STUDIES ON MARINE OLIGOCHAETA FROM BERMUDA, WITH EMPHASIS ON NEW *PHALLODRILUS-SPICIES* (TUBIFICIDAE)

by

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Résumé

La faune d'Oligochètes des Bermudes n'est jusqu'ici connue que par quelques travaux. Le présent article apporte la description de formes marines appartenant aux familles des Enchytraeidae et des Tubificidae, récoltées au cours d'études à la « Bermuda Biological Station for Research ». Parmi les Tubificidae, trois nouvelles espèces du genre *Phallodrilus* sont décrites dont deux sans cavité buccale ni intestin. Les caractères concernant la systématique et l'écologie sont discutés ainsi que la position du genre *Phallodrilus* par rapport à *Adelodrilus.*

Introduction

The marine oligochaete fauna from Bermuda is only little known. During several stays at the Bermuda Biological Station for Research, the author collected oligochaete material which supplements our systematic and faunistic knowledge of this group. Attention has been focussed on new Phallodrilus-species from coralline sands in the Bermudian reefs.

Material **and** methods

The list of sampling stations (see below) exhibits that predominantly interstitial species from the shallow reefs around Bermuda have been collected, a habitat which has rarely been sampled for meiofauna studies.

List **of** stations

(with short notes on their edaphic character) (Fig. 1)

1. Tucker's Town Cove; 32°20'N, 64°42'W. Sheltered tidal flat, calcareous sand.

1A. Sand bar near low-water line, mean grain size 250µm; redox-discontinuity layer in about 0.5cm depth.

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1B. Sand flat at mid-tide level, abiotic situation similar to that in 1A.
1C. 1m below mean high-water line, mean grain size 500 to 250µm; rich in plant debris and gastropod shells; oxidized throughout the sediment column.
2. Castle Harbour, Naval Base; 32°21'N; 64°41'W; high-water line.
3. Gibbet Island; 32°19'N, 64°45'W; near inlet to Harrington Sound; high-water line.
4. Nonsuch Island; 32°21'N, 64°40'W; high-water line; fine, well-sorted sand.
5. Ely's Harbour; 32°17'N, 64°53'W; 3-4m depth; coralline sand, rich in debris.

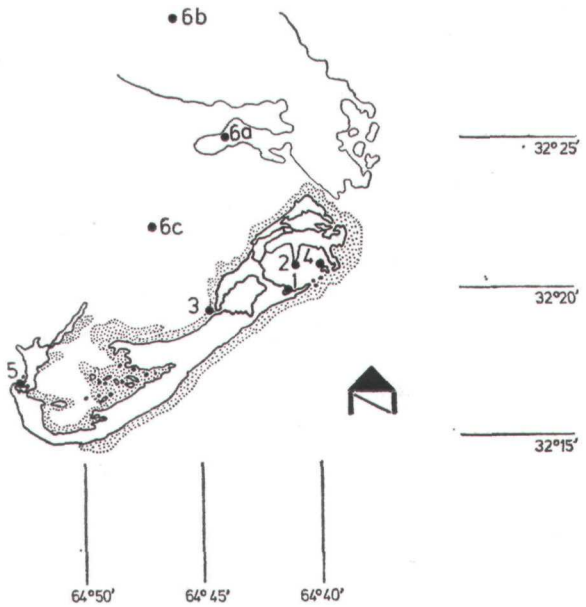

FIG. 1
Investigation area and sampling stations

6. North Shore Reefs, 2-4m depth; coralline sand, mean diameter about 500 to 800µm.
6A. Three Hills Shoals; 32°25'N, 64°44'W.
6B. North Rock; 32°29'N, 64°46'W.
6C. North Lagoon Patch Reefs; 32°11'N, 64°47'W.

The oligochaete fauna was extracted by decantation or elutriation. Specimens were microscopically examined live and photographed (microflash), then anasthetized ($MgCl_2$), preserved (Hollande's Fixative or Worcester Fixative) and kept as whole mounts after staining with Ranvier's Picrocarmine. All tubificid material (except the new *Phallodrilus* species) was fixed (Hollande's) and stored in vials before identification.

If not stated here, synonyme and details of nomenclature are given in Lasserre et Erséus (1976), Erséus and Lasserre (1976) and Erséus (1978).

RESULTS

Family **Enchytraeidae**

***Marionina achaeta* Lasserre, 1964**

Distribution: Tucker's Town Cove (Station **1C),** o-5cm depth; numerous.

Remarks: corresponds in morphological details with original description.

Marionina mesopsamma (Lasserre, **1964)**

Distribution: Gibbet Island (Station **3);** 2-5cm depth; **5** specimens. Nonsuch Island (Station **4), 5-1**0cm depth; **3** subadult specimens. First records for Bermuda.

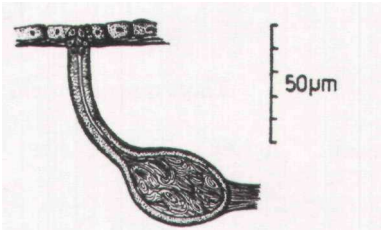

Fig. 2
Marionina mesopsamma
Spermatheca

Remarks: the worms from Bermuda differed somewhat from Lasserre's descriptions (1964, 1966) since they had few small and inconspicuous glandular cells surrounding the ectal opening of the spermathecal duct (Fig. **2)** which was not as long as shown by Lasserre in his figure **4** (1966). Also the lymphocytes were found to be much smaller than mentioned by Lasserre **(1966)** with **a** diameter of half the length of the seta. Despite these smaller differences, the worms certainly belong to *M. mesopsamma* due to good correspondance in all other features.

