

Taxonomic Revision of the Marine Genera *Bathydrilus* Cook and *Macroseta* Erséus (Oligochaeta, Tubificidae), with Descriptions of Six New Species and Subspecies

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Macroseta Erséus, 1975 is considered a junior synonym to *Bathydrilus* Cook, 1970 after examination of the type material of *B. asymmetricus* Cook, 1970. *Bathydrilus* is defined mainly by its organization of the male duct: vas deferens entering ectal half of atrium, one prostate gland attached to ectal part of atrium, near entrance of vas deferens, another prostate attached to apical, ental end of atrium. *B. atlanticus* sp.n., *B. hadalis* sp.n., *B. meridianus* sp.n., *B. graciliatriatus* sp.n. and *B. longus* sp.n. are described from specimens collected from various parts of the world; most of the species are deep-sea forms. *Phalodrilus rohdei* Jamieson, 1977 and *Phalodrilus adriaticus* Hrabě, 1971 are transferred to *Bathydrilus*, and a Caribbean/Bermudian form is described as *B. adriaticus trisetosus* subsp.n. The taxonomy and morphology of the different species, including *B. rarisetis* (Erséus, 1975) comb.n., are discussed. *Bathydrilus* is included in the sub-family Phalodrilinae. It appears closely related to *Phalodrilus* Pierantoni, 1902, from which it is distinguished principally by differences in the relative positions of the vasa deferentia, the atria and the prostate glands.

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Introduction

Though being increasingly studied, marine Tubificidae are still only fragmentarily known. This holds true particularly for the deep-sea species, which have been studied in only a few systematic accounts (Cook 1969, 1970; Erséus 1978a).

Cook (1970) established the genus *Bathydrilus* for *B. asymmetricus* Cook, 1970, a tubificid found at stations of a deep-sea transect between Massachusetts, USA and Bermuda in the North-west Atlantic. According to Cook, the genital organs of *B. asymmetricus* are devoid of external prostate glands, which indicates relationship to *Clitellio* Savigny, 1820. A few years later (Erséus 1975a), another monotypic tubificid genus, *Macroseta*, was defined for the Norwegian species *M. rarisetis* Erséus, 1975. Two pairs of external prostates were noted for *Macroseta*, and the diffuse nature of the pair attached to the ectal part of the atria was considered as an indication of a possible relationship to *Rhyacodrilus* Bretscher, 1901.

Recently, when examining a collection of deep-sea Oligochaeta from the Rockall Trough, west of Scotland in the North-east Atlantic, I found two new species. Both possessed two pairs of prostates and apparently belong to the same genus as *Macroseta rarisetis*. However, one of these, here described as *Bathydrilus atlanticus* sp.n., showed a strong resemblance to *B. asymmetricus*. This made me suspect that prostates had been overlooked when *asymmetricus* was first described. This proved to be the case after examination of the type specimens of Cook's species borrowed from the U.S. National Museum of Natural History.

In this paper, a number of species within *Bathydrilus* are described from material from various parts of the world, and the genus *Macroseta* Erséus is proposed to be a junior synonym to *Bathydrilus* Cook, the definition of which is modified. This is the third contribution in a series of accounts on genera of the sub-family Phalodrilinae. Recently, the genera *Adelodrilus*, *Adelodriloides* (Erséus 1978a) and *Bacescuella* (Erséus 1978b) have been revised.

Material and methods

The tubificids studied in the present paper come from collections made by me and from material received for identification from marine benthic surveys in various geographical areas.

Material of *Bathydrilus adriaticus trisetosus* subsp.n. was collected during periods at the Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA and at the Bermuda Biological Station for Research, Bermuda. *Bathydrilus* sp. was found when studying oligochaetes at the Duke University Marine Laboratory, Beaufort, North Carolina, USA. The specimens of *Bathydrilus rarisetis* comb.n. were taken during stays at different Norwegian marine laboratories: the Institute of Marine Biology of the University of Bergen, Espesgrend, Bergen, and the Biological Stations in Trondheim and Tromsø. Specimens of *Bathydrilus adriaticus* were collected during a visit to Reparto di Ecologia Marina della Stazione Zoologica di Napoli, Ischia, at Naples, Italy. The tubificids were all sorted out from sieved fractions of subtidal sands taken predominantly with various dredges. The animals were fixed in Bouin's fluid. Some specimens were sectioned and stained in Heidenhain's haematoxylin and eosin. The remaining worms were stained in paracarmine and mounted whole in Canada balsam.

One individual of *Bathydrilus asymmetricus* was obtained from deep-sea collections of Dr H. L. Sanders and Dr R. R. Hessler at

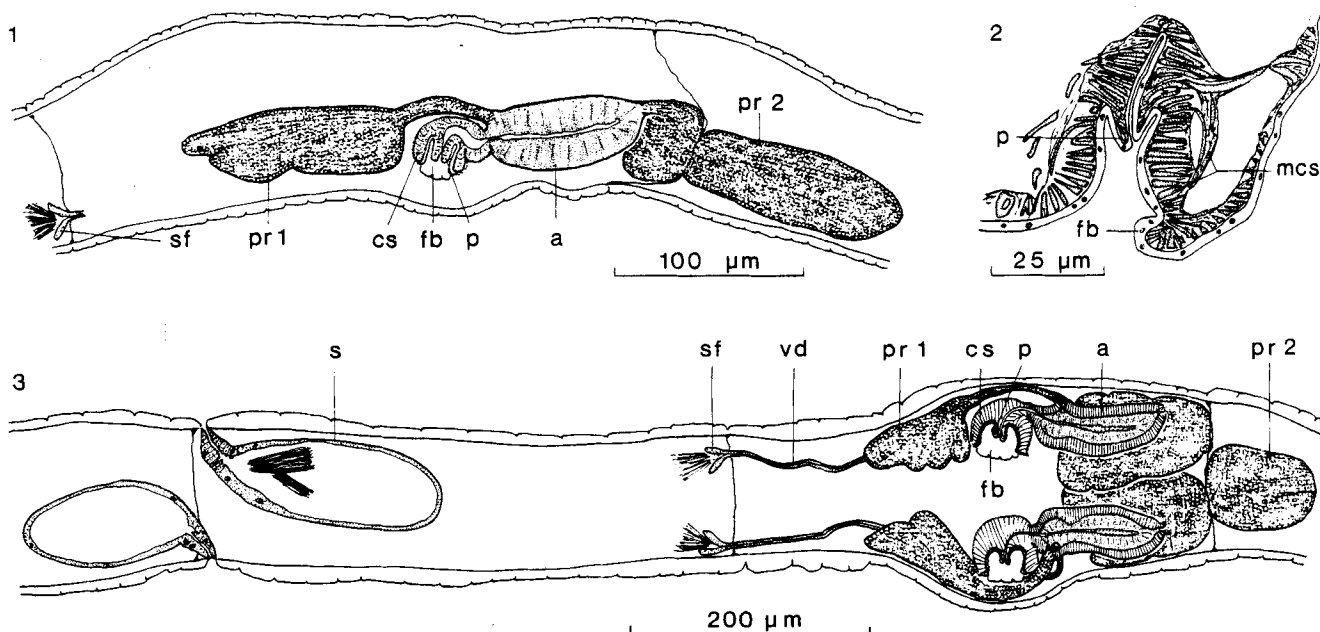


Fig. 1-3. — 1. *Bathydriulus asymmetricus* Cook; lateral view of male genitalia in segment XI of holotype specimen. — 2, 3. *B. atlanticus*

sp.n. 2, transversal section through copulatory sac and penis; 3, horizontal view of genital organs in segments X and XI.

the Woods Hole Oceanographic Institution (WHOI), Woods Hole, Massachusetts, USA. *Bathydriulus atlanticus* sp.n. and *B. graciliatriatus* sp.n. were sorted from deep-sea samples taken on cruises on R.R.S. *Challenger*, made in the Rockall Trough by Dr J. D. Gage, Dunstaffnage Marine Research Laboratory, Oban, Scotland. One specimen of *B. atlanticus* was also found in the material from WHOI. The material of *B. hadalis* sp.n. from the Aleutian Trench, North Pacific Ocean, was sent to me by the courtesy of Dr P. Jumars, Department of Oceanography, University of Washington, Seattle, Washington, USA and Dr G. D. Wilson, Scripps Institution of Oceanography, University of California, La Jolla, California, USA. *Bathydriulus meridianus* sp.n. was sorted by the Centre National de Tri d'Océanographie Biologique, Brest, France, the material being obtained on cruise MD 08 on R.V. *Marion Dufresne* in the South Indian Ocean ("Zone CROZET"). The material of *Bathydriulus longus* sp.n. was found in oligochaete collections from the continental shelf off of New Jersey, eastern USA, made by staff at the Virginia Institute of Marine Science, Gloucester Pt., Virginia (Dr D. Boesch, principal investigator). The methods used for the collection of some of these different materials are described by Sanders, Hessler & Sampson (1965), Jumars & Hessler (1976) and Gage (1977).

Type specimens of *Bathydriulus asymmetricus* Cook, 1970 and *Phalldriulus rohdei* Jamieson, 1977 were placed at my disposal from the U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. and from British Museum (Natural History) (BMNH), London, respectively. Prof. Dr S. Hrabě, Brno, Czechoslovakia, kindly sent me some specimens of *Phalldriulus adriaticus* Hrabě, 1971.

