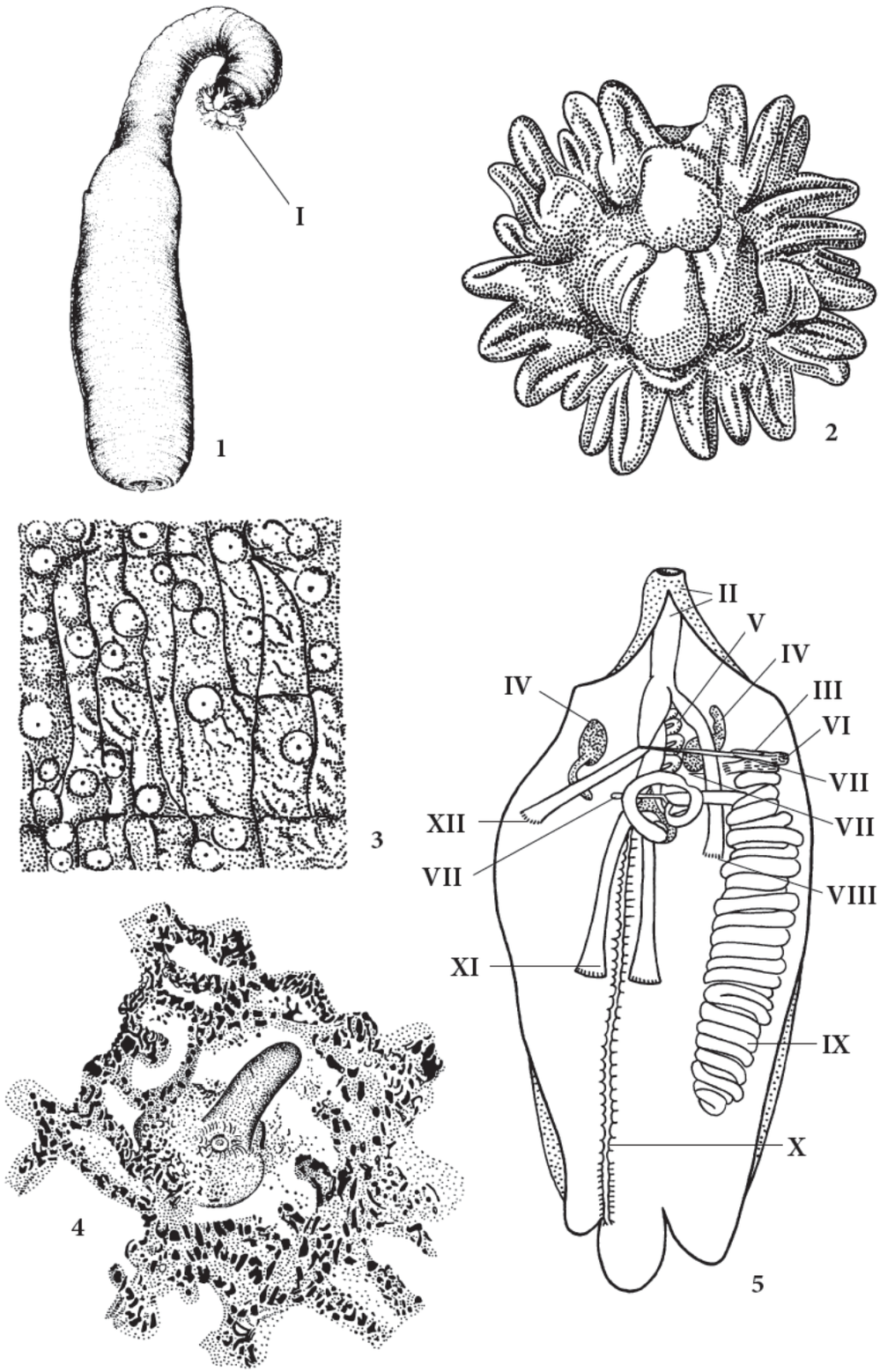

Plate I. ***Golfingia margaritacea margaritacea*** **(Sars, 1851)**

Fig. 1 External view. I: mouth.
Fig. 2 Tentacular crown.
Fig. 3 Section of the skin of the posterior end of the trunk.
Fig. 4 Dermal papilla at high magnification.
Fig. 5 Anatomy. II: introvert. III: anus. IV: nephridium. V: esophagus. VI: winglike muscles. VII: fixing muscle. VIII: gonads near the base of the retractor muscles. IX: spiral and/or looped intestine. X: ventral nerve cord. XI: ventral introvert retractor. XII: dorsal introvert retractor.

(Fig. 1 from Cutler 1994; Figs. 2, 3, 5 from Théel 1905; Fig. 4 from Wesenberg-Lund 1930.)

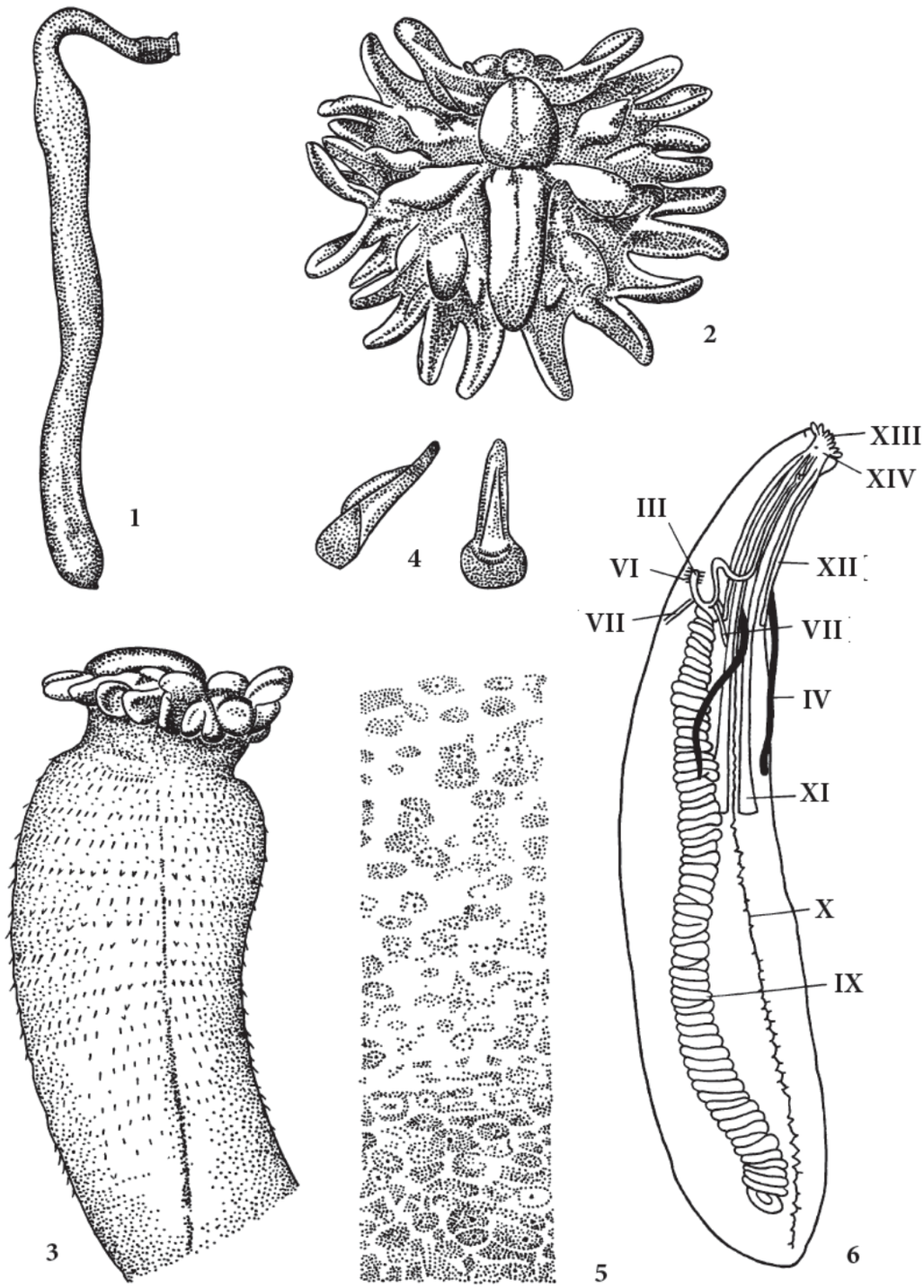

Plate II. ***Golfingia elongata*** **(Keferstein, 1862)**

Fig. 1 External view.
Fig. 2 Tentacular crown.
Fig. 3 Anterior portion of introvert with tentacles and rows (rings) of hooks.
Fig. 4 Introvert hook.
Fig. 5 Section of skin from the posterior end of the trunk.
Fig. 6 Anatomy. III: anus. IV: nephridium. VI: winglike muscles. VII: fixing muscle. IX: spiral and/or looped intestine. X: ventral nerve cord. XI: ventral introvert retractor. XII: dorsal introvert retractor. XIII: introvert tentacles. XIV: eyespots.

(Figs. 1-5 from Théel 1905; Fig. 6 from Keferstein 1865.)

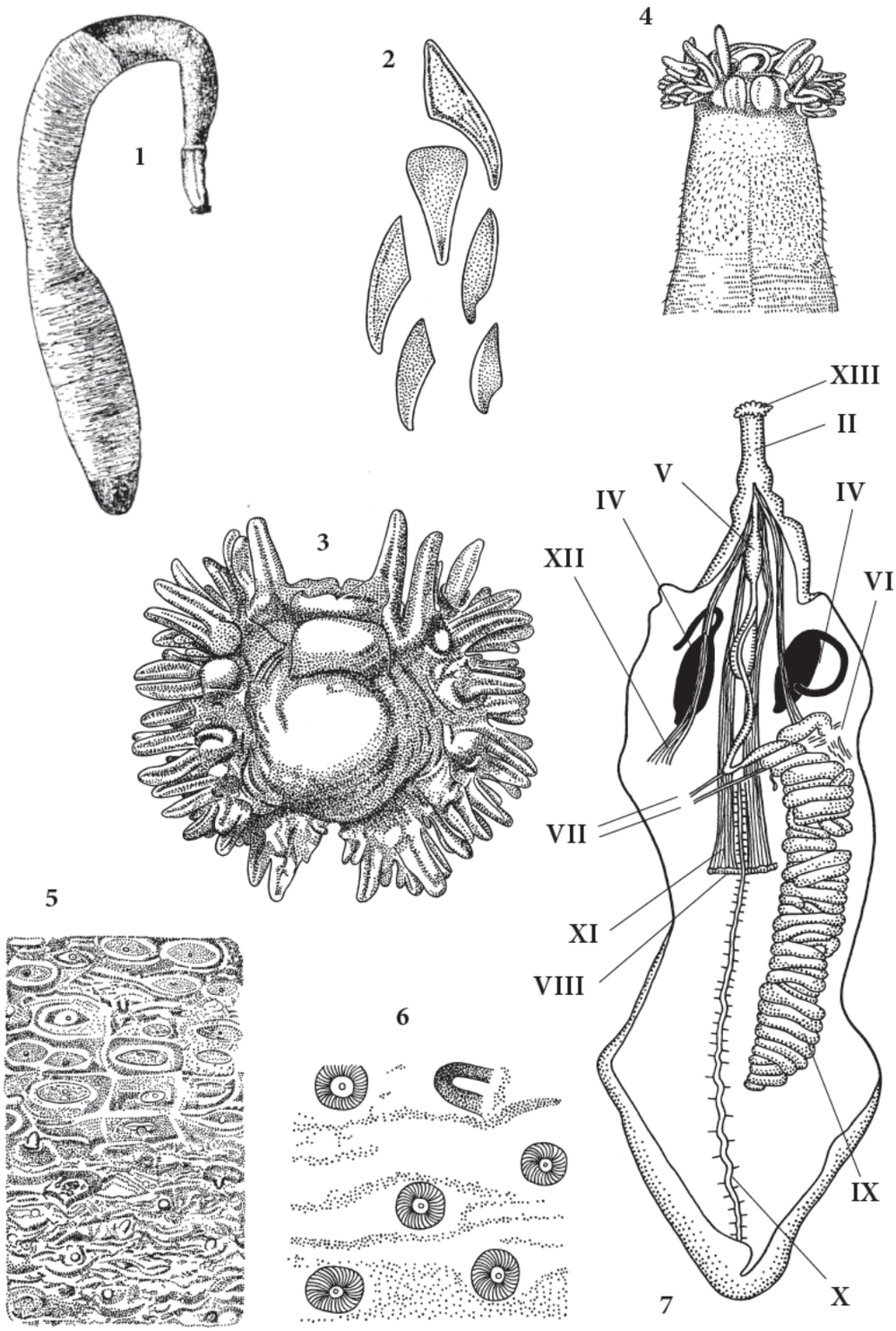

Plate III. ***Golfingia vulgaris vulgaris*** **(Blainville, 1827)**

Fig. 1 External view.
Fig. 2 Introvert hook.
Fig. 3 Tentacular crown.
Fig. 4 Anterior section of the introvert with tentacles and hooks.
Fig. 5 Section of the body wall of the posterior half of the trunk.
Fig. 6 Trunk papillae at high magnification.
Fig. 7 Anatomy. II: introvert. IV: nephridium. V: esophagus. VI: winglike muscles. VII: fixing muscle. VIII: gonads near the base of the retractor muscles. IX: spiral and/or looped intestine. X: ventral nerve cord. XI: ventral introvert retractor. XII: dorsal introvert retractor. XIII: introvert tentacles.

(Figs. 1-5, 7 from Théel 1905; Fig. 6 from Sato 1939.)