Grania macrochaeta (Pierantoni, 1901)
Grania macrochaeta bermudensis Erséus et Lasserre, **1976**

Distribution: North Rock (Station 6B); 0-15cm, rare.

Description: length from **8** to 15mm, diameter 140µm; from **43** to **71** segments. Already in these data the specimens exceeded the metric range given for ***G. macrochaeta*** subsp. ***bermudensis*** by Erséus and Lasserre (1976). Moreover, the author encountered worms which in some ante- and postclitellar segments lacked setae completely, in which the dorsal setation began already in XIII, the ventral one not before **VI.** Other differing features: the shape of the proximal setal

end often displayed all variations, from a curved to a typical "heeled" form (Planche 1), occasionally within the same segmentai pair. The sperm duct extended sometimes into XIV. In some specimens, the spermathecal ampulla was filled with a central, irregular cluster of sperm; in others, the spermatozoa were clearly aggregated in balls or rings, scattered within the walls of the ampulla. Penial bulb of medium size.

Remarks: the occurrence of these features, typical for G. *macrochaeta macrochaeta*, among populations from Bermuda makes a separation of a subspecies *"bermudensis"* (Erséus and Lasserre, 1976) questionable. Even the subspecies differentiation in a statistic-numerical sense on the basis of "degrees of differences" (Mayr, 1969, p. 189) requires comprehensive knowledge of the range and frequency of morphological variations within the G. *macrochaeta* group. Hence, the erection of a subspecies *"bermudensis"* is held to be of preliminary character. As shown above, examination of more material would be desirable.

Family Tubificidae

Thalassodrilus belli Cook, 1974 (1)

Distribution: Tucker's Town Cove (Station 1A, 1B), frequent. First records for Bermuda.

Remarks: the morphology of the species is in good correspondance to Cook's description (1974).

Citellio arenicolus (Pierantoni, 1902) (1)

Distribution: Three Hills Shoals (Station 6A); North Rock (Station 6B).

Remarks: no relevant deviations from the redescription by Brinkhurst (1966).

Phallodrilus monospermathecus (Knöllner, 1935)

Distribution: Tucker's Town Cove (Stations 1A-C), abundant (for distributional details see Giere, 1977); Castle Harbour (Station 2), Gibbet Island (Station 3).

Remarks: among the numerous specimens examined both live and fixed, no individual could be found with a spermatheca as small as shown in Lasserre et Erséus (1976): its average length (about 130µm) was about 1/2 to 2/3 of the segment's length.

(1) Identified **by Dr. 0.** Pfannkuche, Hamburg.