Type materials of the new species and subspecies described in this paper are deposited at USNM (*hadalis* sp.n., *longus* sp.n., *adriaticus trisetosus* subsp.n.), at BMNH (*atlanticus* sp.n., *graciliatriatus* sp.n.), and at the Museum National d'Histoire Naturelle (MNHN), Paris (*meridianus* sp.n.).

The species

Bathydriulus asymmetricus Cook, 1970 (Fig. 1)

Bathydriulus asymmetricus Cook, 1970, pp. 974-976, fig. 1.

Type material. USNM 42024-42025.

Type locality. NW Atlantic, 39°43.2' N, 70°37.8' W, 2 000 m.

New material studied (deposited at USNM). One whole-mounted specimen from WHOI Sta. 73: S of Massachusetts, NW Atlantic, 39°46.5' N, 70°43.3' W, 1 330-1 470 m (Aug. 25, 1964).

Remarks. A careful description of the two type specimens was given by Cook (1970), but it has to be supplemented with respect to some details in the male genital system. Cook did not note any external prostate glands in *B. asymmetricus*. In the types, however, there are two large and distinct prostates attached to each atrium, as shown for the holotype in Fig. 1. One gland (*pr 1*) is situated anterior to the male opening, and it is connected by a long, narrow stalk with the ectal end of the atrial ampulla (*a*). The posterior prostate (*pr 2*), which discharges its secretion into the apical, ental end of the atrium, extends into segment XII.

The new specimen from WHOI lacks its posterior end, and it is contracted and coiled, but its morphology conforms well to the description of *B. asymmetricus*.

Habitat. Bathyal fine sediments. Found at depths ranging from 1 330 to 2 000 metres.

Distribution. Known only from three deep-sea stations near Massachusetts, NW Atlantic.

Bathydriulus atlanticus sp.n. (Figs. 2-3)

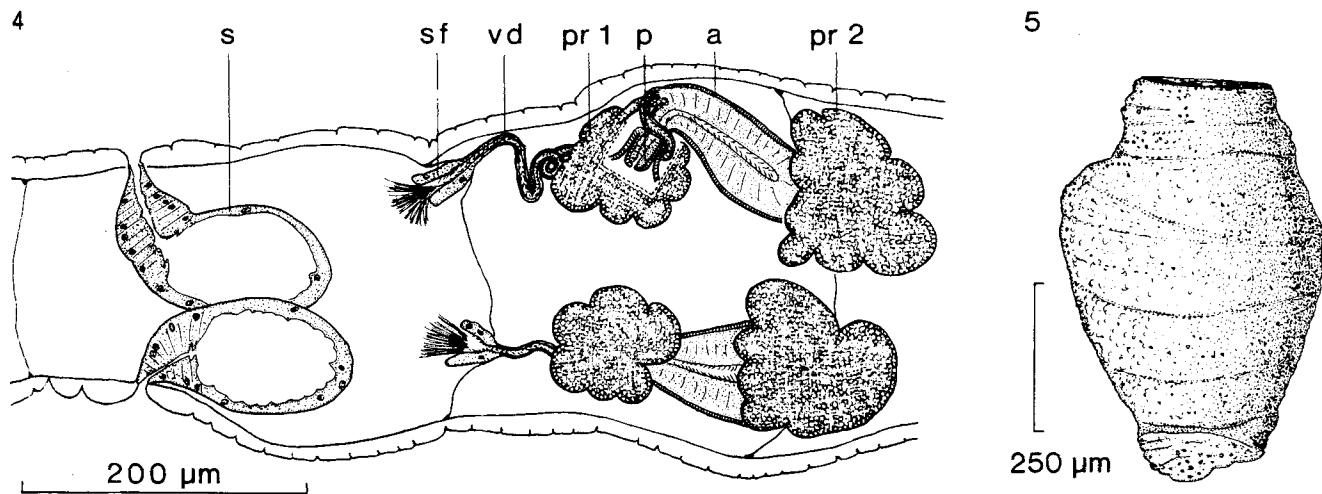
Holotype. BMNH 1978.27.1, whole-mounted specimen.

Type locality. Northern Rockall Trough, NE Atlantic, 58°42' N, 09°43' W, about 1 800 m, hemipelagic ooze (sample taken on July 1, 1976).

Paratypes. BMNH 1978.27.2-7. One specimen from type locality, genital region being sectioned, the rest being whole-mounted. One whole-mounted specimen from Barra Fan (Hebridean slope), Rockall Trough, 56°39' N, 09°40' W, about 1 600 m, hemipelagic ooze (June 26, 1976). One whole-mounted specimen from Southern Rockall Trough, 54°41' N, 12°17' W, about 2 880 m, hemipelagic ooze (June 21, 1976).

Other material examined (deposited at USNM). One whole-mounted specimen from WHOI Sta. G No. 6: S of Massachusetts, NW Atlantic, 39°39.5' N, 70°43.0' W, 2 151 m (Sept. 6, 1962).

Description. Length more than 5.8 mm (only fragments available), more than 20 segments. Diameter in whole-mounted, slightly compressed specimens: 0.12-0.17 mm anteriorly, 0.18-0.20 mm at clitellum, 0.11-0.14 mm posteriorly. Prostomium rounded or pointedly triangular, with a small sa-



Figs 4–5. — 4. *Bathydrilus hadalis* sp.n., horizontal view of genital organs in segments X and XI. Parts of the right-side anterior pro-

state (*pr 1*) is removed to show underlying copulatory organ (*p*). — 5. Tubificid cocoon from hadal sample of Aleutian Trench.

lence apically. Secondary annulations absent. Clitellum poorly developed. Setae all bifid, with teeth almost equal in length. Setae 40–55 μm long, about 1 μm thick. Setae 2–3 (occasionally 4) per bundle anteriorly, 2–3 (occasionally 1) per bundle posteriorly, but absent both ventrally and dorsally in segment XI. Modified genital setae absent. Male pores paired, located on roundish protuberances in line with ventral setae in middle of XI. Each pore is partly covered by a papilla (Figs. 2–3, *fb*) formed by a fold of the body wall, giving the opening a horseshoe-like appearance. Spermathecal pores paired or, in two of the studied specimens, unpaired, located laterally near intersegmental furrow IX/X (cf. fig. 3).

Pharyngeal glands not observed. Chloragogen cells scarce or absent. Male genitalia (all structures paired) (Fig. 3): vas deferens (*vd*) inconspicuous, longer than atrium and about 4–5 μm in diameter, joining ectal end of atrium; atrium (*a*) spindle-shaped to oval, 100–115 μm long, 40–50 μm wide, generally with a slight constriction slightly proximal to entrance of vas deferens; atrium with 7–12 μm thick outer layer of spirally arranged muscles, and inner lining granulated epithelium, leaving a narrow ciliated lumen only; atrium ectally terminating in narrow duct, about 50 μm long, leading to small copulatory organ (Figs. 2–3, *p*) (see remarks below) enclosed in a muscular copulatory sac (*cs*); a large prostate gland (*pr 1*) attached by long stalk to atrium near entrance of vas deferens; a second, very large prostate (*pr 2*) attached to apical, ental end of atrium; the posterior prostate often extends into segment XII. Spermathecae (Fig. 3, *s*) sacciform with indistinct ducts. When two spermathecae are present (cf. above), one is located in X, the other is extending with its ampulla into IX. Sperm generally in distinct bundles in spermatheca, with spermatozoa oriented parallel to the long axis of the bundle.

Remarks. Only fragments of this species are available. The longest piece, the holotype, is 5.8 mm long, and it includes segments V to XX.

I find it difficult to decide whether the copulatory organ of *B. atlanticus* should be termed a penis or a pseudopenis. There appears to be a permanent fold of the copulatory sac around the opening of the male duct, as is shown in Figs. 2–3. This speaks in favour of the term “penis”. At copulation,

however, most of the copulatory sac is probably everted, and, therefore, “pseudopenis” might be as appropriate as “penis” (cf. Discussion).

Habitat. Lower continental slope and upper abyssal rise soft sediments. Depth range at least 1600–2880 m.

Distribution. Known from both the NE and the NW Atlantic.

***Bathydrilus hadalis* sp.n. (Fig. 4)**

Holotype. USNM 55692, three whole-mounted fragments of one specimen (cf. remarks below).

Type locality. Aleutian Trench, N Pacific, 50°58.0' N, 171°37.5' W, 7298 m, top 0–3 cm of soft bottom sediment (sample taken in July, 1970) (cf. Jumars & Hessler 1976).

Description. Length 9.8 mm, 32 segments (cf. remarks). Diameter in whole-mounted, slightly compressed specimen: 0.19 mm anteriorly, 0.28 mm at clitellum, 0.15 mm posteriorly. Prostomium pointedly triangular, about as long as its width at peristomium, with small salience apically. Clitellum poorly developed. Secondary annulations present in segment II–IV, but they are probably due to contractions in the anterior end of the worm. Setae all bifid, with teeth almost equal in length, upper tooth being slightly thinner than lower. Setae 70–75 μm long, about 2 μm thick. Setae 2–4 per bundle anteriorly, 2 per bundle posteriorly. Ventral setae of XI absent. Modified genital setae absent. Male pores paired, located within circular ridges forming protuberances in line with ventral setae, slightly anterior to placement of dorsal setae in segment XI. Each pore partly covered by a lateral fold of the body wall. Spermathecal pores paired, located laterally in anterior portion of X, at some distance from intersegmental furrow IX/X (cf. Fig. 4).