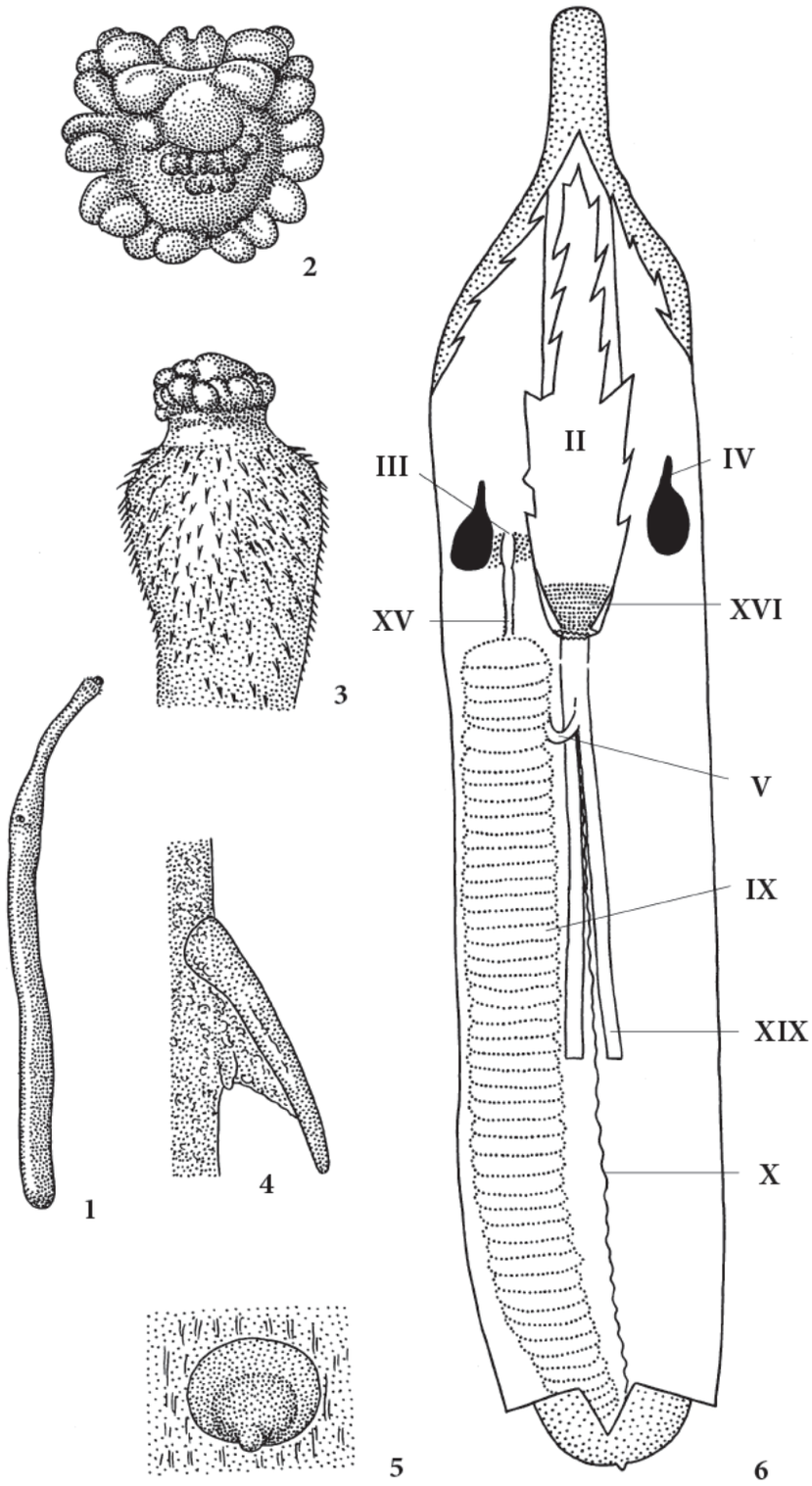

Plate IV. ***Nephasoma abyssorum abyssorum*** **(Koren et Danielssen, 1875)**

Fig. 1 External view.
Fig. 2 Tentacular crown.
Fig. 3 Anterior part of the introvert with tentacles and hooks.
Fig. 4 Introvert hook at high magnification.
Fig. 5 Dermal papilla from the trunk surface at high magnification.
Fig. 6 Anatomy. II: introvert. III: anus. IV: nephridium. V: esophagus. IX: spiral and/or looped intestine. X: ventral nerve cord. XV: rectum. XVI: rows of introvert hooks. XIX: introvert retractor.

(Figs. 1-5 from Théel 1905; Fig. 6 from Murina 1977.)

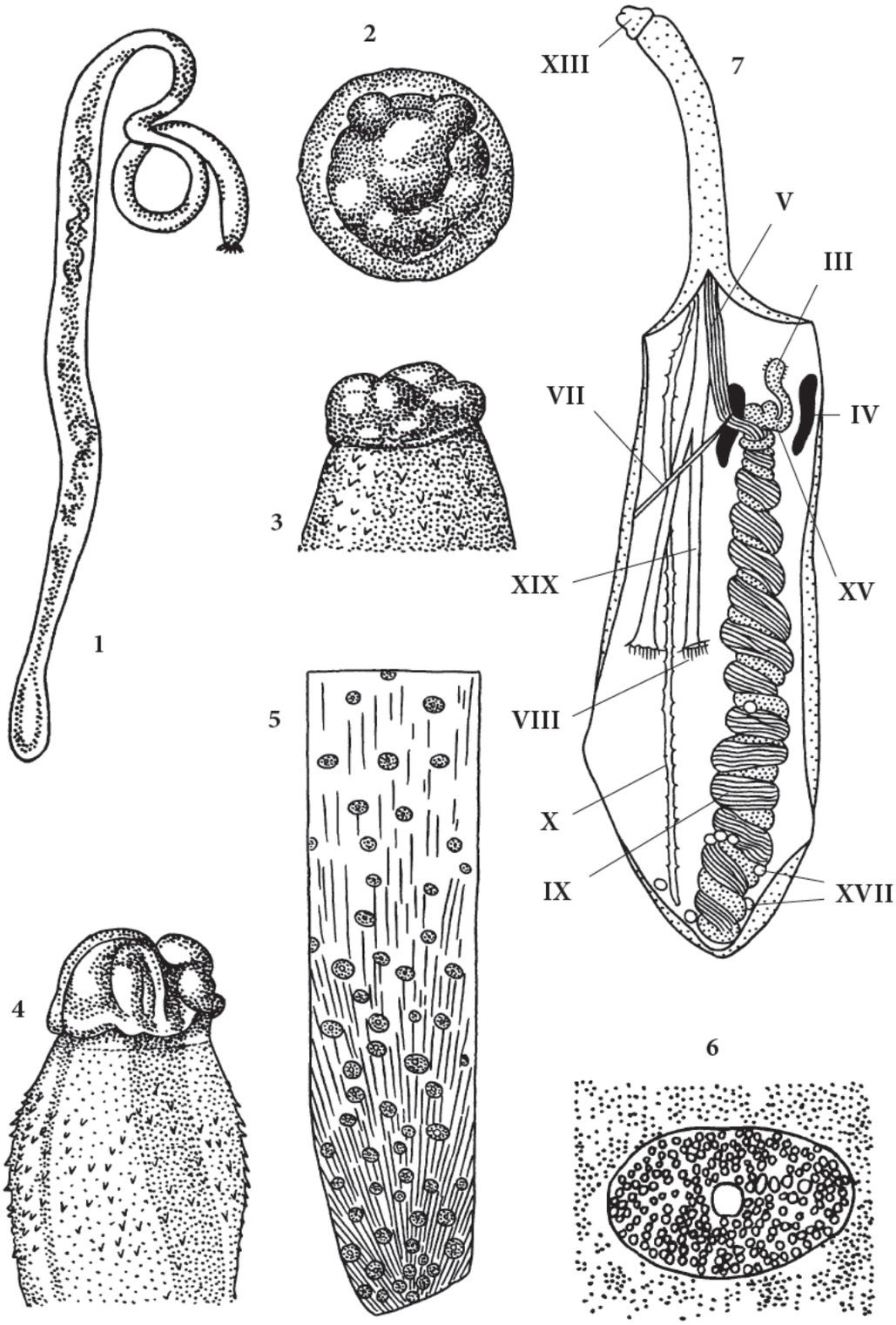

Plate V. ***Nephasoma minutum*** **(Keferstein, 1862). Synonym:** ***N. diaphanes*** **(Gerould, 1913)**

Fig. 1 External view.
Figs. 2-3 Tentacular crown, anterior and lateral view.
Fig. 4 Anterior part of introvert.
Fig. 5 Section of skin from the posterior end of the body.
Fig. 6 Dermal papilla at high magnification.
Fig. 7 Anatomy. III: anus. IV: nephridium. V: esophagus. VII: fixing muscle. VIII: gonads near the base of the retractor muscles. IX: spiral and/or looped intestine. X: ventral nerve cord. XIII: introvert tentacles. XV: rectum. XVII: eggs in the body cavity. XIX: introvert retractor.

(Figs. 1-7 from Théel 1905.)

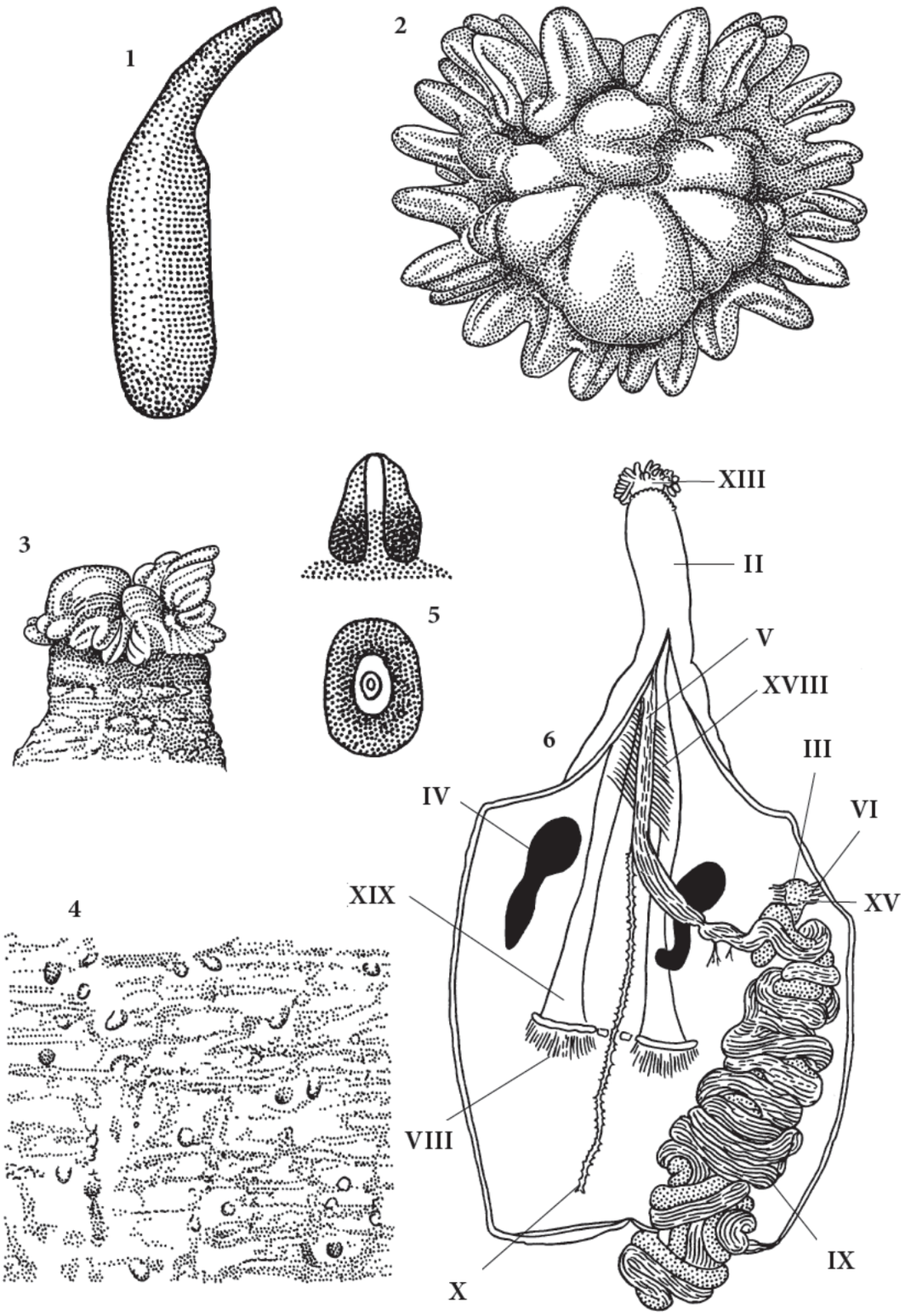

Plate VI. ***Nephasoma eremita*** **(Sars, 1851)**

Fig. 1 External view.
Figs. 2-3 Tentacular crown, anterior and lateral view.
Fig. 4 Skin section from posterior end of body.
Fig. 5 Introvert papillae.
Fig. 6 Anatomy. II: introvert. III: anus. IV: nephridium. V: esophagus. VI: winglike muscles. VIII: gonads near the base of the retractor muscles. IX: spiral and/or looped intestine. X: ventral nerve cord. XIII: introvert tentacles. XV: rectum. XVIII: fixing muscles. XIX: introvert retractor.

(Figs. 1-5 from Théel 1905; Fig. 6 from Selenka et al. 1883.)

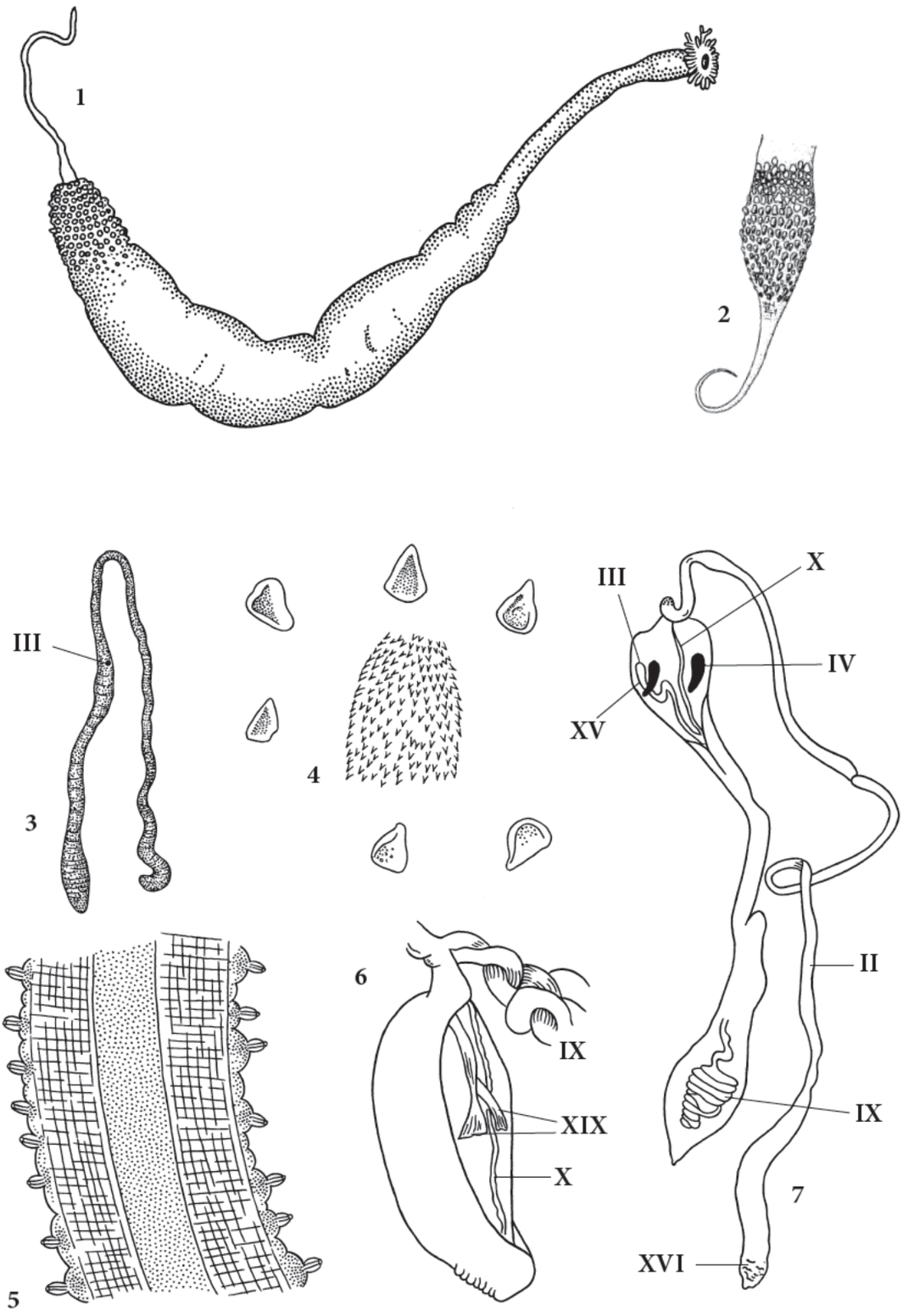

Plate VII

Figs. 1-2 *Nephasoma flagriferum* (Selenka, 1885): 1: external view. 2: posterior end of body with wart-like papillae.
Figs. 3-7 *Nephasoma lilljeborgi* (Danielssen and Koren, 1880). 3: external view. 4: section of the introvert with hooks. 5: section of the introvert with papillae. 6: section of the trunk with origins of retractors. 7: anatomy. II: introvert. III: anus. IV: nephridium. IX: spiral and/or looped intestine. X: ventral nerve cord. XV: rectum. XVI: rows of introvert hooks. XIX: introvert retractor.

