

# The marine Tubificidae (Oligochaeta) of the barrier reef ecosystems at Carrie Bow Cay, Belize, and other parts of the Caribbean Sea, with descriptions of twenty-seven new species and revision of *Heterodrilus*, *Thalassodrilides* and *Smithsonidrilus*

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Fifty-nine species of Tubificidae are recorded from Belize on the Caribbean side of Central America. Twenty-five are new to science: *Ainudrilus geminus* sp.n., *Heronidrilus gravidus* sp.n., *Heterodrilus flexuosus* sp.n., *H. rarus* sp.n., *H. modestus* sp.n., *Corallidrilus rugosus* sp.n., *C. randyi* sp.n., *Phallogrilus compactus* sp.n., *P. singularis* sp.n., *P. vicinus* sp.n., *P. nasutus* sp.n., *P. bipartitus* sp.n., *Inanidrilus reginae* sp.n., *Olavius finitimus* sp.n., *O. vacuus* sp.n., *O. (Olavius) pravus* sp.n., *Bathydrilus vetustus* sp.n., *B. egenus* sp.n., *Thalassodrilides bruneti* sp.n., *Limnodriloides anxius* sp.n., *L. major* sp.n., *L. sacculus* sp.n., *L. adversus* sp.n., *Smithsonidrilus appositus* sp.n., *S. involutus* sp.n. Phylogenetic analyses indicate that *Heterodrilus* Pierantoni, 1902, *Thalassodrilides* Brinkhurst & Baker, 1979, and *Marcusaedrilus* Righi & Kanner, 1979, are paraphyletic taxa as previously defined. They are therefore revised to include also apomorphic species earlier attributed to separate genera; in so doing, *Marcusaedrilus* becomes a junior synonym of *Smithsonidrilus* Brinkhurst, 1966. *Smithsonidrilus pauper* sp.n. (Peru), and *S. multiglandularis* sp.n. (Florida and Puerto Rico) are also described, and *Limnodriloides claviger* Erséus, 1982 is regarded as a synonym of *L. pierantonii* (Hrabě, 1971).

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## Introduction

Most of the marine species within the Oligochaeta belong to the family Tubificidae, and this group has shown to be especially diverse and abundant in shallow subtropical and tropical waters. Parts of the Caribbean region, especially Bermuda, Florida and Barbados, have been better studied than others with regard to the taxonomy of marine Tubificidae (Brinkhurst 1966, 1986; Erséus 1978, 1979a–c, 1980a–b, 1981a–b, 1982a–c, 1983a–b, 1984a–c, 1986a–b, 1987a, 1988a, 1989a; Erséus & Baker 1982; Erséus & Milligan 1988a; Erséus & Loden 1981; Giere, 1979; Helgason & Erséus 1987; Lasserre & Erséus 1976; Råsmark & Erséus 1986), but information on the fauna of the Caribbean coast of Central and South America is scarce (Erséus 1984a, 1987b, 1988a, 1989a; Righi & Kanner 1979).

The present account primarily deals with the tubificid fauna of the barrier reef off Belize in Central America, an area that is biogeographically representative of a large part of the western Caribbean Sea. This reef is the longest continuous barrier reef in the Western Hemisphere, and it has been the site of intensive marine biological research, particularly since the establishment of the Smithsonian Institution's field laboratory at Carrie Bow Cay in

1972. Carrie Bow (16°48'N, 88°05'W) is a tiny island, about 100 m long, situated on top of the barrier reef proper, about 20 km east of the Belizean coast (Fig. 1). Results of studies on the ecosystems of Carrie Bow Cay and its surroundings have been compiled by Rützler & Macintyre (1982). The area is suitable for studies on the diversity of marine fauna, because of its wide range of habitats within short distances. Within kilometres there are bathyal depths, barrier as well as patch reefs, extensive lagoonal bottoms, largely with seagrass, and mangrove systems.

In April–May 1982, the late Dr Howard R. Baker of University of Victoria, Canada, collected marine oligochaetes while acting as station manager at the Carrie Bow Cay laboratory. Unfortunately, he never had the opportunity to publish any results on his study. After Dr Baker's death in 1983, the material was forwarded to me and parts of it were included in a taxonomic study of the gutless general *Inanidrilus* and *Olavius* (Erséus 1984b), the description of *Bathydrilus formosus* (Erséus 1986b), and a revision of the *Phallogrilus rectisetosus*-complex (Erséus 1988a). The other species in Baker's material are treated in the present paper.

The Belizean tubificid material was substantially supplemented by the author's collections in November 1985.

In this paper, 59 species of Tubificidae, 25 of which are new to science, are reported from the area around Carrie Bow Cay, including also many samples collected at Twin Cays and Blue Ground Range (see Fig. 1) by Dr K. Fauchald and colleagues (National Museum of Natural History, Smithsonian Institution, Washington D.C.) at earlier occasions.

As many of the species found in Belize occur also in collections received from other parts of the Caribbean, these other records are accounted for in this study as well (see *Material and methods*).

Some tubificid genera and subfamilies—and probably the family Tubificidae itself (Erséus 1990a)—are, as currently defined, paraphyletic rather than monophyletic taxa. The members of a paraphyletic taxon are descendants of a common ancestor, but other descendants of the most recent common ancestor are excluded from the taxon. Two of the largest tubificid genera, *Limnodriloides* and *Phallogdrilus* are most probably paraphyletic, but they will require an extensive splitting to achieve strict monophyly for each of the resulting genera (Erséus in press). For some other groups, however, monophyly can be hypothesized by merging an assumedly paraphyletic genus with those species that appear to be apomorphic members of the same lineage, but which to date have been kept in separate (often monotypic) genera. In the present paper, a cladistic analysis and re-classification is made of three such paraphyletic groups, which have members among the Belizean Tubificidae: *Heterodrilus* Pierantoni (enlarged to include *Heterodriloides* Erséus and *Giereidrilus* Erséus), *Thalassodrilides* Brinkhurst & Baker (enlarged to include *Kaketio* Righi & Kanner), and *Marcusaedrilus* Righi & Kanner (becoming a junior synonym when merged with the apomorphic *Smithsonidrilus* Brinkhurst).

Two new species of *Smithsonidrilus*, from Peru and Florida/Puerto Rico, respectively, are also described herein, to make them available for the phylogenetic analysis of the genus.

Finally, the type series of the Caribbean taxon *Limnodriloides claviger* Erséus, 1982 is re-examined in this paper; the holotype of *L. claviger* appears identical to *L. pierantonii* (Hrabě, 1971), whereas the paratypes are identified as *Smithsonidrilus minusculus* (Erséus, 1983) comb.n.

## Material and methods

*Material studied and its preparation.* Most of the specimens studied were collected during a three weeks stay at the Carrie Bow Cay field station (November 1985). Eighty-seven stations, listed below, were visited and sampled qualitatively. Sand and mud samples of varying size were elutriated in the field, the animals and organic debris of the sediment were collected on a sieve with a 0.25 mm mesh screen and brought to the laboratory. The oligochaetes were then sorted live under a dissecting microscope, and (mostly sexually mature) specimens were fixed in Bouin's fluid and transferred into 70% ethanol after 1–2 days.

Some specimens collected in the same way, while visiting the Bellairs Institute of McGill University, in Barbados (in 1979), are also included in this study.

Additional Caribbean marine tubificids were obtained from a number of sources: (1) the collections of the late Dr H. R. Baker, Canada (material from Belize and British Columbia); (2) numerous samples collected by Dr K. Fauchald *et al.*, National Museum of Natural History (USNM), Washington D.C. (from mangrove cays in Belize); (3)

material of the R.V. *Alpha Helix* cruise "CARIB I." in 1977, sorted by the Smithsonian Oceanographic Sorting Center, Washington D.C. (from Belize, Panama and Nicaragua); (4) unidentified tubificids at the Institute of Taxonomic Zoology, Zoological Museum, University of Amsterdam (from various Caribbean islands; coll. P. Wagenaar Hummelinck; see Wagenaar Hummelinck 1977); (5) reference material from various benthic surveys, curated by Mr M. R. Milligan, Mote Marine Laboratory, Sarasota, Florida (from Florida and Puerto Rico); (6) intertidal samples sorted by Dr N. Gourbault & Dr J. Renaud-Mornant, Muséum National d'Histoire Naturelle, Paris (from Guadeloupe); (7) one specimen from the Florida Department of Natural Resources Bureau of Marine Research, St Petersburg, Florida (from Hutchinson Island, Florida; see Erséus 1986b); and (8) a sample collected by Dr R. P. Higgins, USNM (from Ft Pierce, Florida).

Included are also a few specimens provided by Mr D. Davis, formerly at Battelle New England Marine Research Laboratory, Duxbury, Massachusetts (from off North Carolina), Dr L. C. Schaffner, Virginia Institute of Marine Science, Gloucester Pt, Virginia (from Virginia), Dr M. L. Jones, USNM (from Ascension Island), and Dr E. Canahuire C., Universidad Nacional Mayor de San Marcos, Lima (from Peru).

When not stated otherwise, the descriptions are based on whole specimens, for most parts stained with paracarmine, compressed and mounted in Canada balsam. Specimens of some species collected by the author, however, were sectioned and stained with Azan or with Heidenhain's haematoxylin and eosin. Generally, the sections are longitudinal through the genital region of the worm. A few large specimens of *Thalassodrilides ineri* were stained in paracarmine, cut into two halves and the genital region cleared from gonadal products and intestinal structures, and the pieces so prepared mounted in Canada balsam on slides.

Some type material and other old reference specimens in museum collections and author's own collection were re-examined. Such material was borrowed from USNM, IRCZM and FSBC (acronyms explained below).

Type specimens of the new species and other new reference material have been deposited in museums listed below.

In the descriptions, length and width measurements refer to fixed, whole-mounted, and slightly compressed specimens. Roman numerals denote segment number.

*Phylogenetic analyses.* Two generic complexes (*Heterodrilus/Heterodriloides/Giereidrilus* and *Marcusaedrilus/Smithsonidrilus*) were analysed for ingroup phylogenetic relationships using Wagner parsimony, which minimizes (but also accepts) all kinds of homoplasy (convergence as well as reversals) during the construction of cladograms. The program used for these analyses was PAUP (Phylogenetic Analysis Using Parsimony, version 2.4; Swofford 1985). Taxa, characters and character states are listed in Tables I–II and VI–VII. Options selected in the PAUP package are specified in captions of Figs 4 and 31.

The third complex revised (*Thalassodrilides/Kaketio*) was cladistically analysed without the aid of a computer.

## Museum acronyms used in the text

FSBC	Old abbreviation for "Florida State Board of Conservation", now Florida Department of Natural Resources Bureau of Marine Research, St Petersburg, Florida
IRCZM	Indian River Coastal Zone Museum, Ft Pierce, Florida
MNH	Muséum National d'Histoire Naturelle, Paris
SMNH	Swedish Museum of Natural History, Stockholm
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington D.C.
ZMA	Zoological Museum, University of Amsterdam, Amsterdam

## Abbreviations used in the figures

a	atrium
aa	atrial ampulla
ad	atrial duct
cg	copulatory gland
cl	clitellum
cs	copulatory sac
d	diverticulum
e	egg
ead	entrance of atrial duct from other side of worm
ec	epidermal crypt

ed	ejaculatory duct
ep	epidermal pad
fp	flap-like papilla
g	gut
gs	gland associated with spermathecal seta
m	muscles
mb	male bursa
mpa	male papilla
ov	ovary
p	penis
pa	papilla
pp	pseudopenis
ppa	prostatic pad
pr	prostate gland
pr 1	anterior prostate gland
pr 2	posterior prostate gland
ps	penial seta
pso	penial seta of other side of worm
ra	rudimentary atrium
s	spermatheca
sa	spermathecal ampulla
sb	sperm bundle
sd	spermathecal duct
se	seta
sep	septum in atrial ampulla
sf	sperm funnel
sg	spermathecal gland
sp	spermathecal protuberance
ss	spermathecal seta
sv	spermathecal vestibule
sz	spermatocugma
vd	vas deferens

### List of stations

The following stations in the barrier reef off Belize (Fig. 1) were sampled by the author in November, 1985. Carrie Bow Cay is abbreviated CBC. The tubificid species encountered are listed for each station. Two station numbers (53, 63) are omitted from the list; the samples so denoted yielded no tubificid oligochaetes.

**Station 1.** N of inner end of dock, CBC, 0.5 m, patch of heterogeneous medium to coarse sand (6 November 1985); *Heterodrilus flexuosus*, *H. paucifascis*, *H. pentcheffi*, *Phallodrilus deminutus*, *P. molestus*, *Olavius vacuus*, *Duridrilus tardus*, *Smithsonidrilus luteolus*, *S. appositus*.

**2.** Under outer end of dock, CBC, 1.5 m, heterogeneous, somewhat muddy, medium to coarse sand (6 November 1985); *Phallodrilus singularis*, *P. molestus*, *Inanidrilus leukodermatus*, *Bathydrius formosus*, *Smithsonidrilus appositus*, *S. hummelincki*, *Tubificoides bermudae*.

**3.** At N tip of CBC, 0.5 m, coarse sand, gravel and rubble (6 November 1985); *Heterodrilus paucifascis*.

**4.** E side of N tip of CBC, 0.2 m, sand bar with loose, greyish, coarse sand (7 November 1985); *Heterodrilus flexuosus*, *Duridrilus tardus*.

**5.** *Thalassia* bed E of CBC, 0.3 m, heterogeneous, somewhat muddy sand and rubble (7 November 1985); *Heterodrilus flexuosus*, *Phallo-*

*lus molestus*, *Inanidrilus leukodermatus*, *Bathydrius formosus*, *Smithsonidrilus hummelincki*, *Tubificoides bermudae*.

**6.** About 25 m N of CBC, 0.5–0.8 m, coarse sand and rubble (7 November 1985); *Heterodrilus flexuosus*, *H. paucifascis*, *Duridrilus tardus*, *Smithsonidrilus luteolus*.

**7.** Sand bar at S tip of CBC, at high-water line (small depression in beach), medium sand (7 November 1985); *Phallodrilus bipartitus*, *Aktedrilus parvithecatus*.

**8.** Inside reef crest, E of CBC, 0.5–1 m, coarse to medium *Halimeda* sand (8 November 1985); *Heterodrilus flexuosus*, *Olavius tenuissimus*, *Bathydrius formosus*, *Smithsonidrilus appositus*.

**9.** About 50 m N of CBC, 0.7 m, rubble bed with coarse to medium sand beneath rubble (8 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Phallodrilus deminutus*, *P. molestus*, *Inanidrilus leukodermatus*, *Duridrilus tardus*, *Bathydrius egenus*, *B. formosus*, *Smithsonidrilus luteolus*, *S. appositus*, *S. hummelincki*, *Tubificoides bermudae*.

**10.** About 30 m N of CBC, 0.3 m, open sand flat without rubble, medium to coarse sand with ripple marks (8 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Duridrilus tardus*, *Smithsonidrilus luteolus*.

**11.** About 10 m N of CBC, 0.5 m, coarse sand accumulated on leeward side of boulder (8 November 1985); *Heterodrilus flexuosus*, *H. paucifascis*, *H. modestus*, *H. pentcheffi*, *Phallodrilus vicinus*, *Inanidrilus leukodermatus*.

**12.** W of N tip of CBC, 0.5 m, patch of medium sand amongst scattered rocks and *Thalassia* (8 November 1985); *Heterodrilus flexuosus*, *Phallodrilus deminutus*, *P. molestus*, *Smithsonidrilus luteolus*.

**13.** W of S tip of CBC, 2 m, sand patch with fine to medium sand (9 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Olavius imperfectus*, *O. vacuus*, *O. (O.) tantulus*.

**14.** About 15 m S of CBC, outer end of rubble zone, 0.5 m, medium to coarse sand (9 November 1985); *Heterodrilus flexuosus*, *H. paucifascis*, *H. modestus*, *Inanidrilus leukodermatus*, *I. aduncosetis*, *Olavius tenuissimus*, *Duridrilus tardus*, *Smithsonidrilus luteolus*.

**15.** *Thalassia* bed about 20 m S of CBC, 0.2 m, rubble and sand (9 November 1985); *Heterodrilus pentcheffi*, *P. compactus*, *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *Duridrilus tardus*.

**16.** Patch reef E of S part of Blue Ground Range, 1 m, fine to medium sand with *Thalassia* (9 November 1985); *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Bathydrius adriaticus*, *Limnodriloides sacculus*.

**17.** Near mangroves on E side of S part of Blue Ground Range, 0.3 m, small patch of sandy mud in *Thalassia* bed (9 November 1985); *Thalassodrilides gurwitschi*, *T. bruneti*, *T. ineri*, *Tectidrilus bori*, *Limnodriloides rubicundus*.

**18.** Hole in the ground, about 5 m from shore, S end of CBC, at ground water level, medium to coarse sand with a lot of small roots (9 November 1985); *Coralliodrilus rugosus*, *Phallodrilus nasutus*.

**19.** Inside breaker, E of laboratory, CBC, 1 m, small patch of medium to coarse *Halimeda* sand (10 November 1985); *Heterodrilus flexuosus*, *Smithsonidrilus appositus*, *S. involutus*.

**20.** Small sandy beach, W side of Wee Wee Cay, at high-water line, fine, somewhat muddy, sand (10 November 1985); *Heterodrilus flexuosus*, *Aktedrilus parvithecatus*.

**21.** Near same beach (Station 20), 0.3 m, fine sand with mud and roots (10 November 1985); *Thalassodrilides gurwitschi*, *Limnodriloides sacculus*, *L. rubicundus*.

**22.** Sand bore between CBC and Wee Wee Cay, 1 m, heterogeneous gravel and sand (10 November 1985); *Heterodrilus flexuosus*, *H. rarus*, *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Olavius (O.) pravus*.

**23.** N of dock, CBC, 1 m, fine to medium sand and rubble (10 November 1985); *Heterodrilus flexuosus*, *Phallodrilus deminutus*, *P. molestus*, *Inanidrilus leukodermatus*, *Bathydrius formosus*, *Smithsonidrilus luteolus*, *S. hummelincki*.

**24.** Edge of *Thalassia* bed, NE of N tip of CBC, 0.3 m, patch of well sorted coarse sand (11 November 1985); *Heterodrilus pentcheffi*, *Duridrilus tardus*.

**25.** N tip of CBC, at high-water line, coarse sand and gravel at groundwater level (11 November 1985); *Coralliodrilus rugosus*.

**26.** About 100 m N of CBC, 1 m, heterogeneous, somewhat muddy sand

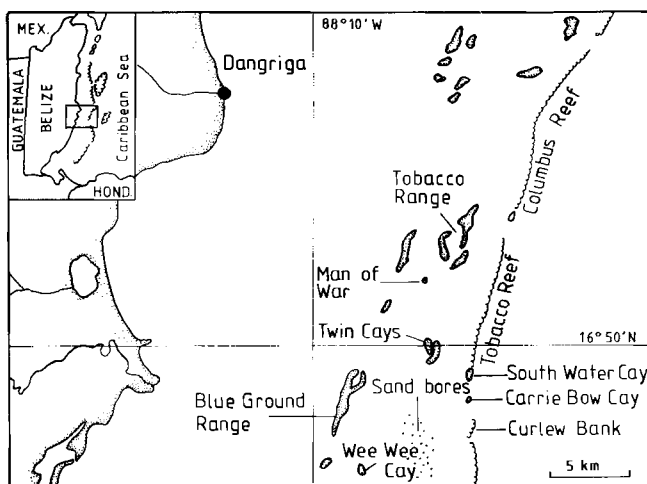


Fig. 1. Map showing studied part of barrier reef off Belize.

- (11 November 1985); *Phallodrilus compactus*, *P. molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Olavius imperfectus*, *O. vacuus*, *Bathydri-  
lus formosus*, *Smithsonidrilus luteolus*, *S. hummelincki*, *Tubificoides bermudae*.
27. NE of N tip of CBC, 0.7 m, small depression with rubble bed, medium to coarse, somewhat muddy, sand under rubble (11 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Inanidrilus leukodermatus*, *I. scalprum*, *Smithsonidrilus luteolus*.
28. *Thalassia* bed NE of N tip of CBC, 0.2 m, medium to coarse sand (11 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Bathydri-  
lus formosus*.
29. Beach above sea wall, E side of CBC, coarse sand at ground water level (12 November 1985); *Phallodrilus bipartitus*.
30. Groove in reef, SW of S tip of CBC, 1.5–1.7 m, coarse *Halimeda* sand (12 November 1985); *Heterodrilus flexuosus*, *Smithsonidrilus hummelincki*.
31. Edge of reef, near *Thalassia* bed, SW of S tip of CBC, 2 m, heterogeneous sand (12 November 1985); *Phallodrilus compactus*, *P. deminutus*, *P. molestus*, *Inanidrilus leukodermatus*, *I. belizensis*, *Olavius imperfectus*, *O. finitimus*, *O. vacuus*, *O. (O.) tantulus*, *Bathydri-  
lus formosus*.
32. Inner end of rubble zone, S tip of CBC, 0.5 m, muddy sand under rubble (slight smell of hydrogen sulfide) (12 November 1985); *Heterodrilus flexuosus*, *H. modestus*, *H. pentcheffi*, *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *I. aduncosetis*, *Bathydri-  
lus formosus*, *Smithsonidrilus hummelincki*.
33. Inside reef 150–200 m N of CBC, 1.5 m, heterogeneous sand (13 November 1985); *Phallodrilus molestus*, *Tubificoides bermudae*.
34. About 40 m NW of N tip of CBC, 0.5 m, medium to coarse sand (13 November 1985); *Heterodrilus paucifascis*, *Smithsonidrilus luteolus*.
35. Rubble zone, S tip of CBC, 0.3 m, muddy coarse sand, with gravel and rubble (13 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Inanidrilus leukodermatus*, *Bathydri-  
lus formosus*.
36. Sand flat at S tip of CBC, 0.2 m, greyish (poorly oxygenated) coarse sand from beneath surface (with smell of hydrogen sulfide) (13 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Duridrilus tardus*, *Bathydri-  
lus vetustus*, *B. formosus*, *Smithsonidrilus appositus*.
37. N end of Big Dipper, Twin Cays, small depression in peat mat at edge of mangroves, 0.3 m, muddy fine sand with *Halimeda* gravel (14 November 1985); *Smithsonidrilus appositus*, *S. hummelincki*, *Tubifi-  
coides bermudae*.
38. Outside entrance channel to Grouper Gardens, Lair Channel, Twin Cays, 1.2 m, muddy fine sand and *Halimeda* gravel (14 November 1985); *Limnodriloides barnardi*, *Tubificoides bermudae*.
39. Inside reef crest SE of laboratory, CBC, 0.5 m, small pockets of heterogeneous sand (15 November 1985); *Bathydri-  
lus formosus*, *Smithsonidrilus appositus*.
40. *Thalassia* bed in front of laboratory, E of CBC, 0.3 m, hetero-  
geneous sand (15 November 1985); *Heterodrilus flexuosus*, *Bathydri-  
lus formosus*, *Limnodriloides barnardi*, *Smithsonidrilus hummelincki*, *Tubificoides bermudae*.
41. Open sand flat W of dock, CBC, 1 m, medium to coarse sand (15 November 1985); *Heterodrilus flexuosus*, *Phallodrilus molestus*, *Inani-  
drilus leukodermatus*, *Tubificoides bermudae*.
42. NW end of reef, N of CBC, 2.5 m, flat inside reef crest with medium to coarse sand (15 November 1985; sediment coll. by C. Brunet); *Heterodrilus pentcheffi*, *Phallodrilus molestus*, *Inanidrilus leukoderma-  
tus*, *Duridrilus tardus*.
43. Inner end of reef flat, NE part of South Water Cay, 0.1 m, heterogeneous, somewhat muddy, sand (15 November 1985); *Phallo-  
dri-  
lus molestus*, *Thalassodrilides bruneti*, *Smithsonidrilus hummelincki*.
44. Inner end of reef flat, at N tip of South Water Cay, 0.1 m, rubble and heterogeneous, somewhat muddy, sand (15 November 1985); *Phallo-  
dri-  
lus compactus*, *P. molestus*, *Bathydri-  
lus formosus*.
45. At dock of "University of Southwater Cay", 0.5 m, muddy (grey) medium to coarse sand (15 November 1985); *Smithsonidrilus humme-  
lincki*, *Tubificoides bermudae*.
46. As Station 45, but 1 m, muddy fine to medium sand, with large mounts and shrimp burrows (15 November 1985); *Heronidrilus gravi-  
dus*, *Limnodriloides barnardi*, *Tubificoides bermudae*.
47. Reef crest NE of CBC, 1 m, patch of heterogeneous medium to coarse sand with *Halimeda* flakes (16 November 1985); *Heterodrilus flexuosus*, *H. paucifascis*, *H. modestus*, *Phallodrilus molestus*.
48. As Station 24, 0.3 m, but deeper (0.1–0.2 m) in sediment, greyish (poorly oxygenated?) sand (16 November 1985); *Heterodrilus paucifas-  
cis*, *Smithsonidrilus luteolus*.
49. *Thalassia* bed E of N tip of CBC, 0.2 m, muddy, heterogeneous, very fine to medium sand (16 November 1985); *Inanidrilus leukodermatus*, *I. reginae*, *Olavius (O.) tantulus*, *Limnodriloides monotheucus*, *L. sacculus*, *Smithsonidrilus hummelincki*.
50. Steep slope on E side of large patch reef at N end of "sand bore" area, between CBC and Wee Wee Cay, 1 m, small patches of somewhat silty, medium to coarse sand (16 November 1985); *Heronidrilus gravi-  
dus*, *Heterodrilus flexuosus*, *H. rarus*, *H. quadrithecatus*, *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *Smithsonidrilus appositus*.
51. As Station 50, slope of reef (E side), but 3 m, heterogeneous fine to coarse sand, with *Penicillum* and a few *Thalassia* (16 November 1985); *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *I. belizensis*, *I. aduncosetis*, *Olavius (O.) tantulus*, *Smithsonidrilus appositus*, *Tubificoides bermudae*.
52. W side of one of the middle group cays in Blue Ground Range, 1 m, coral rubble and fine, somewhat muddy, sand (17 November 1985); *Bathydri-  
lus adriaticus*, *Limnodriloides anxius*, *L. barnardi*, *L. rubicundus*, *Smithsonidrilus hummelincki*.
54. Small sandy beach on W side of one of the cays in the middle group of Blue Ground Range, at high-water line, heterogeneous sand and rubble at groundwater level (17 November 1985); *Aktedrilus longitubularis*, *Jamiesoniella athecata*.
55. SE tip of the largest cay in Tobacco Range, facing Tobacco Cut, 0.7 m, small patch of somewhat muddy and silty coarse *Halimeda* sand near mangroves (18 November 1985); *Tectidrilus hori*, *Smithsonidrilus appositus*, *Tubificoides bermudae*.
56. NE tip of the largest cay in Tobacco Range (i.e., the most north-  
eastern point of the whole group), 0.7 m, patches of muddy, very fine sand, inside *Thalassia* bed (18 November 1985); *Limnodriloides rubi-  
cundus*.
57. Back reef, S end of Columbus Reef, N of Tobacco Cay, 1 m, medium to coarse sand (18 November 1985); *Heterodrilus flexuosus*, *H. modestus*, *H. pentcheffi*, *Phallodrilus molestus*, *Inanidrilus leukodermatus*, *I. belizensis*, *Olavius imperfectus*, *O. finitimus*, *O. vacuus*, *Bathydri-  
lus formosus*, *Smithsonidrilus hummelincki*.
58. In front of laboratory, E of CBC, 0.5 m, medium to coarse sand and rubble under coral clumps (19 November 1985); *Heterodrilus flexuosus*, *H. modestus*.
59. S of dock, CBC, 0.5 m, greyish (poorly oxygenated) sand in *Thalassia* bed (19 November 1985); *Inanidrilus leukodermatus*, *Tubifi-  
coides bermudae*.
60. Rubble zone W of S tip of CBC, 1 m, sand and rubble under coral heads (19 November 1985); *Heterodrilus flexuosus*, *Phallodrilus moles-  
tus*, *Inanidrilus leukodermatus*, *Smithsonidrilus involutus*.
61. At coconut palm tree near house, E side of South Point, Twin Cays, 0.1 m, muddy fine to medium sand (19 November 1985; sediment coll. by C. Brunet); *Thalassodrilides gurwitschi*, *T. bruneti*, *Limnodriloides anxius*, *L. untiampullatus*, *L. barnardi*, *L. rubicundus*, *Smithsonidrilus hummelincki*.
62. Sand trough on outer fore reef, NE of CBC, 24 m, fine to medium sand (20 November 1985; sediment coll. by C. Brunet, SCUBA); *Heterodrilus flexuosus*, *Inanidrilus scalprum*, *I. belizensis*, *Smithsonidri-  
lus luteolus*.
64. Off breakers, SW of CBC, 2.5 m, fine sand (20 November 1985); *Olavius imperfectus*, *O. (O.) tantulus*, *Limnodriloides barnardi*.
65. *Thalassia* bed on reef flat, E of N part of CBC, 0.1 m, greyish coarse sand (21 November 1985); *Phallodrilus molestus*, *Limnodriloides bar-  
nardi*, *Smithsonidrilus appositus*, *S. hummelincki*.
66. Flat on back reef, Curlew Bank, 3 m, fine to medium sand (21 November 1985); *Heterodrilus flexuosus*, *Phallodrilus molestus*, *Inani-  
dri-  
lus leukodermatus*, *Smithsonidrilus luteolus*.
67. Curlew Bank, 1.2–1.5 m, heterogeneous sand (21 November 1985); *Heronidrilus gravidus*, *Heterodrilus flexuosus*, *Bathydri-  
lus formosus*, *Limnodriloides barnardi*, *Smithsonidrilus luteolus*, *S. appositus*, *S. hum-  
melincki*.
68. Top of Curlew Bank, 0.3 m, coarse sand and rubble (21 November 1985); *Heterodrilus flexuosus*, *H. paucifascis*, *H. modestus*, *H. ersei*,

*Olavius (O.) longissimus*.

