

DEEP-SEA *PHALLODRILUS* AND *BATHYDRILUS*
(*OLIGOCHAETA, TUBIFICIDAE*)
FROM THE ATLANTIC OCEAN,
WITH DESCRIPTIONS OF TEN NEW SPECIES

by

Christer Erséus

Swedish Museum of Natural History, Stockholm and University of Göteborg (1)

Résumé

Dix nouvelles espèces bathyales et abyssales des genres *Phallodrilus* et *Bathydrilus* (sous-famille Phalldriliinae), récoltées lors d'un certain nombre de campagnes océanographiques françaises (BIOGAS) et américaines (CHAIN, KNORR, ATLANTIS II), sont décrites. Des remarques sur la distribution géographique et la morphologie de quelques espèces sont fournies.

Introduction

Cook (1969, 1970) was the first to demonstrate the presence of oligochaetes in deep-sea sediments. He described four species of Tubificidae from a transect between Massachusetts and Bermuda, in the North-West Atlantic. Subsequently, numerous such species have also been described from other parts of the world (Erséus, 1979 a, b, 1980, 1982, 1983). One of these, *Bathydrilus hadalis*, was found as deep as 7 298m, in the Aleutian Trench (N. Pacific) (Erséus, 1979 a).

The present paper accounts for additional material of bathyal and abyssal species of the two genera *Phallodrilus* and *Bathydrilus* (subfamily Phalldriliinae), which I have received for identification from French and American expeditions in various parts of the Atlantic Ocean. Most of these species, five of each genus, are new to science.

As both *Phallodrilus* and *Bathydrilus* have been recently revised (Erséus, 1979 a, b, 1981), the main purpose of this paper is to provide descriptions, with taxonomic remarks, of the new material. As to revisionary work, only one thing should be noted here : the discovery of very short vasa deferentia in *Bathydrilus longiatriatus* sp.n. necessitates a slight modification of the revised definition of *Bathydrilus* formulated by Erséus in 1981 (see remarks for *B. longiatriatus* below).

(1) Department of Zoology, Box 25059, S-400 31 Göteborg, Sweden.

Material and methods

The material used in this study comes from two sources: (1) the "BIOGAS VIII-IX" cruises in the Bay of Biscay, the benthos being sorted by the Centre National de Tri d'Océanographie biologique (CENTOB), Brest, France; and (2) various deep-sea cruises undertaken by the Woods Hole Oceanographic Institution (WHOI), Woods Hole, Massachusetts, USA.

Station data for BIOGAS VIII and IX are summarized in Table I; references to Sta. Nos. only are then made in connection with the respective species descriptions. When applicable, details of stations of the other cruises are given at the species descriptions.

The specimens were all stained in paracarmine, and mounted whole in Canada balsam.

Type series of the new species, and some other reference material, have been deposited at the Muséum National d'Histoire Naturelle (MNHN), Paris, France (CENTOB material), and in the United States National Museum of Natural History (USNM), Washington, D.C., USA (WHOI material).

SYSTEMATIC ACCOUNT

GENUS *PHALLODRILUS* Pierantoni, 1902

(Genus definition: see Erséus, 1979 b, p. 203.)

Phalodrilus vulnus sp.n. (Fig. 1)

Holotype: MNHN AS 705, a whole-mounted specimen from KG 151 (BIOGAS VIII; Table I).

Paratypes: MNHN AS 706-707, two specimens, from KG 156 and 157, respectively.

Other material (author's collection): five specimens from BIOGAS IX: two from KG 168, and three from KG 177.

Description: length and segment number not known; available specimens are represented by their anterior ends only, none consisting of more than 11 first segments (hence the name "vulnus" latin=hurt, cut). Clitellum extending from 1/2X and backwards over at least XI. Somatic setae (Fig. 1A) bifid, with teeth almost equal in size; these setae are 30-45 μ m long, 1-1.5 μ m thick, 2-4 per bundle anteriorly (posterior bundles not seen). Ventral setae of XI modified into penial bundles, each of which contains 3-5 straight bifid setae, 37-50 μ m long, 2-2.5 μ m thick at middle. Upper tooth of penial setae shorter and thinner than lower (Fig. 1B). Penial bundles located median to male openings, and their ectal ends are obliquely directed towards the mid-ventral line. Male pores paired in line with ventral somatic

TABLE I

Station data for CENTOB cruises BIOGAS VIII (May 18 to June 8, 1979) and BIOGAS IX (May 9-22, 1980), "Terrasse de Mériadec", W of Brittany, France.

Cruise	Sta. no.	Latitude	Longitude	Depth (m)
BIOGAS VIII	KG 145	47°32'52"N	08°39'04"W	2170
	KG 147	47°33'23"N	08°40'40"W	2190
	KG 148	47°33'03"N	08°40'18"W	2170
	KG 149	47°32'36"N	08°39'08"W	2165
	KG 151	47°33'56"N	08°39'09"W	2205
	KG 152	47°32'27"N	08°39'54"W	2160
	KG 153	47°32'40"N	08°40'49"W	2142
	KG 155	47°33'30"N	08°39'06"W	2187
	KG 156	47°33'49"N	08°39'39"W	2207
	KG 157	47°34'19"N	08°39'46"W	2227
BIOGAS IX	KG 168	47°31.93'N	09°05.47'W	2798
	KG 175	47°31.55'N	09°05.75'W	2825
	KG 177	47°31.80'N	09°04.82'W	2738
	KG 179	47°32.18'N	09°04.52'W	2730
	KG 181	47°31.53'N	09°06.37'W	2811

setae, slightly posterior to middle of XI. Spermathecal pores paired laterally in anterior part of X, near septum IX/X.

Pharyngeal glands extending into IV, or V. Male genitalia (all structures paired) (Fig. 1C): vas deferens very inconspicuous, not seen in holotype, but a few loops of it visible in other specimens; vas deferens thin-walled and ciliated, 7-9 μ m wide, entering apical, ental end of atrium; atrium 75-140 μ m long, maximally 26-47 μ m

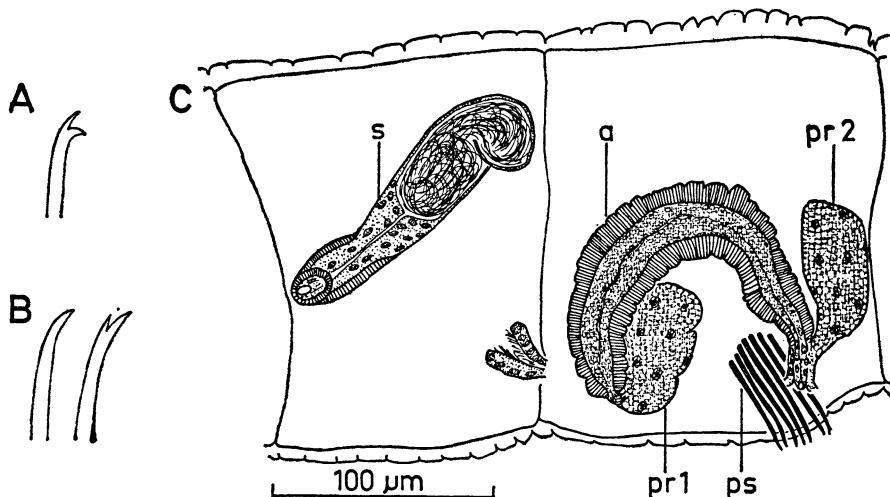


FIG. 1
Phallodrilus vulnus sp.n.

A: free-hand drawing of somatic seta; B: free-hand drawing of penial seta; C: lateral view of spermatheca and male genitalia in segments X-XI.
a, atrium; p, pseudopenis; pr 1, anterior prostate gland; pr 2, posterior prostate gland; ps, penial seta; s, spermatheca.

wide, consisting of large, oval ental portion with slender muscular lining, and thick inner granulated and ciliated epithelium, and short and narrow ectal duct terminating in a protrusible pseudopenis; when protruded, pseudopenis is tubular-to-club-shaped, 20-40 μm long, 10-20 μm wide; two compact prostate glands present, one at each end of atrium, but attachements not observed. Spermathecae (Fig. 1C, s) with thick-walled ducts, 30-70 μm long, 23-40 μm wide, and oblong, thin-walled ampullae, 70-130 μm long, 23-50 μm wide. Outer end of spermathecal ducts muscular; spermathecal ampullae filled with dense, random masses of sperm.