Pharyngeal glands not observed. Chloragogen cells present in thin layer covering alimentary canal. Male genitalia (all structures paired) (Fig. 4): vas deferens (*vd*) inconspicuous, longer than atrium, entering ectal end of atrium; atrium (*a*) ovoid to spindle-shaped, about 140 μm long, 50–55 μm wide, with about 3 μm thick outer, muscular lining, and thick inner ciliated and granulated epithelium, leaving narrow lumen only; atrium apparently terminating in penis-like structure (*p*), the shape and size of which could not be accurately seen in the available material: only its approximate appearance being depicted in Fig. 4; two large prostate glands at-

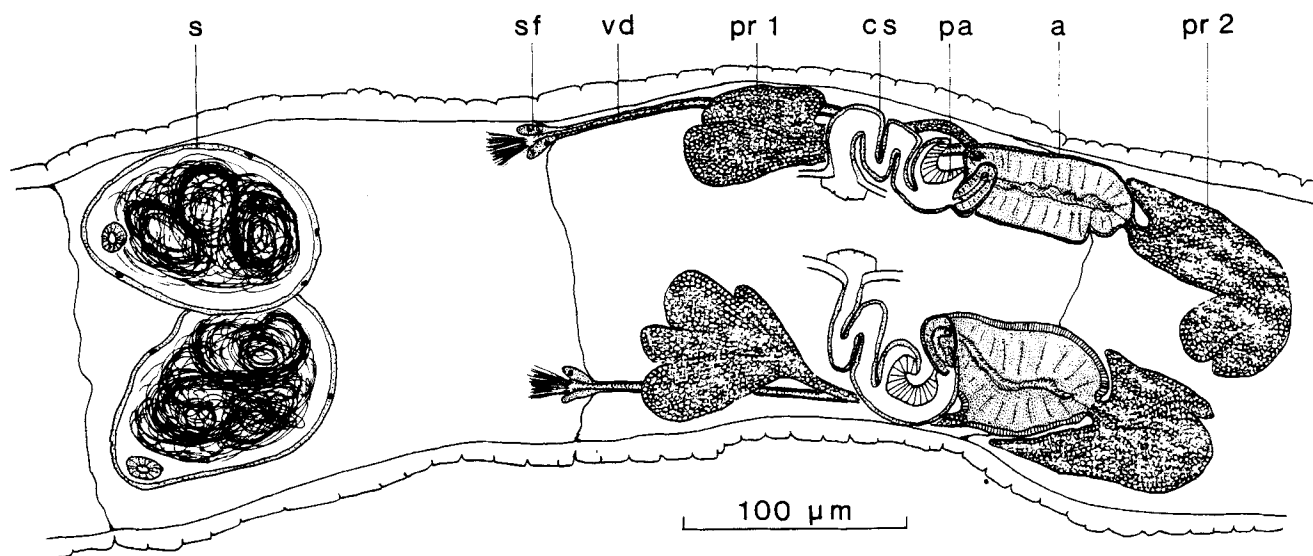


Fig. 6. *Bathydrius meridianus* sp.n., horizontal view of genital organs in segments X and XI.

tached to atrium, one (*pr 1*) at ectal end, near junction with vas deferens, one (*pr 2*) at apical, ental end, which points into most anterior portion of XII. Spermathecae (Fig. 4, *s*) ovoid, ampullae 120–125 μm long, 75–80 μm wide, ducts, 40–50 μm long, not clearly set off from ampullae. No sperm in spermathecae of the available specimen.

Remarks. In the material there are three fragments of this worm, one anterior piece including the genital region, one middle piece, and one posterior piece ending with the pygidium. Evidently these three pieces together make a complete worm, the length of which then becomes 9.8 mm, and which consists of 32 segments altogether. Some details in the genital system could not be satisfactorily studied in the available specimen: the description of which may have to be slightly supplemented by future studies on the species.

In addition to the three fragments comprising the holotype of *B. hadalis* sp.n., the material from the Aleutian Trench includes a sexually immature individual of a tubificid, but it is impossible to judge whether or not it belongs to the same species. This also applies to an oligochaete cocoon (Fig. 5) that was found in the same sample. The cocoon is urn-shaped and incrustated with sediment particles, the length being 670 μm , maximum diameter 430 μm . The cocoon was cut open and pieces of a tubificid embryo was taken out. The worm was probably very close to hatching, since its segmentation and setae were well developed. This noteworthy find indicates that hadal oligochaetes, of which *B. hadalis* is the only known species at present, reproduce in a way similar to what is known for their relatives in shallow marine, freshwater and terrestrial biotops (cf. Lasserre 1975).

Habitat. *B. hadalis* sp.n. is living in hadal soft bottom, being found at 7298 metres depth.

Distribution. Known only from the Aleutian Trench (N Pacific).

***Bathydrius meridianus* sp.n. (Fig. 6)**

Holotype. MNHN AP-446, whole-mounted specimen, with posterior-end missing.

Type locality. W of Iles aux Cochons, Crozet Islands, S Indian Ocean, 46°04.7' S, 49°19.0' E, 480–525 m, sand (April 18, 1976).

Description. Length more than 3.2 mm, more than 16 segments (no complete specimen available). Diameter in slightly compressed specimen: 0.13 mm in segment V, 0.17 mm at clitellum. Postomium rounded. Clitellum extending over $\frac{1}{2}$ X– $\frac{1}{2}$ XII. Secondary annulations absent. Setae bifid, upper tooth thinner and slightly shorter than lower. Setae about 50–55 μm long, about 2 μm thick. Setae 3 per bundle anteriorly, at and posterior to clitellum 2 per bundle. Ventral setae of XI absent. Modified genital setae absent. Male pores paired, located near mid-ventral line in posterior part of XI. Spermathecal pores paired, located dorso-laterally in anterior part of X, very near intersegmental furrow IX/X (cf. Fig. 6).

Pharyngeal glands extending into VII. Chloragogen cells present from VIII. Male genitalia (all structures paired) (Fig. 6): vas deferens (*vd*) straight and inconspicuous, about 6–7 μm wide, longer than atrium, joining ectal end of atrium; main portion of atrium (*a*) ovoid to spindle-shaped, 85–90 μm long, 40–55 μm wide, with 2–5 μm thick outer muscular lining, and thick inner granulated epithelium; ectal end of atrium narrowing and coiled, terminating in deep, folded copulatory sac (*cs*); besides the atrial opening, which is not a typical penis (cf. Discussion), the inner end of the sac contains a large papilla (*pa*) formed by a thickened fold of the wall of the sac; one lobed prostate gland (*pr 1*) situated anterior to copulatory sac, and it is connected with ectal end of atrium by long stalk; a second, large prostate (*pr 2*) located in XII and attached to ental end of atrium, which also points into XII. Spermathecae (Fig. 6, *s*) with inconspicuous ducts and large sacciform ampullae filled with random masses of sperm.

Habitat. Continental slope sand, about 500 metres depth.

Distribution. Known only from the type locality (S Indian Ocean).

***Bathydrius rarisetis* (Erséus, 1975) comb.n. (Fig. 7)**

Macroseta rarisetis Erséus, 1975a, pp. 4–5, fig. 2.

Macroseta rarisetis; Erséus, 1976, pp. 31–32.

Type material. Zoological Museum of the University of Bergen, Norway, 56877–56878.

Type locality. E of Børnestangen, Korsfjorden, western Norway, 60°12'10" N, 05°10'50" E, 40–80 m, coarse shell sand.

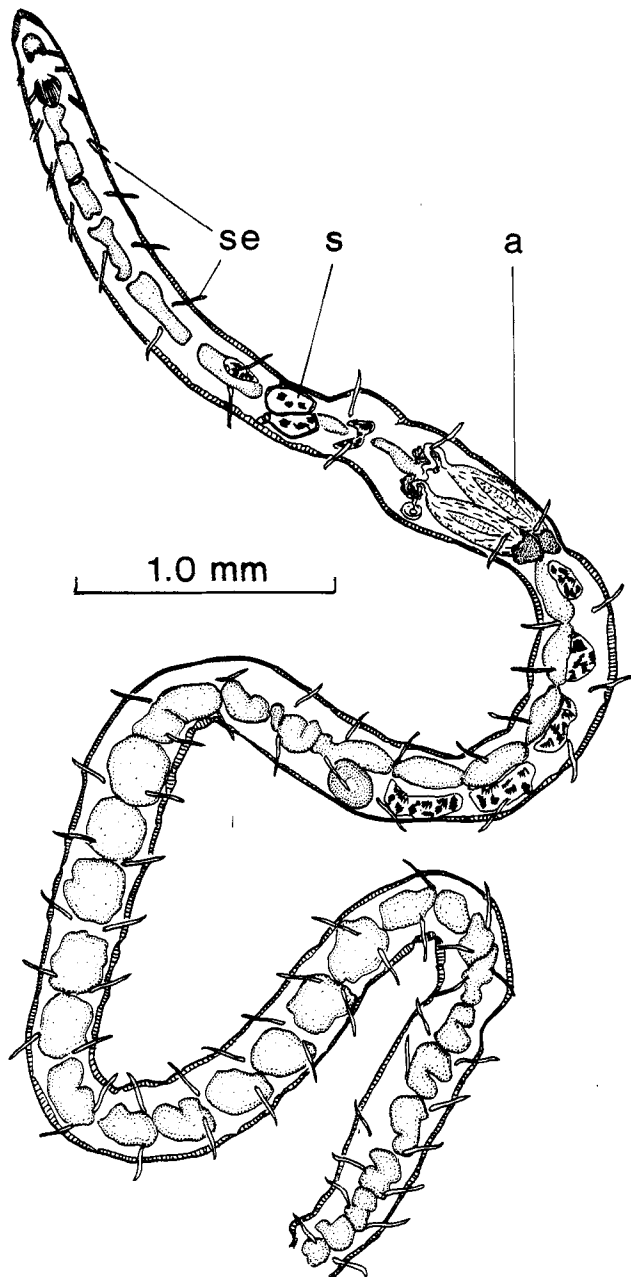


Fig. 7. *Bathydrilus rarisetis* (Erséus) comb.n., whole-mounted specimen, anterior end.