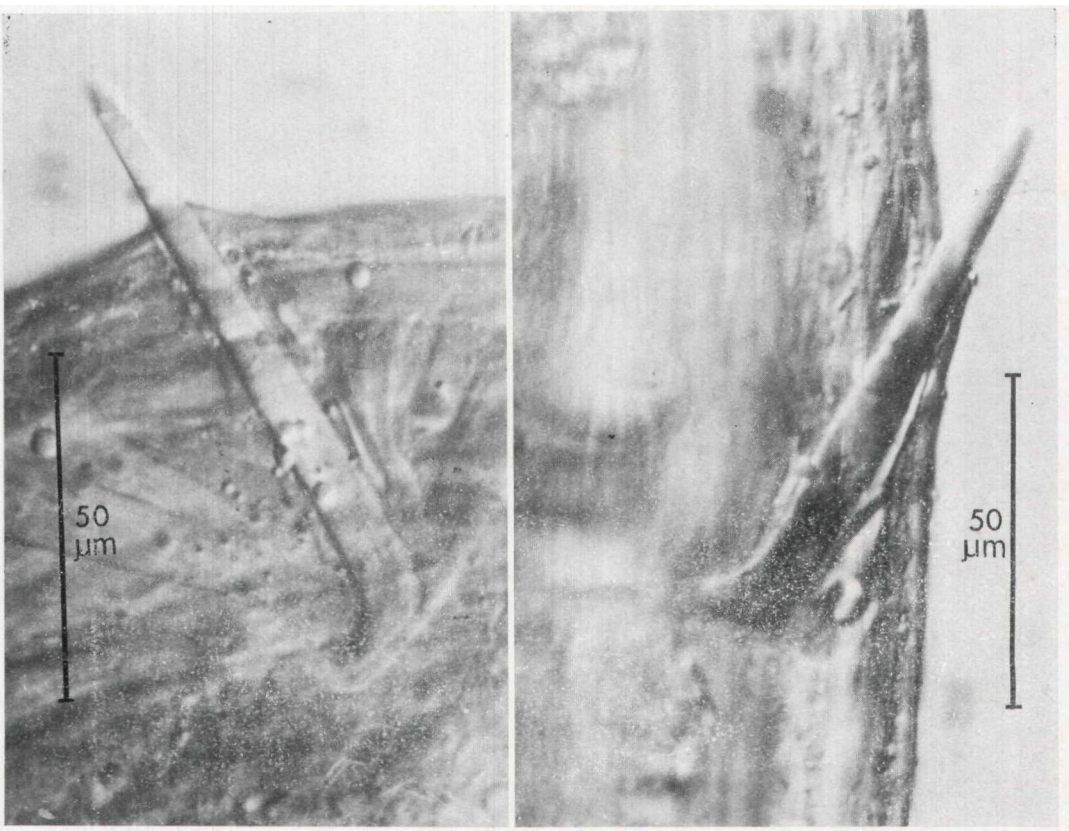

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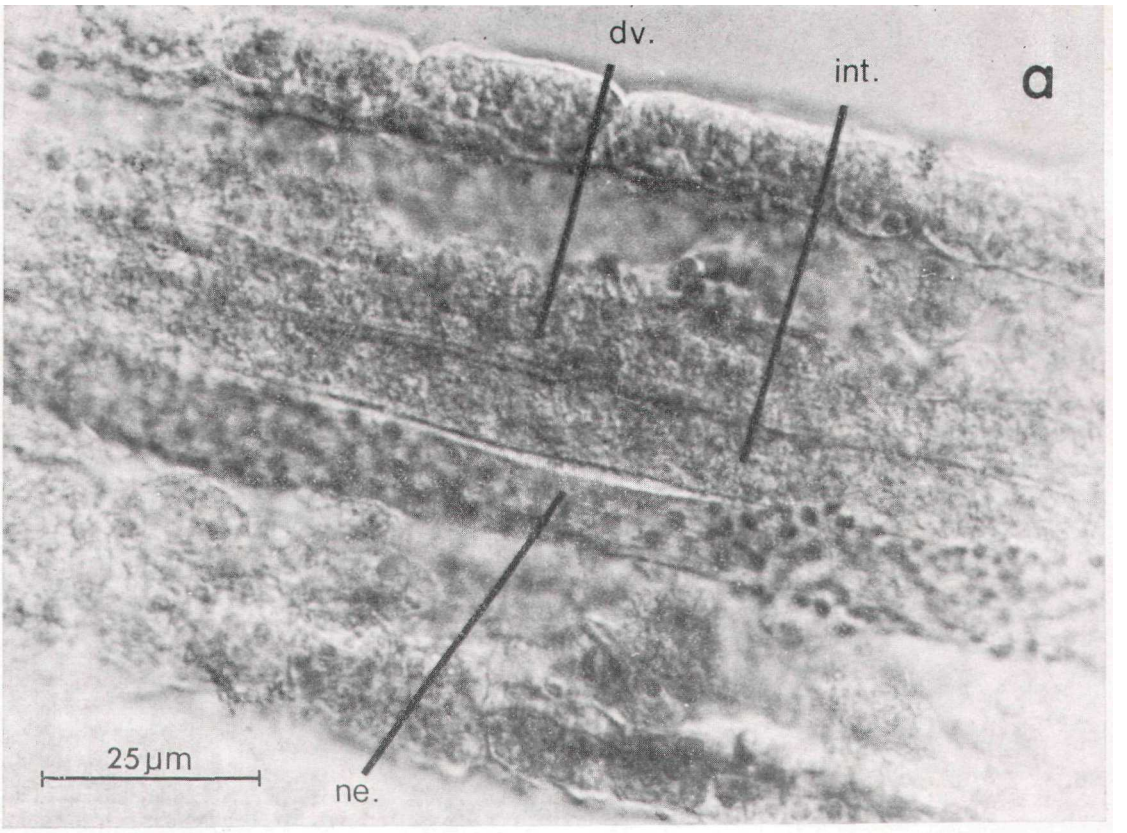
PLANCHE 1

Grenia macrochaeta "bermudensis"

Different shape of setae (Zeiss interference contrast)