(Fig. 1 from Selenka 1885; Fig. 2 from Cutler 1994; Fig. 3 from Wesenberg-Lund 1930; Fig. 4 from Murina 1977; Figs. 5-7 from Wesenberg-Lund 1932.)

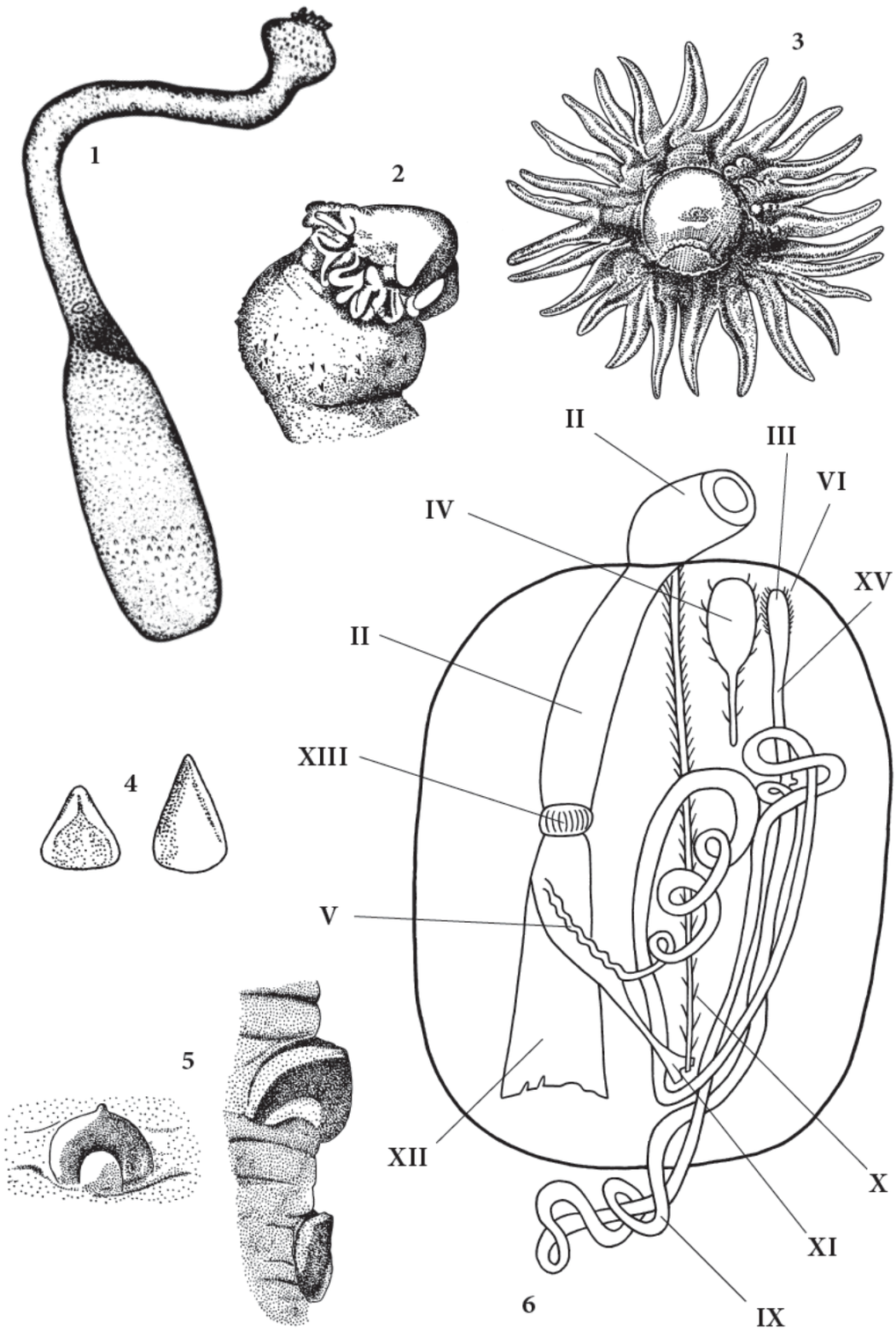

Plate VIII. *Phascolion strombus strombus* Montagu, 1804

Fig. 1 External view.
Fig. 2 Anterior section of introvert with tentacles.
Fig. 3 Tentacular crown.
Fig. 4 Introvert hooks.
Fig. 5 Holdfast papillae at high magnification, anterior and lateral view.
Fig. 6 Anatomy. II: introvert. III: anus. IV: nephridium. V: esophagus. VI: winglike muscles. VII: fixing muscle. IX: spiral and/or looped intestine. X: ventral nerve cord. XI: ventral introvert retractor. XII: dorsal introvert retractor. XIII: introvert tentacles. XV: rectum.

(Fig. 1 original; Figs. 2-5 from Théel 1905; Fig. 6 from Murina 1977.)

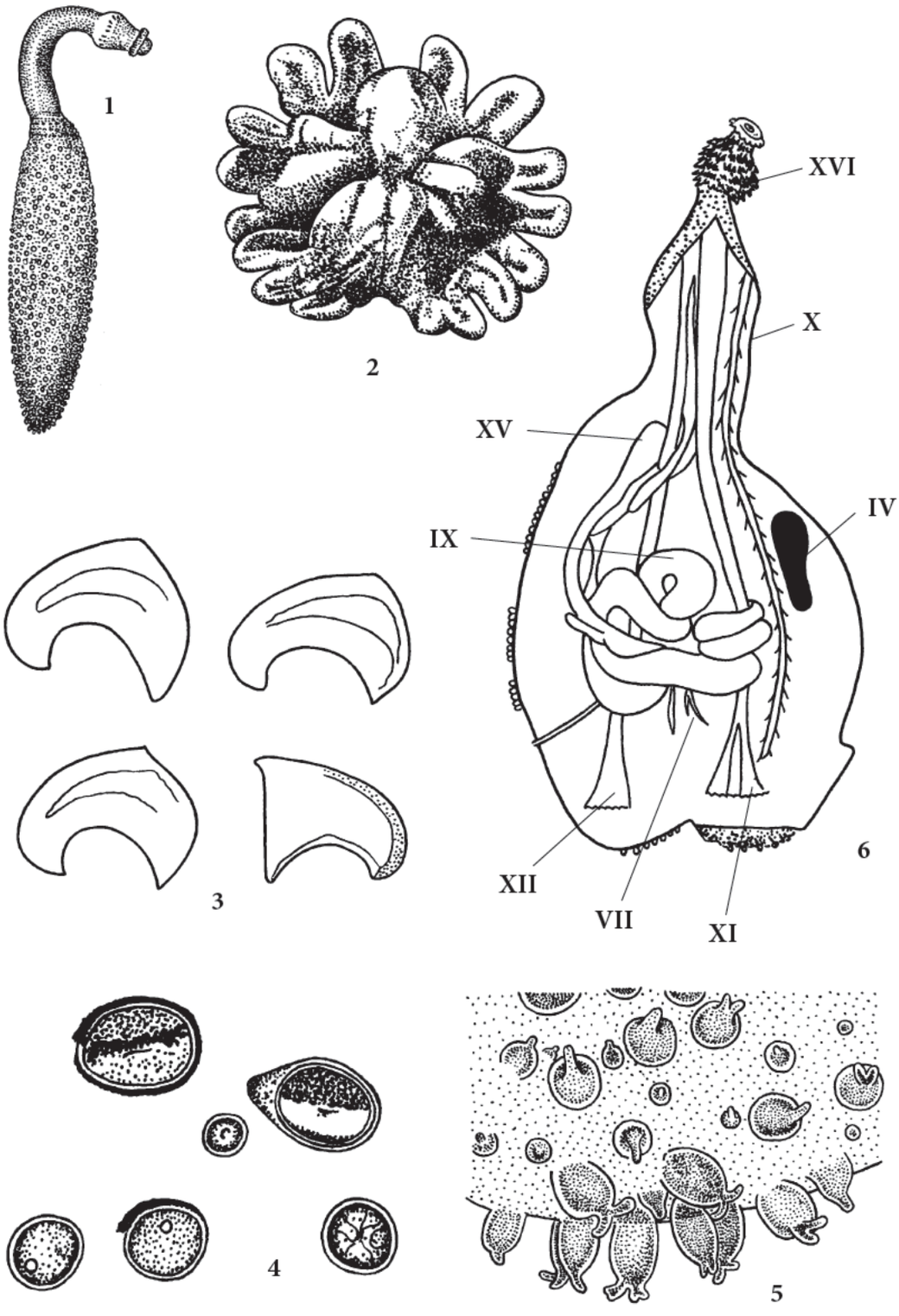

Plate IX. ***Phascolion tuberculosum*** **Théel, 1875**

Fig. 1 External view.
Fig. 2 Tentacular crown.
Fig. 3 Introvert hooks.
Fig. 4 Papillae of the posterior end of the body.
Fig. 5 Holdfast papillae of the posterior end of the body.
Fig. 6 Anatomy. IV: nephridium. VII: fixing muscle. IX: spiral and/or looped intestine. X: ventral nerve cord. XI: ventral introvert retractor. XII: dorsal introvert retractor. XV: rectum. XVI: rows of introvert hooks.

(All from Théel 1905.)

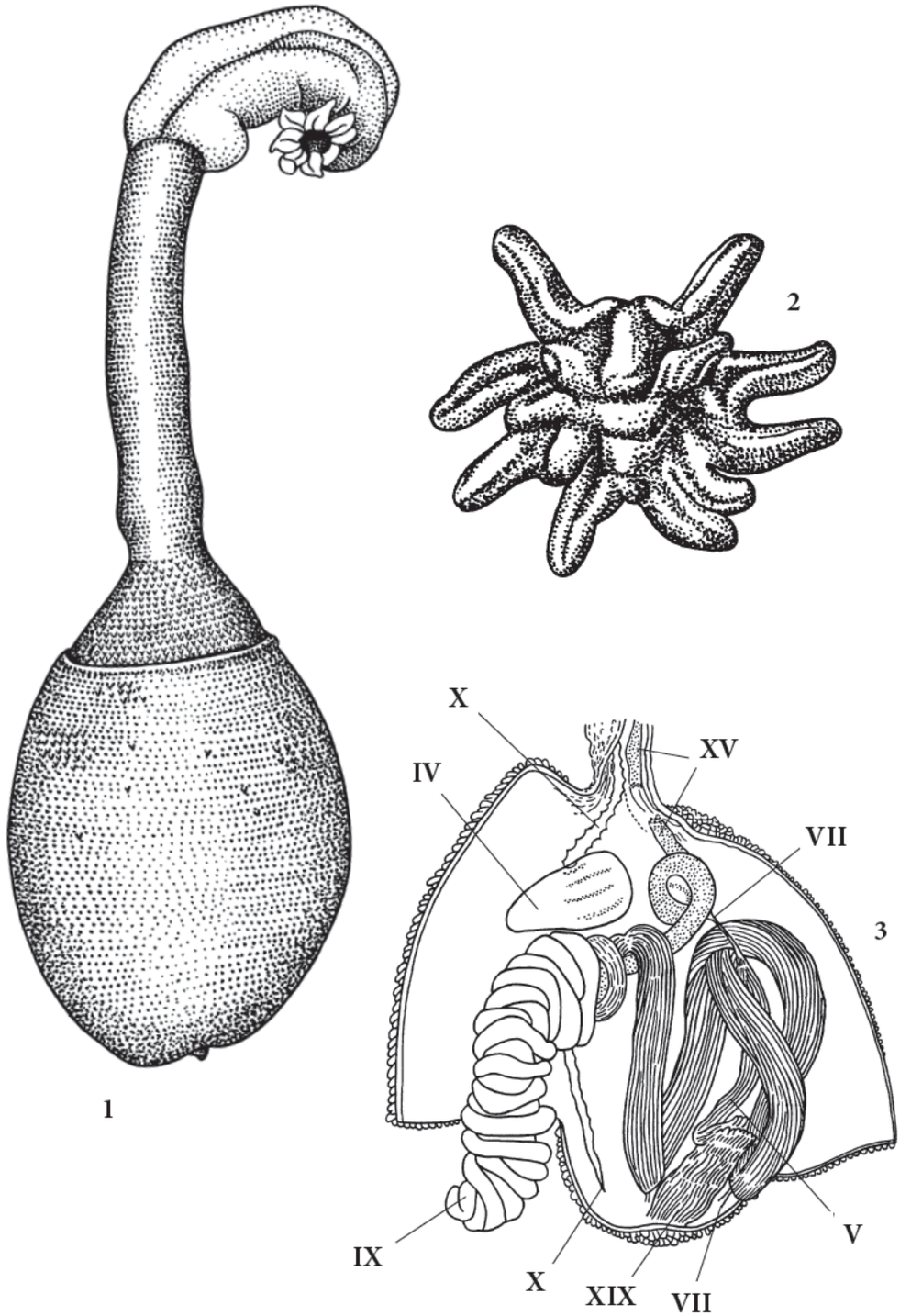

Plate X. ***Onchnesoma squamatum squamatum*** **(Koren and Danielssen, 1875)**

Fig. 1 External view.
Fig. 2 Tentacular crown.
Fig. 3 Anatomy. IV: nephridium. V: esophagus. VII: fixing muscle. IX: spiral and/or looped intestine. X: ventral nerve cord. XV: rectum. XIX: introvert retractor.

(Fig. 1 is original; Figs. 2, 3 from Théel 1905.)

