

SYSTEMATICS, ZOOGEOGRAPHY, AND ECOLOGY OF THE PRIAPULIDA

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With 89 text-figures and five plates

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I INTRODUCTION

The phylum Priapulida is only a very small group of marine worms but, since these animals apparently represent the last remnants of a once undoubtedly much more important animal type, they are certainly of great scientific interest. Therefore, it is to be regretted that a comprehensive review of our present knowledge of the group does not exist, which does not only cause the faulty way in which the Priapulida are treated usually in textbooks and works on phylogeny, but also hampers further studies. The reason for the apparent lack of interest probably is that these worms, although found in many parts of the world, represent important or conspicuous elements of the marine fauna in limited areas only. They are rare or completely absent in many regions, including most areas frequented by zoologists.

After having discovered the aberrant meiobenthic priapulid *Tubiluchus corallicola* a few years ago (Van der Land, 1968), I became more clearly conscious of this lack of a complete monograph. A comparative study appeared to require a time-consuming survey of the extensive but widely scattered and partly unreliable literature. Therefore I decided to undertake not only a further study of this particular species but to include all other species as well.

I.1 PLAN

Nowadays it is beyond one person's capabilities to compile a monograph covering all topics of the natural history of a phylum, however small. The present paper is just designed to give a usable starting point, which means that a nearly complete bibliography is included and that a detailed systematic survey of the Priapulida is presented. Some special topics, namely zoogeography and ecology, are treated of as well, though in a more concise manner. Several aspects of the morphology and the anatomy, larval and post-larval development, and relationships within the group and with other phyla will be dealt with in following papers, partly in cooperation with other authors. It is expected that other important topics such as histology, ultrastructure, physiology, and biochemistry will be covered by experts in these fields, so that the ultimate goal of a comprehensive treatise may come within sight, although embryological and histochemical investigations are still badly needed.

Fossil priapulids (the Middle Cambrian *Ottoidae* of Walcott, 1911) are left out of consideration in the present paper.

1.2 MATERIAL AND METHODS

Most of the relevant literature is present in Dutch libraries. A considerable numbers of papers and books could be consulted in the libraries of the museums in Copenhagen, London, Oslo, and Stockholm, and of the laboratory at Helsingør. Thanks to this, nearly all publications in which priapulids are dealt with, were seen by the author. The bibliography is undoubtedly not complete, but the number of papers missing is small and probably does not include anything of great importance.

Although the preparation of a bibliography and the compilation of data from the literature proved to be quite a task in itself, a direct study of as much material as possible was emphasized in order to facilitate a critical evaluation of the available information and to fill a number of gaps in our knowledge.

Priapulus caudatus is the only species that could be collected and studied alive, viz., in the Gullmarfjord area (Skagerrak) and in the Öresund near Helsingør. In both areas adults were collected with a ring-trawl and larvae with a detritus-sledge. Large adults are usually not very abundant, but in my experience the following collecting method, in use at Kristinebergs Zoologiska Station, is very efficient. A wide-meshed net is attached around the ring-trawl after it has become filled with mud. Both nets are rapidly hauled through the water until all mud has been washed out. Most specimens are retained in the second net. The time-consuming and disagreeable procedure of washing evil smelling mud through sieves on board is thereby avoided. Of course small specimens are lost in this way, but these can more easily be collected with a detritus-sledge. Larvae and postlarvae can be obtained by keeping the detritus for one or more days on plankton gauze over a funnel. I used this method only once so I could not determine how effective it is. It does work but it is not suitable for quantitative studies since especially larvae have a strong tendency to react to changes in their environment by withdrawing into their loricas and remaining immobile. They certainly do this in a warm laboratory so the samples to be treated in this way should be kept at low temperatures in any case.

Living larvae can be forced to protrude their introvert under a coverglass, but some experience should be acquired. There must be a method to make them extend spontaneously since several of the lots of fixed material contained extended specimens, but I did not yet have an opportunity to do experiments; probably some anaesthetic will work.

Specimens of *Tubiluchus corallicola* were washed from samples of coral sand fixed in formalin, Bouin's, or Zenker's. In most samples both larvae and adults were only rarely in an extended condition, so it will be worth-

while to pay attention to a proper treatment before fixation. This is less important for adults of other priapulids, which do not react to fixatives by withdrawing their introvert, although they often contract vigorously.

The greater part of the material was obtained from existing collections. I could visit the museums in Copenhagen and Stockholm, where the richest collections of priapulids in the world are present, and those of London and Oslo. I also visited the Mediterranean Marine Sorting Center at Salammbô (Tunisia), where the collection of Dr. R. P. Higgins and material of the Smithsonian Marine Sorting Center were present at the time. Additional material was borrowed from the museums of Bergen, New York, Trondheim, and Washington, and from the laboratories at Charlottenlund and Woods Hole. Information was received on the collections of the museums in Berlin, Edinburgh, and Hamburg.

A collection of particular importance is present in the Helsingør laboratory. During a period of three years, quantitative meiobenthic sampling was done by Mrs. K. Muus in one locality at two weeks intervals. Larvae and post-larvae of *Priapulus caudatus* were regularly present during a period of about two years. This is the first collection of priapulids of its kind and presents a unique possibility of studying the larval development.

The pharyngeal armature, which shows important taxonomic characters, is visible from the outside when the pharynx is protruded, but usually this is not the case. For routine identification a simple longitudinal slit will do to make it visible, but for a more careful study and for depicting it, removal of the pharynx and making a flat preparation of the armature is necessary. For this and other cuticular structures I prefer temporary preparation in lactic acid, because this fluid does not evaporate, softens the tissues, and has excellent optical properties. The latter is of paramount importance when studying very small specimens. Moreover, lactic acid more or less restores the original condition of wrinkled parts of the cuticle. Specimens of *Priapulus caudatus*, *Halicryptus spinulosus*, and *Tubiluchus corallicola*, including larvae, were serially sectioned and stained in several ways.

All but one of the drawings are original. Most of them were made with the aid of a camera lucida.

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I was allowed to make use of a preliminary manuscript of an English

translation of the important Russian paper by Murina & Starobogatov (1961) prepared at the British Museum (Natural History).

2 SYSTEMATICS

2.1 HISTORICAL INTRODUCTION

The Priapulida constitute one of the smallest groups which has ever been given the rank of a phylum. Consequently, systematics within the group have not presented many difficulties, but the relationship with other groups was and remains a perplexing problem.

The first species was already described as early as 1754 by Odhelius under the name *Priapus humanus*, which was also adopted by Linnaeus (1758). Both authors placed the animal in the same genus as the sea-anemone *Priapus equinus*. Later Linnaeus (1767) considered it to be a sea-cucumber and gave it the name *Holothuria priapus*. De Lamarck (1816) again changed its name and called it *Priapulus caudatus*. Most authors in those times assigned it a position amongst the Echinodermata. De Blainville (1826) first recognized its distinctness and created a separate group for the animal, the Subactinozoaires. In general later authors followed De Quatrefages (1847) in placing *Priapulus* together with the sipunculids and echiurids in the group Gephyrea, thereby indicating that they bridge the gap between worms and echinoderms (gefyra = bridge). In recent times the relationship between priapulids and sipunculids has been disputed more and more, and nowadays there is a general tendency to stress the uniqueness of the Priapulida. As far as I know Vosmaer (1908) for the first time considered the group a separate phylum.

Meanwhile a second species, *Halicryptus spinulosus*, had been discovered by Von Siebold (1849). Although it differs considerably from *Priapulus caudatus* in its outward appearance, their relationship was soon realized. Other species occur in more remote areas or in deep water, so it was only after the onset of scientific expeditions that more species were discovered: *Priapulus tuberculatospinosus* Baird, 1868; *Priapulopsis bicaudatus* (Danielsen, 1868); *Priapulopsis australis* (De Guerne, 1886); *Priapulus horridus* Théel, 1911, none of them surprisingly different from *Priapulus caudatus*. Good progress was made in the fields of anatomy and histology, to which topics a considerable number of publications were dedicated. The discoveries of the peculiar larvae of *Halicryptus spinulosus* by Hammarsten (1913) and *Priapulus caudatus* by K. Lang (1939) also call for mention. The concise systematic monograph by Murina & Starobogatov (1961) was of great importance.

Until 1959 two or three genera with five or six species were generally

recognized. There was only some difference of opinion about the questions whether *Priapulus tuberculatospinosus* is to be considered a separate species or only a subspecies of *P. caudatus*, and whether *Priapulopsis* should be considered a separate genus or be included in *Priapulus*.

However, in the last decade or so the clarity of the situation suffered considerably, due to the descriptions of some new subspecies, some new species, and a new genus, none of them being entirely satisfying:

Priapulus abyssorum Menzies, 1959; *Priapulus tuberculatospinosus* subsp. *bahiensis* Olivier et al., 1961; *Priapulus tuberculatospinosus* subsp. *japonicus* Murina & Starobogatov, 1961; *Priapulus profundus* Sanders & Hessler, 1962; *Priapulopsis atlantisi* (Sanders & Hessler, 1962); *Tubiluchus corallicola* Van der Land, 1968.

The necessity of a critical review of these newly described taxa was one of the first motives for undertaking the present study. Of course the author particularly felt obliged to add to his poor preliminary description of *Tubiluchus corallicola*, which was based on few specimens, mainly larvae.

2.2 PHYLUM PRIAPULIDA

- Subtactinozoaires de Blainville, 1826: 269 (diagnosis; relationship).
 p.p. Proboscephale (ordo) de Blainville, 1826: 549-550 (diagnosis).
 p.p. Gephyrea (classis or phylum) de Quatrefages, 1847: 340; 1865b: 296. — Lankester 1877: 441, 449.
 p.p. Sipunculidea; Diesing, 1859: 753 (monograph).
 Priapulidae (classis); Lankester, 1877: 449.
 p.p. Prosopygii (classis); Lang, A., 1888/94: 182-185.
 Priapuloidea (ordo, classis or phylum); Shipley, 1896: 412-434 (textbook). — Vosmaer, 1908: 275-276 (textbook). — Meyer, 1933: 520-524, 526-527 (relationship with Acanthocephala). — Van Cleave, 1941: 34, 44 (relationship with Acanthocephala). — Lang, K., 1948b: 6-8 (relationship with Kinorhyncha). — Dawydoff, 1959 (textbook, including diagnosis, relationships, bibliography). — Murina & Starobogatov, 1961: 179-199 (monograph). — Hadži, 1963: 296, 397, 426, 460, fig. 54, 60 (systematic status). — Storer & Usinger, 1965: 375-376 (textbook).
 p.p. Sipuncularia (classis) Haeckel, 1896: 315-316.
 Priapulida (subordo, ordo, classis, or phylum); Delage & Hérouard, 1897: 7-11, Pl. I, fig. 2-12, Pl. 2 (textbook). — Théel, 1906: 8, 12-13 (diagnosis). — Schepotieff, 1908: 300-301 (excretory organs; relationship with Acanthocephala). — Hammarsten, 1915: 546-570 (relationships, especially with Kinorhyncha). — Meyer, 1928: 129-130, 203, 214 (relationship with Acanthocephala). — Baltzer, 1934a: 1-14 (textbook, including diagnosis, zoogeography, relationships). — Korschelt, 1936: 407-408 (larval development). — Remane, 1936: 337 (relationship with Kinorhyncha). — Meyer, 1938: 187-188, fig. 33b (relationship with Acanthocephala). — Purasjoki, 1944: 7 (relationships). — von Haffner, 1950: 243-245, 247-252, fig. 3a (comparison with Acanthocephala). — Hyman, 1951: 56, 183-197 (textbook, including history, relationships, bibliography). — Boettger, 1952: 269, 290 (relationship with Annelida). — Wesenberg-Lund, 1957: 12-24 (bibliography 1920-1957). — Golvan, 1958: 541, 566-576, 579-580, 584-586, 589-593, fig. 9, 11, tab. (anatomy, embryology, moult, relationship with Acanthocephala). — Marcus, 1958: 35, 40 (relationships). — Shapeero, 1961: 879-880 (relationships); 1962a: 352 (relationship

with Eucoelomata). — Lang, K., 1963: 256-261 (relationships). — Remane, 1963: 249, 252-254 (relationships). — Hartwich, 1967: 316-318 (textbook). — Hickman, 1967: 254-259 (textbook, including relationships). — Jägersten, 1968: 75-78 (relationships). — Murina, 1968: 89 (zoogeography).

p.p. Sipunculoidea (ordo); Fischer, J., 1913: 91. — ten Broeke, 1929: 156-157. — Wesenberg-Lund, 1939b: 4.

N.B. This synonymy is far from complete; it is only intended to be illustrative. See also under family Priapulidae.

2.2.1 Diagnosis

Vermiform, unsegmented animals; free-living in marine sediments in all stages. Body cylindrical, bilaterally symmetrical with a strong tendency to radial symmetry, divisible in at least two regions: abdomen and introvert, the latter serving as locomotory organ and invaginable into the former. Ectoderm a columnar epithelium, covered with a strong chitinous cuticula with a considerable variety of specializations, externally as well as in the stomodaeum; cuticula subject to moult throughout life.

Mouth terminal, giving entry to an armed and muscular pharynx, the anterior part of which is eversible. Intestine straight and simple, lined with a columnar epithelium; anus at posterior end of abdomen. A single, spacious coelom, filled with coelomic fluid with free coelomocytes containing haemerythrin; lined with a peritoneum. Musculature mainly consisting of the dermomuscular layers of circular and longitudinal muscles and the system of strong retractors; part of the muscles striated. Central nervous system located in the epidermis, consisting of a peribuccal ring and a ventral nerve cord terminating in a preanal ganglion. Sense-organs of different kinds occur all over the body; no eyes. No circulatory system. Sexual reproduction only; sexes separate. One pair of urogenital organs, attached to the body wall by a mesenterium; excretory organs of the solenocytic protonephridial type; urogenital ducts with separate pores near the anus. Cilia completely absent; flagellated cells occur in the urogenital system.

Embryological development incompletely known; bilateral cleavage; blastula and gastrula stages present. Larvae free-living, not ciliated; abdomen enclosed in a relatively strongly cuticularized lorica; metamorphosis to post-larval stage.

2.2.2 Classification

The following taxa are recognized in the present paper:

Familia Priapulidae Gosse, 1855

Priapulus de Lamarck, 1816

1. *Priapulus caudatus* de Lamarck, 1816

2. *Priapulus tuberculatospinosus* Baird, 1868

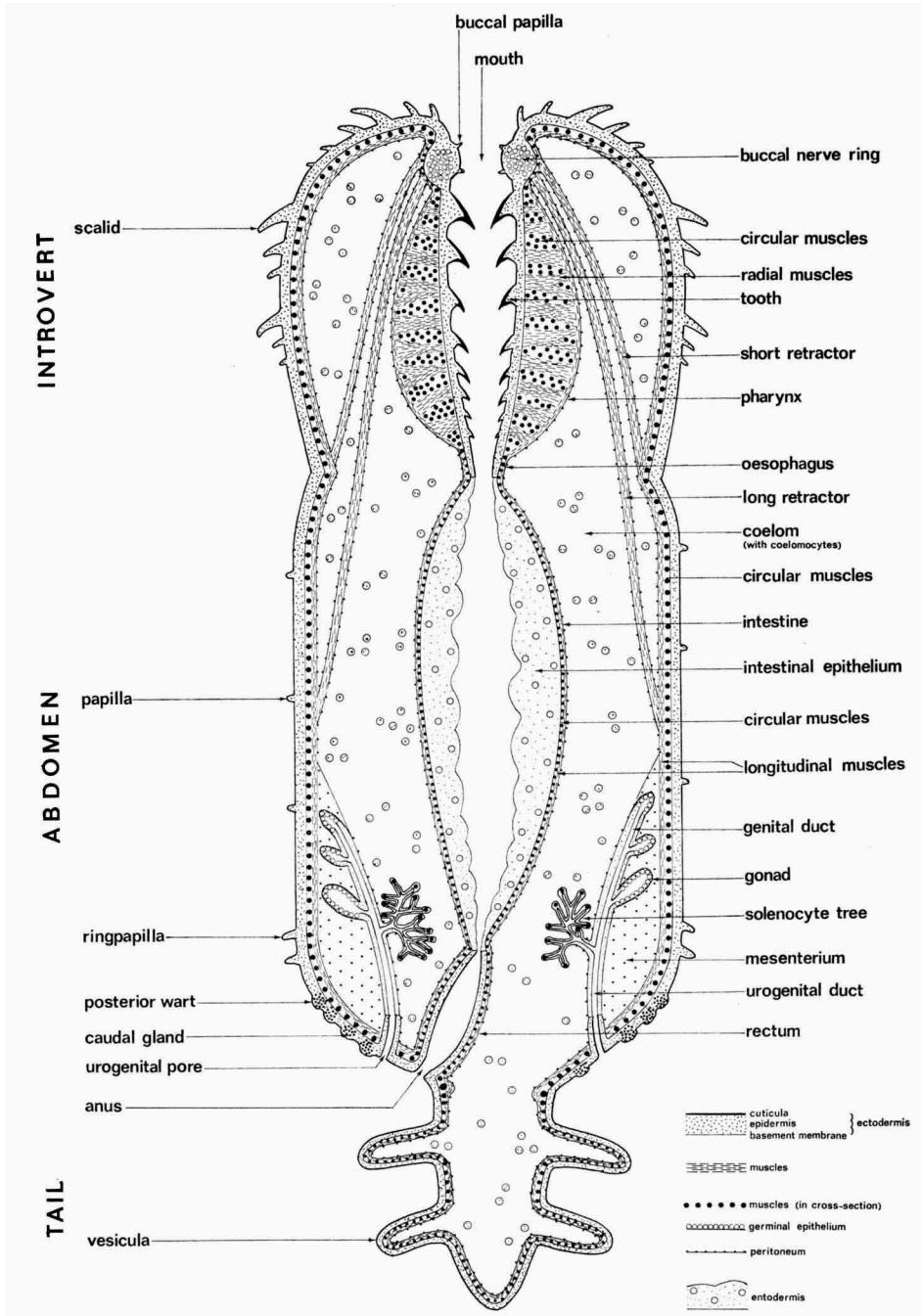


Fig. 1. Diagram of priapulid organization.

Priapulopsis Koren & Danielssen, 1875

3. *Priapulopsis bicaudatus* (Danielssen, 1868)
4. *Priapulopsis australis* (de Guerne, 1886)

Acanthopriapululus n. gen.

5. *Acanthopriapululus horridus* (Théel, 1911) n. comb.

Halicryptus von Siebold, 1849

6. *Halicryptus spinulosus* von Siebold, 1849

Familia Tubiluchidae n. fam.

Tubiluchus van der Land, 1968

7. *Tubiluchus corallicola* van der Land, 1968

2.2.3 Definition of terms

A number of less known morphological terms appearing in the keys, diagnoses, and descriptions are defined below. A complete glossary will be compiled only after completion of my studies.

CAUDAL GLAND. — Epidermal gland occurring in posterior part of abdomen of *Priapululus* (fig. 1, 20) and larval *Halicryptus*.

DENTOSCALID. — Scalid with strongly cuticularized distal part in the shape of a tooth, occurring on the introvert of *Halicryptus* (fig. 42-43).

FIMBRILLA. — Small cuticular ridge provided with a row of tiny hairs, occurring in the posterior part of the pharynx of *Tubiluchus* (fig. 59).

FLOSCULUS. — Small sense organ in the shape of a flower, occurring on neck and abdomen of *Tubiluchus* (fig. 65).

LORICA. — Cuticular encasement of the abdomen of the larva.

POLYTHYRIDIDIUM. — Intricate cuticular organ (?filtering apparatus) between pharynx and intestine, occurring in *Tubiluchus* (fig. 55).

POSTERIOR WART. — Wartlike protuberance occurring on posterior end of abdomen of *Priapululus* (fig. 13).

PRICKLE. — Delicate spine occurring in posterior part of the pharynx of *Tubiluchus* (fig. 58).

RINGPAPILLA. — Papilla occurring on posterior part of abdomen of *Priapulidae* (fig. 1, 13); a number of ringpapillae are typically arranged in one of more circlets around the abdomen.

SCALID. — Protuberance on introvert in one of several different shapes (fig. 11, 19, 27, 42, 56).

TOOTH, CUSPDATE. — Pharyngeal tooth provided with cusps, usually a strong median cusp and a number of smaller lateral cusps (fig. 2, 17, 48).

TOOTH, PECTINATE. — Pharyngeal tooth in the shape of a comb, occurring in *Tubiluchus* (fig. 53-54).

TUBULUS. — Tubelike tactile(?) organ, occurring on the abdomen of *Tubiluchus* (fig. 62, 79) and larvae of Priapulidae (fig. 21).

TUMULUS. — Very small conical protuberance, occurring on abdomen of *Priapulopsis* (fig. 34) and *Tubiluchus* (fig. 64).

VESICULA. — Vesiclelike appendage of the tail, occurring in Priapulidae (fig. 9, 32, 36).

2.2.4 Basic adaptive features

The Priapulidae are burrowing animals living in more or less muddy sediments and are primarily adapted to predaceous habits as appears from their strong pharyngeal armature and as has been proved by observations. They are among the very few actively burrowing predatory worms. It has been suggested (Hickman, 1967) that the small number of species shows that the group has undergone little evolutionary divergence, but the view that they are the last remnants of a once much larger group is more acceptable. It has been shown that at least the same type of animals did already occur in the Middle Cambrium (Walcott, 1911). It is quite understandable that such animals, with their very inefficient means of locomotion (Clark, 1964) in general could not resist the competition of burrowing animals of more advanced types such as arthropods. The fact that the living species are capable of occupying certain marginal, chemically unstable ecologic niches may have been of major survival value.

Tubiluchus, the only psammobiont among the priapulids, undoubtedly represents a sideline, adapted to an interstitial life. Its habits are unknown, but its delicate pharyngeal armature and unrecognizable intestinal contents suggest that it might be a detritus feeder. The characteristic polythyridium also indicates that the food consists of small particles.

2.2.5 General features

Size and colour. — The Priapulida are small to rather large worms, their length ranging from a few mm to about 200 mm, although specimens attaining a length of more than 100 mm are rare even in the largest species. Small specimens are colourless and transparent; larger specimens are opaque and drab or cream-coloured, occasionally with a metallic sheen; the cuticula is often wholly or partly covered with an incrustation resulting in a dark grey, black, or rusty colour, depending on the nature of the sediment. In alcohol or formalin the animals are whitish, cream-coloured, or yellowish-brown; large specimens of *Priapulus* are reddish-brown.

Body-divisions. — The body is thick, cylindrical, with a maximum of four divisions: introvert, neck, abdomen, and tail(s). The introvert, the anterior part of the body, has about the same diameter as the abdomen. A distinct neck-region is only present in larvae; a less distinctly demarcated neck is found in adult *Tubiluchus*. One (*Priapulus*, *Acanthopriapulus*, *Tubiluchus*) or two (*Priapulopsis*) slender tails are implanted on the posterior end of the abdomen, but a tail is lacking in adult *Halicryptus* and in the larvae of all species. The whole body is flexible (except the abdomen of the larvae) so the relative proportions of the various parts of the body are subject to continuous changes in living specimens. The appearance of fixed specimens is highly dependent on the method of fixation and the nature and strength of the fixative; it is unnatural in any case.

Symmetry. — The Priapulida are essentially bilaterally symmetrical animals, but this condition is highly obscured, as is often the case in burrowing animals in which the dorsal, ventral, and lateral surfaces are subject to the same environmental stimuli and perform the same functions. Bilateral symmetry is exhibited internally by the presence of a single nerve cord and a pair of urogenital organs. The location of the nerve cord is postulated as being ventral, the reasonableness of which is confirmed by the presence of male epidermal specializations on the same side in *Tubiluchus*. Conspicuous external bilateral symmetry occurs only in the larvae of the Priapulidae.

Radial symmetry is exhibited by the introvert, which has 20 or 25 longitudinal rows of scalds, and the pharyngeal armature, the anterior circlets of which have five or ten teeth. It is most strongly marked in *Tubiluchus* larvae, in which the lorica, circular in cross-section, is furnished with 20 longitudinal ridges, long ones alternating with shorter ones. It is difficult to relate the two different numbers of radii (20 and 25) to each other. There are two possible theories. In the first place both conditions can be described as pentaradiar, but in that case we must conclude that they developed in different ways. When we prefer to hold the view that they must have developed in the same way, the first condition (occurring in *Tubiluchus*) is to be called tetraradiar, the second one (occurring in Priapulidae) pentaradiar. The fact that in related animals a different way of development is more likely to occur than a different starting-point, supports the first mentioned theory.

Of course the occurrence of pentaradial symmetry was the main reason why the Priapulida were considered to be related to the Holothuria by Linnaeus and other early authors.

Introvert. — The introvert, the anterior part of the body and most important locomotory organ, is characterized externally by the presence of 20

or 25 longitudinal rows of scalids. Until now only descriptive terms such as papillae, cones, spines, and hooks have been used for these organs, which show quite a variety of shapes. The term scalids is proposed here because in *Kinorhyncha* the same term is being used for analogous, if not homologous, organs.

The scalids are arranged in series, in which the size gradually decreases from the first to the last. In adult *Tubiluchus* (fig. 56), adult *Halicryptus* (fig. 42-43), and all larvae (fig. 19, 49, 78) each row of scalids consists of only one such series; in adult *Priapululus* (fig. 11) and *Priapulopsis* (fig. 27-29) each row consists of several subsequent series. Usually a number of scalids near the mouth entrance do not fit in the rows.

In larvae of *Halicryptus* (fig. 49-50), the posterior part of the introvert is provided with adhesive tubes, by which the animals can adhere to objects when the introvert is withdrawn.

The introvert can be completely invaginated into the abdomen, but in adult Priapulidae this is done only in the act of burrowing; in fixed specimens it is usually protruded. However, in fixed specimens of *Tubiluchus* it is commonly introverted. This may be caused by the retractor muscles reacting more vigorously to fixatives, but it possibly indicates that the introvert is withdrawn when the animal is at rest, as is also the case in all larvae.

Neck. — In most adults the introvert is demarcated from the abdomen by a simple constriction only, but a distinct neck-region is present in the larvae. It is characterized by a number of cuticular folds. The system of folds is most elaborate in *Tubiluchus* (fig. 75) where it acts as a fold-up closing apparatus when the introvert is invaginated into the lorica (fig. 76); small sense organs are located on the folds. In *Priapululus* (fig. 14-15) and *Priapulopsis* some of the fields between the ridges are developed into plates, which also serve as a closing apparatus (fig. 16). The larval priapulids have the possession of a closing apparatus in common with adult kinorhynch.

In adult *Tubiluchus* (fig. 66) the neck region is characterized by the absence of tumuli and a more or less conspicuous annulation caused by the circular dermal musculature. Besides it scarcely differs from the abdomen.

Abdomen. — In adult Priapulidae the trunk is distinctly annulated, the large number of annuli (about 30 to about 100) corresponding with the circular muscles of the body wall. It is always provided with many scattered papillae (fig. 8) or setae (fig. 41) and so presents a somewhat warty or spiny appearance. In all genera but *Halicryptus*, one or more annuli close to the posterior end are provided with special papillae, called ringpapillae (fig. 13, 31, 36). In *Priapululus* the last annuli of the abdomen are densely

covered with cushionlike papillae, the posterior warts (fig. 13); each of them shows numerous minute secretory pores of the caudal glands. In *Priapulopsis* the cuticula is provided with numerous, irregularly distributed tumuli, invisible to the unaided eye (fig. 34).

The abdomen of *Tubiluchus* is not annulated but thickly beset with tumuli (fig. 51, 64), characteristically disposed in longitudinal and transverse rows. Moreover, there are many irregularly distributed tubuli and other sense-organs. There is a marked sexual dimorphism, the whole ventral surface being covered with numerous setae of different kinds in the male (fig. 51, 66-74).

In larvae the cuticle of the abdomen is relatively thick and rigid (except at the posterior end) and this is why the cuticular covering of the trunk is called lorica. It is not unlike the lorica of certain rotifers. In Priapulidae (fig. 14-15, 44) the lorica is dorsoventrally flattened, with four longitudinal ridges or folds on each of the lateral sides, two lateral and two dorso-lateral. In *Halicryptus* the cuticula of the dorsal and ventral fields is thicker than that of the lateral fields; therefore it is justified to speak of dorsal and ventral plates in this genus (compare fig. 22 and fig. 47). In *Tubiluchus* (fig. 75) the lorica is circular in cross-section and 10 ridges extend along its whole length, alternating with shorter ridges. In all larvae, except those of *Halicryptus*, the lorica carries a number of tubuli (fig. 21, 79). In *Priapululus* and *Priapulopsis* there are four of them; one tubulus on each of the lateral ridges. In *Tubiluchus* the lorica bears up to 20 tubuli, also associated with ridges. In addition small sense-organs are present in all species. In larval *Priapululus* the posterior end of the abdomen carries a tubelike structure, enclosing the secretory duct of the caudal glands (fig. 20). In the literature this structure has received more attention than it deserves. The reason is that it was described erroneously as a foot with toes by K. Lang (1939) who, therefore, compared it with the foot of the Rotatoria and considered it to be of phylogenetical significance.

Tail. — Basically the tail is a cylindrical post-anal extension of the abdomen. Its skin is continuous with the skin of the abdomen and originally differs from it only in the relative abundance of cuticular structures. Simple original forms are represented by *Tubiluchus* (fig. 51) and postlarval *Priapulopsis* (fig. 30). In *Priapululus* (Pl. 2 A) and *Acanthopriapululus* (fig. 35) the tail is more or less noticeably divided into segments. In *Priapululus* and *Priapulopsis* the original shape is obscured in the course of postlarval development when part of the papillae gradually develop into vesiculae. In adult *Priapululus* the segments are only visible in exceptional cases. Highly

characteristic structures are present in *Acanthopriapulius* in which the tail is beset with posteriorly directed hooks (fig. 35, 37).

There is a great variation in the size of the tail, especially in *Priapulius*, in which it varies from a small stump with few vesicles to an enormous organ of about the same volume as the rest of the body. It is contractile in all species and in living specimens it slowly but continuously changes its shape and volume.

Several discussions about the function of the tail can be found in the literature (see survey given by K. Lang, 1948a), but all of them refer to the type occurring in *Priapulius* and *Priapulopsis*. It is clear that the *Priapulius*-type, the *Acanthopriapulius*-type, and the *Tubiluchus*-type should be considered separately in this connection. The considerable morphological differences are indicative of different functions. Moreover, each type may accomplish more than one function.

It has often been supposed that the vesiculate tail of the *Priapulius*-type has a respiratory function. Evidential facts are the relatively thin cuticle of the vesiculae in comparison with the very thick cuticle of the abdomen, which does not permit a rapid uptake of oxygen, and the considerable increase of the body surface caused by the vesiculae. The observations by Fänge & Mattison (1961) also point this way. However, in the view of K. Lang (1948a) it is not a respiratory organ; its function is uncertain but it possibly serves as an accessory excretory organ or a chemo-receptory organ. Experiments by K. Lang proved that, under normal circumstances, the animals can do without a tail very well. However, when it is cut off it regenerates rapidly. Experiments by Nyholm & Bornö (1969) showed that the oxygen intake is not lowered when the tail is being blocked; according to them the tail has an important respiratory function mainly in conditions of low oxygen concentration.

In *Acanthopriapulius* the tail has a strong circular and longitudinal musculature. The muscles make the impression of being strongly contracted in the only known specimen, leaving only a very narrow cavity in the tail. This is highly suggestive of the possibility that the tail segments can be "blown up" to a considerably larger size (by pressure of the coelomic fluid). One is inclined to think that this very peculiar tail might serve as an anchor, perhaps during burrowing. The structure of the introvert and the presence of ring papillae indicate that burrowing is accomplished in the same way as in *Priapulius*. Since the hooks are directed posteriorly the tail can only act against forces in a posterior direction and most effectively so in a burrow.

The tail of *Tubiluchus* is quite unlikely to have a respiratory function. The animal is so small that it probably does not need a special respiratory

organ at all, let alone one of the size of its tail, which is up to two and a half times as long as the body. We can be sure that this muscular and very contractile tail mainly serves as an anchor and retractor. Such devices are of frequent occurrence among interstitial animals.

Mouth. — The mouth entrance is surrounded by a ring in which the buccal nerve ring is located. The ring has often been called collar, because in fixed specimens it is often visible as an external collar posterior to the everted part of the pharynx (Pl. 1 A, 2 C); the normal condition is shown in Pl. 4. Usually the cuticula bears a number of cuticular structures, here called buccal papillae. Sometimes they are in the form of simple conical papillae terminating in a spinulet, sometimes (e.g., in *Halicryptus*) they look much the same as the scalids. Their number is not very constant and even in one species there may be very few in one specimen and a great many in another one. They seem to be lacking in the larvae.

Pharyngeal armature. — In Priapulidae the whole cuticular lining of the pharynx is covered with cuspidate teeth. The anterior teeth are arranged in circlets of five teeth, commonly called pentagons in the literature. In *Priapulopsis* (fig. 24-25) the first circlet typically comprises ten teeth, being five pairs of small teeth of which each pair apparently originates from one large tooth that lost its median cusp. In large specimens there are hundreds of teeth, gradually decreasing in size posteriorly. The arrangement and relative size of the teeth is of systematic significance.

Each tooth usually is made up of a broad base, a large median cusp, and a number of lateral cusps. Each cusp may be provided with one or more lateral denticles and in postlarvae very small scattered denticles may also be present on the base (fig. 5, 25). The cuticula of the base is not sharply delimited from the surrounding pharyngeal cuticula, especially in younger specimens where the basal part of the teeth is not yet heavily cuticularized. Contrary to the common belief the number of lateral cusps is only of limited systematic significance, for three reasons. (1) There is a considerable individual variation. (2) In teeth of the same pharynx their number first increases backwardly (as is shown in the figures) and then decreases again (not shown in the figures) until only a tiny median cusp is left in the posteriormost teeth; moreover, teeth of the same circlet may be somewhat different and even the left and right sides of one tooth usually differ. (3) Their number decreases after each moult, so in general the number of lateral cusps is higher in younger specimens. There is only a very small change in each moult (fig. 6-7). Possibly there is also a geographical variation but this could not yet be proved.

The anterior part of the pharyngeal cuticula in *Tubiluchus* is beset with pectinate teeth (fig. 52-54), all of about the same size. These teeth consist of a manubrium, embedded in the cuticula, and a comblike distal part, provided with delicate spines. Contrary to the teeth of the Priapulidae they are not hollow, not filled with epidermis. Probably they do not develop as a cuticular sheath, but originate from a cluster of epidermal cells (here indicated as "tooth-glands"), much in the same way as the claws of tardigrades that are formed in so-called claw-glands. The posterior half of the pharynx is devoid of teeth and provided with delicate spines (prickles, fig. 58) and ridges with tiny hairs (fimbriae, fig. 59). The whole structure makes the impression of being a scraping organ rather than being adapted for capturing preys.

The pharyngeal armature of larvae of all species, including *Tubiluchus corallicola*, is basically the same as in adult Priapulidae, the anterior circlets each consisting of five large teeth. They are of the cuspidate type but there is a greater variation than in adults (fig. 17-18, 48, 77). The cusps are often more numerous and frequently have the form of tiny spines or denticles; sometimes they are arranged in more than one row.

Polythyridium. — This cuticular specialization of peculiar and unique construction occurs only in adult *Tubiluchus* (fig. 55). It encircles the entrance of the intestine and consists of a number of hollow cuticular plates (valvulae), arranged in circlets, and is provided with a strong circular muscle. There are two types of valvulae; those of the anterior circlets have a turn-back top, thickly beset with small tubercles (fig. 60), those of the posterior circlets bear a distal fringe of delicate hairs (fig. 61). Its function can only be guessed; possibly it serves as a filtering apparatus. It may be imagined that large particles are prevented from entering the intestine.

Epidermis. — The epidermis is made up of one layer of definite epithelial cells; it is not a syncytium. It does not only cover the body wall but also lines parts of the internal organs. Anteriorly there is a well developed stomodaeum, most elaborate in *Tubiluchus*; posteriorly intrusions of epidermis line the rectum and the terminal parts of the urogenital ducts. Everywhere it secretes a conspicuous cuticle. In many places the epidermis is modified to form the previously described cuticular structures. Most of them are filled with very high columnar cells. Only the smallest, such as small denticles and hairs, are not hollow; the pharyngeal teeth of *Tubiluchus* also seem to be solid structures. Other modifications include the adhesive glands in *Hali-*

cryptus larvae (fig. 50), the caudal glands in the posterior warts of *Priapulius* (fig. 13), and the caudal glands of larval *Priapulius* (fig. 20) and *Halicryptus* (vide Hammersten, 1915, and Hammersten & Runnström, 1920). The function of the caudal glands is uncertain. Sometimes the posterior warts shrink to such a degree that they become almost invisible, so the caudal glands are apparently inactive at times. Probably they have nothing to do with reproduction since they are present in all stages.

In cross-sections the cuticula is seen to be composed of two layers. The outer layer contains chitin, much like α -chitin (Shapeero, 1962a), the inner layer consists of proteins only (Carlisle, 1959). Throughout life the outer layer is shed periodically and replaced by the inner layer, in which chitin is formed after moult and beneath which a new inner layer is secreted. The moulting process has often been described, e.g., by Apel (1885), Hammersten (1915), Wesenberg-Lund (1929), Schulz (1931), K. Lang (1948a), and Shapeero (1962a; 1962b). Cuticular structures such as teeth and scalids are newly formed just before moulting (fig. 6-7). At first they are softer than the old ones, but they have their definite form already and do not confuse the systematist by undergoing a development in the intermoulting period as has been suggested by Murina & Starobogatov (1961: 187). The observer may be confused in a different way, namely by new structures being reduced in size or not being formed at all. Terata of this kind are rare. The present author found one specimen of *Priapulopsis australis* among a number of normal specimens which was completely devoid of scalids. In his opinion *Priapulius tuberculatospinosus japonicus* Murina & Starobogatov was based on a similar teratological specimen, the scalids being absent or reduced to vaguely discernible tubercles; the teeth of the first circler are also strongly reduced.

In fixed specimens the outer layer of the cuticula is often separated from the inner layer. Undoubtedly this is usually an artefact, but it is not impossible that it is natural in the larvae where it can be observed in nearly every specimen. This is especially emphasized by Hammersten (1915) who claims to have seen elastic fibers between the lorica and the body proper, attributing to them a function as accessory retractors. The present author could not find fibers, apart from a number of tiny nerve fibers innervating the sense-organs of the lorica.

Intestine. — The intestine is a quite simple organ. It is straight in extended specimens, curved in contracted specimens. The epithelium consists of a single layer of columnar cells. In small specimens they are of about the same height, but in larger specimens circular areas of low cells alternate

with areas of very tall cells, resulting in a folded appearance of the inner wall of the intestine. According to Shapeero (in Hickman, 1967: fig. 13-5) the cells are provided with a brush border.

Nearly the whole intestinal canal lies free in the body cavity. In *Tubiluchus* larvae retractor muscles run from the posterior part of the pharynx to the body wall of the abdomen. In adult *Tubiluchus* the posterior part of the intestine is attached to the body wall and to the urogenital organs by mesenterial strands. In *Halicryptus* (Lüling, 1940) and *Priapulus* (Théel, 1911: fig. 7) the rectum is attached to the urogenital organs by mesenterial strands and to the body wall by radial muscles.

Nervous system. — In adult Priapulidae the ventral nerve cord is nearly always visible from the outside as a lighter band. In the preanal ganglion the groups of nerve cells are large relative to the nerve cord, especially in *Tubiluchus*; perhaps they have a neurosecretory function.

The peripheral nervous system is not well known; its delicate nerves cannot easily be followed. Only Apel (1885) claims to have seen several of the main peripheral nerves. A study of the nervous system with specific methods is highly desirable.

Sense organs. — In fact not much is known about the sense organs of priapulids. Probably many of the previously mentioned cuticular specializations are associated with receptors. The tubuli of larval *Priapulus*, *Priapulopsis*, and larval and adult *Tubiluchus* perhaps serve as tangoreceptors (they are innervated and are not associated with muscles or glands); the same may hold for the setae of *Halicryptus*. The highly characteristic flosculi of *Tubiluchus* may serve as chemoreceptors. Small spinulets are of common occurrence, e.g., on the tail vesicles, the abdominal papillae, and the ringpapillae of *Priapulus* (fig. 8-10, 13); possibly they too have a sensory function.

Finally mention may be made of the ventral setae of *Tubiluchus*, only occurring in the male (fig. 51, 66-74). Supposedly they serve in copulation and several of them undoubtedly act as sense organs.

Musculature. — The greater part of the tissues of a priapulid consist of muscles. In the first place there is a well developed dermomuscular tube, consisting of an external layer of circular muscles and an internal layer of longitudinal muscles. In large adults these layers may be continuous, but in places the muscles are arranged in definite bundles, e.g., the circular bundles

associated with the abdominal annuli of the Priapulidae. Sometimes additional longitudinal muscles occur between the epidermis and the circular muscles, e.g., underneath the rows of scalids in the introvert of *Priapululus*. Both layers extend over the digestive tract. In the pharynx bundles of radial muscles are present in the circular layer. In *Tubiluchus* there is a peripharyngeal ring-muscle posterior to the peribuccal nerve ring (fig. 55). Circular muscles at the base of the tail serve as a sphincter. In *Tubiluchus* and in larvae of Priapulidae the layers are more or less discontinuous.