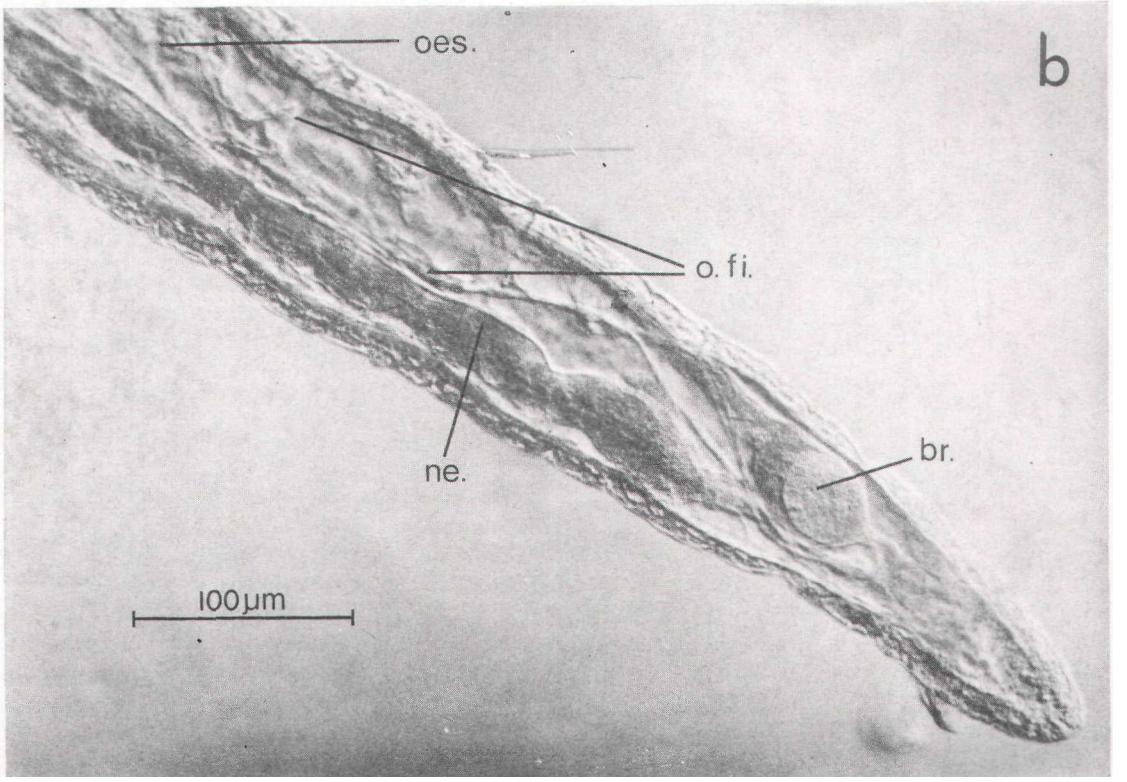


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PLANCHE 2

Phallodrilus longissimus n. sp.

Holotype: Zoological Museum, University of Hamburg, Catalog No. 01.13171, one whole-mounted specimen stained Kith Ranvier's Picro-carmine.

Type locality: Tucker's Town Cove (Station 1B), surface layers, October 3rd, 1975.

Paratype: Zoological Museum, University of Hamburg, Catalog No. 01.13172, one whole-mounted specimen from the type locality.

Derivation: "longissimus"—Latin: the longest, the very long; from its extreme length in relation to width.

Other material examined (author's collection) : several live, whole-mounted and sectioned specimens (juveniles or fragments) from Stations 1B, 6A, 6B.

Description:

External characters: length between 20 to 40mm; diameter only 125µm, in XI: 135µm; about 130 to 155 segments of up to 300am length each. Epidermis with a layer of dermal glands, arranged in 8 to 10 transverse rows per segment, giving the worm a grey to opaque-reddish (incident light) or dark (transmittent light), secondary annulated appearence. Clitellum (little developed) on segments X to 1/2 XII. Prostomium large and elongated, its width 1/2 the length. Mouth opening absent; spermathecal pores paired, lateral, at border between IX and X. Mid-dorsally and mid-ventrally at IX/X one unpaired, deep crypt, each surrounded by massive epidermis cells (Fig. 3, B). One unpaired mid-ventral male pore in posterior part of XI, forming a large, extendible slit (Fig. 3, A).

Setation: (Fig. 3, C) 2 to 3 sigmoid, bifid setae per bundle, about 30µm long, lam thick; (exceptionally, 4 setae in ventral bundles). In some setae, a trend towards a third, minute tooth, derived by differentiation of the upper prong; dorsal tooth longer than ventral; a ligamentous "hood", arising from the shaft of the seta, is attached to the ventral tooth. Many setae with slight indication of a node in the upper half. Segment XI: dorsally only one single-pointed seta/ bundle; penial (ventral) setation highly modified into two bundles containing a marginal giant seta (125µm long, 8µm thick), strongly

PLANCHE 2

Phallodrilus longissimus n. sp.

a: a postclitellar segment, lateral view (whole mount, Zeiss interference contrast): d.v. dorsal blood vessel loosely lined with chloragocytes, int. solid intestinal strand, ne. nerve cord.

b: anterior end (whole mount, Zeiss interference contrast): br. brain, oes. oesophagus, o.fi. oesophageal fibres, ne. nerve cord.

bent, with rounded, simple ectal tip and a thick, curved ental end. Medially are two thin, slightly bent setae of different length (80 and 90µm length resp.) with a strangely club-shaped tip formed by the two flattened teeth.

Blood and nerve system: well developed, corresponding to typical tubificid scheme, blood slightly reddish.