69. Channel S of CBC, 4.5 m, well sorted medium sand (21 November 1985; sediment coll. by C. Brunet, SCUBA); *Heterodrilus modestus*, *H. ersei*, *Phalodrilus molestus*.

70. As Station 69, 4.5 m, but fine to medium sand (21 November 1985; sediment coll. by C. Brunet, SCUBA); *Heterodrilus flexuosus*, *Phalodrilus molestus*, *Smithsonidrilus luteolus*.

71. As Station 68 (but 22 November 1985); *Heterodrilus paucifascis*, *H. modestus*, *H. ersei*, *Olavius (O.) longissimus*.

72. Small patch reef E of S end of middle group of cays, Blue Ground Range, 1 m, greyish (poorly oxygenated) medium sand (22 November 1985); *Phalodrilus molestus*, *Inanidrilus leukodermatus*.

73. Off reef end, NW of CBC, 3.5 m, well sorted medium sand (22 November 1985); *Heterodrilus flexuosus*, *Smithsonidrilus hummelincki*.

74. As Station 17 (but 22 November 1985); *Bathydrius adriaticus*, *Thalassodrilides ineri*, *Smithsonidrilus hummelincki*.

75. As Station 17, but 5–10 m further to the north, 0.2 m, muddy fine sand (22 November 1985); *Thalassodrilides gurwitschi*, *T. bruneti*, *Limnodriloides uniampullatus*, *L. rubicundus*.

76. Hollows at foot of buttress in spur and groove zone of reef, E of CBC, 8–9 m, coarse sand and rubble (23 November 1985; sediment coll. by B. Kensley, SCUBA); *Heterodrilus modestus*.

77. Back reef, about 2 km N of South Water Cay, Tobacco Reef, 1.2 m, fine to medium sand (23 November 1985); *Heterodrilus flexuosus*, *H. modestus*, *H. pentcheffi*, *Phalodrilus molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Olavius vacuus*, *Bathydrius formosus*, *Smithsonidrilus hummelincki*.

78. As Station 77, but immediately behind breakers, 0.7–1 m, small patches of heterogeneous sand with *Halimeda* flakes (23 November 1985); *Heronidrilus gravidus*, *Heterodrilus flexuosus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Limnodriloides sacculus*, *Smithsonidrilus appositus*, *S. hummelincki*, *S. involutus*.

79. As Station 77, back reef, but 0.7 m, medium sand (23 November 1985); *Phalodrilus molestus*, *Inanidrilus leukodermatus*, *Smithsonidrilus luteolus*, *S. appositus*, *Tubificoides bermudae*.

80. Back reef, about 200 m N of South Water Cay, Tobacco Reef, 1 m, coarse sand (23 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Phalodrilus molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Olavius imperfectus*, *Duridrilus tardus*, *Bathydrius formosus*, *Tubificoides bermudae*.

81. E of South Water Cay, 27 m, fine sand with *Halimeda* flakes (23 November 1985; sediment coll. by C. Brunet, SCUBA); *Inanidrilus scalprum*, *Olavius tenuissimus*, *O. (O.) tantulus*, *Tectidrilus bori*.

82. As Station 81, but 16.5 m, medium sand with *Halimeda* flakes (23 November 1985; sediment coll. by C. Brunet, SCUBA); *Phalodrilus molestus*, *Inanidrilus leukodermatus*, *I. scalprum*, *Duridrilus tardus*, *Smithsonidrilus luteolus*, *Tubificoides parviductus*.

83. S end of Man of War, 0.7 m, mud (24 November 1985); *Thalassodrilides gurwitschi*, *T. ineri*, *Limnodriloides rubicundus*.

84. W side of N point, Man of War, lower intertidal, fine sand with some rubble (24 November 1985); *Limnodriloides anxius*.

85. As Station 2 (but 24 November 1985); *Bathydrius adriaticus*.

86. As Station 9 (but 24 November 1985); *Heterodrilus flexuosus*, *H. pentcheffi*, *Phalodrilus deminutus*, *P. molestus*, *Duridrilus tardus*, *Bathydrius formosus*, *Smithsonidrilus luteolus*.

87. E of Man of War, 0.5 m, peaty *Thalassia* bed with some fine sand (24 November 1985); *Phalodrilus compactus*, *Bathydrius adriaticus*.

## List of species treated in this paper

(All except those marked with an asterisk are recorded from Belize.)

### Subfamily Rhyacodrilinae:

- Ainudrilus geminus* sp.n.
- Heronidrilus gravidus* sp.n.
- Heterodrilus flexuosus* sp.n.
- Heterodrilus rarus* sp.n.
- Heterodrilus paucifascis* Milligan, 1987
- Heterodrilus modestus* sp.n.
- Heterodrilus pentcheffi* Erséus, 1981
- Heterodrilus quadrihectatus* (Erséus, 1981) comb.n.
- Heterodrilus ersei* (Giere, 1979) comb.n.

### Subfamily Phalodrilinae:

- Coralliodrilus rugosus* sp.n.
- Coralliodrilus randyi* sp.n.
- Phalodrilus compactus* sp.n.
- Phalodrilus singularis* sp.n.
- Phalodrilus deminutus* Erséus, 1979
- Phalodrilus molestus* Erséus, 1988
- Phalodrilus vicinus* sp.n.
- Phalodrilus nasutus* sp.n.
- Phalodrilus bipartitus* sp.n.
- Aktedrilus longitubularis* Finogenova & Shurova, 1980
- Aktedrilus parvithecatus* (Erséus, 1978)
- Jamiesoniella athecata* Erséus, 1981
- Inanidrilus leukodermatus* (Giere, 1979)
- Inanidrilus scalprum* Erséus, 1984
- Inanidrilus belizensis* Erséus, 1984
- Inanidrilus aduncosetis* Erséus, 1984
- Inanidrilus reginae* sp.n.
- Olavius imperfectus* Erséus, 1984
- Olavius tenuissimus* (Erséus, 1979)
- Olavius finitimus* sp.n.
- Olavius vacuus* sp.n.
- Olavius (Olavius) tantulus* Erséus, 1984
- Olavius (Olavius) pravus* sp.n.
- Olavius (Olavius) longissimus* (Giere, 1979)
- Duridrilus tardus* Erséus, 1983
- Bathydrius vetustus* sp.n.
- Bathydrius egenus* sp.n.
- Bathydrius adriaticus* (Hrabě, 1971)
- Bathydrius formosus* Erséus, 1986

### Subfamily Limnodriloidinae:

- Doliodrilus puertoricensis* Erséus & Milligan, 1988
- Thalassodrilides gurwitschi* (Hrabě, 1971)
- Thalassodrilides bruneti* sp.n.
- Thalassodrilides ineri* (Righi & Kanner, 1979) comb.n.
- Tectidrilus gabriellae* (Marcus, 1950)
- Tectidrilus bori* (Righi & Kanner, 1979)
- Limnodriloides monothecus* Cook, 1974
- Limnodriloides anxius* sp.n.
- Limnodriloides major* sp.n.
- Limnodriloides uniampullatus* Erséus, 1982
- Limnodriloides sacculus* sp.n.
- Limnodriloides adversus* sp.n.
- Limnodriloides barnardi* Cook, 1974
- Limnodriloides rubicundus* Erséus, 1982
- Limnodriloides pierantonii* (Hrabě, 1971)\*
- Smithsonidrilus minusculus* (Erséus, 1983) comb.n.
- Smithsonidrilus luteolus* (Erséus, 1983) comb.n.
- Smithsonidrilus appositus* sp.n.
- Smithsonidrilus pauper* sp.n.\*
- Smithsonidrilus hummelincki* (Righi & Kanner, 1979) comb.n.
- Smithsonidrilus marinus* Brinkhurst, 1966\*
- Smithsonidrilus westoni* Erséus, 1982, stat.n.\*
- Smithsonidrilus multiglandularis* sp.n.\*
- Smithsonidrilus involutus* sp.n.

### Subfamily Tubificinae:

- Tubificoides bermudae* Råsmark & Erséus, 1986
- Tubificoides parviductus* Hølgason & Erséus, 1987

## Descriptive part

### Subfamily Rhyacodrilinae

#### Genus *Ainudrilus* Finogenova, 1982

*Remarks.* This genus, with *Vadicola* Baker, 1983(a) as a junior synonym, was recently revised by Erséus (1990b).

#### *Ainudrilus geminus* sp.n. (Fig. 2)

*Holotype.* USNM 127646.

*Type locality.* West Bay, Twin Cays, Belize, 0–0.3 m, mud (6 April 1981; coll. K. Fauchald *et al.*).

*Paratypes.* USNM 127647–127658, 12 specimens from type locality

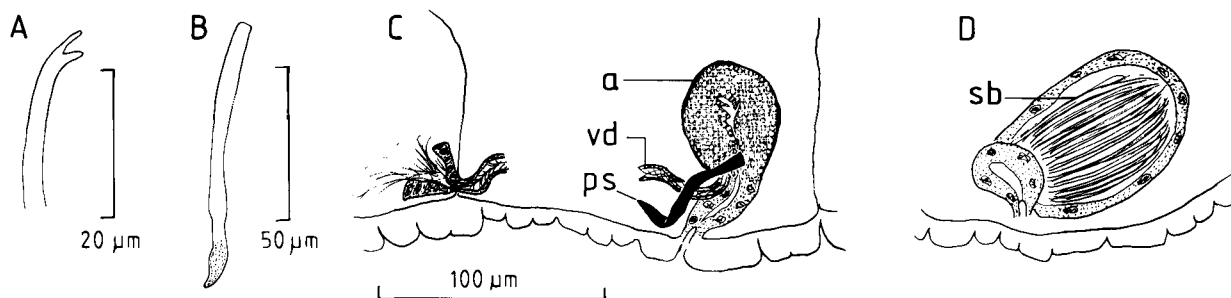


Fig. 2. *Ainudrilus geminus* sp.n.—A. Somatic seta.—B. Penial seta of paratype; dotted area flat.—C. Lateral view of male genitalia in segment XI (holotype).—D. Atrium of another specimen.

(various dates, March–December 1980; coll. K. Fauchald *et al.*). USNM 127659, specimen from W side of middle cay, Blue Ground Range, Belize, intertidal *Caulerpa* mat in mangrove (9 June 1981; coll. K. Fauchald *et al.*).

*Other material.* USNM 127660, specimen from Blue Ground Range (as for paratype above), tentatively identified as *A. geminus* (see *Remarks*).

*Etymology.* The species epithet *geminus* is Latin for 'of double nature' and 'twin', here referring to both the penial setae (generally one on each side of worm, making one pair of penial setae), and the location of the type locality (Twin Cays).

*Description.* Length 2.8–5.2 mm, from about 27 to 40 segments. Width at XI 0.22–0.35 mm. Prostomium variable: rounded and broad, or elongate and well set off from peristomium. Clitellum extending over  $\frac{1}{2}$ X–XII. Somatic setae (Fig. 2A) bifid, with upper tooth longer and slightly thinner than lower. Bifids 50–75  $\mu$ m long, 2–3  $\mu$ m thick, (2)3–6 per bundle anteriorly, (3)4–5 per bundle in postclitellar segments. Penial setae (Figs 2B; C, *ps*) 1(2) per 'bundle', single-pointed, generally somewhat sigmoid, 45–110  $\mu$ m long, 3–7  $\mu$ m wide, with indistinct ectal node and somewhat flattened ectal tip. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores absent.

Pharyngeal glands generally in IV–VI, sometimes indistinct. Gut distended, thick-walled in X. Coelomocytes abundant, globular, 7–12  $\mu$ m wide, granulated. Male genitalia (Figs 2C–D) paired. Vas deferens narrow, longer than atrium, entering latter at base of atrial ampulla, but not well visible in available material. Atrium erect or tilted over to posterior, 40–105  $\mu$ m long, somewhat club-shaped, with round-to-oval ampulla, 25–70  $\mu$ m wide, and short, indistinct duct, 14–21  $\mu$ m wide. Latter opening directly to exterior, pseudopenis (if present at all?) very simple. Atrial ampulla histologically variable, but generally heavily granulated and with narrow lumen (Fig. 2C); see, however, *Remarks*. Lining of atrium thin, not muscular. External prostate glands absent. Spermathecae absent.

*Remarks.* In some of the specimens with very small atria (note wide range in size above), one or two of the ventral setae of segment XI resemble the somatic (bifid) setae and are not penial setae of the kind found in more developed (fully mature) worms. It is therefore concluded that the ventral setae of XI first are normal bifids, and that these are shed and replaced by modified (single-point and ectally flattened) penial setae during sexual maturation.

The non-type specimen from Blue Ground Range is

identified as *A. geminus* with some hesitation. It lacks penial setae on both sides (they may have been shed), and one of its atrial ampullae has thin walls (without granulation) and contains a broad bundle of sperm (Fig. 2D). The latter trait is a common condition for all other species of *Ainudrilus*, and may indicate that this single specimen has reached a later stage of maturity than any of the other specimens of *A. geminus*. However, there is a possibility that the worm represents a separate species.

Regardless of this variation, *A. geminus* is easily separated from its congeners by its (generally) single penial setae (in all others, penial setae at least two per bundle), and consistent lack of spermathecae.

*Distribution and habitat.* Known only from Twin Cays, Belize. Intertidal and barely subtidal, muddy sediment associated with mangroves.

### Genus *Heronidrilus* Erséus & Jamieson, 1981

*Remarks.* The definition of *Heronidrilus* was recently modified (Erséus, 1990b) to include *Macquaridriloides* Erséus & Jamieson, 1981. See also *Remarks* for *H. gravidus* sp.n. below.

### *Heronidrilus gravidus* sp.n. (Fig. 3)

*Holotype.* USNM 127661.

*Type locality.* Curlew Bank, Belize, 1.2–1.5 m (Station 67).

*Paratypes.* USNM 127662–127663, 2 specimens (1 of which sectioned) from type locality. USNM 127664, specimen from Station 78. USNM 127665, specimen from N of Carrie Bow Cay, about 1 m, poorly mixed coral sand under coral overhang (18 April 1982; coll. H. R. Baker).

*Other material* (author's collection). Five specimens from Belize: 1 from near Carrie Bow Cay, shallow water, edge of *Thalassia* bed (7 April 1982; coll. H. R. Baker); 2 from Station 46; and 1 (sexually immature) from each of Stations 20 and 50. Three specimens from Barbados (coll. C. Erséus): 1 from off edge of Bellairs Reef, near sandy beach at Bellairs Research Institute of McGill University, St James, 1–1.5 m, fine sand (22 October 1979); and 2 (1 of which sectioned) from Carlisle Bay, at Bridgetown, 7 m, muddy coarse sand (25 October 1979).

*Etymology.* The species epithet *gravidus* is Latin for 'pregnant', here referring to the presence of large, yolky eggs in all clitellate specimens.

*Description.* Length (only complete specimen) 10.7 mm, 70 segments. Width at XI 0.25–0.45 mm. Prostomium generally pointed triangular. Clitellum extending over  $\frac{1}{2}$ X– $\frac{1}{2}$ XII; well developed in all sexually mature specimens studied. Setae (Fig. 3A) bifid, 40–60  $\mu$ m long, 2–4.5  $\mu$ m thick at node, (1)2–4(5) per bundle anteriorly, (1)2(3) per bundle in postclitellar segments. Bifids with upper tooth distinctly thinner and shorter than lower, and with distinct

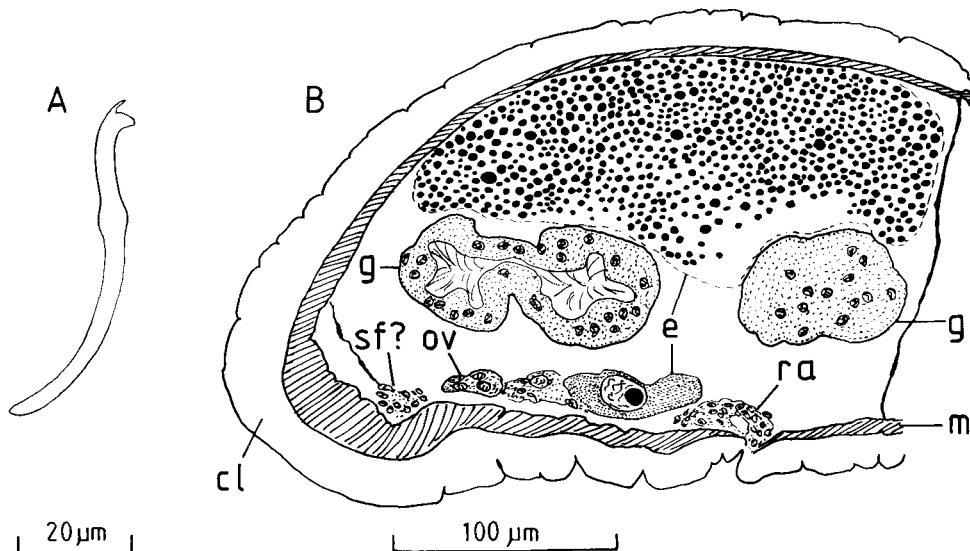


Fig. 3. *Heronidrilus gravidus* sp.n.—A. Seta.—B. Oblique section through clitellar region, largely segment XI.

nodes. Modified penial setae absent; ordinary bifid setae (1–2 per bundle) present or absent, ventrally in XI. Rudimentary male pores sometimes visible in line with ventral setae, posteriorly in XI. Spermathecal pores absent.

Pharyngeal glands extending over III–V, particularly well developed in IV. Oesophagus conspicuously enlarged in VIII. Coelomocytes hyaline, numerous. A pair of testes present anteriorly in X, but maturing or ripe sperm very few or absent. A pair of ovaries (Fig. 3B, *ov*) present anteriorly in XI; one paratype with a second second pair of ovaries in XII. A few large yolky eggs (Fig. 3B, *e*) present in clitellate specimens. Male efferent ducts (Fig. 3B) rudimentary in XI; non-functional sperm funnels (*sf?*), vasa deferentia (visible in sections adjacent to that drawn in Fig. 3B) and poorly developed (non-functional?) atria (*ra*) present in some clitellate specimens. Spermathecae absent.

**Remarks.** The four previously known species of *Heronidrilus*, all from the west Pacific Ocean, have well developed male ducts consisting of ciliated vasa deferentia and tubular atria, latter with numerous prostate cells scattered over surface (Erséus 1990b). The new species from Belize has rudimentary male ducts only, but is recognized as a *Heronidrilus* on the basis of its somatic characters (prostomium triangular; bifid setae with distinct nodes; pharyngeal glands particularly well developed in IV; oesophagus enlarged in segment VIII; coelomocytes numerous, hyaline; cf. Erséus & Jamieson 1981; Erséus 1990b).

Most of the specimens studied are sexually mature, with clitellum thick and eggs well developed. Yet none of them have normally developed male ducts or spermathecae. It is therefore concluded that *H. gravidus* is a uniparental, probably parthenogenetic, species.

**Distribution and habitat.** Belize and Barbados. Intertidal and subtidal sand, to at least 7 m depth.

### Genus *Heterodrilus* Pierantoni, 1902

*Heterodrilus* Pierantoni, 1902: 115–116; Hrabě 1967: 351; Brinkhurst & Baker 1979: 1567; Erséus 1981a: 112.  
*Clitellio* Savigny (*partim*); Brinkhurst 1966: 298–299; 1971: 571.  
*Heterodriloides* Erséus, 1981a: 125.  
*Giereidrilus* Erséus, 1981a: 126.

**Emended definition** (with assumed synapomorphies in *italics*). A group of largely tropical and subtropical marine tubificids. Hair setae absent. *At least some anterior setae trifold (subtilis and hispidus regarded as having lost third tooth secondarily)*. Posterior setae bifid or single-pointed. *Setae two per bundle in most segments anterior to clitellum, only one seta representing each bundle posterior to clitellum*. Setae often large and stout. Penial setae generally present in XI. Spermathecal setae absent. Male pores paired or unpaired, in XI (occasionally in another segment). Spermathecal pores paired or unpaired, generally in X; in one species (*quadrithecatus*) often two pairs, normal pair in XII, supplementary pair rudimentary, in XI. Granulated, round coelomocytes generally abundant. Pharyngeal glands present in IV–V, generally also extending into VI.

Male ducts paired in XI (occasionally in another segment). Vasa deferentia ciliated, short or long, coiled into tight spiral in some species. Atria cylindrical, very long in many species, bearing broadly attached, lobed prostate glands (?secondarily lost in some species). Atria ciliated in all but two species (*ersei* and *inermis*). Spermathecae paired or unpaired, ampullae containing sperm in loose or compact masses, or in loose bundles, often with characteristic granules of secretion. Spermatozeugmata not developed.

**Type species.** *Heterodrilus arenicolus* Pierantoni, 1902.

**Other species.** Listed in Table II. The following taxa are new combinations: *Heterodrilus quadrithecatus* comb.n. (type species of *Heterodriloides*, see below), *H. ersei* comb.n. (type species of *Giereidrilus*, see below), and *H. inermis* (Erséus, 1981a) comb.n. (a South Pacific species, also transferred from *Giereidrilus*, not further treated in present paper).

Table I. Characters and character states used for Wagner analysis of the species of *Heterodrilus* (including the former members of *Heterodriloides* and *Giereidrilus*). Characters with an asterisk (\*) were left unordered. All character transformations are not given unity weight: the factor 2.0 is applied to some (setal, highly diagnostic) features assumed to be less homoplasious than other characters, the factor 0.5 to features for which at least one of the apomorphic states appears very likely to be homoplasious (e.g. loss of penial setae or spermathecae). [See text for further remarks.]