A circle of introvert-retractors originates on the body wall on the level of the buccal nerve ring. Short retractors (lacking in *Tubiluchus*) are attached to the body wall at the posterior end of the introvert. Long retractors are attached to the wall of the abdomen; they are longest in *Priapulopsis* in which they nearly reach the level of the ringpapillae; they are shortest in *Halicryptus* in which they do not extend farther backwards than the anterior fifth part of the abdomen. The number of retractors is subject to some variation, even in one species. There are about 10 to 14 short retractors and about 8 long ones.

In larvae of all species there is also a cirlet of pharyngeal retractors, originating from the posterior part of the pharynx. In *Priapululus* and *Halicryptus* they extend along the dorsal and ventral sides of the intestine (fig. 22, 47) and are attached to the rectum. In *Tubiluchus* they are probably attached to the body wall (Van der Land, 1968). Adult *Priapululus* and adult *Tubiluchus* possess one dorsal and one ventral pharyngeal retractor. In the former they are strong muscles extending along the whole length of the intestine (with which they are connected by a mesenterium) and attached to the rectum. In the latter they are much shorter and attached to the anterior part of the intestine. In adults of *Priapulopsis* and *Halicryptus* pharyngeal retractors are lacking. In the former remnants are present in the form of a dorsal and a ventral muscle running from the anterior to the posterior part of the intestine (with which they are also connected by a mesenterium).

A cirlet of radial muscles is present around the rectum, attaching it to the body wall.

The retractors and part of the muscles of the body wall are striated. The spaces between the muscle-fibers are filled up with connective tissue.

The way in which the muscles of the body wall and the retractors are used in locomotion has been described by Friedrich & Langeloh (1936) (see also: Clark, 1964). *Priapululus* is best adapted to burrowing with the help of the introvert, although peristaltic movements of the abdomen also play a rôle. *Halicryptus* moves much slower because its introvert is very small; perhaps peristaltic movements are relatively more important in this species, as is

also suggested by the very large number (about a hundred) of abdominal annuli. The locomotion of *Tubiluchus* has not yet been observed. Undoubtedly it is capable of burrowing but it is questionable if this is possible in coarse sediments. It is more likely to move by alternately extending and contracting its body and adhering to sand grains by its tail and introvert, respectively.

Coelom. — The body cavity is lined with a very thin membrane. By Apel (1885) and several later authors it was described as a structureless membrane and therefore the body cavity was often considered a "pseudocoel", whatever this may be. In fact the membrane is an extremely flat epithelium in which the nuclei are easily overlooked. It was already observed by Danielssen & Koren (1881) and Molčanov (1908). All internal organs are clothed with the peritoneum, with the possible exception of the solenocytes and the gonads (they are covered with a very thin membrane without any visible structure even under the electron microscope).

Mesenteria are not important in priapulids and the coelom is not divided into compartments by septa. Most conspicuous are the mesenteria by which the urogenital organs are attached to the body wall. Probably these mesenteries are indeed double layers of peritoneum as evidenced by the fact that the urogenital organs grow into it. In this connection the observations by Lüling (1940) are of great importance. Other mesenterial structures include the membrane by which the pharyngeal retractors are attached to the intestine (*Priapulus*; *Priapulopsis*), the mesenterial strands (sometimes forming a nearly complete diaphragma) by which the urogenital organs are attached to the rectum (*Priapulus*, *Halicryptus*), and the strands running from the posterior part of the intestine to the body wall (*Tubiluchus*).

The coelom acts as circulatory system, the coelomic fluid moving freely through the whole body and the tail. There are numerous floating coelomocytes. The vast majority are erythrocytes: disc-shaped cells containing haemerythrin, a red respiratory pigment. According to Fänge & Åkesson (1951) the erythrocytes cannot serve as oxygen carriers and most probably the haemerythrin has only the function of storing oxygen, which can be used when the oxygen concentration of the water is very low. Amoebocytes, with pseudopodia of the petaloid type, are present in much smaller numbers. As was shown by Molčanov (1908) and Hammarsten (1915) the coelomocytes also serve as excretophores, transporting the excreta to the epidermis or to the excretory organs.

Excretory system. — Perhaps priapulids can get rid of products of metabolism in different ways, but the only conspicuous excretory organs are

the solenocyte trees (groups of solenocytes arranged in the shape of a tree), located in the posterior part of the abdomen. In *Tubiluchus* there is only one solenocyte tree on each side, directly entering into the urogenital duct. In Priapulidae there are a few (in the larvae) to a great many of them and (at least in *Priapulius*) they enter into one or more saclike expansions of the excretory duct. The best descriptions are those by Lüling (1940) and Nørrevang (1963c).

Among the solenocyte trees a second type, the glandular tree, was recently discovered by Nørrevang (1963c). The end-bulb cells do not have a flagella; they secrete droplets. This type was found in *Priapulius* and *Priapulopsis* but only in very small numbers.

Genital organs. — As was shown by Lüling (1940) the gonads originate ontogenetically from the wall of the excretory duct. In larvae and postlarvae they are not yet present. They develop as canals penetrating into the mesenterium. In the female these canals develop into ovarian sacs, their walls being the germinal epithelium. In the male the germinal epithelium is formed by the walls of diverticles of the canals.

Hermaphroditic individuals are rare; they have only been reported twice (Molčanov, 1908; K. Lang, 1939).

In all priapulids the situation is basically the same, but of course it is greatly obscured in the large species in which the gonads develop into intricate organs with hundreds of ovarian sacs and thousands of testis diverticles. The most simple condition occurs in *Tubiluchus* in which the gonads consist of a small number of diverticles, in the order of ten to fifteen.

Spermatogenesis has been described by Lüling (1940) and Franzén (1956a). The sperm is of the primitive type, consisting of a short head, a short middle piece and a very long and thin tail. Oogenesis has been described by Lüling (1940) and Nørrevang (1965). There is only one doubtful observation on the chromosomes (Nørrevang, 1963b).

All genital canals, the walls of which are provided with flagellae, open into a common genital duct, which in its turn opens into the common excretory duct to form a simple straight urogenital duct. In Priapulidae the eggs and sperms are shed into the water, where fertilization occurs. Probably internal fertilization occurs in *Tubiluchus*, the occurrence of copulation being the most sensible explanation of the sexual dimorphism. Sperms could not yet be found in the cross-sections of females; in one whole mount of a female small bodies, which could possibly be sperms, were observed in the urogenital ducts. A receptaculum seminis seems to be lacking.

Development. — Little is known of the embryology. Only a few observations have been made on the earliest stages of *Priapulius* and *Halicryptus* (K. Lang, 1939, 1953; Žinkin, 1949; Žinkin & Korsakova, 1953), with partly contradictory results. The fertilized eggs are heavy and sticky; apparently they develop on or in the sediment (K. Lang, 1939). Their cleavage is total and equal, of the bilateral type. Later stages include a coeloblastula and a gastrula, probably resulting from invagination. The origin of the mesoderm is uncertain. According to Lang it arises from the ectoderm; according to Žinkin & Korsakova it is of endodermic origin.

The larva of *Priapulius caudatus* leaving the egg has an extremely simple morphology (K. Lang, 1953). It only consists of an ectoderm and an undifferentiated inner cell mass. It is a very small, oval, strongly contractile, unciliated animal without a cuticle. Its further development is unknown.

As may appear from the present paper the morphology of the later larval stages is fairly well known. The development of the larvae of *Halicryptus* is best known (Purasjoki, 1944); there are four larval stages in this species. The larval development seems to last extraordinarily long; according to K. Lang (1939: 85) the larvae of *Priapulius caudatus* need at least two years to complete their development.

There is a distinct metamorphosis between the last larval stage and the youngest postlarval stage. It has been observed in *Halicryptus* (Hammersten, 1915; Purasjoki, 1944) and in *Priapulius* (K. Lang, 1939). The whole procedure takes place within the larval cuticle.

2.2.6 Systematic notes

Status. — The question of the relationship of the Priapulida with other animals will be dealt with later, when all known facts can be put together. It is useless to make premature statements about such a complicated problem, which can only be solved, if solvable at all, by a group of cooperating experts in several different groups and various different fields of research. The present state of our knowledge does not justify the inclusion of the Priapulida in any of the other phyla. The best solution is to consider the Priapulida a separate phylum for the time being, but we must not hesitate to unite it with another phylum as soon as it has been established that they are more closely related to each other than to other phyla. Undoubtedly the Kinorhyncha are the most serious candidates (K. Lang, 1953, 1963).

Subdivision. — It is proposed to divide the Priapulida into two families: the Priapulidae and the monotypic Tubiluchidae. From what has been stated

above about the structure of *Tubiluchus* it is evident that this meiobenthic genus differs considerably from the other, macrobenthic priapulids. Especially noteworthy in *Tubiluchus* are the pharyngeal armature of the adult, the peculiar polythyridium and several other unique cuticular specializations, the sexual dimorphism and probable internal fertilization, the radial symmetry of the larva and the different number of radii. In other groups of worms such marked differences would probably justify a subdivision on an even higher level, but it is not necessary to do this in such a small group.

For the same reason *Halicryptus* is kept in the family Priapulidae in spite of the fact that it noticeably differs from the other members of the family.

2.3 KEY TO THE TAXA

The following key has been designed to allow the identification of priapulids of all stages, as far as this is possible and as far as the stages are now known. In general it is also possible to identify specimens in which the anterior or posterior half is lacking (this is not uncommon in dredged specimens and in specimens from fish stomachs) or in which certain characters are indistinct (this is not uncommon either). It is mostly not necessary to dissect the pharynx.

1. Body wall of abdomen flexible, capable of peristaltic movements. Tail present in most species. Length about 1 to 200 mm adults (Pl. 1) or postlarvae (Pl. 2B, C, E) 2
- Abdomen enclosed in rigid lorica with longitudinal cuticular ridges. No tail. Length less than 2 mm larvae (Pl. 2A, D, F) 9
2. Pharynx with cuspidate teeth of many different sizes (fig. 2-4). Introvert with 25 rows of scalids. Abdomen with large number of annuli (Pl. 1A-D); sometimes covered with inconspicuous and irregularly distributed tumuli (fig. 34); provided with scattered papillae and sometimes with setae, but not with tubuli. Tail absent or one or two tails present, in the adult provided with vesiculae. Small to large benthic worms (2 to 200 mm) from extra-tropical waters and tropical deep-sea Priapulidae 3
- Pharynx with pectinate teeth (fig. 54), all of about the same size. Introvert with 20 rows of scalids. Abdomen without annuli; covered with tumuli arranged in regular rows (fig. 64); provided with numerous tubuli. One tail, densely covered with tumuli, but without vesiculae. Meiobenthic worms (less than 6 mm long) from tropical waters *Tubiluchus corallicola*

3. Introvert relatively short, with only one series of scalids, including dentoscalids (fig. 42). Abdomen with numerous setae (fig. 41), giving the animal a spiny appearance; no ringpapillae. Tail absent. Length 2 to 40 mm. Northern waters *Halicryptus spinulosus*
- Introvert with several series of scalids in each row; no dentoscalids present (fig. 11). Abdomen without setae; one to several annuli near the posterior end are provided with ringpapillae. One or two tails. Length 2 to 200 mm. Northern and southern waters and deep-sea 4
4. Pharyngeal armature: first circllet consisting of 10 very small teeth (fig. 24-25). Scalids telescopiform (the distal part can be telescoped into the basal part) (fig. 26-29). Abdomen without posterior warts, but ringpapillae quite conspicuous; skin covered with tumuli (fig. 34). Two unsegmented tails; vesiculae with a group of distal spinulae or without spinulae (fig. 32-33) *Priapulopsis* 5
- Pharyngeal armature: first circllet consisting of five (occasionally small) teeth (fig. 2-4). Scalids not telescopiform (fig. 11-12). Skin of abdomen smooth, without tumuli. One segmented tail (Pl. 2A) (intersegmental furrows usually invisible in large specimens); vesiculae with scattered spinulae (fig. 9-10) 6
5. Pharyngeal armature (fig. 25): teeth of first circllet with a row of denticles; teeth of fifth circllet not much smaller than those of fourth one and not followed by a conspicuous gap. Scalids (fig. 28) of a series not very close together, basal parts smooth and never fused; only a small gap between the series of a row. Vesiculae of tail with a conspicuous group of distal spinulae (fig. 32). Northern waters
. *Priapulopsis bicaudatus*
- Pharyngeal armature (fig. 24): teeth of first circllet hardly visible, reduced to a single denticle; teeth of fifth circllet much smaller than those of fourth one and followed by a conspicuous gap. Scalids (fig. 27) of a series close together, basal parts pubescent and often fused; large gap between the series of a row. Vesiculae of tail with a distal group of very few and very small spinulae or without spinulae (fig. 33). Southern waters *Priapulopsis australis*
6. Scalids relatively small and sparse, arranged in indistinct rows; series probably also indistinct (Pl. 1B). Abdomen without posterior warts (fig. 36). Tail covered with strong chitinous hooks and with vesiculae on the first segments only (at least in the only known specimen) (fig. 35). South Atlantic *Acanthopriapululus horridus*
- Scalids arranged in regular rows and in conspicuous series, at least in the anterior part of the introvert. Last annuli of abdomen covered with

- warts (fig. 13) (sometimes they are quite inconspicuous and in small specimens there are only few of them). Tail when fully developed usually completely covered with vesiculae (Pl. 3); in postlarvae with spinulae only (Pl. 2A) *Priapulus* 7
7. Tail without vesiculae or with very few vesiculae only. Small (less than 10 mm) . . . postlarvae of *Priapulus caudatus* or *P. tuberculatospinosus*
- Tail usually densely covered with vesiculae. More than about 10 mm long 8
8. Pharyngeal armature (fig. 3-4): teeth or first circllet much smaller than those of second circllet (e.g., width of tooth of first circllet less than 40% of width of tooth of second one); two of the teeth of the fourth circllet are evidently larger than the other teeth. Southern waters and deep-sea *Priapulus tuberculatospinosus*
- Pharyngeal armature (fig. 2): teeth of first circllet not much smaller than those of second one; teeth of fourth circllet are subequal in size. Northern waters and deep-sea *Priapulus caudatus*
9. Lorica radially symmetrical, with 20 longitudinal ridges and with many scattered tubuli (fig. 75). Tropical waters . . . *Tubiluchus corallicola*
- Lorica bilaterally symmetrical, dorsoventrally flattened, with 8 longitudinal ridges and on each side with two tubuli or without tubuli. Extra-tropical waters and deep-sea
 Priapulidae (larvae of two species unknown!) 10
10. Introvert with adhesive tubuli posterior to the scalids (fig. 49-50). Lorica (fig. 44-46): dorsal and ventral fields developed into thick plates (fig. 47), partially with alveolate sculpture; no tubuli; with anterior and posterior protuberances; no anterior accessory plates. Northern waters *Halicryptus spinulosus*
- Introvert without adhesive tubuli. Lorica (fig. 14-15): cuticula of dorsal and ventral fields not thicker than cuticula of lateral fields (fig. 22), with inconspicuous, non-alveolate sculpture; four lateral tubuli on posterior half of lorica; no anterior or posterior protuberances; anterior accessory plates present 11
11. Lorica with one dorsal and one ventral anterior accessory plate acting as a closing apparatus (fig. 16) *Priapulus* 12
- Lorica with four anterior accessory plates to each of the large fields (detailed description lacking) *Priapulopsis*
12. Tubuli about halfway between the middle of the lorica and the posterior end (fig. 23). Northern waters and deep-sea . . . *Priapulus caudatus*
- Tubuli only slightly posterior to the middle of the lorica (fig. 23). Southern waters and deep-sea *Priapulus tuberculatospinosus*

2.4 SURVEY OF THE TAXA

Priapulidae Gosse, 1855

p.p. Sipunculidea de Blainville, 1828: 553-554 (diagnosis).

p.p. Sipunculea de Quatrefages, 1847: 340.

p.p. Sipunculacea; Maitland, 1851: 96-97.

Priapulidae Gosse, 1855: 73-74 (diagnosis). — Baird, 1868: 104. — Koren & Danielssen, 1875: 135-137. — Théel, 1875: 3, 19-20 (diagnosis). — Koren & Danielssen, 1877: 146. — Levensen, 1884: 273-274 (diagnosis). — Fischer, W., 1894: 22. — Schauinsland, 1912: 1113-1117 (encyclopedia). — Chamberlin, 1920: 8-21 (bibliography). — Fischer, W., 1925: 44-51 (diagnosis; relationships with Sipunculida, Echiurida, and Echinodermata). — ten Broeke, 1929: 164-166 (diagnosis). — Wesenberg-Lund, 1939b: 35-36 (diagnosis). — Dawydoff, 1959: 923 (textbook).

Priapulacea; Keferstein, 1865a: 208; 1865b: 439 (diagnosis).

Priapulea; de Quatrefages, 1865a: 600 (diagnosis); 1865b: 296.

Priapulida; Schmarda, 1871: 349. — von Hayek, 1877: 340 (textbook). — Lang, K., 1953: 326-346 (systematics).

Priapulidea; McIntosh, 1874: 155; 1875: 113.

Priapuliden; Fischer, J., 1913: 91 (diagnosis).

Differential diagnosis. — Pharynx with cuspidate teeth of unequal size; no polythyridium. Introvert with 25 rows of scalids. Abdomen annulated, without tubuli and not showing sexual dimorphism. Larvae with bilaterally symmetrical lorica.

Description. — The Priapulidae are macrobenthic worms, occurring in more or less muddy sediments in extra-tropical waters and in the deep-sea of the tropics. The length of the body (without tail) is at least about 4 mm in mature specimens. The introvert carries 25 rows of scalids, mostly arranged in a number of series. The abdomen is distinctly annulate and is provided with papillae or setae, but tubuli are lacking. There is no tail or there are one or two tails, wholly or partially covered with vesiculae in the adult. The pharyngeal armature consists of numerous cuspidate teeth arranged in circlets of teeth of different sizes; most anterior circlets consist of five large teeth. The oesophagus is short and simple. Each urogenital organ consists of numerous solenocyte trees and numerous testis follicles or ovarial sacs. There is no marked sexual dimorphism and fertilization takes place in the water. The lorica of the larva is dorso-ventrally flattened and is provided with four longitudinal cuticular ridges on each side; it carries four tubuli or none at all.

Subdivision. — *Halicryptus spinulosus* differs from the other species of the family in so many aspects that nobody has ever doubted the validity of the genus *Halicryptus*. However, the other species are usually placed in a single genus. Indeed they are more closely related to each other than to *Halicryptus*, but in the present author's opinion the number and importance

of the characters involved justify a subdivision into three genera. This may make an overdone impression in such a small group but it is the only way to do justice to the diversity. A relatively large number of supraspecific taxa is indicative of either a group with a very rapid evolution or of a group that is nearly extinct. The latter is probably the case since there is no evidence at all for a rapid evolution; on the contrary, evolution is extremely slow as is proved by the fact that the widely distributed species show little geographical variation in spite of their undoubtedly very slow dispersal.

Priapulus de Lamarck, 1816

p.p. *Priapus* Linnaeus, 1758: 656 (diagnosis). — Houttuyn, 1770: 321-326 (diagnosis).
p.p. *Holothuria*; Linnaeus, 1767: 1089-1091 (diagnosis; species). — Stadius Müller, 1775: 94-99 (diagnosis; list of species). — Herbst, 1788: 68-71 (diagnosis; list of species).

Priapulus de Lamarck, 1816: 76-77 (diagnosis). — Schweigger, 1820: 553-554 (diagnosis). — Cuvier, 1825: 38 (diagnosis). — de Blainville, 1828: 554-555 (diagnosis). — Fleming, 1828: 491 (diagnosis). — de Lamarck, 1840: 466-467 (diagnosis). — Forbes, 1841: 256 (diagnosis). — de Quatrefages, 1847: 340 (relationships). — Diesing, 1851: 71 (diagnosis); 1859: 769 (diagnosis). — Leuckart, 1856: 78 (diagnosis). — Ehlers, 1861: 5, 43-47 (diagnosis; relationships). — Keferstein, 1865a: 208 (diagnosis); 1865b: 440 (diagnosis). — de Quatrefages, 1865a: 600-602 (diagnosis). — Théel, 1875: 3, 20 (diagnosis; key to species). — Schauinsland, 1887: 171-173 (histology of nervous system and intestine; coelomocytes). — de Guerne, 1888: 4-8 (history). — Delage & Hérouard, 1897: 4, fig. 2 (diagnosis). — Théel, 1906: 8, 13 (nomenclature). — Molčanov, 1908: 957. — Fischer, J., 1913: 108 (diagnosis). — Thiele, 1922: 142-144 (relationship). — Fischer, W., 1925: 44-45 (diagnosis); 1928: 474 (diagnosis). — ten Broeke, 1929: 164-165 (diagnosis). — Baltzer, 1934a: 2-13 (textbook). — Satô, 1939: 431, 451 (diagnosis; bibliography). — Wesenberg-Lund, 1939b: 37 (diagnosis). — Lang, K., 1953: 329-330, 340, 344, 346. — Bruun, 1957: 655, 658 (deep sea). — Dawydoff, 1959: 911, fig. 720, 722-723, 728A-D, 729-731, 733-734 (textbook). — Murina & Starobogatov, 1961: 181-198 (monograph including diagnosis, key to species, zoogeography). — Lang, K., 1963: 257-259. — Clark, 1964: 73, 87-88, 93, 116, 124, fig. 51 (burrowing). — Guille & Laubier, 1965: 1125-1128 (zoogeography, with map). — Trueman & Ansell, 1969: 326-327, 349-350, fig. 15, 17 (burrowing).

Priapula; de Blainville, 1826: 288-291 (encyclopedia).

p.p. *Lacazia* de Quatrefages, 1865a: 602-604 (diagnosis).

Priapulus s. str. (subgenus); Murina & Starobogatov, 1961: 183 (diagnosis).

Type species: *Priapulus caudatus* de Lamarck.

Differential diagnosis. — Introvert with distinct rows and distinct series of simple scalids. Abdomen with posterior warts. Tail segmented. Larva with closing apparatus consisting of two plates.

Nomenclature. — As appears from the synonymy the generic name *Priapulus* has been used by most authors since it was introduced by De Lamarck in 1816 (see also under *P. caudatus*). It is not necessary to replace it by the older name *Priapus*, as was suggested by Théel (1906) and Hyman (1951),

among others. This latter name was used by Linnaeus (following Odhelius, 1754) for both a sea anemone (*P. equinus*) and a priapulid (*P. humanus*). The inhomogeneity of the genus *Priapus* is also apparent from the original diagnosis: "Corpus oblongus, teres, basi affixum. Os terminale dentibus incurvis: rostro cylindrico radiato". The fixed base refers to the anemone, the incurved teeth are characteristic of priapulids. Poche (1908) designated *P. equinus* as the type species of the genus. Consequently *Priapus* must be considered a genus of coelenterates.

The name of the genus was derived from the name of Priapos, the Greek god of fertility and procreation.

Description. — In the pharyngeal armature (fig. 2-5) the first six or seven circlets consist of five teeth (pentagons). The largest teeth are situated in the fourth circlet. Each tooth bears a median cusp and up to about 16 lateral cusps (the number of lateral cusps and denticles decreases in the course of time; fig. 6-7). In postlarvae teeth of the first circlet (fig. 5-6) do not yet have a conspicuous median cusp and in the fourth circlet two teeth are considerably larger than the others (fig. 5). There are very few to many buccal papillae.

The length of the introvert varies from 25% to 100% of the length of the abdomen, depending on the state of contraction; in small specimens it may be even longer, up to nearly about twice the length of the abdomen. The scalids (fig. 11-12) are simple, conical papillae, in larger specimens strengthened by a cuticular tube. They are usually arranged in conspicuous series, at least anteriorly (Pl. 4), each series consisting of up to six scalids. The two ventral rows on either side of the ventral nerve cord are somewhat nearer to each other than the remaining rows.

The abdomen is provided with 40 to 50 annuli, one to four (to seven?) of them bearing more or less numerous ringpapillae and the last three to eight of them covered with posterior warts (fig. 13). Small, conical papillae (fig. 8) are irregularly dispersed on the entire abdomen. The skin is smooth.

The tail is segmented (there is no fixed number of segments), but this segmentation is usually invisible in larger specimens. In postlarvae it is covered with papillae and spinulets, giving it a spiny appearance (Pl. 2A), in larger specimens it is usually thickly beset with vesiculae. Each vesicula is provided with a number of scattered spinulets (fig. 9-10).

There are typically eight long introvert retractors, two of which are often considerably shorter than the others, 10 to 14 short introvert retractors, and a dorsal and a ventral pharynx retractor attached to the rectum.

In the larvae the pharyngeal armature consists of about six circlets of five teeth (fig. 17-18) followed by about the same number of circlets with

more than five teeth, gradually decreasing in size. Teeth of the first circllet bear two rows, those of the second circllet one irregular row, those of the third circllet two rows of denticles; teeth of the fourth and fifth circllets each bear three rows of fine spines and a number of very small scattered denticles; teeth of the sixth and seventh circllets each have two irregular rows of denticles; the following circllets also bear denticles, in decreasing number and size.

The scalids are curved; the anterior ones have strongly chitinized crests; most of them carry a distal spine (fig. 19). Each row consists of five or six scalids. Adhesive tubules are lacking.

The cuticle of the neck region is divided into a number of fields separated by ridges (best shown in fig. 15), but only two of them have developed into evident plates acting as a closing apparatus (fig. 16).

The lorica is only inconspicuously sculptured (fig. 14-15); there is only a number of rows of very small, curved cuticular ridges. A faint cross-striation is often visible. The cuticula (fig. 22) is equally thick in all fields and the dorsolateral and lateral ridges are hollow throughout. There are four tubuli, each of them associated with one of the lateral ridges (fig. 15). Each tubulus consists of three parts (fig. 21); probably the delicate distal part can be telescoped into the firm shaft to some extent. The excretory duct of the caudal gland (fig. 20) is provided with a cuticularized tube. There are no anterior or posterior protuberances.

Subdivision. — Within the genus in the present sense no less than 16 specific and infraspecific taxa have been described in the course of time. In the present paper only two species are recognized and even this is done with some hesitation: possibly only subspecies are concerned (see under *P. tuberculatospinosus*).

This situation clearly demonstrates the fact that the appearance of the animals exhibits a great variation. In the first place there is a considerable difference between younger and older individuals. Curiously enough the larvae have never been described as separate species, but postlarvae have once been described as a new species (*P. profundus*), and young adults have been described as separate species or varieties several times (*P. pygmaeus*; *P. t. bahiensis*; *P. abyssorum*; *P. c. kristinebergensis*; *P. c. mofjordensis*); on the other hand *P. fuegensis* was based on rather large specimens. In the second place the state of contraction of fixed specimens may be misleading (*P. hibernicus*; *P. glandifer*). In the third place there is a real individual variability as expressed in the names *P. brevicaudatus* and *P. multidentatus*. Once a teratological specimen was described as a new subspecies (*P. t. japonicus*; see p. 20).

Priapulus caudatus de Lamarck, 1816

(fig. 2, 5-8, 10-11, 13-14, 16-17, 19, 22, 23, 80-81, 88, Pl. 1 C, 2 A-B, 3-4)

Priapulus humanus Linnaeus, 1758: 656 (diagnosis; Habitat in Mari Indico; based on *Priapulus humanus* Odhelius, 1754). — Odhelius in: Linnaeus, 1759: 255 (description; no locality). — Houttuyn, 1770: 322 (diagnosis).

Holothuria priapus (pro *Priapulus humanus*) Linnaeus, 1767: 1091 (diagnosis; in Oceano Indiae orientalis & Europae borealis). — Forster, 1771: 337. — Stadius Müller, 1775: 99 (diagnosis). — Müller, 1776: 232 (diagnosis). — Fabricius, 1780: 355-356 (description; predator; Greenland). — Gmelin, 1788: 3140-3141 (diagnosis). — Herbst, 1788: 70 (diagnosis). — Abildgaard, 1789: 133-138, Pl. 3 fig. 1-3 (description; Denmark). — Müller, 1789: 27, pl. 96 fig. 1 (description). — Bosc, 1802: 225. — Turton, 1806: 110. — Rathke, 1806: 18-19, Pl. 135 fig. 2. — Cuvier, 1817: 25 (diagnosis). — Faber, 1829: 206 (Iceland). — Bosc, 1830: 152 (diagnosis). — Cuvier, 1830: 242; 1836: 343 (diagnosis). — Voigt, 1840: 80 (diagnosis).

Hirudo annulis 40, sulcis sive radiis circa orisicium 24 (Madkamoder) Olafsen, 1772: 1001, Pl. 10, fig. 9 [not seen]; 1774: Pl. 10, fig. 9; 1775: 211 (Iceland, Videy, im Thon am Seeufer).

Priapulus caudatus (pro *Holothuria priapus* Linnaeus) de Lamarck, 1816: 77. — Schweigger, 1820: 554. — Cuvier, 1825: 39. — Fleming, 1828: 491-92 (description; Scotland). — de Blainville, 1828: 555. — de Lamarck, 1840: 467. — Forbes, 1841: 256-258, fig. (description; British Isles). — v. Düben, 1844: 115 (Norway). — McCoy, 1845: 272 (Ireland). — Frey & Leuckart, 1847: 40-45 (description; anatomy). — Gray, 1848: 14 (British Isles; catalogue British Museum). — Diesing, 1851: 71, 556 (diagnosis; distribution). — Maitland, 1851: 97 (diagnosis; North Sea). — Sars, 1851: 130, 196 (Norway). — Dalyell, 1853: 253-254, Pl. 35 fig. 1-2 (description; defecation; Scotland). — Phillips, 1854: 70-71 (diagnosis; description living specimen; England). — Schmidt, 1854: 4-5, Pl. 2 fig. 4-4b (description). — Gosse, 1855: 74, fig. 121. — Leckenby, 1855 (morphology; burrowing; England). — Leuckart, 1856: 78. — Reinhardt, 1857: 45 (catalogue Greenland). — Diesing, 1859: 769 (distribution). — Danielssen, 1861: 58 (Norway). — Ehlers, 1861: 1-43, pl. 20 figs. 1-13, pl. 21 fig. 14-22 (history; diagnosis, detailed description, anatomy, histology; food; Greenland; distribution); 1862: 402-404, 407-408, 410 (comparison with *Halicyptus*). — Stimpson, 1864: 141 (predator; Greenland). — Keferstein, 1865a: 208; 1865b: 440 (diagnosis). — de Quatrefages, 1865a: 601 (diagnosis). — MacIntosh, 1866: 613 (Scotland). — Baird, 1868 (bibliography, systematics, nomenclature; Scotland, Greenland). — Zenger, 1870: 227-232, Pl. 9 fig. 1-5 (detailed description, anatomy, histology; Germany). — Schmarida, 1871: 347-349, fig. 247. — Willemoes-Suhm, 1871: 386-387, Pl. 33 fig. 26 (description; postlarva; Germany, Denmark). — Graber, 1873: 61-66, 73, Pl. 1, fig. 1-4 (histology of skin). — Metzger, 1873: 176 (North Sea). — Möbius, 1873: 106, 176 (Baltic Sea). — Heuglin, 1874: 252, 254 (Novaya Zemlya). — Möbius, 1874: 257 (Eastern Greenland). — Whiteaves, 1874: 189 (Canada) — McIntosh, 1874: 148; 1875: 113, Pl. 4, fig. 2 (predators; Scotland). — Koren & Danielssen, 1875: 135-137 (description; Norway). — Lütken, 1875: 178 (catalogue Greenland). — Möbius, 1875: 156 (North Sea). — Théel, 1875: 20-22 (bibliography; diagnosis; distribution in Scandinavia). — von Hayek, 1877: fig. 658, 663. — Koren & Danielssen, 1877: 150-151. — Tauber, 1879: 58-59 (bibliography; Denmark). — Danielssen & Koren, 1881: 47 (Spitsbergen, Norwegian Sea). — Horst, 1881: 13-14, 16, 25-26, 28-29, 33, 36, 38 (Barents Sea). — Verrill, 1881: 294, 307 (list New England). — Lenz, 1883: 172 (Germany). — Levinsen, 1884: 275, 319 (diagnosis; distribution). — Apel, 1885: 459-525, Pl. 15-17, fig. 3, 5-7, 10-11, 15-40 (histology; moult; parasites; Germany). — Scharff, 1885: 193-212, Pl. 14, fig. 1-2, 4-10, 12 (histol-

ogy of skin and nervous system). — Schauinsland, 1886: 574-577 (anatomy urogenital system). — Holm, 1887: 484, 498 (Kara Sea). — Levinsen, 1887: 302 (Kara Sea). — de Guerne, 1888: 4-7, 11-12, 18. — Michaelsen, 1889: 48-51. — Scott, 1890: 332 (predators; Scotland). — Knipovič, 1891: 24, 40 (White Sea). — Levinsen, 1893 (Denmark). — Fischer, 1894: 22 (Greenland, Spitsbergen, North Sea, Germany; Hamburg museum); 1896: 7. — Shipley, 1896: 430, 432-433, fig. 218. — Maitland, 1897: 44. — Gemmil, 1901: 363 (Scotland). — Rauschenplat, 1901: 85, 145-147 (food; parasites; Germany). — Skorikov, 1901: xxi-xxiii (distribution). — Whiteaves, 1901: 89 (catalogue Canada). — Reibisch, 1902: 157-159 (Baltic Sea, deep basin). — Saint-Loup, [n.d.]: 224, fig. 190-191. — Shipley, 1902: 284-285 (Antarctica; zoogeography). — Skorikov, 1902a: 155-157 (distribution). — Norman, 1903: 285 (Norway). — Hérubel, 1904a: 104-109, fig. 1, 3, 4I (description; Norway); 1904b: 126-129 (dimensions; histology of skin). — Théel, 1906: 13, 15-18, Pl. 1, fig. 1-2 (Greenland, Spitsbergen, Iceland, Novaya Zemlya, Scandinavian coasts, Baltic Sea, Siberia; distribution). — Kükenthal, 1907: 21 (bipolarity). — Molčanov, 1908: 957, 966, fig. 1-6, 9 (histology of tail and nervous, digestive and urogenital systems; Russia). — Théel, 1908: 70, 109, 110, 112, 115, 117-118, 123, 125 (Sweden). — Gadd, 1911: 79, 90 (Russia). — Théel, 1911: 15, 18-25, fig. 1, 4-8, Pl. 1, fig. 6-11 (description; Spitsbergen, Sweden). — Marelli, 1912: 139-143 (bipolarity). — Schauinsland, 1912: 1113, 1116, fig. 2 (encyclopedia). — Fischer, J., 1913: 90-91, 108-114, 116-118, 121, fig. 4-5 (description; North Sea, Baltic Sea). — Southern, 1913a: 2, 7, 39 (predators; Ireland); 1913b: 1, 5 (Ireland). — Fischer, W., 1914: 20-21, 23-26 (nomenclature; pharyngeal teeth; Greenland, Spitsbergen, North Sea). — Petersen, 1914: 27, 41, 45, 50 (ecology; Denmark). — Blegvad, 1915: 50, 69, 74 (food; predators). — Derjugin, 1915: 113, 373-375, 773, 796, 863, 871-872 (Russia). — Hammarsten, 1913: 536 (posterior warts). — Blegvad, 1917: 43, 50, 52, lists 1-2, 4-5 (predators; Denmark). — Hempelman & Wagler, 1918: 310-311, fig. (description). — Berg, 1920: 274. — Fischer, W., 1920: 419-421, 424-425, 428 (morphology; Germany; distribution, geography). — Hammarsten & Runnström, 1920: 5-15, fig. 1-3, Pl. 2-3 fig. 1-20 (histology and cyto-physiology of posterior glands; moult). — Thulin, 1920: 2-7 (ecology; Baltic Sea). — Cuénot, 1922: 25. — Fischer, W., 1922b: 17-18; 1922c: 232, 241, 245 (Spitsbergen; distribution). — Eggers, 1925: 170 (Germany). — Fischer, W., 1925: 45-51, fig. 5, 19, 20 (description; food; reproduction; distribution (map) North Sea, Baltic Sea). — Wesenberg-Lund, 1925: 81-82, 84-85 (Greenland; distribution). — MacIntosh, 1927: 67 (Scotland). — Broch, 1928: 7 (Norway). — Fischer, W., 1928: 455, 474-478, fig. 1 (description; Spitsbergen; distribution). — Hertling, 1928: 35, 40-41, 65, 68, 70, 73, 75-76, 83, 94, 96-97, fig. 2, tab. 1, 5-6, 11 (ecology; predators; Baltic Sea). — Wesenberg-Lund, 1928: 1-2 (Færoes); 1929: 165-191, fig. 1, 3 (anatomy; moult, defecation, burrowing; ecology, food, predators; distribution Baltic Sea to Norwegian coast, general distribution). — ten Broeke, 1929: 165, fig. 12-13 (description; Germany). — Hagmeier, 1930: 161, 164-165 (ecology; Baltic Sea). — Stiasny, 1930: 206, 221 (Barents Sea). — Wesenberg-Lund, 1930: 5, 7-17, Pl. 1 fig. 1-8, 10-13, Pl. 2, fig. 16 (histology of skin; ecology, predators; Greenland, Canada, North Atlantic; distribution). — Schulz, 1931: 61-63 (moult; food; Germany). — Wesenberg-Lund, 1932: 3-5, 16-17, fig. 1, 8. (Greenland (map); distribution (map)); 1933: 1-2 (Greenland; Novaya Zemlya; Siberia). — Baltzer, 1934a: 2-3, 7, 10, fig. 4-6, 13 (textbook; distribution (map)). — Okuda, 1934: 115-116, fig. 1-3 (description; Japan). — Stephen, 1934: 160 (predators; Scotland). — Wesenberg-Lund, 1934: 5-6 (Greenland). — Ekman, 1935: 184, 327-328, fig. 160 (zoogeography). — Friedrich & Langeloh, 1936: 249-256, 260, fig. 1-2 (burrowing; Germany). — Langeloh, 1936: 260-268 (geotaxis, phototaxis; burrowing). — Spärck, 1937: 28 (ecology; Iceland). — Wesenberg-Lund, 1937a: 2, 4, 14-15, fig. 1 (predators; Iceland; distribution); 1937b: 3-6, 22-23, fig. 1-2 (ecology, food; Greenland; distribution-map Greenland); 1938: 26-27, fig. (Norway). — Broch, 1939: 61 (bipolarity). — Dons, 1939: 199 (Norway). — Lang, K., 1939: 80-87,

fig. 1-7 (spawning; embryology; larval and postlarval development; hermaphroditism; Sweden). — Satô, 1939: 348, 431-432, 439, 451 (Japan). — Wesenberg-Lund, 1939a: 3, 7-8 (Sweden); 1939c: 37-39, fig. 21 (description; ecology; distribution). — Lilling, 1940: 136-138, 141, 153, 167, 169, 173-174 (anatomy, histology, and development urogenital system; Germany). — Remane, 1940: 146 (ecology). — Brown & Cheng, 1946 (predators; Iceland). — Okuda, 1946: 221-222 (Japan). — Brattström, 1947: 67, 73 (Öresund). — Lang, K., 1948a: 1-11, fig. 1, Pl. 1 fig. 1-3, Pl. 2 fig. 1-4 (tail, caudal glands; regeneration, moult, spawning; burrowing, feeding, defecation; Sweden); 1948b: 1-8, fig. 1, 3-6, Pl. 1 fig. 2, Pl. 2 (morphology larva). — Žinkin, 1949: 410-412, fig. 1-2 (embryology; Russia). — Fänge, 1950: 613 (haemerythrin). — Wesenberg-Lund, 1950: 488-489, 4 fig. (description; Denmark). — Fänge & Akesson, 1951: 25-31, fig. 1-3 (coelomocytes, haemerythrin; respiration; Sweden). — Hyman, 1951: 183-197, fig. 87B-C, 92A-B, D (textbook). — Lang, K., 1951: 565-567, fig. 1-2a (pharyngeal teeth, larva; Sweden, Iceland, Spitsbergen); 1953: 321-326, 329, fig. 1-3 (embryology; spawning). — Žinkin & Korsakova, 1953: 571-573 (embryology). — Demel & Mulicki, 1954: 84-88, 101, 104 (ecology; Baltic Sea). — Jones, 1954: 32, tab. 17 (predators). — Smith, et al., 1954: 111 (California). — Dell, 1955: 1129-1130. — MacGinitie, 1955: 72, 81, 126 (Alaska). — Sjöblom, 1955: 37, 40 (Baltic Sea). — Forsman, 1956: 396, 415 (Baltic Sea). — Franzén, 1956a: 377-379, fig. 33-34 (spermatozoon; spermiogenesis); 1956b: 7, 11 (spermiogenesis). — Bassindale & Barrett, 1957: 265 (Wales). — Mulicki, 1957: 313-314, 360, 363-365, 367, 371-373, 376-377, fig. 29-31, 35-37 (ecology; Baltic Sea, Poland). — Hedgpeth, 1957: 377, fig. 14 (bipolarity). — Segerstråle, 1957b: 789, fig. 15 (ecology; Baltic Sea). — Demel & Mulicki, 1958: 51, fig. 9 (ecology; Baltic Sea). — Golvan, 1958: 568-569. — McIntyre, 1958: 14, 21 (Scotland). — Carlisle, 1959: 79-81 (nomenclature; moult, biochemistry of cuticula). — Dawydoff, 1959: 909, 916, 922-923, fig. 727 (textbook). — Hyman, 1959: 741-742 (textbook, additions). — Segerstråle, 1960: 5 (ecology; Baltic Sea). — Stephen, 1960: 25-26, fig. 17 (description; British Isles). — Fänge & Mattisson, 1961: 1216-1217, fig. 1 (coelomic fluid, coelomocytes; respiratory function of tail). — Murina & Starobogatov, 1961: 181-188, 195-196, 198, fig. 1a, 2a-b, 3a-b, 4a-b, 5a-b, 6a-b, 7a, 8a-b, 9 (bibliography; description; distribution (map)). — Olivier et al., 1961: 259. — Shapeero, 1961: 879-880, fig. 1A-B (histology: muscles, peritoneum). — Hurley, 1962: 14. — Préfontaine & Brunel, 1962: 247 (Canada). — Sanders & Hessler, 1962: 130, fig. 3-4. — Shapeero, 1962a: 352-355, fig. 1-4 (histology epidermis; biochemistry cuticula; moult); 1962b: 237-241, fig. 1-3 (moult; distribution Pacific coast N.-America (map)). — Bruce, et al., 1963: 110 (England). — Holmquist, 1963: 116 (Alaska). — Kühlmorgen-Hille, 1963: 59-60, fig. 17 (Germany). — Lang, K., 1963: fig. 18-1, 18-3. — Nørrevang, 1963a: 33 (anatomy, histology and cytology ♀ urogenital system); 1963b: 603-606, fig. 1-4 (karyology oocyte, chromosomes?); 1963c: 700-701, fig. 1-3 (anatomy, histology and fine structure of excretory organs). — Arndt, 1964: 140, 143 (ecology; Baltic Sea). — Murina, 1964: 873-875 (distribution-map). — Guille & Laubier, 1965: 1125-1128 (description; Mediterranean; distribution-map). — Nørrevang, 1965: 1-84, Pl. 1-20, fig. 1-55 (anatomy, histology, and cytology of ovarium; oogenesis). — Tulkki, 1965: 457-458, 461 (ecology; Baltic Sea) — Bull, 1966: 15 (England). — Crothers, 1966: 44 (Wales). — Hartwich, 1967: 316-318, fig. (textbook). — Hickman, 1967: 254-259, fig. 13-1-13-6 (textbook). — de Lattin, 1967: 157-159, 503, fig. 53. — Jägersten, 1968: 75-78, fig. 16 (larvae; Sweden). — Murina, 1968: 88-89 (geographical and bathymetrical distribution). — Tommasi, 1968: 1-2. — Nyholm & Bornö, 1969: 262-263 (oxygen consumption).