Remarks: *P. vulnus* sp.n. is similar to *P. aquaedulcis* Hrabé, 1960, which also has oblong atria with slender musculature, and penial setae that are bifid. However, *P. vulnus* has elaborate pseudo-penes (Fig. 1C), whereas the atria of *P. aquaedulcis* open directly on the body surface (Hrabé, 1960, fig. 3).

P. vulnus is probably closely related to *P. cristolatus* sp.n., described below, the main distinction between the two being the difference in thickness of atrial musculature; that of *P. cristolatus* is very conspicuous (Fig. 2C). In addition, in *P. cristolatus*, only some of the penial setae are bifid, not all as in *P. vulnus*.

Habitat and distribution: bathyal and abyssal fine sediments, 2 205-2 798m. Known only from W of Brittany, France.

Phallodrilus cristolatus sp.n. (Fig. 2)

Holotype: MNHN AS 701, a whole-mounted specimen from KG 149 (BIOGAS VIII; Table I).

Paratypes: MNHN AS 702-704, three specimens from type locality.

Other material (author's collection): seven specimens from BIOGAS VIII: one from KG 148, one from KG 151, three from KG 152, one from KG 156, and one from KG 157.

Description: length more than 3.0mm, more than 23 segments; no complete specimens available. Clitellum extending over 2/3X-2/3XII. Somatic setae (Fig. 2B) bifid, with teeth almost equal in size; these setae are 40-60 μm long, 1-1.5 μm thick, 3-6 per bundle anteriorly, 2-3 per bundle in post-clitellar segments. Ventral setae of XI modified into penial bundles, each of which contains (3)5-7 straight penial setae (Fig. 2C, ps), 50-70 μm long, about 2.5 μm thick. Ectal tips of penial setae (Fig. 2B) either single-pointed and slightly bent, or bifid with upper tooth shorter than lower. Penial bundles located median to male openings, and their ectal ends are obliquely directed towards the mid-ventral line. Male pores paired in line with ventral somatic setae, slightly posterior to middle of XI. Spermathecal pores paired laterally in anterior part of X, near septum IX/X.

Pharyngeal glands extending into V. Male genitalia (all structures paired) (Fig. 2C): vas deferens difficult to observe in available material, but narrow and coiled, entering apical, ental end of atrium; atrium cylindrical, curved, 150-215 μm long, 30-42 μm wide, with 7-14 μm thick layer of circular muscles, and granulated inner epithelium (ciliation not seen); atrium narrowing ectally, and ending as small

pseudopenis, which is protruded in some specimens (slightly shorter than, and about half as wide as, that of *P. vulnus*; cf. Fig. 1C; two compact and small prostate glands present, one at each end of atrium. Spermathecae (Fig. 2C, s) with thick-walled, ectally muscular ducts, 45-65 μ m long, 16-23 μ m wide, and thin-walled slender ampullae, 80-105 μ m long, 30-50 μ m wide; ampullae often wider entally than ectally (not so in holotype, which is depicted in Fig. 2C); sperm in compact random masses.

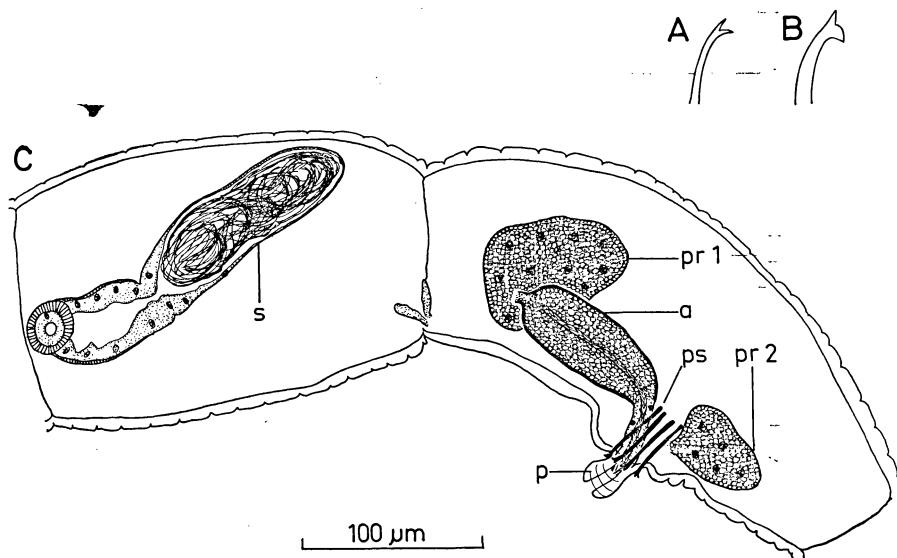


FIG. 2
Phalodrilus cristolatus sp.n.

A: free-hand drawing of somatic seta; B: free-hand drawing of penial setae; C: lateral view of spermatheca and male genitalia in segments X-XI. Abbreviations as for Fig. 1.

Remarks: as noted above, *P. cristolatus* sp.n. appears to be closely related to *P. vulnus* sp.n., but can be separated from that species by virtue of its very thick atrial muscles, and some setal differences.

The atrial musculature of *P. cristolatus* is reminiscent of that of *P. hallae* Cook and Hiltunen, 1975 (cf. Cook and Hiltunen, 1975, fig. 1A-B), but other features (morphology of spermathecae, arrangement of penial setae) clearly distinguish that freshwater species (known from the N. American Great Lakes) from the deep-sea *P. cristolatus*.

Habitat and distribution: bathyal fine sediments, 2 160-2 227m. Known only from W of Brittany, France.

Phalodrilus pinguis sp.n. (Fig. 3)

Holotype: MNHN AS 699, a whole-mounted specimen from KG 149 (BIOGAS VIII; Table I).

Paratype: MNHN AS 700, one specimen from KG 147.

Other material (author's collection): one specimen from KG 156.