Character	Character states	Weight
1.	Trifid setae confined to preclitellar segments (0); present also in some postclitellar segments (1)	1.0
2.	Setae in segments II–IX (or thereabout) all trifid (0); some 'trifid' setae modified, with third (lower) tooth indistinct, subdistally located (as in Figs 6B, 7B) (1); no trifid setae present, all anterior setae bifid (as in Fig. 6A) (2)	2.0
3.	Postclitellar setae 'normal' bifids, with lower tooth at least as large as upper (see Figs 5B, F) (0); most posterior setae with lower tooth merely as a subdistal swelling (as in Figs 7C–D) (1); most posterior setae all single-pointed, dorsal setae about as long as ventral ones (2); posterior setae single-pointed, dorsal setae distinctly larger than ventral ones (3)	2.0
4.	Penial setae large (0); minute (1)	2.0
5.*	Penial setae two (occasionally three) per bundle (0); one per 'bundle' (1); absent (2)	0.5
6.*	Penial setae straight, evenly thick (0); straight, but with inner ends much wider than rest (1); with outer ends bent (2); curved (at middle), somewhat sigmoid (3); with hooked tips (4)	1.0
7.*	Spermathecal pores paired (0); unpaired, mid-ventral (1); spermathecae absent (2)	0.5
8.	Vas deferens short (0); long, coiled, but not forming spiral (1); long, forming tight spiral (2)	1.0
9.	Vas deferens more or less evenly wide throughout its length (0) distinctly widened at middle (1)	0.5
10.*	Atrium short (0); moderately long, generally C-shaped (1); very long, generally M-shaped (2)	1.0
11.	Atrium ciliated throughout (0); not ciliated throughout (1)	1.0
12.	Atrial musculature thin or only moderately developed (0); very thick (1)	0.5
13.*	Prostate glands as small lobes along atrium (0); absent, or very poorly developed (1); as two large bodies, one on each side of atrium (2)	1.0
14.	Ectal part of atrium (atrial duct) without swelling (0); with swelling (1)	1.0
15.*	Copulatory organ simple, merely a pore (0); distinct, pendent penis present (1); atrium ending in small slender 'peg' inside (glandular?) simple pseudopenis (2)	1.0

**Remarks.** In a revision of tubificid species with trifid (anterior) setae (Erséus, 1981a) three separate taxa were recognized: *Heterodrilus*, *Heterodriloides* and *Giereidrilus*. The two latter are small genera, distinguished from the former, much larger genus by some unique, probably apomorphic features. Many specimens of the monotypic *Heterodriloides* have two pairs of spermathecae instead of one pair, and these spermathecae are located in segments XI–XII, not in X which otherwise is the normal position in Tubificidae. *Giereidrilus* was established for two species with unpaired spermathecal and male pores.

A cladistic analysis of this complex is summarized in Tables I–II and Fig. 4. The phylogenetic implication of the cladogram in Fig. 4, which is only one of many possible trees, is that *Heterodriloides* and *Giereidrilus* in a cladistic sense are advanced members of *Heterodrilus* rather than other taxa of the same rank; *Heterodrilus* as

previously defined (Erséus 1981a) appears paraphyletic, not strictly monophyletic. I therefore suggest that all the species with trifid setae (or modified such setae) rather should be regarded as one large genus, *Heterodrilus*, of which *Heterodriloides* and *Giereidrilus* are junior synonyms.

In an initial analysis (with PAUP) all character transformations were given equal weight, but this resulted in a high number of equally parsimonious trees with very limited congruence in their branching patterns. Moreover, some of the homoplasy suggested by these trees did not seem biologically feasible. Therefore, a second analysis, with *a priori* weighting of some characters (see Table I) was performed; it resulted in fewer, and very similar, cladograms, one shown in Fig. 4. The weighting was admittedly subjective, but as for all phylogenetic analyses (whether or not based on parsimony), a phylogenetic

Table II. Data matrix for Wagner analysis of the species of *Heterodrilus* (including the former members of *Heterodriloides* and *Giereidrilus*). For characters, character states and weights, see Table I. The outgroup is a hypothetical ancestor, resembling species of the genus *Heterodrilus*, but with trifid setae in anterior segments; the latter feature is regarded as a synapomorphy for *Heterodrilus* (see text). NA not applicable

Taxa	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
outgroup	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0
<i>arenicolus</i> Pierantoni, 1902	0	0	1	1	1	3	2	0	0	0	0	0	1	0	2
<i>minisetosus</i> Erséus, 1981a	0	0	0	1	1	4	0	0	0	1	0	0	0	0	1
<i>ascensionensis</i> Erséus, 1981a	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>queenslandicus</i> (Jamieson, 1977)	0	0	0	0	0	2	0	1	1	1	0	0	0	0	0
<i>lacetosus</i> Erséus, 1981a	0	0	0	0	0	2	0	1	1	2	0	1	0	0	0
<i>scitus</i> Erséus, 1981a	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>keenani</i> Erséus, 1981a	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>claviatriatus</i> Erséus, 1981a	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0
<i>subtilis</i> (Picantoni, 1917)	NA	2	1	NA	2	NA	0	2	0	1	0	0	1	0	0
<i>jamiesoni</i> Erséus, 1981a	0	1	1	0	0	0	0	2	0	1	0	0	0	0	0
<i>occidentalis</i> Erséus, 1981a	0	1	2	0	0	1	0	2	0	2	0	0	0	1	0
<i>pentcheffi</i> Erséus, 1981a	0	0	1	0	0	1	0	2	0	2	0	0	0	0	0
<i>bulbiporus</i> Erséus, 1981a	0	0	0	0	0	1	0	2	0	2	0	1	0	0	1
<i>maccaini</i> Erséus, 1985	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
<i>maiusculus</i> Erséus, 1988b	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0
<i>hispidus</i> Erséus, 1986b	NA	2	3	0	0	0	0	2	0	1	0	0	0	0	0
<i>perkinsi</i> Erséus, 1986b	0	0	0	1	0	4	0	0	0	2	0	1	0	0	1
<i>paucifascis</i> Milligan, 1987	0	1	3	0	0	0	0	2	0	1	0	0	0	1	0
<i>flexuosus</i> sp.n.	0	0	0	1	1	0	2	1	0	1	0	0	0	0	1
<i>rarus</i> sp.n.	0	0	0	1	1	3	0	1	0	0	0	0	1	0	2
<i>modestus</i> sp.n.	0	1	2	NA	2	NA	2	1	0	0	0	0	1	0	0
<i>quadrithectatus</i> (Erséus, 1981a) comb.n.	0	0	0	0	0	4	0	2	0	1	0	0	0	0	0
<i>ersei</i> (Giere, 1979) comb.n.	1	0	0	0	0	1	1	1	0	0	1	0	2	0	0
<i>inermis</i> (Erséus, 1981a) comb.n.	1	0	0	NA	2	NA	1	1	0	0	1	0	2	0	0

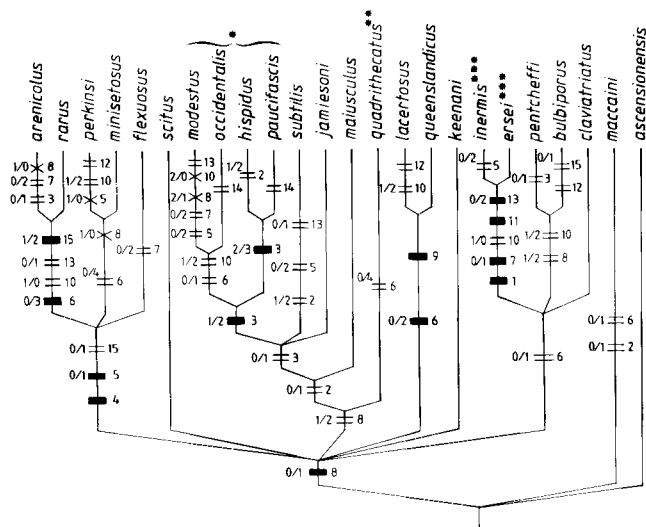


Fig. 4. One of three equally parsimonious cladograms obtained with the PAUP program for the 24 ingroup taxa of *Heterodrilus* (Table II) and their 15 characters (Table I). Character weights are applied (see Table I). Length of tree 57.5 steps, consistency index 0.522. Rooting at the hypothetical ancestor (see head of Table II). The two other trees differ only with regard to the internal topology of the group marked with one asterisk (\*): *hispidus* and *paucifascis* cannot be unambiguously resolved from *modestus* and *occidentalis*. The species previously placed in other genera are marked with two asterisks (\*\*; *Heterodriloides*) and three asterisks (\*\*\*; *Giereidrilus*), respectively. Numbers to the right of symbols refer to characters (Table I), numbers to the left indicate transformations of character states (e.g. 1/2 means 'going from state 1 to state 2'). Filled rectangle represents autapomorphy; two parallel lines, convergence; cross, reversal of character state.

The following options were selected for the execution of the PAUP program: ADDSEQ=CLOSEST, SWAP=ALT, MULPARS, OPT=FARRIS.

hypothesis always remains a hypothesis, and is always only one of several possible hypotheses. Furthermore,

the purpose here is to show that *Heterodriloides* and *Giereidrilus* are members of *Heterodrilus*, not to examine the phylogeny of all species in detail.

The description of the hypothetical ancestor of *Heterodrilus* (Table II) is also based on the subjective assumption that the ancestor already had the trifid setae today characterizing most members of the group, and that this feature has been secondarily lost in the other members. This assumption, which is the most important support for the monophyly of *Heterodrilus*, may of course be challenged.

#### *Heterodrilus flexuosus* sp.n. (Figs 5A–D)

*Holotype*. USNM 127666.

*Type locality*. Columbus Reef, Belize, 1 m (Station 57).

*Paratypes*. USNM 127667–127669, 3 specimens (1 of which sectioned) from type locality. USNM 127670–127676, 7 specimens, 1 from each of Stations 6, 8, 19, 22, 40, 73 and 78.

*Other material* (author's collection). 147 specimens from several stations: 4 from type locality; 6 (2 of which sectioned) from Station 6; 25 (2 of which sectioned) from Station 10; 10 (1 of which sectioned) from Station 19; 1 (sectioned) from Station 22; 6 (1 of which sectioned) from Station 40; 1 from each of Stations 1, 4, 13, 23, 27, 28, 41, 68, 70, 77 and 80; 2 from each of Stations 5, 11, 60 and 73; 3 from each of Stations 12, 14, 30, 58 and 66; 4 from each of Stations 35, 36, 50 and 62; 6 from each of Stations 9 and 78; 7 from each of Stations 32 and 67; 8 from Station 47; and 11 from Station 8.

*Etymology*. This species has long, 'tortuous' (Latin *flexuosus*) vasa deferentia (see *Remarks*).

*Description*. Length (8 specimens measured) 6.0–9.7 mm, 44–65 segments. Width at XI 0.20–0.36 mm. Prostomium large, rounded. Clitellum extending over  $\frac{1}{2}$ X–XII. Setae of II–(IX)X(XI) 2 per bundle, 'bundles' unisetal thereafter. Anterior setae (in II–XII(XIII), or thereabouts)

Table III. Intraspecific variation in number of penial setae of *Heterodrilus flexuosus* sp.n.

Number of penial setae (two sides of worm)	Number of specimen	Percentage of total specimens
0 + 0	2	1
1 + 0	19	13
1 + 1	95	64
2 + 1	23	16
2 + 2	8	5
2 + 0	1	1
Total:	148	99

trifid (Fig. 5A), with uppermost tooth thinner than middle and lower ones. Trifids 50–80  $\mu\text{m}$  long, 3.5–7  $\mu\text{m}$  thick at node. Setae from XIII, XIV or thereabouts, bifid (Fig. 5B), with widely diverging, broad teeth. Bifids 40–75  $\mu\text{m}$  long, 3.5–7  $\mu\text{m}$  thick at node. Some somatic setae with subdental ligament. Penial setae (Figs 5C; D, *ps*) single-pointed, small, 1(2) (occasionally absent) at each male pore (variation shown in Table III). Penials 30–45  $\mu\text{m}$  long, 2.5–3.5  $\mu\text{m}$  thick, straight or very slightly curved (Fig. 5C). Male pores in line with ventral setae, posteriorly in XI. Spermathecal pores absent.

Pharyngeal glands in IV–V(VI). Coelomocytes round,

granulated, abundant. Male genitalia (Fig. 5D) paired. Vas deferens 8–19  $\mu\text{m}$  wide, much longer than atrium, tightly coiled in anterior part of XI and entering apical end of atrium. Atrium cylindrical, generally curved in the way shown in Fig. 5D, 140–225  $\mu\text{m}$  wide, 19–23  $\mu\text{m}$  wide, with outer muscular lining thin but distinct, and inner epithelium ciliated and, at least in its ectal part, granulated. Prostate glands broadly attached to most of length of atrium. Atrium terminating in small, but distinct, penial papilla inside small copulatory sac. Spermathecae absent.

*Remarks.* The genitalia are shifted one segment forward in the paratype from Station 19.

*Heterodrilus flexuosus* is one of the most common tubificids in the coarse sediments of the reefs around Carrie Bow Cay. It was found in no less than 36 of the 87 samples collected by the author. This new form has setae (including the minute penial setae) and atria that are virtually identical to those of *H. minisetosus* Erséus, 1981, known from southeastern United States, Bahamas and Bermuda (Erséus 1981a, 1986b). *Heterodrilus flexuosus* is, however, considered as a separate species, as its vasa

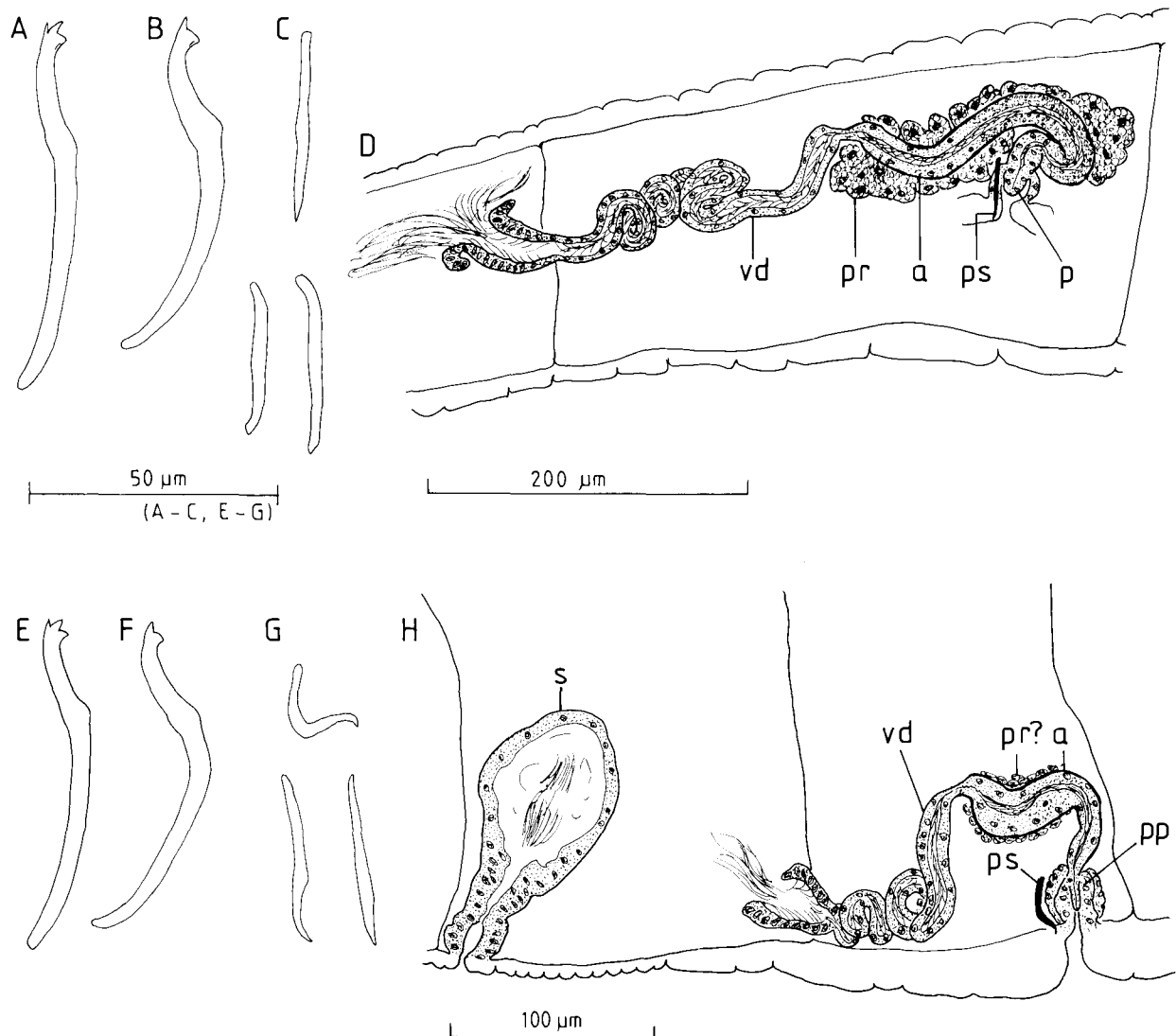


Fig. 5.—A–D. *Heterodrilus flexuosus* sp.n.—A. Anterior somatic seta.—B. Posterior somatic seta.—C. Penial setae of three different specimens.—D. Lateral view of male genitalia in segment XI.—E–H. *Heterodrilus rarus* sp.n.—E. Anterior somatic seta.—F. Posterior somatic seta.—G. Penial setae of three different specimens.—H. Lateral view of spermatheca and male genitalia in segments X–XI.

deferentia are consistently longer than the atria (vasa shorter than atria in *minisetosus*), and by its lack of spermathecae. More than 150 clitellate specimens of *H. flexuosus* were examined, but none had spermathecae.

Spermathecae are, however, present in an additional species with minute penial setae, described below (see *Remarks* for *H. rarus* sp.n.).

*Distribution and habitat.* Known only from the barrier reef off Belize. Subtidal, largely coarse, sands, to at least 24 m depth.

### *Heterodrilus rarus* sp.n. (Figs 5E–H)

*Holotype.* USNM 127677.

*Type locality.* Sand bore between Carrie Bow Cay and Wee Wee Cay, Belize, 1 m (Station 22).

*Paratypes.* USNM 127678–127680, 3 specimens from type locality.

*Other material* (author's collection). One specimen from Station 50.

*Etymology.* This is, in comparison with the very similar *H. flexuosus* described above, an 'uncommon' (Latin *rarus*) species in the area investigated: it was only found at two stations.

*Description.* Length (4 complete specimens) 6.7–8.0 mm, 65–72 segments. Width at XI 0.27–0.37 mm. Prostomium large, rounded. Clitellum extending over  $\frac{1}{2}$ X–XII. Setae of II–X 2 per bundle, 'bundles' unisetal thereafter. Anterior setae (in II–X) trifid (Fig. 5E), with uppermost tooth thinner than middle and lower ones. Trifids 45–90  $\mu$ m long, 2.5–5  $\mu$ m thick at node. Setae from XI, bifid (Fig. 5F) with widely diverging, broad teeth. Bifids 35–70  $\mu$ m long, 2–5  $\mu$ m thick at node. Some somatic setae with subdental ligament. Penial setae (Figs 5G; H, *ps*) single-pointed, very small, (invariably) 1 at each male pore. Penials 27–40  $\mu$ m long, 2.5–3.5  $\mu$ m thick, straight or (sometimes strongly) curved (Fig. 5G). Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores paired in line with ventral setae, anteriorly in X.

Pharyngeal glands in IV–V(VI). Coelomocytes round, granulated, abundant. Male genitalia (Fig. 5H) paired. Vas deferens 12–16  $\mu$ m wide, much longer than atrium, tightly coiled in anterior part of XI and entering apical end of atrium. Atrium cylindrical, 95–120  $\mu$ m long, with a somewhat swollen ental part, 21–42  $\mu$ m wide, outer muscular lining thin but distinct, and inner epithelium ciliated but not much granulated. Prostate glands not large, represented only by small cells scattered in a thin layer over atrial surface. Atrium terminating in a small, slender 'peg' inside simple pseudopenis, but peg not pendent within copulatory sac. Spermathecae (Fig. 5H, *s*) with distinct ducts, and oval ampullae; latter 55–95  $\mu$ m long, 40–60  $\mu$ m wide, and containing a few broad bundles of sperm.

*Remarks.* The five specimens, described here as a separate species (*H. rarus*), were initially sorted as the same taxon as the preceding species (*H. flexuosus*); the trifid, bifid and penial setae are very similar in the two forms. The two samples (from Stations 22 and 50), in which *Heterodrilus rarus* was found, contained also specimens of *H. flexuosus*.

*Heterodrilus rarus* is, however, discriminated from the latter by its shorter atria, less developed prostate glands (note that the specimens are clitellate, sexually mature), and its possession of spermathecae. Moreover, in all five specimens of *H. rarus* the trifid setae occur only through segment X, whereas in *H. flexuosus* they are generally present through segment XII or XIII. This character, however, may vary between different populations of the same species, and, therefore, the difference noted may not hold for other areas of the distribution of the two taxa.

As shown in Figs 5C and G, the penial setae tend to be more curved in *H. rarus* than in *H. flexuosus*, but the difference is hardly diagnostic.

*Heterodrilus rarus* appears closely related to the Mediterranean *H. arenicolus* Pierantoni, 1902, the type species of the genus. The latter has short atria ending in pseudopenes identical to those of *H. rarus* (see Pierantoni 1902; Erséus 1981a), and its penial setae are minute, sigmoid. There are, however, discrepancies indicating that the two forms are different species: in *H. arenicolus*, the upper tooth of the bifid setae is much larger than the lower tooth, the vasa deferentia appear shorter and not as coiled as in *H. rarus*, and spermathecae are absent. [The absence of spermathecae in *H. arenicolus*, noted by Pierantoni (1902), was challenged by Erséus (1981a: 113). However, now that both *H. flexuosus* and *H. modestus* sp.n. are known to lack spermathecae, Pierantoni's statement appears more likely to be accurate.]

The *Heterodrilus* species with minute penial setae (Table IV), including *H. flexuosus* and *H. minisetosus* discussed above, appear to constitute (or be parts of) a monophyletic subgroup within the genus. Monophyly is based on the assumption that the small, generally single (one per 'bundle') penial setae are synapomorphic for the four species in question; all other members of *Heterodrilus*, except *H. subtilis* (Pierantoni, 1917) and *H. modestus* sp.n. described below, which lack penial setae altogether, have two large penial setae at each male pore (see Erséus 1981a, 1986b; Milligan 1987). As for the internal phylogeny of this group, however, the characters are not all compatible with each other. The pattern within the taxa indicate that at least some character states have evolved convergently. The most parsimonious interpretation of

Table IV. Morphological differences between four species of *Heterodrilus* with minute, single penial setae. The apomorphic states of the characters at this level, inferred from the phylogenetic analysis of the whole genus (Tables I–II, Fig. 4), are indicated in *italics*

Character	<i>arenicolus</i> Pierantoni	<i>rarus</i> sp.n.	<i>minisetosus</i> Erséus	<i>flexuosus</i> sp.n.
Vasa deferentia	<i>short</i>	long, coiled	<i>short</i>	long, coiled
Atria	<i>short</i>	<i>short</i>	long	long
Prostate glands	<i>poorly developed</i>	<i>poorly developed</i>	well developed	well developed
Copulatory organs	<i>'reduced' to slender pegs inside simple pseudopenes</i>	<i>'reduced' to slender pegs inside simple pseudopenes</i>	pendent penes <sup>1</sup>	pendent penes
Spermathecae	<i>absent</i>	present	present	<i>absent</i>

<sup>1</sup>In the original description (Erséus 1981a), the copulatory organ was termed pseudopenis for this species. It is, however, more appropriate to regard it as a true penis.

the states shown in Table IV is that short atria, poorly developed prostate glands, and simple pseudopores are synapomorphies for *H. arenicolus* and *H. rarus*, and that short vasa deferentia (characterizing *H. minisetosus*) and lack of spermathecae (characterizing *H. flexuosus*) occur by convergence also in *H. arenicolus*. Thus, there is strong evidence for *H. arenicolus* being the sister taxon of *H. rarus*, which is illustrated also in Fig. 4 (phylogenetic hypothesis of whole genus). The relationships of *H. minisetosus* and *H. flexuosus*, however, are less clear and involve also the position of the highly apomorphic *H. perkinsi* (included in Fig. 4).

*Distribution and habitat.* Known only from the barrier reef off Belize. Subtidal medium to coarse sand, 1 m depth.

### *Heterodrilus paucifascis* Milligan, 1987 (Fig. 6)

*Heterodrilus paucifascis* Milligan, 1987: 481–482, fig. 1.

*Material re-examined.* USNM 101443–101445 (type series) and 1 specimen in Milligan's collection, all from type locality, Puerto Rico.

*New material.* USNM 127681, specimen from Station 48. USNM 127682–127687, 6 specimens (1 of which sectioned) from Station 6. ZMA 2854, specimen from Drunkemans Key, Jamaica, 0–0.5 m, sandy debris (15 June 1973; P. Wagenaar Hummelinck, station no 1683). M. R. Milligan collection: specimen from off Hollywood Beach, Hollywood, E coast of Florida, 36 m, medium sand (22 March 1989). Author's collection: 104 specimens; 8 from Station 8, 3 from Station 1, 4 from each of Stations 3 and 34, 36 from Stations 6, 21 (2 of which sectioned) from Station 11, 9 (1 of which sectioned) from Station 14, 1 from Station 47, 11 from Station 68, and 7 from Station 71.

*Description of material from Belize.* Length (8 specimens measured) 8.5–12.3 mm, 64–80 segments. Width at XI 0.33–0.48 mm. Prostomium round or rounded triangular. Clitellum extending over  $\frac{1}{2}$ X–XII. Setae of II–IX 2 per bundle, somatic 'bundles' unisetal thereafter. Anterior setae (to IX or thereabouts) bifid, with somewhat diverging teeth, and with upper tooth slightly shorter than lower (Fig. 6A); these setae 45–105  $\mu$ m long, 3–5  $\mu$ m thick. Setae of 2–3 following segments with indistinct third tooth (merely a swelling) developing subdistally, and with upper tooth much reduced (Fig. 6B); these setae about

90–100  $\mu$ m long, about 5  $\mu$ m thick. Postclitellar dorsal setae sharply single-pointed (Fig. 6C), up to 115  $\mu$ m long, 7  $\mu$ m thick. Postclitellar ventral setae bifid with a very poorly developed lower tooth (Fig. 6D), these setae distinctly smaller than dorsal ones. Penial setae (Figs 6E; F, *ps*) single-pointed, straight, 2 per bundle, 60–85  $\mu$ m long, 3–3.5  $\mu$ m thick. Penial bundles erect, with proximal ends of setae wider apart than distal ends. Male pores paired in posterior part of XI, not far apart: on each side, male pore located approximately halfway between line of ventral (somatic) setae and mid-ventral line. Spermathecal pores paired, ventral to lines of ventral setae, anteriorly in X.