Priapula priapus; de Blainville, 1826: 289 (diagnosis).

Priapula caudatus; de Blainville, 1826: 290 (diagnosis).

Priapula caudata; Guérin-Méneville, 1829-1844: Zoophyta pl. 5 fig. 2, p. 8.

Priapululus vulgaris (pro *Holothuria priapus*) Cuvier, 1836: 401.

Priapululus hibernicus McCoy, 1845: 272, pl. 16 fig. 1 (description; Connemara, Ireland,

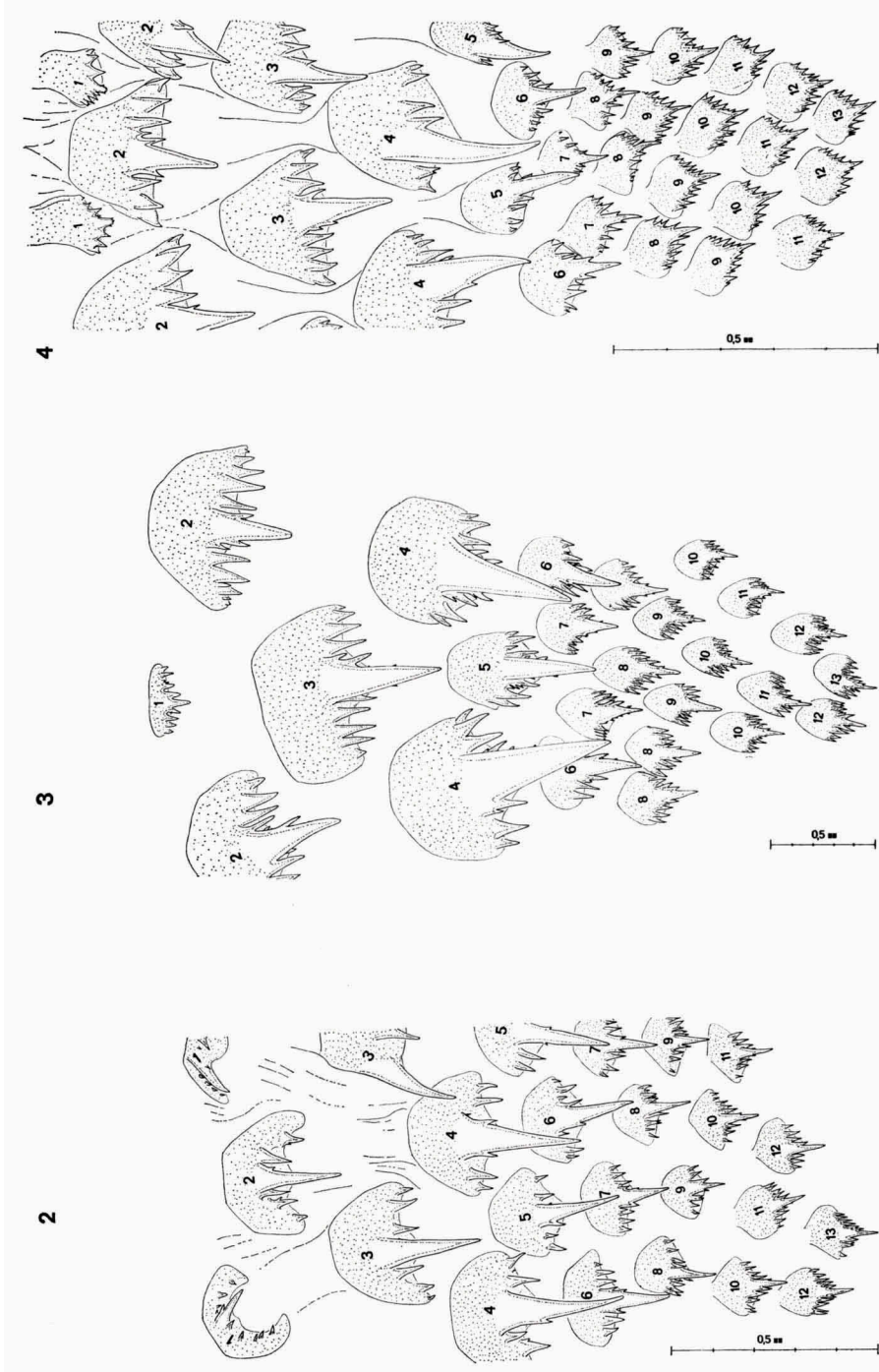


Fig. 2-4. *Priapulus*, anterior pharyngeal teeth. 2, *P. caudatus*, length about 13 mm, Greenland (Mus. Copenhagen); 3-4, *P. tuberculatospinosus*; 3, length about 45 mm, Falkland Islands (Mus. Stockholm 252); 4, length about 12 mm, Palmer Archipelago (Mus. Washington).

low water mark). — DIESING, 1851: 71-72 (diagnosis); 1859: 770. — EHLERS, 1861: 6 (syn. of *P. caudatus?*).

Priapulus brevicaudatus Ehlers, 1861: 5, 12-14, 35, Pl. 21 fig. 23 (diagnosis, description; probably from the German coast of the Baltic Sea). — de Quatrefages, 1865a: 601 (diagnosis). — Keferstein, 1865a: 208; 1865b: 441 (Norway). Baird, 1868: 106. — Théel, 1875: 20, 22-23 (diagnosis). — Lenz, 1878: 10-11 (short description; Germany). — Shipley, 1896: 432 — Skorikov, 1902: 155 (syn. of *P. caudatus*). — Hérubel, 1904a: 104.

Priapulus glandifer Ehlers, 1861: 5, 12-14, 34, Pl. 21 fig. 24 (diagnosis, description; Greenland). — de Quatrefages, 1865a: 601 (diagnosis). — Keferstein, 1865a: 208; 1865b: 440-441 (diagnosis). — Baird, 1868: 106. — Lütken, 1875: 178 (catalogue Greenland). — Théel, 1875: 20, 22 (diagnosis). — Shipley, 1896: 430, 432. — Skorikov, 1902: 155 (syn. of *P. caudatus*).

Lacazia hibernica; de Quatrefages, 1865a: 604 (diagnosis).

Priapulus multidentatus Möbius 1873: 106 (diagnosis; Kiel, Germany). — Lenz, 1878: 10, pl. I fig. 1-4 (description; Germany). — Fischer, W., 1920: 419.

Priapulus intermedius (pro *P. multidentatus*) Lenz, 1878: 10.

Priapulus pygmaeus Verrill, 1879: 11 (nomen nudum; checklist New England); 1880: 182-183 (description; Massachusetts Bay, off Plymouth, 27 fm; New England); 1881: 306, 310, 319, 321 (list New England). — de Guerne, 1888: 8. — Whiteaves, 1901: 89 (catalogue Canada).

Priapulus spec. Verrill, 1885: 525, fig. 191-191a (North Atlantic, off New England).

Priapulus humanus; de Guerne, 1888: 4-5 (copy of description by Odhelius, 1754). — Collin, 1901: 302. — Derjugin, 1906: 87 (Russia). — Averincev, 1908: 190 (Russia). — Chamberlin, 1920: 3 (predators; Alaska, Canada). — Ricketts & Calvin, 1952: 316 (California).

Priapulus pygmaeus [lapsus] Collin, 1901: 301-302.

Priapulus caudatus var. *antarcticus*; (p.p.) Skorikov, 1902: 155-157 (distribution-map). — Wesenberg-Lund, 1925: 82, 85 (Greenland; distribution); 1928: 1-2 (Færoes).

Priapulus caudatus kristinebergensis Hérubel, 1904a: 104-109, fig. 2, 4III (description; Gullmarfjord, Sweden); 1904b: fig. 3.

Priapulus caudatus mofjordinensis Hérubel, 1904a: 104-109, fig. 1, 4II (description; Mofjord near Bergen, Norway).

Priapulus priapus Derjugin, 1906: 140 (Russia). — Skorikov, 1910: 226-227, 236 (distribution Baltic Sea).

Priapulus caudatus var. *multidentatus*; Fischer, J., 1913: 113-114, fig. 6-7 (pharyngeal teeth; Baltic Sea). — Fischer, W., 1914: 21-22, fig. 13-14 (pharyngeal teeth; Baltic Sea); 1928: 475-476.

(?) *Priapulus tuberculatospinosus japonicus* Murina & Starobogatov, 1961: 183, 191-192, 195, fig. 1v, 3d, 4d, 5d, 6g, 7g, 8v, 10, 12 (description; one specimen; Sea of Japan, "Vitjaz" sta. 206, 45°20'5"N 142°55'E, 130 m). — Murina, 1964: 873-875; 1968: 89.

Priapulus profundus Sanders & Hessler, 1962: 128-129, fig. 2-4 (description; North Atlantic off New England; 2 specimens, 37°27'N 68°41'W, 4483 m; 1 specimen, 38°00'N 69°31'W, 3800 m). — Murina, 1964: 873-875. — Guille & Laubier, 1965: 1125-1126. — Hickman, 1967: 254. — Murina, 1968: 89. — Tommasi, 1968: 1-2.

(?) *Priapulus tuberculatospinosus abyssorum* p.p.; see under next species.

Material. — The author has seen many hundreds of specimens from all areas except from the northwestern Pacific. Many hundreds of larvae were available from Scandinavia and Iceland. Type specimens were not studied, but the following types are known to be present in collections: *P. pygmaeus* (Mus. Washington), *P. profundus* (Mus. Washington; coll. Sanders), *P.*

tuberculatospinosus japonicus (coll. Lab. Sevastopol), *P. glandifer* (Mus. Berlin).

Diagnosis. — In the pharyngeal armature of adults teeth of first circler not much smaller than those of second circler; all teeth of fourth circler subequal in size; seventh circler with five teeth. Tubuli of larvae situated at distance of about one fifth of total length of lorica from posterior end.

Nomenclature. — It appears from the synonymy that *P. humanus* has priority over all other names, but also that *P. caudatus* has been used much more frequently. One of the reasons is that *P. humanus* was supposed to be based on material from China or the East Indies because it was first described by Odhelius (1754) in a dissertation titled "Chinensia Lagerströmiana". However, there is no reason to believe that this supposition was correct. Firstly Odhelius did not mention the country of origin of his priapulids. Secondly most of his material of other animals does not come from China so it is incorrect to draw a conclusion from the title of his work. Thirdly it is extremely unlikely that he has seen other than European material of *Priapulus*. Linnaeus himself was also of the opinion that the material described by Odhelius (probably also seen by Linnaeus) was identical with Scandinavian material. Moreover, *P. caudatus* was just a replacement name for *P. humanus*. De Lamarck did not even know the animal, he just changed its name as was often done in those times.

We may conclude that the only way to preserve the commonly used name *P. caudatus* is to suppress both *P. humanus* and *H. priapus*. The argument that the name *P. caudatus* has been used more often is not very convincing in the case of a relatively obscure animal, only familiar to a restricted number of specialists. Nevertheless I have made a relevant proposal to the International Commission on Zoological Nomenclature and continue to use *Priapulus caudatus* for the time being.

Description. — Living specimens in extended condition may reach a length of about 200 mm, but large specimens are rare and the great majority apparently does not even reach a length of 100 mm.

Pharyngeal armature: In postlarvae (fig. 5) teeth of the first circler do not yet have a median cusp; they grow just as fast as the other teeth and gradually get a conspicuous median cusp (fig. 2, 6). (In one case the teeth of the first circler were found to be just as small as those of *P. tuberculatospinosus*; in the specimen described as *P. tuberculatospinosus japonicus* the teeth of the first circler were also very small). On the contrary the initial growth of the two large teeth of the fourth circler is slower than that of the others, so that in animals with a length greater than about 10 mm, all teeth of the fourth circler have about the same size (fig. 2). In mature

specimens the teeth of the anterior circlets usually bear 4 to 6 lateral cusps, but a greater number is certainly not exceptional. The seventh circlet still consists of five teeth, but from the eighth circlet the number of teeth per circlet is higher, steadily increasing backwards, diagonal rows becoming more conspicuous than the circlets.

Usually the spinulets on the vesiculae of the tail are small and sparse (fig. 10); vesiculae with large and numerous spinulets as in *P. tuberculatospinosus* (fig. 9) are less common.

The larvae reach a length of up to 2 mm.

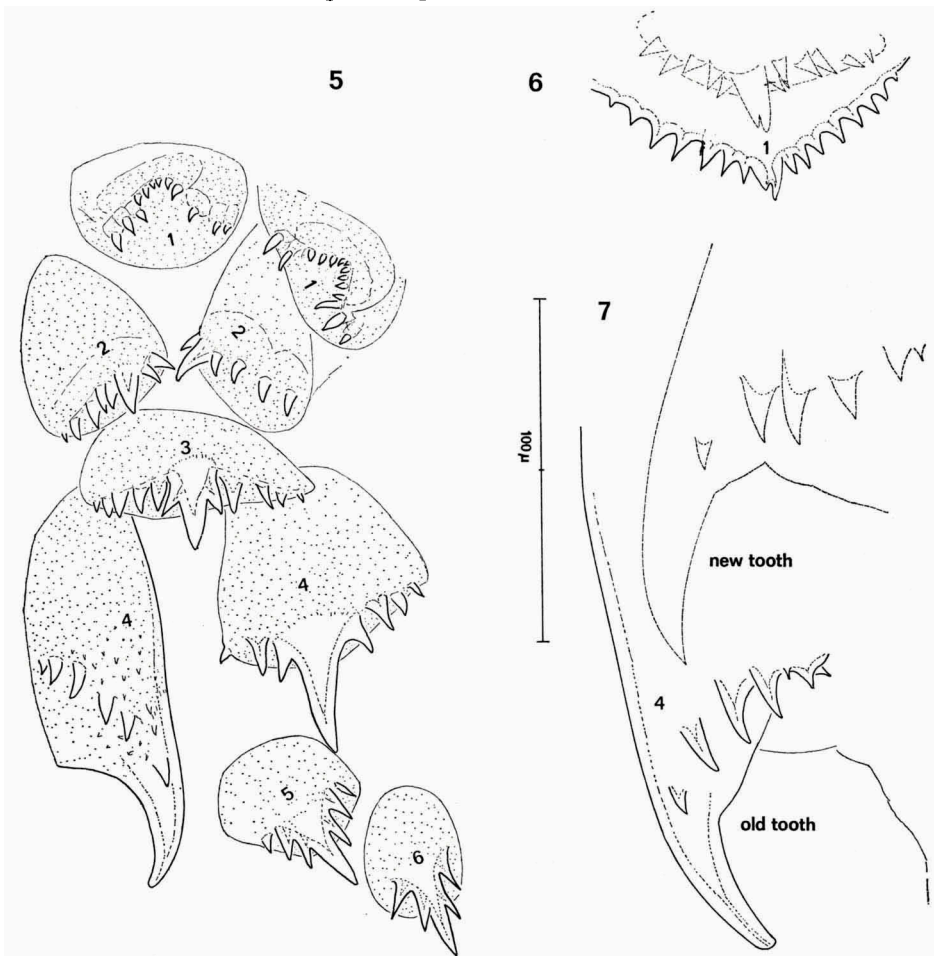


Fig. 5-7. *Priapulus caudatus*, anterior pharyngeal teeth of postlarvae. 5, Iceland (Mus. Stockholm); 6-7, old and new teeth just before moulting, Denmark (Lab. Helsingør); 6, tooth of first ring; 7, large tooth of fourth ring. Note the decrease in the number of lateral denticles and cusps.

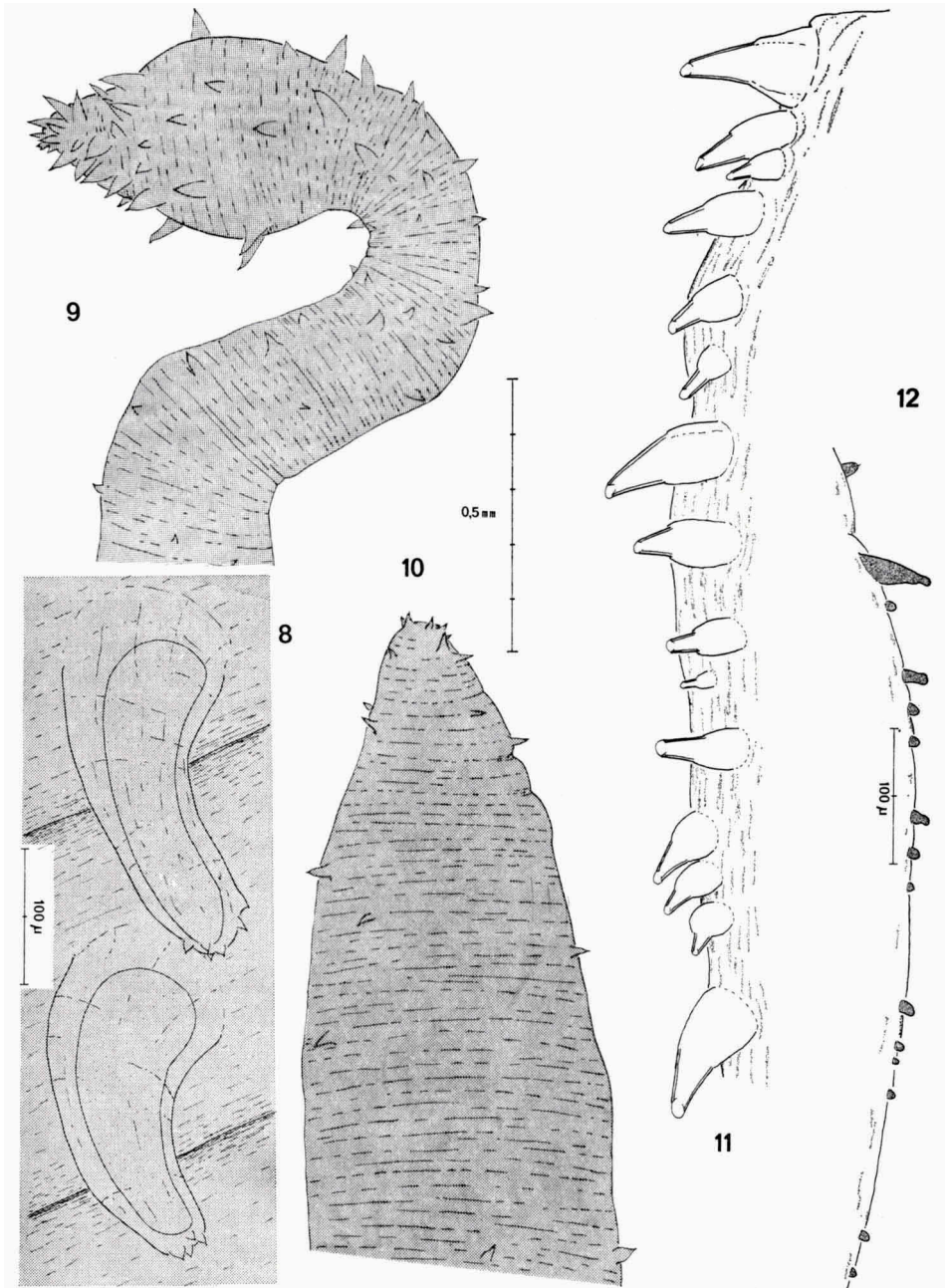


Fig. 8-12. *Priapulus*. 8, *P. caudatus*, abdominal papillae, Sweden (Mus. Leiden 4918); 9-10, distal part of tail vesicula; 9, *P. tuberculatospinosus*, Chili (Mus. Stockholm); 10, *P. caudatus*, Sweden (Mus. Leiden 4918); 11-12, anterior scalds; 11, *P. caudatus*, Sweden (Mus. Leiden 4918); 12, *P. tuberculatospinosus*, postlarva, South Georgia (Mus. Stockholm 357).

The tubuli of the larvae are all situated at about the same level, namely at a distance of about one fifth of the total length of the lorica from the posterior end. Of course there are often small differences between the individual tubuli and between the specimens (partly due to different states of contraction), but in general there is only a slight variation (see fig. 23).

Discussion. — Two recently described taxa that are synonymized here, demand some discussion.

Priapulus profundus Sanders & Hessler, 1962.

I have not seen type specimens but the original description is sufficiently clear to conclude that it was based on postlarvae of *P. caudatus*. The authors were undoubtedly misled by the morphology of the tail, which is conspicuously segmented and not yet provided with vesiculae. Tails of young specimens have not very often been depicted in the literature (Zenger, 1870; Willemoes-Suhm, 1871; K. Lang, 1938). The presence of an annulus with ringpapillae was also mentioned as an important differential character of *P. profundus*. Indeed it has not often been stressed in the literature that *P. caudatus* has ringpapillae even in young stages. The pharyngeal teeth of postlarvae had never been described at that moment.

P. caudatus was already known to occur in the area, though not at such great depths as those from which Sanders & Hessler got their material (3800 and 4483 m). It had often been found on the shelf off New England, but only once at a greater depth (Verrill, 1885; about 1900 m).

Priapulus tuberculatospinosus subsp. *japonicus* Murina & Starobogatov, 1961.

The description of this subspecies was based on a single specimen dredged near the island of Hokkaido. It was considered to be a subspecies of *P. tuberculatospinosus* because the first cirlet of pharyngeal teeth consists of very small teeth and two teeth of the fourth cirlet are somewhat larger than the others. However, the specimen involved was very small (about 9 mm) and there is not much difference between *P. tuberculatospinosus* and *P. caudatus* of that size. Considering the facts that *P. caudatus* is known to occur along the coasts of Hokkaido (Okuda, 1934) and that it has never been proved with certainty that *P. tuberculatospinosus* does occur in northern waters it is highly likely that the specimen belongs to *P. caudatus*. The occurrence of another peculiarity (the absence of scalids) has been discussed earlier (see page 20).

Distribution. — See fig. 80-81 and 88.

This species has a northern circum-polar distribution. Of course it has never been collected under the permanent polar ice cap, but it undoubtedly occurs there. It is known to be common along the coasts of Scandinavia, Scotland,

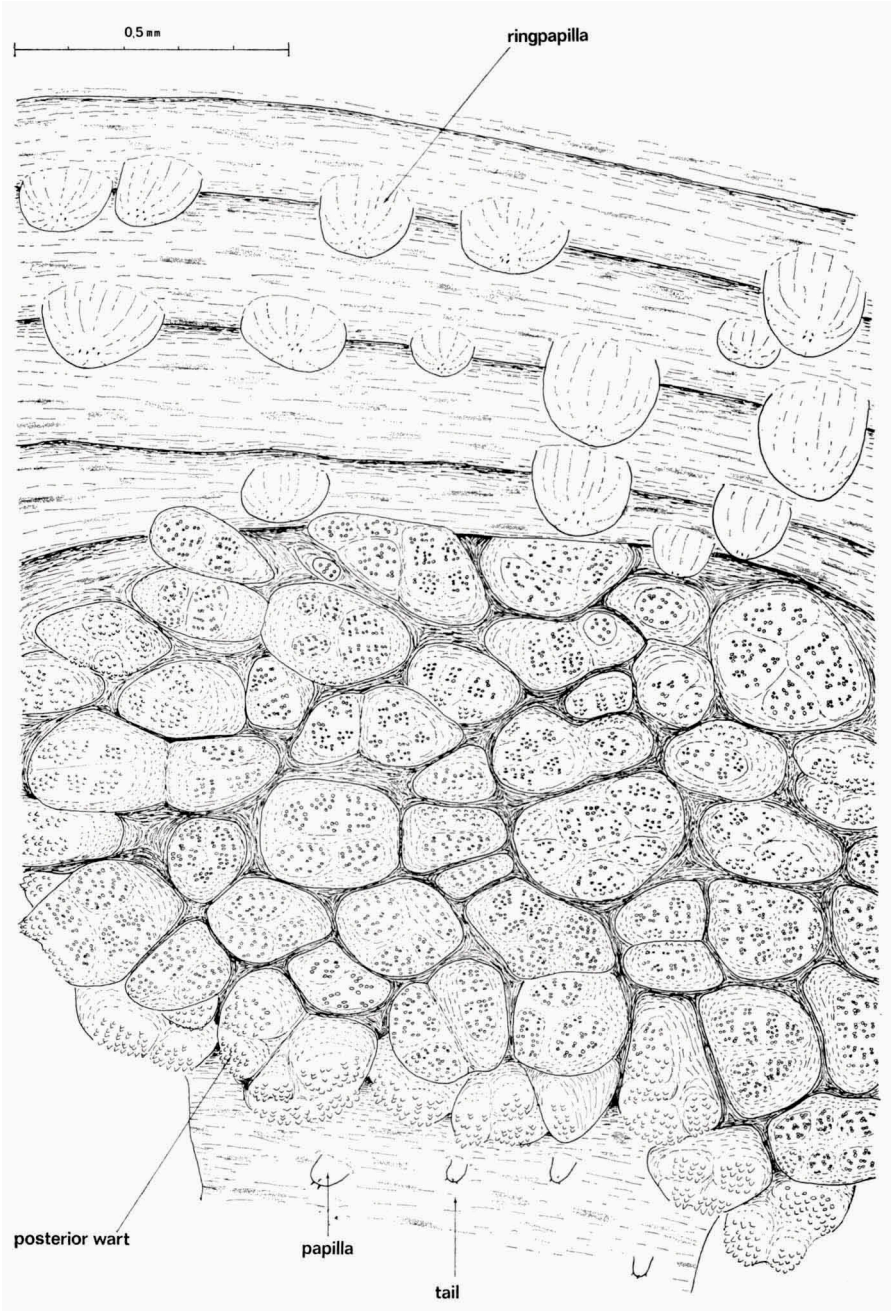


Fig. 13. *Priapulus caudatus*, fragment of posterior end of abdomen, Sweden (Mus. Leiden 4918).

Iceland, Spitsbergen, Greenland, and the far eastern coasts of the USSR. Probably it is just as common along the coasts of northern Siberia, northern Canada and Alaska, but not many collections have been made in these areas. The species shows a much more scattered occurrence in more southern regions: the southern North Sea, along the coasts of England, Ireland, eastern Canada, New England, the western United States, and northern Japan.

P. caudatus has been reported from the Belgian coast, for the first time by Fischer (1925), who referred to Ehlers. This record probably goes back to Maitland's checklist of the fauna of the Netherlands (1855). This author only stated that the species occurred „aan de kusten der Noordzee” (along the coasts of the North Sea) and did not specifically report it from the Dutch coast. The Latin title of his book (*Fauna belgii septentrionalis* . . .) led to the assumption that *P. caudatus* had been found along the Belgian coast. As far as I know this worm has never been found on or near the Belgian and Dutch coasts, unattractive to so many animals.

The most remarkable recent record is the one by Guille & Laubier (1965). They found one specimen in the Mediterranean off Banyuls (France) at a depth of about 100 m. Dr. Guille was kind enough to send the specimen and I can affirm the identification. In fact it has been stated to occur in the Mediterranean already a long time ago, viz., by Gmelin (1788); however, he did not mention his source of information and therefore this record has always been considered unreliable.

P. caudatus is a rather large and easily recognizable animal. Therefore we can be sure that we now have a fairly good idea of its distribution in shallow water. However, we have only a scanty knowledge of its distribution in deep water. We only know that it is not extremely common in the Norwegian Sea; it has been found there only rarely although many collections have been made in the course of time (compare fig. 81 with fig. 85). A few records from deep water off New England, off Kamchatka, and off Japan (perhaps also off California, see fig. 88) suggest that the species may have a wide distribution in the deep sea and this might explain its occurrence in the Mediterranean. Seemingly isolated populations (the one of Tomales Bay, California, is another example) are most likely to originate from the deep sea.

In certain areas there are considerable fluctuations in the abundance. Schulz (1931) stated that this worm was relatively rare in the Kieler Förde (Germany), where it had been very common a few years before. According to Segerstråle (1960) *P. caudatus* was numerous in the deeper parts of the Baltic Sea in 1949 and 1950. After 1955 it became less common and in 1958

and 1959 the Gotland, Gdansk, and Bornholm Deep were practically lifeless deserts. Tulkki (1965) also found an azoic region in the Bornholm Deep, according to him due to mass mortality in the 1950's.

Priapulus tuberculatospinosus Baird, 1868

(fig. 3-4, 9, 12, 15, 18, 20-21, 23, 82, 88)

Priapulus tuberculatospinosus Baird, 1868: 106-107, Pl. 11 fig. 3 (description; Falkland Islands.) — de Guerne, 1886: 1 (description; Tierra del Fuego); 1888: 6-15, 18, Pl. 1 fig. 1-9, Pl. 2 fig. 1-6 (description; Tierra del Fuego). — Shipley, 1896: 432-433. — Lahille, 1899: 50-51 (bipolarity). — Collin, 1901: 300-302. — Hérubel, 1904a: 109, fig. 4IV. — Théel, 1906: 18. — Fischer, W., 1914: 22-25 (systematics). — Lang, K., 1951: 565-567, fig. 1, 2b (pharyngeal teeth, larva; South Georgia, Falkland Islands). — Dell, 1955: 1129-1132, fig. 1-5 (description; New Zealand; distribution, zoogeography). — Wesenberg-Lund, 1955: 3-5 (Chile; distribution). — Hedgpeth, 1957: 377, fig. 14 (bipolarity). — Golvan, 1958: 568. — Hyman, 1959: 742 (textbook). — Menzies, 1959: 1585-1586. — Shapeero, 1962a: 355 (chitin in cuticula). — Guille & Laubier, 1965: 1125-1126 (distribution-map). — Hickman, 1967: 254, 259, fig. 13 (textbook). — Murina, 1968: 88-89. — Tommasi, 1968: 1-4, fig. 1 (diagnosis; Brasil; distribution).

Priapulus caudatus var. *antarcticus* Michaelsen, 1889: 48-51, fig. 3 (description; South Georgia; zoogeography). — Pfeffer, 1890: 512 (South Georgia). — Fischer, W., 1894: 22 (South Georgia); 1896: 6-7 (Tierra del Fuego). — Skorikov, 1901: xxi-xxiii (Kerguelen); 1902a: 155-157 (Kerguelen). — Fischer, W., 1914: 22-26, fig. 12 (description, South Georgia; Tierra del Fuego); 1920: 414, 419-420, 428 (morphology; distribution); 1922a: 34 (South Georgia); 1922b: 3, 17, 19, 24 (description; Kerguelen); 1922c: 242; 1928: 475 (distribution).

Priapulus fuegensis Lahille, 1899: 51-52 (description; Ushuaia, Tierra del Fuego; zoogeography).

Priapulus humanus var. *antarcticus*; Collin, 1901: 299-302 (description; Kerguelen).

Priapulus caudatus (non Linnaeus); Benham, 1916: 165 (Australian waters N. of Antarctic circle); 1932: 890 (New Zealand).

Priapulus caudatus var. or forma *tuberculatospinosus*; Théel, 1911: 15-24, fig. 2, Pl. 1 fig. 1-5 (description, systematic status; Patagonia, Tierra del Fuego, Falkland Islands, Graham region, South Georgia). — Fischer, J., 1913: 109, 113-144 (perhaps only individual variation). — Benham, 1922: 5-6 (description; Macquarie, Antarctica). — Derjugin, 1927: 20 (bipolarity). — Baltzer, 1934a: 10-11 (textbook). — Stephen, 1941: 237, 241, 243-244, 258-259 (Falkland islands, South Georgia, South Orkneys, South Shetlands). — Dawydoff, 1959: 923 (textbook). — de Lattin, 1967: 158, 503, fig. 53 (distribution-map; bipolarity).

Priapulus tuberculatospinosus var. *fuegensis* Marelli, 1912: 139-143 (description; Tierra del Fuego; zoogeography).

Priapulus caudatus tuberculatospinosus; Derjugin, 1915: 863, 871. — Ekman, 1935: 327 (zoogeography).

Priapulus abyssorum Menzies, 1959: 1585-1586, fig. 1 (description, 1 specimen; Pacific Ocean, Mid-America trench, 12° 11' N 80° 34' W, 5680 to 5690 m). — Wolff, 1961: 142, 144, 158, fig. 10 (Pacific Ocean, off Costa Rica). — Tommasi, 1968: 1-2.

Priapulus tuberculatospinosus tuberculatospinosus; Murina & Starobogatov, 1961: 183, 188-190, 195-198, fig. 3v, 4v, 5v, 7b, 10, 12 (bibliography; description; Macquarie; distribution-map). — Olivier, et al., 1961: 259-260, 269, fig. 1 (Argentina). — Hurley, 1962: 13-15. — Sanders & Hessler, 1962: fig. 3-4. — Murina, 1964: 873-875 (distribution-map, zoogeography).

Priapulus tuberculatospinosus abyssorum; Murina & Starobogatov, 1961: 183, 190-191,

195, 197, fig. 1b, 3g, 4g, 5g, 6v, 7v, 8v, 10, 12 (description; North Pacific Ocean, New Zealand; distribution-map). — Sanders & Hessler, 1962: 125, fig. 3-4. — Hurley, 1962: 13-15. — Murina, 1964: 873-875 (distribution-map; zoogeography). — Guille & Laubier, 1965: 1125-1126 (distribution-map). — Murina, 1968: 88-89 (geographical and bathymetrical distribution).

Priapulus tuberculatospinosus bahiensis Olivier, Rapoport, & García, 1961: 259-269, fig. 1-5 (description; ecology, food; Puerto Ing. White, Bahía Blanca, 38°47'S 62°16'W, Argentina, zona intercotidal). — Tommasi, 1968: 1-2.

Material. — Hundreds of adults from many localities in Antarctica, the Antarctic Islands, Chile, and Argentina were studied. The author has seen larvae and postlarvae from South Georgia only. Type specimens were not studied, but the following types are known to be present in collections: *P. tuberculatospinosus* (Mus. London), *P. caudatus* var. *antarcticus* (Mus. Hamburg 2003), *P. abyssorum* (Lamont Geological Observatory), *P. t. bahiensis* (Museo de La Plata).

Diagnosis. — In the pharyngeal armature of adults teeth of first circler much smaller than those of second circler; two teeth of fourth circler larger than the others; seventh circler with more than five teeth. Tubuli of larvae situated at distance of about two fifths of total length of lorica from posterior end.

Description. — Living specimens in extended condition reach a length of nearly 200 mm in exceptional cases (Lahille, 1899: 194 mm). Most specimens in collections are even much shorter than 100 mm.

Pharyngeal armature: In postlarvae it does not differ from that of *P. caudatus* (fig. 5). Later (fig. 3-4) the teeth of the first circler stay behind in their growth and remain quite small in comparison with the other teeth, although they commonly develop a distinct median cusp. Usually the two large teeth of the fourth circler (the latero-dorsal ones) remain evidently larger than the other teeth of the same circler. (Sometimes the difference is quite small. Sometimes the two ventral teeth are of nearly the same size as the latero-dorsal ones, the dorsal tooth only distinctly smaller). In mature specimens the large teeth of the anterior circlers usually bear 6 to 10 lateral cusps but a number of 4 lateral cusps is not exceptional. The sixth circler consists of five teeth but from the seventh circler the number of teeth per circler is higher.

Tail: The spinulets of the vesiculae (fig. 9) are usually large and numerous (hence the name of the species); specimens with vesiculae with small and sparse spinulets are less common.

Larva: the tubuli are situated at a distance of about two fifths of the total length from the posterior end (fig. 23).

Discussion. — When the descriptions of *Priapulus caudatus* and *P. tuber-*

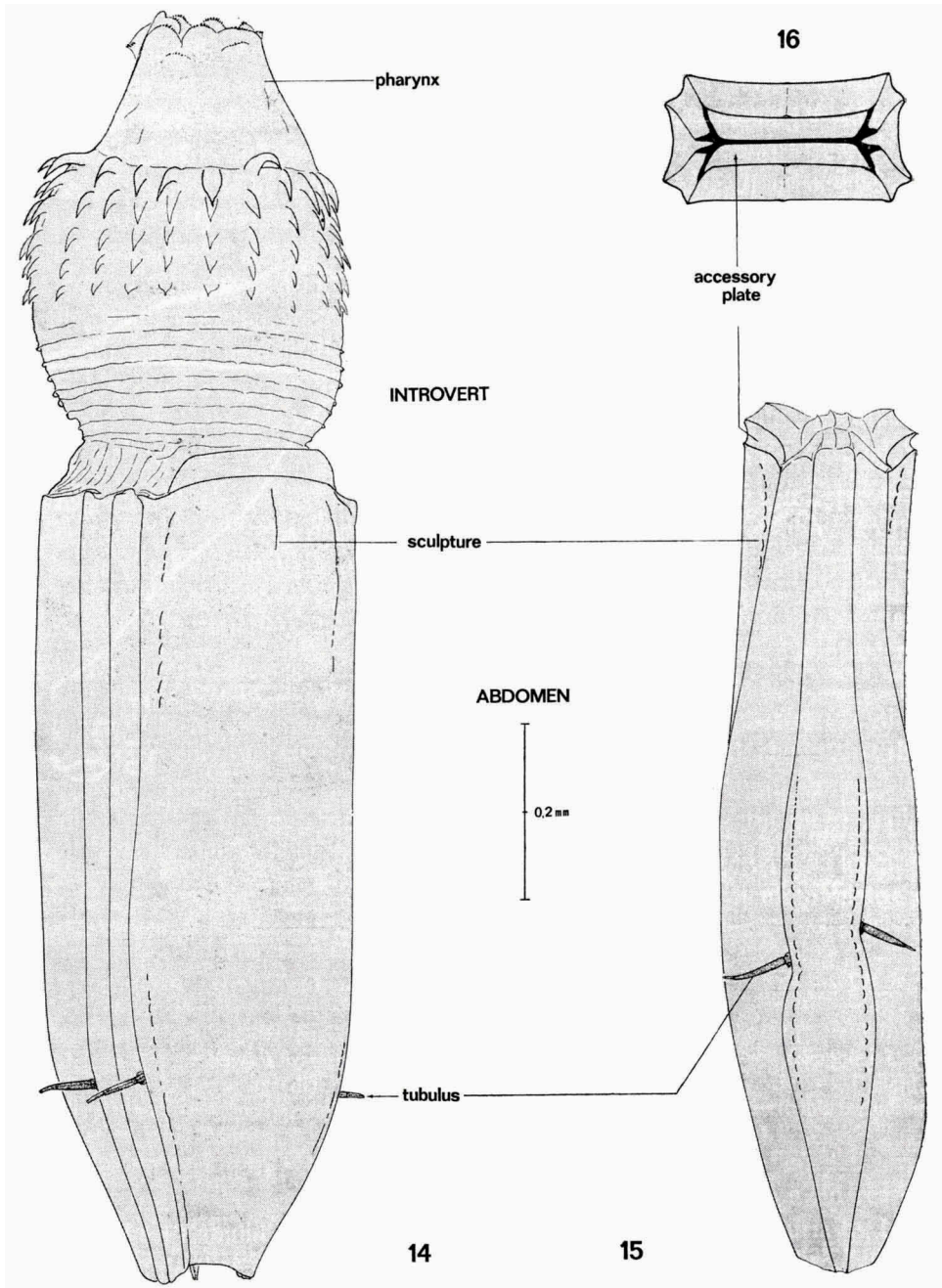


Fig. 14-16. *Priapulus*, larvae; 14, *P. caudatus*, latero-dorsal or latero-ventral view, Iceland (Mus. Stockholm); 15, *P. tuberculatospinosus*, lateral view, introvert withdrawn, South Georgia (Mus. Stockholm); 16, *P. caudatus*, frontal view, introvert withdrawn, Öresund (after sketch of living specimen).

culatospinosus are compared, it is evident that these two species differ but slightly. The very few differences mentioned in the literature proved to be less reliable than they were considered to be.