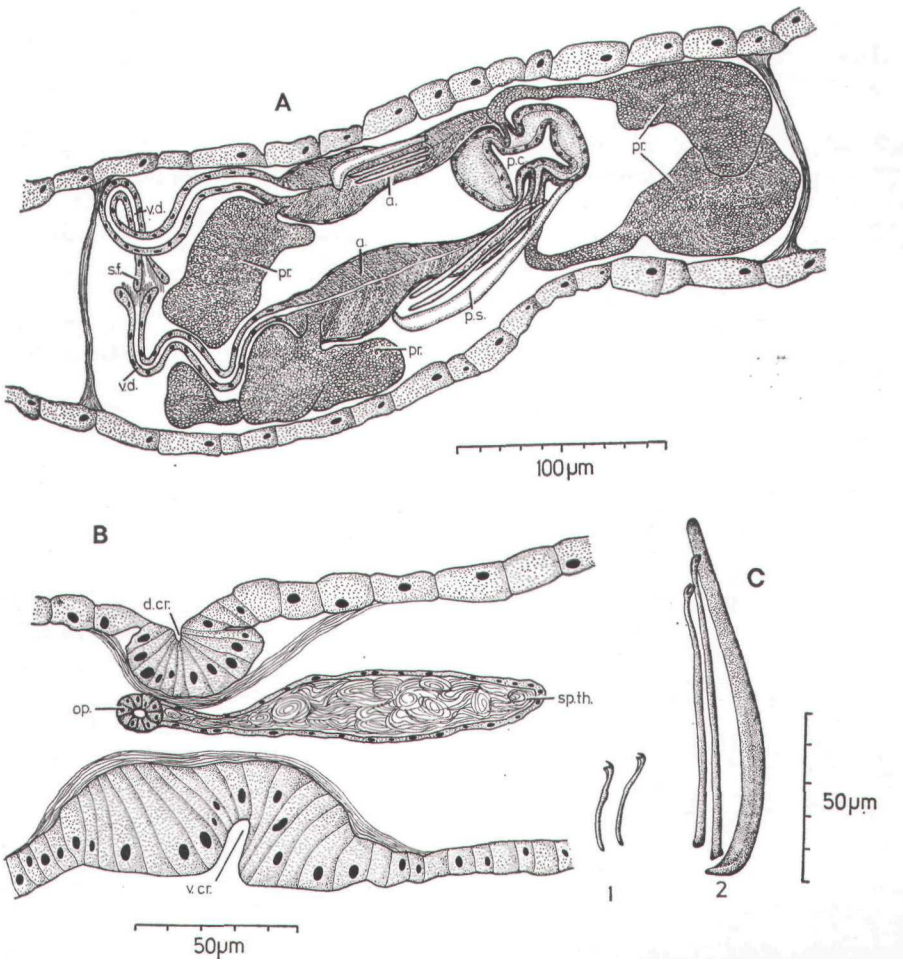


FIG. 3
Phallodrilus longissimus n. sp.
A: male genitalia (one pair of penial setae cut off), ventral view: a. atrium, p.c. penial chamber, pr. prostate glands, p.s. penial setae, s.f. sperm funnel, v.d. vas deferens.
B: spermatheca, lateral view: d.cr. dorsal crypt, op. opening of spermatheca (lateral), sp.th. spermatheca, v.cr. ventral crypt.
C: setation: 1 normal setae (note hood!), 2 penial setae.

Digestive system: gut much reduced, forming a massive strand of tissue without lumen (Planche 2, a). In II, the "oesophagus" splits up into several fibres which loosely adhere to the body walls in segment I and the adjacent organs without any connection to the "mouth region" (Planche 2, b). Pharyngeal glands absent.

Coelomic system: due to the degeneration of the gut, the coelomic cavity is wide and contains relatively large, transparent lymphocytes with central nucleus. In the typical phallodriline mode, the large prostomial walls are lined with numerous small globular cells. Chloragocytes unusually large, surrounding the intestinal tissue as a regular layer from VI/VII (Planche 2, a).

Nephridia: inconspicuous, relatively long and slender, closely parall-eling the body wall.

Genital organs (all structures paired except for male pore) (Fig. 3, A) : small, thick-walled sperm funnels (sf) near septum IX/X, the coiled vas deferens (vd) about 150µm long, about 15µm wide, the thick walls enclosing a narrow, ciliated duct. Atrium (a) very long (length 115µm, width 30µ), with solid, glandular walls and narrow, inconspicuous lumen, opening on a dorso-lateral papilla into the spacious penial chamber (pc). Its aperture, neighboured by the distal ends of the penial setae, is usually slit-like, but along its deep folds widely extendible. The large, lobed anterior prostate gland (pr) in XI joins the atrium with a short duct near the transition to the vas deferens. A second, smaller and more globular prostate gland in the posterior part of XI enters the atrium with a long duct near its ectal orifice. Two huge, unpaired seminal vesicles, filled with irregularly accumulated sperm and spermatocytes, can extend in fully mature specimens from XI anteriorly into IX, the second one posterior-ly untill XV. Small ovaries in their usual ventral position at septum X/XI. One large egg (up to 2 1/2 segments long !) mature at a time in XV-XIII. The slender, thin-walled and sack-like spermatheca (Fig. 3, B) (120µm long; max. 20µm wide) opens with short duct between the dorsal and ventral crypts laterally at transition IX/X. It contains irregular, compact masses of sperm.

Remarks: *Ph. longissimus* n. sp. is, despite its extremely long body, a truly interstitial worm. Its relatively thick body wall, together with its thread-like shape, give it a nematoid appearance which is supported by the rather "stiff", but quick movements with which the worm "glides" through the crevices of grains. Occasionally, the large prostomium was observed to alternatively extend and contract. The meaning of this strange "pumping" habit remains unclear. Under the dissecting microscope, the worm displayed "seeking" and "grop-ing" movements with its anterior end. In water, it coiled up rapidly. In nature, the worm is, apparently, not selective for a defined grain size since it occurred both in fine sand (Station 1 C) and in the coarse shelly sediment of Station 6.

Phallodrilus leukodermatus n. sp.

Holotype: Zoological Museum, University of Hamburg, Catalog No. 01.13173, one whole-mounted specimen, stained with Ranvier's Picro-carmine.

Type locality: North Shore Reef, Bermuda (Station 6), Sept. 14, 1975, 2m depth.

Paratype: Zoological Museum, University of Hamburg, Catalog No. 01.13174, one whole-mounted specimen from the type locality, broken into two pieces, stained with Ranvier's Picrocarmine.

Derivation: ”leukos”—Greek: white; ”derma”—Greek: skin; characterizing the white dermal wall of the worm.

Other material examined (author's collection) : several live or whole-mounted, immature and mature specimens from Stations 3, 5, 6A, 6B, 6C.

Description.

External characters: length 20mm, occasionally 25mm, diameter 180 to 200µm; about 62 to 66 segments. Epidermis with a thick "mantle" of warty dermal glands. Arranged in 6-7, in the median segments up to 13 transverse rows per segment. They give the worm a strong secondary annulation and make it shining in the same bright white (incident light) which characterizes the coralline sediments thus perfectly camouflaging it (in transmittent light, the glandular epidermis makes the live animal completely non-transparent). The glandular layer is less thick in the pregenital segments and the terminal region where the colour of the worm turns to an opaque reddish due to its red blood. Clitellum little differentiated, on segments 1/2 X to 1/2 XII. Prostomium rather pointed, of conical shape, only slightly longer than wide (at its base); mouth opening absent; spermathecal pores paired, in lateral position at transition IX/X. Paired male genital openings ventrally in XI.