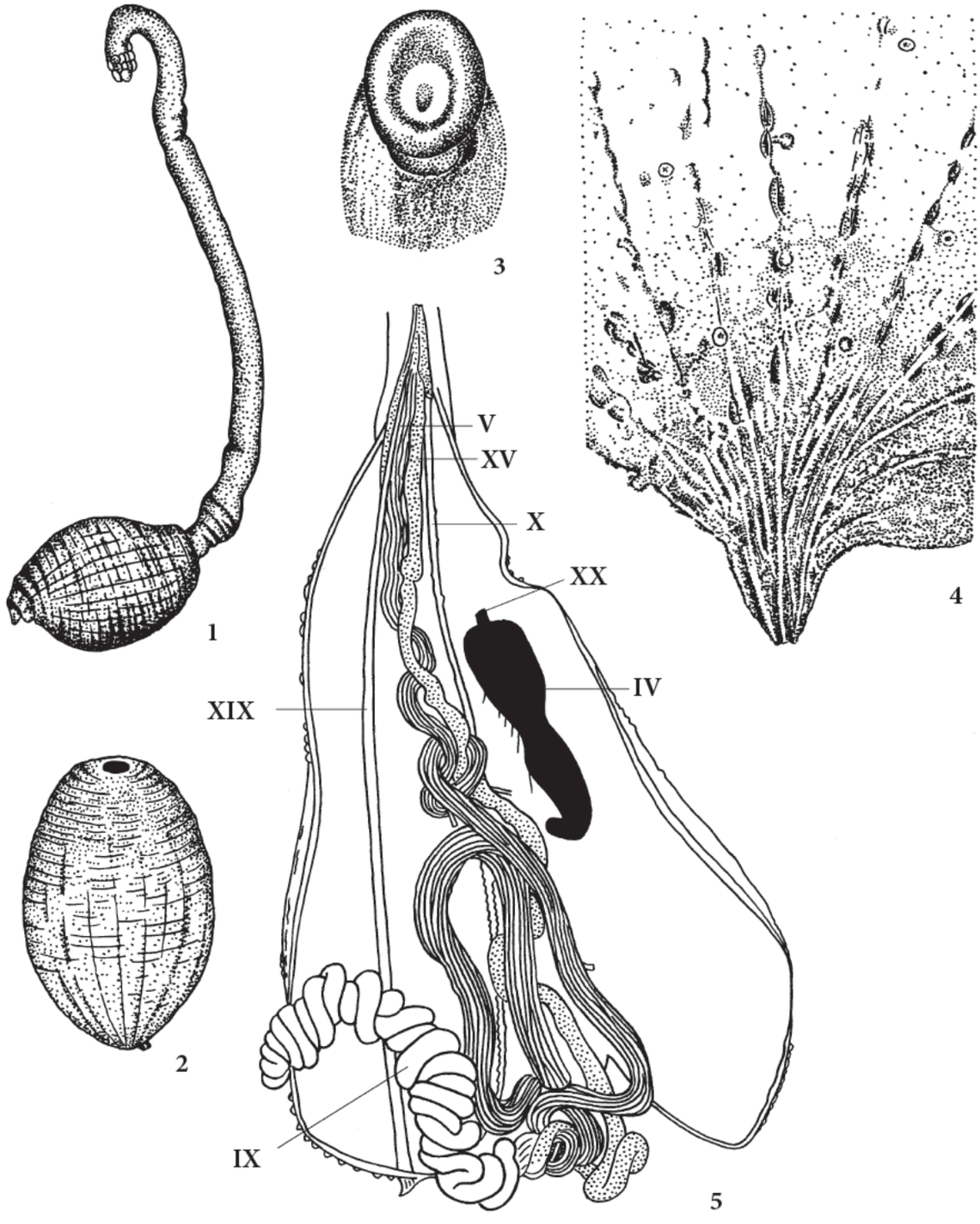

Plate XI. ***Onchnesoma steenstrupii steenstrupii*** **(Koren and Danielssen, 1875)**

Fig. 1 Animal with completely everted introvert.
Fig. 2 Animal with retracted introvert.
Fig. 3 Oral disk.
Fig. 4 Section of the skin from the posterior end of the body.
Fig. 5 Anatomy. IV: nephridium. V: esophagus. IX: spiral and/or looped intestine. X: ventral nerve cord. XV: rectum. XIX: introvert retractor. XX: nephrostome.

(Figs. 1, 2 from Wesenberg-Lund 1930; Figs. 3-5 from Théel 1905.)

Phylum Phoronida

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The phylum Phoronida Hatschek, 1888, consists of a small group of marine worm-like coelomates, with a tentacular extension called the lophophore surrounding the mouth (Pl. I). A similar organ with tentacles is shared with bryozoans and lamp shells (brachiopods), grouped in the Lophophorata (previously sometimes called Tentaculata). The phoronids have a loop-shaped digestive tract, the anus being located close to the mouth (but outside the lophophore). During metamorphosis, the phoronid body occurs through evagination of the ventral wall of the actinotroch larvae, drawing down the gut and a pair of body coelomic cavities into the developing ventral trunk. During this process, the coelomic spaces fold in two, thus forming the lateral mesenteries, but do not reach the back end of the body (Mamkaev 1962).

Phoronids live in slender chitinous tubes embedded in soft substrates or boring in hard substrates (i.e., mollusk shells, barnacle shells, skeletal tubes of ceriantharians, lithothamnionic algae, and rocks). The body length ranges from 3-4 mm to about 50 cm. The lophophore is generally horseshoe-shaped. In large specimens the ends of the horseshoe are coiled and the lophophore becomes a spiral or helicoidal shape depending on the species. In small individuals the lophophore is slightly bent or rounded. The mouth is separated from the anus by an epithelial fold, the epistome, which is located inside the lophophore and runs along the inner row of tentacles. Longitudinal muscle fibers form muscle bundles. The body in cross section is divided into four sectors, in each of which is a certain number of muscle bundles revealed by a "muscle formula" used in taxonomy. The muscle bundles do not reach to the rear end of the body, where the digestive tract loops. This section of the body is often somewhat distended and is referred to as the "end bulb." The nervous system consists of an epidermal diffuse nerve plexus with an agglomeration of nerve cells and branches in the region between the mouth and anus and in the base of the lophophore, and nerves running into the tentacles and along the lateral mesenteries to the rear end of the body as giant nerve fibers (there are two, a right and left fiber, or only one, a left fiber). The excretory system consists of a pair of nephridia, which open to the outside by the nephridiopore near the anus by separate papillae. The inner end consists of a ciliated funnel opening into the coelom. During spawning the nephridia serve as gonoducts. The tubes of the nephridia are variable in shape and are used as taxonomic characters. The tubes are usually U-shaped or V-shaped, and the ciliated funnels sometimes form complex lobes. The circulatory system is closed. It includes longitudinal vessels (one medial and one or two lateral), and transverse connecting vessels and capillaries (including blind capillaries entering the tentacles). Blood flows forward in the medial vessel and backward in the lateral vessel(s).

Phoronids are separated into two genera: *Phoronis* Wright, 1856 (eight species) and *Phoronopsis* Gilchrist, 1907 (four species) within the phylum Phoronida, without class, order, and family. The genus *Phoronopsis* is characterized by the presence of a collar (an epithelial fold beneath the base of the lophophore), which covers the well-developed nerve ring (Pl. I, Figs. 5-6). Only one species, *Phoronis ovalis*, has been recorded in the Arctic Basin.

Phoronis ovalis Wright, 1856 (Pl. II)

Lateral mesenteries are absent. Giant fibers absent. Two lateral vessels. The lophophore is oval or transitional between oval and horseshoe-shaped. The middle tentacles on the anal side of the lophophore are displaced inward (unpublished data of N.N. Shunatova); tentacle numbers are 15-50 (21-30 in White Sea specimens). Tubes are leathery. Body length 3-90 mm (White Sea specimens 3-4 mm). Larvae are simplified, crawling, lecithotrophic.

Barents Sea (unpublished data of N.N. Shunatova, along the north coast of the Kola Peninsula in Dalne-Zelenetskaya Bay on Krechetov Island). Depth 10-17 m.

White Sea, Onezhskiy Bay near the Solovetskiye Islands and Kandalakshsky Bay in the strait between Velikiy and Malyi Eremeevskiy islands (Temereva et al. 2000). Depth 0.5-4 m.

Boring species, inhabiting (in arctic seas) the shells of mollusks (*Modiolus modiolus, Chlamys islandicus*), barnacles (*Balanus balanus* and *B. crenatus*), and calcifications of lithothamnionic algae and rocks.

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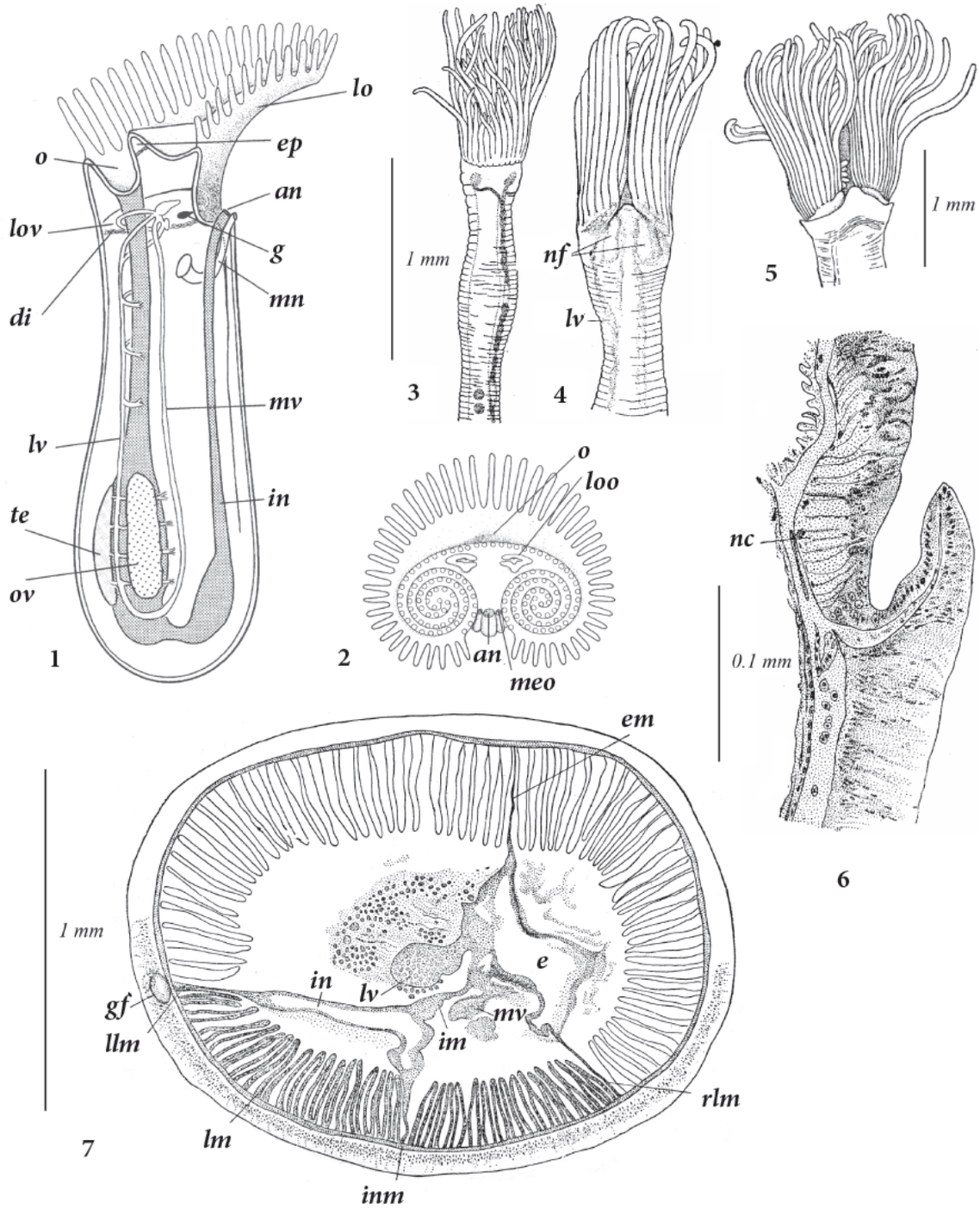
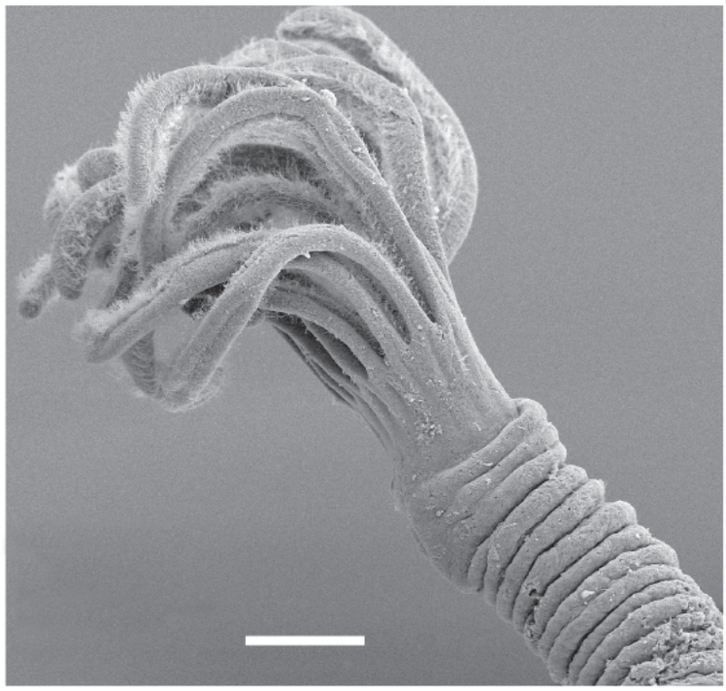


Plate I. Phoronida body structure

Fig. 1 Schematic of a longitudinal section through the body of *Phoronis* with horseshoe-shaped lophophore.
Fig. 2 Schematic illustration of the distal end of the body of a phoronid with a coiled lophophore (inner row of tentacles outlined only).
Figs. 3-4 Distal end of the body with oral (3) and anal (4) view (here *Phoronis muelleri*).
Fig. 5 Front end of the body with the collar characteristic of the genus *Phoronopsis*, view from the anal side (*Phoronopsis harmeri*).
Fig. 6 Collar, covering the nerve ring, longitudinal section (*Phoronopsis harmeri*).
Fig. 7 Cross section through the middle of the body (*Phoronopsis harmeri*).

Abbreviations: *an*: anus. *di*: dissepiments. *e*: esophagus (descending branch of intestine), *em*: esophageal mesentery. *ep*: epistome. *g*: nerve ganglion. *gf*: left giant nerve fiber. *im*: interintestinal mesentery. *in*: intestine (ascending branch of the gut). *mm*: gut mesentery. *llm*: left lateral mesentery. *lm*: longitudinal musculature. *lo*: lophophore. *loo*: lophophore organ. *lov*: lophophore blood vessel. *lv*: lateral blood vessel. *meo*: nephridiopore. *mn*: metanephridia. mv: medial blood vessel. *nc*: nerve ring. *nf*: ascending branches of nephridial canals. *o*: mouth. *ov*: ovary. *rlm*: right lateral mesentery. *te*: testis.

(Figs. 1-2 from Hermann 1996; Figs. 3-7 from Mamkaev 1962.)