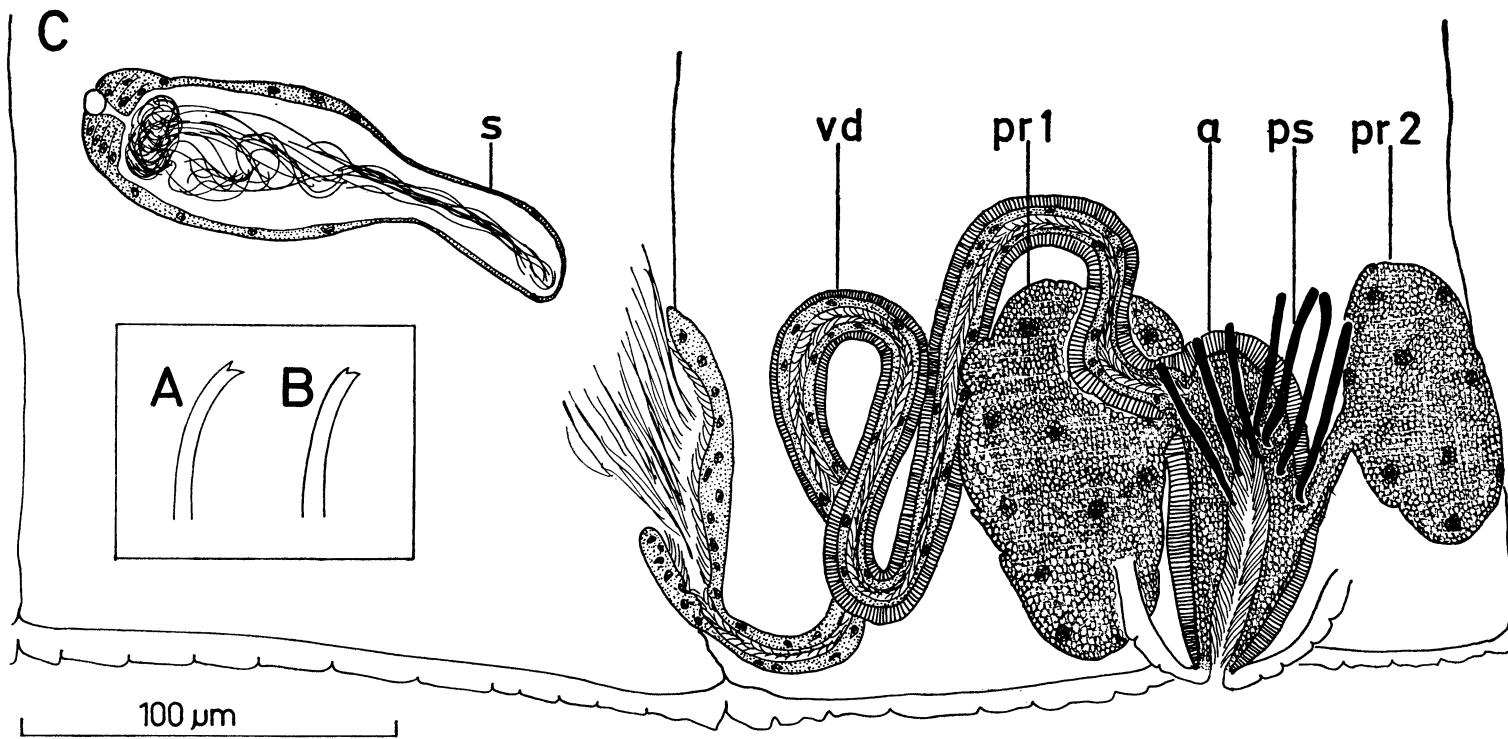


FIG. 3
Phalodrilus pinguis sp.n.

A: free-hand drawing of anterior somatic seta; B: free-hand drawing of posterior somatic seta; C: lateral view of spermatheca and male genitalia in segments X-XI.
vd, vas deferens; other abbreviations as for Fig. 1.

Description: length (holotype) 7.4mm, 60 segments. Clitellum extending over 1/2X-XII. Somatic setae bifid, anteriorly with upper teeth shorter and thinner than lower (Fig. 3A), posteriorly upper teeth even more reduced (Fig. 3B). Somatic setae 70-85 μ m long, 2.5-3 μ m thick, (2.3)4-6 per bundle anteriorly, (2)3-4 per bundle in post-clitellar segments. Ventral setae of XI modified into penial bundles, each of which contains 6-7 more or less straight, single-pointed, somewhat hooked, penial setae (Fig. 3C, ps). Penial setae 35-47 μ m long, 2-2.5 μ m thick, located at inner ends of narrow invaginations median to male openings. Male pores paired, on small protuberances, in line with ventral somatic setae, in posterior part of XI. Spermathecal pores paired, located laterally in anterior part of X, near septum IX/X.

Pharyngeal glands poorly developed. Male genitalia (all structures paired) (Fig. 3C): vas deferens about 13-14 μ m wide, much longer than atrium, heavily muscular along most of its length, and entering atrium sub-apically; atrium pear-to-comma-shaped, more or less erect, 80-90 μ m long, 35-40 μ m wide, with 3.5-7 μ m thick outer lining of (circular) muscles, and inner granulated and ciliated epithelium; atrium opening directly to exterior on summit of ventral protuberance; two compact prostate glands present, one communicating with atrium at entrance of vas deference, another attached by stalk to middle of posterior face of atrium. Spermathecae (Fig. 3C, s), slender, 115-140 μ m long, basally 40-55 μ m wide, entally narrower, with very short, thick-walled ducts; ampullae thin-walled, containing loose or compact mass of sperm.

Remarks: *P. pinguis* sp.n. is distinguished from the closely related *P. parvatriatus* Cook, 1971, known from the continental shelf of Eastern USA (Erséus, 1979 b), by its much more heavily muscular vasa deferentia and atria, and its smaller penial setae, when compared to the latter species. *P. pinguis* may also be closely related to *P. marionensis*, described from the South Indian Ocean by Erséus (1979 b). However, these two are easily separated on the basis of the morphology of their penial setae (cf. op. cit., fig. 10).

Habitat and distribution: bathyal fine sediments, 2165-2207m. Known only from W of Brittany, France.

Phallodrilus biparis sp.n. (Fig. 4)

Holotype: MNHN AS 696, a whole-mounted specimen from KG 152 (BIOGAS VIII; Table I).

Paratypes: MNHN AS 697-698, two specimens from KG 148.

Other material (author's collection): two specimens from BIOGAS VIII, from KG 155 and KG 156, respectively. One specimen from BIOGAS IX, KG 168.

Description: length more than 5.5mm, more than 20 segments; no complete specimens available. Clitellum extending over 1/2X-XII. Somatic setae (Fig. 4A) bifid, with upper tooth slightly longer than lower; these setae are slender, about 55-60 μ m long, about 1.5 μ m thick, 3-4 per bundle anteriorly, generally 2 per bundle in post-clitellar segments. Ventral setae of XI modified into penial bundles,

each of which contains 4 penial setae arranged in two distinct pairs (Fig. 4C, ps); anterior pair with setae 80-115 μm long, about 3 μm thick, sharply single-pointed, and with ental ends strongly bent; posterior pair with setae 70-95 μm long, about 3 μm thick, slightly sigmoid, and with ectal tips strongly hooked. Penial setae pointing in an almost antero-posterior direction, with their ectal ends protruding into lateral walls of a male invagination. Male pores (i.e. atrial openings) paired in lateral walls of unpaired, shallow horse-shoe-shaped ventral invagination (Fig. 4C, mi). Spermathecal pores paired laterally in most anterior part of X. A circular, glandular epidermal crypt (Fig. 4B, ec), 22-35 μm in diameter, located immediately ventral to each spermathecal pore.

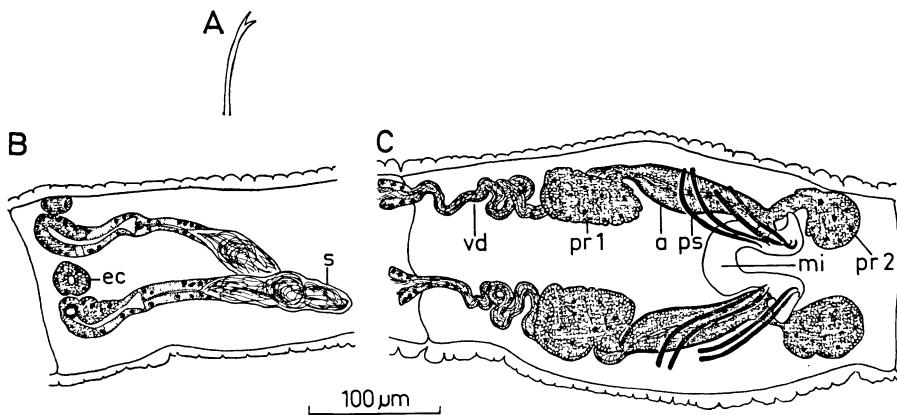


FIG. 4
Phallodrilus biparis sp.n.

A: free-hand drawing of somatic seta; B: oblique view of spermathecae; C: ventral view of male genitalia.

ec, epidermal crypt; mi, male invagination; vd, vas deferens; other abbreviations as for Fig. 1.

Pharyngeal glands extending into V, or VI. Male genitalia (all structures paired) (Fig. 4C): vas deferens about 7 μm wide, longer than atrium, entering apical, ental end of atrium; atrium spindle-shaped, 105-140 μm long, 24-35 μm wide, with about 2 μm thick outer lining of muscles, and thicker, granulated and ciliated, inner epithelium; atrium terminating in simple protrusible pseudopenis; two compact glands present, one at each end of atrium. Spermathecae (Fig. 4B, s) very slender, each consisting of (1) a duct, 80-115 μm long, ectally glandular and 19-31 μm wide, entally not glandular and only 10-18 μm wide, with lumen characteristically dilated at about halfway from ampulla, and (2) a very thin-walled ampulla, 115-185 μm long, 16-32 μm wide, filled with a random mass of sperm.