(1) The pharyngeal teeth of the first cirlet are very small in *P. tuberculatospinosus*. However, there is no difference in very small specimens, and in mature *P. caudatus* small teeth occur occasionally.

(2) Two teeth of the fourth cirlet are larger than the others in *P. tuberculatospinosus*. However, this is not always the case and certainly not always evident; two of the other teeth may be of nearly the same size. Moreover, small specimens of *P. caudatus* have the same character.

(3) Perhaps there is a slight statistical difference in the number of lateral cusps (J. Fischer, 1913).

(4) There are seven "pentagons" in *P. caudatus* and six in *P. tuberculatospinosus*. This statement is based on few observations because in most specimens, especially small ones, it is quite difficult to determine with certainty

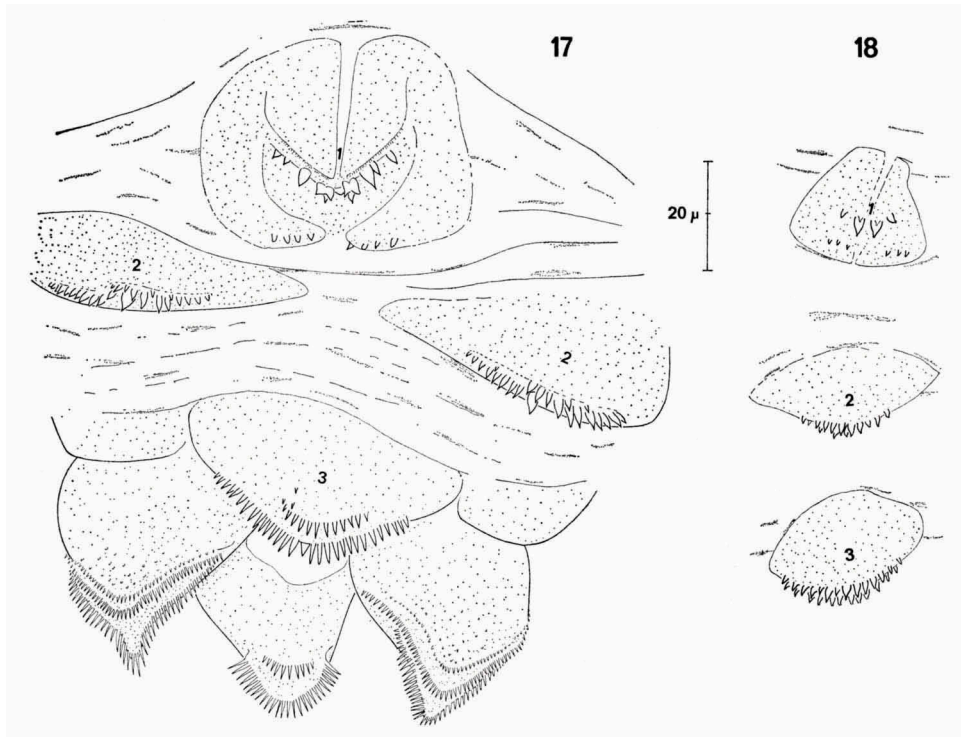


Fig. 17-18. *Priapulus*, larvae, anterior pharyngeal teeth. 17, *P. caudatus*, Iceland (Mus. Stockholm); 18, *P. tuberculatospinosus*, younger stage, South Georgia (Mus. Stockholm).

whether there are five teeth in the sixth circllet or more. Anyhow, it cannot be considered a reliable character.

(5) The larvae differ only in one character, viz., the position of the tubuli (see fig. 23). This difference was discovered by K. Lang (1951). However, it was based on observations on few populations only. The material of *P. tuberculatospinosus* mentioned by K. Lang, collected by the Swedish Antarctic Expedition 1901-1903, is still the only material present in collections (Mus. Stockholm). My measurements (fig. 23) refer to the same samples.

We may conclude that there are no qualitative differences but only quantitative differences, often with a large overlap. One is inclined to consider *P. tuberculatospinosus* a subspecies of *P. caudatus* as has been done by several other authors. However, a decision can better be made when more is known about the fauna of the tropical deep sea (see later). The question is of some interest because of its relevance to the bipolarity problem.

In this connection mention may be made of a problematical specimen. Shipley (1902) recorded *Priapulus caudatus* from Antarctica (two specimens washed ashore at Cape Adare). One would expect that the material had been misidentified or that Shipley considered the southern and northern species to be identical. The latter was probably the case. However, curiously enough the large specimen (the second one is only a fragment without introvert) indeed has all characters of the northern form. For the time being I do not want to base any conclusion on this single observation, and just mention it. Mislabeling or shift of specimens are not likely to have occurred; the British Museum was not overloaded with priapulids in those times.

The following taxa are synonymized here for the first time:

Priapulus tuberculatospinosus bahiensis Olivier, Rapoport, & García, 1961.

The authors gave a detailed description of their material, with interesting ecological notes, but no characteristic differences from the typical *P. tuberculatospinosus*. The specimens were described as a new subspecies only because they were considered to be relatively small. The pharyngeal armature, in which the most important characters are to be expected, was not described at all; there is only a simple diagram of the arrangement of the teeth, but this is almost certainly incorrect: the largest teeth are situated in the first circllet and the teeth gradually diminish in size from the first to the sixth circllet (In *P. tuberculatospinosus* the teeth of the first circllet are very small and the largest teeth are situated in the fourth circllet); the first circllet has a mid-dorsal tooth (there should be a mid-ventral one); the teeth of the fourth circllet are of equal size.

Priapulus abyssorum Menzies, 1959.

The original description was based on one small specimen (total length

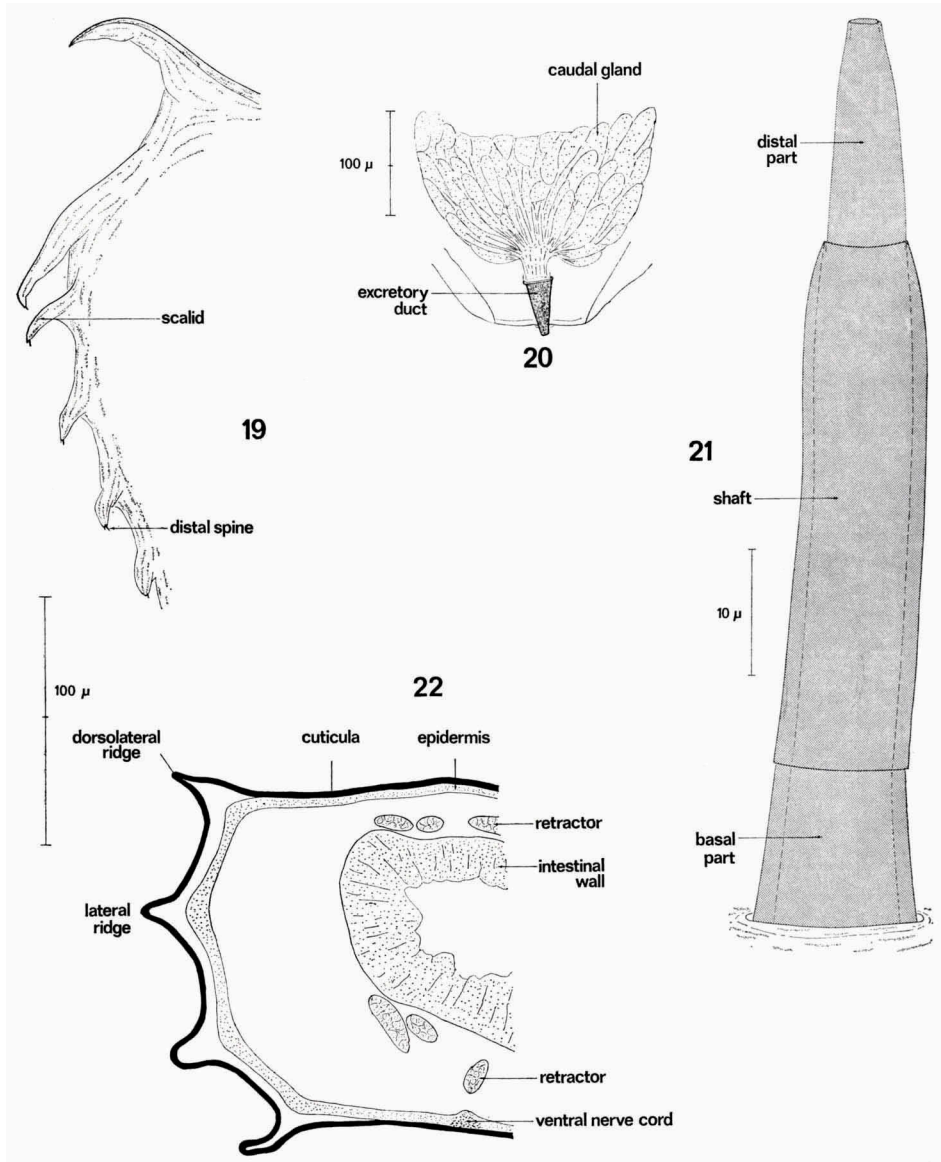


Fig. 19-22. *Priapulus*, details of larvae. 19, *P. caudatus*, scalids, Iceland (Mus. Stockholm); 20-21, *P. tuberculatospinosus*, South Georgia (Mus. Stockholm); 20, caudal gland; 21, tubulus; 22, *P. caudatus*, cross-section of abdomen, Öresund (Mus. Leiden).

22 mm) from the tropical deep sea. The fact that the pharyngeal teeth of the first cirlet are very small indicates that the specimen most probably belongs to *P. tuberculatospinosus* and Menzies was quite right in concluding: "The animal is allied so closely to *Priapulus tuberculatospinosus* that some may doubt whether the two are distinct species. A positive decision can not be reached without additional specimens of various sizes". Curiously enough he nevertheless described it as a new species, probably because the specimen was dredged from the deep sea or just for safety's sake.

Meanwhile a number of similar small specimens have been reported from the deep sea; all localities are indicated in fig. 88. Wolff (1961) found one

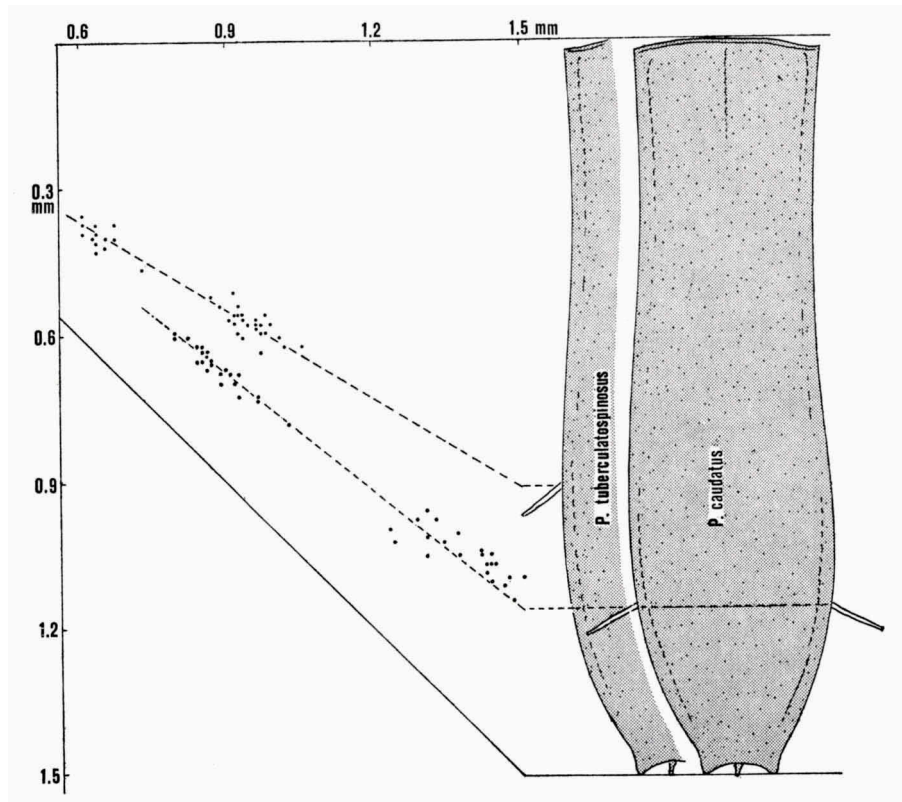


Fig. 23. *Priapulus caudatus* and *tuberculatospinosus*, larvae, distance from anterior end of loric to level of tubuli plotted against total length of loric (based on measurements of about 50 specimens of each species; *P. caudatus* from Denmark and *P. tuberculatospinosus* from South Georgia). Two distinct size groups can be recognized in both species, but it should not be concluded that there are only two larval stages. This aspect will be treated in another paper.

specimen in the same area (depth 3570 m). Murina & Starobogatov (1961), who considered the animals to belong to a subspecies of *P. tuberculatospinosus*, reported them from several localities in the North Pacific (depths 3300 to 7600 m). Murina (1964) indicated a find in the Java trench on her map. She wrote to me that this refers to Vitjaz sta. 5168, depth 6433 m. According to the logbook of the Galathea expedition, present in the Copenhagen museum, a second specimen was found in the Java trench at a depth of 3920 m (sta. 474).

It is to be regretted that until now only very few, small specimens have been dredged from the deep sea. I have seen none of them and separate descriptions of the various specimens are lacking. Therefore it is impossible to decide to which species the animals belong. They have all been mentioned as *P. tuberculatospinosus abyssorum* or as *P. abyssorum*, but given the fact that small specimens cannot easily be identified, it is quite possible that the records from the trenches in the North Pacific refer to *P. caudatus*, which is known to occur in these areas. The tropical records may refer to *P. tuberculatospinosus*. It is not impossible that the two species intergrade in the deep sea.

Distribution. — See fig. 82 and 88.

This species shows about the same pattern of distribution on the southern hemisphere as the preceding species on the northern hemisphere. The inaccurate record by Benham (1916), who reported this species from Australian waters north of the Antarctic circle, could not be indicated on the map. In this case there is also an isolated record from subtropical waters: Tommasi (1968) found one specimen in Brazilian coastal waters. There are also two records from deep water: Murina & Starobogatov (1961) reported the find of one specimen at a depth of about 3000 m in New Zealand waters (they referred the specimen to *P. t. abyssorum*, but only because it was found at a great depth). The "Vema 17" expedition dredged one specimen from a depth of 2657 m in Chilian waters (sta. V-17-13). The records from the tropical deep sea were discussed above.

As in the case of the preceding species we would like to know more about the distribution in the deep sea, particularly in the tropics.

Priapulopsis Koren & Danielssen, 1875.

Priapulopsis Koren & Danielssen, 1875: 135 (diagnosis).

Priapuloides Koren & Danielssen, 1877: 146 (diagnosis). — Delage & Hérouard, 1897: 11, fig. 3-4 (diagnosis). — Molčanov, 1908: 957, 959, 961 (status). — Dawydoff, 1959: 923 (textbook).

Priapulopsis (subgenus of the genus *Priapululus*); Murina & Starobogatov, 1961: 193, 196 (diagnosis).

Type species: *Priapulius bicaudatus* Danielssen.

Differential diagnosis. — Scalids telescopicform. First cirlet of pharyngeal armature consisting of 10 small teeth. Two unsegmented tails. Larva with closing apparatus consisting of several plates.

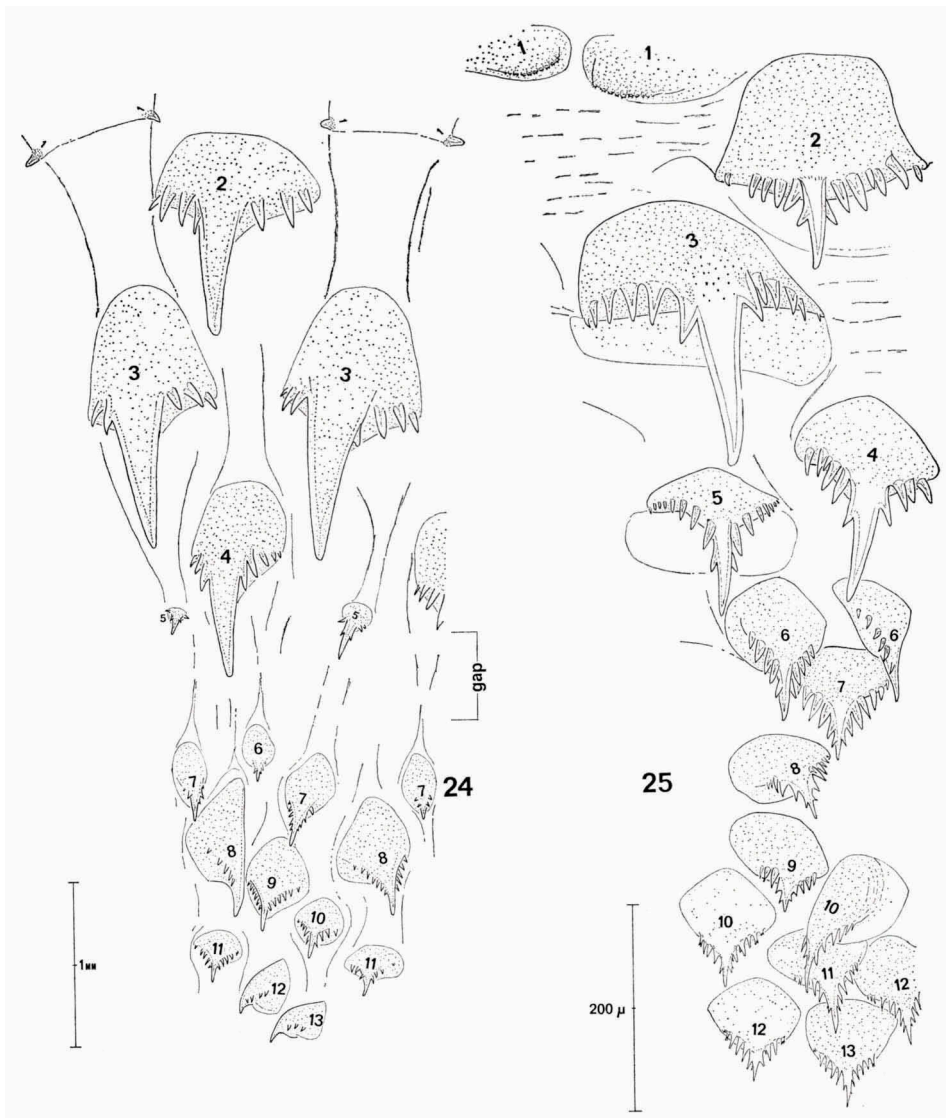


Fig. 24-25. *Priapulopsis*, anterior pharyngeal teeth. 24, *P. australis*, length about 30 mm, Chili (Mus. Stockholm); 25, *P. bicaudatus*, postlarva, Greenland (Mus. Copenhagen), (the pharyngeal teeth of the adults do not differ essentially from those of the postlarvae).

Description. — In the pharyngeal armature (fig. 24-25) the first circlet consists of ten rudimentary teeth (each pair can be considered to have developed from a single tooth by reduction of its median part); the second to the fifth circlets consist of five teeth (pentagons). The largest teeth are situated in the third circlet. The normal teeth always bear a strong median cusp and up to about 20 lateral cusps; the rudimentary teeth of the first circlet bear one to about ten small denticles. There are few to many buccal papillae.

The relative length of the introvert is somewhat larger than in *Priapulus*; depending on the state of contraction it is 40% to more than 100% of the length of the abdomen; in small specimens it may reach more than twice the length of the abdomen. The scalids (fig. 26-29) are telescopiform. The distal part, in larger specimens strengthened by a cuticular tube, can be telescoped into the broad basal part. Anteriorly they are usually arranged in conspicuous series, each consisting of up to seven scalids. The two ventral rows are nearer to each other than the other rows (fig. 26).

The abdomen is provided with 35 to 50 annuli, three to five of them bearing numerous, conspicuous ringpapillae (fig. 31), at least in the adult. Posterior warts are lacking, but small, conical papillae are present all over the body. The skin is densely covered with irregularly distributed tumuli (fig. 31, 34).

The tail is not segmented. In postlarvae (fig. 30; Pl. 2C) it is covered with papillae. These papillae are more or less conspicuously arranged in circlets and gradually grow into vesiculae. Each vesicula is tipped with a group of spinulets (fig. 32-33) or completely smooth.

Usually there are eight long introvert retractors; two of them are shorter than the others, which are very long and nearly reach the level of the ringpapillae. There are about ten short introvert retractors, but pharynx retractors are lacking (the latter are apparently reduced to a dorsal and a ventral muscle running from the anterior to the posterior part of the intestine).

Larvae are poorly known. The brief description of larvae of *P. bicaudatus* by Sanders & Hessler (1962) is the only one available until now. It can not easily be interpreted but it is clear that *Priapulopsis*-larvae have essentially the same morphology as those of *Priapulus*. According to Sanders & Hessler an important difference is to be found in the structure of the closing apparatus: there are not two but eight accessory plates. The posterior chitinous tube seems to be lacking and the scalids are probably different.

Discussion. — In my opinion *Priapulopsis* deserves the status of a separate genus. The presence of two tails is very important, and the peculiar structure of the tail, the telescopiform scalids, and the tumuli are also quite charac-

teristic, not to speak of many other peculiarities of minor importance.

Subdivision. — There are two well defined species; only one species has to be synonymized.

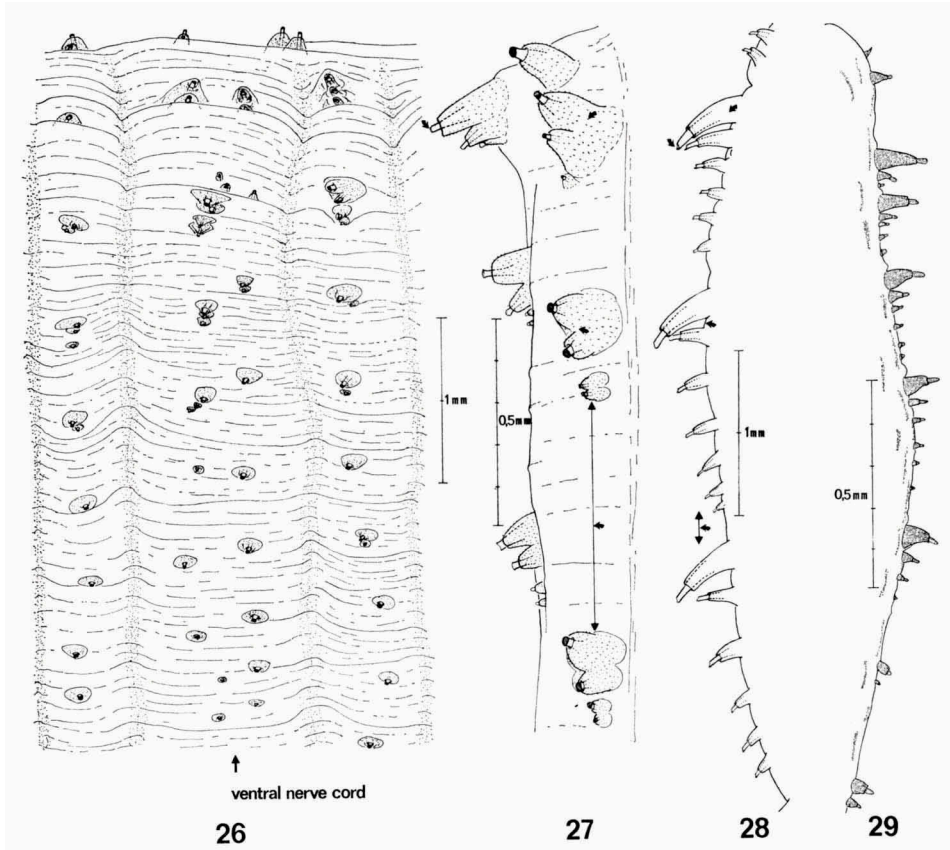


Fig. 26-29. *Priapulopsis*, anterior scalids. 26-27, *P. australis*, Chili (Mus. Stockholm); 26, the four rows closest to the ventral nerve cord; 27, two lateral rows; 28-29, *P. bicaudatus*; 28, Greenland (Mus. Copenhagen); 29, postlarva, western North Atlantic ("*P. atlantisi*" from coll. Sanders). In fig. 27 and 28 the differences between *P. australis* and *P. bicaudatus* are indicated by arrows.

Priapulopsis bicaudatus (Danielssen, 1868)

(fig. 25, 28-32, 34, 84-85, Pl. 1 A, 2 C)

Priapulopsis bicaudatus Danielssen, 1868: 542 (description; Varangerfjord, Norway, 120 fm) [type locality here restricted to Vadsö]. — Théel, 1875: 20, 23 (diagnosis). — Horst, 1881: 13-38, Pl. 2, fig. 1-12, Pl. 3, fig. 13-20 (anatomy, histology; Barents Sea). — Apel, 1885: 460, 466-468, 470-471, 480, 482, 483, 497-501, 524 (histology). — Scharff, 1885: 194, 196, 198, 200, 203, 210. — Shipley, 1896: 430, 432 (textbook; North Sea [?]);

1902: 285. — Skorikov, 1902b: 277 (Norway). — Théel, 1906: 13, 18-19, Pl. 1 fig. 3-6, Pl. 2 fig. 9-10 (Greenland, Spitsbergen, Norway, distribution). — Gadd, 1911: 79, 90 (Russia). — Théel, 1911: 20-21, fig. 3, Pl. 1 fig. 12 (pharyngeal teeth; Greenland). — Schauinsland, 1912: 1113, 1116, fig. 3 (encyclopedia). — Fischer, J., 1913: 91. — Fischer, W., 1914: 26 (South Atlantic [lapsus?]). — Derjugin, 1915: 30, 373, 375, 741 (Russia). — Fischer, W., 1920: 420-421 (morphology; North Atlantic; distribution, zoogeography); 1922b: 3, 17, 19, 22 (nomenclature; description; North Atlantic; zoogeography); 1922c: 232, 243, 245 (Spitsbergen, Arctic Ocean; distribution). — Wesenberg-Lund, 1925: 82, 85-86 (Greenland; distribution). — Fischer, W., 1925: 51 (tail); 1928: 455, 474, 476-478, fig. 2 (description; Spitsbergen, Arctic Ocean; distribution). — Wesenberg-Lund, 1928: 5; 1929: 177-182, fig. 2 (musculature, nervous system). — Stiasny, 1930: 204, 206 (Barents Sea). — Wesenberg-Lund, 1930: 5-7, 14-17, Pl. 1 fig. 9, Pl. 2 fig. 14-15, 17-18, 21-26 (histology of skin; North Atlantic, Greenland; distribution); 1932: 3, 5-6, 16-17, fig. 2, 8 (western Greenland (map); distribution-map); 1933: 1, 3, Pl. 1 fig. 1 (Siberia); 1934: 5-6 (Greenland) — Baltzer, 1934a: 3, 11, fig. 1-2 (textbook). — Okuda, 1934: 115. — Satô, 1934: 1, 23-28, fig. 26-31, Pl. 1 fig. 11 (description; Japan). — Ekman, 1935: 382 (zoogeography). — Satô, 1937: 139, 168, Pl. 4 fig. 22 (Japan). — Wesenberg-Lund, 1937a: 2, 4-5, 14-15, fig. 1 (ecology; Iceland; distribution); 1937b: 3, 6-7, 22-24, fig. 2 (ecology; Greenland); 1939c: 38. — Satô, 1939: 348, 432, 434, 439, 451 (bibliography; distribution Japan). — Lüling, 1940: 136, 153. — Brown & Cheng, 1946: 66 (predators; Iceland, Barents Sea). — von Haffner, 1950: fig. 1. — Hyman, 1951: 184, 187, fig. 87A (textbook). — Lang, K., 1951: 567. — Wesenberg-Lund, 1954: 1-2 (Iceland). — Dell, 1955: 1129. — Golvan, 1958: 568-569. — Stephen, 1960: 25-26. — Murina & Starobogatov, 1961: 183, 193, 195-196, 198, fig. 3e, 4e, 5z, 7e, 8g, 11 (bibliography; description; distribution-map). — Olivier, et al., 1961: 259. — Sanders & Hessler, 1962: fig. 3-4. — Hurley, 1962: 14. — Nørrevang, 1963c: 701 (histology excretory organs). — Murina, 1964: 873-875 (distribution-map, zoogeography). — Hickman, 1967: 254, 259 (textbook). — Murina, 1968: 89. — Tommasi, 1968: 1-2.

Priapulopsis typica (pro *Priapulus bicaudatus*) Koren & Danielssen, 1875: 135 (diagnosis; Varangerfjord, Norway). — Norman, 1903: 285-286.

Priapuloides typicus; Koren & Danielssen 1877: 147-150, Pl. 16 fig. 10-14 (description, histology, anatomy; Norwegian Sea). — Levinsen, 1884: 275, 318 (diagnosis; distribution). — de Guerne, 1886: 1-3 (Norway). — Fischer, 1896: 7. — Marelli, 1912: 139.

Priapuloides bicaudatus; de Guerne, 1888: 7-8, 10, 15-16, 18 (Norway). — Averincev, 1908: 192 (Russia). — Molčanov, 1908: 957, 964, 966. — Dawydoff, 1959: 909, 911, fig. 718A.

Priapulus atlantisi Sanders & Hessler, 1962: 125-126, 129-130, fig. 1, 3-5 (description postlarvae and larvae; North Atlantic, continental slope S. of New England, 39°42'N 70°39'W, 2000 m, and 39°42'N 70°45'W, 1500 m). — Murina, 1964: 873-875. — Guille & Laubier, 1965: 1125-1126. — Hickman, 1967: 254. — Murina, 1968: 89. — Tommasi, 1968: 1-2.

Material. — Several dozens of specimens (including postlarvae) from many localities were studied. Material from the North Pacific and larvae were not available. The author has seen the two type specimens of *P. bicaudatus* (Mus. Bergen) and one specimen of *P. atlantisi* (more specimens in Mus. Washington and coll. Sanders).

Diagnosis. — Pharyngeal armature: teeth of first circler with number of denticles; teeth of fifth circler not much smaller than those of fourth one and not followed by conspicuous gap. Scalids of one series not very close

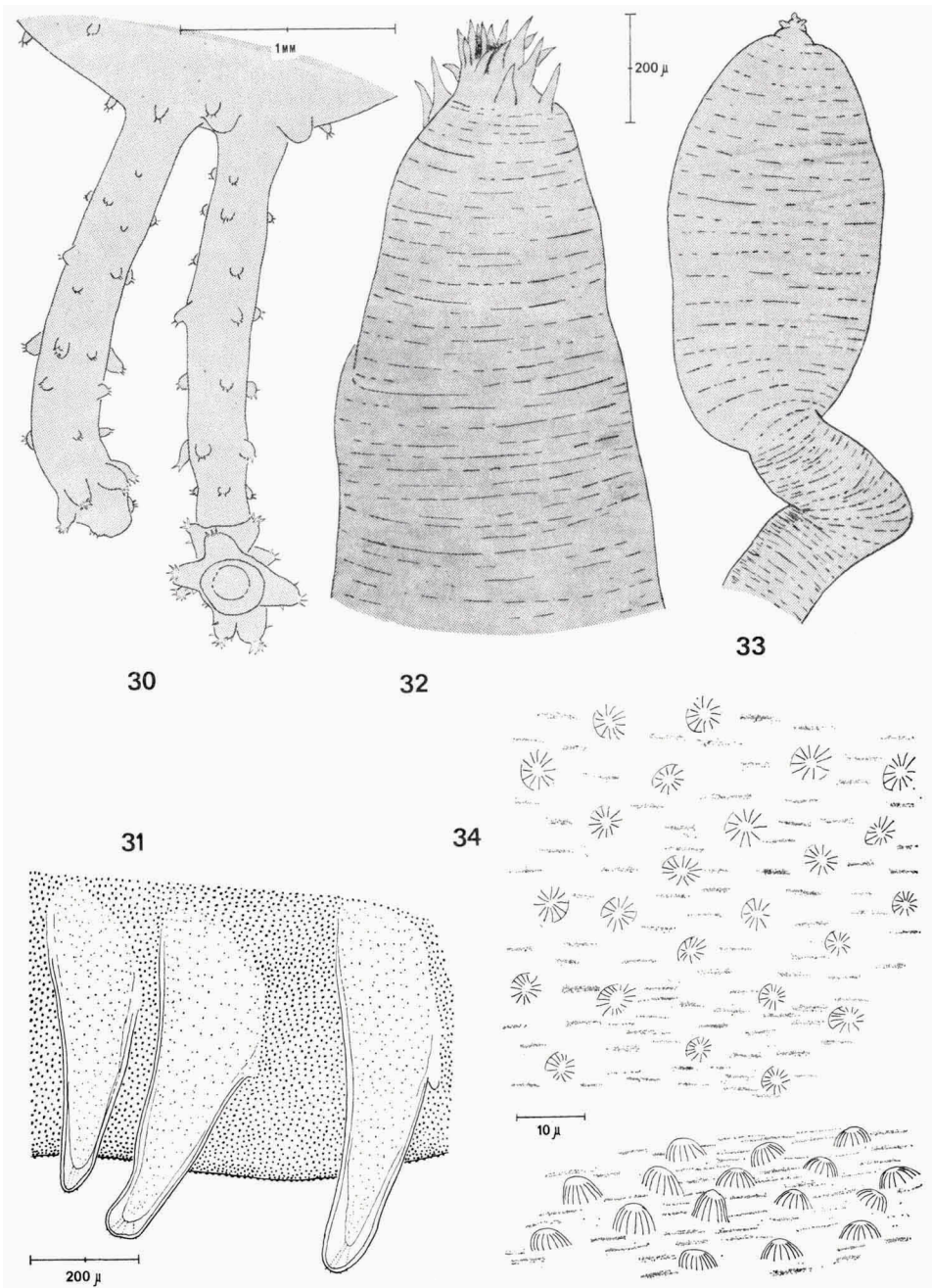


Fig. 30-34. *Priapulopsis*. 30-32, *P. bicaudatus*; 30, tails of postlarva, western North Atlantic ("*P. atlantisi*" from coll. Sanders); 31, ringpapillae, Greenland (Mus. Copenhagen); 32, vesicula of tail, Greenland (Mus. Copenhagen); 33, *P. australis*, vesicula of tail, Chili (Mus. Stockholm); 34, *P. bicaudatus*, tumuli, Greenland (Mus. Copenhagen).

together; small gap between the anterior series. Vesiculae of tail tipped with group of conspicuous spinules.

Description. — Living specimens in extended condition have a maximum length of about 100 mm, but specimens of this size seem to be very rare.

Pharyngeal armature (fig. 25): The small teeth of the first circlet bear five to ten small denticles; the other anterior teeth all have a conspicuous median cusp and 6 to 20 lateral cusps. The teeth of the fourth and following circlets gradually decrease in size and there is no conspicuous gap between any of the circlets.

Scalids (fig. 28-29): The individual scalids are always separated from one another; their basal parts are smooth; their distal tips are obliquely cut off. The anterior series, consisting of up to seven scalids, are not separated by large gaps. In large specimens there are up to 19 series in one row.

The vesiculae of the tail (fig. 32) are always provided with a group of distinct spinulae.

The present author has not seen larvae. Part of the description of *P. atlantisi* by Sanders & Hessler (1962), based on nine specimens, is copied here:

“The larvae differed little in size, the lorica varying from 0.82 to 1.02 mm in length. Two tactile spines arise near posterior end of lorica from dorsal and ventral margins of middle lateral plate. Along anterior margin of dorsal plate is small, narrow, crescent-shaped plate; two minute, somewhat triangular plates are at its anterolateral edges, and a minute narrow plate, rounded laterally, is at its anteromedial margin. An identical set of plates are found anterior to the ventral plate. All of the plates anterior to the dorsal and ventral plates are light tan and have roughened punctate appearance. Anterior to each lateral plate is minute narrow anterior lateral plate. Eight large papillae of spines form circle on introvert posterior to mouth. Arising from surface of trunk (within lorica) are numerous fine spines.”

Discussion. — Postlarvae of *P. bicaudatus* had never been described in the literature so Sanders & Hessler (1962) can hardly be blamed for describing their material of postlarvae as a new species (*Priapulidus atlantisi*). Dr. Sanders was kind enough to send one of his specimens and so to present me an opportunity to correct some obscure points in the original description.

(1) According to the description and the figure teeth of the second circlet do not have a median cusp. However, a distinct median cusp is present in the specimen sent to me.

(2) It is not clear from the original description and figures whether the scalids are telescopiform or not. They proved to be telescopiform.

(3) According to the description "no warts or small papillae are evident either on posterior extremity or elsewhere on trunk". However, abdominal papillae (some are visible in fig. 30) as well as ringpapillae proved to be present.

(4) The papillae on the tail are of the type found in *P. bicaudatus*, which was not quite clear from the original figures.

Distribution. — See fig. 84-85.

This species has a more restricted distribution when compared with *P. caudatus*. It is quite remarkable that the numerous Russian expeditions in the North Pacific did not obtain a single specimen (Murina & Starobogatov, 1961). One is inclined to conclude that this species does not have an uninterrupted circumpolar distribution and that the Japanese populations are indeed isolated from the main area. (It is to be regretted that the author could not obtain material from Japan).

In comparison with *P. caudatus* there is a remarkably large number of records from the Norwegian Sea and the Barents Sea. In coastal waters it is only common along the coasts of Eastern Greenland and Spitsbergen, but even in these areas it shows a definite preference for deeper water when compared with *P. caudatus* (Wesenberg-Lund, 1937b). It is not allowed to conclude that *P. bicaudatus* can be expected to have a wide distribution in the deep sea. Until now it has never been dredged from abyssal depths.

The following records are considered to be erroneous: Shipley (1896) stated that the species occurs in the North Sea and W. Fischer (1914) reported it from the South-Atlantic.

Priapulopsis australis (de Guerne, 1886)

(fig. 24, 26-27, 33, 83)

Priapuloides australis de Guerne, 1886: 1-3; 1888: 13-18, pl. 1 fig. 10-21, pl. 2 fig. 7-15 (description; South Atlantic, off Argentina, 44°47'S 65°56'W of Paris [= 63°36'W of Greenwich], 90 m; the island of Vauverlandt, Ponsonby Sound, S. of Navarino, Tierra del Fuego-region, Chile). — Fischer, W., 1896: 7. — Marelli, 1912: 139, 143. — Shipley, 1902: 285.

Priapulus australis; Wesenberg-Lund, 1955: 3, 5 (systematic status; Chile; distribution). — Hyman, 1959: 742 (textbook). — Murina & Starobogatov, 1961: 183, 193-196, fig. 3ž, 4ž, 5z, 8d, 11 (bibliography; description; distribution-map). — Sanders & Hessler, 1962: fig. 3-4. — Hurley, 1962: 13-15 (description; ecology; New Zealand). — Murina, 1964: 873, 875 (distribution-map; zoogeography). — Estcourt, 1967: 356, 364, 366 (ecology; New Zealand). — Hickman, 1967: 254. — Murina, 1968: 88-89. — Tommasi, 1968: 1-2 (distribution).

Priapulus bicaudatus var. *australis*; Fischer, W., 1921: 414, 420, 428 (morphology); 1928: 477. — Stephen, 1941: 237, 244, 258. — Stephen & Cutler, 1969: 112, 118 (South Africa).

Priapulus bicaudatus australis; Dell, 1955: 1129.

Material. — I have only seen the five specimens collected by the Lund University Chile Expedition (Mus. Stockholm), and studied earlier by Wesenberg-Lund (1955).

Diagnosis. — Pharyngeal armature: teeth of first cirlet with only one denticle; teeth of fifth cirlet much smaller than those of fourth one and followed by conspicuous gap. Scalids of one series close together; large gap between anterior series. Vesiculae of tail glabrous or with very few, very small spinulets.

Description. — Living specimens may reach a length of at least 50 mm.

Pharyngeal armature (fig. 24): The teeth of the first cirlet are reduced to a single denticle (they are so small that they have previously been overlooked); the other anterior teeth all have a conspicuous median cusp and 4 to about 12 lateral cusps (perhaps more in postlarvae). The teeth of the fifth, sixth, and seventh cirlets are unusually small (smaller than those of the eighth cirlet) and there is a distinct gap between the fifth and sixth cirlets.

Scalids (fig. 26-27): Usually the scalids of one series lie close together and the basal parts of two or three subsequent scalids are often fused; their basal parts are pubescent (covered with tiny hairs of peculiar shape; see De Guerne, 1888); their distal tips are rectangularly cut off. The anterior series, consisting of up to four scalids, are separated by wide gaps; the posterior series are often indistinct. There are up to about ten series in one row.

The vesiculae of the tail are mostly smooth; once a group of reduced spinulets was observed (fig. 33).

Remarks. — Hitherto only small adults, ranging in size from about 10 to about 40 mm in fixed condition, have been described. Larvae and postlarvae are unknown. The smallest specimen (10 mm long; extended) seen by the present author did already have well developed vesiculae on its tails.

The description by De Guerne (1888), based on the study of 11 specimens, is the only extensive description in the literature. Not much was added to this by Wesenberg-Lund (1955), who had a quick glance at five specimens from Chile, and Hurley (1962) who superficially studied seven specimens from New Zealand.