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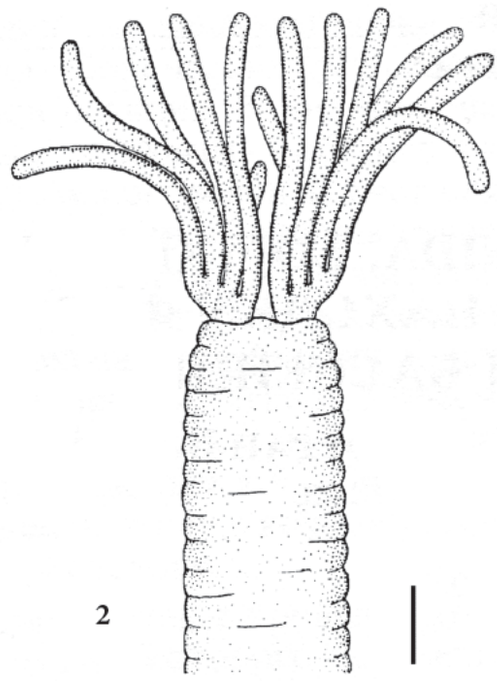

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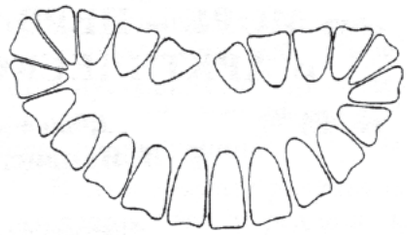

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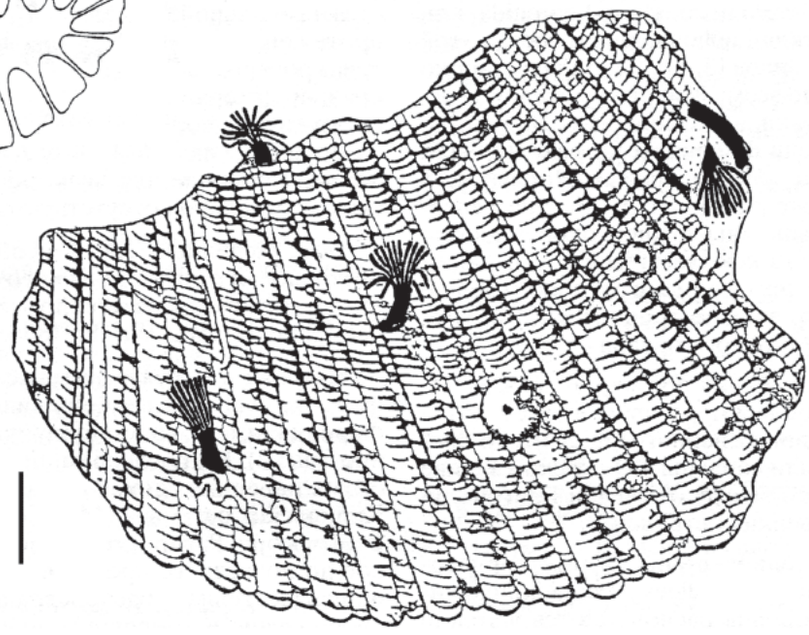

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Plate II. *Phoronis ovalis* from the White Sea

Fig. 1 Distal end of the body on the oral side, taken with a scanning electron microscope.
Fig. 2 Diagram of the distal end of the body on the anal side.
Fig. 3 Transverse section through the lophophore.
Fig. 4 Fragment of a *Chlamys islandicus* shell with the tops of *Phoronis ovalis* protruding from it.

(Fig. 1 photograph by N.N. Shunatova; Figs. 2-4 from Temereva et al. 2000.)

Scale: Figs. 1-3, 0.1 mm; Fig. 4, 1 mm.

Phylum Brachiopoda

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Brachiopods are sessile, non-parasitic, exclusively marine animals inhabiting predominantly the lower sublittoral to the upper bathyal zones (30-1500 m) on hard substrates; they are rarely attached to sand grains. A total of about 390 recent species are known. They feed on small, suspended particles in the water column including bacteria, detritus, marine snow, and particles of organic matter aggregated from colloidal material in suspension.

The body is bilaterally symmetrical including the lophophore (a feeding and respiratory organ) enclosed within a bivalved shell, formed by a dorsal and a ventral valve. The dorsal valve can be viewed as brachial valve, since the lophophore is located within it and in articulated forms (as we can see in the class Rhynchonellata) the skeletal support for the lophophore attaches at the back edge or at the inner bottom of this valve. The ventral valve can be viewed as the pedal valve, since the muscular peduncle (or "foot") is attached to the inner bottom of it, and the pedal[1] valve has an opening, named foramen, through which the foot protrudes to attach to the substrate.

The foramen in articulated forms (class Rhynchonellata) is framed by deltidial plates (Pl. I, Figs. D, E), which either leave it opened in the front (non-closing) or they close along the center line or even fuse to a greater or lesser extent, even to the point of forming a single plate completely isolating the foramen from the hinge edge, as in *Liothyrella arctica*[2] and *Dallina septigera* (Pl. III, Figs. 1, 9). The shell cavity, which contains the lophophore, is lined by the mantle, the margin of which is equipped with setae. The longest setae occur in *Pelagodiscus atlanticus* (Pl. II, Fig. 1), while short setae occur in all others with the exception of *Craniata*, which lack marginal setae altogether.

A groove is present along the coils of the lophophore at the base of tentacles, through which food particles are carried to the mouth (Pl. I, Figs. A, B, C). The groove is bounded by a thickened lower lip on the side where the water stream enters the mantle cavity. The tissue of the mantle and lophophore in members of the families Cancellothyrididae and Terebratulidae are filled with delicate star-shaped plates (spicules).

The skeleton of the lophophore (or the brachidium) is formed by anteriorly directed processes of the hinge margin (crura) and bands that are formed into more or less complicated loops. The branches of the loops are referred to as descending (they descend to the bottom of the valve) or ascending (they ascend from the bottom of the valve). Descending branches develop from the crura and, in addition to the loops, they form the crural appendices (horizontal flat processes on the edges of the crura and descending loops; they are pointed toward one another) and they are sometimes fused (Pl. II, Fig. 17), forming a ring as in *Terebratulina retusa*. Ascending branches develop in the upper section of the middle septum, and later during ontogenesis of the highly developed forms (such as *Dallina septigera* and *Macandrevia cranium*) they lose their connection to the septum and retain a connection only to the descending branches and to one another by the ribbon of the transverse band.

[1]Editorial note: other taxonomists use the term pedicle.

[2]Editorial note: per the World Register of Marine Species, *Arctosia arctica* is the accepted name.

Key to classes, families, genera, and species of the phylum Brachiopoda

1(2) Shell chitinous-phosphatic, impunctate (without pores). . . . . **Lingulata Gorjansky et Popov, 1985, family Discinidae, genus *Pelagodiscus, P. atlanticus* (King, 1868) (Pl. II, Figs. 1-3)**

Synonymies: *Discina atlantica* King, 1868. *Discinisca atlantica* Davidson, 1888.
Length 5 mm.
Cosmopolitan (from the northern Atlantic and Pacific to the Southern Ocean and Antarctica).
Bathyal-abyssal at 300-6000 m.
A single dorsal valve of an empty shell was collected in the northern Canadian Basin at 2747 m depth in the sediments of a trawl sample (Drift Station North Pole 22 in 1976-1977).

2(1) Shell calcitic, with pores or without them.

3(4) Dorsal (brachial) valve cap-shaped, punctate, joined to ventral (pedal) valve only by muscles, ventral valve cemented to substrate. When soft tissue is destroyed (e.g., torn off the substrate), valves are easily separated. . . . . **Craniata Williams et al., 1996, family Craniidae, genus *Novocrania*, *N. anomala* (Müller, 1776) (Pl. II, Figs. 4, 5)**

Synonymies: *Crania anomala* Davidson, 1888. *Neocrania anomala* Lee et Brunton, 1986.
Length 20 mm.
Atlantic widespread boreal. Southwestern and northern Barents Sea, east to White Island (east of Spitsbergen).
Depth 30-1478 m. On rock and gravel bottoms.

4(3) Brachial and pedal valves joined by a hinge consisting of teeth on the pedal valve and tooth cavities on the brachial valve. When valves are separated, hinge breaks. . . . . **Rhynchonellata Williams et al., 1996**

Key to orders of the class Rhynchonellata

1(2) Shell impunctate. Coils of lophophore in form of two symmetrical soft spirals, lacking skeleton (spirolophous lophophore, Pl. I, Fig. C) . . . **Rhynchonellida Kuhn, 1949**

2(1) Shell with punctae (pores). Coils of lophophore have complex shape (plectolophous lophophore, Pl. I, Fig. B), and are supported by bands of brachial skeleton or spicule network within soft tissue. . . . . **Terebratulida Waagen, 1883**

Key to families, genera, and species of the order Rhynchonellida

1(2) Large triangular septum present in brachial valve. Crura hand-shaped (maniculiform). Shell small, thin-walled, brittle, white, semitransparent with smooth outer surface . . . **Cryptoporidae, genus *Cryptopora*, *C. gnomon* Jeffreys, 1869 (Pl. II, Figs. 10-12)**

Synonymy: *Neatretia gnomon* Fischer and Oehlert, 1891.
Length 6 mm.
Atlantic widespread boreal. Western and northern Barents Sea east to Graham-Bell Island.
Depth 300-520 m. On agglutinated foraminiferan shells.

2(1) Middle septum of brachial valve absent or very low and short (threadlike). Crura shaped like flat hooks. Shell medium size, strong, dark (grayish-brown to dark brown or black) with ribbed outer surface .... **Hemithirididae, genus *Hemithiris*, *H. psittacea* (Gmelin, 1790) (Pl. II; Figs. 6-9)**

Synonymies: *Anomia psittacea* Gmelin, 1790. *Rhynchonella psittacea* Davidson, 1887.
Length 30 mm.
Widespread boreal Arctic, circumpolar.
Depth 6-916 m. On rock, gravel, boulders.
This is the only species of brachiopod in the White Sea.

Key to suborders of the order Terebratulida

1(2) Lateral coils of lophophore supported only by spicules filling the soft tissue. Brachial skeleton consists of ring or short loop in base of middle lobe of lophophore. . . . . **Terebratulidina Waagen, 1883**

2(1) Lateral coils of lophophore supported by bands of brachial skeleton having long loops with descending and ascending branches . . . . . **Terebratellidina Muir-Wood, 1955**

Key to families, genera, and species of the suborder Terebratulidina

1(2) Shell ribbed. Deltidial plates not fused to one another; foramen open anteriorly. Crural processes fused at both ends forming a ring together with short brachial loop. Spicules fill all soft tissue of lophophore. Along entire length of tentacles, spicule plates are rolled into unclosed tubules (grooves). **Cancellothyrididae, genus *Terebratulina*, *T. retusa* (Linnaeus, 1758) (Pl. II, Figs. 13-17)**

Length 24 mm.
Atlantic widespread boreal. Western Barents Sea near Spitsbergen and Murmansk coast east to 39°E.
Depth 141-1478 m.

2(1) Shell smooth. Foramen bounded anteriorly by fused deltidial plates. Crural processes never fused together and short brachial loop is open posteriorly. Lophophore spicules enter base of tentacles as cone-shaped socles. . . . . **Terebratulidae, genus *Liothyrella*, *L. arctica* (Friele, 1877) (Pl. III, Figs. 1-4)**

Synonymies: *Terebratula arctica* Friele, 1877. *Arctosia arctica* Cooper, 1983.
Length 20 mm.
Atlantic high boreal. Western and central Barents Sea.
Depth 136-415 m. On rocks and gravel.

Key to families, genera, and species of the suborder Terebratellidina

1(2) Foramen is open anteriorly. Deltidial plates rectangular, very narrow, or absent. Middle septum in brachial valve is short, low; its connection with loop of brachial skeleton is lost during development . . . . . **Macandreviidae, genus *Macandrevia*, *M. cranium* (Müller, 1776) (Pl. III, Figs. 15-22)**

Length 28 mm.
Atlantic widespread boreal. Southwestern Barents Sea along European coast east to 42°E.
Depth 75-525 m.

2(1) Foramen framed by deltidial plates, which are very close or fused together anteriorly.

3(4) Deltidial plates fused anteriorly into one wide plate. Middle septum of brachial valve high, stretching anteriorly along entire length of lophophore, almost reaching anterior edge of shell. Septum loses its connection with loop of brachial skeleton during ontogenesis. Shell grayish-white or yellowish . . . . . **Dallinidae, genus *Dallina*, *D. septigera* (Loven, 1840) (Pl. III, Figs. 9-14)**

Length 27 mm.
Atlantic widespread boreal. Southwestern Barents Sea.
Depth 37-1910 m.

4(3) Deltidial plates well developed but touch one another only near hinge edge, leaving a wide slit at edge of foramen. Middle septum in brachial valve is tall, stretching anteriorly to half the length of lophophore, never losing its connection with descending branches of brachial skeleton. Shell bean-shaped, greenish olive color. . . . . **Dallinidae, genus *Glaciarcula*, *G. spitzbergensis* (Davidson, 1852) (Pl. III, Figs. 5-8)**

Length 13 mm.
Widespread boreal Arctic, circumpolar.
Depth 32-2450 m.

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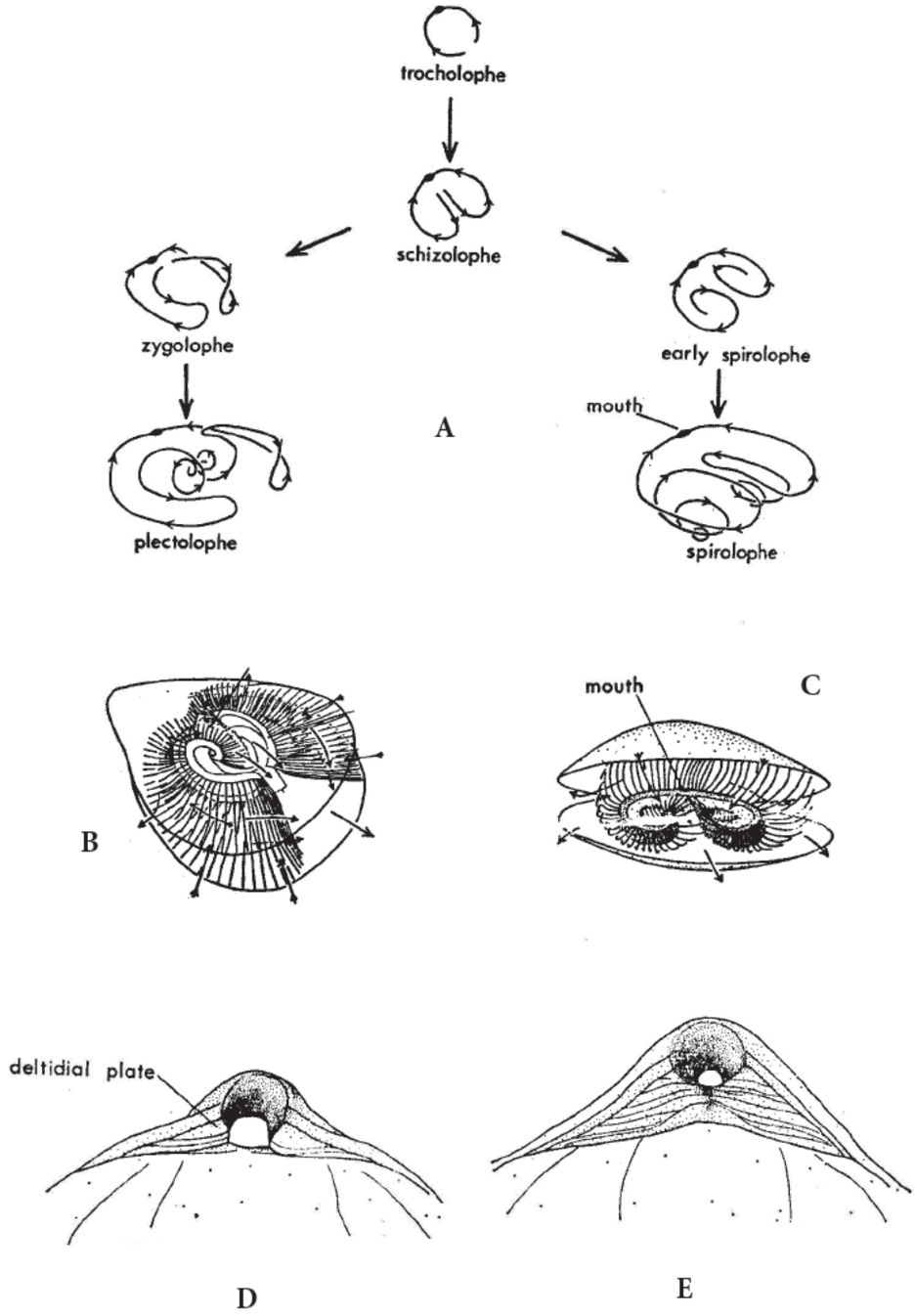


Plate I. Organization of the lophophore, foramen, and deltidial plates in hinged brachiopods.