Remarks: the heterogeneous complements of penial setae in *P. biparis* sp.n. are interesting from two points of view.

1.—This special case of anisomorph penial setation, together with other genital features, speaks in favour of a close phylogenetic

relationship between *P. biparis* and *P. longissimus* Giere, 1979; the latter species also has heterogeneous penial bundles, long coiled vasa deferentia, slender atria opening into a median male invagination, very slender spermathecae, and epidermal crypts associated with the spermathecal openings (cf. Giere, 1979, fig. 3). However, *P. longissimus* belongs to a very aberrant group of marine Tubificidae, viz. those lacking an alimentary canal (cf. Erséus, 1979 b, 1981; Giere, 1979, 1981), and is thus certainly a species well separated from *P. biparis*. Many other gutless species of *Phalodrilus* have penial setae that are uniform within the bundle, and thus clearly different from those of *P. longissimus*. As it appears likely that *P. longissimus* has been derived from a *biparis*-like ancestor, the fact that *P. biparis* does have a gut supports the view that the gutless condition has evolved more than once within the Phalodrilinae.

2.—One may allow oneself to speculate about the function of the penial setae of *P. biparis*. It seems plausible to assume that the strongly hooked setae, the posterior pair within each bundle (Fig. 4C, ps), are used for the mutual holding of copulating worms. The peculiar crypts near the spermathecal pores are then possibly anchoring sites for these hooks (cf. Giere, 1979, who provides a similar interpretation for penial setae and crypts in *P. longissimus*). The anterior pairs of penial setae in *P. biparis*, however, are not hooked, and may well be inserted into the spermathecal openings. They would hence aid in adjusting the atrial openings over the spermathecal openings during copulation, and perhaps also secure the free passage of sperm into the spermathecal ducts.

Such a functional differentiation of penial setae is assumed also for the species of *Inanidrilus* Erséus, 1979 and *Adelodrilus* Cook, 1969 (cf. Erséus 1979 c, d), but the various components of the heterogeneous penial bundles of these genera are not necessarily homologous to the functionally corresponding setae of *P. biparis*.

Habitat and distribution: bathyal fine sediments, 2 160-2 798m. Known only from W of Brittany, France.

Phalodrilus lobatus sp.n. (Fig. 5)

Holotype: USNM 72983, a whole-mounted specimen from N of Surinam, W Atlantic, 08°58.0'N, 54°04.3'W, 1 456-1 518m (WHOI cruise "KNORR 25", Sta. 293; Feb. 27, 1972).

Description: length more than 2.9mm, more than 22 segments; holotype not complete. Clitellum extending over 1/2X-XII. Somatic setae (Fig. 5A) very slender, bifid, with upper tooth thinner and slightly longer than lower. Bifids 47-55 μ m long, about 1 μ m thick, 2-3 per bundle anteriorly, 2 per bundle in post-clitellar segments. Ventral setae of XI modified into penial setae (Fig. 5B, ps), one or two at each male pore (see Remarks). Penial setae up to 80 μ m long, 1.5-2 μ m thick at middle, ectally tapering and single-pointed, entally strongly curved. Male pores inconspicuous and paired, ventrally in middle-to-posterior part of XI. Unpaired roundish epidermal crypt located in mid-ventral line, between male pores,

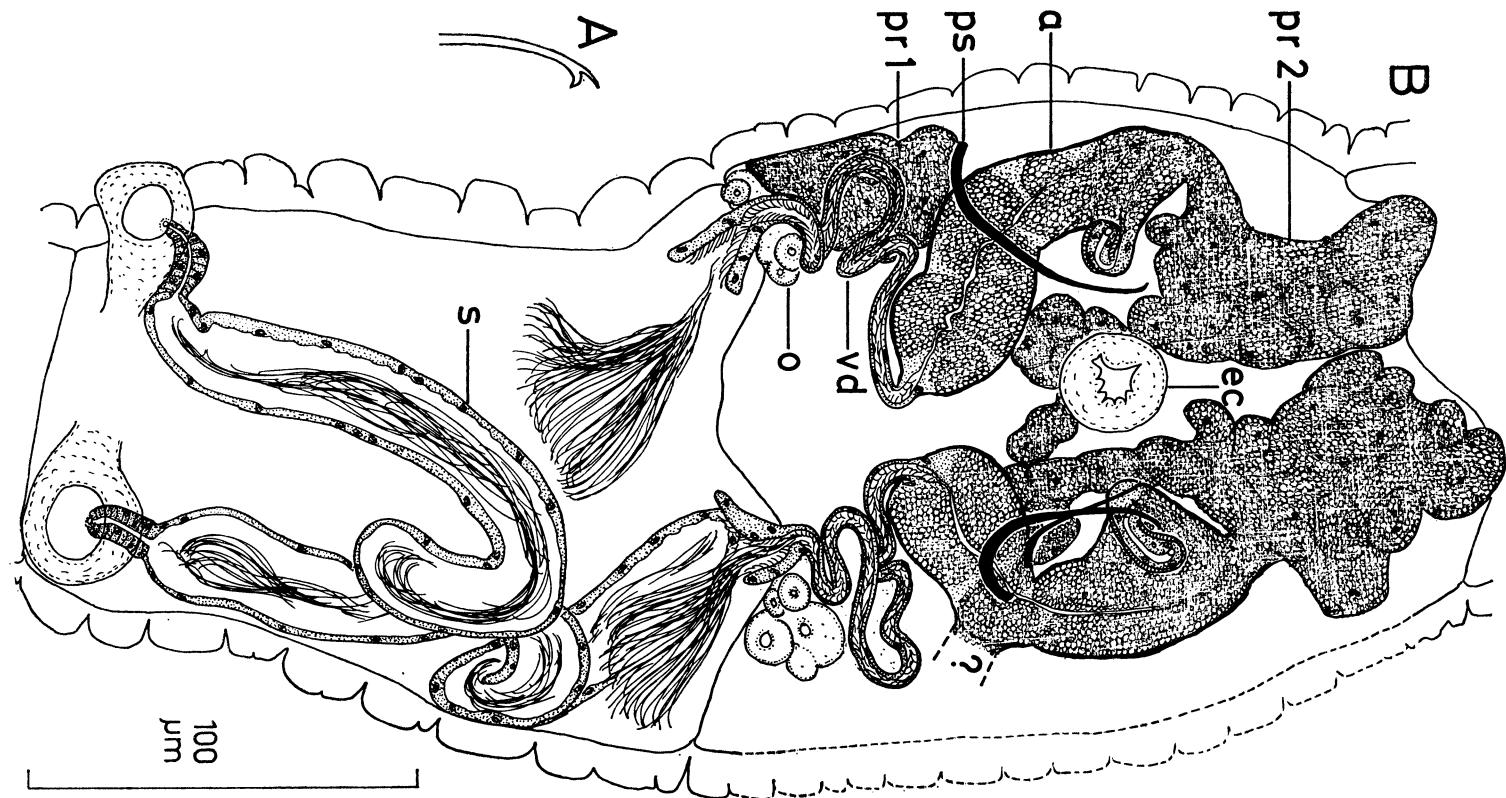


FIG. 5
Phalldodrilus lobatus sp.n.

A: free-hand drawing of somatic seta; B: ventral view of spermathecae and male genitalia in segments X-XI.
ec, epidermal crypt; o, ovary; vd, vas deferens; other abbreviations as for Fig. 1.

but function of it is unknown. Spermathecal pores paired on pear-shaped papillae, located in line with ventral setae, anteriorly in X.

Pharyngeal glands extending into V. Male genitalia (all structures paired) (Fig. 5B): vas deferens coiled, about 180 μ m long, 4-6 μ m wide, entering apical, ental end of atrium; atrium slender, about 150 μ m long, entally 25-33 μ m wide, ectally tapering and curved; atrial muscles only 1-2 μ m thick, inner epithelium granulated and thick, leaving very narrow lumen; atrial ciliation not observed; an anterior prostate gland attached to ental part of atrium, but apparently at some distance from apical end (cf. Remarks); a very large, lobed posterior prostate attached to ectal part of atrium, but ental to the tapering, most ectal portion; pseudopenis absent, atrial duct opening directly to the exterior. Spermathecae (Fig. 5B, s) with distinct ducts, 20-25 μ m long, about 9 μ m wide, and slender, thin-walled ampullae, about 200-225 μ m long, about 25 μ m wide; each ampulla with a long bundle of sperm.