Discussion. — Contrary to the situation in the genus *Priapulius* the southern species of *Priapulopsis* clearly differs from the northern one in characters of the pharyngeal armature, the scalids, as well as the tail vesicles.

Distribution. — See fig. 83.

Until now this species has only been found on a few localities in New Zealand, South-American, and South-African waters. It is remarkable that it has never been found in Antarctic waters, where so many collections have

been made. We may conclude from this that, unlike *P. bicaudatus*, it prefers somewhat warmer regions.

***Acanthopriapulus* n. gen.**

Type species: *Priapulus horridus* Théel.

Differential diagnosis. — Scalids relatively small and sparse, arranged in indistinct rows. Abdomen with about 30 annuli. Tail segmented and provided with hooks.

Description. — The introvert is at least up to half as long as the abdomen. The diminutive conical scalids are sparse and arranged in indistinct rows; probably not arranged in distinct series. Structure and disposition of the pharyngeal teeth are unknown (probably much like *Priapulus*). The abdomen has about 30 annuli; abdominal papillae are very small and sparse; ringpapillae are present but posterior warts are lacking. The anus has a mid-ventral position close to the base of the tail. The tail is club-shaped, segmented, and provided with strong, posteriorly directed hooks. There are eight long retractors; six of them are inserted on the body wall in about the middle of the abdomen, the others are inserted more anteriorly, one dorsal and one ventral. The number of short retractors is unknown.

Discussion. — The unique construction of its tail is the main reason for proposing a new genus for *Priapulus horridus*. Moreover, due to the loose arrangement of the scalids, the habitus of this species differs considerably from that of other priapulids in which the scalids are relatively larger and lie closer together, forming very distinct longitudinal rows.

***Acanthopriapulus horridus* (Théel, 1911) n. comb.**

(fig. 35-37, 83, Pl. 1 B)

Priapulus horridus Théel, 1911: 24-26, Pl. 2 fig. 13-19 (description; 1 ♀ specimen; South Atlantic, off Uruguay, 33°S 51°10'W, 80 m). — Fischer, W., 1920: 414, 420 (morphology; zoogeography). — Baltzer, 1934a: 10-11, fig. 13 (textbook). — Lüling, 1940: 136. — Stephen, 1941: 237, 244, 257. — Lang, K., 1951: 567. — Dell, 1955: 1129. — Dawydoff, 1959: 909, 924, fig. 720, 721, (non 725) (textbook). — Menzies, 1959: 1585. — Olivier, et al., 1961: 259. — Murina & Starobogatov, 1961: 182, 192-193, 196, fig. 5e, 7d, 9 (description). — Sanders & Hessler, 1962: fig. 3. — Murina, 1964: 873-875. — Guille & Laubier, 1965: 1125-1126. — Hickman, 1967: 254 (textbook). — Murina, 1968: 89. — Tommasi, 1968: 1-2.

Material: Abdomen and tail of the holotype (Mus. Stockholm 1296).

Description. — The following description of a sexually mature female is partly based on the original description by Théel (1911), partly on own observations.

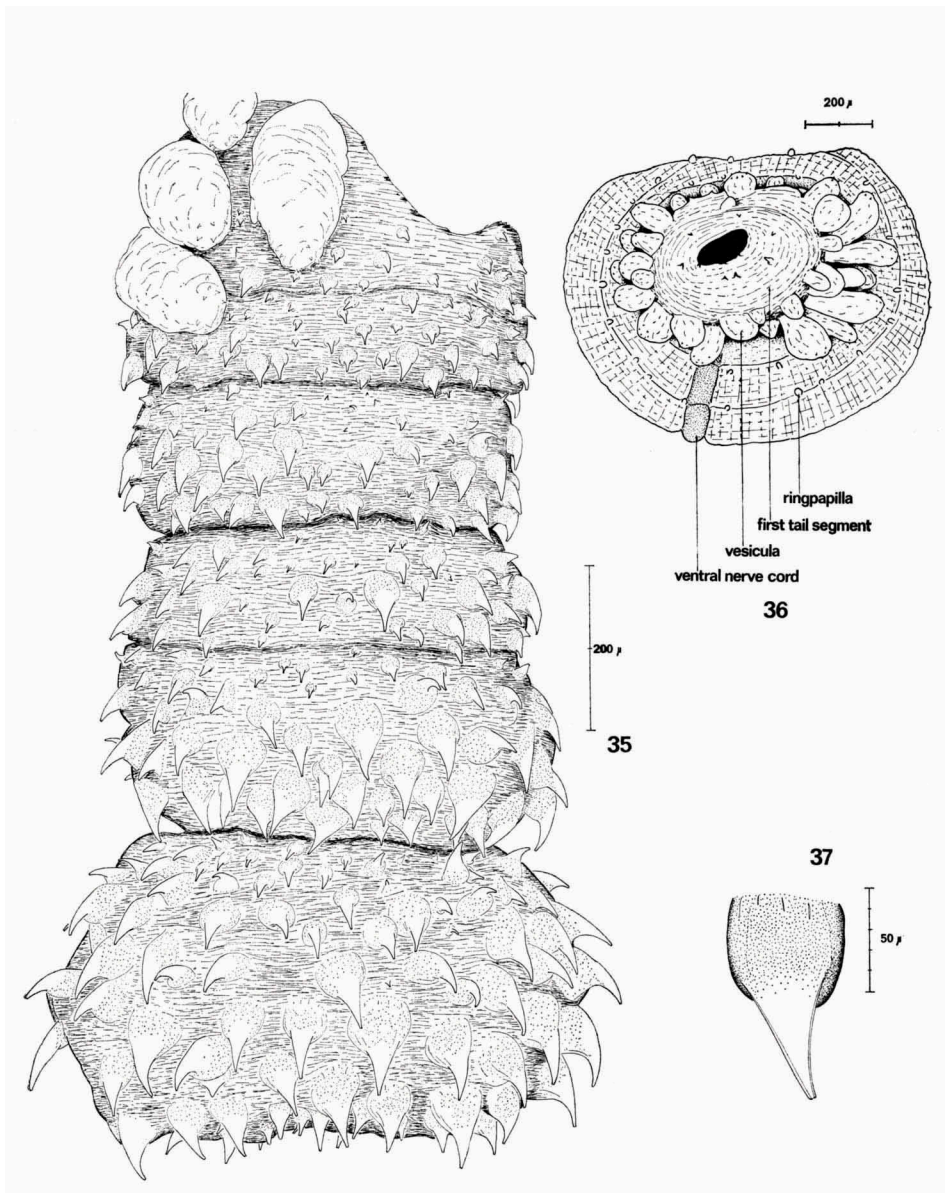


Fig. 35-37. *Acanthopriapulus horridus*, off Uruguay (holotype, Mus. Stockholm). 35, tail (first and last segments missing); 36, last annuli of abdomen and first segment of tail, posterior view; 37, hook of tail.

The total length is approximately 6 mm (introvert: 1.3 mm; abdomen: 2.6 mm; tail: 1.9 mm).

The pharynx was lost during preparation so next to nothing is known about the structure and disposition of the pharyngeal teeth. The very few, small teeth seen by Théel were not different from those of other species of the family.

The abdomen carries two series of ringpapillae (fig. 36).

Tail (fig. 35-36): The number of tail segments cannot be indicated exactly because some of them are apparently just dividing. All segments are provided with hooks. They are small and rather sparse on the first segments and gradually increase in size towards the posterior segments. On each individual segment they also increase in size posteriorly. The slightly curved, posteriorly directed, blunt tipped hooks (fig. 37) are heavily chitinized. Although the thick cuticle has a hole on top of the hook there is probably no aperture. The broad, rounded base has a much thinner cuticle, which undoubtedly gives the hook some flexibility. The first segments bear vesicles. A small number of spinulae is present on the distal part of each vesicula.

Remarks. — The holotype is the only known specimen of this species. Théel dissected it but lost the pharynx and the greater part of the introvert. Apparently no one else has ever studied the remains of the animal.

Distribution. — The type locality is indicated on fig. 83. The fact that until now only one specimen of this species has been found, shows that the discovery of more species of the Priapulidae is certainly not quite impossible, although this has not happened since 1911. Possibly this species has only a local distribution, but the fauna of the southern oceans is so poorly known that the animal can be expected anywhere on the southern hemisphere.

Halicryptus von Siebold, 1849

Halicryptus von Siebold, 1849: 184-185 (description of *H. spinulosus*). — Diesing, 1859: 779 (diagnosis). — Kefenstein, 1865a: 208 (diagnosis); 1865b: 441 (diagnosis). — de Quatrefages, 1865b: 296 (gen. incert. sedis). — Théel, 1875: 3, 23 (diagnosis). — Delage & Hérouard, 1897: 10, fig. 1 (diagnosis). — Fischer, J., 1913: 108 (diagnosis). — Fischer, W., 1925: 45 (diagnosis). — ten Broeke, 1929: 164-165 (diagnosis). — Baltzer, 1934a: 2-13 (textbook including diagnosis). — Dawydoff, 1959: 923 (textbook including diagnosis). — Murina & Starobogatov, 1961: 181, 194-195 (diagnosis).

Halicryptus Meyer, 1928: 130, 210-211, 214, fig. 56a.

Type species: *Halicryptus spinulosus* von Siebold.

Differential diagnosis. — Introvert short (about 10% of total length) with one series of scalids, including dentoscalids. Abdomen with large number of annuli (up to 100), provided with setae. No tail. Lorica of larva with alveolate sculpture, without tubuli; no closing apparatus.

Nomenclature. — The name of the genus was formed by combining the Greek words halos (sea) and kryptos (hidden).

Description. — In the pharyngeal armature (fig. 38-39) the first six circlets consist of five teeth (pentagons). The largest teeth are situated in the second and third circlets. Each tooth bears a median cusp and up to about ten lateral cusps (sometimes there are no lateral cusps at all; see fig. 39). Buccal papillae are present and are of about the same appearance as the scalids.

The introvert is very short (less than 20% of the length of the abdomen). There are two types of scalids (fig. 42-43): a "normal" type in the shape of a conical, slightly curved papilla, strengthened by a cuticular tube, and a type provided with one or two teeth (dentoscalid). The latter are situated in the posterior part of the introvert. The total number is very small (only

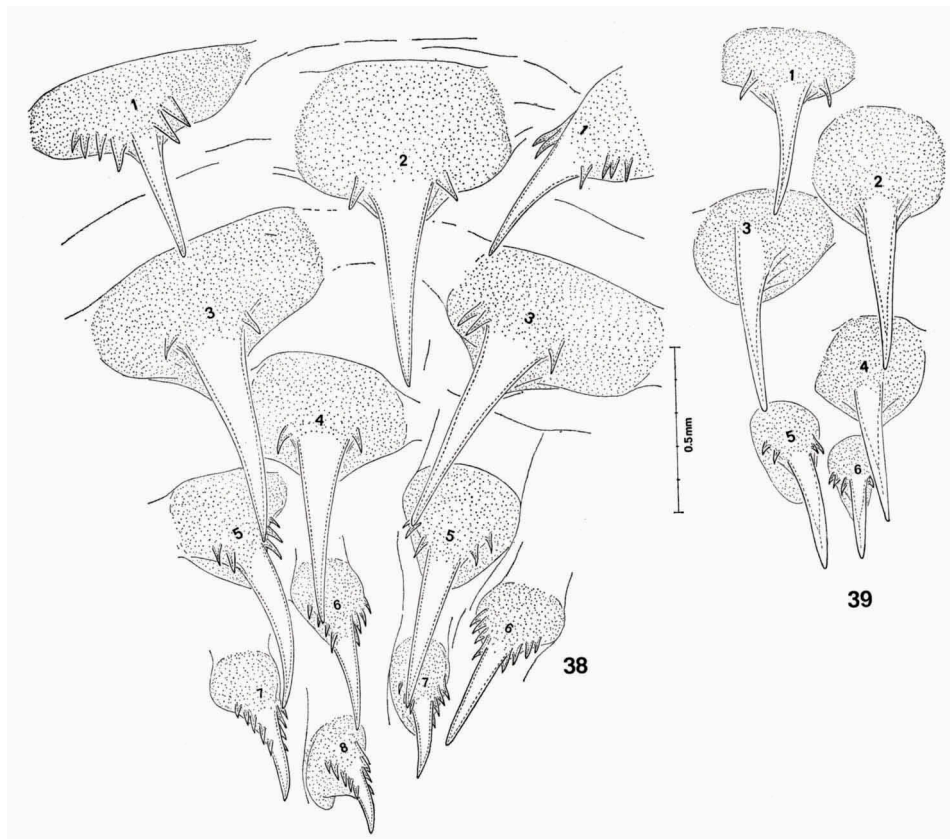


Fig. 38-39. *Halicyptus spinulosus*, anterior pharyngeal teeth. 38, Sweden (Mus. Stockholm 108); 39, Novaya Zemlya (Mus. Stockholm 109).

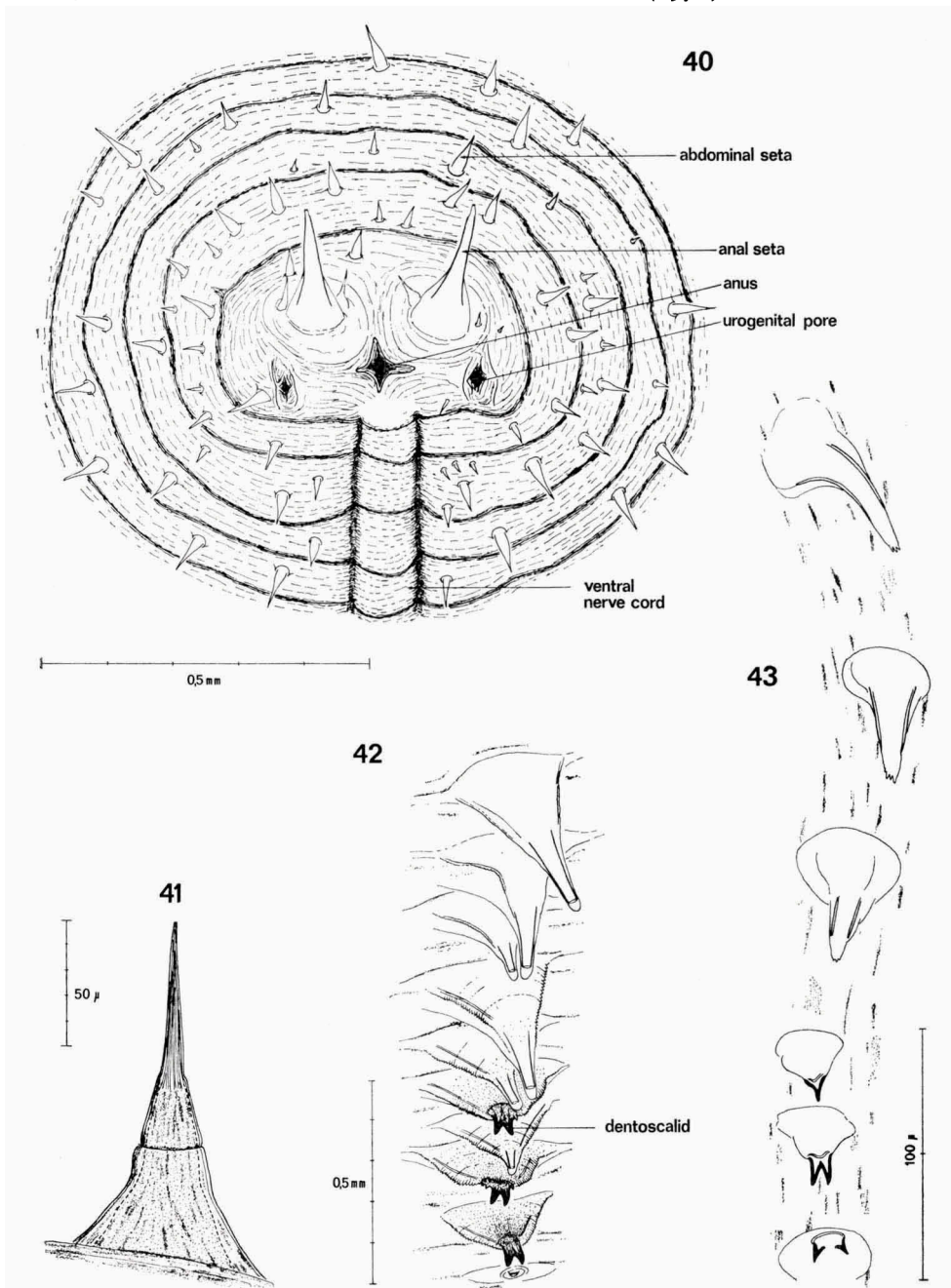


Fig. 40-43. *Halicyrtus spinulosus*. 40, anal region and last annuli, posterior view, Alaska (Mus. Stockholm); 41, abdominal seta, Sweden (Mus. Stockholm 108); 42, scalids of adult, Sweden (Mus. Stockholm 108); 43, scalids of postlarva, Sweden (Mus. Stockholm).

up to about ten) and there are no series. The two ventral rows are scarcely closer to each other than the other rows.

The abdomen is provided with a very large number of annuli (up to about 100). There are no papillae and warts, but the whole abdomen is beset with setae (fig. 40-41). The skin is smooth. The anal region bears two very large setae (fig. 40).

There is no tail.

The long introvert retractors are relatively short, attached to the body wall in the anterior third part of the abdomen; there are seven to ten of them, all of about the same length. There are about 10 short introvert retractors. Pharynx retractors are lacking.

In the larvae the pharyngeal armature consists of about six circlets of five teeth, followed by a number of circlets with more than five teeth, gradually decreasing in size. The large teeth of the anterior circlets (fig. 48) consist of a median spine, decreasing in size posteriorly, and tiny lateral spines and denticles, increasing in number posteriorly.

The slightly curved scalids (fig. 49) do not show any particular specialization; each row consists of about five scalids. The posterior part of the introvert is provided with a circlet of adhesive tubules (fig. 44, 49-50).

The neck region is not provided with cuticular plates nor with conspicuous folds; there is no closing apparatus.

The anterior and posterior parts of the dorsal and ventral plates of the lorica are provided with an alveolate sculpture (fig. 44-46). The cuticula (fig. 47) of the dorsal and ventral plates is thicker than that of the lateral fields; only the basal part of the ridges is hollow. Tubuli are lacking. The excretory duct of the caudal gland is not provided with a tube. The dorsal and ventral plates are provided with protuberances on the inner side of the anterior edge and at the posterior end.

***Halicryptus spinulosus* von Siebold, 1849.**

(fig. 38-50, 86-87, Pl. 1 D, 2 D-E)

Halicryptus spinulosus v. Siebold, 1849: 184-185 (description; washed ashore on beach between Weichselmünde and Heerbucht, Germany, now Poland). — Leuckart, 1856: 77-78. — Diesing, 1859: 779 (diagnosis). — Ehlers, 1861: 46 (systematic status); 1862: 401-413, pl. 34 fig. 1-11 (long description; Germany). — von Siebold, 1862: 413-415 (description; predator; Germany). — Lovén, 1864: 383-384 (Sweden, Spitsbergen; zoogeography). — Keferstein, 1865a: 208; 1865b: 441 (diagnosis; Germany, Spitsbergen). — Baird, 1868: 107. — Leuckart, 1869: 281-282 (morphology, anatomy; Germany, Poland, Estonia). — Zenger, 1870: 209-229, Pl. 10-11 fig. 1-41 (morphology, anatomy, histology). — Willemoes-Suhm, 1871: 385-386 (reproduction, moult; Germany). — Ehlers, 1871: 84-85 (morphology; Spitsbergen, Germany, Poland, Latvia, Estonia; zoogeography). — Möbius, 1873: 98, 106 (Baltic Sea, Germany, Poland). — Heuglin, 1874: 247-248 (pharyngeal teeth; Spitsbergen; zoogeography). — Théel, 1875: 23-24

(bibliography; diagnosis; Sweden). — Lenz, 1878: 10 (Germany). — Horst, 1881: 28, 34. — Ackermann, 1881: 11 (relict). — Danielssen & Koren, 1881: 47. — Lenz, 1883: 172 (Germany). — Levinsen, 1884: 275, 319 (diagnosis; distribution). — Apel, 1885: 459-525, Pl. 15-17, fig. 1-2, 4, 8-9, 12-14 (histology; moult; Germany). — Scharff, 1885: 193-212, Pl. 14 fig. 3, 11 (histology of skin, external organs, and nervous system). — Schauinsland, 1886: 574-577 (anatomy urogenital system); 1887: 171-173 (nervous system, coelomocytes, histology of intestine). — Nordqvist, 1890: 86-88, 97, 125 (Sweden). — Levinsen, 1893 (Denmark). — Fischer, W., 1894: 22 (Germany). — Shipley, 1896: 432-433, fig. 219 (textbook). — Rauschenplat, 1901: 85, 145 (food). — Reibisch, 1902: 157, 159 (Baltic Sea). — Skorikov, 1902b: 278 (Baltic Sea). — Norman, 1903: 286 (Norway). — Théel, 1906: 13, 19-22, Pl. 2 fig. 11-13 (Greenland, Spitsbergen, Novaya Zemlya, Siberia, Baltic Sea, Sweden). — Derjugin, 1906: 87, 140 (Russia). — Molčanov, 1908: 957, 962-966, fig. 7-8 (histology excretory system; Russia). — Skorikov, 1910: 212-213, 226, 228, 235-236 (Baltic Sea). — Gadd, 1911: 79, 90 (Russia). — Schauinsland, 1912: 1113, 1116, fig. 1 (encyclopedia). — Fischer, J., 1913: 91, 117-118, 121 (diagnosis; Baltic Sea). — Hammarsten, 1913: 501-505, fig. 1-3 (description of larva and its movements; Sweden). — Skorikov, 1913: 101-102 (Baltic Sea). — Petersen, 1914: 9, 46, 48-49, 56 (ecology; Kattegat). — Levander, 1915: 5 (Finland). — Derjugin, 1915: 20, 373-375, 773, 796 (Russia). — Blegvad, 1915: 50, 69, 74 (food). — Hammarsten, 1915: 527-571, fig. 1-15 (histology of larva; metamorphosis). — Blegvad, 1917: list 4 (predators; Denmark). — Hempelmann & Wagler, 1918: 311. — Thulin, 1920: 2-8. — Fischer, W., 1922c: 243-245 (distribution). — Hesse, 1923: 150-151 (Baltic Sea); 1924: 23, 30-34, 36-39, tab. 5 (ecology; Baltic Sea, Sweden). — Fischer, W., 1925: 46-51, fig. 5 (description; larva; distribution in Baltic Sea). — Eggers, 1925: 170-173 (larva; anatomy and ontogeny of urogenital system). — Wesenberg-Lund, 1925: 82, 86 (Greenland; distribution). — Meyer, 1926: 355-356. — Fischer, W., 1928: 455, 474 (diagnosis; distribution). — Hertling, 1928: 35, 40-41, 56, 59, 61, 65, 68, 70, 73, 75-76, 80, 83-88, 92-94, 97-98, 101, 104, fig. 2, tab. 1-11 (ecology; predators; Baltic Sea). — Meyer, 1928: 130, 210-211, 214, fig. 56a (larva). — ten Broeke, 1929: 166 (description; Germany). — Wesenberg-Lund, 1929: 165, 167; 1930: 5-7, 17, Pl. 2 fig. 19-20 (Greenland; distribution). — Hagmeier, 1930: 163-167 (ecology; Baltic Sea). — Stiasny, 1930: 206, 221 (Germany). — Schulz, 1931: 62 (moult). — Ekman, 1932: 19-20, 34, 37, fig. 9-10 (distribution-map Scandinavia and Baltic Sea; zoogeography). — Segerstråle, 1933: 4, 11-12, 43-45, 52, 56-58, tab. 1-2, 4, Pl. 3 fig. 2, 6-7 (ecology; Finland). — Välikangas, 1933: 91, 95-96, fig. 6 (Baltic Sea). — Wesenberg-Lund, 1933: 1, 3, Pl. 1 fig. 2 (Novaya Zemlya). — Baltzer, 1934a: 2-3, 5, 7, 11, fig. 3, 7-12 (textbook). — Schulz, 1934: 59-61 (larva; Germany). — Ekman, 1935: 206, fig. 112 (zoogeography). — Friedrich & Langeloh, 1936: 249, 253-260, fig. 3-4 (burrowing and physiology of dermal musculature; Germany). — Korschelt, 1936: 407-408, fig. 445-446 (larva). — Langeloh, 1936: 260-267, fig. 1-5 (burrowing, geotaxis, phototaxis). — Spärck, 1937: 9, 30, 31 (ecology; Iceland, glacial relict). — Wesenberg-Lund, 1937a: 2, 5-6, 14-15, fig. 1 (ecology; Iceland; distribution, zoogeography); 1937b: 3, 7-9, 22-24, fig. 2 (ecology; Greenland); 1938: 26-27, fig. (Norway); 1939a: 3, 8-9 (Sweden; zoogeography). — Dons, 1939: 199-200 (Norway). — Lang, K., 1939: 80, 83-85 (larva). — Lüling, 1940: 136-179, fig. 1-34 (anatomy, histology and development of urogenital system; Germany). — Remane, 1940: 7, 24, 124, 146, 149, 152, 185, 198 (ecology; Baltic Sea). — Spärck, 1942: 70, fig. 19 (distribution-map Denmark). — Purasjoki, 1944: 1-14 (description larval stages; ecology; Finland). — Brattström, 1947: 67, 73 (Sweden, Denmark). — Lang, K., 1948a: 5, 10; 1948b: 1-8, fig. 2, 4, Pl. 1 fig. 1 (description larva; Sweden). — Segerstråle, 1949: 137, fig. 6 (relict; Finland). — von Haffner, 1950: 247, 250-251. — Wesenberg-Lund, 1950: 489 (Denmark). — Fänge & Åkesson, 1951: 29-31 (coelomocytes; respiration; Sweden). — Hyman, 1951: 183-197, fig. 88A-B, G, 90-91, 92C (textbook). — Lang, K., 1953: 326, 332-333, 336, fig. 4a-b. — Žinkin & Kors-

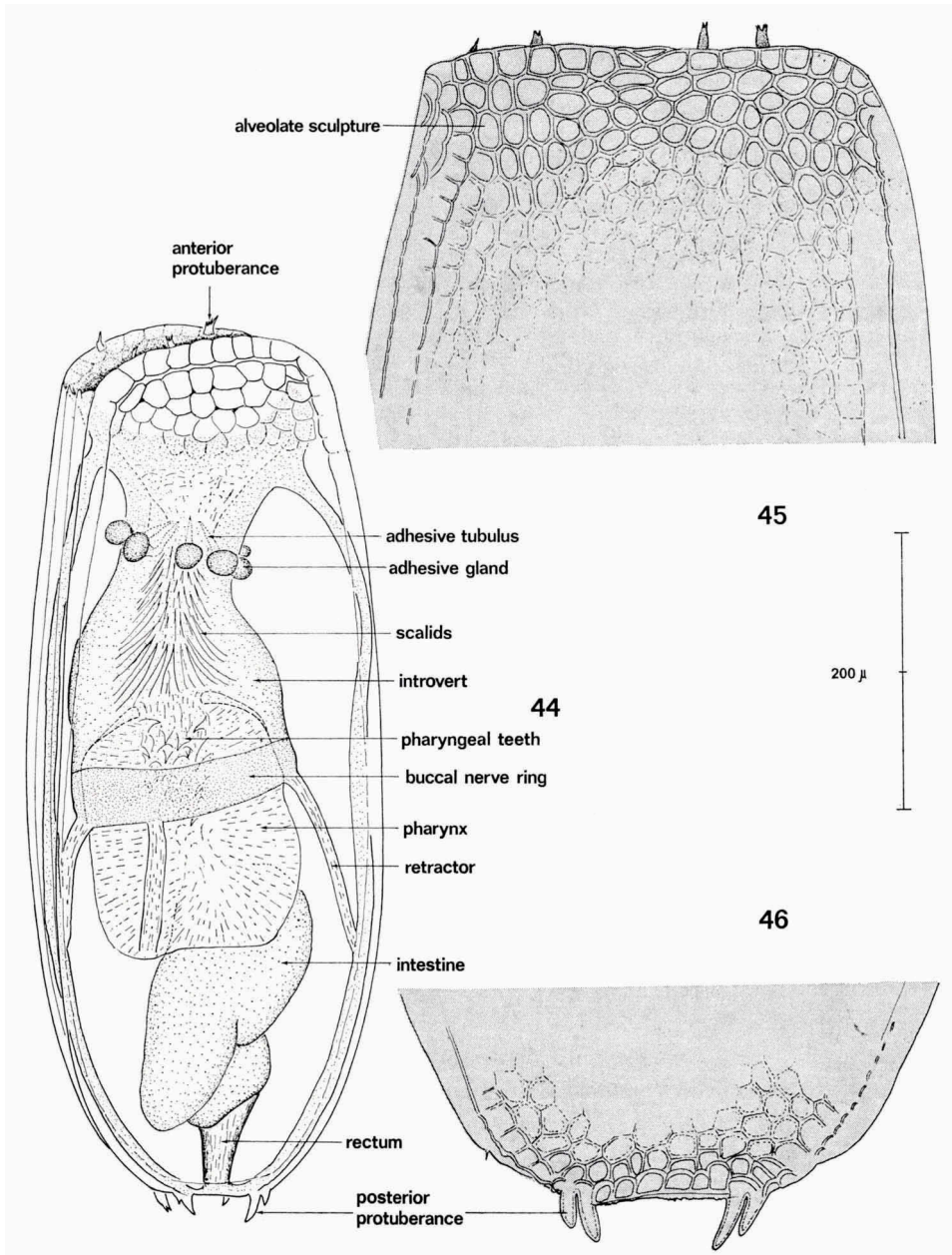


Fig. 44-46. *Halicryptus spinulosus*, larvae, Sweden. 44, small larva, contracted (Mus. Stockholm); 45-46, anterior and posterior parts of lorica of large larva (Mus. Leiden 7215).

kova, 1953: 571-573, fig. 1 (embryology; Russia). — Demel & Mulicki, 1954: 77, 82-91, 101, 104, 107, fig. 4-5, 13 (ecology; Baltic Sea). — Granqvist, 1955: 44, 51, 55 (ecology; Finland). — MacGinitie, 1955: 61, 65, 101, 126 (Alaska). — Sjöblom, 1955: 37-40 (ecology; Baltic Sea). — Forsman, 1956: 397 (food; Baltic Sea). — Mulicki, 1957: 313-314, 360-365, 367, 371-373, 376-377, fig. 29-31, 34-36 (ecology; Baltic Sea, Poland; distribution-map Baltic Sea). — Segerstråle, 1957a: 12 28 (zoogeography, relict-fauna); 1957b: 774, 783, 785, fig. 15, Pl. 4 fig. 2 (ecology; Baltic Sea). — Thorson, 1957: 516 (ecology). — Demel & Mulicki, 1958: 51, fig. 9 (ecology; Baltic Sea). — Golvan, 1958: 567-570, 573. — Dawydoff, 1959: 909, 918, 921-923, fig. 718B, 724, 726, 728E-F, 732, 735 (textbook). — Hyman, 1959: 742. — Segerstråle, 1959: 5 (relict); 1960: 7 (Finland). — Stephen, 1960: 25-26, fig. 18 (diagnosis) — Tulkki, 1960: 7, 9-12, 18, 20, 26, fig. 4, 15 (ecology; Finland). — Murina & Starobogatov, 1961: 195, 196, 198, fig. 2v-g, 3z (bibliography; description; Kara Sea; distribution). — Olivier et al., 1961: 259. — Sanders & Hessler, 1962: 130, fig. 3. — Shapeero, 1962b: 238. — Holmquist, 1963: 115-116, 120 (Alaska; ecology). — Kühlmorgen-Hille, 1963: 60, fig. 17 (Germany). — Lang, K., 1963: 257, 260, fig. 18 1-2. — Arndt, 1964: 47, 140, 143, 153, 163, fig. 78 (ecology; Baltic Sea; zoogeography). — Murina, 1964: 873. — Tulkki, 1964: 181-186, fig. 5 (ecology; Finland). — Bagge, et al., 1965: 43-44, 50-51, fig. 12 (ecology; Finland). — Tulkki, 1965: 457-458, 460-461 (ecology; Baltic Sea). — Carter, 1966: 438-439, fig. 1-2 (Labrador; relict). — Hartwich, 1967: 316-318, fig. (textbook). — Hickman, 1967: 254-255, 259 (textbook). — de Lattin, 1967: 140, 507 (Baltic Sea relict fauna) — Jägersten, 1968: 75-78 (larva). — Holmquist, 1969: 82-83 (Alaska; zoogeography, relict-problem). — Särkkä, 1969: 281, 286 (ecology; Finland).

Halicryptus spinulosus var. *multidentatus* Zenger, 1870: pl. 10 [probably lapsus; name not mentioned in text].

Material. — The author has seen hundreds of postlarvae and adults from all areas, except Labrador and Norway. Numerous larvae from the Baltic Sea were available.

Description. — The length ranges from about 1.5 mm (postlarvae) to about 40 mm; specimens with a length of over 25 mm are rare.

Pharyngeal armature (fig. 38-39): Usually the teeth of the first circlet have four to eight, those of the second to fourth circlets two to four, and those of the following circlets four to twelve lateral cusps. The pharyngeal armature of the postlarvae scarcely differs from that of the adults. In large specimens from Novaya Zemlya (fig. 39) and Alaska the teeth of the first circlet were found to have only two lateral cusps and those of the second to fourth circlets were even devoid of lateral cusps; the numbers of lateral cusps were also unusually small in the following circlets.

Scalids (fig. 42-43): In postlarvae there are usually three or four normal scalids and two or three dentoscalids in each row. In adults there are three to six normal scalids, two to four dentoscalids, and usually a very small rudimentary scalid at the end of the row. The anterior scalids are always of the normal type; the posterior scalids are always dentoscalids (not counting the small rudimentary scalid); in the middle part of the row the two types may be mixed (as shown in fig. 42).

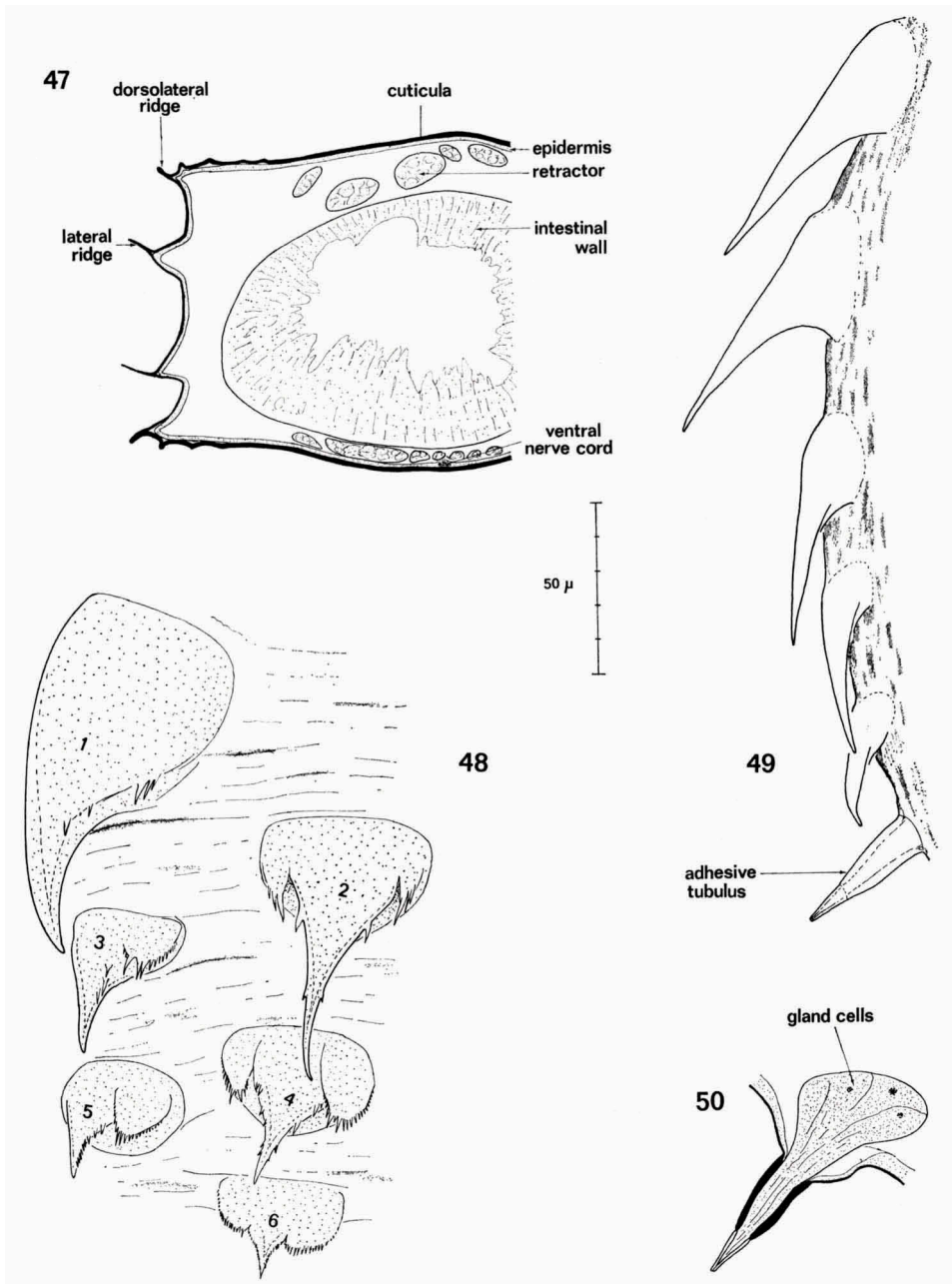


Fig. 47-50. *Halicryptus spinulosus*, details of larvae, Sweden. 47, cross-section of abdomen (Mus. Leiden 7217); 48, anterior pharyngeal teeth (Mus. Leiden 7216); 49, scalds (Mus. Stockholm); 50, adhesive tubulus, from cross-section (Mus. Leiden 7217).

Larva (fig. 44-50): According to Purasjoki (1944) there are four larval stages, in which the length of the lorica ranges from 0.3 to 1.3 mm, the total length being up to about 1.5 mm. In the youngest stage there are no posterior protuberances and only very few alveoli on the anterior part of the lorica. In the course of development the number of alveoli increases and in the last stages they are also present on the posterior part of the lorica (compare fig. 44 and 45-46).

Distribution. — See fig. 86-87.

This species has a definite northern circum-polar distribution. It also appears from the maps that it is restricted to coastal waters in cold areas, the Baltic Sea forming an exception. It may be quite abundant in suitable habitats (see later). The fact that it was found in Alaska and Canada only quite recently (Mac Ginitie, 1955; Holmquist, 1963; Carter, 1966), is probably due to the fact that the habitats in which it occurs there (shallow lagoons and coastal lakes) were not investigated during earlier expeditions. The species will undoubtedly be found in many places along the northern Canadian and Siberian coasts. It is not to be expected in deep water.

The occurrence at St. Andrews (Scotland) is considered to be doubtful. One specimen (Mus. London 1965.1042) was supposedly collected there.

The animal seems to have vanished from the Kattegat area in recent times. In the 19th century it has been found in a number of fjords in the Göteborg region (Wesenberg-Lund, 1939a) but it disappeared there since (the fauna of that region is very well known). Petersen (1914) mentions a few finds in the southern part of the Kattegat and there are also a few old specimens from the Kattegat in the Oslo Museum (C 1323). There are old records from the northern entrance of the Öresund, but now this species only occurs in the southern part and even there it is not as common as it used to be (I could collect only a few larvae).

Tubiluchidae n. fam.

Differential diagnosis. — Pharynx with pectinate teeth of equal size; polythyridium at entrance of intestine. Introvert with 20 rows of scalids. Abdomen not annulated, carrying many tubuli and in the male also ventral setae. Larvae with radially symmetrical lorica.