Material examined. From the Bergen area, Norway, see Erséus (1975a, 1976). New records: Tromsø area, northern Norway: Balsfjorden, W of Kuberg, 69°35.3' N, 18°55.0' E, 50–60 m, shells and shell gravel, two mature (one sectioned, one whole-mounted) and ten immature specimens (Aug. 5, 1975). Trondheimsfjorden, middle Norway: Rörviksgrund, NW of Tautra, 63°35.6' N, 10°32.0' E, 40–80 m, shell gravel and sand, with dead coral (*Lophelia*), nine mature and five immature specimens (all whole-mounted) (Aug. 2, 1976); SSE of Rödberg, 63°28.5' N, 09°43.6' E, 180–240 m, corals (living and dead *Lophelia* and *Paragorgia*), with some clay, one mature and four immature specimens (whole-mounted) (Aug. 4, 1976); at Gjetnes, 63°26.6' N, 09°59.4' E, 17–30 m, coarse sand, with stones, pebbles and shells, eight mature (one sectioned, seven whole-mounted) and five immature specimens (Aug. 4, 1976).

Remarks. This species was described as *Macroseta rarisetis* from the Bergen area, Norway (Erséus 1975a). When alive, the worms are characteristically transparent and iridescent, with large, single-pointed and straight setae, arranged in uni-

setal “bundles” in all parts of the body, except for the most anterior segments (cf. Fig. 7, *se*).

The new material of *B. rarisetis* comb.n. enables me to modify the original description (Erséus 1975a) with respect to the prostate glands. The anterior prostate attached to the ectal end of the atrial ampulla is not as diffuse as was said before: the prostate is lobed in its outline, but parallelly oriented strands of its tissue enter the atrium in a stalk-like structure, together with the vas deferens, the loops of which lie mixed with the lobes of the prostate (cf. op.cit., fig. 2).

The outer muscular layer of the spindle-shaped atria of *B. rarisetis* is extremely well developed (Erséus 1975a), the thickness being up to 45 μm . Ectally the atria narrow into long “ejaculatory ducts” (op. cit.), which terminate into “penes”. This terminology can be discussed, since the two are histologically continuous with the rest of the atrial structure, with the exception of the thick muscular layer around the atrial ampulla. The most ectal portion of the atrial duct, however, protrudes into a very small copulatory sac, and it most probably functions as a true penis (cf. Discussion).

One sexually mature specimen of *B. rarisetis* from the investigation on the Oligochaeta of the Bergen area (Erséus 1976, sta. 27) was found to possess two pairs of almost fully developed spermathecae. One pair is located in its normal position in segment X and the second pair is present in segment XI. The posterior spermathecae have their openings located near the intersegmental furrow X/XI. This arrangement is most probably abnormal: it has not been seen in any of the other specimens of this species studied from different localities.

Habitat. Subtidal coarse sand and gravel. Depth range 17–400 m.

Distribution. *B. rarisetis* appears common all along the Norwegian coast, including the most northern, sub-arctic regions.

Bathydrilus graciliatriatus sp.n. (Fig. 8)

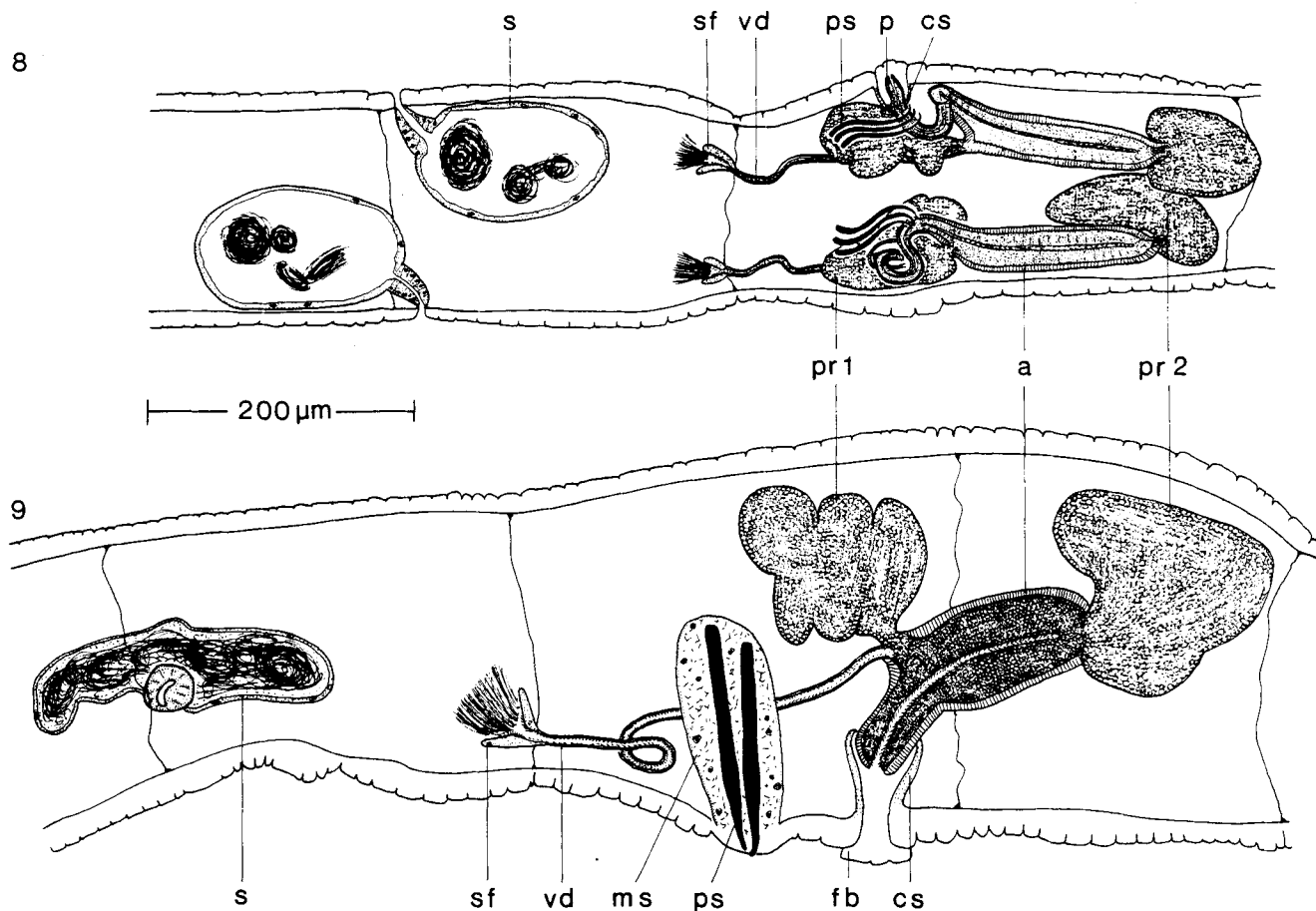
Holotype. BMNH 1978.27.8, whole-mounted specimen.

Type locality. Northern Rockall Trough, NE Atlantic, 58°42' N, 09°43' W, about 1 800 m, hemipelagic ooze (July 1, 1976).

Paratypes. BMNH 1978.27.9–16. Six whole-mounted specimens from the type locality. Two whole-mounted specimens from Barra Fan (Hebridean Slope), Rockall Trough, one being from 56°37' N, 10°12' W, about 1 800 m (June 25, 1976), the other from 56°39' N, 09°40' W, about 1 600 m (June 26, 1976).

Description. Length more than 4.5 mm, more than 23 segments (no complete specimen available). Diameter in slightly compressed specimens: 0.14–0.17 mm anteriorly, 0.16–0.22 mm at clitellum, 0.11–0.15 mm posteriorly. Prostomium rounded or pointedly triangular, generally slightly shorter than its width at peristomium. Apically the prostomium bears a small salience. Secondary annulations absent. Clitellum very poorly developed, even at full maturity. Anterior setae bifid, with upper tooth slightly shorter and thinner than lower. Posterior setae single-pointed. Setae 50–60 μm long, less than 2 μm thick, 3–4 (occasionally 2) per bundle anteriorly, 2 (occasionally 3) per bundle posteriorly. Ventral setae of XI modified into penial bundles, each of which contains 3 sigmoid, single-pointed setae (Fig. 8, *ps*), 70–80 μm long, entally about 3 μm thick, with ectal ends strongly curved and very thin. Penial setae situated together with paired male openings on small protuberances in line with ventral setae, slightly posterior to the middle of segment XI. Spermathecal pores paired, located laterally in anterior part of X, very near intersegmental furrow IX/X (cf. Fig. 8).

Pharyngeal glands extending into segment VII or VIII.



Figs 8–9. — 8. *Bathydrius graciliatriatus* sp.n., horizontal view of genital organs in segments X and XI. — 9. *B. longus* sp. n., lateral view of genital organs in segments X and XI.