Remarks: when the holotype was mounted, unfortunately a chunk of the clitellar wall was squashed out from its original position at one side of segment XI (indicated by broken lines in Fig. 5B). The chunk is not depicted in the figure, but within it lies a glandular body, which probably is the anterior prostate gland of that side of the worm, and which appears to have been removed from the atrium, at the point indicated by a question-mark.

In the examined specimen, a "spine" protrudes through the opening of the median epidermal crypt in segment XI. However, as light is very strongly refracted by this spine, it is considered as a foreign object entrapped by the crypt, rather than a seta or any other appendage belonging to the worm.

Without additional material of *P. lobatus* sp.n., it cannot be established whether the small, second penial seta at one side of the holotype (cf. Fig. 5B) is a common feature of this species.

P. lobatus is similar to *P. exiguum*, which was described from shallow waters of the Bermuda platform (Erséus, 1979 b). Both species have very slender spermathecae and slender, curved penial setae. The new species, however, possesses an epidermal crypt between the male pores, and spermathecal papillae, neither of which are present in *P. exiguum*. Moreover, the posterior prostates of *P. lobatus* are very elaborate and lobed, not compact as those of *P. exiguum*.

Habitat and distribution: bathyal fine sediments, about 1 500m. Known only from the continental slope off Surinam.

***Phalldrilus profundus* Cook, 1970 (Fig. 6)**

Cook, 1970, pp. 978-980, fig. 3; Erséus, 1979 b, pp. 197-198.

Material examined: MNHN AS 693-695, three specimens from KG 148 (BIOGAS VIII; Table I).

Author's collection: twelve specimens from BIOGAS VIII: one from KG 145, two from KG 147, three from KG 149, one from

KG 151, one from KG 152, two from KG 153, one from KG 156, and one from KG 157. One specimen from S of Massachusetts, USA, $38^{\circ}14.4' - 17.6'N$, $70^{\circ}20.3' - 22.8'W$, 3 264-3 356m (WHOI cruise "KNORR 35", Sta. 340; Nov. 24, 1973).

Remarks: it was noted by Erséus (1979 b) that there are morphological differences between the populations of *P. profundus* of the two sides of the Atlantic. All specimens known from the NW Atlantic have modified genital setae in all three segments IX, X and

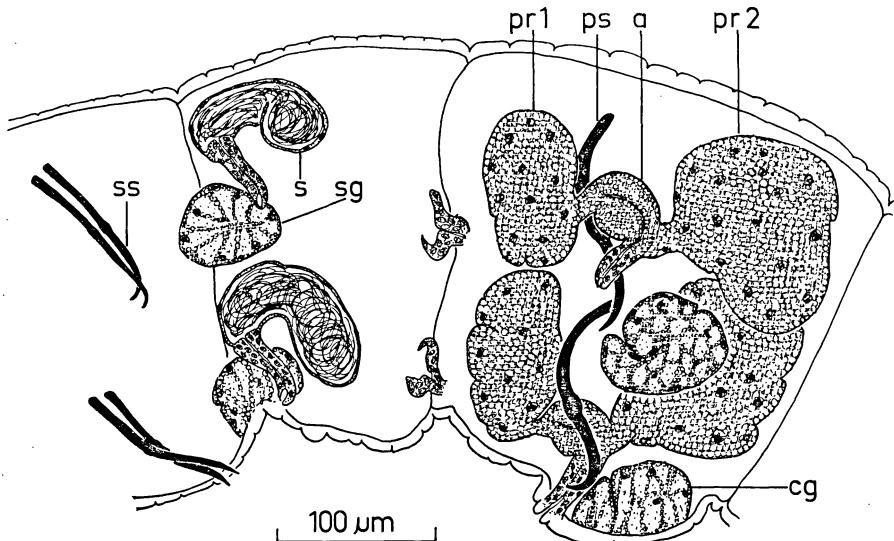


FIG. 6
Phallodrilus profundus Cook, 1970

Oblique view of spermathecae and male genitalia in segments X-XI.
cg, copulatory gland; sg, spermathecal gland; ss, spermathecal seta; other abbreviations as for Fig. 1.

XI, and these setae are generally 2 per bundle (occasionally only one per "bundle"), whereas the NE Atlantic form is characterized by its lack of genital setae in segment X, and its reduced average number of genital (=penial) setae in XI. The latter setae were 1-2 per bundle in the material from the Rockall Trough (W of Scotland) examined by me (Erséus, 1979 b), but in the present material from further south (W of France), the penial "bundles" are always unisetal.

Fig. 6 shows the genital organs of one of the specimens from off France.

Habitat and distribution: bathyal and abyssal fine sediments, 1 800-3 753m. Known from three areas: S to SSE of Massachusetts (NW Atlantic), W of Scotland, and W of Brittany, France (both NE Atlantic); the species may thus be continuously distributed over a large area in the North Atlantic.

GENUS *BATHYDRILUS* Cook, 1970

(Genus definition: see Erséus, 1981, p. 22; for a slight modification, see Remarks for *B. longiatriatus* sp.n. below.)

Bathydrilus asymmetricus Cook, 1970

Cook, 1970, pp. 974-976, fig. 1; Erséus, 1979 a, p. 140, fig. 1.

Material examined (author's collection): one specimen from S of Massachusetts, USA, 39°43.0'-43.2'N, 70°46.0'-49.5'W, 2 024-2 064m (WHOI cruise "CHAIN 88", Sta. 210; Feb. 22-23, 1969).

Remarks: this single new specimen, which was collected in the same area as all previously known material of *B. asymmetricus*, conforms fully to the description emended by Erséus (1979 a).

Habitat and distribution: bathyal fine sediments, 1 330-2 064m. Known only from four closely situated stations, S of Massachusetts (NW Atlantic).

Bathydrilus desbruyeresi sp.n. (Fig. 7)

Holotype: MNHN AS 689, a whole-mounted specimen from KG 168 (BIOGAS IX; Table I).

Paratypes: MNHN AS 690-692, three specimens from KG 177.

Other material (author's collection): three specimens, from KG 175, 179, and 181, respectively.

Description: length more than 2.2mm, more than 16 segments; no complete specimens available. Clitellum poorly developed. Setae (Fig. 7A) bifid, with upper tooth thinner and distinctly shorter than lower (particularly pronounced in setae of H). Setae about 35-40 μ m long, 1-1.5 μ m thick, 2-3 per bundle anteriorly, 2 per bundle in post-clitellar segments. Ventral setae absent from XI. Male pores paired, ventrally and posteriorly in XI. Each male pore partly covered by a papilla formed by a lateral fold of the body wall (Fig. 7C, mp). Spermathecal pores paired slightly dorsal to lateral lines, in most anterior part of X.

Pharyngeal glands poorly developed. Male genitalia (all structures paired) (Fig. 7C): vas deferens not observed, but obviously much longer than atrium; atrium comma-shaped, somewhat erect, 60-70 μ m long, about 25 μ m wide, with very thin outer layer of muscles, and thick inner epithelium, ciliation not observed; atrium opening directly into male pore, but this pore is partly covered by the male papilla; anterior prostate gland attached with long stalk to middle (anterior face) of atrium, probably together with vas deferens, but latter not seen; large posterior prostate attached to apical, ental end of atrium, which is obliquely pointing towards septum XI/XII. Spermathecae (Fig. 7B) oval or elongated, highly variable in size (55-230 μ m long), with short, thick-walled ducts, and thin-walled ampullae, latter with random masses of sperm. Often one spermatheca extending with its ampulla into IX.

Remarks: this species is named for Dr. Daniel Desbruyères (Centre Océanologique de Bretagne), the principal investigator of the "BIO-GAS" expeditions.

B. desbruyeresi sp.n. is closely related to *B. asymmetricus*. However, the atria of the new species are smaller and simpler than those of *B. asymmetricus*. For instance, in *B. desbruyeresi*, the atria are not ectally constricted, and discrete pseudopenes are absent.