Description. — Tubiluchids are meiobenthic worms occurring in sandy sediments in tropical and semi-tropical waters. The length of the body (without tail) is less than 2 mm. The introvert carries 20 rows of scalids. The abdomen is not annulated and is provided with tumuli, arranged in neat rows, and many tubuli. There is a long, slender tail without vesiculae. The pharyngeal armature consists of numerous pectinate teeth of approx-

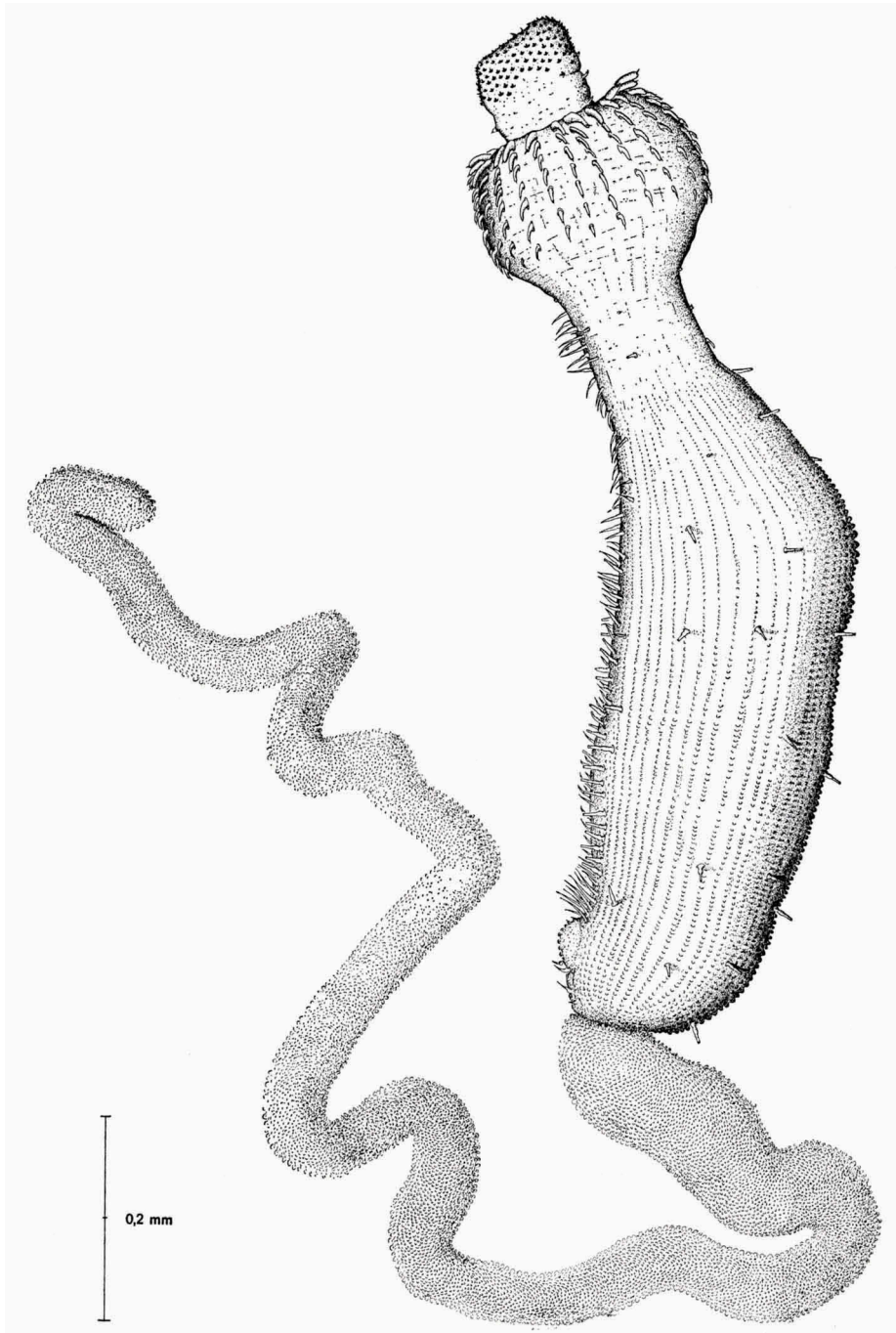


Fig. 51. *Tubiluchus corallicola*, habitus, male, pharynx protruded, lateral view, Bonaire (Mus. Leiden).

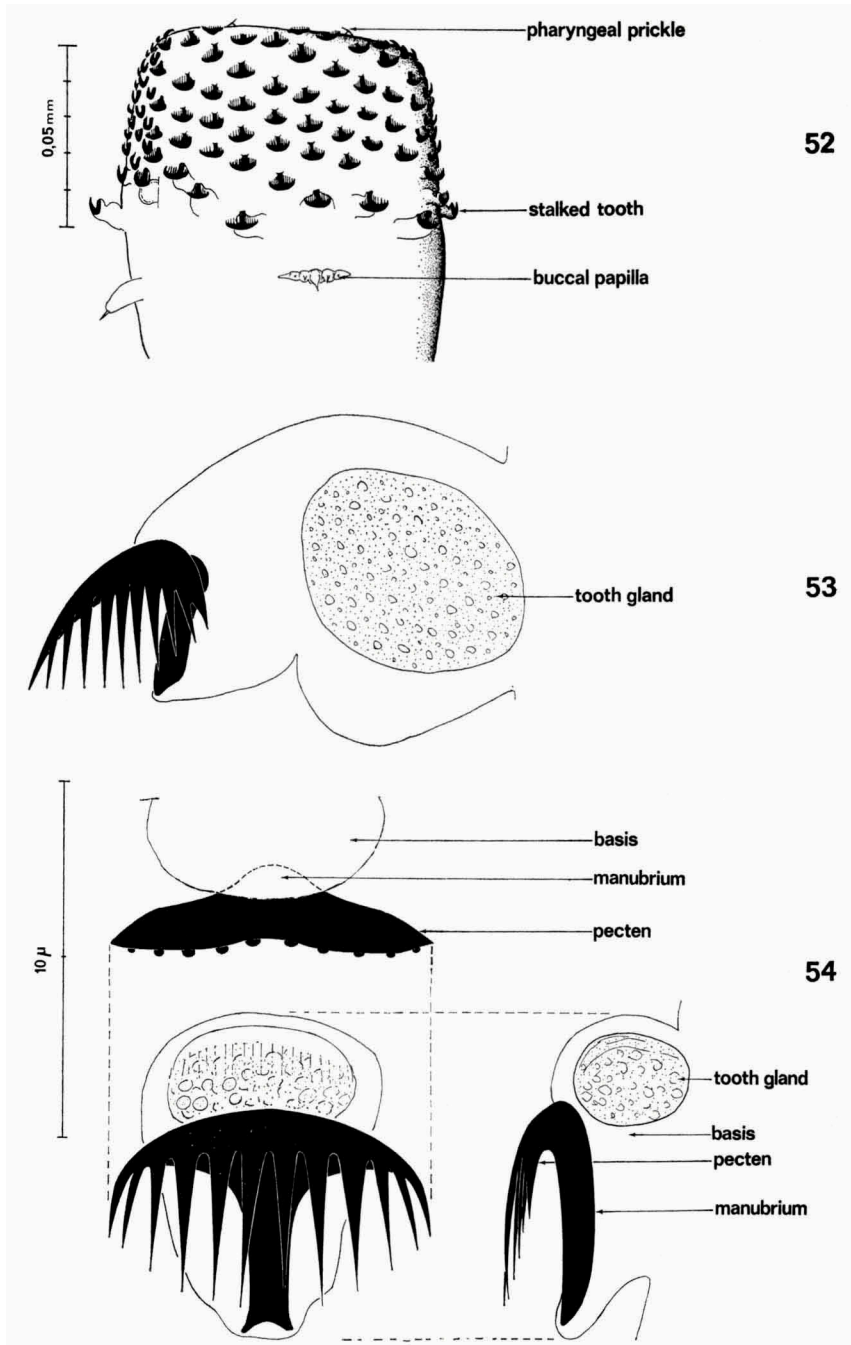


Fig. 52-54. *Tubiluchus corallicola*, pharyngeal teeth, Bonaire (Mus. Leiden). 52, arrangement of teeth as seen on protruded pharynx; 53, stalked tooth; 54, normal tooth in frontal, axial and lateral views.

imately equal size and a small number of prickles and fimbriellae. The oesophagus is rather long and terminates in a polythyridium. Each urogenital organ consists of one solenocyte tree and about ten testis or ovarium follicles. There is a marked sexual dimorphism (the abdomen of the male is provided with numerous ventral setae) and fertilization probably takes place in the urogenital duct. The lorica of the larva is round in cross-section and is provided with 20 longitudinal cuticular ridges; it carries up to about 20 tubuli.

This is a monotypic family.

Tubiluchus van der Land, 1968

Tubiluchus van der Land, 1968: 239-250 (description of type species).

Type species: *Tubiluchus corallicola*.

Diagnosis and description. — As of family.

Nomenclature. — The name of the genus was formed by combining the word tubulus with the Latin suffix -uchus (carry).

Remarks. — Tubiluchid larvae were found first by Remane and Schulz who mention the find of a few specimens in a report (Remane & Schulz, 1964: 16) on their investigations in the Red Sea in the vicinity of the biological station of Al Ghardaqa (Egypt), describing it as follows: „Der sackförmige Körper trug ein hakenbesetztes Vorderende, ähnlich dem der Priapuliden-Larve. Der Rumpf war aber nicht wie bei dieser in Platten gegliedert, sondern trug eine Anzahl typischer Haftröhrchen“. From this description and from a simple sketch given by Remane (1963: fig. 17-3) it is evident that the animal is a tubiluchid, but it is impossible to say whether it is conspecific with *Tubiluchus corallicola* or represents another species. It is remarkable that in Remane's figure of a contracted specimen a tubulus is present at the anterior edge of the lorica, which is never the case in *T. corallicola* (compare fig. 76).

Tubiluchus corallicola van der Land, 1968

(fig. 51-79, 89, Pl. 1 E, 2 F, 5)

Tubiluchus corallicola van der Land, 1968: 237-250, fig. 1-18 (description; Curaçao, Piscadera Baai). — Coull, 1970: 337 (ecology; Bermuda).

Priapulida spec. Coull, 1968: 1, 58, 65, 68, 70, 80, 151-153, fig. 16 A-D (ecology; Bermuda).

Material: About a hundred specimens of all stages from Curaçao, Bonaire (Lagoon of Lac), and Bermuda, including many whole mounts and serial sections of several specimens. Material from Curaçao (including type specimens) and Bonaire in Mus. Leiden, from Bermuda in coll. Higgins.

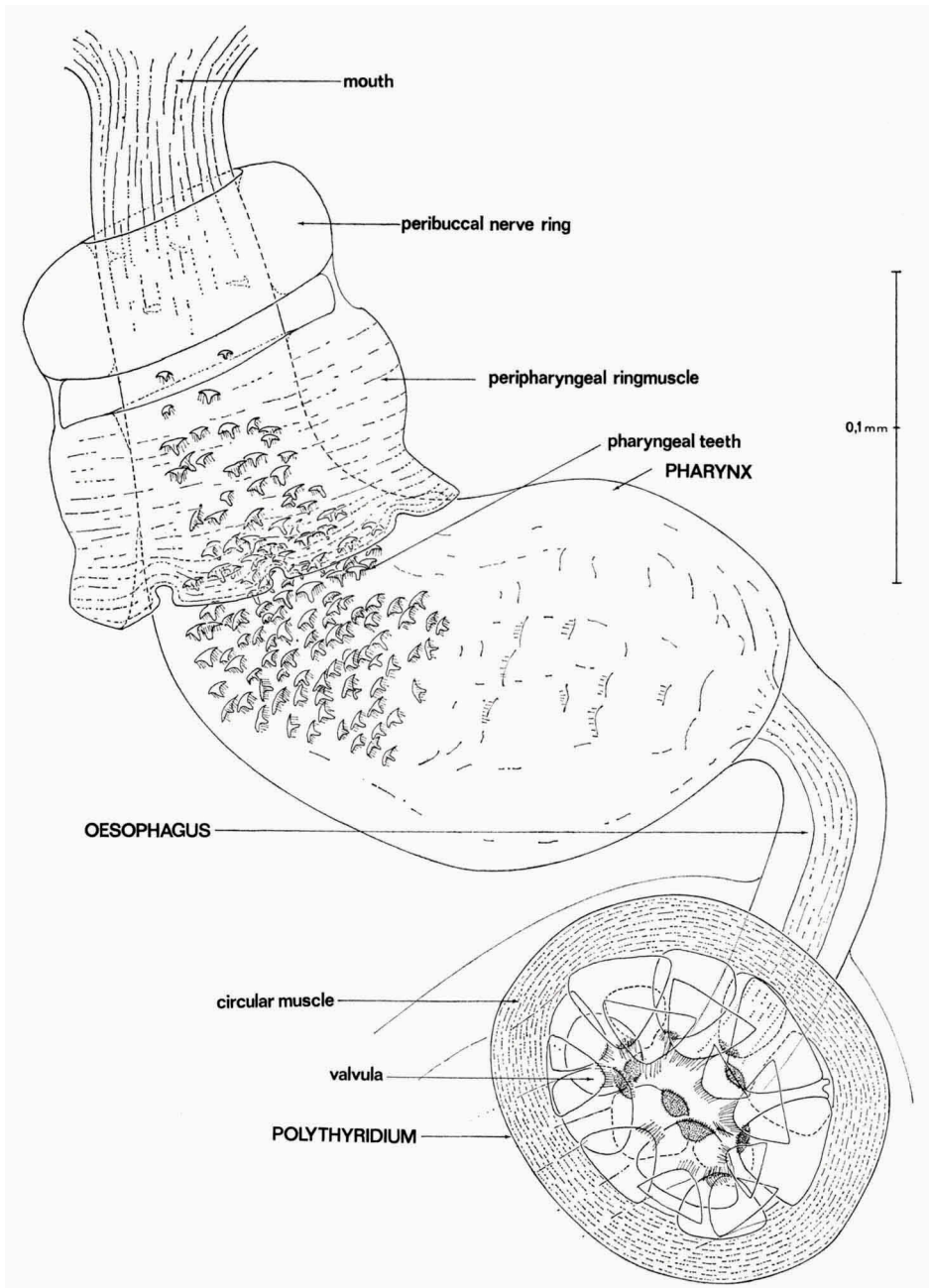


Fig. 55. *Tubiluchus corallicola*, pharynx and polythyridium, Bonaire (Mus. Leiden).

Nomenclature. — The name of the species refers to the fact that it was found in coral sand.

Description. — The animals are strongly contractile, so the length and width are largely dependent of the state of contraction. The length of the body ranges from about 0.4 mm in small, contracted specimens to about 1.5 mm in large, extended specimens. The longest specimen had a total length of about 5.7 mm (body: 1.2 mm; tail: 4.5 mm), but this is quite exceptional; the shortest specimens had a total length of approximately 1 mm (body: about 0.4 mm; tail: about 0.6 mm).

The pharyngeal teeth (fig. 53-54) are of a peculiar type, hitherto unknown among priapulids (pectinate teeth). They are all of approximately the same size (in a large specimen their width varied from 7.5μ to 9μ). Each tooth consists of a manubrium embedded in an elevation (basis) and a comb-shaped distal part (pecten) provided with about 12 delicate spines. The anteriormost teeth have very tall bases (stalked teeth); their disposition is somewhat irregular. The other teeth are arranged in diagonal and longitudinal rows (fig. 52); there are no distinct circlets. The number of longitudinal rows cannot easily be determined; it must be approximately 35 in large specimens. The teeth are followed by a number of "prickles" (fig. 52, 58), conical papillae terminating in a long, delicate spine. The wall of the posterior part of the pharynx is provided with fimbriae (fig. 59), small cuticular ridges provided with a row of tiny hairs. The structure of the polythridium was already described on p. 19.

Each row of scalids (fig. 56) consists of one series of up to seven scalids. They gradually decrease in size posteriorly and all have basically the same structure, which is unusually intricate (see diagram, fig. 57). The first and second scalid have a very tall basal part, on which a collaret seems to be lacking, and a very small distal part, without an apical seta. The other scalids have a much smaller basal part, which bears a ridge provided with a hair fringe (collaret) and a larger distal part, which is provided with an apical seta and a tuft of tiny hairs. (It should be stressed that details of the scalids can only be observed with a good microscope and if the animals are prepared in a medium with good optical properties such as lactic acid).

Cuticular specializations occurring on the abdomen in both males and females are tubuli (fig. 62-63), tumuli (fig. 64, Pl. 5), and flosculi (fig. 65). Tubuli are strongly cuticularized, tube-shaped organs, jointed into a smaller or larger elevation of the body-wall (basis); they are always provided with a small accessory seta near the base; the basis is often provided with ridges, just like the tumuli. Tumuli are simple conical elevations of the cuticle, and characterized by approximately 12 ridges (best shown in the scanning elec-

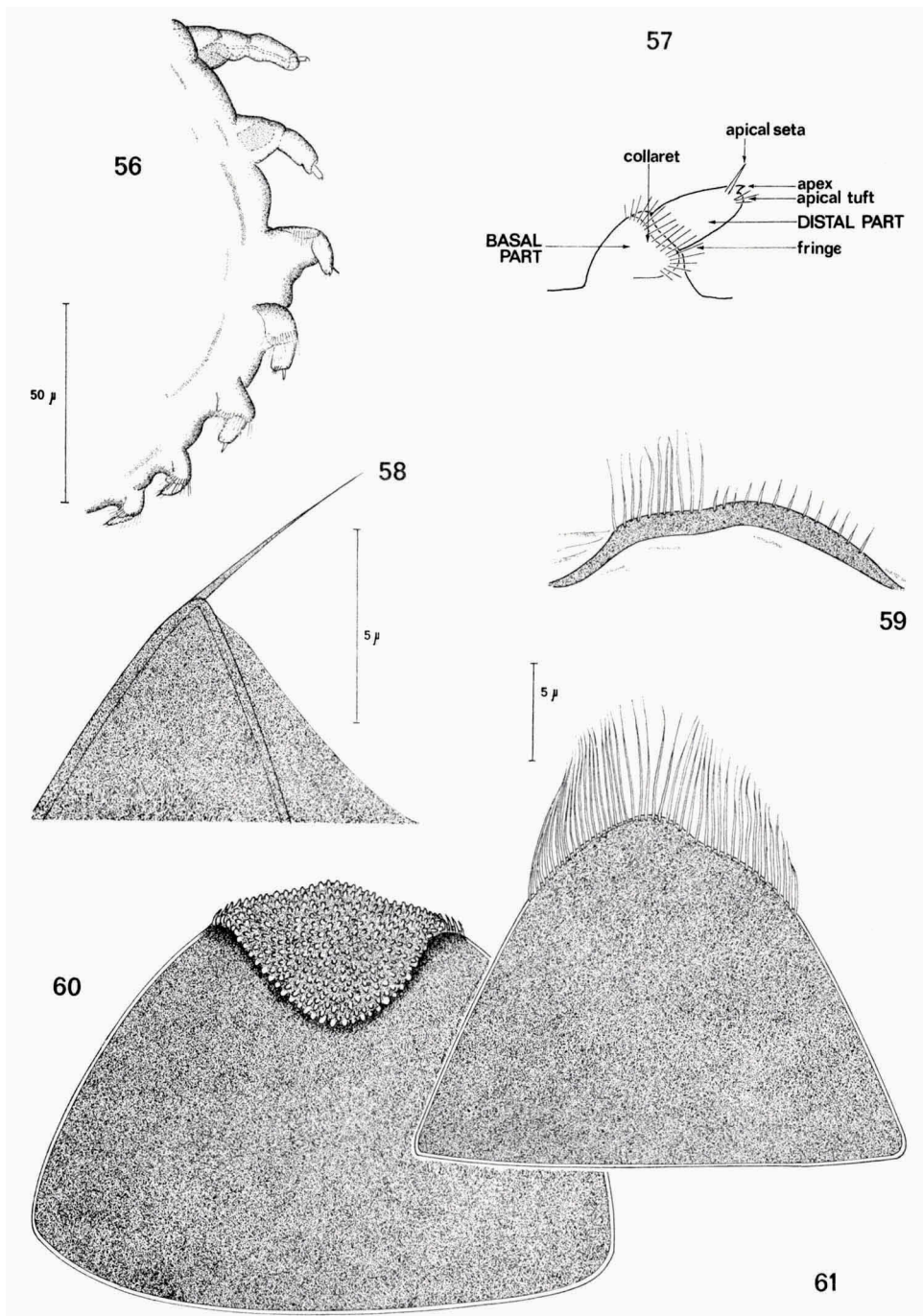


Fig. 56-61. *Tubiluchus corallicola*, Bonaire (Mus. Leiden). 56, row of scalids; 57, diagram of scalid with morphological terms; 58, pharyngeal prickle; 59, pharyngeal fimbrilla; 60, valvula of polythyridium with knobby distal part; 61, valvula with distal fringe.

tron micrographs of Pl. 5). Flosculi are small organs in the shape of a flower with 10 or 11 "petals"; they are situated on an elevation and always accompanied by an accessory seta. The tubuli and flosculi are sparsely strewn over the abdomen, but concentrations of tubuli occur in the preanal region of the male (fig. 67) and flosculi are more common in the neck region and on the anterior part of the abdomen (fig. 66) than elsewhere. The tumuli are arranged in longitudinal (approximately 40) and circular rows; they are absent in the anal region of the male (fig. 67).

Cuticular specializations only occurring on the ventral surface of the abdomen in males (fig. 51, 66-74) include clavulae, bullulae, and various kinds of setae. There are two club-shaped clavulae (fig. 68), situated just anterior to the urogenital pores. Bullulae (fig. 72) are very small, rounded elevations of the cuticle (much smaller than the tumuli); a small number of them occurs on the lateral sides of the preanal bulge, close to the smallest perigenital setae. The "normal" setae (fig. 69-70) are heavily cuticularized throughout and always provided with an accessory seta close to the base on the dorsal side (fig. 66). Sometimes the accessory seta is replaced by a flosculus. These setae are usually jointed into an elevation of the body wall (basis). They extend over the whole length of the neck and the abdomen, ending in two dense groups of very tall setae anterior to the urogenital pores (fig. 67). The perigenital setae only occur in the regions just anterior to the urogenital pores (fig. 67) and differ from the other setae in that they possess a distinctly differentiated distal part with a delicate cuticle and that they do not have an accessory seta. Three types are depicted here (fig. 71-74), but they shade off into one another. The smallest perigenital setae (fig. 72) are arranged in two distinct rows anterior to the two clavulae (fig. 67); the others are irregularly distributed in the area between the two groups of tall setae. The largest perigenital setae are usually jointed into a distinct basis, provided with ridges.

The tail is long and slender up to nearly four times as long as the body in extended condition; when contracted it is much thicker but still one to two times as long as the body. Particular cuticular specializations do not occur. It is much more densely covered with tumuli (Pl. 5) than the abdomen and the rows are less distinct; there are also about 40 longitudinal rows. Tubuli are lacking, but flosculi sometimes occur.

The anatomy and histology will be dealt with later. The most important facts were already mentioned among the general features of the phylum.

Larvae: The total length is up to about 0.75 mm, of which the introvert constitutes about 25%, the neck about 20%, and the abdomen about 55%.

The pharyngeal armature (fig. 77) is of the same type as that of the

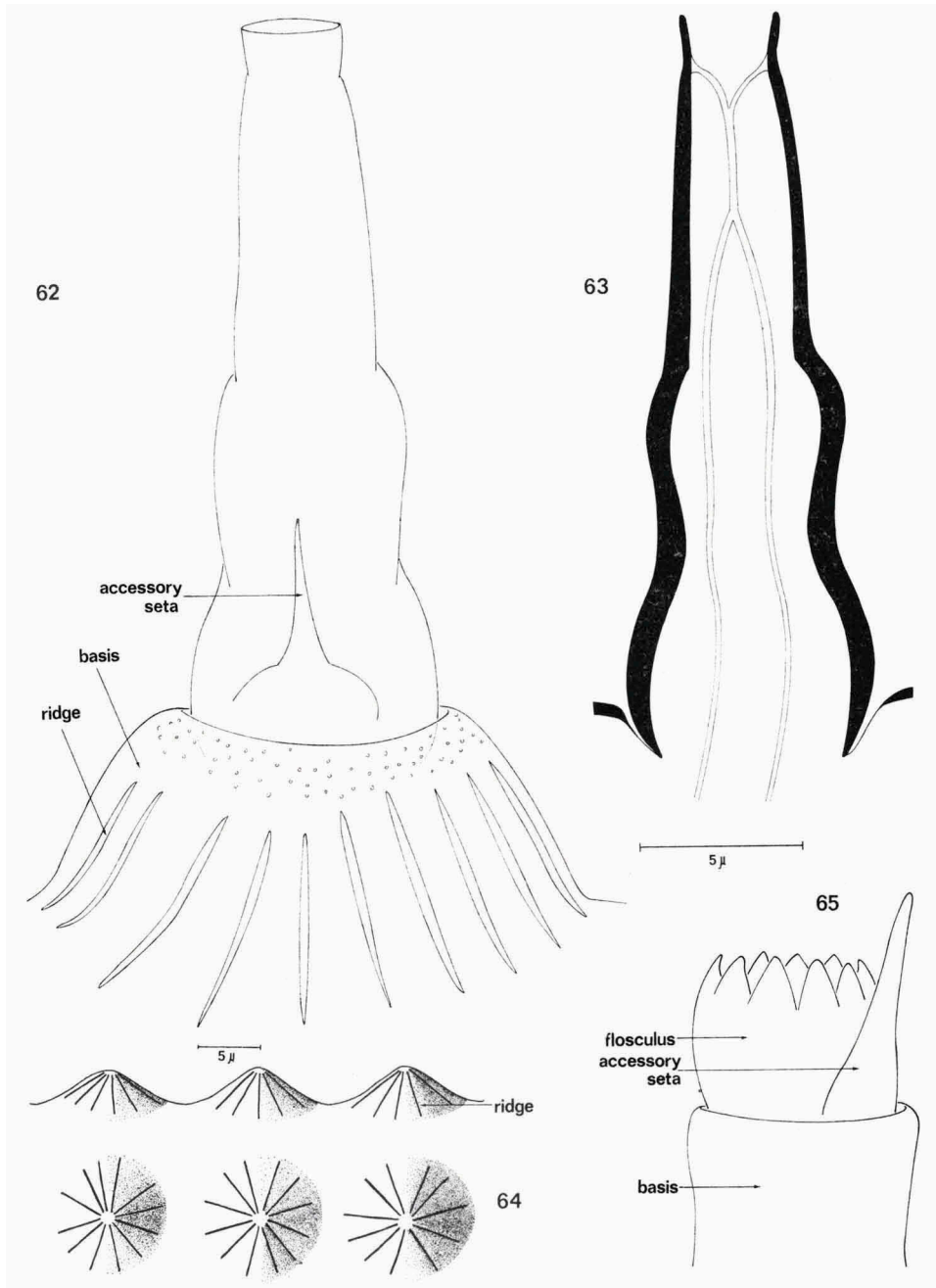


Fig. 62-65. *Tubiluchus corallicola*, cuticular structures of abdomen. 62, tubulus, Bonaire (Mus. Leiden); 63, optical length-section of the same; 64, tumuli, Curaçao (after Van der Land, 1968); 65, flosculus, Bonaire (Mus. Leiden).

Priapulidae, the teeth being of the cuspidate type and the anteriormost circlets each consisting of five teeth. The teeth of the first circlet are provided with a number of delicate spines and numerous minute denticles; a median cusp is lacking. The teeth of the second circlet have a strong median cusp (with lateral denticles), about 10 lateral cusps, and a small number of dorsal denticles. The teeth of the third circlet have a slender median cusp and about 15 lateral cusps. The teeth of the fourth circlet have a long and slender median cusp and only about four lateral cusps. The teeth of the fifth circlet have a short median cusp and about four very small lateral cusps. The teeth of the following circlets do not have a median cusp and are only provided with a row of denticles.

The rows of scalids (fig. 78) consist of one series of four or five scalids of simple construction, all provided with a distinct apex; the last one is very small and bulbous.

The cuticle of the neck shows up to seven distinct circular ridges, ten distinct longitudinal ridges, being extensions of the primary ridges of the abdomen, and ten indistinct longitudinal folds, being in a direct line with the secondary ridges of the abdomen.

The lorica is provided with ten distinct longitudinal ridges extending over its whole length (primary ridges), alternating with ten less distinct ridges which usually do not reach the anterior and posterior ends (secondary ridges).

The tubuli (fig. 79) have essentially the same morphology as those of the adults and they have about the same size; a distinct basis is lacking. There are up to about 20 tubuli; they are regularly distributed (see Van der Land, 1968) and all situated on the primary ridges.

The flosculi are considerably smaller than those of the adults and it is not always easy to find them. They neither have a distinct basis nor an accessory seta. They occur on the neck, where they are irregularly distributed, and on the posterior part of the abdomen, where they are arranged according to a certain pattern (see Van der Land, 1968).

The larvae were described in some more detail in my 1968 paper. The larval development will be the subject of a later paper.

Discussion. — In the foregoing description special attention has been paid to those characteristics that could possibly be of systematic significance. At present much work is being done in the field of tropical meiobenthology, so it is not at all impossible that more species will be found in the near future. They are most likely to differ from the present species in the structure of the polythyridium, the pharyngeal armature, and the scalids. Experience with other animals has shown us that they will almost certainly differ in characters

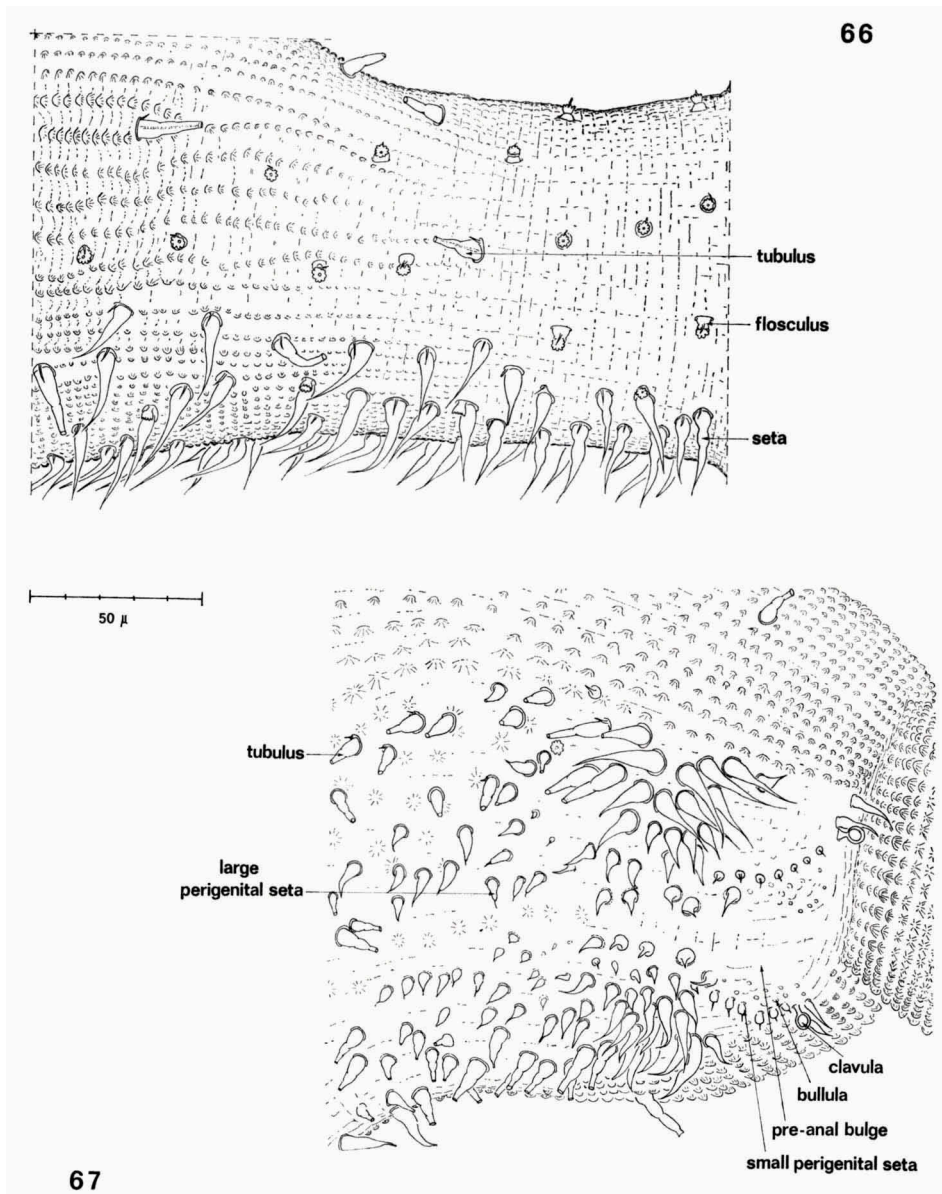


Fig. 66-67. *Tubiluchus corallicola*, male, Bonaire (Mus. Leiden). 66, neck and anterior part of abdomen, latero-ventral view; 67, posterior part of abdomen, latero-ventral view.

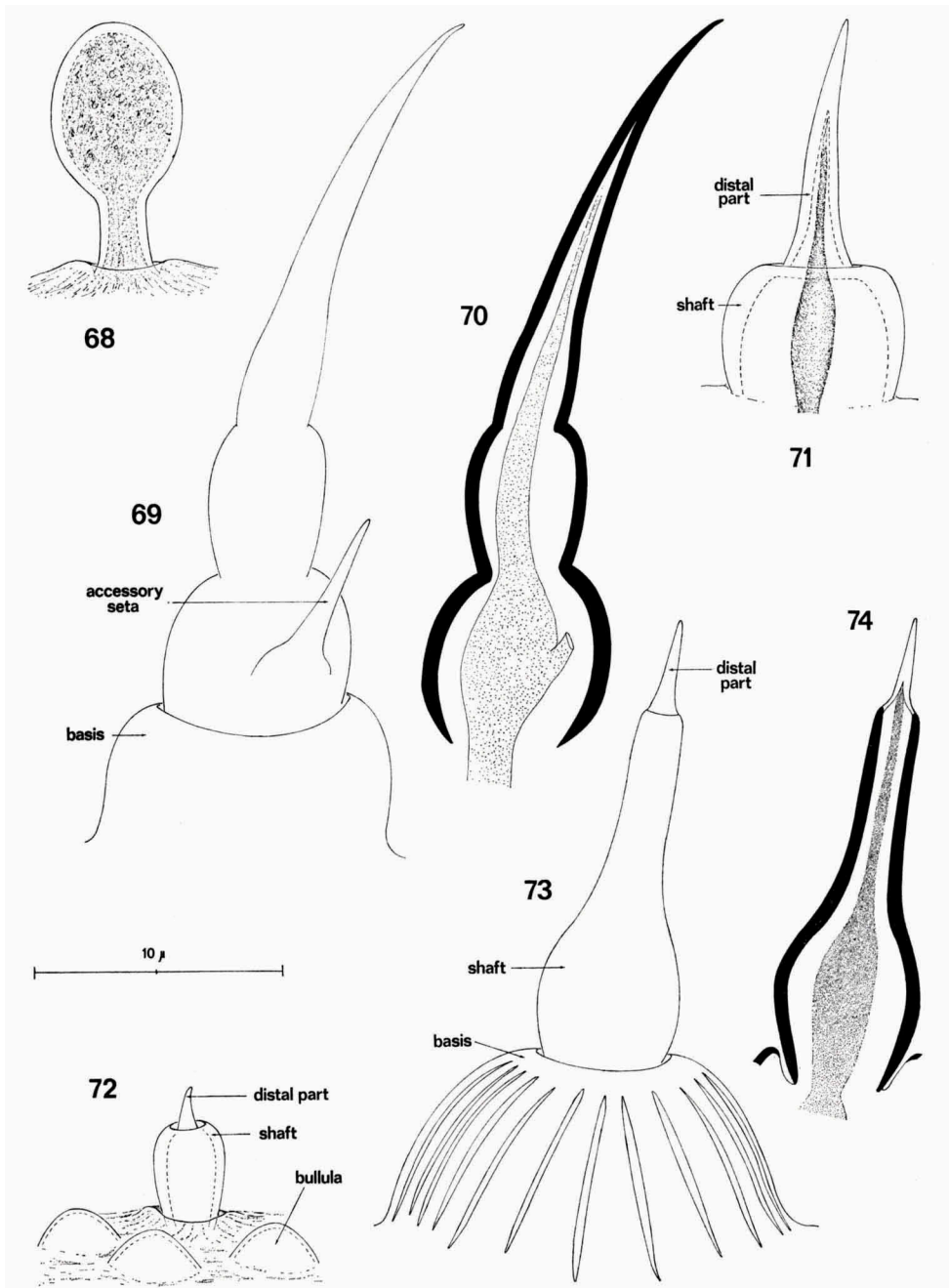


Fig. 68-74. *Tubiluchus corallicola*, male, cuticular structures of abdomen, Bonaire (Mus. Leiden). 68, clavula; 69, ventral seta; 70, optical length-section of the same; 71, perigenital seta; 72, small perigenital seta and bullae on preanal bulge; 73, large perigenital seta; 74, optical length-section of the same.

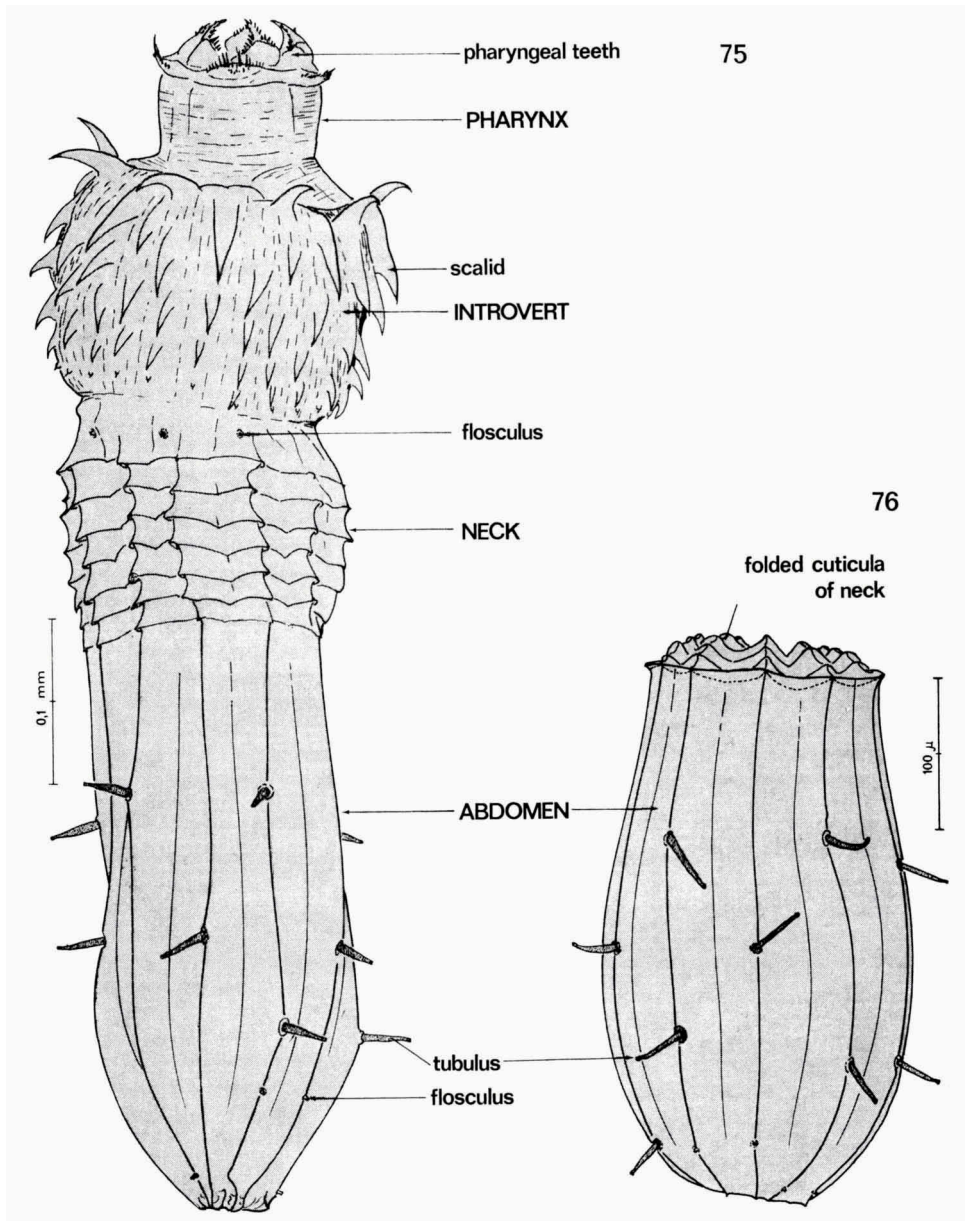


Fig. 75-76. *Tubiluchus corallicola*, larvae, habitus. 75, with introvert and pharynx protruded, Bermuda (coll. Higgins); 76, contracted, Curaçao (after Van der Land, 1968).