Fig. A Diagram of the development and morphology of various lophophores. Arrows indicate the direction of movement of food particles in the food groove at the base of the tentacles.

Figs. B, C Distribution of tentacles in plectolophal (B) and spirolophal lophophores during feeding. Arrows show the direction of water currents in the mantle cavity.

Figs. D, E Foramen and deltidial plates, separate (D) and fused (E).

(From Rudwick 1970.)

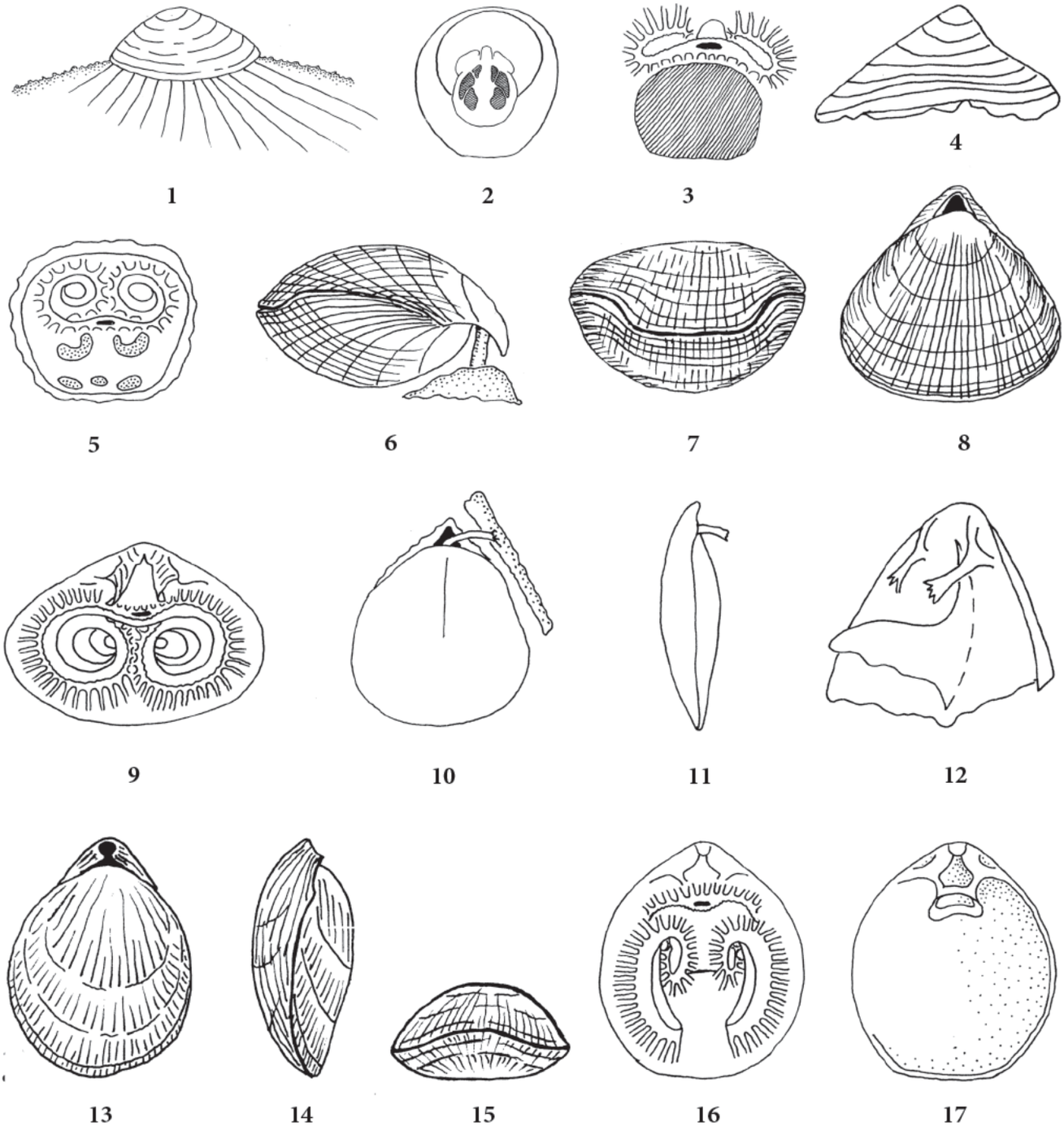


Plate II

Figs. 1-3 *Pelagodiscus atlanticus* (King, 1868) (1: position of the shell and setae of the dorsal mantle on the substrate, lateral right view. 2: view through the transparent dorsal valve: relative positions of the ventral valve and body [with the gullet and lophophore], muscle fields on the inner surface of the dorsal valve are shown by striations. 3: view of the body from the ventral side: surface of the foot (peduncle) attached to the substrate [hatched], slit-shaped mouth [black fill], gullet, and lophophore [lip shown by a solid wavy line, the tentacle bases are depicted by broken lines].)

Figs. 4-5 *Novocrania anomala* (Müller, 1776) (4: dorsal valve, anterior view. 5: ventral view: relative position of the lophophore and muscle attachments [stippled] on the inner surface of the dorsal valve.)

Figs. 6-9 *Hemithiris psittacea* (Gmelin, 1790) (6: lateral view of an attached individual. 7: anterior view of shell. 8: dorsal view of shell. 9: interior view of the dorsal [brachial] valve from the inside: position of the crura and spiral coils of the lophophore.)

Figs. 10-12 *Cryptopora gnomon* Jeffreys, 1869 (10: dorsal view of an attached individual. 11: lateral view of attached individual. 12: interior view of the brachial valve: maniculiform crura and high, triangular median septum.)

Figs. 13-17 *Terebratulina retusa* (Linnaeus, 1758) (13: dorsal view of the shell. 14: lateral view of the shell. 15: anterior view of the shell. 16: position of the plectolophous lophophore in the dorsal [brachial] valve: median and lateral coils, mouth and preoral portion of the lip, and tentacles. 17: interior view of the brachial valve of an empty shell: crura and short ring-shaped loop of the brachial skeleton.)

(Figs. 1-9 from Zezina 1997b; Figs. 10-12 from photographs in Gorbunov 1946; Figs. 13-17 from Davidson 1880.)

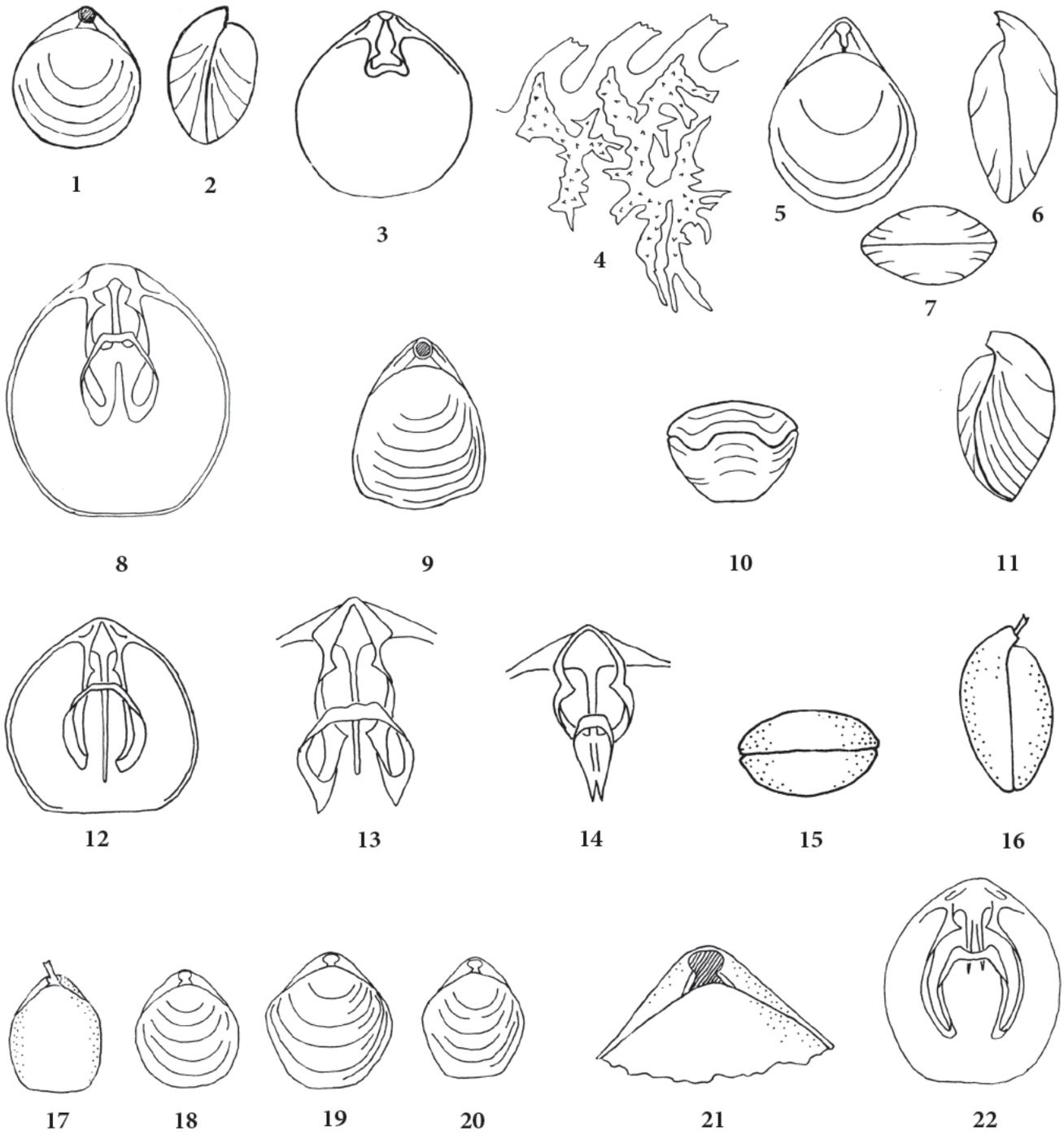


Plate III

Figs. 1-4 *Liothyrella arctica* (Friele, 1877) (1: dorsal view of the shell, foramen is bounded anteriorly by fused deltidial plates. 2: lateral view of shell. 3: dorsal valve interior: hinge edge and short loop of the brachial skeleton. 4: spicules in the soft tissue of the lophophore, running into the base of the tentacles as cone-shaped socles.)

Figs. 5-8 *Glaciarcula spitzbergensis* (Davidson, 1852) (5: dorsal view of the shell, with deltidial plates not fused near the edge of the foramen. 6: lateral view of shell. 7: anterior view of shell. 8: interior view of an empty dorsal valve from adult: long loop of the brachial skeleton attached to the median septum by descending branches.)

Figs. 9-14 *Dallina septigera* (Loven, 1840) (9: dorsal view of the shell; the foramen is bounded anteriorly by fused deltidial plates. 10: anterior view of shell. 11: lateral view of shell; 12: interior view of empty dorsal valve of adult: long loop of brachial skeleton not attached to the long, high median septum. 13, 14: brachial loop of juveniles at various developmental stages showing detaching of the descending branches from median septum.)

Figs. 15-22 *Macandrevia cranium* (Müller, 1776) (15: anterior view of shell. 16: lateral view of shell. 17, 18, 19, 20: dorsal view of shell: variations of shell outline. 21: dorsal view of posterior end of adult: foramen open [not closed] anteriorly, such that the deltidial plates are narrow and not fused to one another. 22: interior view of empty dorsal valve of adult: long loop of brachial skeleton not connected to the short, low septum, transforming into a median groove at its anterior end.)

(Figs. 1-14 from Davidson 1886; Fig. 4 from Blochmann 1908; Figs. 15-17, 21 from Fischer and Oehlert 1891; Figs. 18-20, 22 from Davidson 1886.)

Ranges of Species Inhabiting the Arctic Ocean

This is a refinement and addition to Appendix 1 in *Explorations of the Fauna of the Seas*, vol. 54(62), 2004: "Fauna and ecosystems of the Laptev Sea and adjacent deep-water areas of the Arctic Basin, Part II."

Please see maps on following pages. In addition, see map of Eurasian seas on page 2 of this volume.

Major Ranges of Species Inhabiting the Shelf

I. Arctic species

Arctic or arctic circumpolar: Arctic non-circumpolar and arctic circumpolar species. Widely distributed in arctic waters on the shelves of the marginal arctic seas and on the continental slopes of the Arctic Basin. Arctic circumpolar species have an uninterrupted distribution in the Arctic Ocean.

Arctic Eurasian: The western boundary of their range runs along the line from the mouth of the MacKenzie River and the Amundsen Gulf to the Fox Basin and Hudson Strait. The eastern boundary occurs at the New Siberian Banks.

Arctic Amerasian: These species occur to the east of the New Siberian Banks to the mouth of the MacKenzie River, and can penetrate through the Canadian Arctic to the Fox Basin and Hudson Strait.

II. Boreal arctic species

Widespread boreal arctic non-circumpolar and circumpolar species: Widely distributed in temperate waters of the Atlantic and Pacific oceans. The southern boundary of the range goes to Cape Hatteras on the American Atlantic coast and to the southwestern English Channel on the European coast. The southern boundary in the western Pacific is the line between Wonsan, Korea, and Sado Island on the Japan Sea side of Japan in the eastern Pacific to Cape Conception or San Diego on the American coast.

High boreal arctic non-circumpolar and circumpolar species: Inhabit the North Atlantic south to Cape Cod on the American coast and to southwest Norway in Europe. The southern boundary in the Pacific is to Cape Terpeniye (Sakhalin Island) and Ekaterina Strait (south of Iturup Island) and the Strait of Juan de Fuca (south of British Columbia). They also occur in the Arctic Ocean.

Atlantic widespread boreal arctic species. Inhabit the North Atlantic (south to Cape Hatteras on the American coast and to the English Channel on the European side); they also occur in the Arctic eastward to the New Siberian Banks.

Atlantic high boreal arctic circumpolar species: Occur in temperate waters of the Atlantic north of Cape Cod (on the American coast) and southwestern Norway; also circumpolar in the Arctic.