Habitat and distribution: abyssal fine sediments, 2 730-2 825m. Known only from W of Brittany, France.

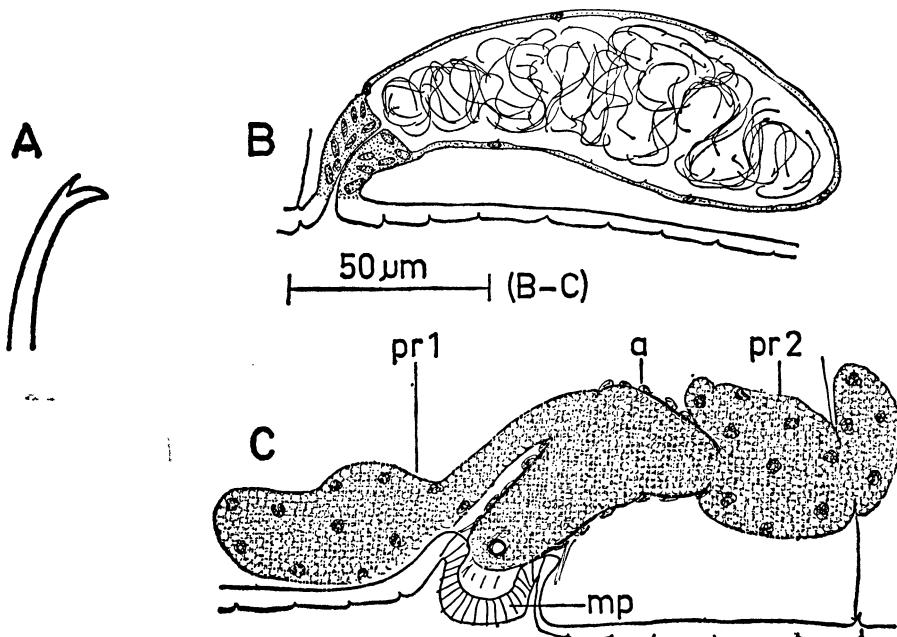


FIG. 7
Bathydrilus desbruyeresi sp.n.

A: free-hand drawing of seta; B: spermatheca; C: male genitalia.
mp, male papilla; other abbreviations as for Fig. 1.

Bathydrilus atlanticus Erséus, 1979

Erséus, 1979 a, pp. 140-141, figs. 2-3.

Material examined: MNHN AS 687-688, two specimens from KG 148 and 151, respectively (BIOGAS VIII; Table I).

Author's collection: one specimen from WSW of Ireland, 50°43.5'-43.4'N, 17°51.7'-52.9'W, 4 632m (WHOI cruise "CHAIN 106", Sta. 330; Aug. 24, 1972).

Remarks: the three new specimens conform to the original description. *B. atlanticus* is characterized by its very stout, heavily muscular atria (muscle layer up to 14μm thick in the new material), and its conspicuous male protuberances.

Habitat and distribution: bathyal and abyssal fine sediments; 1 600-4 632m. Known from S of Massachusetts (NW Atlantic), W of Scotland, WSW of Ireland, and W of France (all NE Atlantic); the species may thus be continuously distributed over a large area in the North Atlantic.

Bathydrilus sandersi sp.n. (Fig. 8)

Holotype: USNM 72984, a whole-mounted specimen from SW of Ireland, $50^{\circ}08.3'N$, $13^{\circ}53.7\text{-}50.9'W$, 3 338-3 356m (WHOI cruise "CHAIN 106", Sta. 323; Aug. 21, 1972).

Paratype: USNM 72985, one specimen from type locality.

Other material (author's collection): one specimen from $50^{\circ}12.3'N$, $13^{\circ}35.8'W$, 2 868-2 890m (CHAIN 106, Sta. 321; Aug. 20, 1972).

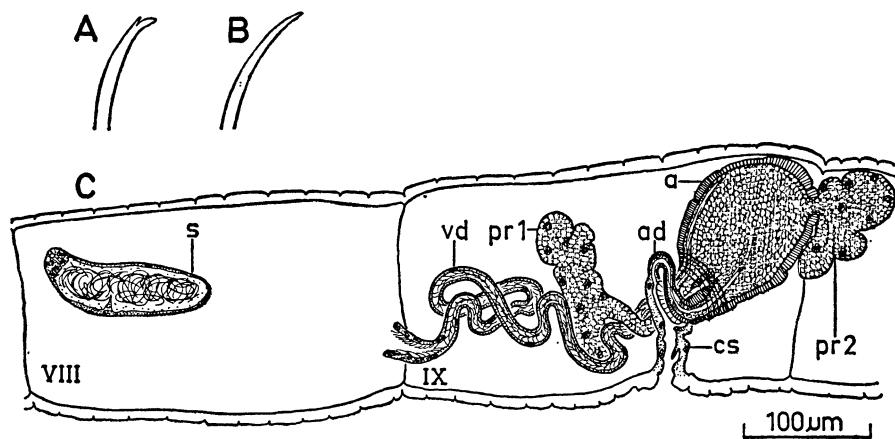


FIG. 8
Bathydrilus sandersi sp.n.

A: free-hand drawing of anterior seta; B: free-hand drawing of posterior seta; C: lateral view of spermatheca and male genitalia in segments VIII-IX. ad, atrial duct; cs, copulatory, sac; vd, vas deferens; other abbreviations as for Fig. 1.

Description: length more than 4.4mm, more than 20 segments; no complete specimens available. In type specimens, mouth large and everted; in third specimen (author's collection), mouth absent, and anterior end of worm appears to be regenerating. Clitellum extending over IX-X in holotype, poorly developed in other two worms. Setae in a few, most anterior, segments (Fig. 8A) bifid, with upper tooth reduced. Setae in all other segments (Fig. 8B) sharply single-pointed. Setae 35-60 μ m long, 2.5-3 μ m thick, 2-4 per bundle anteriorly, 2 per bundle in post-clitellar segments, but absent ventrally from segment bearing male pores. Male pores paired in slight (median) depression of body wall in posterior part of IX (in holotype), or X (in other two specimens). Spermathecal pores paired, dorsal to lateral lines, in anterior part of VIII (holotype), or IX (other two specimens).

Pharyngeal glands poorly developed. Male genitalia (all structures paired) (Fig. 8C): vas deferens up to 15 μm wide, very long and coiled, entering atrium, together with stalk of anterior prostate gland, immediately ental to narrow part of atrium; atrium consisting of an ental, spindle-shaped-to-globular ampulla, 70-100 μm wide, and an ectal duct, which is much narrower; total length of atrium about 150-225 μm (exact length difficult to establish); atrium heavily muscular, muscle layer up to 12 μm thick in ental ampulla, and with granulated and thick inner epithelium; posterior prostate gland, at least a part of which extends into the next segment, attached to sub-apical, posterior face of atrial ampulla; atrial duct opening into a deep invagination, the wall of which is thickened at inner end (possibly a papilla is present here, as in *B. meridianus* Erséus, 1979 a, fig. 6; but this is not quite clear in available material). Spermathecae (Fig. 8C, s) 130-205 μm long, 45-55 μm wide, with very short ducts, and oblong, thin-walled ampullae; latter filled with random masses of sperm.

Remarks: *B. sandersi* sp.n. is named for Dr. Howard L. Sanders (WHOI), a renowned deep-sea biologist, and one of the principal investigators of the expedition (CHAIN 106), from which the material of the species originates.

It is noteworthy that, in this species, the genital organs are shifted from segments X-XI, the normal location in a tubificid, to segments VIII-IX (holotype), or IX-X. This may prove to be a reliable specific character, but should perhaps first be confirmed by some additional specimens.

As indicated in the description, *B. sandersi* appears to be closely related to *B. meridianus*, a bathyal species described on the basis of a single individual from near the Crozet Islands in the South Indian Ocean (Erséus, 1979 a). The two species are easily distinguished by their different setae, most setae being single-pointed in *B. sandersi*. In addition, the copulatory sacs appear to be deeper in *B. meridianus* than they are in *B. sandersi*, but as to other male duct differences, we must await further material, especially of *B. meridianus*.