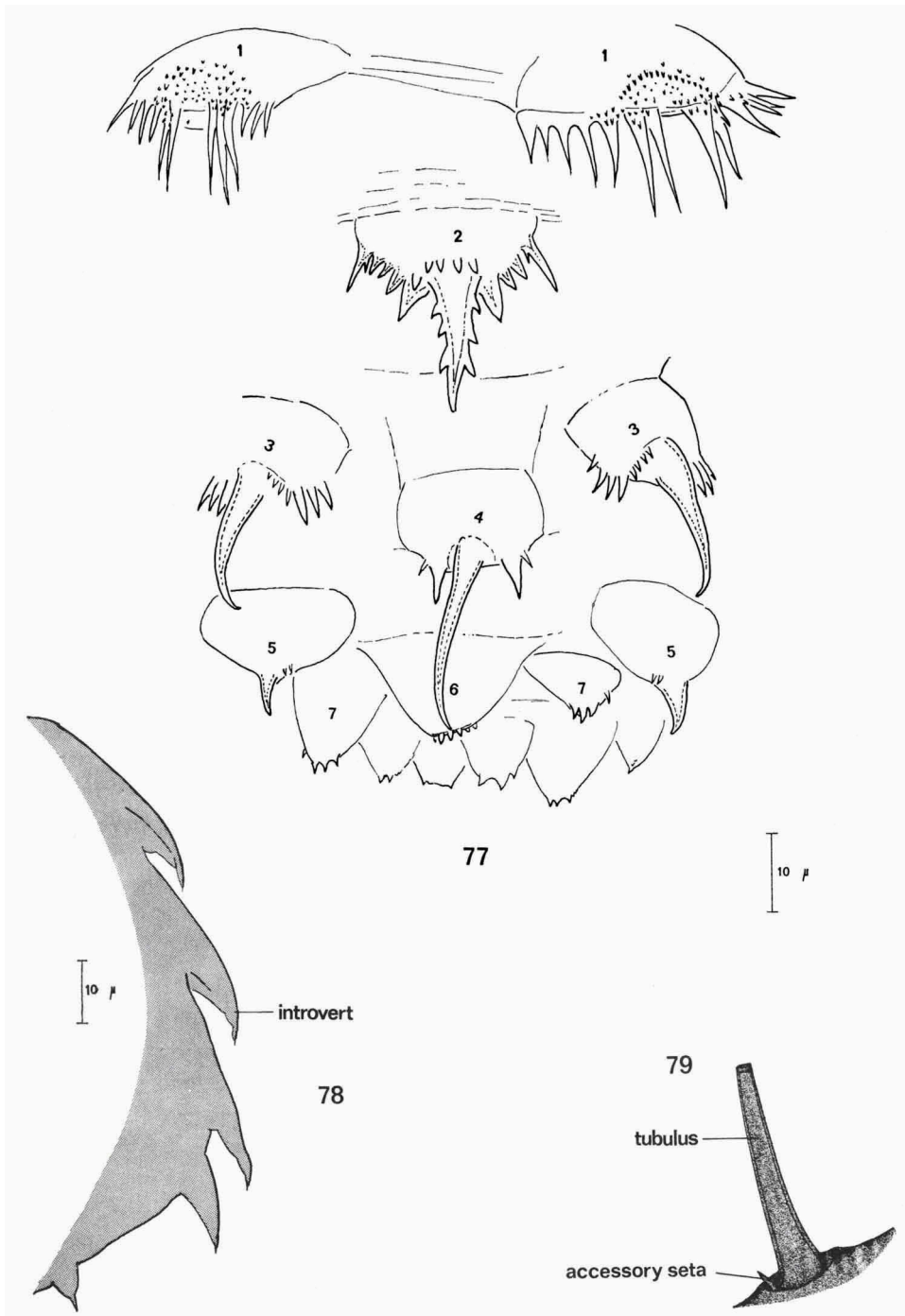


Fig. 77-79. *Tubiluchus coralicola*, details of larvae, Bermuda (coll. Higgins). 77, anterior pharyngeal teeth; 78, row of scalids; 79, tubulus.

of the copulatory apparatus; in this case special attention has to be paid to the arrangement of the perigenital setae. Specimens from Curaçao, Bonaire and Bermuda were strikingly similar in these details.

The larvae might differ in the structure of the pharyngeal armature and the arrangement of the tubuli, but it should be stressed that the youngest stages have not yet been described.

Distribution. — See fig. 89.

The study of the marine meiobenthos of tropical waters has begun quite recently. Therefore it is not at all astonishing that this relatively conspicuous animal has not been found earlier than 1958. The fact that it has since been found on a number of localities on four islands is a demonstration of the fact that meiobenthology has become more popular in recent years. There is no doubt about it that tubiluchids will turn up in many other tropical or semi-tropical localities. The most intriguing question is whether there are more species or only one.

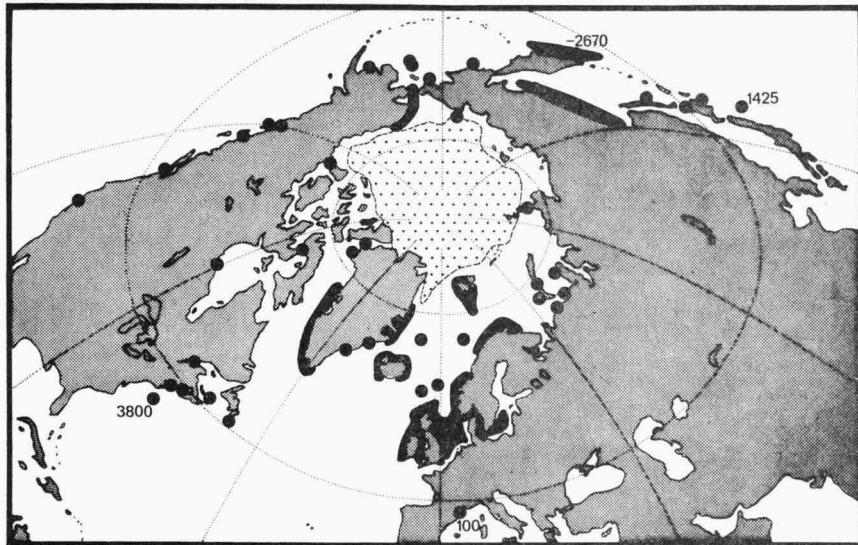
The identity of the material from the Red Sea is unknown. The author has not seen specimens from Barbados, but according to Dr. Kirsteuer (New York) the material collected by him is identical with the material on which the original description was based.

3 ZOOGEOGRAPHY AND ECOLOGY

Synthetical zoogeography is only possible on the basis of a fair knowledge of both distribution and ecology. Therefore, these subjects are dealt with first. It will become clear that much remains to be done in these fields. The distribution of several, if not all, species is insufficiently known and our knowledge of their ecology is extraordinarily poor. Because of this lack of a firm basis theoretical subjects can only be treated tentatively. Nevertheless they are presented here in order to stimulate further research.

3.1 DISTRIBUTION

It is a regular practice in systematic monographs to give lists of localities where the species have been found or from which the author has seen material. However, when these lists are becoming very long this procedure is neither practical nor useful. Moreover, by far the greater part of the material studied by the author has already been mentioned in the literature before; most of it was enumerated by Danielssen, Koren, K. Lang, Théel, Stephen, and Wesenberg-Lund. One is practically never confronted with real misidentifications. Material worth mentioning has either been recorded specifically in the present paper or will be recorded in faunistic papers. For these reasons and in order to save labour and money a more useful system



Priapulus caudatus

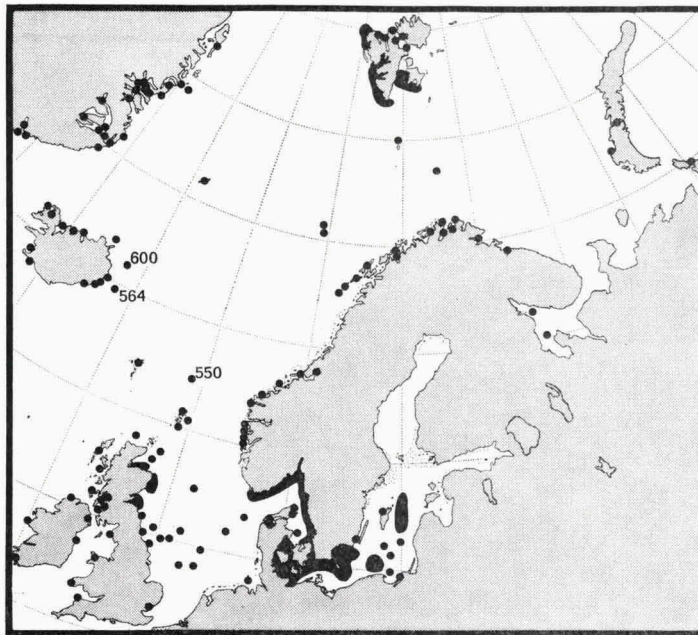


Fig. 80-81. *Priapulus caudatus*. 80, general distribution (but see also fig. 88); 81, distribution in northern European waters.

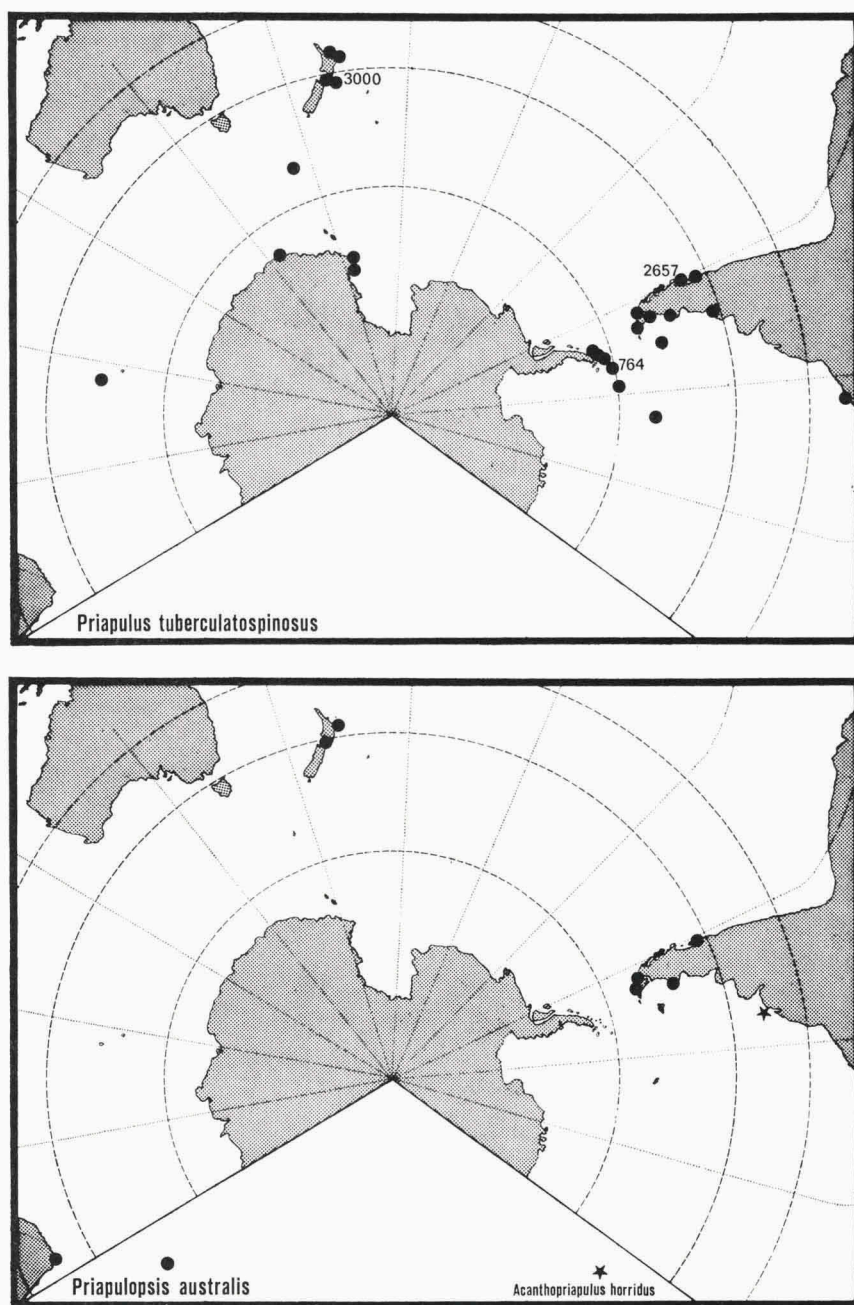
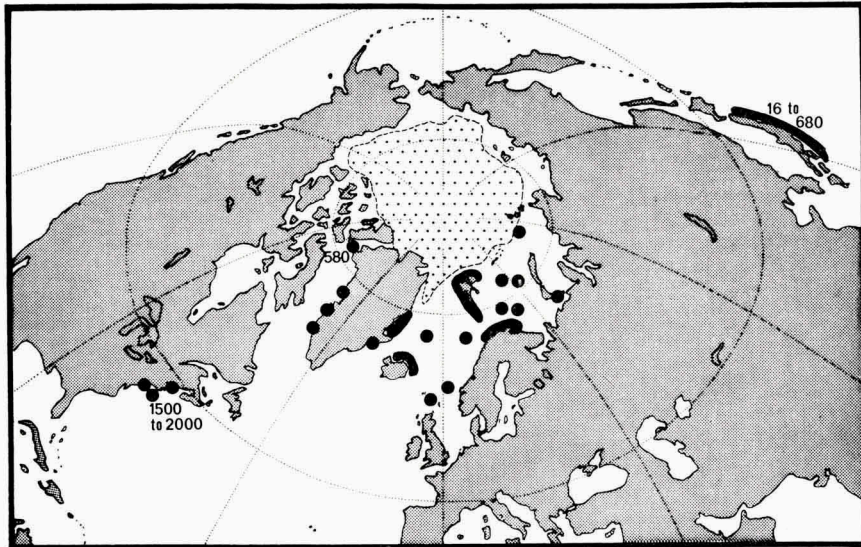


Fig. 82. Distribution of *Priapulus tuberculatospinosus* (but see also fig. 88).
Fig. 83. Distribution of *Priapulopsis australis* and locality of *Acanthopriapulus horridus*.



Priapulopsis bicaudatus

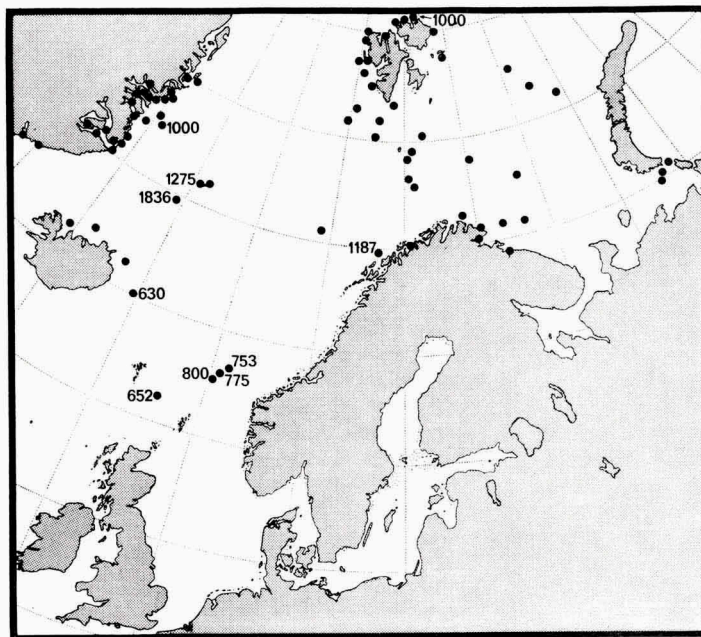


Fig. 84-85. *Priapulopsis bicaudatus*. 84, general distribution; 85, distribution in northern European waters.

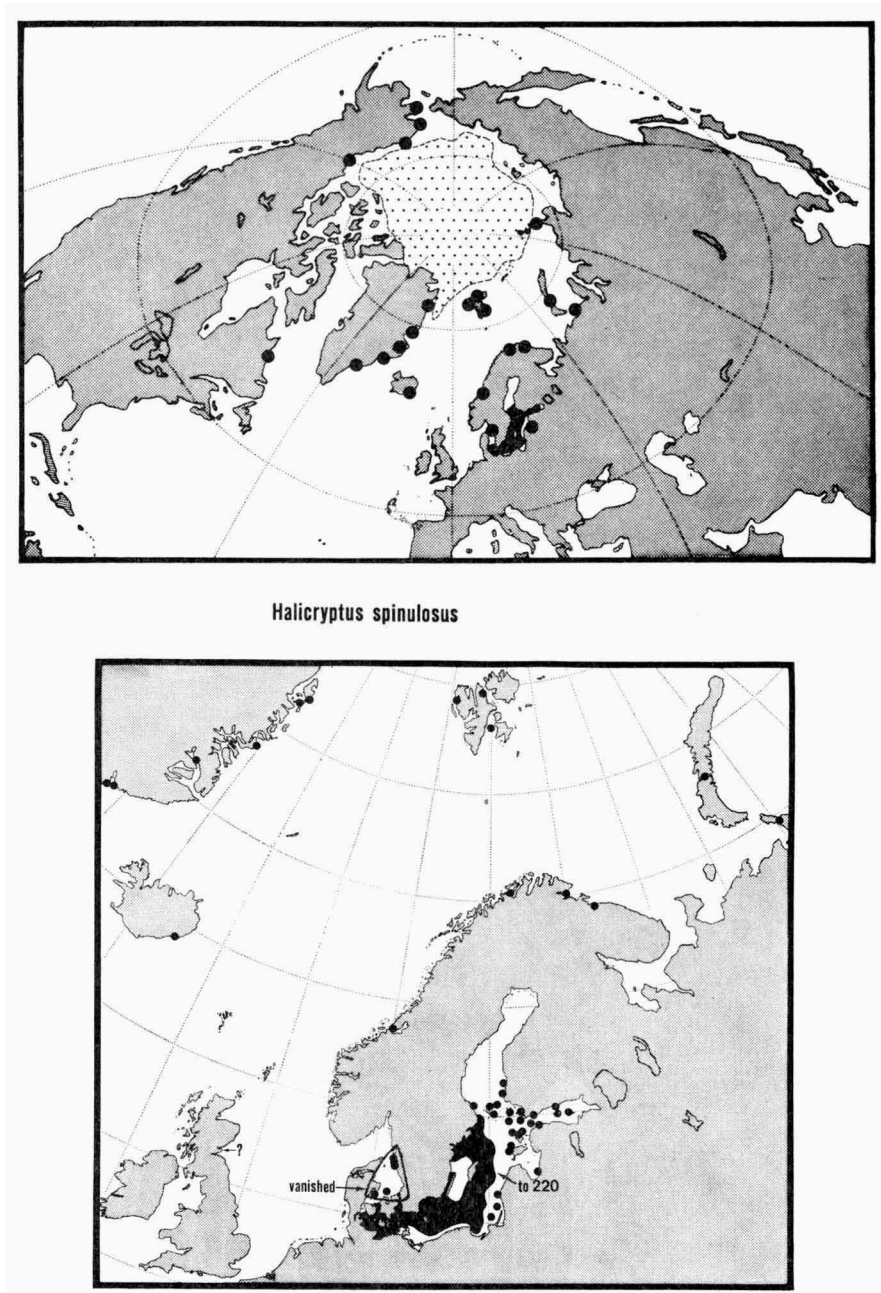
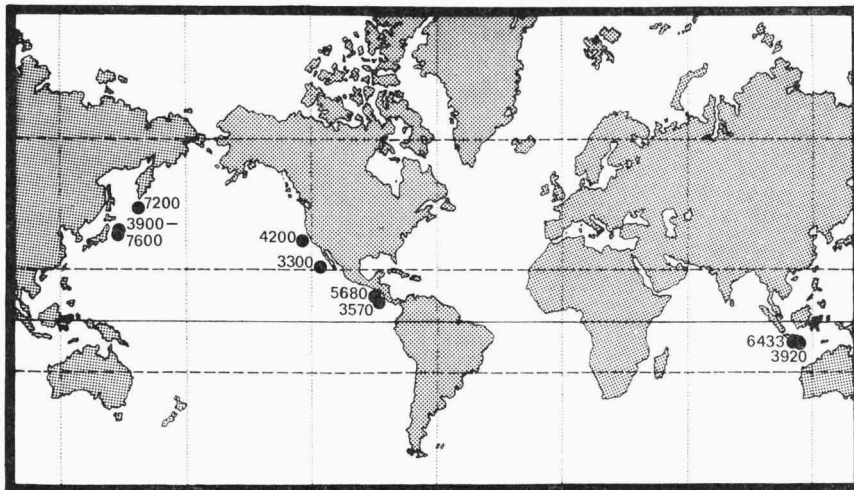
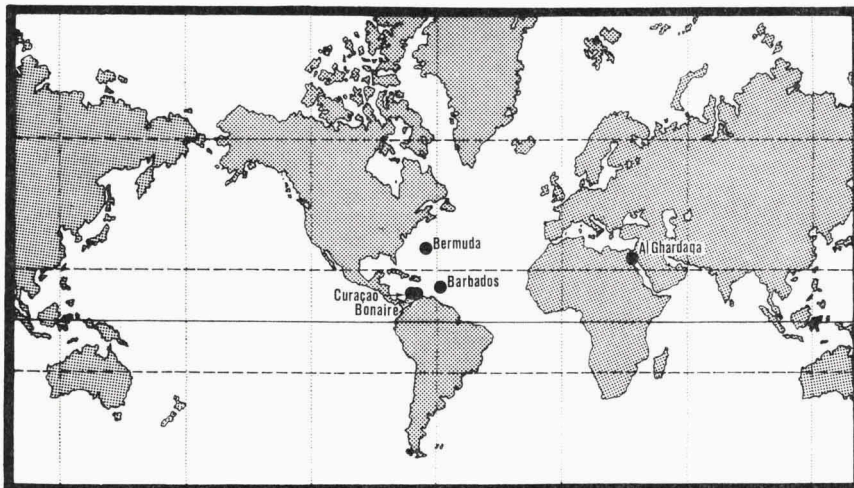


Fig. 86-87. *Halicryptus spinulosus*. 86, general distribution; 87, distribution in northern European waters.



Priapulus spec.



Tubiluchus

Fig. 88. Records of *Priapulus caudatus* or *P. tuberculatospinosus* from the deep sea. The specimen described as *P. abyssorum* (depth 5680 m) most probably belongs to *P. tuberculatospinosus*; separate descriptions of the other specimens are lacking.

Fig. 89. Localities where *Tubiluchus* has been found. The identity of the material from Al Ghardaqa is unknown; the other records refer to *T. corallicola*.

has been adopted for the present paper. (Of course more information is available to those interested in it).

In the introductory and systematic chapters the reader could get a general impression of the amount and variety of material on which this monograph is based. The distribution of the species is only given on maps. In order to meet the drawbacks of the absence of locality records, the sources of information on the distribution (both literature and collections) are specified in the following sections.

Remarks on the distribution of each of the species separately are already given in the systematic part. The distribution in European waters is known in much more detail than that in other parts of the world. Therefore maps of northern European waters are added for the three species occurring in this region. Most records refer to depths of less than 500 m. For localities in deeper water the depth, when known, has been indicated on the maps.

3.1.1. Faunistics

In the following lists the sources of information on the distribution of priapulids are specified for a number of areas, chosen for convenience. In the first place references to the literature are given, with indications as to where the species were recorded from the area in question for the first time. Secondly collections are mentioned in which material is present that was not mentioned in the literature before. The shelf regions of the continents are treated separately from the oceans and oceanic islands. For coastal waters national boundaries are taken into account. They are biologically irrelevant, but those engaged in faunistic studies, which are usually done on a national basis, are probably best served in this way.

North America

1. Alaska: Skorikov, 1902a (*P. caudatus*); Chamberlin, 1920; Mac Ginitie, 1955 (*H. spinulosus*); Shapeero, 1962b; Holmquist, 1963, 1969; Mus. Washington; Mus. Stockholm.
2. United States, West coast: K. Lang, 1951 (*P. caudatus*); Ricketts & Calvin, 1952; Smith et al., 1954; Shapeero, 1962b; Mus. Washington.
3. Canada, North and East coasts: Whiteaves, 1874 (*P. caudatus*), 1901; Verrill, 1880, 1881; Chamberlin, 1920; Wesenberg-Lund, 1930; Préfontaine & Brunel, 1962; Carter, 1966 (*H. spinulosus*); Mus. Washington; Mus. Stockholm.
4. United States, East coast; Verrill, 1879 (*P. caudatus*), 1880, 1881; Mus. Washington (*P. bicaudatus*).
5. Greenland: Fabricius, 1780 (*P. caudatus*); Ehlers, 1861; Stimpson, 1864; Baird, 1868; Möbius, 1874; Théel, 1875, 1906 (*P. bicaudatus*; *H. spinulosus*), 1911; Fischer, W., 1894, 1914; Wesenberg-Lund, 1925, 1930, 1932, 1933, 1934, 1937b; Mus. Copenhagen; Mus. Washington; Mus. London; Mus. Bergen.

North Atlantic Ocean

1. Western North Atlantic: Verrill, 1885 (*P. caudatus*); Sanders & Hessler, 1962 (*P. bicaudatus*).
2. Bermuda: Coull, 1968 (*T. corallicola*), 1970; coll. Higgins.
3. Norwegian and Greenland Seas: Danielssen & Koren, 1881 (*P. caudatus*; *P. bicaudatus*); Fischer, 1920, 1922b; Wesenberg-Lund, 1930, 1937a; Mus. Bergen.
4. Iceland: Olafsen, 1772 (*P. caudatus*), 1775, Faber, 1829; Théel, 1906; Wesenberg-Lund, 1930 (*P. bicaudatus*), 1937a (*H. spinulosus*); Spärck, 1937; Brown & Cheng, 1946; K. Lang, 1951; Mus. Stockholm.
5. Færoes: Wesenberg-Lund, 1928 (*P. caudatus*), 1930.
6. Spitsbergen: Lovén, 1864 (*H. spinulosus*); Keferstein, 1865b; Ehlers, 1871; Heuglin, 1874; Danielssen & Koren, 1881 (*P. caudatus*); Fischer, W., 1894, 1914, 1922c, 1928; Skorikov, 1902a; Théel, 1906 (*P. bicaudatus*), 1911; K. Lang, 1951; Mus. Bergen.
7. Barents Sea: Horst, 1881 (*P. caudatus*; *P. bicaudatus*); Stiasny, 1930; Brown & Cheng, 1946; Mus. Hamburg; Mus. Copenhagen.

Europe.

1. British Isles and Ireland: Fleming, 1828 (*P. caudatus*); Forbes, 1841; McCoy, 1845; Dalyell, 1853; Phillips, 1854; Leckenby, 1855; McIntosh, 1866, 1874, 1875; 1927; Baird, 1868; Scott, 1890; Gemmil, 1901; Southern, 1913a, 1913b; Stephen, 1934, 1960; Bassindale & Barrett, 1957; McIntyre, 1958; Bruce et al., 1963; Bull, 1966; Crothers, 1966; Hammond and Sims (personal communication); Mus. London; Mus. Edinburgh.
2. Norway: v. Düben, 1844 (*P. caudatus*); Sars, 1851; Danielssen, 1861, 1868 (*P. bicaudatus*); Koren & Danielssen, 1875, 1877; de Guerne, 1886, 1888; Skorikov, 1902b; Norman, 1903 (*H. spinulosus*); Hérubel, 1904a; Théel, 1906; Broch, 1928; Wesenberg-Lund, 1929, 1938; Dons, 1939; Mus. Oslo; Mus. Bergen; Mus. Trondheim; Mus. Stockholm; Mus. London.
3. North Sea: Metzger, 1873 (*P. caudatus*); Möbius, 1875; Fischer, W., 1894, 1914, 1925; Fischer, J., 1913; Stephen, 1934; Coll. Charlottenlund laboratory.
4. Denmark and Kattegat: Abildgaard, 1789 (*P. caudatus*); Willemoes-Suhm, 1871; Tauber, 1879; Levinsen, 1893; Théel, 1906 (*H. spinulosus*); Petersen, 1914; Blegvad, 1915, 1917; Wesenberg-Lund, 1929, 1950; Spärck, 1942; Brattström, 1947; Nørrevang, 1965; Mus. Copenhagen.
5. Sweden: Lovén, 1864 (*H. spinulosus*); Möbius, 1873; Nordqvist, 1890; Théel, 1906 (*P. caudatus*), 1908, 1911; Hérubel, 1904a; Hammarsten, 1913; Wesenberg-Lund, 1929, 1939a; K. Lang, 1939; Brattström, 1947; K. Lang, 1948a, 1948b, 1951; Fänge & Åkesson, 1951; Nørrevang, 1965; Jägersten, 1968; Mus. Stockholm; Mus. Leiden.
6. Finland: Levander, 1915 (*H. spinulosus*); Segerstråle, 1933, 1949, 1960; Purasjoki, 1944; Granqvist, 1955; Tulkki, 1960, 1964; Bagge et al., 1965; Särkkä, 1969.
7. Estonia: Leuckart, 1869 (*H. spinulosus*); Ehlers, 1871.
8. Latvia: Ehlers, 1871 (*H. spinulosus*).
9. Poland: von Siebold, 1849 (*H. spinulosus*); Leuckart, 1869; Ehlers, 1871; Möbius, 1873; Mulicki, 1957.
10. Baltic Sea: Möbius, 1873 (*H. spinulosus*); Théel, 1875 (*P. caudatus*), 1906; Nordqvist, 1890; Reibisch, 1902; Skorikov, 1902b, 1910, 1913; Fischer, J., 1913; Fischer, W., 1914, 1925; Thulin, 1920; Hessle, 1923, 1924; Hertling, 1928; Wesenberg-Lund, 1929; Hagmeier, 1930; Välikangas, 1933; Demel & Mulicki, 1954, 1958; Sjöblom, 1955; Forsman, 1956; Segerstråle, 1957b, 1960; Mulicki, 1957; Arndt, 1964; Tulkki, 1965; Mus. Stockholm.

11. Germany: von Siebold, 1862 (*H. spinulosus*), 1871; Keferstein, 1865b; Leuckart, 1869; Zenger, 1870 (*P. caudatus*); Willemoes-Suhm, 1871; Möbius, 1873; Lenz, 1878, 1883; Apel, 1885; Fischer, W., 1894, 1920; Eggers, 1925; ten Broeke, 1929; Schulz, 1931, 1934; Friedrich & Langeloh, 1936; Lüling, 1940; Kühlmorger-Hille, 1963.
12. France: Guille & Laubier, 1965 (*P. caudatus*).
13. Novaya Zemlya: Heuglin, 1874 (*P. caudatus*); Théel, 1906 (*H. spinulosus*); Wesenberg-Lund, 1933.
14. Kara Sea: Levinsen, 1887 (*P. caudatus*); Holm, 1887; Skorikov, 1902a; Wesenberg-Lund, 1933 (*P. bicaudatus*); Murina & Starobogatov, 1961 (*H. spinulosus*); Mus. Copenhagen.
15. Russia, North coast: Knipovič, 1891 (*P. caudatus*); Skorikov, 1902a; Derjugin, 1906 (*H. spinulosus*), 1915; Averincev, 1908 (*P. bicaudatus*); Molčanov, 1908; Gadd, 1911; Zinkin, 1949; Zinkin & Korsakova, 1953.

Asia.

1. Siberia: Skorikov, 1902a (*P. caudatus*); Théel, 1906 (*H. spinulosus*); Murina & Starobogatov, 1961.
2. Japan: Satō, 1934 (*P. bicaudatus*), 1937, 1939; Okuda, 1934 (*P. caudatus*); Murina & Starobogatov, 1961.

North Pacific Ocean

1. Sea of Okhotsk and Bering Sea: Murina & Starobogatov, 1961 (*P. caudatus*).
2. Western North Pacific: Murina & Starobogatov, 1961 (*P. caudatus*; *P. ?tuberculatospinosus*).
3. Eastern North Pacific: Menzies, 1959 (*P. ?tuberculatospinosus*); Wolff, 1961; Murina & Starobogatov, 1961.

South America

1. Chile: Wesenberg-Lund, 1955 (*P. tuberculatospinosus*; *P. australis*); Mus. New York.
2. Curaçao and Bonaire: van der Land, 1968 (*T. corallicola*); Mus. Leiden.
3. Barbados: Kirsteuer (personal communication) (*T. corallicola*).
4. Brasil: Tommasi, 1968 (*P. tuberculatospinosus*).
5. Uruguay: Théel, 1911 (*A. horridus*).
6. Argentina: de Guerne, 1886 (*P. australis*), 1888; Théel, 1911 (*P. tuberculatospinosus*); Olivier et al., 1961.
7. Tierra del Fuego-region (Argentina and Chile): de Guerne, 1886 (*P. australis*; *P. tuberculatospinosus*), 1888; Fischer, W., 1896, 1914; Lahille, 1899; Théel, 1911; Marelli, 1912.
8. Falkland Islands: Baird, 1868 (*P. tuberculatospinosus*); Théel, 1911; Stephen, 1941; K. Lang, 1951; Mus. London.

South Atlantic Ocean

1. South Georgia: Michaelsen, 1889 (*P. tuberculatospinosus*); Pfeffer, 1890; Théel, 1911; Fischer, W., 1914, 1922a; Stephen, 1941.

Africa

1. Egypt: Remane, 1963 (*Tubiluchus spec.*); Remane & Schulz, 1964.
2. South-Africa: Stephen & Cutler, 1969 (*P. australis*); Day (personal communication).

Indian Ocean

1. Java Deep: Murina, 1964 (*P. ?tuberculatospinosus*).
2. Kerguelen: Collin, 1901 (*P. tuberculatospinosus*); Skorikov, 1901, 1902; Fischer, W., 1922b.

South Pacific Ocean

1. New Zealand: Benham, 1932 (*P. tuberculatospinosus*); Dell, 1955; Murina & Starobogatov, 1961; Hurley, 1962 (*P. australis*); Estcourt, 1967.
2. Macquarie: Benham, 1922 (*P. tuberculatospinosus*); Murina & Starobogatov, 1961.

Antarctica

1. South Shetland and South Orkney Islands: Théel, 1911 (*P. tuberculatospinosus*); Stephen, 1941; Mus. Washington; Mus. New York.
2. The continent: Shipley, 1902 (*P. tuberculatospinosus*); Benham, 1922; Mus. Washington; Mus. London.

3.1.2 Expeditions

Much work can be done within the range of marine biological stations, but for marine zoogeography we are largely dependent on special expeditions. In the following list those expeditions are specified which have contributed to our knowledge of the distribution of priapulids.

Sometimes the expeditions have received a special name but mostly the name of the ship (here given between quotation marks) or the name of the leader of the expedition is used. The area and the time in which the expedition operated are indicated and also the nationality and sometimes the leader or zoologist of the expedition (sometimes only their names occur on the labels). After the colon references are given to the literature in which the priapulids of the expedition have been treated and the collections are mentioned in which the material is known to be kept now. The results of a small number of expeditions are being used for the first time in the present paper.

- "Albatross", off New England, 1883; Alaska, 1905 (U.S.): Verrill, 1885; Mus. Washington.
- Amdrup's East Greenland Exps, 1898/1900, with Jensen (Danish): Wesenberg-Lund, 1930; Mus. Copenhagen.
- Amondson, Greenland, 1862, 1872 (Swedish): Théel, 1906; Mus. Stockholm.
- "Antarctic", Swedish Antarctic Expedition, 1901-1903, Nordenskjöld: Théel, 1911; Lang, K., 1951; Mus. Stockholm.
- Antarctic Research Program, 1964-1969 (U.S.): Mus. Washington.
- "Aranda", Baltic Sea, 1954 (Finnish): Sjöblom, 1955; Granqvist, 1955.
- "Armauer Hansen", Norwegian Sea, 1926 (Norwegian): Mus. Bergen.
- "Atlantis", Western North Atlantic, 1961 (U.S.): Sanders & Hessler, 1962; Mus. Washington.
- "Aurora", see next.
- Australasian Antarctic Exp. with the "Aurora", 1911-1914: Benham, 1922.
- Baltic Exp., Russian, see "Kompass".
- Bartlett, Greenland, 1937 (U.S.): Mus. Washington.
- "Belgica", Spitsbergen, 1905 (Belgian): Mus. Bergen.
- Berthelsen, Iceland, 1936 (Danish): Wesenberg-Lund, 1937a; Mus. Copenhagen.
- "Beskytteren", Eastern North Atlantic (Danish): Wesenberg-Lund, 1930.
- "Blåfjell", Norwegian Sea, Spitsbergen, 1923 (Norwegian): Mus. Bergen.

- Bock, Sweden, 1940-1946 (Swedish): Mus. Stockholm.
- Broch, see Lindesness.
- Canadian Arctic Exp., 1913-1916: Chamberlin, 1920.
- Cap Horn, Mission scientifique du, 1882-1883, with the "Romanche" (French): de Guerne, 1886.
- Clare Island Survey, 1909-1911 (Irish): Southern, 1913b.
- "Dana", Baltic Sea, Danish waters, Færoes, Iceland, 1900-1902, 1926-1927, 1931-1934 (Danish): Wesenberg-Lund, 1930, 1937; Spärck, 1937; Mus. Copenhagen.
- "Danmark", Eastern North Atlantic, 1906-1908 (Danish): Wesenberg-Lund, 1930; Mus. Copenhagen.
- "Dannevig", Southern Norway, 1950-1953 (Norwegian): Mus. Oslo.
- Deepfreeze I, Antarctic waters, 1956 (U.S.): Mus. Washington.
- Degerbøl, Greenland, 1932 (Danish): Wesenberg-Lund, 1937b; Mus. Copenhagen.
- Deutsche Südpolar Exp. with the "Gauss", Drygalski, Vanhöffen, 1901-1903: W. Fischer, 1921; Mus. Berlin.
- Deutsche Tiefsee-Expedition, see "Valdivia".
- "Discovery", Greenland (British): Mus. London.
- "Discovery", Southern Oceans, 1926-1937 (British): Stephen, 1941; Mus. London.
- "Dijmphna", Kara Sea, 1882-1883 (Danish): Levinsen, 1873; Metzger, 1873; Mus. Copenhagen.
- Drygalski, see Deutsche Südpolar Exp.
- East Greenland Exp., Scoresby Sound Committee's 2nd, 1932 (Danish): Wesenberg-Lund, 1934; Mus. Copenhagen.
- Eastwind, Antarctic waters, 1966 (U.S.); Mus. Washington.
- "Edisto", see Deepfreeze I. (ED on labels).
- "Eltanin", see Antarctic Research Program.
- "Endeavour", Australian waters, 1909-1914 (Australian): Benham, 1916.
- "Ermák", Baltic Sea, 1901 (Russian): Skorikov, 1902b.
- "Eugénie", Southern oceans, 1851-1853, Virgin (Swedish): Théel, 1911; Mus. Stockholm.
- Eystrasalts exp., Baltic Sea, 1919-1923 (Swedish): Hessle, 1923, 1924.
- "Fylla", North Atlantic, 1884-1896, Holm and Wandel (Danish): Wesenberg-Lund, 1930; Mus. Copenhagen.
- "Galathea", around the world, 1950-1952 (Danish): Wolff, 1961; Mus. Copenhagen.
- "Gauss", see Deutsche Südpolar Exp.
- "Gazelle", Southern oceans, 1874-1876, Schleinitz (German): Collin, 1901; Mus. Berlin.
- Godthaab Exps., Greenland, 1928, 1932-1933 (Danish): Wesenberg-Lund, 1932; Mus. Copenhagen.
- Grönlands Exp., 1899 (Swedish): Théel, 1906; Mus. Stockholm.
- "Gunhild", Baltic Sea, 1878-1879, Théel (Swedish): Théel, 1906; Mus. Stockholm. (abbreviated as Gunh. Exp.).
- Hamburger Magalhaensischen Sammelreise, 1892-1893, Michaelsen (German): Fischer, W., 1896; Mus. Hamburg.
- Hansen, Greenland, 1927-1929 (Danish): Wesenberg-Lund, 1930; Mus. Copenhagen.
- Hayes, Arctic Expedition, 1862 (U.S.): Stimpson, 1864.
- "Hekla", Scoresby Sound, Greenland, 1891-1892, Ryder (Danish): Wesenberg-Lund, 1930; Mus. Copenhagen.
- Heuglin & Waldburg-Zeil Spitsbergen Exp., 1870-1871 (German): Ehlers, 1871; Heuglin, 1874.
- Holm, see "Fylla".
- Holmquist, Northern Alaska, 1961-1968 (Swedish and U.S.): Holmquist, 1963, 1969; Mus. Stockholm.
- Hummelincq, West Indies, 1963-1967 (Dutch): van der Land, 1968; Mus. Leiden.

- "Ikatere", New Zealand, 1957 (New Zealand): Hurley, 1962.
- "Ingegerd & Gladan", Swedish Arctic Expedition, Greenland, 1871, Lindahl: Théel, 1906; Mus. Stockholm. (abbreviated as Ing. & Gl. Exp.).
- "Ingolf"-Exps., North Atlantic, 1895-1896 (Danish): Wesenberg-Lund, 1930; Mus. Copenhagen.
- Karskoj Naučnoj Exp., 1944-1946 (Russian): Murina & Starobogatov, 1961.
- Koldewey, see Zweite Deutsche Nordpolarfahrt.
- "Kompass", Russian Baltic Exp., 1908, Knipovič: Skorikov, 1910, 1913.
- Lindessness Exp. with the "Spinax", Southern Norway, 1926, Broch (Norwegian): Broch, 1928; Mus. Oslo.
- Lund University Chile Exp., 1948-1949 (Swedish): Wesenberg-Lund, 1955; Mus. Stockholm.
- "Medusa", Scotland (British): Gemmil, 1901.
- "Michael Sars", North Atlantic, 1902 (Norwegian): Wesenberg-Lund, 1930; Mus. Bergen. (M.S. on labels).
- Nordenskiöld, see "Vega" and Yenessei Exp.
- Nordenskiöld, Southern Oceans, 1896 (Swedish): Théel, 1911; Mus. Stockholm. (Erdsf. Exp. on labels).
- Nordenskiöld, see "Antarctic".
- Nordsee Exp., 1872 (German): Möbius, 1875.
- Norske Nordhavs Exp., Norwegian North-Atlantic Exp., 1876-1878: Danielssen & Koren, 1881; Mus. Bergen; Mus. Oslo; Mus. Copenhagen; Mus. London. (N.N.Eks. on labels).
- Nova Semlja Exp., 1875, Théel (Swedish): Théel, 1906; Mus. Stockholm.
- "Ob", Antarctic waters, 1956 (Russian): Murina & Starobogatov, 1961.
- "Olga", Spitsbergen, 1898 (German): Fischer, W., 1922, 1928.
- Ostsee Exp., (German): Reibisch, 1902.
- "Pervenec", Bering Sea, 1958-1959 (Russian): Murina & Starobogatov, 1961.
- "Pommerania", Baltic Sea, 1871 (German): Möbius, 1873; Metzger, 1873.
- "Poseidon", North Sea, 1902-1912 (German): Fischer, J., 1913. Barents Sea, Fischer, W., 1922c. Baltic Sea, 1925, 1926, 1929: Hertling, 1928; Hagmeier, 1930.
- "Romanche", see Cap Horn.
- Römer & Schaudinn's Spitsbergen Exp., 1898 (German): Fischer, W., 1922c, 1928; Mus. Berlin.
- Salomonsen, Greenland, 1936 (Danish): Mus. Copenhagen.
- "Severnyj Poljus", Chukotsk Sea, 1946 (Russian): Murina & Starobogatov, 1961.
- "Skagerak", Southern Baltic, 1963-1964 (Swedish): Tulkki, 1965.
- "Sofia", Greenland, 1883 (Swedish): Théel, 1906.
- "Solveig I", Spitsbergen, 1937-1939 (Norwegian): Mus. Bergen.
- "Sotra", Norwegian Sea, 1930-1931 (Norwegian): Mus. Bergen.
- "Southern Cross", Antarctic waters, 1898-1900 (British): Shipley, 1902.
- "Sôyô-Maru", Japan, 1922-1930 (Japanese): Satô, 1934.
- Spärck, Greenland, 1932 (Danish): Wesenberg-Lund, 1937; Mus. Copenhagen.
- „Speedwell", New England (U.S.): Mus. Washington.
- Spitsbergen Exps. 1861, 1864, 1868, 1872-1873, 1898 (Swedish): Lovén, 1864, Théel, 1906; Mus. Stockholm.
- Süd-Georgien-Exp., 1882-1883 (German): Michaelsen, 1889; Mus. Hamburg.
- "Sven Lovén", Baltic Sea, 1911 (Swedish): Mus. Stockholm.
- Swedish Antarctic Exp., see "Antarctic".
- Swedish Arctic Exp., 1871, see "Ingegerd & Gladan".
- Swedish Arctic Exp., 1900: Théel, 1906; Mus. Stockholm.
- Théel, see "Gunhild" and Nova Semlja Exp.