Chloragogen cells covering alimentary canal in very thin layer from VIII. Male genitalia (all structures paired) (Fig. 8): vas deferens (*vd*) inconspicuous, probably slightly longer than atrium; main portion of atrium (*a*) slender and spindle-shaped, 160–200 μm long, 30–40 μm wide, with outer muscular layer about 4–5 μm thick, and thick inner granulated epithelium leaving almost no lumen open; atrium narrowing ectally, continuously terminating into long duct, about 10–15 μm wide, making at least one loop before ending in small penial structure (*p*), about 10 μm wide, and which is enclosed in small copulatory sac (*cs*); one irregular prostate gland (*pr 1*) attached to ectal end of main portion of atrium; one large prostate (*pr 2*) at apical, ental end of atrium, which extends into XII. Spermathecae (Fig. 8, *s*) with small indistinct ducts and large, sacciform ampullae. Spermathecal ampullae lying side by side in X of precopulatory specimens. In postcopulatory individuals generally one spermathecal ampulla is situated in IX, the other in X, and they contain roundish aggregates of sperm.

Remarks. Attempts at sectioning two additional specimens from the type locality were made. Because of the poor quality of the result no additional morphological information was gained.

The copulatory organ of *B. graciliatriatus* resembles the same structure in *B. rarisetis* (cf. remarks for the latter species).

Habitat. Bathyal fine sediments, known from 1600–1800 m.

Distribution. Known only from the Rockall Trough (NE Atlantic).

***Bathydrius longus* sp.n. (Fig. 9)**

Holotype. USNM 55693, whole-mounted specimen.

Type locality. Continental shelf off the coast of New Jersey, USA. NW Atlantic, 39°06.6' N, 72°59.0' W, 70 m, medium to coarse sand (material coll. on Aug. 23, 1976).

Paratypes. USNM 55694–55700 (on seven slides). Two specimens from the type locality; three specimens from 39°07.5' N, 72°48.9' W, 91 m, coarse sand (Aug. 22, 1976); one specimen from 38°44.7' N, 73°17.3' W, 76 m, medium sand (Nov. 11, 1976); six specimens from 38°44.8' N, 73°17.4' W, 79 m, medium sand (Nov. 11, 1976). All paratypes whole-mounted.

Description. Length (fixed specimens) 18–25 mm, 94–109 segments. Diameter in slightly compressed specimens: 0.17–0.26 mm anteriorly, 0.23–0.35 mm at clitellum, 0.14–0.26 mm posteriorly. Prostomium roundedly triangular, about as long as its width at peristomium. Secondary annulations absent. Clitellum extending over segments X to XII. Somatic setae all bifid, 50–70 μm long, about 4 μm thick, with upper tooth shorter and thinner than lower. Setae 2–3 per bundle anteriorly, 2 per bundle posteriorly. Ventral setae of XI modified into penial bundles, each of which contains 2 (occasionally 3) large, single-pointed and straight setae (Fig. 9, *ps*), 150–180 μm long, maximally 7–11.5 μm thick. Penial setae narrowing ectally, most ectal tip being slightly curved (in some specimens more strongly curved). Penial bundles enclosed in compact muscular sac (Fig. 9, *ms*). Ends of penial setae protruding out from a pair of ventral papillae anterior to male pores. The penial setae, as well as the papillae, are directed obliquely towards mid-dorsal line of body. Male

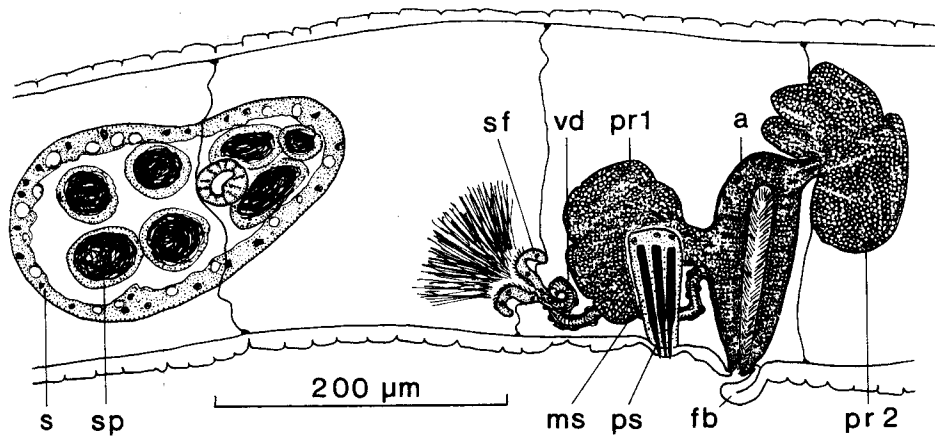


Fig. 10. *Bathyrilus adriaticus trisetosus* subsp.n., lateral view of genital organs in segments X and XI.

pores paired, located in line with ventral setae in posterior part of XI. Spermathecal pores paired, located laterally in X, very near intersegmental furrow IX/X (cf. Fig. 9).

Pharyngeal glands extending into segment VII (occasionally VIII). Chloragogen cells present from VIII. Male genitalia (all structures paired) (Fig. 9): vas deferens (*vd*) inconspicuous, 7–9 μm wide, longer than atrium, joining ectal part of atrium; atrium (*a*) more or less spindle-shaped, 185–250 μm long, 55–90 μm wide, with outer layer of muscles 5–7 μm thick, and inner well developed, granulated epithelium; ectally atrium narrowing and ending in a copulatory sac (*cs*), the opening of which is partly covered by a lateral fold of the body wall (*fb*); one lobed prostate (*pr 1*) attached by long stalk to atrium at entrance of vas deferens; a second, large prostate (*pr 2*) attached to apical, ental end of atrium, which is situated in segment XII. Spermathecae (Fig. 9, *s*) with short, indistinct ducts and sacciform, irregular ampullae. In many specimens the ampulla is elongated with the entrance of the duct at its middle portion. Generally at least one of the spermathecae extends into IX. Sperm in loose masses in spermathecae.

Remarks. This description is based upon 13 specimens. In 11 there are two setae in each penial bundle, in one individual there is one penial bundle with two setae and one with three setae. In one worm the penial setae are completely absent, though the muscular setal sacs and the setal papillae ventrally in XI (cf. Fig. 9) are present.

Habitat. Off-shore medium to coarse sand. Known depth range 70–91 m.

Distribution. Continental shelf off New Jersey, NW Atlantic.

Bathyrilus adriaticus (Hrabě, 1971) comb.n., polytypic species

Bathyrilus adriaticus adriaticus (Hrabě, 1971)

Phallodrilus adriaticus Hrabě, 1971, pp. 220–221, figs. 19–25.

Phallodrilus adriaticus; Cook & Hiltunen 1975, p. 936.

Phallodrilus adriaticus; Jamieson 1977, p. 340.

Type material. Hrabě collection.

Type locality. Maslinica, Šolta Island, Adriatic Sea, Yugoslavia, 0.5–0.7 m, sand under stones.

Material examined. From Hrabě's collection: three sectioned, mature specimens and a few whole-mounted, immature specimens, all from the Adriatic Sea. Author's collection: two whole-mounted specimens from the Bay of Naples, Italy: one from Lacco Ameno, Ischia, 40°45.5' N, 13°53.5' E, 32 m, muddy fine sand with *Posidonia* (sample taken by Dr J Ott, Vienna) (May 25, 1978); one from Ischia Porto, at entrance of harbour, 40°44'42" N, 13°56'40" E, about

0.2 m below low water mark, coarse sand with detritus between boulders (May 25, 1978).

Remarks. Hrabě (1971) gave a detailed description of the nominate form of *B. adriaticus* comb.n. under the name *Phallodrilus adriaticus*. According to Hrabě, the muscular layer of the atria of this form is "slender"; in the examined material from the Mediterranean the layer is only 1–2 μm thick.

The two specimens from Italy are slightly smaller than Hrabě's material, the only complete individual being about 7 mm long and consisting of 55 segments (Hrabě: about 10 mm, 67–86 segments). The penial setae are also smaller, only 67 μm long in the most developed specimen.

Habitat. Subtidal sands, depths ranging from 0.2 to 32 metres.

Distribution. Known from Yugoslavia (Hrabě 1971, 1975), and the Bay of Naples, Italy (new record).

Bathyrilus adriaticus trisetosus subsp.n. (Fig. 10)

Holotype. USNM 55701, longitudinally sectioned specimen.

Type locality. Ferry Reach, at Bermuda Biological Station, Bermuda, 32°22'05" N, 64°41'44" W, 0.2 m below low water mark, calcareous medium to coarse sand (Nov. 30, 1977).

Paratypes. USNM 55702–55703, two whole-mounted and two sectioned specimens from the type locality. USNM 55704, one whole-mounted specimen from W of Soldier Key, Biscayne Bay, Miami, Florida, USA, 25°35.6' N, 80°10.0' W, 2 m, calcareous gravel, sand and clay, with a lot of mud (seaweed debris) (Nov. 18, 1977). USNM 55705, two sectioned specimens from Black Ledge, Biscayne Bay, Florida, 25°35.2' N, 80°14.2' W, 2 m, muddy sand (Nov. 21, 1977).

Other material examined (author's collection). Two sectioned specimens, one from the type locality, one from the locality W of Soldier Key, Florida.