Setation (Fig. 4, b) : segments IV to IX with 3 sigmoid bifid setae/bundle, the other segments only with 2 setae/bundle (about 65µm long; 4µm thick). Dorsal tooth of about equal length as ventral; a ligamentous ”hood” (as in Ph. *longissimus* n. sp.) clearly visible. Segment XI (Fig. 4, a) : the dorsal bundles with 2 normal setae, the ventral bundles consisting of 2 strongly sigmoid penial setae (about 75µm long). Their flattened inner part (7µm wide) tapers ectally. The outer (distal) end is sharply bent into a strong hook.

Blood and nerve system: well developed acc. to the typical tubificid scheme, blood reddish; brain posteriorly deeply incised.

Digestive system: as in *Ph. longissimus*, gut much reduced, connected only by few strands to the oral region; no lumen. Pharyngeal glands absent.

Coelomic system: with wide coelomic cavity, oval lymphocytes; the large chloragocytes surround remainders of the gut from V. The prostomial walls are lined, as in other *Phallodrilus*-species, with numerous small globular cells.

Genital organs (all structures paired) (Fig. 4, a) : small, thick-walled sperm funnels (sf) ventrally attached to septum IX/X, the slightly bent vas deferens (vd) about 110µm long, 65µm thick; the relatively thick walls enclosing a narrow, ciliated duct which widens only little when entering the small, spindle-shaped atrium (a). The atrial

opening always near the distal ends of the penial setae (ps). The two prostate glands (pr) kidney-shaped to spherical; the anterior one entering the atrium with a short duct near the transition to vas deferens. The posterior prostate joins the atrium distally with a long duct. Two large seminal vesicles irregularly filled with spermatocytes; the anterior (arising in **X)** extends into **IX,** the posterior fills **XI.** One mature egg at a time in **XV.** The paired spermathecae (sth) form long, relatively thick-walled sacs (about **145µm** long, **25-**40µm wide), filled with irregular masses of sperm. Their glandular short ectal ducts open laterally.

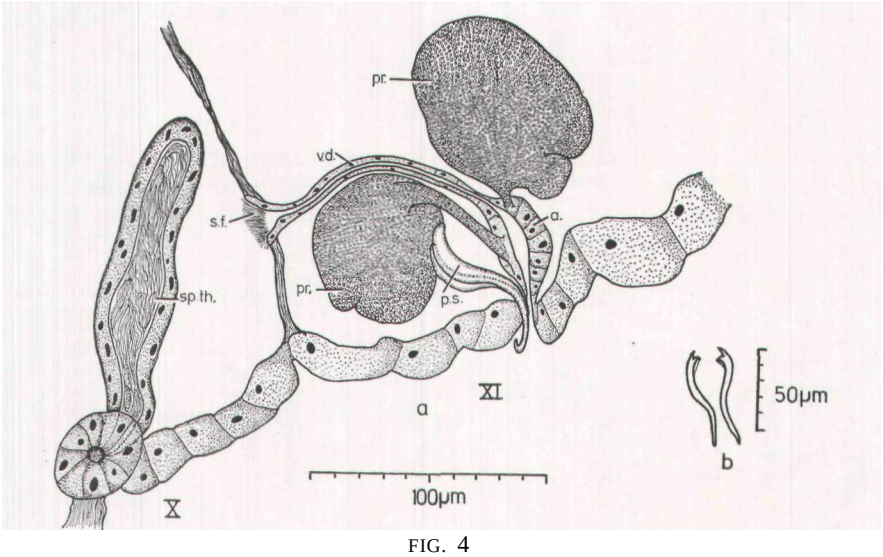


FIG. 4
Phallodrilus leukodermatus n. sp.
a: genitalia, lateral view: a. atrium, pr. prostate glands, p.s. penial setae, s.f. sperm funnel, sp.th. spermatheca, v.d. vas deferens.
b: normal setae (note hood!).

Remarks: the thick, glandular epidermis gives the worm a stiff, nematoid appearence. It moves very slowly.

Phallodrilus ersei n. sp.

Holotype: Zoological Museum, University of Hamburg, Catalogue No. 01.13175, one whole-mounted specimen, stained with Ranvier's Picrocarmine.

Type locality: Three Hills Shoals (Station **6A),** Sept. 9, **1976.** No paratype, no other specimens available.

Derivation: the species is named for fil. kand. Christer Erséus, Göteborg, Sweden, to acknowledge his substantial contributions to the faunistic and taxonomical knowledge of marine oligochaeta.

Description.