Habitat and distribution: abyssal fine sediments, 2 868-3 356m. Known only from SW of Ireland.

Bathydrilus medius sp.n. (Fig. 9)

Holotype: USNM 72986, a whole-mounted specimen from SW of Ireland, 50°08.3'N, 13°53.7-50.9'W, 3 338-3 356m (WHOI cruise "CHAIN 106", Sta. 324; Aug. 21, 1972).

Paratype: USNM 72987, one specimen, comprising 10 first segments only, from type locality.

Description: length more than 2.9mm, more than 16 segments; no complete specimens available. Clitellum extending over X-XII. Setae (Fig. 9A) bifid, with diverging teeth, almost equally long. Bifids 50-70 μm long, about 2 μm thick, 3-4 per bundle anteriorly, 2 per bundle in segments immediately posterior to clitellum. Ventral setae of

XI absent. Male pores paired, in line with ventral setae, near middle of XI; each pore partly covered by a papilla formed by a fold of body wall, but pores not elevated on protuberances (cf. *B. atlanticus*; Erséus, 1979 a). Spermathecal pores paired, laterally very near septum in anterior part of X.

Pharyngeal glands poorly developed. Male genitalia (all structures paired) (Fig. 9B): vas deferens not observed, except for most ectal part, which enters ectal end of atrial ampulla; atrium with

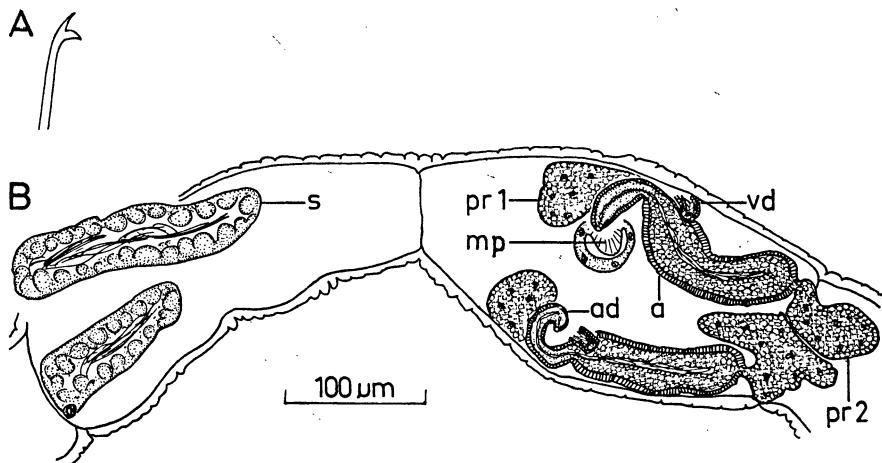


FIG. 9
Bathydrilus medius sp.n.

A: free-hand drawing of seta; B: ventral (somewhat oblique) view of spermathecae and male genitalia.
ad, atrial duct; mp, male papilla; vd, vas deferens; other abbreviations as for Fig. 1.

spindle-shaped-to-cylindrical ampulla, 130-140 μm long, about 40 μm wide, with 3.5-5.5 μm thick outer layer of circular or somewhat spirally arranged muscles, and thick inner granulated epithelium; ampulla ectally terminating into narrow, muscular duct, about 50 μm long, opening into small copulatory sac (=“male pore”); this sac is not conspicuously muscular (cf. *B. atlanticus*); ental, apical end of atrium pointing towards posterior end of XI; one prostate gland located anterior to male pore, communicating with ectal part of atrium, another attached to apical end of atrium. Spermathecae (Fig. 9B, s) 125-175 μm long, about 45 μm wide, with irregular lumen containing loose bundles of sperm and globules of secretion; ducts inconspicuous.

Remarks: the atria of *B. medius* sp.n. take an “intermediate” (=medius Latin) position if compared with those of other deep-sea species of *Bathydrilus*; they are neither as stout as those of the large complex of *asymmetricus/atlanticus/hadalis/desbruyereri/sandersi/meridianus* (many of which were treated above), nor as slender as those of *graciliatriatus/longitriatus/argentinae* (treated below). If compared to those species, which are morphologically the most

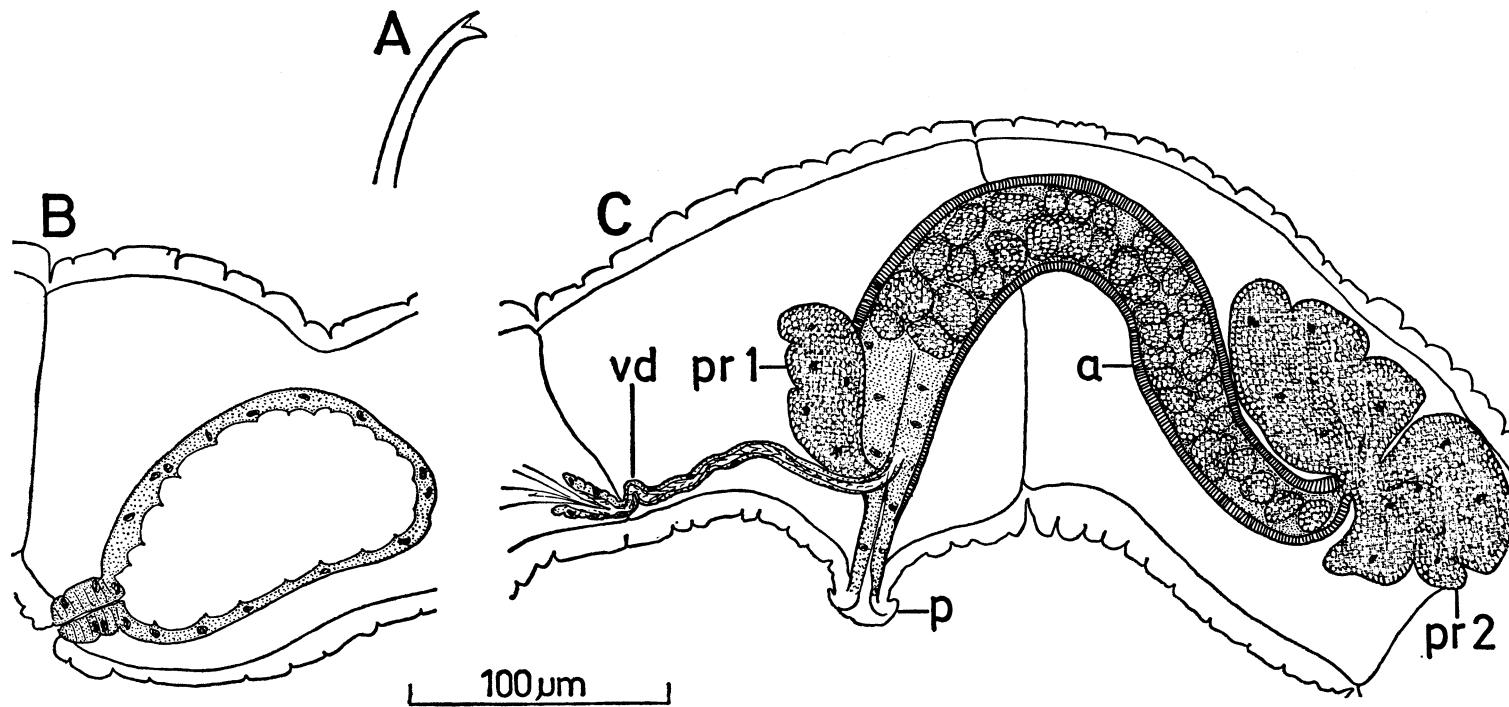


FIG. 10
Bathydrilus longiatriatus sp.n.

A: free-hand drawing of seta; B: spermatheca; C: male genitalia.
vd, vas deferens; other abbreviations as for Fig. 1.

similar to it, *B. medius* differs from *B. asymmetricus* by its thicker atrial musculature and simpler copulatory organs, and from *B. graciliatriatus* by its lack of penial setae.

Habitat and distribution: abyssal fine sediment, 3 338-3 356m. Known only from the type locality, SW of Ireland.