Description. Length (fixed specimens) about 9 mm, 66–67 segments (only two complete specimens available). Diameter in slightly compressed specimens: 0.22–0.26 mm anteriorly, 0.26–0.33 mm at clitellum, 0.18–0.24 mm posteriorly. Prostomium roundedly triangular, about as long as its width at peristomium. Secondary annulations absent. Clitellum extending over segments $\frac{1}{2}$ X to XII, especially well developed ventrally in XII. Somatic setae all bifid, 45–50 μm long, about 2 μm thick, with upper tooth slightly shorter and thinner than lower. Setae 3 (occasionally 2) per bundle anteriorly, 2 per bundle posteriorly. Ventral setae of XI modified into penial bundles, each of which contains 3 straight, sharply single-pointed setae (Fig. 10, *ps*), 80–85 μm long, maximally 4–5 μm thick, with ectal part tapering towards end. Penial setae enclosed in compact, muscular sac (*ms*), and their ends point-

ing almost in a latero-ventral direction towards ventral mid-line of body, from a pair of inconspicuous papillae anterior to male pores. Male pores paired, located in line with ventral setae in posterior part of XI. Spermathecal pores paired, located laterally in X, very near intersegmental furrow IX/X (cf. Fig. 10).

Pharyngeal glands extending into VII. Chloragogen cells in thin layer covering alimentary canal from VIII. Male genitalia (all structures paired) (Fig. 10): large sperm funnel (*sf*) on X/XI; vas deferens (*vd*) 7–9 μm wide and thin-walled, longer than atrium; vas deferens entering ectal part of atrium, but near middle of latter; atrium (*a*) cylindrical to spindle-shaped, about 150 μm long, maximum diameter about 50 μm ; atrium erect and not extending into XII; ectal end of atrium narrowing and ending in small opening partly covered by latero-posterior fold of body wall (*fb*), the whole structure forming a pseudopenis; atrium with very thin, only 1–2 μm thick, outer muscular layer and thick inner epithelium, which is granulated and ciliated; one prostate (*pr 1*) broadly attached to middle, anterior face of atrium, just above entrance of vas deferens; a second prostate (*pr 2*) entering apical or slightly sub-apical part of atrium from posterior. Spermathecae (Fig. 10, *s*) sacciform, of varying shape and extension. The short duct often opens into the middle of an elongated ampulla, the anterior part of which extends into segment IX. Spermathecal ampullae of postcopulatory specimens containing simple spermatophores (*sp*), globular or semi-globular in shape, with compact masses of sperm.

Remarks. This description conforms well to the description of *B. adriaticus* comb.n. made by Hrabě (1971). *B. adriaticus trisetosus* subsp.n. is more or less identical to the nominate form, with respect to most somatic characters, such as body dimensions, the segment number and the shape and arrangement of somatic setae, as well as to most genital features, i.e. the appearance of the atrium, the arrangement of prostate glands, the shape and location of spermathecae, and the presence of spermatophores. Taxonomically, *trisetosus* is distinguished by its possession of invariably three straight setae in each penial bundle, the number being only two in *adriaticus adriaticus*. Even though specimens of *trisetosus* with, for instance, only two setae could be expected to occur (cf. remarks for *B. longus* sp.n.), the available material suggests that the degree of difference in the number of penial setae in the two forms is sufficient to allow subspecies recognition (cf. Mayr 1969, p. 189 ff.).

Brinkhurst (1965*b*) described briefly two specimens of Tubificidae from Puerto Rico, which were identified as “*?Spiridion insigne* Knöllner, 1935”. The depicted setae (op.cit., fig. 10D), the dimensions of the worms and the presence of “massive, discrete prostates opening about in the middle of the atria”, indicate a possible relationship of Brinkhurst’s material to *B. adriaticus trisetosus*.

Habitat. *B. adriaticus trisetosus* inhabits sands in shallow water. Depth range 0.2–2 m.

Distribution. Bermuda and Florida. ?Puerto Rico (cf. above).

Bathydrilus sp.

Material examined (author’s collection). Two whole-mounted specimens from an inshore locality in the Beaufort area, North Carolina, USA: between Carrot Island and Middle Marsh, 34°42’06” N, 76°37’13” W, 5 m, shells and shell gravel, with some coarse sand (Oct. 19, 1977).

Remarks. *Bathydrilus* sp. shows close taxonomic affinity to *B. longus* sp.n. It is, like *B. longus*, a large form, width being up to 0.42 mm at clitellum in the slightly compressed specimens, and its somatic setae are up to about 80 μm long (thickness about 4 μm). Its length and segment number are unknown, since the two available specimens are not complete, but evidently one of them originally consisted of more than the remaining 79 segments. The penial setae are three in each ventral bundle of XI, the length being 150–173 μm , which falls within the range described for *longus*. The atria of *B. sp.* are erect or obliquely pointed into most anterior part of XII, the male openings being identical to those of *B. longus*. The doubt regarding the two specimens’ identity, however, is raised by the very thin muscular layer of their atria: this layer is only about 2 μm thick, while in all specimens of *B. longus*, from the maturing and poorly developed individuals to the fully mature ones, exhibit the 5–7 μm thick layer of atrial muscles. In this way, the atria of *B. sp.* resemble those of *B. adriaticus*. However, in both subspecies of the last-mentioned, the atria open to the exterior almost directly on the ventral surface of the body wall, copulatory sacs being represented by very shallow horseshoe-like furrows (cf. Fig. 10; Hrabě 1971, fig. 23). The spermathecae of one of the specimens from North Carolina contain the type of spermatophores reported for *B. adriaticus*. In the second specimen, the spermathecae are filled with loose masses of sperm.

Habitat. Subtidal coarse sand and gravel, depth 5 metres.

Distribution. Known only from North Carolina (NW Atlantic).

Bathydrilus rohdei (Jamieson, 1977) comb.n.

Phallogdrilus rohdei Jamieson, 1977, pp. 342–344, fig. 4, plate 1 D–F.

Type material. In Queensland Museum, Australia, in BMNH and in Jamieson Collection.

Type locality. Heron Reef, Great Barrier Reef, E of Australia, S Pacific, 0.1–1 m, coral sand.

Material examined. One whole-mounted, half-mature specimen from BMNH.

Remarks. A good description of this species is given by Jamieson (1977), who included it within *Phallogdrilus*. However, *P. rohdei* resembles in many respects the assemblage of *Bathydrilus longus* sp.n. and *B. adriaticus*, and it is, therefore, transferred to *Bathydrilus* here.

B. rohdei has atria that are erect, but which always curve dorso-posteriorly from its base (Jamieson 1977), and which possess two pairs of prostates, one attached to apical, ental and posterior ends of atria, and one, more pedunculate, entering anterior face of ectal parts of atria. These atrial feature, the presence of penis-like structures, the presence of two straight penial setae anterior to each male pore, and the shape of the spermathecae, indicate a close relation to other species of *Bathydrilus*. Unfortunately, in the type series, the vasa deferentia are “not detectable” (op.cit., p. 344). The location of the entrances of the sperm ducts into the atria is, therefore, not yet established.

The atrial muscle layer in *B. rohdei* is maximally about 10 μm thick, as can be judged from Jamieson’s figs. 4 C–D. *B. rohdei* is the only known species of the genus that possesses prespermathecal setae in segment IX.

Habitat. Subtidal coral sand, 0.1–1 metre depth.

Distribution. Known only from Heron and Wistari Reefs in the Great Barrier Reef (S Pacific).

Definition of the genus *Bathydrilus* Cook, 1970

(Modified after Cook 1970). A group of marine tubificids, many of which are deep-water forms. Hair setae absent. Penial setae, ventrally in XI, present or absent. Prespermathecal setae occasionally present in IX. Coelomocytes, if present, small and sparse, not of the "Rhyacodrilus-type".

Vasa deferentia inconspicuous, longer than atria, joining ectal halves of atria. Atrial oval, ovoid or spindle-shaped, erect or, more often, with apical, ental ends pointing to the posterior and extending into XII. Atrial wall with more or less developed muscular layer. Ectal ends of atria participating in pseudopenial or penis-like structures, often enclosed in copulatory sacs. One pair of prostate glands entering atria at entrances of vasa deferentia. A second pair of prostates attached to apical, ental ends of atria. Spermathecae sacciform, often one spermatheca extending into IX, the second remaining in X. Sperm in loose masses or as simple, roundish spermatophores in spermatheca.

Type species. *Bathydrilus asymmetricus* Cook, 1970.

Junior synonym. *Macroseta* Erséus, 1975.

Discussion*The genus definition*

When *Macroseta* was established (Erséus 1975a), its status as a separate genus was considered appropriate, because no previously described tubificid appeared closely related to *Macroseta rarisetis* Erséus, 1975. Though two pairs of prostate glands were known for *Phallogdrilus* Pierantoni, 1902, for instance, the location of the entrance of the vas deferens at the ectal end of the atrium made the systematic position of the species unclear. The recent studies on the available material of *Bathydrilus asymmetricus* Cook, 1970, however, clarified the situation: *B. asymmetricus* had not been adequately described regarding its prostate glands, which, in the original description, were said to be absent. Two pairs of prostates are present in *asymmetricus*, and they are arranged exactly in the same way as in *rarisetis*. Especially in the holotype of *B. asymmetricus* the prostates (Fig. 1, *pr 1-2*) are very large, and they were apparently interpreted as an egg sac by Cook (1970, fig. 1 A). The atria of both *asymmetricus* and *rarisetis* have their ectal ends pointing to the posterior, and the vasa deferentia of *asymmetricus* enter the ectal ends of the atria, as in *rarisetis*, though the junctions are very difficult to observe in the whole-mounted specimens (cf. Erséus 1975a).