Pharyngeal glands in (III)IV–V. Coelomocytes round, granulated, abundant. Male genitalia (Fig. 6F) paired. Vas deferens 11–17  $\mu$ m wide, longer than atrium, tightly coiled in anterior part of XI, entering apical end of atrium. Atrium cylindrical, C-shaped, 200–260  $\mu$ m long, 21–32  $\mu$ m wide, with thin outer lining, and ciliated and granulated inner epithelium. Prostate glands well developed, as large lobes covering most of atrial surface. Ectal part of atrium with a bulbous swelling, but opening to exterior small and simple; penial apparatus absent. Spermathecae (Fig. 6F, *s*) with up to about 100  $\mu$ m long, 30  $\mu$ m wide, ducts, and large, elongate ampulla; sperm random or arranged in large bundle in lumen of spermathecae. Granules of secretion generally present in spermathecal walls.

*Brief description of specimen from Jamaica.* Length 8.0 mm, 70 segments. Width at XI 0.25 mm. Many setae broken off, but those remaining intact with tips morphologically similar to those of specimens from Belize. Setae of II–IX 2 per bundle, up to about 80  $\mu$ m long, 3.5–4  $\mu$ m thick, setae 1 per 'bundle' thereafter. Dorsal posterior setae sharply single-pointed, up to about 90  $\mu$ m long, 5  $\mu$ m thick. Ventral posterior setae bifid, up to about 75  $\mu$ m long, 4.5  $\mu$ m thick, with poorly developed lower tooth (as in Fig. 6D). Penial setae about 50  $\mu$ m long, 3  $\mu$ m thick, 2 per bundle. Male genitalia as described above, but somewhat smaller. Spermathecae poorly developed.

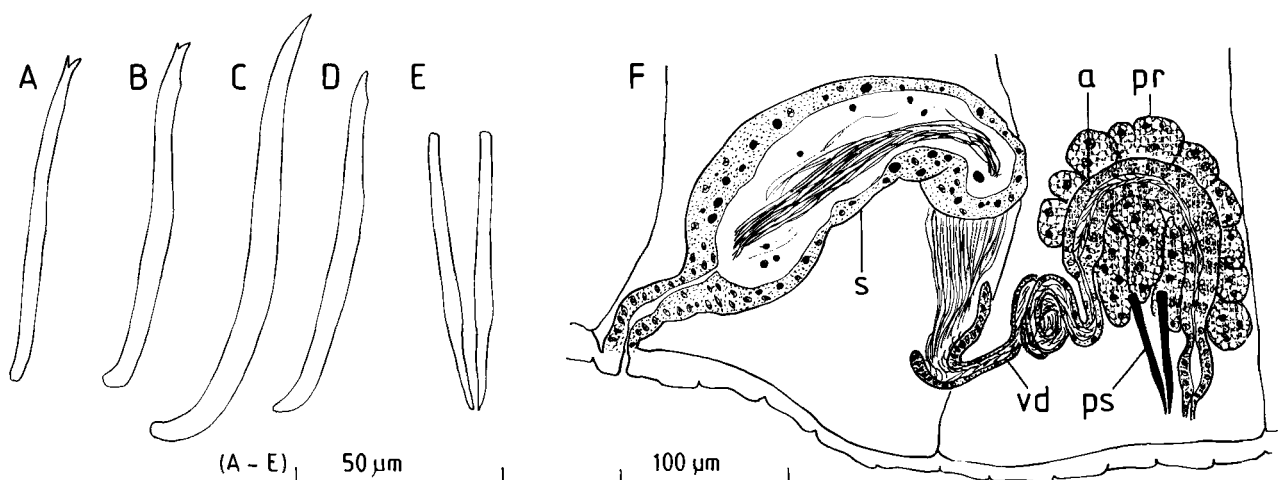


Fig. 6. *Heterodrilus paucifascis* Milligan.—A. Somatic seta of segment VII.—B. Somatic seta of segment X.—C–D. Dorsal (C) and ventral (D) somatic setae of the same postclitellar segment.—E. Penial setae.—F. Lateral view of spermatheca and male genitalia in segments X–XI.

*Brief description of specimen from Florida.* Length 4.4 mm, 60 segments. Width at XI 0.21 mm. Setae of II–IX 2 per bundle, up to 40  $\mu\text{m}$  long, 2.5  $\mu\text{m}$  thick. ‘Trifid’ setae (kind shown in Fig. 6B) present as far back as segment XVIII, thereafter both dorsal and ventral setae somewhat bifid (as in Fig. 6D), to about XXXV; posterior to this, dorsal setae sharply single-pointed and clearly larger (about 55–60  $\mu\text{m}$  long, 2.5  $\mu\text{m}$  thick) than ventral setae (only about 30  $\mu\text{m}$  long, 2  $\mu\text{m}$  thick). Penial setae about 50  $\mu\text{m}$  long, 3  $\mu\text{m}$  thick, 2 per bundle. Male genitalia as described above. Spermathecae with ducts 40  $\mu\text{m}$  long, 16  $\mu\text{m}$  wide, ampullae oval, 85–90  $\mu\text{m}$  long, about 55  $\mu\text{m}$  wide; sperm as large, coiled bundles.

*Remarks.* In one aberrant specimen from Belize (Station 6), two pairs of male ducts are present, in segment XII as well as in (the normal) XI. In this worm the clitellum extends over  $\frac{1}{2}$ X–XIII.

The new material of *H. paucifascis* differs slightly from the original description by Milligan (1987). First, the specimens from Belize and Jamaica are larger than those from Puerto Rico; the latter were only 3.3–6.3 mm long, with up to 56 segments. Second, as indicated by the name *paucifascis* (“few bundles”), the original material had bisetal bundles in segments II–VIII only, whereas in the present material, as in almost all other species of *Heterodrilus*, these bundles invariably occur also in IX. However, a one-segment variability of this kind has been reported from within populations of other species. For instance, specimens of *H. pentcheffi* from Bermuda have bisetal bundles in II–VIII (IX, XI) (Ers us 1981a: 122).

Third, Milligan (1987) did not note any difference in size between the dorsal and ventral setae of the posterior parts of the body, all being described as somewhat bifid (with a “subdistal tooth”). In the new individuals, the dorsal setae of at least a majority of the postclitellar setae are in fact sharply single-pointed, and distinctly larger than the ventral setae in the same segments.

I therefore examined Milligan’s type specimens in the USNM, as well as the single specimen in Milligan’s collection (see Milligan 1987). The holotype is not complete, and very few postclitellar segments remain. The two paratypes, however, are complete; they have many posterior segments in which the dorsal setae are larger than the ventral ones. Moreover, in these segments, the dorsal setae are often distinctly single-pointed, without any lower tooth developed. It is thus concluded that the new material from Belize, Jamaica and Florida reported on here is conspecific to *H. paucifascis* from Puerto Rico.

As already noted by the original author, *H. paucifascis* is very similar to the South Pacific *H. jamiesoni* Ers us, 1981(a), the only diagnostically useful difference being the more pronounced subdistal swelling (=third, lower tooth) on the preclitellar setae from about segment V and onwards, as well as on all postclitellar setae, in the latter species. In the original description of *H. jamiesoni*, the spermathecal ducts were characterized as “short, indistinct”. As pointed out by Milligan (1987), this appears to support the separate status of *H. paucifascis*, which has distinct such ducts. However, after re-examining specimens of *H. jamiesoni* in my possession, I can conclude

that their spermathecal ducts are virtually indistinguishable from those of *H. paucifascis*.

*Distribution and habitat.* Belize, Jamaica, SE Florida (new records), and Puerto Rico. Subtidal, medium to coarse sands, to at least 39 m depth.

### *Heterodrilus modestus* sp.n. (Fig. 7)

*Holotype.* USNM 127688.

*Type locality.* At S tip of Carrie Bow Cay, Belize, 0.5 m (Station 32).

*Paratypes.* USNM 127689, specimen from type locality. USNM 127690–127691, 2 specimens from Station 47. USNM 127692, specimen from Station 57.

*Other material* (author’s collection). Twenty-nine specimens: 1 from each of Stations 11, 14, 32 (type locality), 58, 69 and 77; 4 from Station 47; 10 from Station 68; 7 from Station 71; and 2 from Station 76.

*Etymology.* This species lacks penial setae, prostate glands and spermathecae; the name *modestus* (Latin for ‘moderate’, ‘keeping within bounds’) alludes to this.

*Description.* Length (7 complete specimens) 3.8–6.0 mm, 43–57 segments. Width at XI 0.28–0.37 mm. Prostomium round or rounded triangular. Clitellum extending over  $\frac{1}{2}$ X–XII. Setae of II–(VIII)IX 2 per bundle, ‘bundles’ unisetal thereafter. Anterior setae (to VIII or thereabouts) bifid, with somewhat diverging teeth, and with upper tooth slightly shorter than lower (Fig. 7A); these setae 45–85  $\mu\text{m}$  long, 2.5–4  $\mu\text{m}$  thick. Setae of 2–3 following segments with indistinct third tooth (merely a swelling) developing subdistally, and with upper tooth more reduced than in anterior setae (Fig. 7B); these setae about 80–90  $\mu\text{m}$  long, about 4  $\mu\text{m}$  thick. Postclitellar setae bifid, with poorly developed lower tooth, or more or less single-pointed (Figs 7C–D); these setae up to 100  $\mu\text{m}$  long, up to 7  $\mu\text{m}$  thick, those of most posterior segments however much smaller (Fig. 7D). In postclitellar segments, dorsal setae not larger than ventral ones. Penial setae generally absent (but see *Remarks*). Male pores paired, slightly ventral to lines of ventral setae, in posterior part of XI. Spermathecal pores absent.

Pharyngeal glands in (III)IV–V. Coelomocytes round, granulated, abundant. Male genitalia (Fig. 7E) paired. Vas deferens 8–13  $\mu\text{m}$  wide, much longer than atrium, tightly coiled, entering atrium subapically. Atrium comma-to-club-shaped, 65–95  $\mu\text{m}$  long, 23–33  $\mu\text{m}$  wide, with thin, but distinct outer lining, and moderately thick inner epithelium; i.e. lumen of atrium wider than in most other species of *Heterodrilus*. Atrium epithelium ciliated, at least in ental part, and granulation restricted to ectal part. Ectally, atrium tapering and opening directly to exterior through simple pore; penial apparatus absent. Small cells, possibly representing undeveloped prostatic tissue, scattered over atrial surface, but typical prostate glands absent. Spermathecae absent.

*Remarks.* In the paratype from Station 57, three small penial setae (two of which very short, appearing supernumerary) are developed on one side of the worm, and in the specimen from Station 77, one small penial seta is present on both sides. In all other individuals, penial setae are absent. Penial setae are, however, present in specimens from Nicaragua described below. It is therefore concluded that their occurrence in a few worms in the Belize population of *H. modestus* is an atavism indicating

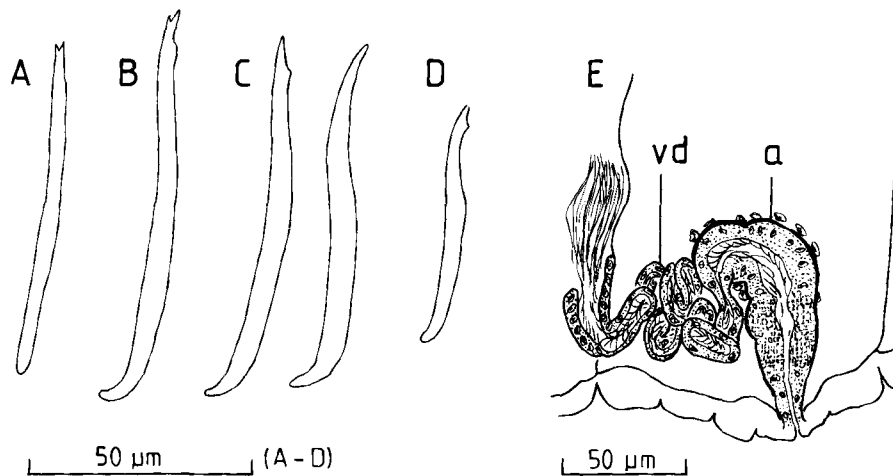


Fig. 7. *Heterodrilus modestus* sp.n., material from Belize.—A. Seta of segment VII.—B. Seta of segment X.—C. Postclitellar setae.—D. Seta of posterior end of worm.—E. Lateral view of male genitalia in segment XI.

the close phylogenetic relationship with forms always bearing such setae.

*Heterodrilus modestus* appears closely related to *H. paucifascis* and *H. jamiesoni*; the morphology and arrangement of somatic setae are similar in the three taxa. As most of the examined specimens of *H. modestus* are clitellate, many also bearing well developed eggs, the lack of penial setae (except for one specimen noted above), prostate glands and spermathecae in this form justifies its specific status. The new species is probably apomorphic with regard to these characters, all of which seem to suggest that *H. modestus* is a uniparental form, reproducing by parthenogenesis or self-fertilization.

In the area studied here (barrier reef off Belize), *H. modestus* is consistently smaller (measured specimens not longer than 6.0 mm, with maximally 57 segments) than *H. paucifascis*, which is at least 8.5 mm long, with at least 64

segments. It is further discriminated from *H. paucifascis* by having dorsal and ventral setae of about the same length in postclitellar segments.

*Distribution and habitat.* Belize and possibly Nicaragua (see below). Intertidal(?) and subtidal medium to coarse sands, to at least 9 m depth.

#### *Heterodrilus* (?) *modestus* (Fig. 8)

*Material.* USNM 127693–127696, 4 specimens from about 30 km off Costa de Mosquitos (between Puerto Cabo Gracias á Dios and Punta Gorda), Caribbean Sea, Nicaragua, 14°34.2'N, 82°58.0'W, lower intertidal, sediment unknown (11 January 1977; CARIB I. *Alpha Helix* Station no. MS-39-500).

*Description.* Length (2 complete specimens) 4.9–5.2 mm, 53–54 segments. Width at XI 0.19–0.25 mm. Prostomium generally rounded triangular. Clitellum extending over

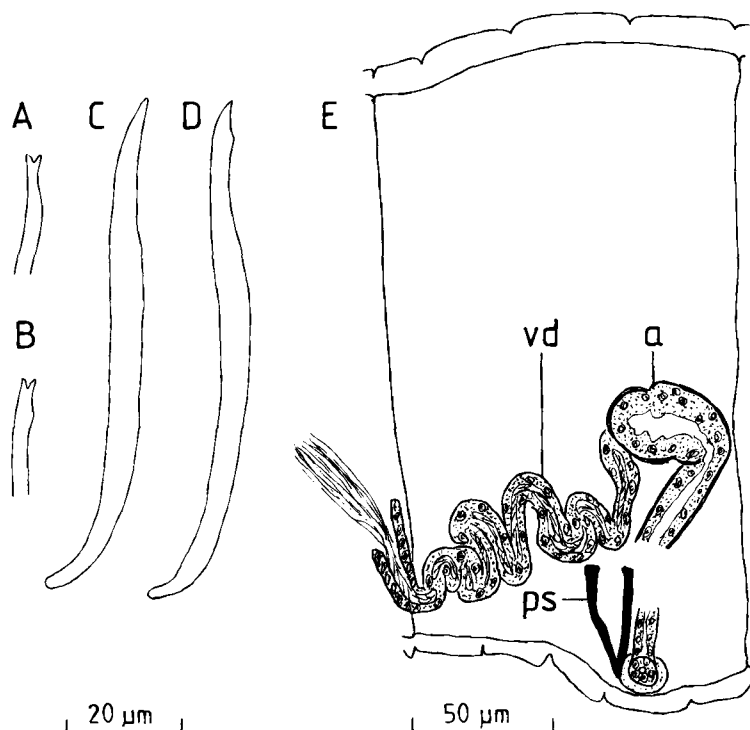


Fig. 8. *Heterodrilus* (?) *modestus* sp.n., material from Nicaragua.—A. Somatic seta of segment III.—B. Somatic seta of segment VIII.—C. Dorsal postclitellar seta.—D. Ventral postclitellar seta.—E. Lateral view of male genitalia in segment XI.

$\frac{1}{2}$ X–XII. Setae of II–(VIII)IX 2 per bundle, ‘bundles unisetal thereafter. Anterior setae (to VII) bifid, with somewhat diverging teeth (Fig. 8A); these setae 45–85  $\mu\text{m}$  long, 2.5–4.5  $\mu\text{m}$  thick. Setae of 2–3 following segments with indistinct third tooth (merely a swelling) developing subdistally (Fig. 8B); these setae about 80–90  $\mu\text{m}$  long, about 4  $\mu\text{m}$  thick. Postclitellar setae first (both dorsal and ventral setae) bifid, with poorly developed lower tooth, but after a varying number of segments, dorsal setae sharply single-pointed (Fig. 8C), ventral setae remaining bifid (Fig. 8D); these setae 75–95  $\mu\text{m}$  long, 4.5–5  $\mu\text{m}$  thick, dorsal setae tending to be somewhat larger than corresponding ventral ones (but not in all segments). Setae of most posterior segments all bifid, smaller. Penial setae (Fig. 8E, *ps*) straight, single-pointed, about 60  $\mu\text{m}$  long (oblique in all mounted specimens), 3.5  $\mu\text{m}$  thick, 2 per bundle. Male pores paired, in line with ventral somatic setae, in posterior part of XI. Spermathecal pores absent.

Pharyngeal glands in IV–V. Male genitalia (Fig. 8E) paired. Vas deferens about 7–10  $\mu\text{m}$  wide (difficult to see), much longer than atrium, tightly coiled, entering atrium subapically. Atrium comma-to-club-shaped, about 90–110  $\mu\text{m}$  long, entally 23–30  $\mu\text{m}$  wide, with thin, but distinct outer lining, and moderately thick inner epithelium; ciliation and granulation of epithelium not observed, but material not well preserved. Ectal part of atrium narrow; opening to exterior simple. Spermathecae absent.

**Remarks.** In one of these four specimens from Nicaragua, the genitalia are shifted forwards two segments; the male pores are in segment IX instead of XI.

This Nicaraguan form appears very closely related to *H. modestus* from Belize (above). However, it differs from the latter by invariably having penial setae. As both forms lack spermathecae and thus may have an uniparental mode of reproduction, they may be regarded as two different strains within the same species, the alternative preferred here. Otherwise, they could be considered as two different (morpho-)species.

### *Heterodrilus pentcheffi* Erséus, 1981

*Clitellio arenicolus* (*partim*); Giere 1979; but not *Clitellio arenicolus* Picranтони, 1902 (= *Heterodrilus arenicolus* s.str.).

*Heterodrilus pentcheffi* Erséus, 1981a: 121–123, fig. 12, table I; 1984d: 196; 1986b: 289–290, fig. 1.

*Heterodrilus* sp.; Erséus 1981a: 123–124, fig. 14.

**New material.** USNM 127697–127701, 5 specimens from Station 80. Author's collection: 43 specimens; 3 (1 of which sectioned) from Station 13, 1 from each of Stations 1, 9, 11, 15, 24, 28 and 86; 2 from each of Stations 10, 27, 32, 42 and 80; 4 from each of Stations 35 and 36; 7 from Station 77; and 8 from Station 57.

**Remarks.** The new material fits within the variation noted in the previous descriptions (Erséus 1981a, 1986b). The bisetal bundles are generally located in II–IX, but end in VII or VIII in specimens in which the genital organs are shifted correspondingly forwards. The penial bundles generally contain two setae, but in a few cases these bundles contain three or four setae.

The spermathecal pores are located approximately midway between the lateral lines and the lines of the ventral setae. In this respect the Belize individuals resemble the worms from the U.S. east coast (with pores “slightly ventral to lateral lines”) more than they do the material from Bermuda (with pores “in line with ventral setae”) (Erséus 1981a).

**Distribution and habitat.** Belize (new record), Bermuda, United States east coast (New Jersey through Florida), Galapagos Islands (Pacific Ocean); this is thus the only species of *Heterodrilus* that has been recorded from both sides of the isthmus of Panama. Subtidal, largely coarse sands, to at least 39 m depth.

### *Heterodrilus quadrithecatus* (Erséus, 1981) comb.n.

*Heterodriloides quadrithecatus* Erséus, 1981a: 125–126, fig. 15.

**New material.** USNM 127702, specimen from Station 50.

**Brief description of new material.** Length 3.4 mm, 41 segments. Width at XI 0.16 mm. Trifid setae in II–IX, 2 per bundle, 40–50  $\mu\text{m}$  long. Bifid setae from X, 1 per ‘bundle’, 40–50  $\mu\text{m}$  long. Penial setae 2 per bundle, about 40  $\mu\text{m}$  long. Atrium about 85  $\mu\text{m}$  long, 12–14  $\mu\text{m}$  wide, with about 1  $\mu\text{m}$  thick outer lining of muscles. Spermathecae in anterior part of XII, but poorly developed; spermathecae not observed in XI.

**Remarks.** This species, the type species of the monotypic *Heterodriloides*, is now regarded as a cladistic member of *Heterodrilus* (see *Remarks* for genus above).

The specimen from Belize is slightly smaller than the worms from Bermuda, but otherwise it conforms very well with the original description (see Erséus 1981a). *Heterodrilus quadrithecatus* is an aberrant tubificid as its spermathecae are located posterior to the normal position in segment X. In the Bermudian individuals, there generally were two pairs of spermathecae, one more or less rudimentary pair anteriorly in XI, the other (containing sperm) anteriorly in XII. The present worm appears to have spermathecae in XII only.

**Distribution and habitat.** Belize (new record) and Bermuda. Subtidal medium to coarse sand, to at least 15 m depth.

### *Heterodrilus ersei* (Giere, 1979) comb.n.

*Phallogrilus ersei* Giere, 1979; 309–312, figs. 5–7.

*Gielaideilus ersei*; Erséus 1981a: 126–127, figs. 16–17.

**New material.** USNM 127703–127704, 2 specimens from Station 71. Author's collection: 4 specimens; 1 from each of Stations 68 and 71; and 2 from Station 69.

**Remarks.** This large tubificid (up to 25 mm long) was originally described, from Bermuda, as a member of the subfamily Phallogrilinae and placed in the genus *Phallogrilus* Picranтони by its author (Giere 1979). The systematic position near *Heterodrilus* was recognized when the species was redescribed, as a member of a separate genus *Gielaideilus*, by Erséus (1981a). To render *Heterodrilus* a monophyletic taxon, *Gielaideilus* is now considered as a

part of, and thus as a junior synonym of, it (see *Remarks* for genus above).

The setae of *H. ersei* are similar to those of most species of *Heterodrilus*: there are bisetal bundles anteriorly followed by unisetal 'bundles' throughout the rest of the worm, the anterior setae are trifid, and the penial bundles each contain two large, straight, single-pointed setae. In *H. ersei* and the closely related *H. inermis* (Erséus, 1981a) comb.n., the atria are shorter than in most other species of *Heterodrilus* and lack cilia throughout most of their length (atria fully ciliated in all congeners).

The new individuals from Belize conform well with the previous descriptions, but their penial setae are only 100–140  $\mu\text{m}$  long, i.e. slightly shorter than those of the worms from Bermuda (135–160  $\mu\text{m}$ ).

*Distribution and habitat.* Belize (new record) and Bermuda. Subtidal, largely coarse sand, to at least 9 m depth.

### Subfamily Phallodrilinae

#### Genus *Coralliodrilus* Erséus, 1979

*Remarks.* *Coralliodrilus* comprises phallodriline species that lack external prostate glands (an assumed synapomorphy), but which possess a normal alimentary system; a few gutless species within *Olavius* also lack prostate glands (Erséus 1984b). The definition of the genus was recently modified by Erséus (in press).

#### *Coralliodrilus rugosus* sp.n. (Fig. 9)

*Holotype.* USNM 127705.

*Type locality.* N tip of Carrie Bow Cay, Belize, at high-water line (Station 25).

*Paratypes.* USNM 127706–127707. 2 specimens from type locality.

*Other material* (author's collection). Specimen from Station 18.

*Etymology.* The name *rugosus* is Latin for 'wrinkled', here referring to the appearance of the body wall. Each segment bears a high number of small secondary annuli.

*Description.* Length (2 complete specimens) 3.2–3.4 mm, 39–44 segments. Width at XI 0.32–0.39 mm. Prostomium short, rounded. Secondary annuli numerous. Clitellum extending over  $\frac{1}{2}$ X–XII. Somatic setae (Fig. 9A) bifid, with upper tooth thinner and shorter than lower and with inconspicuous subdental ligament. Bifids 33–40  $\mu\text{m}$  long, 1.5–2.5  $\mu\text{m}$  thick at node (which is well developed, particularly in postclitellar segments), (3)4–6 per bundle anteriorly, (2)3–5 per bundle in postclitellar segments. Penial setae (Fig. 9B; C, *ps*) 7–9 per bundle, very slender, straight or somewhat curved, 40–50  $\mu\text{m}$  long, entally about 1.5  $\mu\text{m}$  thick, ectally much thinner with single-pointed, curved tips. Male pores paired in line with ventral setae, slightly posterior to middle of XI. Spermathecal pores paired in lateral lines, anteriorly in X.