External characters: length about 25mm, diameter 340-350µm, in XI: 460µm; 86 segments (holotype). Epidermis with numerous small, irregularly scattered dermal glands, giving the worm a whitish

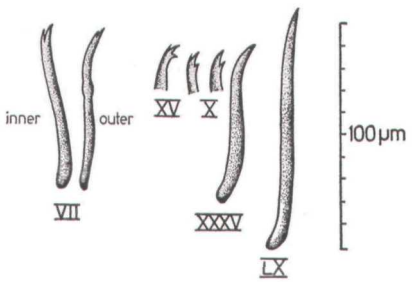
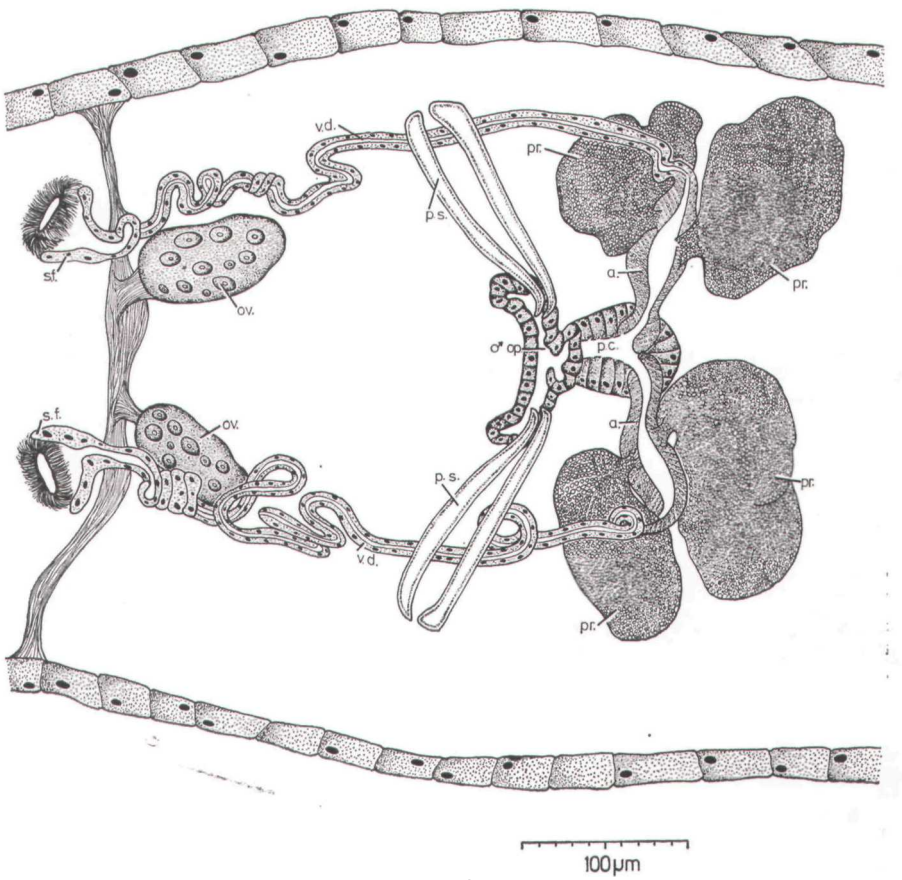


FIG. 5
Phallodrilus ersei n. sp.
Setation in different body regions (for genital setae see Fig. 6).

appearence in incident light. No secondary annulation. No clitellar region in genital segments discernible. Prostomium pointed, relatively small and of conical shape, its base being as wide as its length.



Fio. 6
Phallodrilus ersei n. sp.
Genitalia in XI, ventral view: a. atrium, ♂ op. male opening, ov. ovaries, p.c. penial chamber, pr. prostate glands, s.f. sperm funnel, v.d. vas deferens.

Mouth small; anus terminal. Two spermathecal pores ventrally in X, near septum IX/X; one unpaired mid-ventral male pore in posterior part of **XI** forming a wide, transverse, extensible slit (Fig. 5, 6, 7).

Setation (Fig. 5): segments **II-IX:** 2 slender, sigmoid bifid setae/ bundle (length: 75-105µm, maximal width: 7µm); their ventral prong longer than the dorsal which is particularly small in the outer seta. From the postclitellar region onward, the ventral tooth becomes smaller again, so that the dorsal now exceeds the ventral and often differentiates a third little prong. These tridentate setae are typical for segments **XII** to **XX.** Further caudal, this third tooth disappears gradually, the ventral gets rapidly reduced and from about **XXV** the

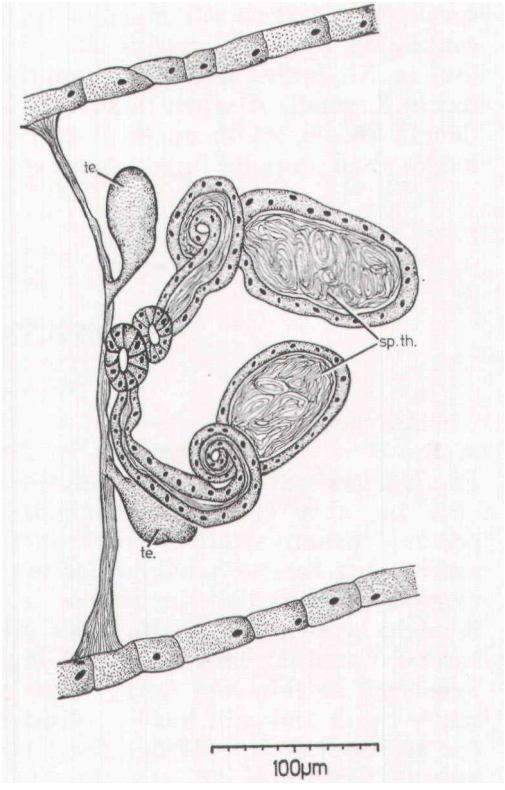


FIG. 7
Phallodrilus ersei n. sp.
Genitalia in X, ventral view (slightly displaced): sp.th. spermathecae, te. testes.

setae are single-pointed, bent needles of different length. Segment **XI:** dorsally normal setae; ventrally 2 thick (12-13µm) and straight, slightly noded giant setae (length: 153µm) directing median; their inner end rather blunt, outer (distal) end hooked, ending near male opening.