Bathydrilus graciliatriatus Erséus, 1979

Erséus, 1979 a, pp. 143-144, fig. 8.

Material examined: USNM 72992, one specimen from W of Ireland, 51°32.2'N, 12°35.9'W, 1 491-1 500m (WHOI cruise "CHAIN 106", Sta. 313; Aug. 17, 1972).

Remarks: this single specimen conforms to the original description in all characters; for instance, it has sigmoid penial setae, three per bundle, in segment XI.

Habitat and distribution: bathyal fine sediments, 1 491-1 800m. Known only from W of Scotland and Ireland.

Bathydrilus longiatriatus sp.n. (Fig. 10)

Holotype: USNM 72988, a whole-mounted specimen from N of Surinam, W Atlantic, 08°28.8'N, 56°04.5'W, 2 842-2 853m (WHOI cruise "KNORR 25", Sta. 303; Mar. 1, 1972).

Description: length more than 1.9mm, more than 13 segments. Ciliellum poorly developed. Setae (Fig. 10A) bifid, with upper tooth slightly thinner and shorter than lower. Bifids 50-70 μ m long, 1.5-2 μ m thick, 3-4 per bundle anteriorly, 2-3 per bundle in XII and XIII (thereafter, no information available). Ventral setae absent from XI. Male and spermathecal pores paired in line with ventral setae, male pores in posterior part of XI, spermathecal ones in most anterior part of X.

Pharyngeal glands poorly developed. Male genitalia (all structures paired) (Fig. 10C): vas deferens inconspicuous and narrow, shorter than atrium, entering ectal half of atrium; atrium cylindrical, very slender, about 350 μ m long, 27-45 μ m wide, with 4-5 μ m thick muscular layer, and thick inner epithelium consisting of large, granulated cells; atrial lumen not observed; atrium extending into XII; ectally atrium tapering and terminating in simple pseudopenis; anterior prostate gland small, without stalk, attached at entrance of vas deferens; posterior prostate larger, communicating with apical, ental end of atrium, in posterior part of XII. Spermathecae (Fig. 10B) with short ducts, about 25 μ m long, about 22 μ m wide, and large oval ampullae, 130-135 μ m long, 50-70 μ m wide; sperm not observed.

Remarks: none of the previously known species of *Bathydrilus* has such slender atria, as those of *B. longiatriatus* sp.n.

In my revised definition of *Bathydrilus* (Erséus, 1981), I stated that vasa deferentia are "longer than atria". As the vasa deferentia

are distinctly shorter than the atria in *B. longiatriatus*, as well as in *B. argentinae* sp.n. (cf. below), this statement now has to be modified.

Habitat and distribution: abyssal fine sediment, about 2 850m. Known only from the type locality, N. of Surinam.

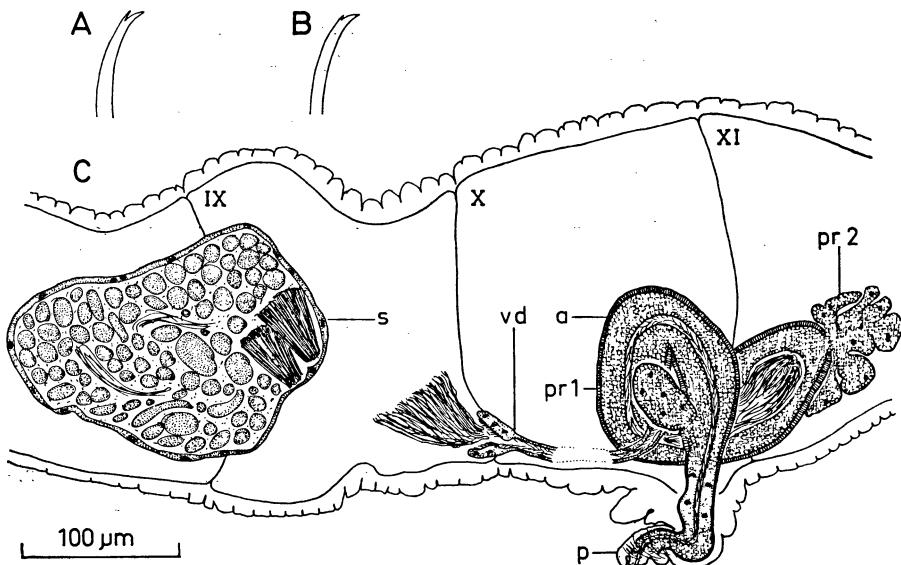


FIG. 11
Bathydrilus argentinae sp.n.

A: free-hand drawing of anterior seta; B: free-hand drawing of posterior seta; C: lateral view of spermatheca and male genitalia in segments IX-XI. vd, vas deferens; other abbreviations as for Fig. 1.

Bathydrilus argentinae sp.n. (Fig. 11)

Holotype: USNM 72989, a whole-mounted specimen from Argentine Basin, off Rio de la Plata, SW Atlantic, 36°32.6'S, 53°23.0'W, 993-1 011m (WHOI cruise "ATLANTIS-II 60" Sta. 237; Mar. 11, 1971).

Paratypes: USNM 72990-72991, two specimens from type locality.

Description: length more than 3.1mm, more than 22 segments; no complete specimens available. Clitellum extending over 1/2IX-XI (holotype and one paratype), or 1/2X-XII (second paratype). Setae bifid, anteriorly with upper tooth thinner and shorter than lower (Fig. 11A), posteriorly upper tooth even further reduced (Fig. 11B). Bifids 55-75μm long, 2-2.5μm thick, (2)3-4 per bundle anteriorly, 2-3 per bundle in post-clitellar segments. Ventral setae absent from segment bearing male pores. Male pores paired on small protuberances in line with ventral setae in posterior part of X (two specimens), or XI (one specimen); cf. extension of clitellum above. Spermathecal pores not observed, but judging from the location of the spermathecal ampullae (Fig. 11C, s), they appear to be located anteriorly in the segment anterior to the one bearing the male pores.

Pharyngeal glands poorly developed. Male genitalia (all structures paired (Fig. 11C): vas deferens inconspicuous, entering ectal end of atrium; atrium slender, generally convulted, but with ental end extending into the segment immediately posterior to the one bearing male pores; atrium 380-430 μ m long, entally 40-65 μ m wide, with 2-3.5 μ m thick lining of muscles, and granulated inner epithelium; in two specimens, atrial lumen entally filled with sperm, but ectally, atrium narrowing, with few sperm; atrium ciliated; most ectal part of atrium tapering into long duct, opening to exterior at summit of small protuberance, the whole complex forming an elaborate, protrusible pseudopenis; anterior prostate gland very small, without stalk, attached at entrance of vas deferens; posterior prostate larger, lobed, attached at apical, ental end of atrium. Spermathecae (Fig. 11C, s) sacciform and large, without discrete ducts, containing a few, very dense bundles of sperm, and numerous granules of secretion.

Remarks: *B. argentinae* sp.n. appears to be closely related to *B. longiatriatus*, but differs from that species by (1) its stouter setae, which have very much reduced upper teeth, (2) its more weakly developed atrial musculature (its atria are not as "stiff" as those of *B. longiatriatus*), and (3) its more elaborate pseudopenes (for instance, compare the lengths of the ectal atrial ducts in Figs. 10C and 11C).

Habitat and distribution: bathyal fine sediment, about 1 000m. Known only from the type locality in the Argentine Basin.

Acknowledgements

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Summary

Ten new bathyal and abyssal species of the genera *Phallodrilus* and *Bathydrilus* (subfamily Phallodrilinae), collected during some French (BIO-GAS) and American (CHAIN, KNORR, ATLANTIS II) oceanographic cruises, are described. Notes on the geographical distribution and morphology of some other species are given.

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In the paper entitled "Deep-sea *Phallodrilus* and *Bathydrilus* (Oligochaeta, Tubificidae) from the Atlantic Ocean, with descriptions of ten new species", by C. Erséus, the illustrations of *Phallodrilus vulnus* sp.n. and *P. cristolatus* sp.n. were transposed. Thus the legend of Fig. 1 actually refers to the drawings of Fig. 2 and *vice versa*.