Pharyngeal glands in IV–V. Male genitalia (Fig. 9C) paired. Vas deferens 9–11  $\mu\text{m}$  wide, slightly longer than atrium, coiled, entering apical end of atrium. Atrium bipartite, distinctly folded at middle, total length about 100  $\mu\text{m}$ . Ental half of atrium 28–47  $\mu\text{m}$  wide, with granulated inner epithelium, ectal part 26–33  $\mu\text{m}$  wide,

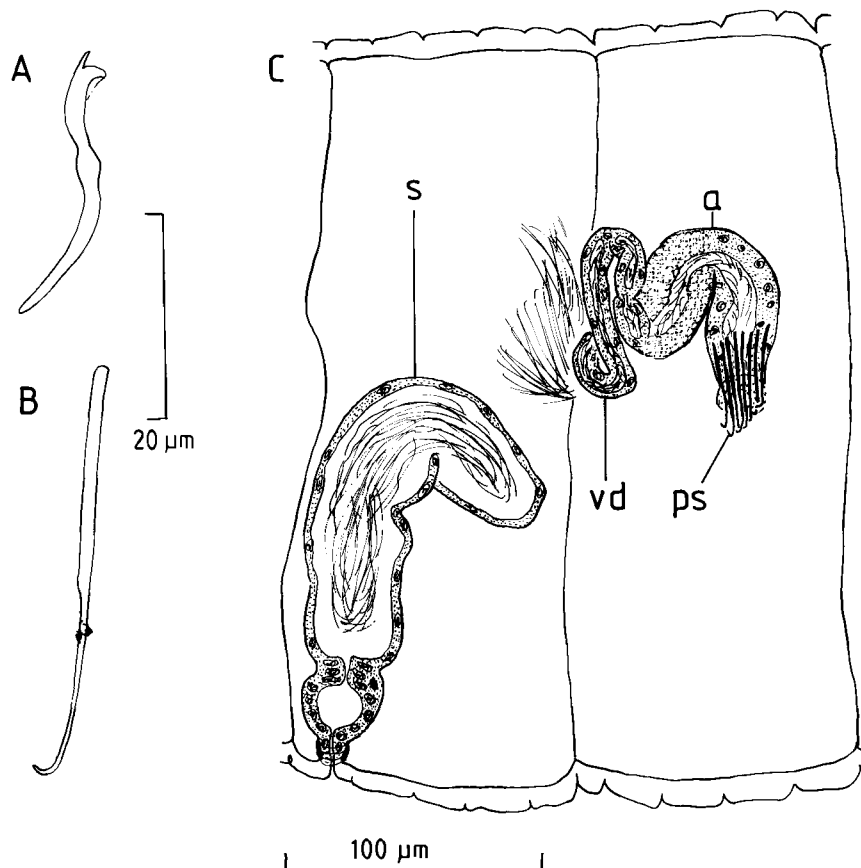


Fig. 9. *Coralliodrilus rugosus* sp.n.—A. Somatic seta.—B. Penial seta.—C. Somewhat lateral view of spermatheca and male genitalia in segments X–XI.

without granulation; muscular lining nowhere thicker than about  $1\ \mu\text{m}$ , lumen wide and ciliated throughout. Atrium opening to exterior through simple pore. Prostate glands absent. Spermathecae (Fig. 9C, *s*) with  $40\text{--}45\ \mu\text{m}$  long, up to  $28\text{--}35\ \mu\text{m}$  wide, ducts, and elongate, up to about  $150\ \mu\text{m}$  long, about  $40\ \mu\text{m}$  wide, thin-walled ampullae. Ectal part of spermathecal ducts narrow, with muscular 'sphincter', middle part of ducts with roundish cavity. Sperm as large bundle in spermathecae.

*Remarks.* Four previously known species of *Coralliodrilus* have bipartite atria similar to those of *C. rugosus*. The new species is, however, distinguished from *C. atriobifidus* Erséus, 1981(c) by its slenderer and more numerous penial setae, shorter spermathecal ducts and longer spermathecal ampulla; from *C. oviatriatus* Erséus, 1981(c) by its wider vasa deferentia, and much wider ectal part of the atria; from *C. giacobbei* Erséus, 1983(c) by its smaller number of penial setae (about 20 per bundle in *giacobbei*), and wider ectal part of the atria; and from *C. hamatilis* Erséus, 1985 by its lack of penes. [Due to a typographical error a part of the description of the setae is missing in the description of the last-mentioned species (*op. cit.*); in *C. hamatilis*, the bifid, somatic setae are two to six per bundle in postclitellar segments, and the hooked penial setae are seven to nine per bundle.]

The bulbous appearance of the spermathecal ducts (see Fig. 9C) is a very characteristic feature of *C. rugosus*, distinguishing it from all other members of the genus.

*Distribution and habitat.* Known only from Carrie Bow Cay, Belize. Upper intertidal and subterranean marine waters, sand.

### *Coralliodrilus randyi* sp.n. (Fig. 10)

*Holotype.* USNM 127708.

*Type locality.* W side of South Point, Twin Cays, Belize, 0.3 m, coarse coral sand with some mangrove debris (5 April 1982; coll. H. R. Baker).

*Etymology.* Named for the late Dr H. R. (Randy) Baker, who collected the material but never had the opportunity to describe it.

*Description.* Length more than 1.6 mm, more than 20 segments (specimen not complete), but clearly a very small species. Width at XI  $0.13\ \text{mm}$ . Prostomium rounded triangular, large, somewhat longer than wide. Clitellum well developed, extending over  $\frac{1}{2}\text{X}\text{--XII}$ . Setae (Fig. 10A) bifid, with upper tooth thinner but about as long as lower. Anterior setae slender,  $25\text{--}38\ \mu\text{m}$  long, about  $1\ \mu\text{m}$  thick, 3–4 per bundle. Postclitellar setae stouter,  $24\text{--}28\ \mu\text{m}$  long, about  $1.5\ \mu\text{m}$  thick, 3 per bundle. Penial setae absent. Male pores paired, in line with ventral setae, posteriorly in XI. Spermathecal pores, in line with ventral setae, in most anterior part of X.

Pharyngeal glands in IV–V(VI?), but not well developed. Male genitalia (Fig. 10B) paired. Vas deferens  $4\text{--}5\ \mu\text{m}$  wide, with a few coils, entering apical end of atrium. Atrium divided into slender, spindle-shaped ampulla, about  $60\ \mu\text{m}$  long,  $20\ \mu\text{m}$  wide, and narrow ectal duct, about  $25\ \mu\text{m}$  long,  $5.6\ \mu\text{m}$  wide. Atrial ampulla with very thick ( $3\text{--}4\ \mu\text{m}$ ) outer lining of muscles; lumen narrow, but inner epithelium not particularly granulated. Atrial duct without muscular lining, terminating in small penial apparatus, about  $20\ \mu\text{m}$  long,  $15\ \mu\text{m}$  wide; however, whether inner 'core' of apparatus is pendent within sac (i.e. whether it is a proper penis) cannot be ascertained. Prostate glands absent. Spermathecae (Fig. 10B, *s*) slender, with  $15\ \mu\text{m}$  long,  $10\ \mu\text{m}$  wide ducts, and  $40\ \mu\text{m}$  long,  $10\text{--}12\ \mu\text{m}$  wide ampullae; sperm absent (specimen precopulatory).

*Remarks.* The atria of *C. randyi* are similar to those of *C. longiductus* Erséus, 1983, a meiobenthic species from bathyal depths off Angola in the South Atlantic (Erséus 1983d). The new species is, however, discriminated from *C. longiductus* by its lack of penial setae, and by the morphology of its penial apparatuses (in *longiductus*, the atrial ducts terminate in small, muscular, protrusible pseudopenes in the lateral walls of male invaginations).

*Distribution and habitat.* Known only Twin Cays, Belize. Barely subtidal, muddy coarse sand.

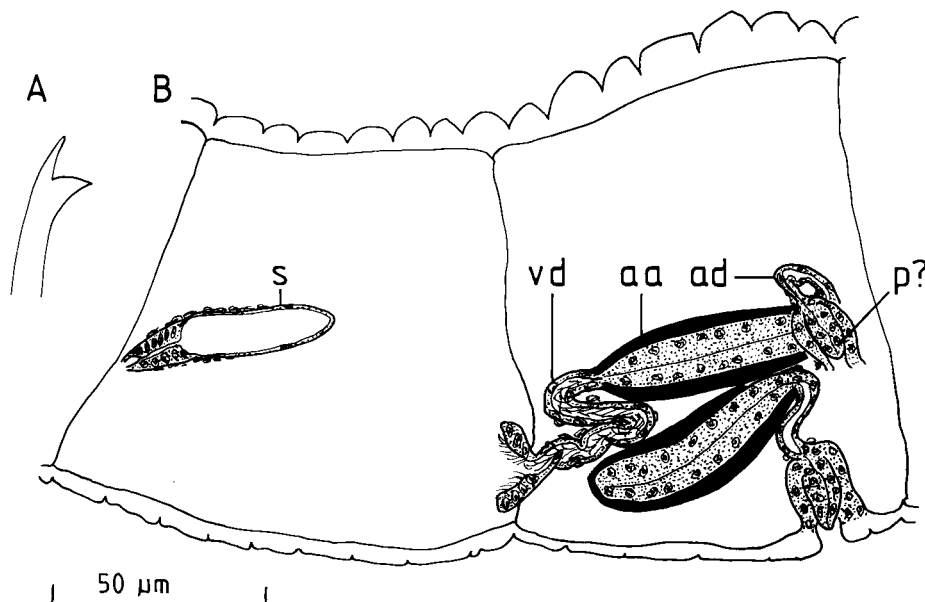


Fig. 10. *Coralliodrilus randyi* sp.n.—A. Free-hand drawing of seta.—B. Somewhat lateral view of spermatheca (one of two) and male genitalia in segments X–XI; both atria shown.

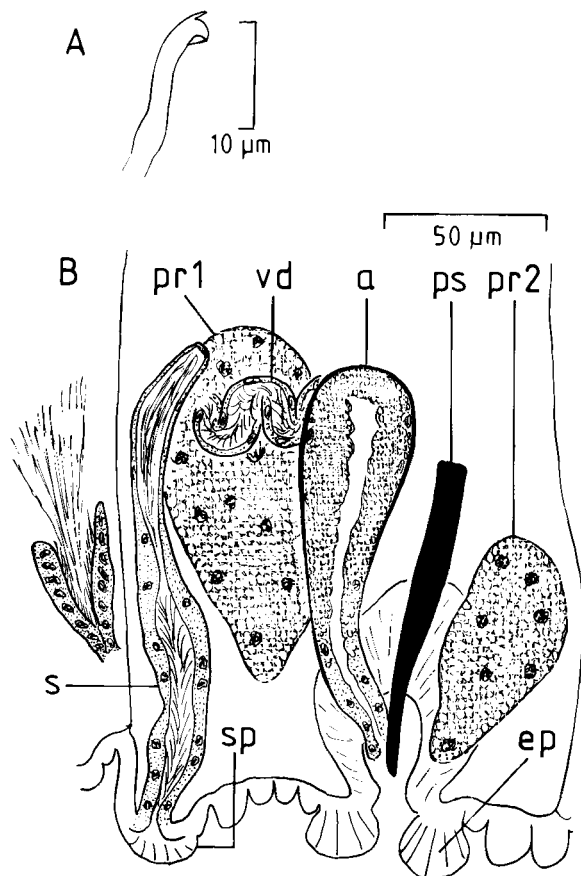


Fig. 11. *Phalldrilus compactus* sp.n.—A. Somatic seta.—B. Lateral view of spermatheca and male genitalia in segment XI.

### Genus *Phalldrilus* Pierantoni, 1902

**Remarks.** With over 70 species, *Phalldrilus* is the largest genus within the subfamily. The most recent definition of the genus was given by Erséus (in press), but as noted before (Erséus 1984a, 1987c, in press) it is a paraphyletic taxon in need of a major revision.

#### *Phalldrilus compactus* sp.n. (Fig. 11)

**Holotype.** USNM 127709.

**Type locality.** N tip of South Water Cay, Belize, 0.1 m (Station 44).

**Paratypes.** USNM 127710–127713, 4 specimens from type locality.

**Other material** (author's collection). Four specimens: 1 from each of Stations 15, 26 (specimen sectioned), 31 and 87.

**Etymology.** The species is named for the 'compact' (Latin *compactus*) arrangement of its genitalia.

**Description.** Length 2.0–2.9 mm, 30–38 segments. Width at XI 0.22–0.41 mm. Prostomium and pygidium similar, rounded triangular, both well set off from rest of body, but pygidium generally somewhat smaller than prostomium. Secondary annulation inconspicuous. Clitellum extending over  $\frac{1}{2}$ X– $\frac{2}{3}$ XII. Somatic setae (Fig. 11A) bifid, with upper tooth shorter and much thinner than lower, and with subdental ligament. Bifids 34–41  $\mu$ m long, 2–2.5  $\mu$ m thick at node, (1)2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae (Fig. 11B, *ps*) 1–2 per bundle, straight, single-pointed, 77–100  $\mu$ m long, entally flat and 5–15  $\mu$ m wide, ectally narrower and more solid. Tips of penial setae protruding into small copulatory chambers surrounded by thick-walled sacs.

Male pores paired in line with ventral setae posteriorly in XI. Two transverse epidermal pads located mid-ventrally, one anterior and one posterior to level of male pores (cf. Fig. 11B, *ep*). Spermathecal pores paired in line with ventral setae in most anterior part of XI. Discrete unpaired roundish protuberance (Fig. 11B, *sp*) present mid-ventrally between spermathecal pores.

Pharyngeal glands in IV–V(VI). Male genitalia (Figs. 11B) paired. Vas deferens inconspicuous, up to about 10  $\mu$ m wide and entering apical end of atrium, but not observed in its full length in any of available specimens. Atrium club-shaped, erect, 115–140  $\mu$ m long, entally 23–30  $\mu$ m wide, with 1–2  $\mu$ m thick outer lining of muscles and thick inner epithelium, latter apparently lacking cilia, but granulated at least entally. Two large and compact prostate glands present, but attachments to atrium not seen. Atrium ectally tapering and opening into copulatory chamber. Spermathecae (Fig. 11B, *s*) slender, 140–200  $\mu$ m long, with long, ciliated(?), 17–28  $\mu$ m wide ducts, and shorter, thin-walled, 12–21  $\mu$ m wide ampullae; each ampulla with loose bundle of sperm.

**Remarks.** This species is unique within *Phalldrilus* having the spermathecae located in the same segment as the male ducts, i.e. in segment XI. In the northeast Atlantic *P. postspermathecatus* Erséus, 1980(c), and the Italian, fresh-water *P. cuspis* Erséus & Dumnicka, 1988, however, the spermathecae are shifted backwards even further, into segment XII, behind the male genitalia. The penial setae and atria of *P. compactus* bear some resemblance to those of *P. parthenopaues* Pierantoni, 1902 (see Erséus 1987c) and *P. sabulosus* Erséus, 1979 (see Erséus 1979d), which may be two of its closest relatives among the known species of the genus.

**Distribution and habitat.** Known only from the barrier reef off Belize. Subtidal sand, to at least 2 m depth.

#### *Phalldrilus singularis* sp.n. (Fig. 12)

**Holotype.** USNM 127714.

**Type locality.** Outer end of dock at Carrie Bow Cay, Belize, 1.5 m (Station 2).

**Etymology.** The specific name *singularis*, Latin meaning 'with one only' alludes to the single penial setae at each male pore.

**Description.** Length more than 2.4 mm, more than 21 segments (holotype not complete). Width at XI 0.25 mm. Prostomium rounded, triangular. Secondary annuli numerous. Clitellum extending over  $\frac{1}{2}$ X–XII, but not well developed. Somatic setae (Fig. 12A) bifid and slender, with upper tooth about as long as but thinner than lower, and with subdental ligament. Bifids 33–40  $\mu$ m long, 1–1.5  $\mu$ m thick, (1,2)3–4(5) per bundle anteriorly, 1–3 per bundle in segments posterior to clitellum. Penial setae (Figs 12B; C, *ps*) single-pointed, slightly curved, about 50  $\mu$ m long, entally 2.5  $\mu$ m thick, ectally thinner, 1 on each side of worm. Tips of penial setae in holotype sharply bent (which, however, may be an anomaly for this single individual). Male pores paired in line with ventral somatic setae in posterior part of XI. Spermathecal pores paired in line with ventral setae, in furrow between IX and X.

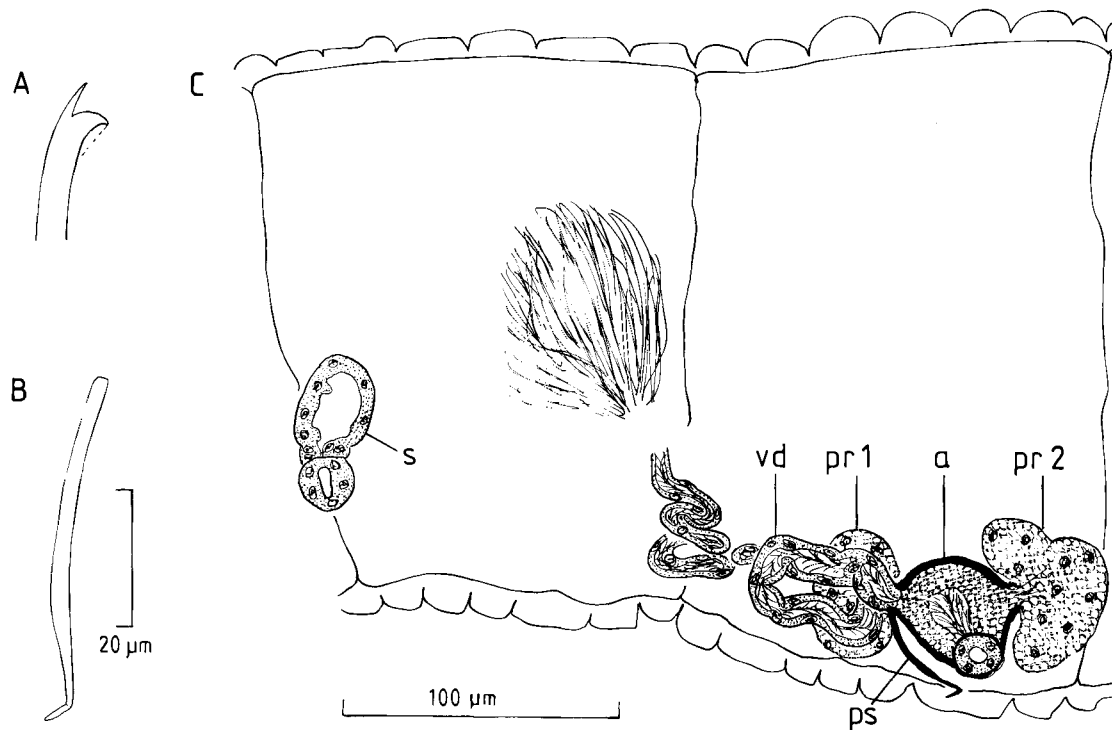


Fig. 12. *Phalldrilus singularis* sp.n.—A. Free-hand drawing of somatic seta.—B. Penial seta (sharply bent tip may be an artifact).—C. Lateral view of spermatheca and male genitalia in segments X–XI.

Pharyngeal glands not observed. Male genitalia (Fig. 12C) paired. Vas deferens 6–15  $\mu\text{m}$  wide, very long and coiled, entering atrium subapically. Atrium erect, oval, about 50  $\mu\text{m}$  long (both atria of holotype observed from an oblique view), 40  $\mu\text{m}$  wide, with up to 4  $\mu\text{m}$  thick lining of muscles, and ciliated and granulated inner epithelium. Prostate glands both subapical, attached to atrium opposite to each other. Spermathecae (Fig. 12C, *s*) small, with short ducts and oval ampulla, probably not fully developed in holotype; sperm absent.

**Remarks.** Among the few species of *Phalldrilus* possessing only one (or very few) penial seta per 'bundle', *P. singularis* is unique in having erect, oval, heavily muscular atria. It is possible that additional specimens would prove to have, e.g. two penial setae per bundle, but this would not speak against it being separate from all other known species.

**Distribution and habitat.** Known only from Carrie Bow Cay, Belize. Subtidal, somewhat muddy sand, 1.5 m.

#### *Phalldrilus deminutius* Erséus, 1979

*Phalldrilus rectisetosus deminutius* (partim) Erséus, 1979d: 191–192, fig. 7; Erséus 1981c: table I.  
*Phalldrilus deminutius*: Erséus 1988a: 786–787, figs 2A–C, 4.

**Material.** See Erséus (1988a). Author's samples from Belize, 8 specimens (3 of which deposited in the USNM): 1 from each of Stations 1, 9, 31 and 86; and 2 from each of Stations 12 and 23.

**Remarks.** The *Phalldrilus rectisetosus*-complex was treated in a recent taxonomic revision (Erséus 1988a), in which the *deminutius* form, previously regarded as a subspecies of *P. rectisetosus* Erséus, 1979(d), was elevated to specific status.

*Phalldrilus deminutius* is distinguished from the closely related *P. molestus* (see below) by its smaller number of somatic setae (generally two per bundle anteriorly, one per 'bundle' posteriorly) and greater number of penial setae (four to eleven per bundle); *P. molestus* has almost invariably two setae in all somatic bundles, but generally only three to five penial setae per bundle.

This species is not as common in Belize as *P. molestus*, but wherever it occurs it appears to be sympatric with the latter.

**Distribution and habitat.** Bermuda, Barbados and Belize, probably present throughout the Caribbean. Intertidal and subtidal sand, to at least 14 m depth.

#### *Phalldrilus molestus* Erséus, 1988

*Phalldrilus rectisetosus deminutius* (partim) Erséus 1979d: 191–192; Erséus 1981c: table I.  
*Phalldrilus molestus* Erséus, 1988a: 787–789, figs 1B–D, 2D–F, 4.

**Material.** See Erséus (1988a). Author's collection from Belize, 199 specimens (5 of which deposited in the USNM) from following Stations (number of specimens given in parentheses: Stations 1(3), 2(type locality)(25), 5(2), 9(9), 12(9), 13(6), 15(5), 16(2), 22(4), 23(10), 26(7), 31(2), 32(1), 33(1), 41(10), 42(5), 43(1), 44(3), 47(1), 50(1), 51(10), 57(6), 60(1), 65(2), 66(5), 69(1), 70(6), 72(5), 77(20), 79(11), 80(23), 82(1), and 86(1).

**Remarks.** This species was described in the revision of the *P. rectisetosus*-complex (Erséus 1988a). It is one of the most common tubificids on the barrier reef off Belize. See also *Remarks* for *P. deminutius* above.

**Distribution and habitat.** Bermuda, Florida, Belize, Barbados, Hawaii, Great Barrier Reef, Fiji, probably circumtropical. Lower intertidal and subtidal sands, to at least 70 m depth.

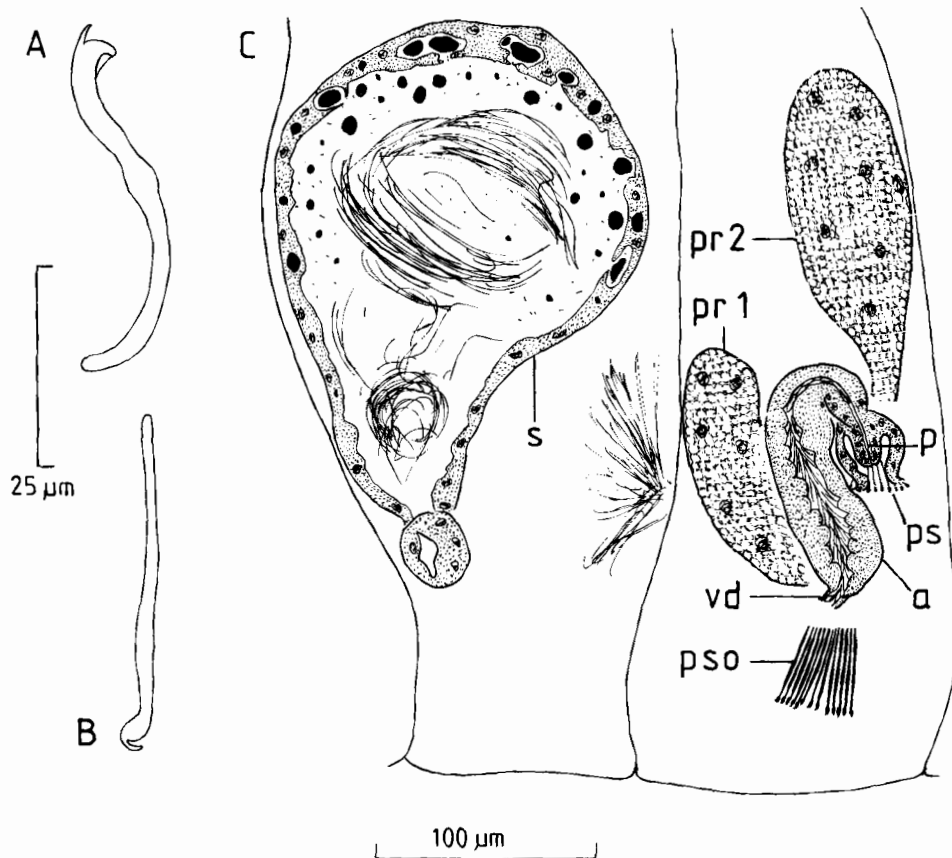


Fig. 13. *Phallodrilus vicinus* sp.n.—A. Somatic seta.—B. Penial seta.—C. Somewhat lateral view of spermatheca and male genitalia in segments X–XI.

***Phallodrilus vicinus* sp.n. (Fig. 13)**

*Holotype*. USNM 127715.

*Type locality*. About 10 m N of Carrie Bow Cay, Belize, 0.5 m (Station 11).

*Paratypes*. USNM 127716–127718, 3 specimens from S tip of Carrie Bow Cay, sand flat, near rubble zone, barely subtidal, medium to coarse sand (7 April 1982; coll. H. R. Baker).

*Other material* (author's collection). Three specimens from locality of paratypes.

*Etymology*. The name *vicinus* is Latin for 'neighbouring, near', which recognizes the species' very close relationship to *P. caviatriatus* (see *Remarks* below).

*Description*. Length (2 complete specimens) 4.2–4.5 mm, 38–39 segments. Width at XI 0.23–0.48 mm. Prostomium rounded triangular. Secondary annulation present in anteriormost segments. Clitellum extending over  $\frac{2}{3}$ X– $\frac{2}{3}$ XII in holotype, poorly developed in paratypes. Somatic setae (Fig. 13A) bifid, with upper tooth thinner and shorter than lower, and with subdental ligament. These setae 35–48  $\mu$ m long, 2.5–3.5  $\mu$ m thick at node, 2–3 per bundle anteriorly, (1)2 per bundle in postclitellar segments. Penial setae (Figs 13B; C, *ps*, *pso*), (6–8)9–13(14) per bundle, straight, 35–42  $\mu$ m long, about 2  $\mu$ m thick, ectally clubbed setae; each 'club' bearing a curved apical hook. Male pores paired in line with ventral somatic setae, posteriorly in XI. Spermathecal pores paired, located between lines of ventral setae and lateral lines, in most anterior part of X.