- "Thor", North Sea, North Atlantic, 1903-1908 (Danish): Wesenberg-Lund, 1937; Mus. Copenhagen. Iceland, 1935: Spärck 1937.
- Thorson, Greenland, 1931-1933 (Danish): Wesenberg-Lund, 1937b; Mus. Copenhagen.
- Thule Exp. V, Northern Canada, 1921-1923 (Danish): Wesenberg-Lund, 1930; Mus. Copenhagen.
- Thule, Greenland, 1933 (Danish): Mus. Copenhagen.
- Torell, Greenland, Iceland (Swedish): Théel, 1906.
- "Tovik", Norwegian Sea, 1925 (Norwegian): Mus. Bergen.
- "Valdivia", Southern Oceans, 1898-1899 (German): Fischer, W., 1922b; Mus. Berlin; Mus. Hamburg.
- "Vega", Siberia, 1878, Nordenskiöld (Swedish): Théel, 1906; Mus. Stockholm.
- "Veiding", Norwegian Sea, 1931 (Norwegian): Mus. Bergen.
- "Vema" 15, Pacific Ocean, 1958 (U.S.): Menzies, 1959.
- "Vema" 17, Southern Oceans, 1961 (U.S.): Mus. New York.
- Vibe, Greenland, 1936, 1939 (Danish): Mus. Copenhagen.
- "Vitjaz", Pacific Ocean, 1950-1960 (Russian): Murina & Starobogatov, 1961; Murina, 1964, 1968.
- Wandel, see "Fylla".
- Whiteaves, with the "J. H. Nickerson", Gulf of St. Lawrence, 1873 (Canadian): Whiteaves, 1874.
- "Willem Barents", Barents Sea, 1879 (Dutch): Horst, 1881, Stiasny, 1930; Mus. Leiden.
- Yenessei Exp., Northern Siberia, 1875, Nordenskiöld (Swedish): Théel, 1906, Mus. Stockholm.
- "Žemčug", Bering Sea, 1958-1959 (Russian): Murina & Starobogatov, 1961.
- Zweite Deutsche Nordpolarfahrt 1869-1870: Möbius, 1874.

3.2 ECOLOGY

Ecological data can be obtained from the labels of museum specimens; usually the depth and the nature of the sediment are indicated and sometimes also the salinity and the temperature; a considerable number of specimens was obtained from the stomachs of predators. A number of incidental observations are mentioned in the literature (see survey by K. Lang, 1948a). It is to be regretted that very few relevant ecological investigations have been carried out until now. Most important are the investigations in the Baltic Sea, where *Priapulius caudatus* and *Halicryptus spinulosus* are dominant species of the very poor fauna. Several references to the literature were given for both species, but special mention should be made of the investigations by scientists from Poland (Demel & Mulicki, 1954; Mulicki, 1957) and Finland (Bagge, et al., 1965; Segerstråle, 1933, 1957b, 1960; Tulkki, 1960-1965).

3.2.1 Substratum

The Priapulidae are not at all fastidious in the choice of their habitats. I confine myself to giving a few examples in which this fact is clearly demonstrated. Théel (1906) recorded *Priapulius caudatus* from mud, clay, clay

and stones, gravel and clay, clay with sand, mud and clay, sand and clay, and *Priapulopsis bicaudatus* from clay, mud, mud and stones, sand and stones. Sjöblom (1955) found *Halicryptus spinulosus* in the Baltic Sea in clay, clayey sand and gravel, clayey mud, clayey gravel, sand, and gravel. The same may hold for the other species. Nevertheless it is obvious from the numerous observations mentioned in the literature that the sediments in which the animals are found, are nearly always more or less muddy or clayey. They are certainly most common in muddy sediments with a poor fauna. In my experience one has to dredge on muddy bottom, preferably with evil smelling blue mud, when one wants to have a really good chance of obtaining *P. caudatus* in the Gullmarfjord area or in the Öresund. The reason is perhaps that competition is too strong in biotopes with a richer fauna.

Tubiluchus has been found in poorly sorted coral sand with a rich interstitial fauna. In Bermuda (Coull, 1968) it inhabited a very fine sediment.

3.2.2 Depth

Priapulidae occur from the intertidal zone to the trenches in the deep sea. The species of *Priapulus* have the widest bathymetrical distribution; both species have been found in the intertidal zone several times, but both have also been reported from abyssal depths, down to about 7500 m. On the contrary the species of *Priapulopsis* occur neither in the littoral zone nor at abyssal depths. *P. bicaudatus* occurs at a depth of 10 to 2000 m; it was found at bathyal depths several times. *P. australis* has been recorded from depths of 40 to 400 m. *Acanthopriapulus horridus* was found at a depth of 80 m. *Halicryptus spinulosus* usually occurs in very shallow water (also in the intertidal zone) but in the Baltic Sea it is common even in the deepest basins, down to 220 m.

Tubiluchus has been collected only in the sub-littoral zone from the low-water mark to a depth of 13 m.

3.2.3 Temperature

The Priapulidae are practically restricted to cold water as is apparent from the distribution pattern. According to Mulicki (1957) *Priapulus caudatus* occurs in the Baltic Sea in areas where the temperature does not exceed 8° C and *Halicryptus spinulosus* where the temperature does not exceed 11° C. *Priapulopsis bicaudatus* prefers still colder water: Danielssen & Koren (1881) recorded temperatures of -1.1° C to +3.5° C. The Japanese populations of *Priapulopsis bicaudatus* are exceptional in that they occur off southern Japan in rather warm water (in shallow water *Priapulus caudatus* does not go farther south than the island of Hokkaido).

Tubiluchus was found only in warm water. The climate of Bermuda is semi-tropical due to the warm Gulf Stream. According to Coull (1968) the surface temperature of the water varied from 17° C in winter to 27.5° C in summer at the locality where *Tubiluchus* was found.

3.2.4 Salinity

Priapulopsis, *Acanthopriapululus* and *Tubiluchus* have only been found in localities with a high salinity, but *Priapululus* and *Halicryptus* are more or less euryhalinous.

Priapululus caudatus is usually found in typically marine habitats but in the Baltic Sea it occurs in areas with a salinity of down to 7‰ (Mulicki, 1957). Undoubtedly it also occurs in brackish water elsewhere, e.g., in fjords and estuaries.

Halicryptus spinulosus has never been found in a typically marine environment. In the area of the Baltic Sea it is restricted to brackish water. According to Mulicki (1957) the optimal salinity is 13 to 15‰, but it was found in localities with a much lower salinity (Purasjoki, 1944: down to 3.7‰; Särkkä, 1969: down to 5‰; Granqvist, 1955: down to 6‰). In other areas it was also found in definitely brackish water: Trondheimsfjord (Wesenberg-Lund, 1938); Iceland, salinity 6‰ (Wesenberg-Lund, 1937); Labrador, salinity 10 to 15‰ (Carter, 1966). Records from other areas may as well refer to brackish water habitats, although this was not mentioned on the labels. In spite of the fact that records from typically marine habitats are completely lacking, the animal is not a brackish-water species, as was proved by Holmquist (1963; 1969). In the course of her investigations in Alaska *Halicryptus spinulosus* was not only found in brackish water (salinity from about 4‰ to about 20‰), but also in a lagoon with a salinity of 29‰ and in a coastal pond with hypersaline water (salinity up to 65‰!). According to her the localities where the species occurs in Alaska are often characterized by considerable fluctuations in salinity.

3.2.5. Oxygen

It is to be regretted that there are only very few observations on the oxygen requirements of priapulids. Perhaps *Priapululus* and *Halicryptus* can withstand very low concentrations of oxygen in the water, at least for some time, and this may be of major survival value for these animals. Although measurements are lacking we can be sure that the water in their burrows in foul smelling mud is often poor in oxygen (see Fänge & Åkesson, 1951).

Mulicki (1957) did a large number of observations in the Baltic Sea. According to him the oxygen contents of the water near the bottom becomes

favourable for *Halicryptus* at a concentration of 3 ml/l, a lower concentration causing a decrease of the biomass. For *Priapulus* the oxygen contents of the water should not drop to less than 2 ml/l. Sometimes the whole fauna disappears from the deeper parts of the Baltic Sea due to oxygen deficiency (Tulkki, 1965).

3.2.6 Food

The structure of the pharyngeal armature of adult Priapulidae suggests that they are predaceous. However, observations on this point mentioned in the literature are contradictory. A survey of the available data is given below. The intestine often contains only a small amount of indeterminable material and mostly it is even completely empty, so that many specimens are required for investigations (in itself this fact is also evidence of predaceous habits).

Priapulus caudatus:

Frey & Leuckart (1847): intestine with sand, a shell fragment, and some small bodies of unknown nature.

Ehlers (1861): intestine with sand, many spores, and algae; it is a plant-eater.

Rauschenplat (1901): intestine with mud, plant remains, and chaetae of Polychaeta; it is not a plant-eater but a mud-eater.

Blegved (1915): it is a carnivorous detritus-eater.

Wesenberg-Lund (1929): *Chiridota laevis* (Holothuroidea) in mouth; intestine with *Pectinaria* and *Terebellides* (Polychaeta); mainly feeds on detritus.

Schulz (1931): intestine with *Nephtys* (Polychaeta); fed with flesh of *Mytilus* (Mollusca) in aquarium; but mainly plant-eater.

Wesenberg-Lund (1937b): intestine with Polychaeta.

K. Lang (1948a): observed many cases of cannibalism in aquarium; fed on *Aphrodite*, *Terebellides*, *Melinna* and *Amphicteis* (Polychaeta) and *Amphiura* (Ophiuroidea); the victims are usually swallowed with unbelievable speed; dead preys were not eaten; swift polychaetes like *Nereis* could not be seized.

Priapulus tuberculatospinosus:

Olivier, et al., 1961: Polychaeta in intestine; fed on earthworms.

I found a nearly undamaged mite in the intestine of a small specimen from the Palmer Archipelago (Mus. Washington).

Halicryptus spinulosus:

Blegvad (1915): intestine with *Nephtys* and spionid polychaetes; it is a carnivorous detritus-eater.

Forsman (1956): fragments of worms.

I found some holothurians in the intestine of a specimen from Alaska (Mus. Stockholm).

We may conclude that adult Priapulidae are carnivorous animals living on slow-moving prey, particularly on polychaetes. According to K. Lang (1948a) the mud and plant remains found in most cases in its intestine have been ingested together with the victims or are from the intestinal canal of the victims. Occasionally *Priapulus* may swallow mud but only in cases of emergency. The fact that it can live a couple of months in azoic mud, must not be taken as evidence that it is a mud-eater. In fact it is a real hunger artist. Lang kept it without food in mudless aquaria for six weeks and after that period it showed no signs of starvation.

On the other hand larvae of *Priapulus* are indeed detritus-eaters, as was observed by K. Lang (1939). Probably the same holds for adult *Tubiluchus*; I have seen quite a number of serial sections and the intestinal contents always proved to consist of indeterminable material. This was also the case in preparations of larvae of *Halicryptus* and *Tubiluchus*, but it should be recalled that their pharyngeal armature (fig. 48, 77) is of a type different from the one of *Priapulus* (fig. 17-18), which is indicative of at least a different way of feeding.

3.2.7 Predators

In the table on p. 101 a list of given of fishes and mammals in which priapulids were found among the stomach contents. Probably all animals feeding on benthic invertebrates will occasionally capture priapulids. In general they are not important as fish food because of their low densities. However, in areas with a nearly uninhabitable muddy bottom they are often relatively more abundant and in such areas they may be of some importance, especially for flatfishes and gadids. The best examples of such areas are the deep basins of the Baltic Sea where the benthic fauna is very poor and where both *Priapulus caudatus* and *Halicryptus spinulosus* are relatively common (Blegvad, 1917; Thulin, 1920; Hessle, 1924; Hertling, 1928). In Scottish waters *Priapulus caudatus* is rather common and frequently found in fish stomachs (MacIntosh, 1874, 1875; Stephen, 1934).

According to Leckenby (1855) fishermen at Scarborough (England) used *Priapulus caudatus*, which they called "sea mushrooms", as bait. They obtained the worms by digging in the harbour at half tide. In Germany *Halicryptus spinulosus* is used for the same purpose under the name "Rutenwurm" (Hartwich, 1967).

Predators of Priapulida

<i>Predator</i>	<i>Prey</i>	<i>Area</i>	<i>Source</i>
Scyliorhinidae (Sharks): Scyliorhinus caniculus (L.)	P. caudatus	Ireland	Southern, 1913a
Acipenseridae (Sturgeons): Acipenser stureo L.	H. spinulosus	Baltic Sea	v. Siebold, 1862
Gadidae: Gadus morhua L.	P. caudatus	Scotland	MacIntosh, 1874, 1875
	"	Denmark	Blegvad, 1917
	"	Norwegian Sea	Mus. Bergen
	"	Iceland	Brown & Cheng, 1946
	P. bicaudatus	Norwegian Sea	Mus. Bergen
	"	Iceland	Brown & Cheng, 1946
	"	Barents Sea	Brown & Cheng, 1946
Melanogrammus aeglefinus (L.)	P. caudatus	Scotland	McIntosh, 1874, 1875; Stephen, 1934
	"	North Sea	Jones, 1954
	"	Spitsbergen	Mus. Bergen
	"	Iceland	Brown & Cheng, 1946
	P. bicaudatus	Spitsbergen	Mus. Bergen
	"	Barents Sea	Brown & Cheng, 1946
Pollachius virens (L.)	P. caudatus	Norway	Mus. Oslo
Anguillidae: Anguilla anguilla (L.)	P. caudatus	Denmark	Blegvad, 1917
Gobiidae: Gobius niger L.	P. caudatus	Denmark	Blegvad, 1917
Cottidae: Cottus spec.	P. caudatus	Greenland	Fabricius, 1780
Gymnocanthus pistilliger (Pallas)	"	Canada	Chamberlin, 1920
Congiopodidae: Zanclorhynchus spinifer Günther	P. tuberculato-spinosus	Macquarie	Benham, 1922
Nototheniidae: Notothenia rossi Richardson	P. tuberculato-spinosus	S. Georgia	Stephen, 1941
Zoarcidae (Eel pouts): Zoarces viviparus (L.)	P. caudatus	Denmark	Blegvad, 1917
Lycodes endopleurostictus Jensen	"	Ireland	Wesenberg-Lund, 1937a
	"	Greenland	Wesenberg-Lund, 1930
Pleuronectidae (Flatfishes): Pleuronectes platessa (L.)	P. caudatus	Ireland	Southern, 1913a
	"	Scotland	Stephen, 1934
	"	Iceland	Wesenberg-Lund, 1937a
	"	Denmark	Blegvad, 1917; Mus. Copenhagen
	"	Baltic Sea	Hertling, 1928
	H. spinulosus	Baltic Sea	Blegvad, 1917; Hertling, 1928
Pleuronectes flesus L.	P. caudatus	Baltic Sea	Hertling, 1928
	H. spinulosus	Baltic Sea	Hertling, 1928
Limanda limanda (L.)	P. caudatus	Ireland	Southern, 1913a
	"	Iceland	Wesenberg-Lund, 1937a
	"	Denmark	Blegvad, 1917
	"	Baltic Sea	Hertling, 1928
	"	Greenland	Wesenberg-Lund, 1930
	H. spinulosus	Baltic Sea	Hertling, 1928
Hippoglossoides platessoides (Fabricius)	P. bicaudatus	Norwegian Sea	Mus. Bergen
Platichthys stellatus (Pallas)	P. caudatus	Alaska	Chamberlin, 1920
Phocidae (Seals): Erignathus barbatus (Erxleben)	P. caudatus	Greenland	Mus. London
Odobenidae (Walrusses): Odobenus rosmarus (L.)	P. caudatus	Greenland	Stimpson, 1864
	"	Spitsbergen	Théel, 1906

3.2.8 Communities

Probably most species of the Priapulida are not restricted in their occurrence to certain bottom communities. However, locally they may show definite preferences. It would be interesting to know more about this, but until now only very few observations are available.

Priapulus caudatus undoubtedly occurs in many different bottom communities. According to Spärck (1937) it prefers the *Macoma calcarea* community in Icelandic waters. This community has a wide distribution in arctic and boreal coastal waters. *P. caudatus* will certainly be found in it in other areas too.

According to Estcourt (1967) *Priapulopsis australis* is a characterizing species of the *Asychis-Echinocardium-Amphiura* association in New Zealand waters. This community of soft muddy bottoms in coastal waters can be compared with the northern *Maldane sarsi-Ophiura sarsi* community in which *Priapulopsis bicaudatus* may well occur although this has never been stated in the literature.

Halicryptus spinulosus occurs in the *Macoma baltica* community in the Baltic Sea (Hertling, 1928). According to Spärck (1937) and Thorson (1957) it is a characterizing species of the *Pontoporeia* community, one of the boreo-arctic amphipod communities, occurring on silty bottoms with more or less sand in brackish water.

3.3 THEORETICAL ZOOGEOGRAPHY

In most textbooks and treatises on marine zoogeography one or more priapulids are mentioned. In the first place the distribution of *Priapulus* is often used to demonstrate bipolar distribution. Secondly the distribution of *Halicryptus spinulosus* is frequently presented as an example of a typical marine-glacial relict distribution. General discussions of these topics can be found in the literature (e.g., Ekman, 1935; Hedgpeth, 1957; De Lattin, 1967). I confine myself to an evaluation of the known facts only as far as priapulids are concerned.

3.3.1 Bipolarity

Several animal taxa show a bipolar distribution. There are three theories to explain such a distribution pattern (Stiasny, 1935): (1) Relict theory: the warmer regions were once much cooler than they are now. (2) Migration theory I: the animals migrated through the deep sea in southern or northern direction. (3) Migration theory II: the animals were once adapted to warm water, but competition has driven them to the cold regions.

The distribution of the genus *Priapulus* has always been considered one of the best examples of bipolarity. However, recent discoveries have shown that *Priapulus* probably has a world-wide distribution in cold water. There are now several records from the deep sea (fig. 88) and a few isolated finds in rather warm water (Brasil; Mediterranean; California) are also indicative of this fact (see also p. 50-51).

However, zoogeographers can still use the distribution of the genus *Priapulopsis* as an example. The species of this genus have never been found at abyssal depths and the fact that the two species clearly differ in several aspects indicates that they possibly have been isolated for a long time already. Perhaps migration theory I gives the best explanation in this case, given the facts that probably there has always been an area with warm water and that there is no indication that these animals ever have occurred in warm water. *Priapulopsis bicaudatus* has often been found at bathyal depths, so one can easily imagine a migration through the bathyal zone of the tropics.

The tropical regions form an effective barrier for shallow-water species as is shown by the fact that *Halicryptus* has no representative on the southern hemisphere.

3.3.2 Relict distribution

One can speak of a relict distribution when a taxon occurs in isolated areas forming the remnants of a once wider distribution range. In the case of glacial relicts isolated populations are supposed to form the remnants of a wider distribution range in a period when the cold, arctic water extended farther south; they could survive for some special reason.

Halicryptus spinulosus in the Baltic Sea is a famous example of a marine-glacial relict. It is usually ranked among the animals occurring in the Arctic Ocean and being euryhalinous there, that entered the Baltic Sea when the Kattegat had an arctic fauna and that could survive there because they became adapted to brackish-water conditions (Segerstråle, 1957; Arndt, 1964). However, it is questionable whether this view is correct.

The post-glacial history of the Baltic Sea can be summarized as follows (De Lattin, 1967; Segerstråle, 1957):

- 15.000 B.C. : End of last glaciation.
- 15.000-7.500 B.C.: Baltic Ice Lake with fresh water.
- 7.500-7.000 B.C.: *Yoldia Sea*, with subarctic-boreal marine fauna.
- 7.000-5.000 B.C.: *Ancylus Lake*, with boreal fresh-water fauna.
- from 5.000 B.C.: *Littorina Sea*, with boreal brackish-water fauna, gradually becoming slightly warmer and more brackish until the present situation (*Lymnaea Sea*) was reached.

The brackish-water animals were certainly absent in the *Ancylus* period. Therefore, the term glacial relict is certainly incorrect, as was already remarked by De Lattin (1967: 140): the relicts in question originate from post-glacial times. Segerstråle (1957) used the term *Yoldia*-relicts, supposing that the animals could survive in the Kattegat during the *Ancylus* period.

Important is that the animals were supposed to be primarily arctic, marine animals that could survive because they became adapted to brackish water. In the case of *Halicryptus spinulosus* this is probably not true. This species indeed has a wide distribution in arctic regions, but in the first place it also occurs in the boreal zone (western Alaska, Iceland, ?Scotland, Norway, northern Russia) and in the second place it has never been found with certainty in a typical marine environment (see p. 70).

From a strictly physiological point of view *Halicryptus spinulosus* is not a genuine brackish-water animal (it has occasionally been found in water with a high salinity, even in hypersaline water), but nevertheless it is practically restricted to brackish water; perhaps because competition is too strong in marine environments. From an ecological point of view *Halicryptus* does not have a relict distribution. It has a scattered distribution simply because suitable habitats are not present everywhere. Moreover, in the present time the Baltic Sea in fact forms the main area; elsewhere it has a more scattered distribution in estuaries, coastal lakes, and lagoons.

It is clear that it is incorrect to consider *Halicryptus spinulosus* a marine-glacial relict in the Baltic Sea: (1) It is not a typically marine animal. (2) It entered the Baltic Sea in post-glacial times. (3) It is not a relict.

The seemingly isolated populations of *Priapulus caudatus* (California; Mediterranean) and *Priapulus tuberculatospinosus* (Brasil) are probably connected with the main area through the deep sea, but it is not impossible that the genus *Priapulopsis* has a relict distribution, the two species occurring in three isolated areas (see p. 58).

3.3.3 Concluding remarks

The distribution of the Priapulidae is mainly determined by ecological factors. Of course they need sediments in which they can dig, but these are present everywhere; the same holds for suitable preys. In my opinion the main reason why Priapulidae do not occur everywhere is that these "primitive" animals cannot withstand strong competition. The reason that they survived nevertheless is that they can live in marginal biotopes: they can withstand low oxygen contents in the water, hydrogen sulphide poisoning, low salinities (*Priapulus*; *Halicryptus*), considerable fluctuations in salinity (*Halicryptus*), low temperatures, and high hydrostatic pressure in the deep

sea (*Priapulus*, *Priapulopsis*); moreover, they can do without food for a long time. The facts that they produce large numbers of eggs and that the larvae are protected by a resistant lorica are also of survival value.

Historical factors have been of minor importance, at least in recent times, probably because evolution is extremely slow. Perhaps historical events have caused the isolation of the Japanese *Priapulopsis bicaudatus* and of *Priapulopsis australis*.

As yet it is of no use to discuss the position of *Tubiluchus* from a zoogeographical point of view.

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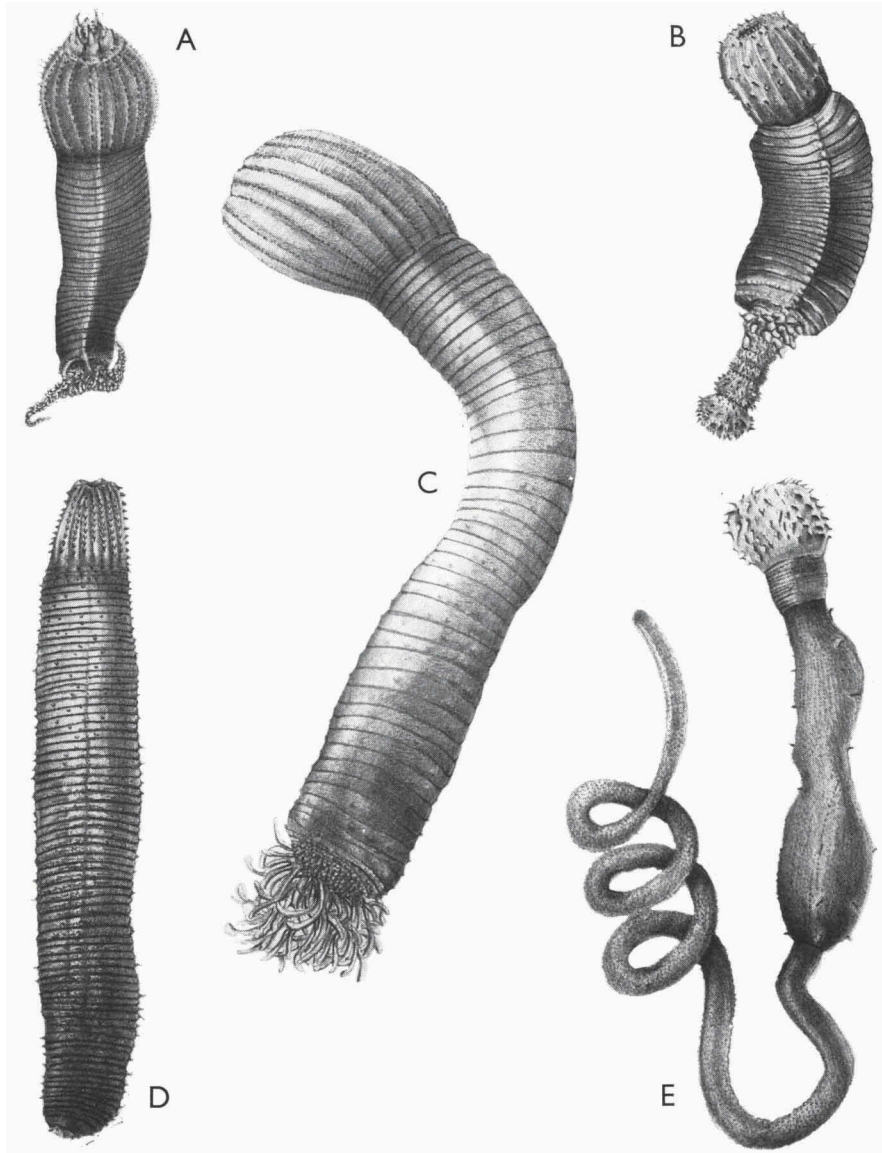
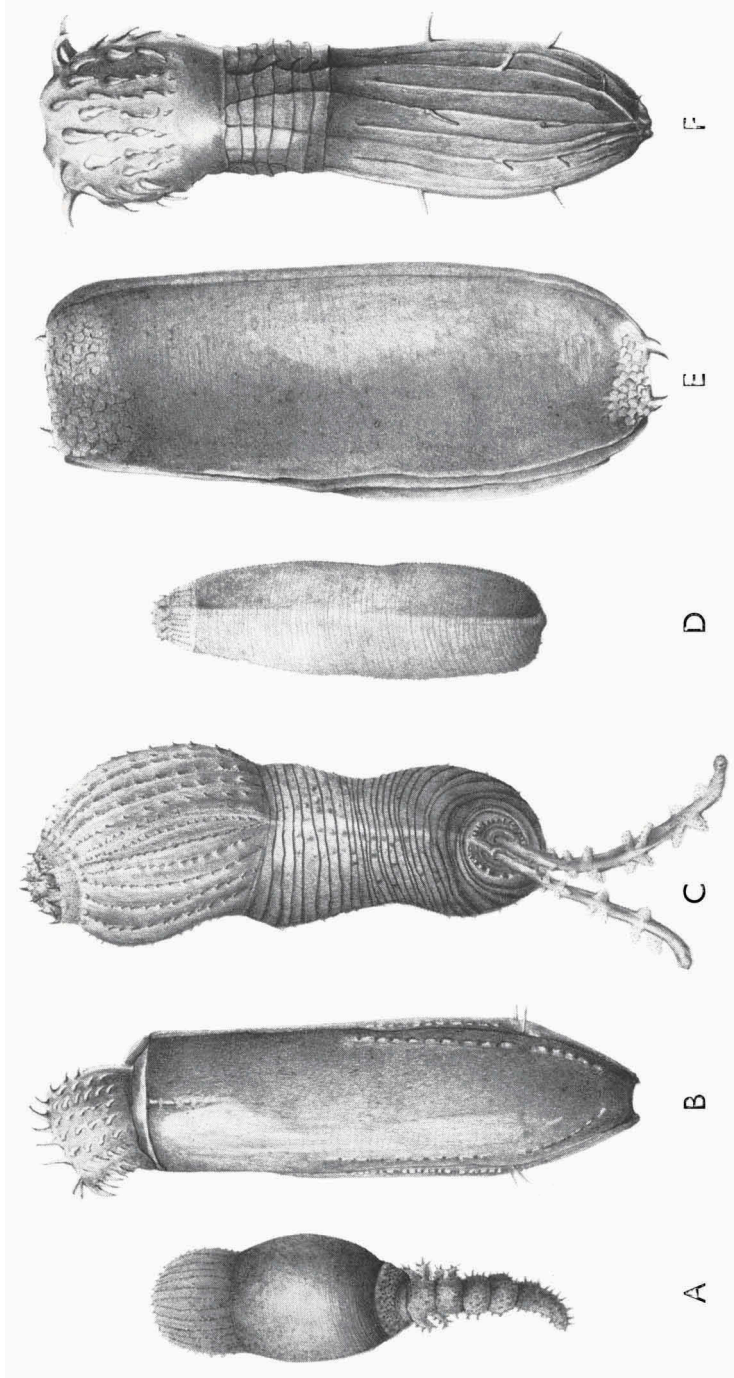
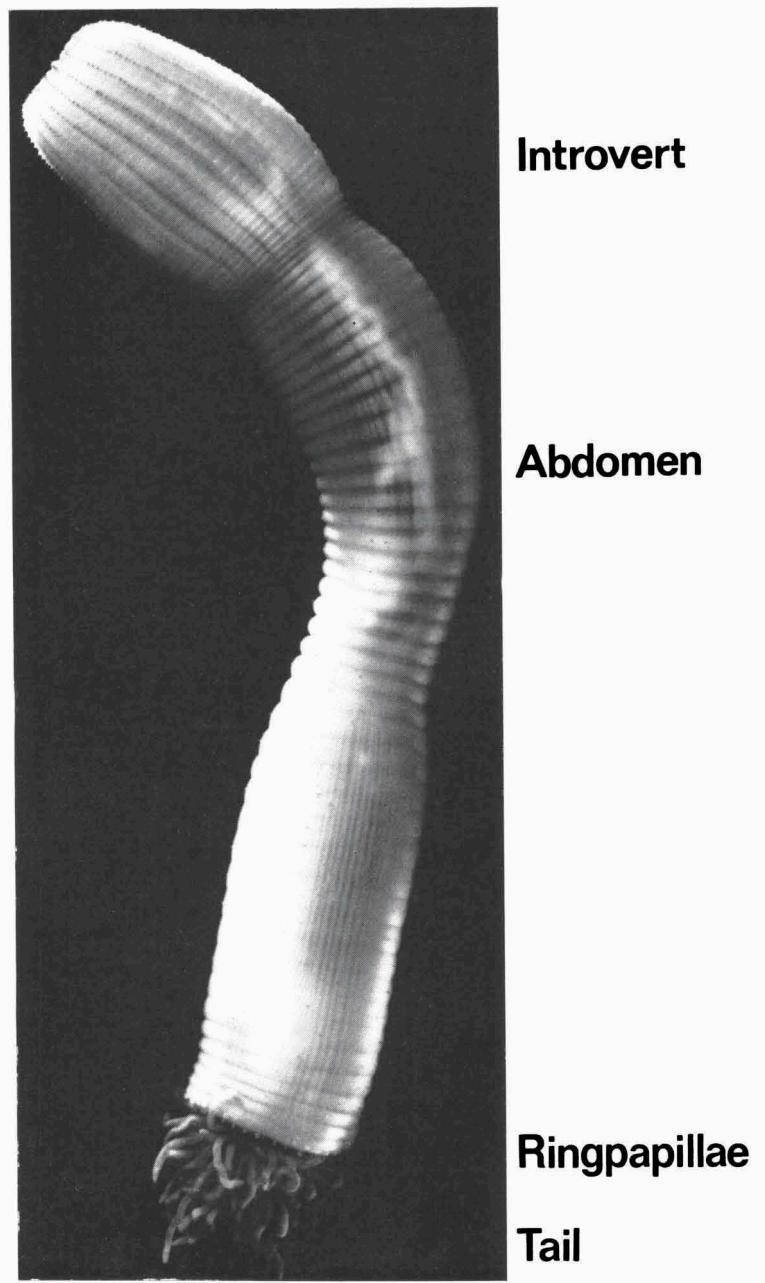


Plate 1

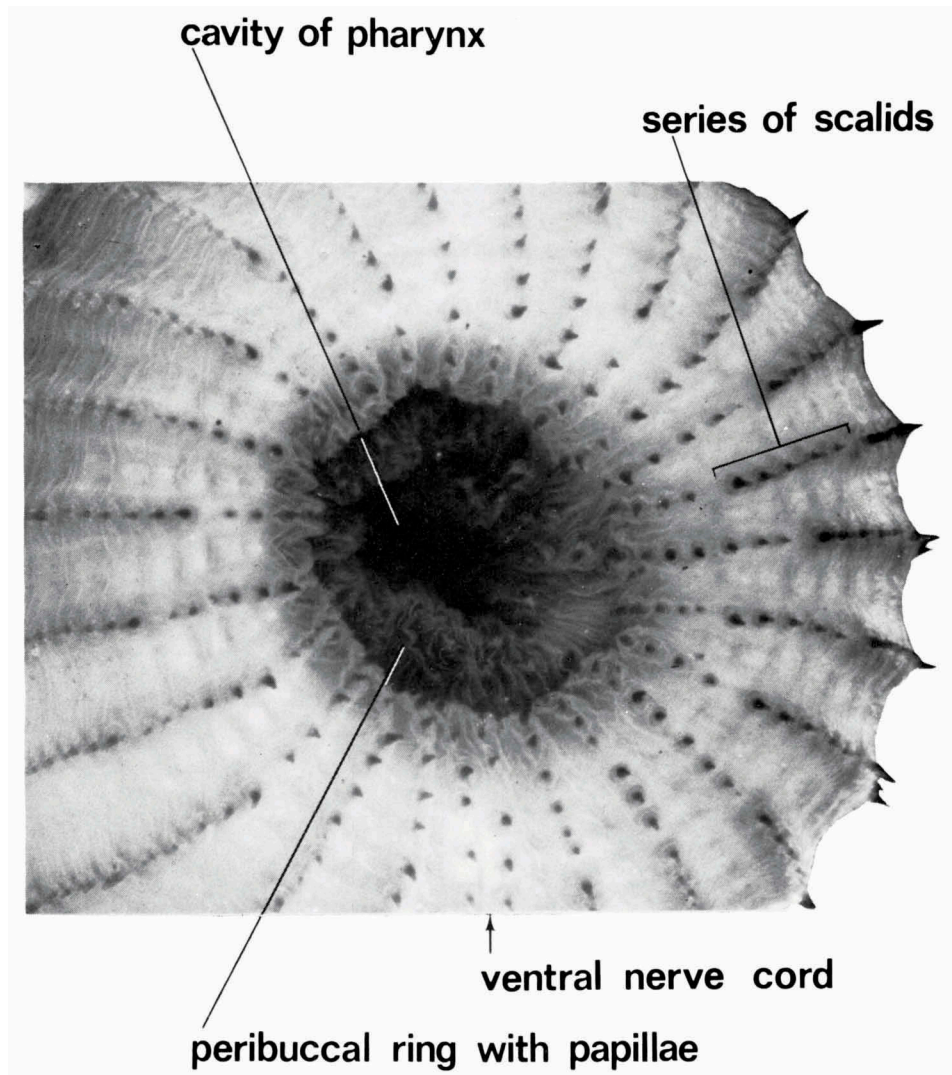
Representatives of the five known genera of the Priapulida. A, *Priapulopsis bicaudatus*, 25 mm long, contracted, pharynx protruded; Greenland (Mus. Stockholm 106). B, *Acanthopriapulus horridus*, about 6 mm long, contracted; off Uruguay (after Théel, 1911). C, *Priapulus caudatus*, about 120 mm long, relaxed, after photograph of living specimen; Öresund (Mus. Leiden 7211). D, *Halicryptus spinulosus*, 40 mm long, extended; Sweden (Mus. Stockholm). E, *Tubiluchus corallicola*, body about 1.8 mm long, extended; Curaçao (after Van der Land, 1968)



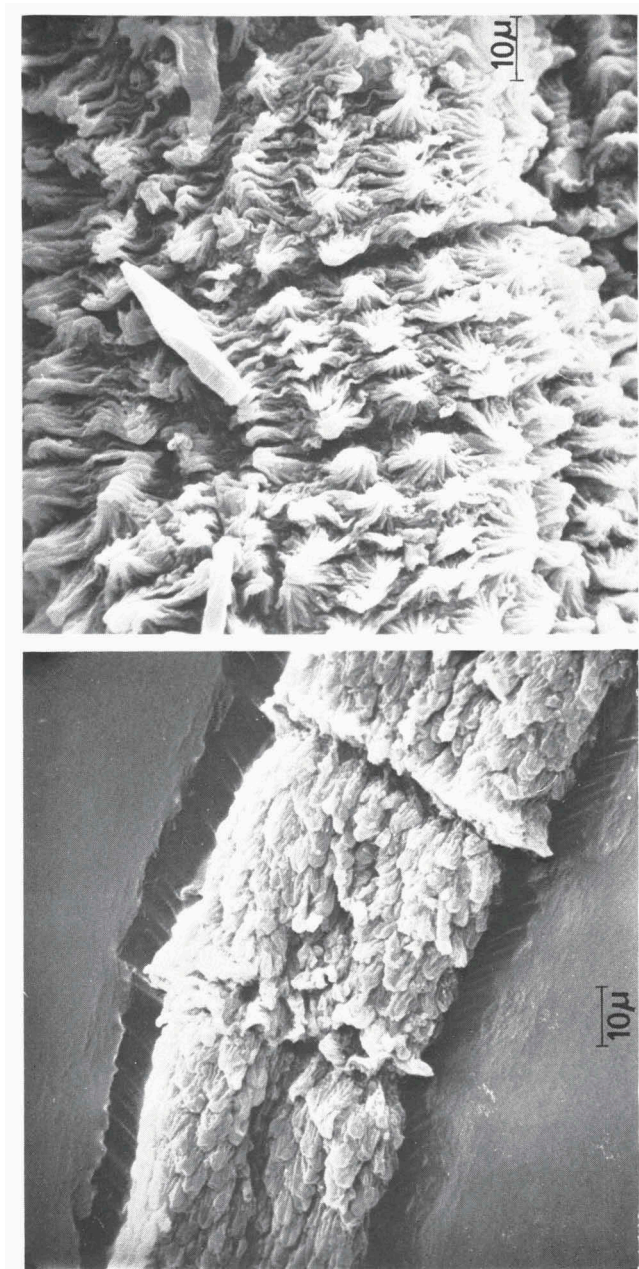
Larvae and postlarvae. A, B, *Priapulius caudatus*, A, 5 mm long, strongly contracted; Denmark (Helsingør Lab. 336). B, 1.5 mm long, introvert partially protruded; Öresund (Mus. Leiden 7212). C, *Priapulopsis bicaudatus*, 16 mm long, contracted, pharynx protruded; Greenland (Mus. Copenhagen). D, E, *Halicryptus spinulosus*. D, 10 mm long, contracted, pharynx protruded; Baltic Sea (Mus. Stockholm 186). E, 1.6 mm long, introvert entirely withdrawn; Sweden (Mus. Leiden 7215). F, *Tubiluchus corallicola*, 0.7 mm long, extended; Curaçao (after Van der Land, 1968).



Priapulus caudatus, large, living specimen, in relaxed condition; Öresund (Mus. Leiden 7212).



Priapulus caudatus, mouth of large, living specimen, relaxed (note that the pharynx and the buccal ring are both completely withdrawn in this condition); Öresund (Mus. Leiden 7212).



Tubiuchus coralicola, tumuli of abdomen (top) and detail of tail (bottom), Curaçao; scanning electron micrographs, copyright British Museum (Natural History), London.