It becomes evident that *Macroseta* Erséus, 1975 has to be considered as a junior synonym to *Bathydrilus* Cook, 1970. This is supported by the discovery of the other deep-water species described in this paper, *B. atlanticus* sp.n., *B. hadalis* sp.n., *B. meridianus* sp.n. and *B. graciliatriatus* sp.n., some of which are morphologically intermediate between *B. asymmetricus* and *B. rarisetis*.

The copulatory organs

Terms such as "penis" and "pseudopenis" have been subject to much confusion in the tubificid literature; Brinkhurst (1965a, pp. 370–371) has attempted to clarify the meaning of these two terms. He distinguishes between "eversible pseudopenis", "protrusible pseudopenis", "true penis", and "true penis with cuticular sheath" (op.cit., fig. 4). In the typical cases these different terms are applicable, though inter-

mediate types do occur (cf. e.g. Cook 1974). Also, much of the difficulty is due to the fact that homologies and analogies in different copulatory structures are not always evident, and in some instances provisional determination of these has to be accepted.

Furthermore, when describing the male genitalia of species of *Bathydrilus*, problems regarding the terminology of the copulatory structures arise (cf. remarks for *B. atlanticus*, *B. rarisetis* and *B. graciliatriatus*). In one species, *B. hadalis* sp.n., the ectal ends of the male ducts are poorly visible in the available material. In *B. meridianus*, *B. rarisetis*, *B. graciliatriatus* and *B. longus* the ectal ends of the atria appear histologically continuous with the rest of the atria (with the exception for the outer muscular lining), but they protrude into the copulatory sac, which is well developed in *meridianus* and *longus*. The same situation occurs in the species of *Adelodrilus* (cf. Erséus 1978a). In this way the penial structures of these species are not penes "formed from folds in the body wall, the cuticle being retained", as they are defined by Cook (in Brinkhurst & Jamieson 1971, pp. 32–33).

In *B. asymmetricus*, *B. atlanticus* and *B. rohdei* the copulatory organs are much more like true penes or, possibly, protrusible pseudopenes (cf. Figs. 1–3; remarks for *atlanticus*; Jamieson 1977, fig. 3D). In *B. adriaticus* the atria end as pseudopenes in very shallow horseshoe-like furrows (cf. Fig. 10; Hrabě 1971, p. 221, fig. 23).

Taxonomy of the different species

Some principal distinguishing characteristics for the different species of *Bathydrilus* are summarized in Table I. Unfortunately, complete information on the length and segment number is not available for *atlanticus*, *meridianus* and *graciliatriatus*. It is likely that all the deep-sea forms are less than about 10 mm in length and possess relatively few segments. Both *B. longus* and *B. rohdei*, on the contrary, are up to at least 25 mm long and consist of up to more than 100 segments. The forms of *B. adriaticus* are no longer than about 10 mm and possess 55–86 segments. *B. rarisetis* is intermediate in size (about 15 mm, about 70 segments), but it is easily distinguished from the rest of the genus by its giant somatic setae, which are all single-pointed and straight, up to 190 μm long, and in mid-body 11–15 μm thick. In addition, the setae are arranged in unisetal "bundles" in all segments except for II–IV (cf. Fig. 7; Erséus 1975a). All the other species have bifid setae of more ordinary size. Penial setae are present in *rarisetis*, *graciliatriatus*, *longus*, *adriaticus* and *rohdei*. The last-mentioned is the only species with (pre-)spermathecal setae.

Even though there occurs a certain degree of variation within the different species, the thickness of the atrial muscles is considered taxonomically important. Again, *rarisetis* represents the extreme by its thick muscular layer (up to 45 μm). In *atlanticus* (7–12 μm), *hadalis* (about 3 μm), *meridianus* (2–5 μm), *graciliatriatus* (4–5 μm), *longus* (5–7 μm) and *rohdei* (up to 10 μm), the atrial muscles are moderately developed, while they are very slender in *asymmetricus* and *adriaticus* (maximally 2 μm). The atria are of different shape and size in the different species, their appearances being shown in Figs. 1, 3, 4, 6–10, in Erséus (1975a, fig. 2), in Hrabě (1971, fig. 23), and in Jamieson (1977, fig. 4). Other important characters are found in some other parts of the genital system of the species. The different kinds of copulatory structures were discussed above. However, note the

Table I. Principal distinguishing characteristics for the species of *Bathydrilus*

	Length (mm)	Segments	Length of somatic setae (Thickness)	Penial setae	Thickness of atrial muscle	Other important characters	Depth range (m)
<i>asymmetricus</i>	About 8	32–37	37–48 μm (<2 μm)	Absent	0.7–2.0 μm	–	1 330–2 000
<i>atlanticus</i> sp.n.	>5.8	>20	40–55 μm (1 μm)	Absent	7–12 μm	–	1 600–2 880
<i>hadalis</i> sp.n.	9.8	32	70–75 μm (about 2 μm)	Absent	About 3 μm	Spermathecal pores at some distance from furrow IX/X	7 298
<i>meridianus</i> sp.n.	>3.2	>16	50–55 μm (about 2 μm)	Absent	2–5 μm	Very deep, folded copulatory sacs	About 500
<i>rarisetis</i> comb.n.	About 15	About 70	130–190 μm (11–15 μm)	Present 1 small seta per bundle	Up to 45 μm	Unisetal "bundles"	17–400
<i>graciliatriatus</i> sp.n.	>4.5	>23	50–60 μm (<2 μm)	Present 3 sigmoid setae per bundle	4–5 μm	Very slender atria	1 600–1 800
<i>longus</i> sp.n.	18–25	94–109	50–70 μm (4 μm)	Present 2 (3) straight large setae per bundle	5–7 μm	Male pores as deep invaginations	70–91
<i>adriaticus</i> comb.n. (polytypic species) <i>adriaticus</i> nominate form	About 10	55–86	About 50 μm (2 μm)	Present 2 straight small setae per bundle	1–2 μm	Male pores as shallow horseshoe-like furrows	0.2–32
<i>trisetosus</i> subsp.n.	About 9	66–67	45–50 μm (2 μm)	Present 3 straight small setae per bundle	1–2 μm	Male pores as shallow horseshoe-like furrows	0.2–2
<i>rohdei</i> comb.n.	18.4–27.8	90–119	40–61 μm (3–5 μm)	Present 2 straight large setae per bundle	Up to 10 μm	Prespermathecal setae present ventrally in IX (1–2 per bundle)	0.1–1

very deep, folded copulatory sac of *B. meridianus*, which has a characteristic papilla in the innermost part of the sac (Fig. 6, *pa*). This papilla is probably homologous to the lateral thickened fold of the body wall described for many of the other species. The internal location of the fold in *meridianus* can thus be explained by the invagination of the body wall during the evolution of the deep sac. Unique within the genus is the location of the spermathecae of *B. hadalis*, which do not open immediately posterior to the furrow between IX and X, but more posteriorly in the anterior part of segment X (cf. Fig. 4).

Bathydrilus longus sp.n., *B. adriaticus adriaticus*, *B. adriaticus trisetosus* subsp.n. and *B. sp.*

These four forms are evidently monophyletic and very closely related, and they certainly illustrate the shortcomings of the almost purely typological species concept that is still applied in practical oligochaete taxonomy. At present, however, the taxonomic decisions regarding these forms have to be based upon the available morphological data plus some information on habitat and geographical distribution. The weighting of the different features, as always, is subjective. Taxonomically, there are at least four different ways of acting in this particular case: (1) The whole assemblage could be

considered as one variable species, with or without the designation of different subspecies. (2) The complex could be treated as four different species, and specific names be given for each of them, allowing them to become synonyms, if necessary after future studies. (3) The three North-west Atlantic forms, *B. longus*, *B. adriaticus trisetosus* and *B. sp.*, could be interpreted as one variable species and considered as a sister species to the Mediterranean *adriaticus*. This gives much weight to the prospective genetic differences due to the great geographical distance between the two areas, and to the presence of a morphologically and geographically somewhat intermediate form, *B. sp.*, between the northern *longus* population and the Bermudian/Caribbean *trisetosus*. (4) The very close morphological similarity between *trisetosus* and *adriaticus*, despite the wide geographical separation, could be taken as an indication for conspecific status; *B. longus* would be kept as a separate species, because of its relatively large dimensions, its possession of deep copulatory sacs, and possibly because of its thick atrial muscles (cf. below).