Pharyngeal glands in IV–V, generally also extending into VI. Male genitalia (Fig. 13C) paired. Vas deferens not seen in its entire length in available material, but

entering apical end of atrium. Atrium cylindrical, about 130–140  $\mu$ m long, ectally sharply bent, with very thin outer lining of muscles and thick inner epithelium; latter ciliated but not granulated. Ental part of atrium 28–35  $\mu$ m wide, ectal part much narrower and terminating in inconspicuous penis; latter enclosed in small copulatory sac in immediate vicinity of penial setae (for clarity, penial setae of other side of worm depicted in Fig. 13, *pso*). Prostate glands large (at least of same size as atrium), but attachments to atrium not seen. Spermathecae (Fig. 13C, *s*) with short, in some specimens bulbous, ducts, and large ampullae. Latter of variable shape and size, containing somewhat bundled sperm; in holotype wall and lumen of ampullae also with globules of secretion.

*Remarks*. This species is closely related to *P. caviatriatus* Erséus, 1984, known from a lower intertidal (possibly somewhat brackish) habitat in Barbados (Erséus 1984a). With regard to non-genital characters and the penial setae, the two forms are virtually identical, the new species having on average fewer penial setae per bundle (range 6–14 as opposed to about 13–18 in *P. caviatriatus*). However, the atria are fundamentally different in the two species. Those of *P. caviatriatus* are heavily muscular (muscle layer 5–9  $\mu$ m thick) and have a thin inner epithelium rendering the lumen very wide (epithelium thick and lumen narrow in *P. vicinus*). In addition, the prostate glands are much larger in *P. vicinus*.

*Distribution and habitat*. Known only from Carrie Bow Cay, Belize. Barely subtidal, rather loose sand, about 0.5 m.

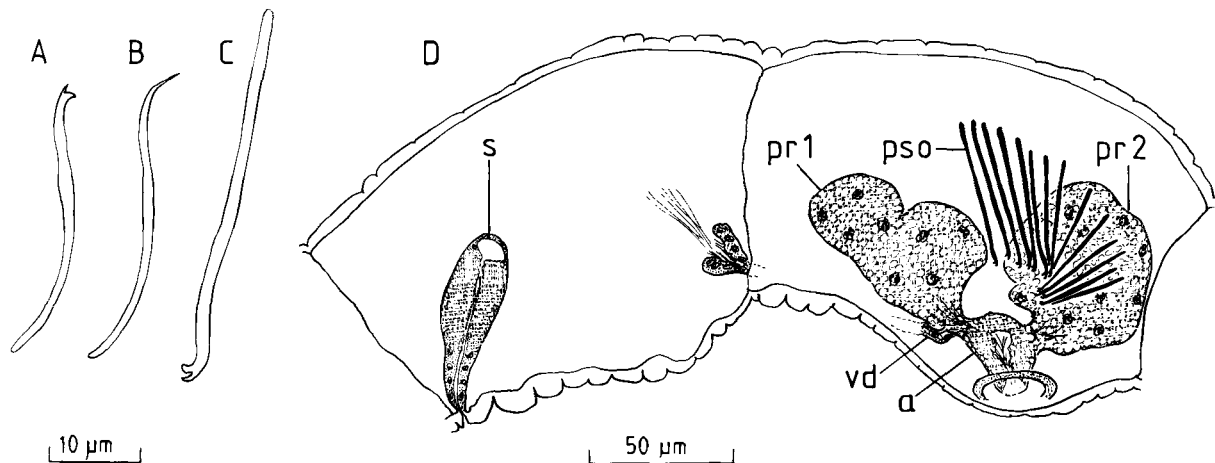


Fig. 14. *Phalldrilus nasutus* sp.n.—A. Anterior somatic seta.—B. Dorsal somatic seta of posterior end of worm.—C. Penial seta.—D. Lateral view of spermatheca and male genitalia in segments X–XI.

### *Phalldrilus nasutus* sp.n. (Fig. 14)

*Holotype*. MNHN MA 1.

*Type locality*. Anse Laborde, N part of Grand-Terre, Guadeloupe, 16°29.2'N, 61°30.3'W, intertidal, sand (9 December 1982; coll. N. Gourbault).

*Paratype*. USNM 127719, specimen from Station 18 (Belize).

*Other material* (author's collection). Specimen from La Gourde beach, E part of Grande-Terre, Guadeloupe, 16°15.7'N, 61°12.7'W, high intertidal, coarse sand (November 1984; coll. J. Renaud-Mornant & N. Gourbault).

*Etymology*. The name *nasutus* is Latin for 'large-nosed', here referring to the species' prominent prostomium.

*Description*. Length 1.9–2.0 mm, 24–29 segments. Width at XI 0.10–0.14 mm. Prostomium elongate, snout-like. Secondary annulation indistinct. Clitellum extending over  $\frac{1}{2}$ X–XII. Somatic setae 23–45  $\mu$ m long, 1–1.5  $\mu$ m thick, 4–7(8) per bundle anteriorly, (3)4–6 per bundle in postclitellar segments. Anterior and ventral posterior setae (Fig. 14A) bifid, with upper tooth thinner and shorter than lower; dorsal setae of posteriormost segments (Fig. 14B) sharply single-pointed. Penial setae (Figs 14C; D, *pso*) straight, 13–17 per bundle, 25–50  $\mu$ m long, 1.5–2  $\mu$ m thick, bifid, with upper tooth thinner, but as long as, lower. Penial setae in fan-shaped formation within bundle, with posterior half of bundle 'tilted over' in a characteristic way and anterior setae of bundle distinctly longer than posterior ones (for clarity, penial setae of other side, not side of atrium shown, are drawn in Fig. 14D). Male and spermathecal pores paired in line with ventral somatic setae, posteriorly in XI, and in most anterior parts of X, respectively.

Pharynx cavity large and ciliated. Pharyngeal glands well developed, in IV–VI. Male genitalia (Fig. 14D) paired. Vas deferens not seen in its entire length, but entering atrium subapically. Atrium small, erect, somewhat pear-shaped, 26–33  $\mu$ m long, 19–28  $\mu$ m wide, with very thin outer lining and granulated and ciliated inner epithelium. Prostate glands large, both subapical, attached to atrium almost opposite to each other. Atrium opening into copulatory sac, latter also containing tips of penial setae. Spermathecae club-shaped, 47–63  $\mu$ m long, 15–19  $\mu$ m wide, with elongate, granulated ducts, and very short, thin-walled ampulla; sperm random in spermathecae of 1 specimen.

*Remarks*. *Phalldrilus nasutus* and *P. bipartitus* sp.n.

(described below) are closely related and share a number of characters which appear apomorphic: (1) an elongate, snout-like prostomium, (2) a large pharynx cavity (probably their feeding biology is different from that of most other members of *Phalldrilus*), (3) granulated spermathecae with very small ampullae, and (4) numerous bifid penial setae, each bundle of which shows a clear tendency of breaking up into two groups of setae, in *P. bipartitus* more so than in *P. nasutus* (cf. Figs 14D, 15C). Moreover, both species have been found in ground water near or above the high-water line.

In addition to the differences in the arrangements of the penial setae, *P. nasutus* is distinguished from *P. bipartitus* by its possession of sharply single-pointed setae in posterior dorsal bundles and the larger size of its penial setae.

These two new species are in some respects similar to *P. scirpiculus* Erséus, 1985 (see also Erséus 1989b) from Saudi Arabia. The latter species also has a snout-like prostomium, simple atria, and a clear granulation in the spermathecae. *Phalldrilus scirpiculus*, however, has very characteristic penial setae, distinguishing it from all congeners. Each bundle of penial setae tend to be arranged in a ring, with one seta very large and strongly hooked, followed by 5–6 gradually smaller, and not as hooked, setae (Erséus 1985: fig. 5b).

*Distribution and habitat*. Guadeloupe and Belize. Intertidal and subterranean water; sand.

### *Phalldrilus bipartitus* sp.n. (Fig. 15)

*Holotype*. USNM 127720.

*Type locality*. Beach above sea wall, E side of Carric Bow Cay, Belize, at groundwater level (Station 29).

*Paratypes*. USNM 127721–127722, 2 specimens from Station 7.

*Other material* (author's collection). Two specimens from Station 7.

*Etymology*. The name *bipartitus* is Latin for 'in two parts', 'in two ways', and refers to the very unusual arrangement of the penial setae.

*Description*. Length of 2 complete specimens 3.2–3.6 mm, 32–33 segments; a third specimen, lacking posterior end, more than 3.8 mm long, more than 33 segments. Width at XI 0.25–0.34 mm. Prostomium elongate, snout-like. Secondary annulation indistinct. Clitellum extending over X–XII. Somatic setae (Fig. 15A) all bifid, with upper tooth somewhat thinner than lower, and with

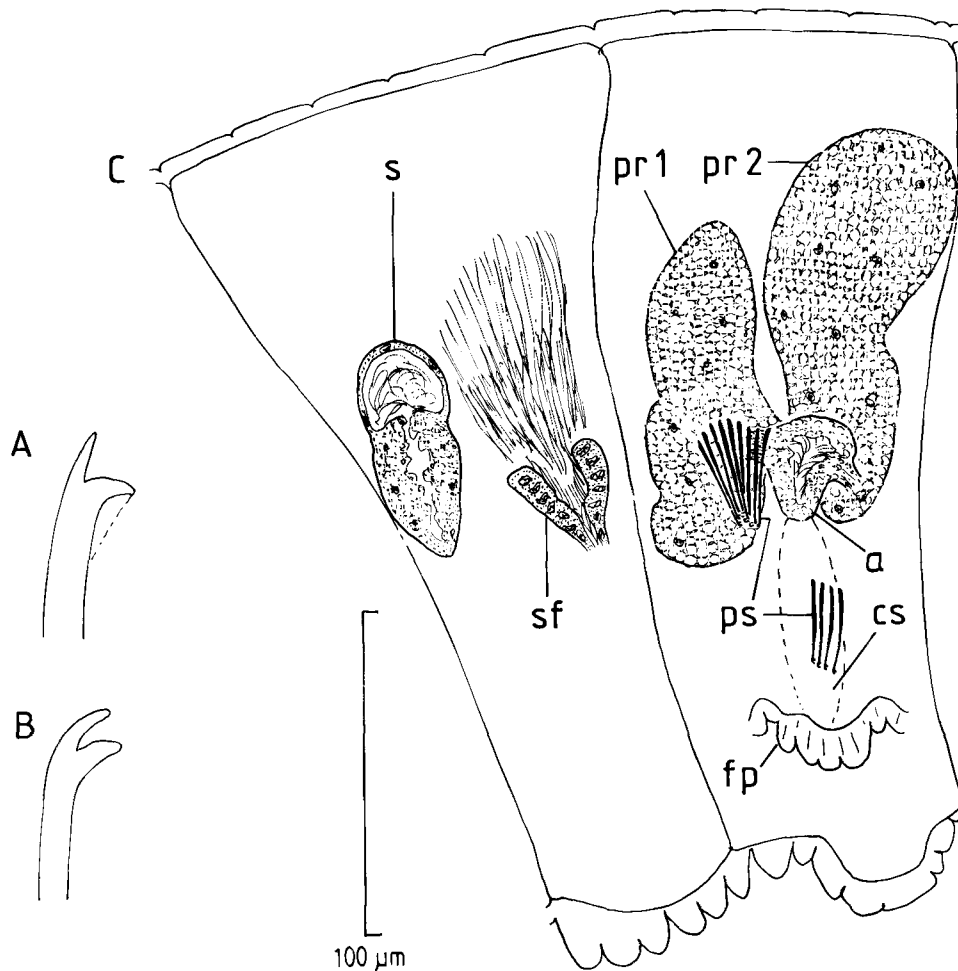


Fig. 15. *Phalodrilus bipartitus* sp.n.—A. Free-hand drawing of somatic seta.—B. Free-hand drawing of penial seta.—C. Somewhat lateral view of spermatheca and male genitalia in segments X–XI.

inconspicuous subdental ligament. These setae 35–50  $\mu\text{m}$  long, about 2  $\mu\text{m}$  thick, 5–7 per bundle anteriorly, 4–6 per bundle in postclitellar segments. Penial setae (Figs 15B; C, *ps*) more or less straight, bifid, with teeth closer together than in somatic setae, 26–35  $\mu\text{m}$  long, 1.5–2  $\mu\text{m}$  thick, arranged in two separate bundles at each male pore: one with about 8–17 setae (exact number sometimes difficult to establish) located near atrium, another with 2–5 setae located halfway down copulatory sac. Setae of larger bundle forming a semicircular, those of smaller bundle a straight, row. Male pores close together ventrally, slightly posterior to middle of XI, between two flap-like papillae (Fig. 15C, *fp*). Spermathecal pores paired in line with ventral setae, anteriorly in X.

Pharynx cavity large and ciliated. Pharyngeal glands well developed, in IV–VI. Male genitalia (Fig. 15C) paired. Vas deferens not seen in its entire length, but entering atrium subapically. Atrium small, erect, somewhat pear-shaped, 24–40  $\mu\text{m}$  long, 20–28  $\mu\text{m}$  wide, with very thin outer lining and sparsely granulated and ciliated(?) inner epithelium. Prostate glands very large, both subapical, attached to atrium opposite to each other. Atrium appear to open into deep copulatory sac, but details not clear in available material. Spermathecae 50–80  $\mu\text{m}$  long, 20–35  $\mu\text{m}$  wide, consisting of elongate, partly granulated ducts, and short, thin-walled ampullae; latter with some random sperm in postcopulatory specimens.

**Remarks.** See *Remarks* for *P. nasutus* above.

**Distribution and habitat.** Known only from Carrie Bow Cay, Belize. Upper intertidal and subterranean water; sand.

#### Genus *Aktedrilus* Knöllner, 1935

**Remarks.** Almost 30 of the meiobenthic species of Tubificidae living in intertidal habitats of sandy beaches are members of *Aktedrilus*. The genus was most recently revised by Erséus (1987a). Subsequent additions of species are those by Erséus (1990b, in press).

#### *Aktedrilus longitubularis* Finogenova & Shurova, 1980 (Fig. 16)

*Aktedrilus longitubularis* Finogenova & Shurova, 1980: 65–69, figs 1–8; Erséus 1989b: 17, figs 2q–r; Erséus 1990b: 279–280, fig. 6.

**New material.** USNM 127723, specimen from Station 54.

**Description of new material.** Length 2.5 mm, 34 segments. With at XI 0.12 mm. Epidermal glands not observed. Clitellum extending over  $\frac{1}{2}$ X–XII. Setae (Fig. 16A) all bifid, with upper tooth thinner and shorter than lower and with inconspicuous subdental ligament. Setae about 30  $\mu\text{m}$  long, about 1.5  $\mu\text{m}$  thick, 3–4 per bundle anteriorly, (2)3 per bundle in postclitellar segments. Spermathecal pore mid-dorsal, anteriorly in X.

Pharyngeal glands in IV–VI. Male genitalia (Fig. 16B) paired. Vas deferens about 8  $\mu\text{m}$  wide, not observed in its

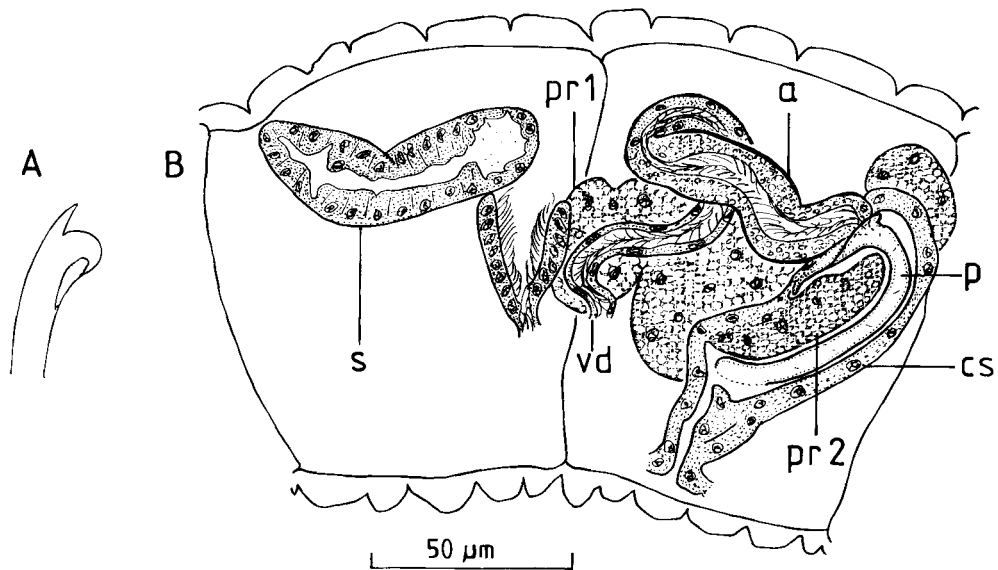


Fig. 16. *Aktedrilus longitubularis* Finogenova & Shurova.—A. Free-hand drawing of seta.—B. Lateral view of spermatheca and male genitalia in segments X–XI.

entire length, but entering apical end of atrium. Atrium about 115  $\mu\text{m}$  long, strongly curved, tubular, bipartite, ciliated and with very thin outer muscular lining. Ental part of atrium 10–16  $\mu\text{m}$  wide, ectal part 18  $\mu\text{m}$  wide, latter more granulated than ental part. Penis curved and elongated funnel-shaped, with cuticular sheath, inner end of which forming asymmetrical collar at base. Penis about 80  $\mu\text{m}$  long, diameter 26  $\mu\text{m}$  at base, about 5  $\mu\text{m}$  at middle and tip, enclosed in deep penial (copulatory) sac. Anterior prostate gland very large. Posterior prostate smaller, partly as a glandular pad in anterior wall of copulatory sac. Spermatheca (Fig. 16B, s) cylindrical, 65  $\mu\text{m}$  long, 21  $\mu\text{m}$  wide, with duct much longer than ampulla; sperm absent (specimen precopulatory).

**Remarks.** This species is now known from all major oceans (Erséus 1989b, 1990b, present paper). The single specimen from Belize fits the original description by Finogenova & Shurova (1980) remarkably well considering that their material was from the Sea of Japan. Except for some dimensional differences (the original specimens were somewhat larger), the only more fundamental discrepancy between the original and the present description is that Finogenova & Shurova did not note any subdental ligaments on the setae. Such ligaments were reported for material from Hong Kong (Erséus 1990b), but were not seen in worms from Saudi Arabia (Erséus 1989b). This difference is not considered as sufficient to suggest that two species are involved.

*Aktedrilus martiniquensis* Erséus, 1983e, however, is regarded as a separate species, despite the fact that it has male genitalia that are virtually indistinguishable from those of *A. longitubularis*. The former, known from Martinique and Guadeloupe, is discriminated from the latter by its sharply single-pointed posterior setae (Erséus 1983e: fig. 3B) and, possibly also, by its slightly longer spermathecal ampulla.

**Distribution and habitat.** Sea of Japan (Pacific U.S.S.R.), South China Sea (Hong Kong), Saudi Arabia, and Belize (new record). Intertidal sand.

### *Aktedrilus parvithecatus* (Erséus, 1978)

*Bacescuella parvithecata* Erséus, 1978: 264–265, fig. 2, table I; Erséus 1980a: 106–107, fig. 10B; Erséus 1984d: 195–196; Erséus & Cantú-Martínez 1984: 183–184, fig. 2.

*Bacescuella pilicrepus* Erséus, 1984e: 153–154, fig. 11.

*Aktedrilus parvithecatus*; Erséus 1987a: 117–119, fig. 6; Erséus 1989b: 17–18, figs 2s–t; 1990b: 281.

**New material.** USNM 127724–127726, 3 specimens from Station 7. Author's collection, 7 specimens: 6 from Station 7; and 1 from Station 20. MNHN MA 2, specimen from Anse Petite Rivière, La Désirade, Guadeloupe, 16°19.9'N, 61°00.4'W, intertidal, sand (28 March 1983; coll. N. Gourbault). Author's collection, specimen from same locality (Guadeloupe).

**Remarks.** This species, which appears to have a circum-tropical distribution (Erséus 1987a), was originally described from Bermuda, but has not been reported from the Caribbean proper to date. The worms from Belize are 2.6–3.0 mm long (36–40 segments), those from Guadeloupe 2.1–2.3 mm (both 36 segments). Three of the Belizean specimens bear roundish external spermatophores, 14–16  $\mu\text{m}$  in diameter.

**Distribution and habitat.** Belize and Guadeloupe (new records), Bermuda, Pacific coast of Mexico, Galapagos, Hong Kong, Saudi Arabia and France. Intertidal and barely subtidal sand.

### Genus *Jamiesoniella* Erséus, 1981

**Remarks.** The definition of *Jamiesoniella* Erséus, 1981(c) was recently modified by Erséus (1990b). The genus contains three meiobenthic, littoral species.

### *Jamiesoniella athecata* Erséus, 1981 (Fig. 17)

*Jamiesoniella athecata* Erséus, 1981c: 28–29, figs 27–29.

**New material.** USNM 127727, specimen from Station 54.

**Description of new material.** Length more than 1.3 mm, more than 15 segments (specimen not complete). Width

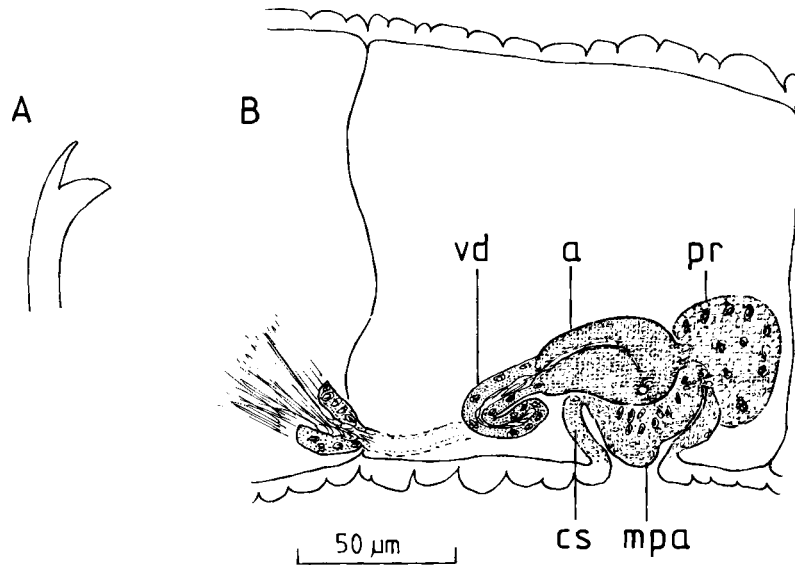


Fig. 17. *Jamiesoniella athecata* Erséus.—A. Free-hand drawing of somatic seta.—B. Lateral view of male genitalia in segment XI.

at XI 0.15 mm. Prostomium round, not large. Clitellum extending over  $\frac{1}{2}$ X–XII. Setae (Fig. 17A) bifid with upper tooth as long as but thinner than lower. Setae 28–35  $\mu\text{m}$  long, 1–1.5  $\mu\text{m}$  thick, (1–)3–5 per bundle anteriorly, 2–3 per bundle in postclitellar segments. Ventral setae of XI absent. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores and spermathecae absent.

Pharyngeal glands in (III)IV–V(VI). Male genitalia (Fig. 17B) paired. Vas deferens longer than atrium, wider ectally (about 10  $\mu\text{m}$ ) than entally (entall parts poorly visible in specimen). Atrium somewhat ovoid, about 50  $\mu\text{m}$  long, about 30  $\mu\text{m}$  wide, with very thin outer lining and thick inner epithelium; lumen narrow. Compact prostate gland attached to ectal end of atrium. Atrium opening into small copulatory sac, at base of flap-like, somewhat triangular papilla; papilla and wall of sac granulated.

**Remarks.** This species was originally described from Australia's Great Barrier Reef (Erséus 1981c), from a habitat similar to that of the present material. The new and the old specimens are remarkably similar even in dimensional features. Another species, *J. bahamensis* Erséus, 1981, is known from Bahamas (Erséus 1981d), and one would have expected this species rather than the South Pacific *J. athecata* to occur in Belize. However, the Belizean material of *Jamiesoniella* does not have curved and heavily muscular atria, and large copulatory sacs, which characterize *J. bahamensis*.

The wide geographic separation of the two records indicates that *J. athecata* is a widely distributed, possibly circumtropical, species.

**Distribution and habitat.** Belize (new record) and Great Barrier Reef. Intertidal, largely coarse, sand.

### Genus *Inandrilus* Erséus, 1979

**Remarks.** This genus, as well as *Olavius* (treated below), comprise a large group of aberrant Tubificidae, viz. those lacking a normal alimentary system, but instead bearing

symbiotic bacteria in their body wall (Giere & Langheld 1987). *Inandrilus* and *Olavius* were defined in a revision of these gutless species by Erséus (1984b).

### *Inandrilus leukodermatus* (Giere, 1979)

*Phallogrilus leukodermatus* Giere, 1979: 307–309, fig. 4; Giere 1981: 353–356, figs 1–8; Erséus 1981c: tables II–III; Erséus & Baker 1982: fig. 3A.

*Inandrilus leukodermatus*; Erséus 1984b: 240–241, fig. 1.

**New material.** USNM 127728–127732, 5 specimens from Station 13. Author's collection, 279 specimens from 30 different stations: 59 from Station 13; 29 from Station 22; 27 from Station 51; 23 from each of Stations 26 and 77; 20 from Station 57; 10 from each of Stations 27, 31 and 72; 9 from each of Stations 14 and 80; 6 from each of Stations 35 and 66; 4 from each of Stations 2, 16 and 60; 3 from each of Stations 15, 41, 42, 50 and 79; 2 from each of Stations 9 and 32; and 1 from each of Stations 5, 11, 23, 49, 59, 78 and 82.

**Remarks.** *Inandrilus leukodermatus*, which was described first from Bermuda (Giere 1979) and later from Belize (Erséus 1984b), is the most common gutless species in the present material. It occurred at 30 of the stations sampled and sometimes in high numbers (see above). This is similar to the situation in Bermuda, where the species sometimes reaches densities of about 85,000 ind.  $\text{m}^{-2}$  (Giere *et al.* 1982).