Blood and nerve system: well developed acc. to the general tubificine scheme, blood reddish.

Digestive system: gut well developed, intestine in postclitellar segments very wide; pharyngeal glands in IV and V.

Coelomic system: normally developed, in postclitellar segments narrow due to extension of intestine; lymphocytes spherical to oval

with central nucleus, not abundant; spherical, small chloragocytes scattered over walls of gut.

Nephridia: long and slender, closely paralleling the body wall.

Genital organs (all structures paired except for male opening) (Fig. 6) : large, thick-walled sperm funnels (sf) in X attached to septum X/XI. Vas deferens (vd) very long (400-450µm), heavily coiled, about 9µm wide; its narrow duct enclosed by thick walls. Atrium (a) small (length 75µm), oval; lumen spindle-shaped and narrow; opens laterally into posterior part of spacious, extendible penial chamber (pc). 2 solid, globular prostate glands (pr), closely surrounding the atrium, entering it mid-laterally with short ectal ducts. In type specimen, a large median seminal vesicle developed from XI to XIV, containing irregular masses of sperm and spermatocytes. Ovaries (ov) in XI, large, attached to ventral parts of septum X/XI; testes (te) in X, small, attached to septum IX/X. Spermatheca (Fig. 7) long (length 280µm, width up to 65µm), irregularly twisted; its ectal duct longer than ampulla in which no sperm was discernible.

DISCUSSION

Absence of direct observation leaves any functional interpretation of the large and morphologically aberrant penial setae in the above *Phallodrilus-species* a matter of speculation. Their frequent occurrence in other sublittoral phallodriline forms (Erséus, 1978; and personal communication) underlines this setal complication not to represent a rare and unique feature. It is well to imagine that in exposed habitats like the shallow coral reef sands around Bermuda it might be advantageous for successful fertilization to develop structures for mutual hold fast and clinging together. This is especially necessary in thin and long worms which certainly will be twisted many times and will hardly adjust themselves in the right position for sperm transfer without the large penial setae and their strong musculature (not indicated in the figures). The thread-like *Ph. longissimus* has possibly developed the 2 deep crypts as additional ancoring organs for the giant setae.

But also in their "normal" setation, *Ph. longissimus* and *Ph. leukodermatus* seem to be aberrant: possession of a ligamentous ”hood” attached to the lower tooth of the bifid seta is a feature unlike all other oligochaetes and common only in some polychaetes. It seems too early, however, to try any interpretation of the ecological or taxonomical relevance of this feature.

Erséus discussed in a recent paper (1978) the relationships between the genera *Phallodrilus* and *Adelodrilus*, and stressed the uniformity of penial setae in *Phallodrilus* as a main contrast to the heterogeneous and complicated penial setation in *Adelodrilus.* The new *Phallodrilus*-species, described above, with their rather complic-

ated and in two cases even anisomorph penial setation invalidate this character as a crucial feature separating the two genera. A feature both genera have in common are the prostates with their "stalk-like attachments to the male duct" (Brinkhurst and Jamieson, 1971). Even the more or less spoon-or scoop-like shape of the penial setae in *Adelodrilus* can hardly be taken as a good, consistant apomorphic character since this trend, apparently, also occurs in *Phallodrilus* (see Ph. *longissimus* n. sp. with the spoon-shaped ends in its inner penial setae).

Hence, there remains the dilation and functional change of the vas deferens in *Adelodrilus,* a feature which varies very much even within this genus (compare *A. anisosetosus* and *A. voraginus* in Erséus, 1978) and, thus, is, acc. to Remane's (1952) criteria of homology, hardly suitable as a good character to separate genera.

Consequently, for the moment, the maintenance of the *Adelodrillus*-group is a good means of bringing some order into the large, heavily radiating and eurytopic subfamily Phallodrilinae. But the author hesitates to definitely establish the separate generic rank for it since the possible range of morphological diversity is by far not to be foreseen.

Moreover, the great number of new *Phallodrilus-species* to be described soon by Erséus (personal communication), makes it advisable to postpone any discussion about the systematic position of the three *Phallodrilus*-species described here, in relation to other relatives.

One of the most striking features among the phallodriline species described above, is the degeneration of mouth and gut in *Ph. longissimus* and *Ph. leukodermatus.* This trend, unique in annelids, underlines the interstitial system as a biotope still insufficiently understood in its ecological and chemical properties. And it again stresses the relevance of solved organics as a nutritional base for many higher invertebrates. To fully meet the importance of these aspects, a special study is required : it is planned by the author to investigate the chemical ecology of the interstitial system of coralline sands, the ultrastructure of the morphologically and physiologically specialized organs of these *Phallodrilus*-species and, also, to examine the development of the gut in their juvenile stages.

Acknowledgements

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Summary

The oligochaete fauna of Bermuda, known only from few studies, is further investigated and marine species belonging to the families Enchytraeidae and Tubificidae, three of which new to science, two new for Bermuda, are described.

They were collected during stays at the Bermuda Biological Station for Research. Among the tubificids are 3 new Phallodrilus-species, two of them without mouth opening and normal gut. Their systematically and ecologically relevant features and the position of the much radiating genus *Phallodrilus* in respect to *Adelodrilus* are discussed briefly.

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