Pacific widespread boreal arctic species: Occur in temperate waters of the Pacific Ocean south to the line between Wonsan, Korea, and Sado Island on the Japan Sea side of Japan; on the American coast they occur south to Point Conception or San Diego. They also occur in the Arctic but are not found in temperate waters of the North Atlantic.

Pacific high boreal arctic species: Occur in the North Pacific (southern boundary reaches Cape Terpeniye, Sakhalin Island), Ekaterina Strait (south of Iturup Island) and the Strait of Juan de Fuca (south of British Columbia), and in the Arctic Ocean. They do not occur in temperate waters of the Atlantic.

Pacific western Atlantic boreal arctic species: Widely distributed in boreal waters of the North Pacific and along the west side of the Atlantic from Newfoundland to Greenland. In the Arctic they have been observed in the southeastern Chukchi Sea and along the arctic coast of Canada and northern Greenland.

III. Boreal species penetrating the arctic seas

Atlantic widespread boreal species: Found in the western Atlantic from Cape Hatteras to the Greenland-Canadian region (almost to the Arctic Circle) and Denmark Strait. They are seen on the European coast from the English Channel to Cape Kanin Nos (in the Barents Sea) and north to the west coast of Spitsbergen.

Atlantic high boreal species: Occur along the coast of North America north of Cape Cod and the European coast to north of northeastern Scotland and southwestern Norway. The northern boundary is similar to that of the Atlantic widespread boreal species.

Eastern Atlantic (Atlantic European) widespread boreal species: Seen in the Atlantic Ocean along the coast of Europe from the English Channel to Cape Kanin Nos (Barents Sea) and north to the west coast of Spitsbergen.

Pacific widespread boreal species: Inhabit the Pacific Ocean along the Asian coast north of the line between Wonsan, Korea, and Sado Island on the Japan Sea side of Japan and Cape Inubo (Pacific coast of Japan) to Bristol Bay. They occur on the American coast from Point Conception or San Diego to the Bering Strait, some to Wrangel Island and Point Barrow (Chukchi Sea), and in refuges for boreal species in the area adjacent to the mouths of the Mackenzie and Kolyma rivers and in Chaunsk and Kolyuchin bays.

Pacific high boreal species: Occur in the Pacific to north of Cape Terpeniye (Sakhalin Island), the Ekaterina Strait (south of Iturup Island), and the Strait of Juan de Fuca (south of British Columbia) up to Bering Strait; some occur north to Wrangel Island and Point Barrow (Chukchi Sea), and in refuges for boreal fauna in the area adjacent to the mouths of the Mackenzie and Kolyma rivers and in Chaunsk and Kolyuchin bays.

Western Pacific (Pacific Asian) widespread boreal species: Seen along the Asian coast north of the line between Wonsan, Korea, and Sado Island on the Japan Sea side of Japan and Cape Inubo (Pacific coast of Japan) to Bristol Bay and the Bering Strait; some found north to Wrangel Island and Point Barrow (Chukchi Sea), and in refuges for boreal fauna in the area adjacent to the mouths of the Mackenzie and Kolyma rivers and in Chaunsk and Kolyuchin bays.

Western Pacific (Pacific Asian) high boreal species: Seen along the Asian coast to the north of Cape Terpeniye (Sakhalin Island) and Ekaterina Strait (south of Iturup Island) to the Bering Strait; some occur north to Wrangel Island and Point Barrow (Chukchi Sea), and in refuges for boreal fauna in the area adjacent to the mouths of the Mackenzie and Kolyma rivers and in Chaunsk and Kolyuchin bays.

Eastern Pacific (Pacific American) widespread boreal species: Occur along the Pacific coast of North America north of Point Conception or San Diego. Can be found in the southeastern Chukchi Sea.

Eastern Pacific (Pacific American) high boreal species: Distributed along the North American coast north of the Strait of Juan de Fuca (south of British Columbia). Can be found in the southeastern Chukchi Sea.

Amphiboreal species: Distributed in temperate waters of the North Atlantic and North Pacific; sometimes seen in the southwestern Barents Sea and the southern Chukchi Sea.

IV. Subtropical-arctic species

Subtropical-arctic species: Distributed in the Atlantic Ocean where the southern boundary on the west side reaches South Carolina and on the east side to the coast of Morocco and the Mediterranean Sea; in the Pacific Ocean the southern boundary on the west side is the Yellow Sea and Kyushu Island and on the east side from the tip of the Baja California peninsula; also in the Arctic Ocean.

V. Subtropical-boreal species.

Atlantic subtropical-boreal species: Occur in the North Atlantic north of South Carolina and Morocco including the Mediterranean, and in temperate waters of the Barents, Norwegian, and Greenland seas.

Pacific subtropical-boreal species: Occur in the Pacific north of Kyushu Island, the northern Yellow Sea, and southern tip of the Baja California peninsula, in temperate waters of the Chukchi Sea, and in refuges for boreal fauna in the area adjacent to the mouths of the Mackenzie and Kolyma rivers and in Chaunsk and Kolyuchin bays.

VI. Bipolar species.

Bipolar species: Inhabit primarily the temperate and polar waters of the northern and southern hemispheres with a break in the range in the tropics.

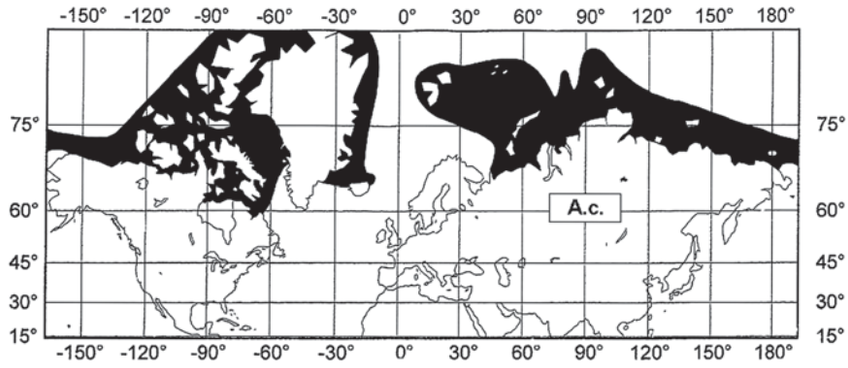
VII. Panoceanic species.

Panoceanic species: Inhabit almost all latitudes of the world's oceans.

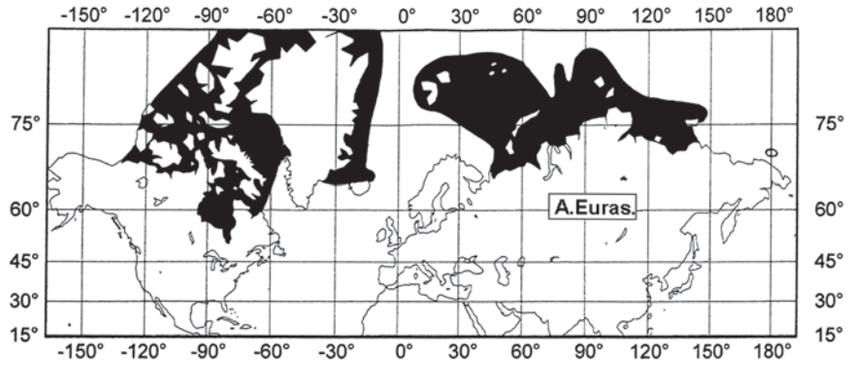
Major Range Types of Bathyal and Abyssal Species (below 200 m)

Arctic bathyal, abyssal, or bathyal-abyssal species
Atlantic-arctic (Arcto-Atlantic) bathyal or bathyal-abyssal species
Atlantic-Pacific-Arctic bathyal or bathyal-abyssal species
Bipolar bathyal-abyssal species
Panoceanic bathyal or bathyal-abyssal species

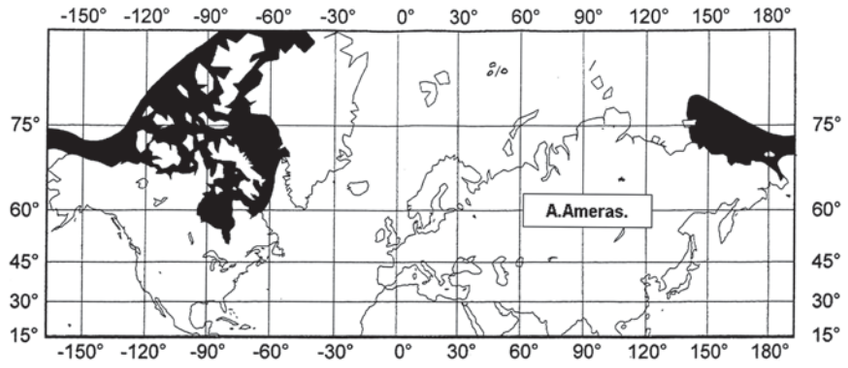
I. Arctic species



Arctic or Arctic Circumpolar

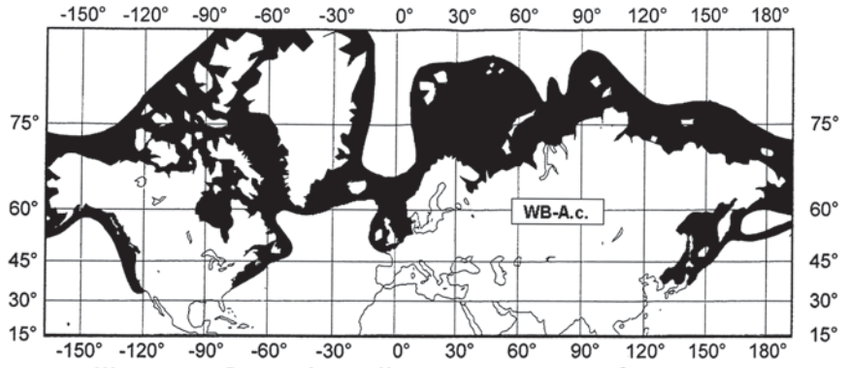


Arctic Eurasian

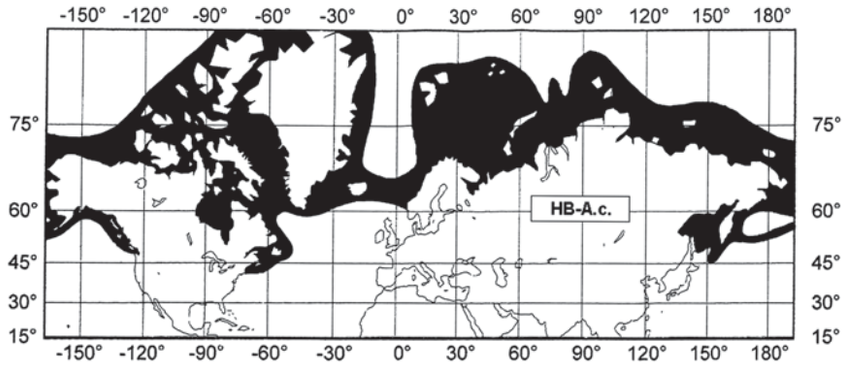


Arctic Amerasian

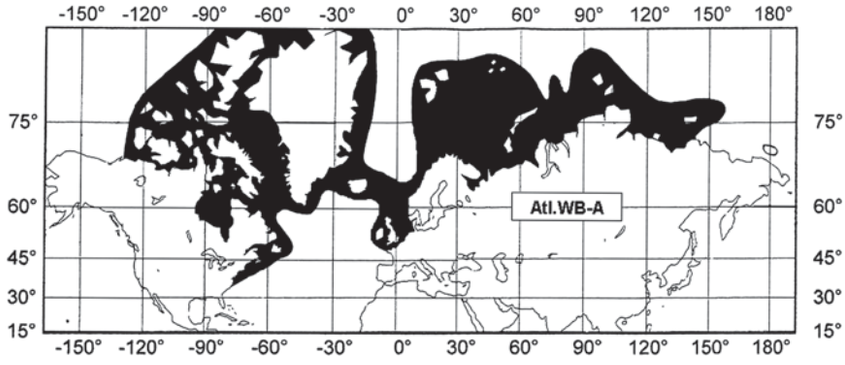
II. Boreal arctic species



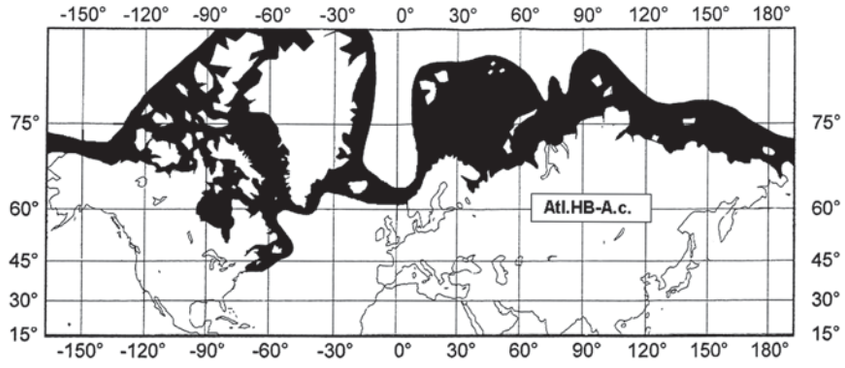
Widespread Boreal Arctic Non-circumpolar and Circumpolar



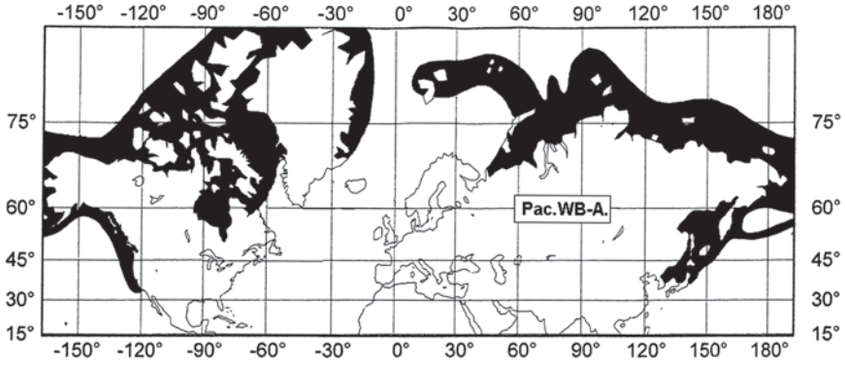
High Boreal Arctic Non-Circumpolar and Circumpolar