The penial setae are very characteristic, sickle-shaped with conspicuous ectal hooks, and arranged in bisetal bundles (Erséus 1984b: fig. 1).

**Distribution and habitat.** Bermuda, Belize. Various kinds of intertidal and subtidal sands, to at least 16.5 m depth. According to Giere *et al.* (1982) the species prefer the reduced layers of the carbonate sediments.

### *Inandrilus scalprum* Erséus, 1984

*Inandrilus scalprum* Erséus, 1984b: 247, fig. 9.

**New material.** USNM 127733, specimen from Station 27. USNM 127734, specimen from Station 78. Author's collection, 16 specimens: 5 from Station 62; 2 from each of Stations 26 and 27; and 1 from each of Stations 13, 16, 22, 51, 80, 81 and 82.

**Remarks.** This species was originally described from very shallow bottoms near Carrie Bow Cay (Erséus 1984b),

but has now also been found off the reef crest down to 27 m depth. The penial setae are characteristic, somewhat chisel-shaped, and the spermathecal ampullae are oval; otherwise the species is similar to *I. belizensis*. Seven worms of the present material are complete, they are 7.5–10.9 mm long, with 53–66 segments. This extends the known size range of the species (original material: 7.1–8.3 mm, 61–63 segment).

The two worms from about 100 m N of Carrie Bow Cay (Station 26) lack penial setae, but are otherwise clearly attributable to *I. scalprum*.

*Distribution and habitat.* Belize. Subtidal coral sand, to at least 27 m depth.

#### *Inanidrilus belizensis* Erséus, 1984

*Inanidrilus belizensis* Erséus, 1984b: 248, fig. 10.

*New material.* USNM 127735, specimen from Station 57. USNM 127736, specimen from Station 62. Author's collection: 1 specimen from each of Stations 31 and 51.

*Remarks.* *Inanidrilus belizensis*, characterized by sickle-shaped penial setae with bifid tips, and very short spermathecal ampullae, was originally described from Belize (Erséus 1984b). The new specimens, up to 8.8 mm long with up to 69 segments (the old worms were 6.2–6.6 mm long, with 50–68 segments), fit the original description well.

*Distribution and habitat.* Belize. Subtidal coral sand, to at least 24 m depth.

#### *Inanidrilus aduncosetis* Erséus, 1984 (Fig. 18)

*Inanidrilus aduncosetis* Erséus, 1984b: 248–249, fig. 11.

*New material.* USNM 127737–127738, 2 specimens from Station 14. Author's collection, 5 specimens: 3 from Station 51; 1 from Station 32; and 1 from reef flat N of Carrie Bow Cay, 1.2 m, poorly mixed medium coral sand in small sand grooves (15 April 1982; coll. H. R. Baker).

*Description of new material.* Length (2 complete specimens) 10.8–13.4 mm, 81–84 segments. Width at XI 0.17–0.28 mm. Prostomium elongate, rounded. Clitellum extending over  $\frac{1}{2}X$ – $\frac{2}{3}XII$ . Secondary annuli 7 per (postclitellar) segment. Bifid setae (Fig. 18A) with upper tooth thinner and slightly shorter than lower, and with subdental ligament. Bifids 30–45  $\mu\text{m}$  long, 1.5–2  $\mu\text{m}$  thick, (1)2–3 per bundle anteriorly, (1)2 per bundle in postclitellar segments. Penial setae (Figs 18B; C, *ps*) 2 per bundle, resembling fish-hooks, sharply single-pointed, about 50  $\mu\text{m}$  long, 4.5–6  $\mu\text{m}$  thick. Male and spermathecal pores in line with ventral setae.

Alimentary canal absent. Male genitalia (Fig. 18C) paired. Vas deferens 7–9  $\mu\text{m}$  wide, much longer than atrium, with thin but distinct muscular lining for most parts. Atrium erect, somewhat pear-shaped, 60–70  $\mu\text{m}$  long, 35–42  $\mu\text{m}$  wide, with 1–2  $\mu\text{m}$  thick outer muscular lining, and thick granulated inner epithelium. Prostate glands very large. Spermathecae (Fig. 18C, *s*) with (1) 'vestibules' at pores, (2) spindle-shaped, thick-walled ducts, 125–130  $\mu\text{m}$  long, 35–55  $\mu\text{m}$  wide, and (3) oblong, thin-walled ampullae, 70–110  $\mu\text{m}$  long, 33–51  $\mu\text{m}$  wide, containing large bundle of sperm. Spermathecae completely lined with 1–2  $\mu\text{m}$  thick layer of muscles.

*Remarks.* This species was previously known only from Bermuda, where it was found in coarse coral sand at 8 m depth (Erséus 1984b). The specimens from Belize basically conform to the original description, but there are some dimensional differences; the new worms are smaller with regard to setae, male ducts and spermathecae. A more qualitative difference is that their secondary annuli are seven per segment, not six as in the material from Bermuda. The differences are not regarded as specific, but as geographic variation.

*Distribution and habitat.* Belize (new record) and Bermuda. Various kinds of subtidal coral sand, to at least 8 m depth.

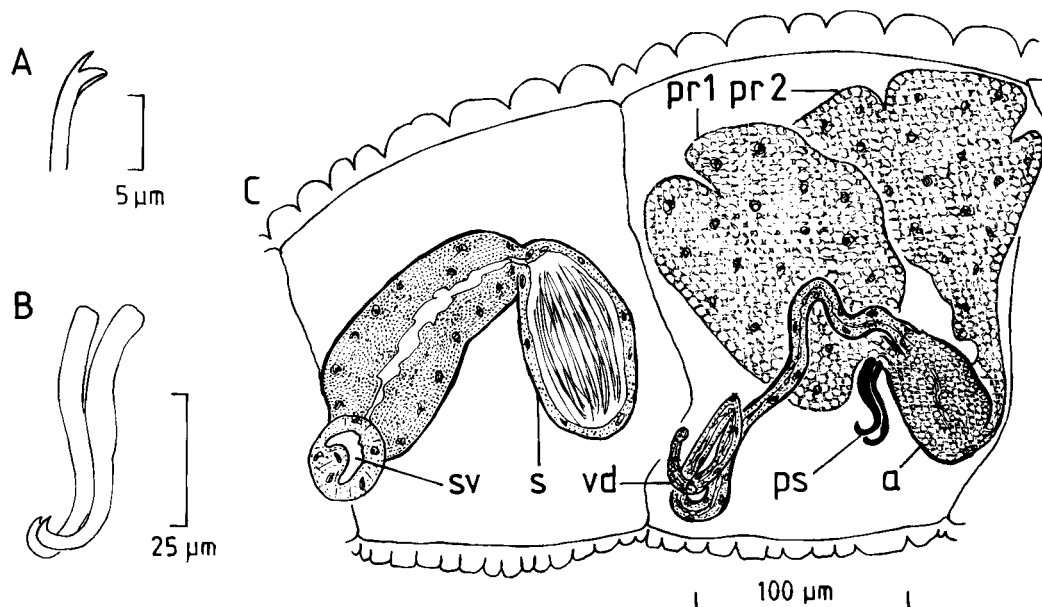


Fig. 18. *Inanidrilus aduncosetis* Erséus.—A. Somatic seta.—B. Penial setae.—C. Lateral view of spermatheca and male genitalia in segments X–XI.

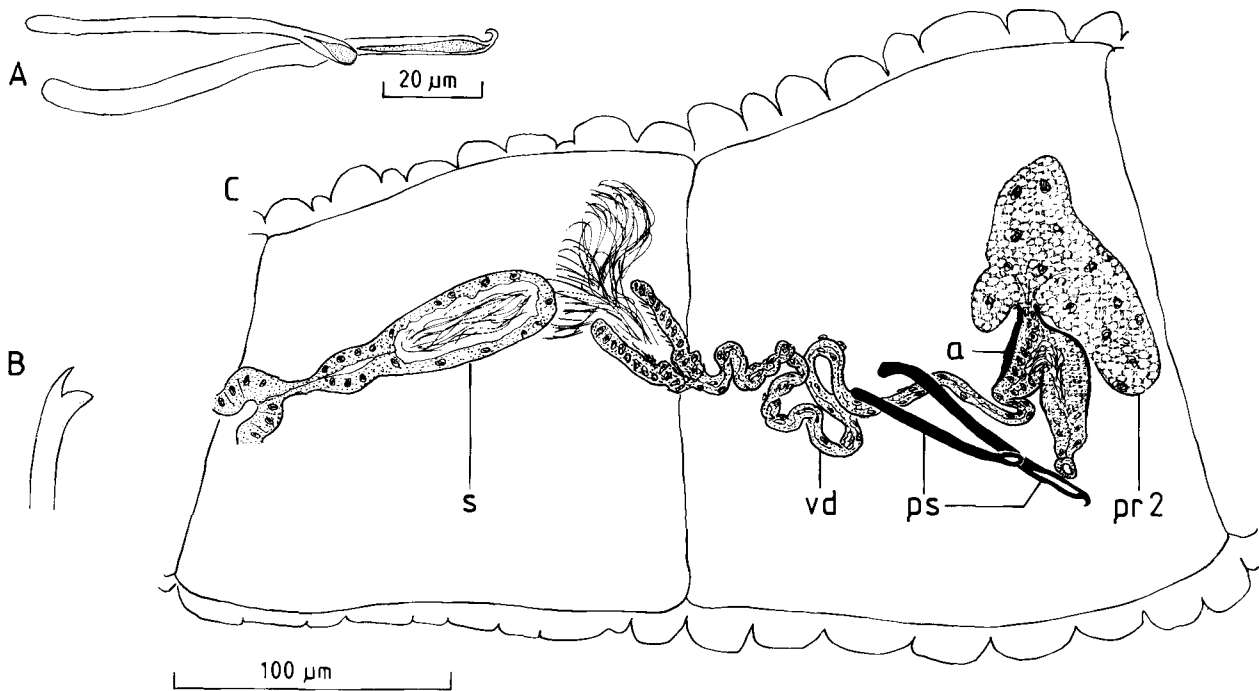


Fig. 19. *Inandrilus reginae* sp.n.—A. Penial setae.—B. Free-hand drawing of somatic seta.—C. Lateral view of spermatheca and male genitalia in segments X–XI.

***Inandrilus reginae* sp.n. (Fig. 19)**

*Holotype*. USNM 127739.

*Type locality*. *Thalassia* bed E of N tip of Carrie Bow Cay, Belize, 0.2 m (Station 49).

*Paratype*. USNM 127740, specimen from type locality.

*Etymology*. Named for Ms Regina Lewis (Dangriga, Belize), for many years a most appreciated cook at the field laboratory on Carrie Bow Cay.

**Description.** Length more than 2.7 mm, more than 25 segments (specimen not complete). Width at XI 0.22–0.24 mm. Prostomium pointed triangular. Secondary annuli 7 per (postclitellar) segment. Clitellum extending over  $\frac{1}{2}$ X–XII. Somatic setae (Fig. 19B) bifid, with upper tooth somewhat thinner than but about as long as lower, and with indistinct subdental ligament. Bifids 25–35  $\mu$ m long, about 1  $\mu$ m thick, 2–3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae (Figs 19A; C, *ps*) 2 per bundle, slightly curved, each bundle consisting of: (1) a large seta, 95–100  $\mu$ m long, 4–5  $\mu$ m thick, with curved inner end, and grooved outer part ending in small hook; (2) a smaller seta, 58–66  $\mu$ m long, 3.5–4  $\mu$ m thick, with straight inner end and rounded, somewhat spoon-shaped outer tip. Male pores paired, inconspicuous, in line with ventral setae, posteriorly in XI. Spermathecal pores paired in line with ventral setae, anteriorly in X.

Alimentary canal absent. Male genitalia (Fig. 19C) paired. Vas deferens about 5  $\mu$ m wide, very long, coiled, ectally with distinct muscular lining. Atrium about 70  $\mu$ m long, maximally 19–26  $\mu$ m wide, somewhat spindle-shaped but abruptly bent  $\frac{1}{3}$  from inner end, with 1–2.5  $\mu$ m thick outer lining of muscles and ciliated and partly granulated inner epithelium. Large prostate gland (probably homologous to posterior prostate in related spp.) communicating with atrium at point of bend; anterior prostate gland not observed. Spermathecae (Fig. 19C, *s*)

slender, 110–125  $\mu$ m long, with narrow, maximally 13–16  $\mu$ m wide ducts (most ectal part of ducts very narrow, appearing ‘stretched’), and oblong, 25–30  $\mu$ m wide ampullae, latter with loose bundles of sperm; epithelium surrounding spermathecal pores thickened.

**Remarks.** *Inandrilus reginae* belongs to a group of apomorphic species within *Inandrilus*, namely those with elongated, folded atria and anisomorph penial setae (see Erséus 1984b). Other species with this combination of characteristics are *I. manae* Erséus, 1984(b), *I. falcifer* Erséus and Baker, 1982, and *I. renaudae* Erséus, 1984(b). These others possess structures that at least have been interpreted as anterior prostate glands, although in the case of *I. falcifer* and *I. manae*, the ‘glands’ are associated with the vasa deferentia rather than the proper atria (Erséus 1984b). No anterior prostate gland could be established to occur in *I. reginae*, but developing eggs of the ovaries are sometimes located among the coils of the vasa deferentia and may erroneously be interpreted as prostates.

The detailed morphology of the penial setae and the spermathecae distinguishes *I. reginae* from the other species: the smaller penial setae are ending with rounded, somewhat spoon-shaped tips, not with hooks, and the spermathecal ducts are not muscular as in *I. manae*, *I. falcifer* and *I. renaudae*.

**Distribution and habitat.** Known only from the barrier reef off Belize. Barely subtidal sand with seagrass, 0.2 m depth.

**Genus *Olavius* Erséus, 1984**

**Remarks.** See *Remarks* for *Inandrilus* above.

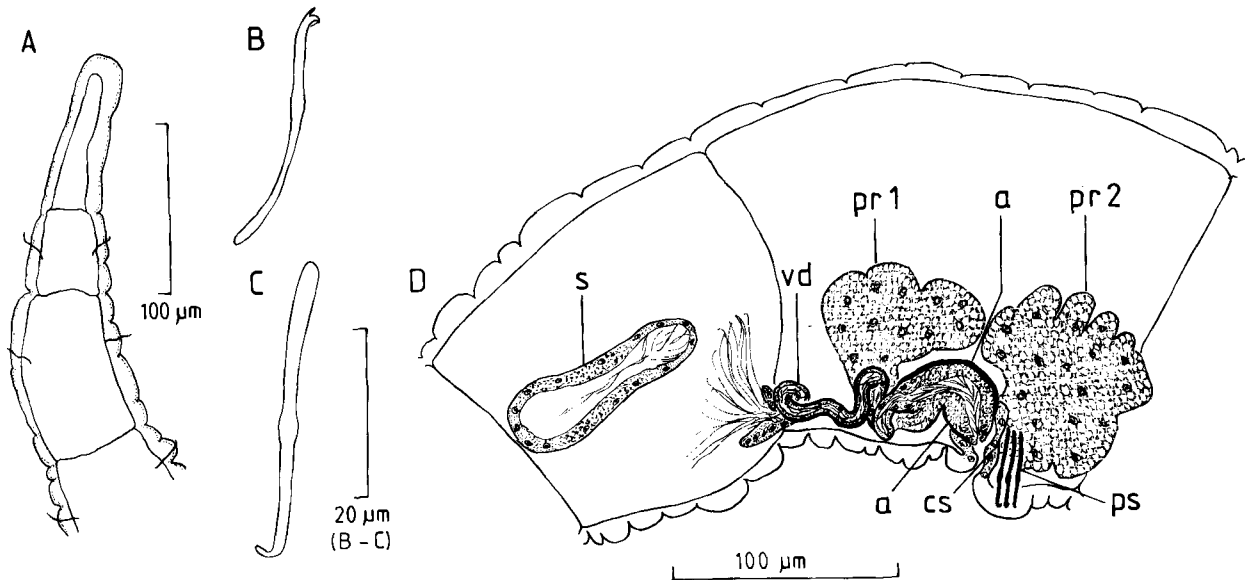


Fig. 20. *Olavius imperfectus* Erséus.—A. Posterior end of worm showing pygidium (top) and three segments.—B. Somatic seta.—C. Penial seta.—D. Lateral view of spermatheca and male genitalia in segments X–XI.

### *Olavius imperfectus* Erséus 1984 (Fig. 20)

*Olavius imperfectus* Erséus, 1984b: 255–256, fig. 18.

**New material.** USNM 127741–127742, 2 specimens from Station 31. Author's collection, 38 specimens: 16 from Station 64; 15 from Station 31; 3 from Station 13; 2 from Station 26; and 1 from each of Stations 57 and 80. M. R. Milligan collection, 2 specimens from 2 km W of mouth of Withlacoochee River, west coast of Florida, 4 m, coarse sand with shell hash (November 1984; coll. M. R. Milligan, for South West Florida Water Management District).

**Amended description.** Length (8 complete specimens measured) 5.6–8.6 mm, 42–57 segments; 1 specimen, with undifferentiated posterior end, only 3.6 mm long, about 31 segments. Width at XI 0.14–0.19 mm. Prostomium rounded. Pygidium (Fig. 20A) slender, generally much longer than wide. Secondary annuli generally 7 per (post-clitellar) segment. Small, roundish gland(?) cells scattered in epidermis throughout body; not visible in all specimens. Clitellum extending over  $\frac{1}{2}$ X–XII, well developed in some specimens. Somatic setae (Fig. 20B) bifid, with upper tooth thinner and shorter than lower, and with subdental ligament. Bifids 30–35  $\mu$ m long, 1–1.5  $\mu$ m thick, 2–3 per bundle anteriorly, (1)2 per bundle in postclitellar segments. Penial setae (Figs 20C; D, *ps*) (2)3(4) per bundle, straight and more or less parallel, 30–45  $\mu$ m long, about 2  $\mu$ m thick, with single-pointed and strongly curved tips. Male pores paired posteriorly in XI. Spermathecal pores paired, slightly dorsal to lateral lines anteriorly in X.

Alimentary canal absent. Male genitalia (Fig. 20D) paired. Vas deferens 5–9  $\mu$ m wide, ectally with distinct muscular lining, entering apical end of atrium. Atrium elongate oval, somewhat curved, 40–52  $\mu$ m long, 23–35  $\mu$ m wide, with up to 4.5  $\mu$ m thick (generally much thinner) outer lining of muscles, and granulated and ciliated inner epithelium. Prostate glands large, anterior one attached to ental end of atrium near entrance of vas deferens, posterior one stalked and attached to ectal part of atrium. Atrium ectally tapering and opening into small copulatory sac; latter with a few folds, at least in some specimens. Spermathecae (Fig. 20D, *s*) elongate, 70–105

$\mu$ m long, each with ectal, duct-like, thick-walled and partly granular portion, 26–34  $\mu$ m wide, and ental oval and more thin-walled ampulla, 16–25  $\mu$ m wide; sperm few and scattered in spermathecae, often partly embedded in wall of ampullae.

**Remarks.** *Olavius imperfectus* was originally described on the basis of a single, incomplete specimen from Columbus Reef, Belize (Erséus 1984b). The old description fits the new material rather well, but it has now been amended to include some of the variation noted.

In six of the 42 new specimens studied, the penial setae are two at one side, but three (the normal number) at the other side of the worms. In another specimen, there are four setae in one of the penial bundles. The stalk of the posterior prostate gland generally appears longer than is shown in Erséus' (1984b) fig. 18B.

**Distribution and habitat.** West coast of Florida (new record) and Belize. Subtidal sand, to at least 8 m depth.

### *Olavius tenuissimus* (Erséus, 1979) (Figs 21A–F)

*Phallogdrilus tenuissimus* Erséus, 1979d: 199–200, fig. 20; Erséus 1981c: tables II–III.

*Olavius tenuissimus* (*partim*); Erséus 1984b: 259; Davis 1985: 166–167.

**New material.** USNM 127743, specimen from Station 8. USNM 127744, specimen from Station 81. Author's collection: 2 specimens from Station 14.

**Description of new material.** Length (3 complete specimens) 4.4–9.5 mm, 24–47 segments. Width at XI 0.12–0.16 mm. Prostomium and pygidium elongate, rounded. Clitellum extending over  $\frac{1}{2}$ X–XII. Secondary annulation irregular. Bifid setae (Fig. 21A) with upper tooth shorter and distinctly thinner than lower, and with subdental ligament. Bifids 35–50  $\mu$ m long, 1.5–2  $\mu$ m thick, 3 per bundle throughout body (occasionally 2 per bundle in postclitellar segments). Penial setae (Figs 21B; F, *ps*) 1 at each side, slender, 63–70  $\mu$ m long, 2.5–3.5  $\mu$ m thick, almost straight but with somewhat bent, single-pointed

tips. Male pores paired ventrally in posterior part of XI. Spermathecal pores paired, located between lines of dorsal setae and lateral lines, immediately anterior to dorsal setae in X.

Alimentary canal absent. Male genitalia (Fig. 21F) paired. Vas deferens about 5–7  $\mu\text{m}$  wide, much longer than atrium. Atrium small, pear-shaped, 30–35  $\mu\text{m}$  long, 20–25  $\mu\text{m}$  wide, with very thin outer lining and thick, granulated inner epithelium, opening into inner part of very large, folded copulatory sac. Prostate glands small, anterior one attached at entrance of vas deferens into

atrium, posterior one located immediately posterior to copulatory sac and attached to middle-to-ectal part of atrium by long stalk. Spermathecae (Fig. 21F, *s*) with short, discrete ducts and elongate ampulla, latter 125–145  $\mu\text{m}$  long, 30–42  $\mu\text{m}$  wide and filled with random sperm.

**Remarks.** This species was originally described from the east coast of Florida, North Carolina and Bermuda, as a member of *Phallogdrilus* (Erséus 1979*d*). In the revision of the gutless Phallogdrilinae (Erséus 1984*b*), it was transferred to *Olavius* and was recorded from the Gulf of

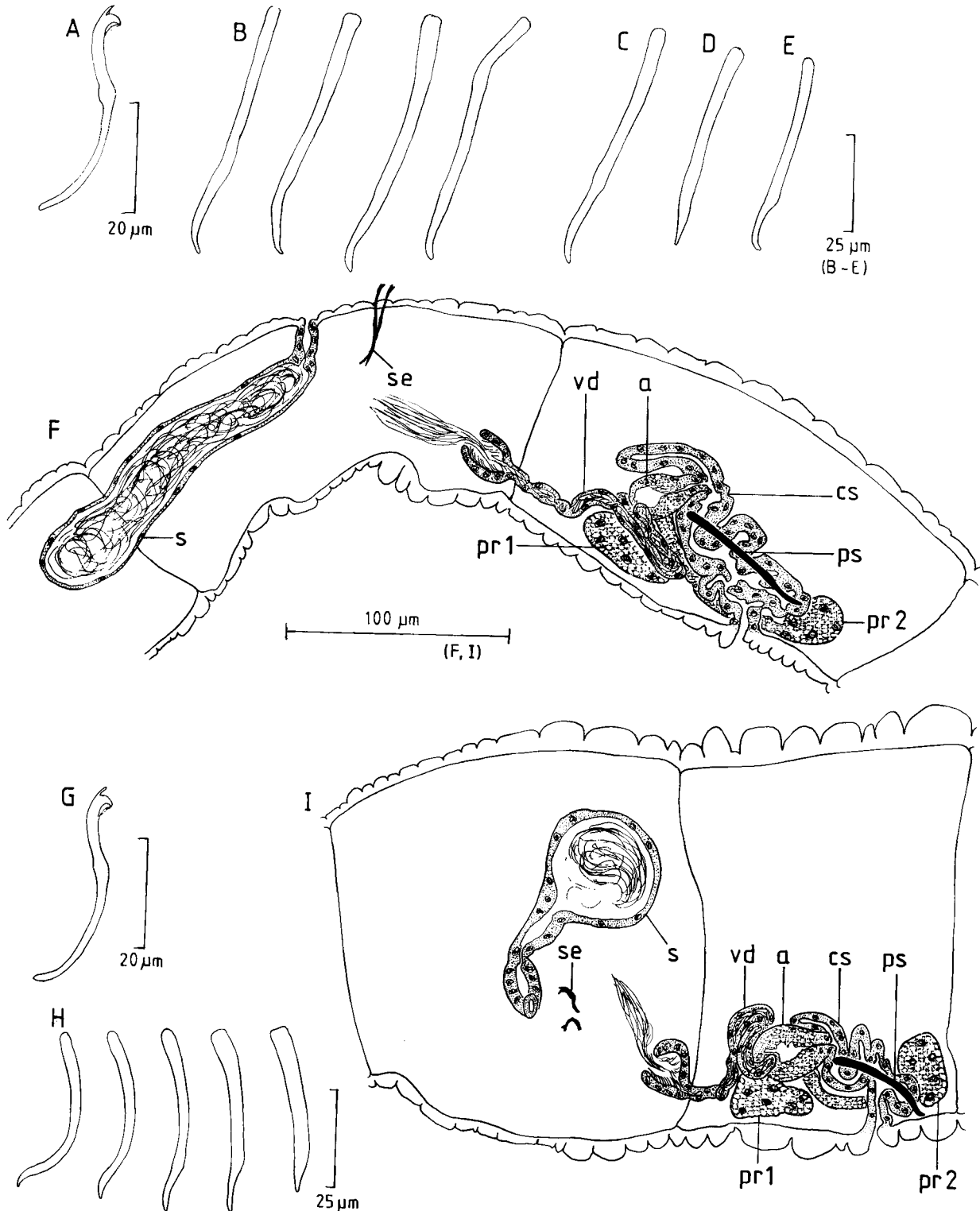


Fig. 21.—A–F. *Olavius tenuissimus* (Erséus).—A. Somatic seta.—B–E. Penial setae of specimens from Belize (B), Gulf of Mexico (C), New Jersey (D) and Bermuda (E).—F. Lateral view of spermatheca and male genitalia in segments X–XI.—G–I. *Olavius finitimus* sp. n.—G. Somatic seta.—H. Penial setae of various specimens (from Belize).—I. Somewhat lateral view of spermatheca and male genitalia in segments X–XI.