The fourth alternative has been chosen in the present account. Until future studies provides contradicting evidence, it is proposed that *adriaticus* Hrabě and *trisetosus* subsp.n. be treated as different subspecies of *Bathydrilus adriaticus* (Hrabě), and *Bathydrilus longus* sp.n. is given full species rank. In addition to the discrepancies in morphology, the dif-

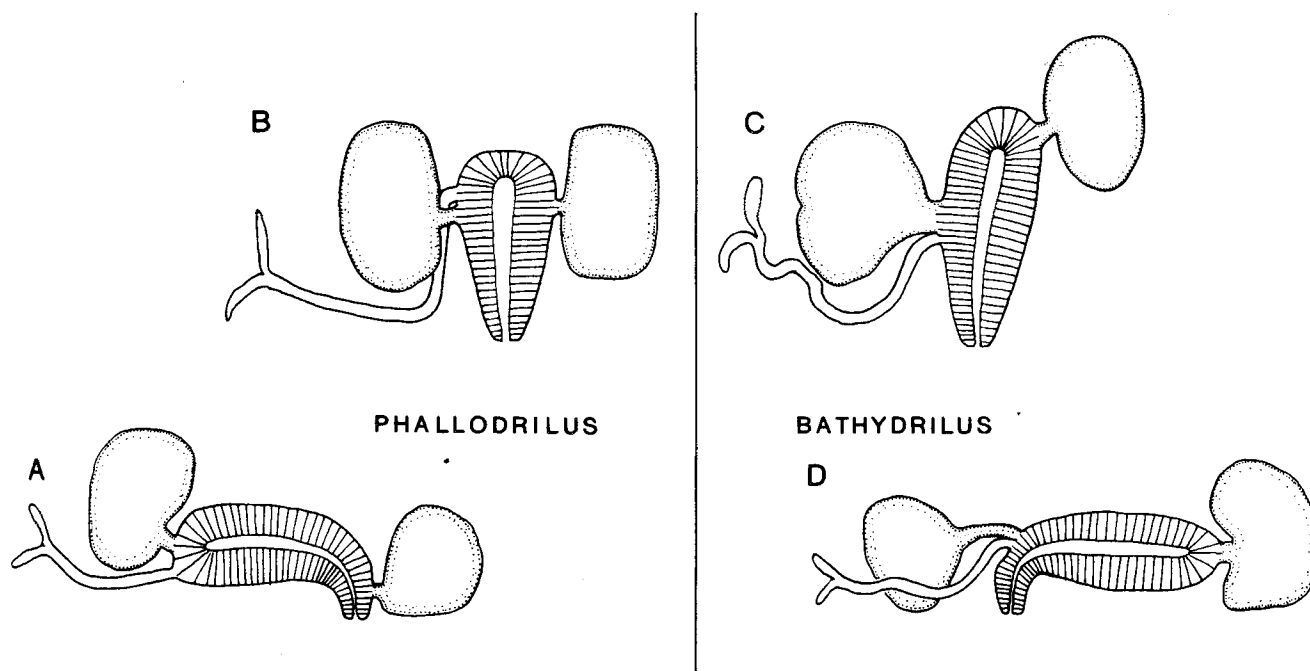


Fig. 11. Principal organization of male efferent duct in *Phallodrilus* and *Bathydrilus*. (A) "Typical" *Phallodrilus* (e.g. *P. obscurus* Cook);

(B) *Phallodrilus parviatriatus* Cook; (C) *Bathydrilus adriaticus* (Hrabě) comb.n.; (D) "Typical" *Bathydrilus*.

ferent habitats and distribution of *adriaticus/trisetosus* and *longus* support this arrangement: both subspecies of *adriaticus* inhabit shallow, tropical and subtropical sands, while *longus* is found on the continental shelf (depths 70–91 m) at much more northern latitudes (off the coast of New Jersey, USA), where the temperature seldom reaches more than about 10–12°C (R. Diaz, personal communication). *Bathydrilus* sp.n. is left without further change in nomenclature. It is quite possible that this form is conspecific to *B. longus*; the differences in, for instance, the thickness of the atrial muscles might be explained simply by the different fixation methods used, the type material of *longus* being fixed in large samples in formalin, the specimens from North Carolina individually in Bouin's fluid. The different fixations could also explain why no spermatophores of the kind found in both *B. adriaticus* and *B. sp.* were observed in *B. longus*. In all of the latter, the spermathecae appear slightly shrunken, and their contents are very poorly fixed (cf. Fig. 9).

The taxonomic arrangement proposed here, which partly follows the proposal by Mayr (1969, p. 197) to treat allopatric populations of doubtful rank as subspecies, might, of course, have to be modified after future studies. For instance, the *trisetosus* form from Bermuda and Florida can easily be given full species rank, if further analysis suggests it. After all, the wide geographical separation of *trisetosus* from the nominate form of *adriaticus* most probably is accompanied by genetic isolation. This isolation might have been large enough for a reproductive barrier to have been established, but such theories have to be checked with methods other than the traditional, purely morphological ones.

Problems regarding the taxonomy and geographical separation of marine Oligochaeta have been discussed by Erséus & Lasserre (1976) for the enchytraeid genus *Grania*.

Relation of *Bathydrilus* to other Tubificidae

The division of the family Tubificidae into genera is mainly based on differences in the male genital system, most of the

other, somatic characters are useful on the specific level only. The same applies to *Bathydrilus*, which is characterized by the arrangement of its vasa deferentia, atria and prostate glands (cf. genus definition above).

The new information on the prostate glands of the type species of both *Bathydrilus* and *Macroseta* explains the systematic position of *Bathydrilus*. It is a proper member of the sub-family Phallodrilinae (cf. Brinkhurst & Jamieson 1971). Note that the "spermatophores", which are said to be absent in the Phallodrilinae (op.cit.), are referring to the special kind of spermatophores, "spermatozeugmata", characteristic for, i.e., the sub-family Tubificinae (cf. Erséus 1978b).

Bathydrilus is evidently closely related to *Phallodrilus* Pierantoni, 1902. In fact, *B. adriaticus* is morphologically intermediate between some species of *Phallodrilus* and the more "typical" members of *Bathydrilus*, with emphasis on the arrangement of the male genitalia; in *Phallodrilus*, the vasa deferentia enter the apical or subapical, ental ends of the atria, while the "typical" *Bathydrilus* species has sperm ducts that enter the ectal ends of the atrium. The more or less continuous transition between the two genera, as shown in Fig. 11, almost support a union of them into one large genus, *Phallodrilus*. In addition to the eleven species already recognized (according to Jamieson (1977), but excluding *adriaticus* and *rohdei*), there are at least sixteen species to be described (Erséus, in press; Giere, in preparation). If the species included in *Bathydrilus* in the present account are added, the genus *Phallodrilus* becomes extremely large, inhomogeneous and very difficult to handle. Such a union would also, for consistency, necessitate the consideration of the genera *Aktedrilus* Knöllner, *Bacescuella* Hrabě, and *Adelodrilus* Cook (cf. Cook & Hiltunen 1975; Erséus 1978a, b) as junior synonyms to *Phallodrilus*. Recently (Jamieson 1977), *Phallodrilus* was enlarged to include the monotypic genus *Torodrilus* Cook, 1970.

It is argued that the generic distinction between *Phallo-*
dri-
lus and *Bathydri-*
lus, though being relatively subjective, is

most conveniently settled between the genital arrangements found in *Phalldrilus parviatriatus* Cook, 1971 and *Bathydri- lus adriaticus* (Hrabě, 1971) (Fig. 11, B–C). It should be stressed that this does not necessarily mean that the two species are phylogenetically very closely related, but it is likely that one of the genera has evolved from the other, the direction of the evolution, at present being unclear.

The removal of *adriaticus* from *Phalldrilus* has been considered previously, both by Cook & Hiltunen (1975), who mentioned the occurrence of spermatophores in the species as an aberrant character for *Phalldrilus*, and by Erséus (1975b), who noted the peculiar organization of the male efferent duct.

It is noteworthy that the separation of *Phalldrilus* and *Bathydri- lus* based on discrepancies in the male genitalia is accompanied by a difference in the general appearance of the spermathecae of the two genera. Most species of *Phalldri- lus* possess elongated, narrow spermathecal ampullae, while the spermathecae of *Bathydri- lus* are all sacciform.

The superficial resemblances between *Bathydri- lus* and *Clitel- lio*, noted by Cook (1970), and between *Macroseta* and *Rhyacodrilus*, noted by Erséus (1975a), have probably little systematic relevance, since *Bathydri- lus*, according to its new definition, is included in the sub-family Phalldrilinae. *Clitel- lio* and *Rhyacodrilus* belong to other sub-families (cf. Brink- hurst & Jamieson 1971).

Geographical distribution and habitat

Bathydri- lus exhibits a cosmopolitan distribution with repre- sentatives described from the North Atlantic, the Mediter- ranean Sea, the South Indian Ocean and the North and South parts of the Pacific Ocean. The knowledge of the distribu- tion and diversity of the genus, however, is still very far from complete. Most of the species are known from very few speci- mens only. The main reason for the fragmentary nature of the findings is probably the fact that *Bathydri- lus* to a large extent is a deep-sea genus (cf. Table I), the name itself im- plying this.

Bathydri- lus hadalis sp.n. from the Aleutian Trench is the first hadal oligochaete ever described, its type locality being more than 7000 metres deep. The available specimen is there- for unique and it is considered justifiable to establish a new species on a holotype only. The same applies to *B. meridia- nus* sp.n., which also is a deep-water species described on the basis of one individual, from about 500 metres depth near the Crozet Islands in the South Indian Ocean.

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Abbreviations in the figures

<i>a</i>	atrial ampulla
<i>cs</i>	copulatory sac
<i>fb</i>	fold of body wall
<i>mcs</i>	muscles of copulatory sac
<i>ms</i>	muscular setal sac
<i>p</i>	penis
<i>pa</i>	papilla
<i>pr 1</i>	anterior prostate gland
<i>pr 2</i>	posterior prostate gland
<i>ps</i>	penial seta
<i>s</i>	spermatheca
<i>se</i>	seta
<i>sf</i>	sperm funnel
<i>sp</i>	spermatophore
<i>vd</i>	vas deferens

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Addendum

In a recent article in *Zool. Scr.* (6: 298, 1977), I cited "Erséus, C., in press. A new species of *Bathydrilus* (Oligochaeta, Tubificidae) from the High Arctic deep sea. — *J. Nat. Hist.*" This paper has been withdrawn and will not be published, since, during the preparation of the present account, the species considered was found not to belong to *Bathydrilus*.

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