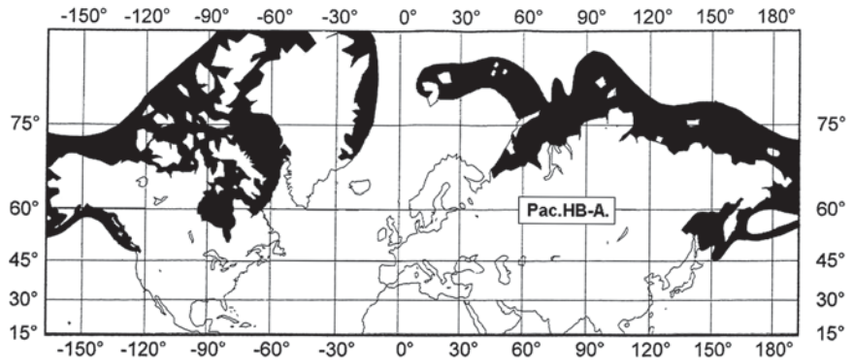
Atlantic Widespread Boreal Arctic



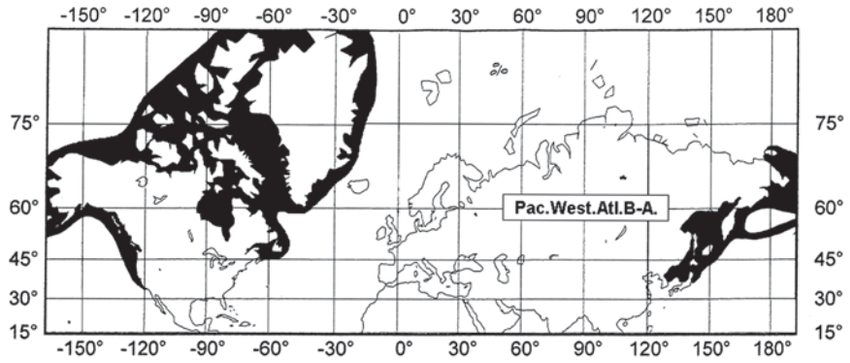
Atlantic High Boreal Arctic Circumpolar



Pacific Widespread Boreal Arctic

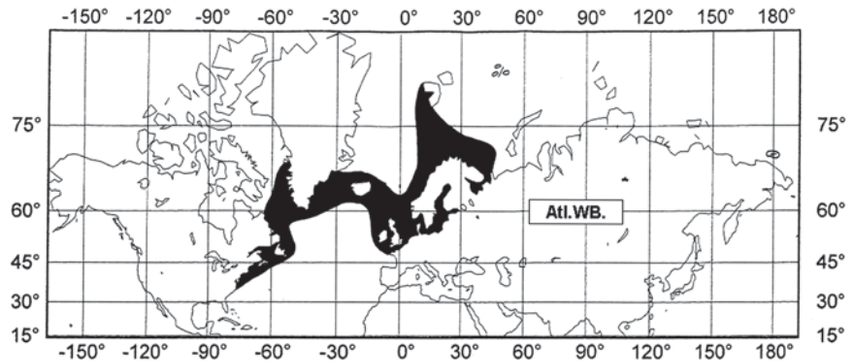


Pacific High Boreal Arctic

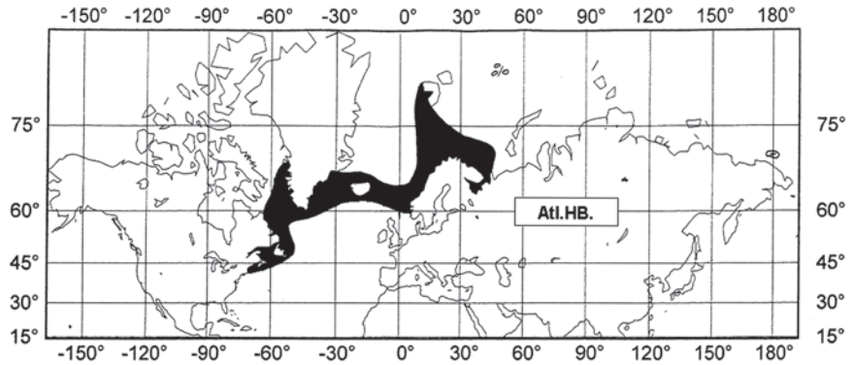


Pacific-Western Atlantic Boreal Arctic

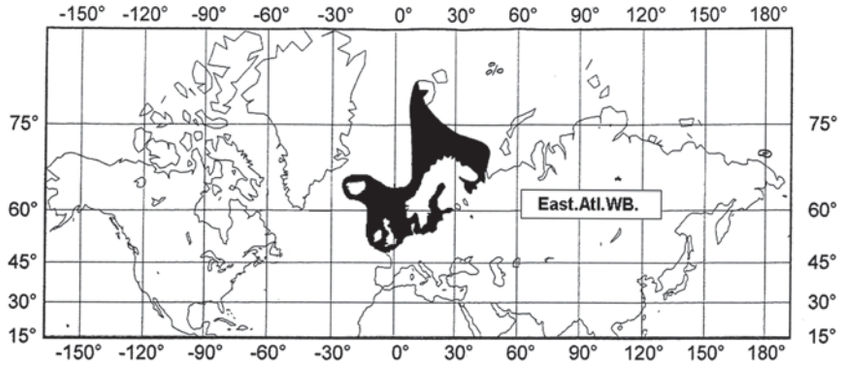
III. Boreal species penetrating the arctic seas



Atlantic Widespread Boreal



Atlantic High Boreal



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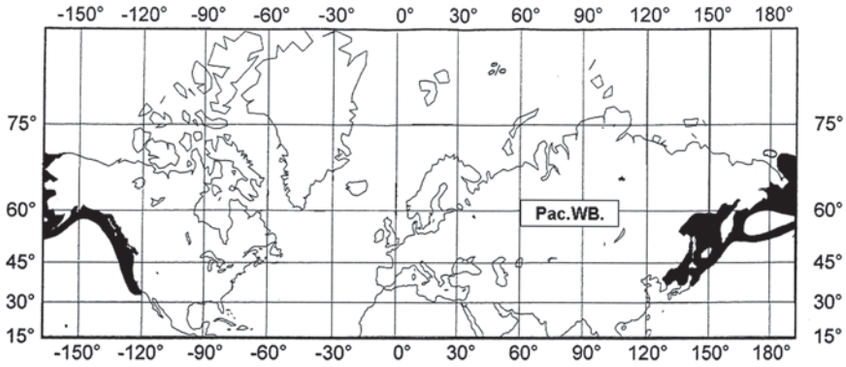

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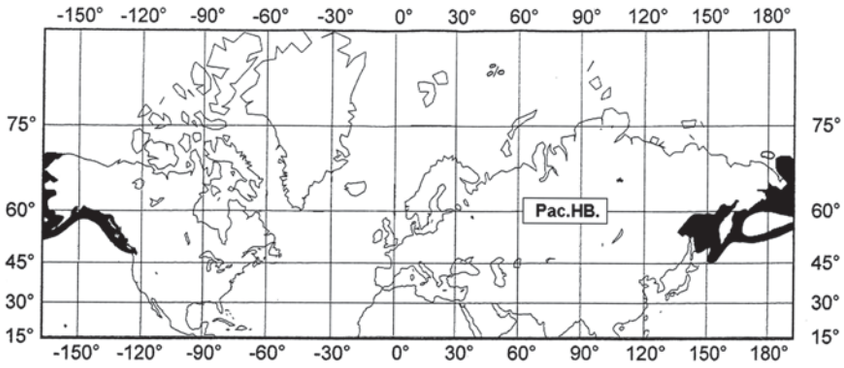

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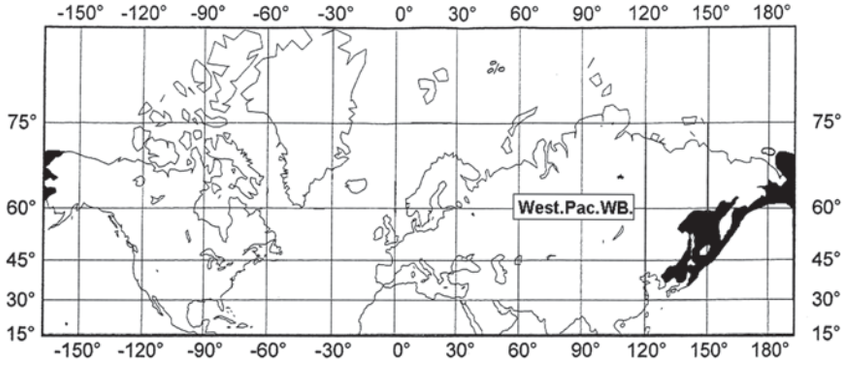

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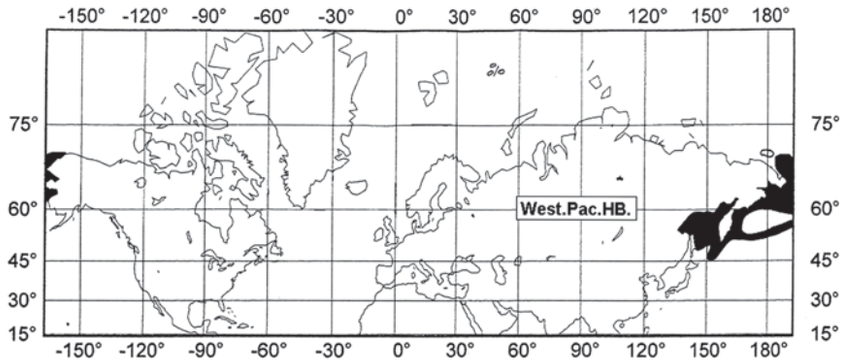

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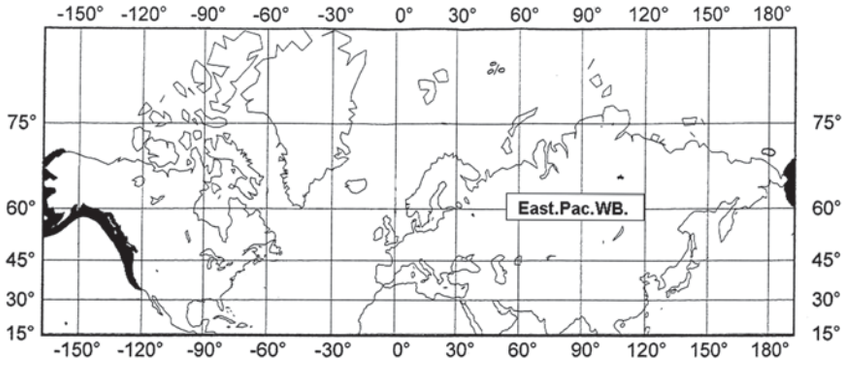

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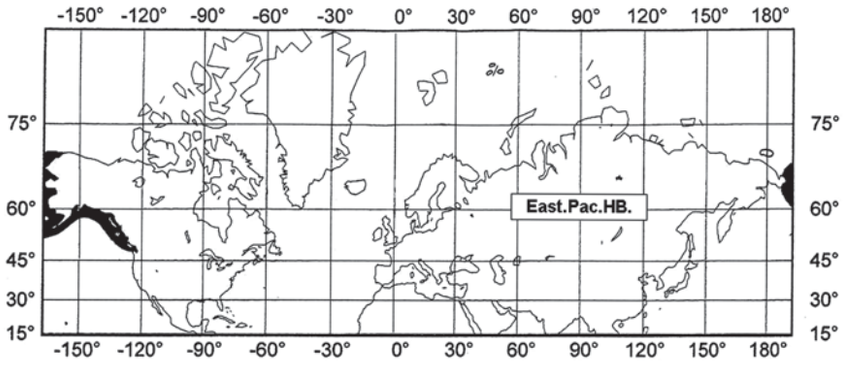

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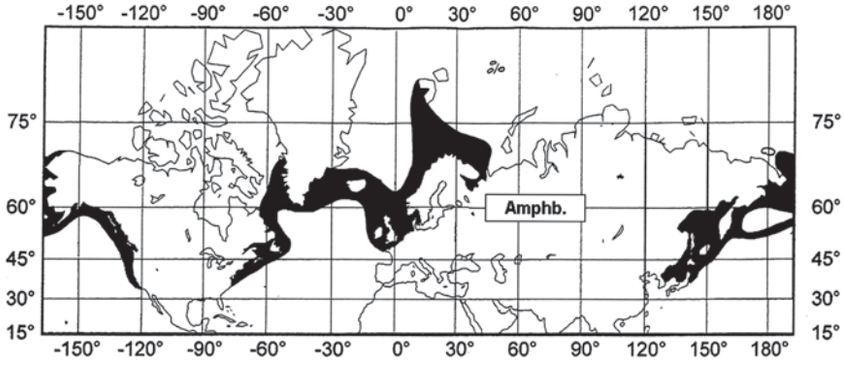
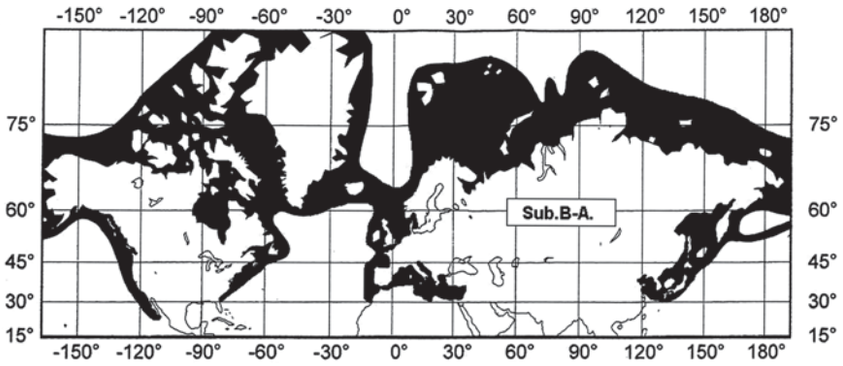


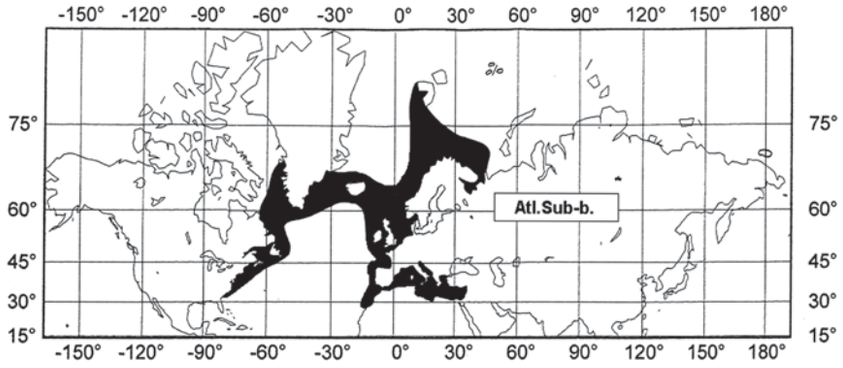
Amphiboreal

IV. Subtropical-arctic species

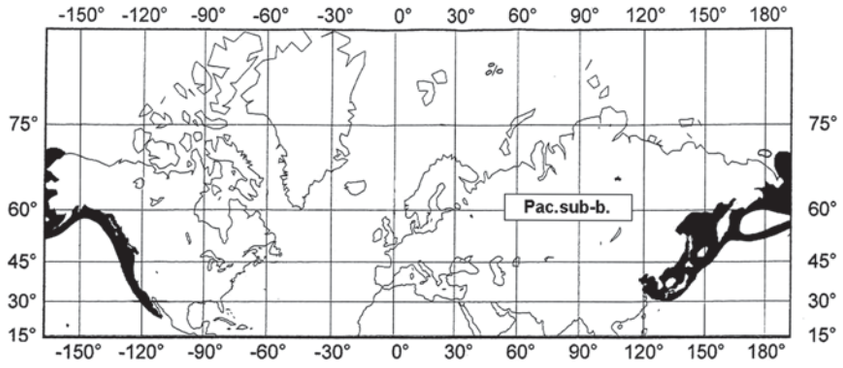


Subtropical-Arctic

V. Subtropical-boreal species.



Atlantic Subtropical-Boreal



Pacific Subtropical-Boreal

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