Mexico. Davis (1985) found the species as far north as from off Massachusetts. Two specimens from Belize collected by H. R. Baker were also identified as *O. tenuissimus* by Erséus (1984b), but upon re-examination these worms proved to belong to the new species *O. finitimus* described below. The presence of *O. tenuissimus* in Belize is nevertheless confirmed by the new material collected by the present author. The new specimens have penial setae and spermathecae morphologically very similar to those of the worms from more northern populations of *O. tenuissimus* (cf. Figs 21C–E). Two individuals collected near Rosentiel School of Marine and Atmospheric Science, Miami, Florida, with penial setae only 41–44  $\mu\text{m}$  long, and which were identified as *tenuissimus* by Erséus (1979d) actually neither represent that species nor *O. finitimus*, but most probably yet another new form that cannot be described in detail until additional material becomes available. Thus, the known range of the length of the penial setae of *O. tenuissimus* is 45–74  $\mu\text{m}$  in the populations of the southeastern United States and Bermuda, which overlaps with the range noted for the four specimens from Belize (63–70  $\mu\text{m}$ ). Still, however, the worms reported from off Massachusetts by Davis (1985) have somewhat shorter penial setae (38–51  $\mu\text{m}$ ).

The distinction between *O. tenuissimus* and *O. finitimus* is discussed in *Remarks* for the latter species.

*Distribution and habitat.* East coast of U.S.A. (Massachusetts through Florida), Gulf of Mexico, Bermuda and Belize. Subtidal sand, to at least 141 m depth.

### *Olavius finitimus* sp.n. (Figs 21G–I)

*Olavius tenuissimus* (*partim*): Erséus 1984b: 259.

*Holotype.* USNM 127745.

*Type locality.* Edge of reef, near *Thalassia* bed, SW of S tip of Carrie Bow Cay, Belize, 2 m (Station 31).

*Paratypes.* USNM 127746–127747, 2 specimens from Station 57.

*Other material* (author's collection). Five specimens: 2 from type locality; and 3 from area near permanent study transect, N of Carrie Bow Cay, 1 m, sand with some organic matter (April 1982; coll. H. R. Baker).

*Etymology.* The name *finitimus* is Latin meaning 'connected with', 'nearly related' and alludes to the species' close relationship to *O. tenuissimus*.

*Description.* Length (1 complete specimen) 6.6 mm, 40 segments. Width at XI 0.15–0.29 mm. Prostomium and pygidium elongate, rounded. Secondary annulation irregular. Clitellum extending over  $\frac{1}{2}$ X–XII. Somatic setae (Fig. 21G) bifid, with upper tooth shorter and distinctly thinner than lower, and with subdental ligament. Bifids 35–45  $\mu\text{m}$  long, 2–2.5  $\mu\text{m}$  thick, (2)3 per bundle anteriorly, 2(3) per bundle in postclitellar segments. Penial setae (Figs 21H; I, *ps*) curved and somewhat flattened, with single-pointed tips. Penial setae 40–50  $\mu\text{m}$  long, 3–4.5  $\mu\text{m}$  thick (but 'thickness' depending on from which angle seta is viewed; cf. variation in Fig. 21H). Male pores paired ventrally in posterior part of XI. Spermathecal pores paired in line with, and immediately anterior to, dorsal setae in X.

Alimentary canal absent. Male genitalia (Fig. 21I) paired. Vas deferens 6–8  $\mu\text{m}$  wide, much longer than atrium. Atrium small, pear-shaped, 30–40  $\mu\text{m}$  long, 25–

30  $\mu\text{m}$  wide, with very thin outer lining and thick, granulated inner epithelium, opening into inner part of large, folded copulatory sac. Prostate glands small, anterior one attached at entrance of vas deferens into atrium, posterior one located immediately posterior to copulatory sac and attached to middle-to-ectal part of atrium by long stalk. Spermathecae (Fig. 21I, *s*) with discrete, about 15  $\mu\text{m}$  wide ducts, and ampullae characteristically divided into an outer narrow part and an inner distended, oval-to-spherical part; latter 50–75  $\mu\text{m}$  wide and containing random sperm.

*Remarks.* This form was first identified as *O. tenuissimus* by the author. However, the seven specimens studied (including the two reported by Erséus 1984b) all have slightly curved penial setae (which also appear stouter than those of *O. tenuissimus*) and more roundish spermathecal ampullae than the material of *O. tenuissimus* from northern areas (see *Remarks* for *tenuissimus* above). As other specimens from Belize (with slender and straight penial setae, and elongate spermathecal ampullae) are clearly attributable to *tenuissimus*, it was concluded that the whole material in fact consists of two, very closely related species. In addition to the discrepancies noted in the morphology of the penial setae and spermathecae, the two forms are, in the Belizean material, distinguished by the number of postclitellar setae: these setae are commonly three per bundle in the four specimens of *O. tenuissimus*, but almost invariably two per bundle in the seven individuals of *O. finitimus*. However, when comparing the Belizean *O. finitimus* with *O. tenuissimus* from other areas, there is no longer such a clear difference; many specimens of the northern populations of the latter species also have bisetal postclitellar bundles.

Additional material of this complex from various parts of the Caribbean is needed for a more definite settlement of the status of the two forms. It is possible that *O. finitimus* is a southern species that is sympatric with *O. tenuissimus* in Central America, but which does not occur further north.

*Distribution and habitat.* Known only from Belize. Subtidal sand, 1–2 m depth.

### *Olavius vacuus* sp.n. (Fig. 22)

*Olavius* sp. A; Erséus 1986b: 308.

*Holotype.* USNM 127748.

*Type locality.* Back reef, S end of Columbus Reef, N of Tobacco Cay, Belize, 1 m (Station 57).

*Paratypes.* USNM 127749–127750, 2 specimens from type locality. USNM 127751–127752, 2 specimens from Station 26. FSBC 1 37860, specimen from off Hutchinson Island, E coast of Florida, 27°21.6'N, 80°13.1'W, 11.5 m, clean shell hash, very coarse to coarse sand with granule-sized shell (5 July 1972; coll. R. Gallagher *et al.*).

*Other material.* Author's collection, 10 specimens: 3 from Station 13; 1 from each of Stations 1, 31, 57 (type locality) and 77; 2 from near Carrie Bow Cay (exact locality unknown), about 1 m, sand (15–16 April 1982; coll. H. R. Baker); and 1 from offshore of the army base Fort Monroe, southern Chesapeake Bay, Virginia, 37°01'N, 76°17'W, 3 m, sand, salinity range about 25–30 ppt (27 June 1988; coll. L. C. Schaffner). M. R. Milligan collection, 11 specimens: 5 from southwest shelf of Florida, 26°45'50"N, 82°45'11"W, 24.4 m, fine sand (November 1980; coll. for Bureau of Land Management); 1 from same source and collection, but 24°47'07"N, 83°13'05"W, 58.5 m, fine sand (November 1980); and 5 from 2 km W of mouth of Withlacoochee River, west coast

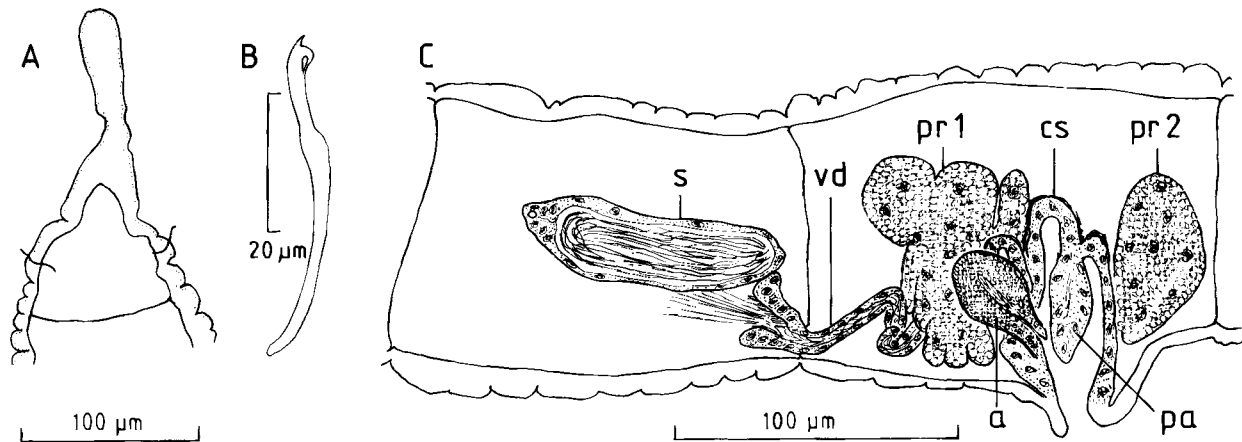


Fig. 22. *Olavius vacuus* sp.n.—A. Posterior end of worm with prolonged pygidium.—B. Setae.—C. Lateral view of spermatheca and male genitalia in segments X–XI.

of Florida, 4 m, coarse sand with shell hash (November 1984; coll. M. R. Milligan, for South West Florida Water Management District).

**Etymology.** The species name *vacuus* is Latin for “void, empty, lacking”, here alluding to the lack of both an alimentary canal and penial setae.

**Description.** Length 3.6–20.4 mm, 53–132 segments. Width at XI 0.15–0.28 mm. (Body not flat; see *Remarks*.) Prostomium elongate with rounded apex. Pygidium with long filiform process (Fig. 22A), sometimes however lost. Secondary annulation conspicuous, irregular, 4–7 annules per segment. Epidermal glands scattered along body, but not always visible. Clitellum extending over  $\frac{1}{2}$ X–XII. Somatic setae (Fig. 22B) bifid, with upper tooth thinner and shorter than lower, and with subdental ligament. Setae 30–60  $\mu$ m long, 1.5–3  $\mu$ m thick, (2)3(4) per bundle anteriorly, (1)2(3) per bundle postclitellar segments. Penial setae absent. Male pores paired in line with ventral setae posteriorly in XI. Spermathecal pores paired anteriorly in X, at some distance from septum between IX and X, in line with dorsal setae or slightly ventral to this line.

Alimentary canal absent. Male genitalia (Fig. 22C) paired. Vas deferens longer than atrium, 7–14  $\mu$ m wide, entering atrium more or less apically. Atrium somewhat oval, tapering ectally, 30–60  $\mu$ m long, 15–28  $\mu$ m wide, with thin muscular lining and thick, granulated inner epithelium. Atrium opening into anterior face of large, convoluted and generally heavily muscular copulatory sac; one ‘fold’ of sac often appearing as pendent papilla. Prostate glands two per atrium, anterior one large and lobed. Spermathecae (Fig. 22C, s) consisting of short ducts and slender ampullae, latter 50–115  $\mu$ m long, 13–42  $\mu$ m wide, thin-walled and containing large bundle of sperm.

**Remarks.** *Olavius vacuus* is closely related to *O. latus* Erséus, 1986b, a flat species known only from Hutchinson Island, Florida. It is, however, easily distinguished from the latter by its round body shape, its lack of penial setae, its low number of somatic setae (only 3 per bundle anteriorly, 2 per bundle posteriorly, as opposed to up to 4 anteriorly and up to 3 posteriorly in *O. latus*), and its smaller spermathecae (those of *O. latus* 155–185  $\mu$ m long including ducts, and with bipartite ampullae).

**Distribution and habitat.** Virginia, east and west coasts of Florida, Belize. Subtidal sand, to at least 58.5 m depth.

### *Olavius (Olavius) tantulus* Erséus, 1984

*Olavius (Olavius) tantulus* Erséus, 1984b: 261–262, fig. 24.

**New material.** USNM 127753, specimen from Station 51. USNM 127754, specimen from Station 64. Author’s collection, 16 specimens: 12 from Station 13; 2 from Station 49; and 1 from each of Stations 31 and 81.

**Remarks.** Four of the new specimens are complete and they are 6.0–7.9 mm long and consist of 46–55 segments. They are thus larger than the original material described from Belize (Erséus 1984b; 4.5–5.8 mm, 44–45 segments). In all other respects, however, they fit the original description. The penial setae, which are very small (up to about 25  $\mu$ m long) in this species, are consistently two per bundle in all new specimens.

**Distribution and habitat.** Known only from Belize. Subtidal, largely fine sands, to at least 27 m depth.

### *Olavius (Olavius) pravus* sp.n. (Fig. 23)

**Holotype.** USNM 127755.

**Type locality.** Sand bore between Carrie Bow Cay and Wee Wee Cay, Belize, 1 m (Station 22).

**Paratype.** USNM 127756, specimen from type locality.

**Other material** (author’s collection). One specimen from type locality.

**Etymology.** The name *pravus* is Latin for ‘crooked, distorted, deformed’, here referring to the appearance of the penial setae (in comparison with those of closely related species).

**Description.** Length 5.7–7.2 mm, 41–44 segments. Width at XI 0.20–0.21 mm. Prostomium pointed triangular. Secondary annuli generally 7 per (postclitellar) segment. Clitellum poorly developed in available material. Pygidium elongate with rounded tip in paratype, damaged in holotype. Somatic setae (Fig. 23B) bifid with upper tooth thinner than lower, and with subdental ligament. Bifids 32–37  $\mu$ m long, about 2  $\mu$ m thick, (2)3 per bundle anteriorly, 2 per bundle in postclitellar segments. Penial setae (Figs 23A; C, ps) blunt, abruptly bent near ectal ends, 125–150  $\mu$ m long, 4.5–7.5  $\mu$ m thick, 3 per bundle, with small roundish depressions in tips. Penial setae more

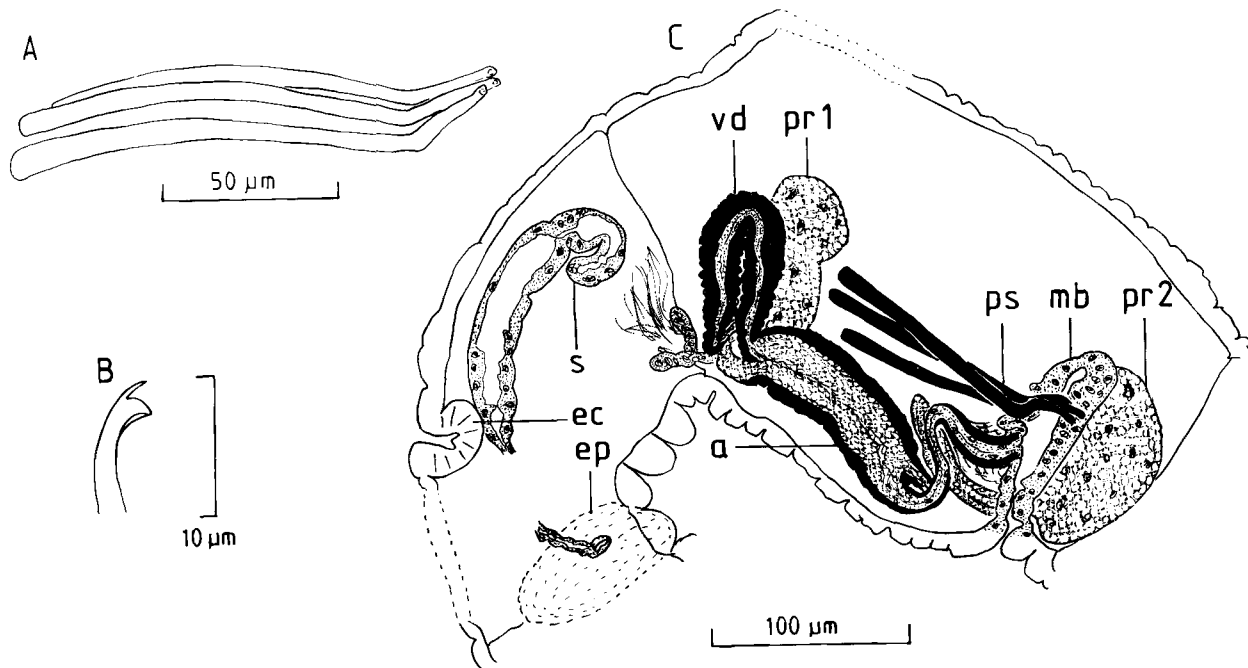


Fig. 23. *Olavius (Olavius) pravus* sp.n.—A. Penial setae.—B. Somatic seta.—C. Lateral view of spermatheca and male genitalia in segments X–XI; specimen somewhat distorted at spermathecal pore.

or less parallel within bundle, oriented along long axis of worm, ental ends to the anterior. Male pores (=atrial openings) in walls of unpaired, large, complex, folded male bursa, ventrally and posteriorly in XI. Spermathecal pores paired, immediately ventral to lateral lines, opening on unpaired pad extending up along lateral sides of worm, anteriorly in X. Round and distinct epidermal crypt present mid-dorsally and anteriorly in X.

Alimentary canal absent. Male genitalia (Fig. 23C) paired. Vas deferens 21–23  $\mu\text{m}$  wide, ectally with very thick layer of (circular) muscles, about as long as atrium, entering apical end of atrium. Atrium slender, 230–250  $\mu\text{m}$  long, maximally 33–42  $\mu\text{m}$  wide, with up to 6–7  $\mu\text{m}$  thick muscular lining; inner epithelium of atrium ciliated, ental (wide) part granulated; ectal part of atrium long, narrow, somewhat coiled duct. Anterior prostate gland attached to ental end of atrium, near entrance of vas deferens; posterior prostate with very long, somewhat coiled stalk, attached at transition between wide and narrow parts of atrium. Spermathecae (Fig. 23C, s) very slender, about 190–210  $\mu\text{m}$  long; ducts not muscular, ectally only 5–7  $\mu\text{m}$  wide, middle part of spermatheca (probably a part of duct too) 19–23  $\mu\text{m}$  wide, hollow; ampullae small, oblong and curved, but without sperm (not fully developed?; specimens precopulatory).

**Remarks.** In the revision of the gutless Tubificidae (Erséus 1984b), the nominate subgenus *Olavius* was defined to include three highly modified species, *O. (O.) longissimus* (Giere, 1979), *O. (O.) alius* Erséus, 1984(b) and *O. (O.) tantulus* Erséus 1984(b), all with heavily muscular vasa deferentia, an unpaired male bursa, slender spermathecae, and a dorsal epidermal crypt (in segment X). The new species appears intermediate between *O. (O.) longissimus*/*O. (O.) alius* (spermathecal pore in line with dorsal setae; penial setae oriented along long axis of worm; penial setae of two different kinds; tips of

penial setae somewhat clubbed) and *O. (O.) tantulus* (spermathecal pores ventral to lines of ventral setae; penial setae obliquely pointing towards mid-ventral line of worm, and less modified, of one kind only). *Olavius (O.) pravus* is distinguished from all the others by its abruptly bent penial setae, and its non-muscular, ectally very narrow, spermathecal ducts.

**Distribution and habitat.** Known only from type locality, Belize. Subtidal sand and gravel, 1 m depth.

#### *Olavius (Olavius) longissimus* (Giere, 1979)

*Phallogdrilus longissimus* Giere, 1979: 305–307, fig. 3, plate 3; Erséus 1981c: tables II–III.

*Olavius (Olavius) longissimus*; Erséus 1984b: 262–263, figs 25, 26A–C.

**New material.** USNM 127757–127758, 2 specimens from Station 71. Author's collection, 6 specimens: 5 from Station 71; and 1 from Station 68.

**Remarks.** This species was originally described from Bermuda by Giere (1979), subsequently from Belize by Erséus (1984b). The penial setae of *O. (O.) longissimus* are oriented along the long axis of the worm (ectal ends of setae pointing towards posterior), each bundle consisting of (2)3(4) straight setae of which one is larger than the other two. The species was named for its great length; Giere reported a range of 20–40 mm with up to 155 segments. One of the new specimens from Curlew Bank is (fixed) 46 mm long and consists of about 184 segments, but its posterior end is still not fully differentiated, which indicates that the species can attain even greater lengths. The greatest seta within the penial bundles is up to 215  $\mu\text{m}$  long in the present material, which extends the size range for this character (up to 190  $\mu\text{m}$  in the old material).

**Distribution and habitat.** Bermuda and Belize. Intertidal and subtidal sand, to at least 2 m depth.

**Genus *Duridrilus* Erséus, 1983**

**Remarks.** The definition of *Duridrilus* was recently modified by Erséus (in press). The genus comprises a few phallo-driline species with more or less papillated body wall.

***Duridrilus tardus* Erséus, 1983**

*Duridrilus tardus* Erséus, 1983b: 29–32, figs 1–2; 1990b: 285–287, fig. 10; Milligan 1987: 484–485, fig. 3.

**New material.** USNM 127759–127762, 4 specimens from Station 6. Author's collection, 26 specimens: 10 (1 of which sectioned) from Station 6; 4 from Station 24; 2 from Station 9; and 1 from each of Stations 1 (sectioned specimen), 4, 10, 14, 15, 36, 42, 80, 82, 86.

**Remarks.** This stiff and sluggish, often characteristically pinkish (when alive), species is known from several parts of the Caribbean area (Erséus 1983b; Milligan 1987), but also recently reported from the West Pacific (Erséus 1990b). The new material fits the previous descriptions well.

**Distribution and habitat.** Belize (new record), Bermuda, Puerto Rico, Barbados, Hong Kong. Subtidal, medium to coarse sand, to at least 39 m depth.

**Genus *Bathydriilus* Cook, 1970**

**Remarks.** *Bathydriilus*, as defined by Erséus (1981c), is a large genus with about 25 species, about half of which constitutes a uniform group of shallow-water forms, whereas the other half, as the generic name implies, is a deep-sea group.

***Bathydriilus vetustus* sp.n. (Fig. 24A–C)**

**Holotype.** USNM 127763.

**Type locality.** West Bay, Twin Cays, Belize, 0–0.3 m, mud (11 April 1981; coll. K. Fauchald *et al.*).

**Paratypes.** USNM 127764, specimen from type locality (type date). USNM 127765–127767, 3 specimens from Station 36.

**Other material.** USNM 127768–127782, 15 specimens from type locality (various dates, October 1979–April 1981; coll. K. Fauchald *et al.*). Author's collection, specimen from SW of Holetown, Barbados, 6 m, silty sand and coral rubble (25 October 1979; coll. C. Erséus).

**Etymology.** This species is considered as 'ancient, old-fashioned' (Latin *vetustus*) with regard to the position of the spermathecal pores and the appearance of the male ducts (see *Remarks*).

**Description.** Length (4 complete specimens) 9.6–12.2 mm, 60–73 segments. Width at XI 0.22–0.31 mm. Prostomium rounded, not elongate. Clitellum extending over  $\frac{1}{2}$ X–XII ( $\frac{1}{3}$ XIII). Epidermal glands present in most segments, in four distinct patches per segment, one patch around each bundle of setae. Setae 32–55  $\mu$ m long, 2–2.5  $\mu$ m thick, 2 per bundle in II–IX, thereafter 'bundles' unisetal for most parts of body, bisetal bundles becoming increasingly common again in posterior end of worm. Anterior setae (Fig. 24A) bifid with upper tooth much thinner and shorter than lower, most of postclitellar setae (Fig. 24B) rather bluntly single-pointed. Penial setae absent. Male pores paired in line with ventral setae,

posteriorly in XI. Spermathecal pores paired in line with ventral setae, anteriorly in X.

Pharyngeal glands inconspicuous, extending into VII or thereabouts. Male genitalia (Fig. 24C) paired. Vas deferens 7–12  $\mu$ m wide, with thin walls, much longer than atrium, coiled. Vas appears to attach to middle of anterior face of atrium, but runs outside atrium proper to apex, where it joins actual lumen of atrium. Atrium somewhat club-shaped, 130–165  $\mu$ m long, maximally 26–46  $\mu$ m wide, with apex tilted over to posterior. Outer (muscular) lining of atrium very thin, inner epithelium granulated, lumen narrow. Ectal part of atrium tapering into short, narrow duct leading to inconspicuous male pore. Latter surrounded by some tissue, forming a small bulb, but no pseudopenis formed. Prostate glands small, anterior one attached to middle of anterior face of atrium, posterior one to apex of atrium. Spermathecae (Fig. 24C, *s*) consisting of distinct ducts, 45–60  $\mu$ m long, 23–28  $\mu$ m wide, and ampullae of variable shape, 70–190  $\mu$ m long, 40–75  $\mu$ m wide. Spermathecal ampullae containing a mixture of loose sperm, skein-like balls of sperm and droplets of secretion.

**Remarks.** Three other shallow-water species of *Bathydriilus* lack penial setae: *B. torosus* Baker, 1983 (*b*), *B. edwardsi* Erséus, 1984 (*e*) and *B. egenus* sp.n. *Bathydriilus vetustus* differs from all of these by its fewer setae (anterior bundles generally with three, posterior bundles with two setae, in the other three), and by the more ventral position of its spermathecal pores (these pores in lateral lines in the others). Moreover, it is distinguished from *B. torosus* by its lack of thick atrial musculature, from *B. edwardsi* by having posterior single-pointed setae (all setae bifid in *edwardsi*), and from *B. egenus* by its slenderer atria and smaller prostate glands (cf. description of *egenus* below).

Although it has been noted for several other species of *Bathydriilus* that the vas deferens runs under the muscular lining of the atrium to join the proper atrial lumen at apex of the atrium (Erséus 1981c; Baker 1983b), this part of the vas nowhere seems to be as superficial as in *B. vetustus*. In the new species, the terminal end of the vas merely attaches to the atrial surface (Fig. 24C). This condition supports the view that *Bathydriilus* and *Duridrilus* are very closely related genera (Erséus in press), and *B. vetustus* is with regard to atrial features intermediate between a new species of *Duridrilus* simultaneously described from Australia (Erséus in press) and the other species of *Bathydriilus*. This neither refutes the assumed monophyly of *Duridrilus* (with body wall papillation and prolongation of vasa deferentia as two apomorphies), nor that of *Bathydriilus* (with the apomorphic incorporation of the vas deferens in the atrium), but it suggests that *B. vetustus* is a plesiomorphic member of the latter.

The ventral location of the spermathecal pores in *B. vetustus* is probably also an additional assumed plesiomorphic trait (shared with the majority of phallo-drilines); in most other shallow-water species of *Bathydriilus*, the spermathecae open in the lateral lines.

**Distribution and habitat.** Belize and Barbados. Subtidal sand, to at least 6 m depth.

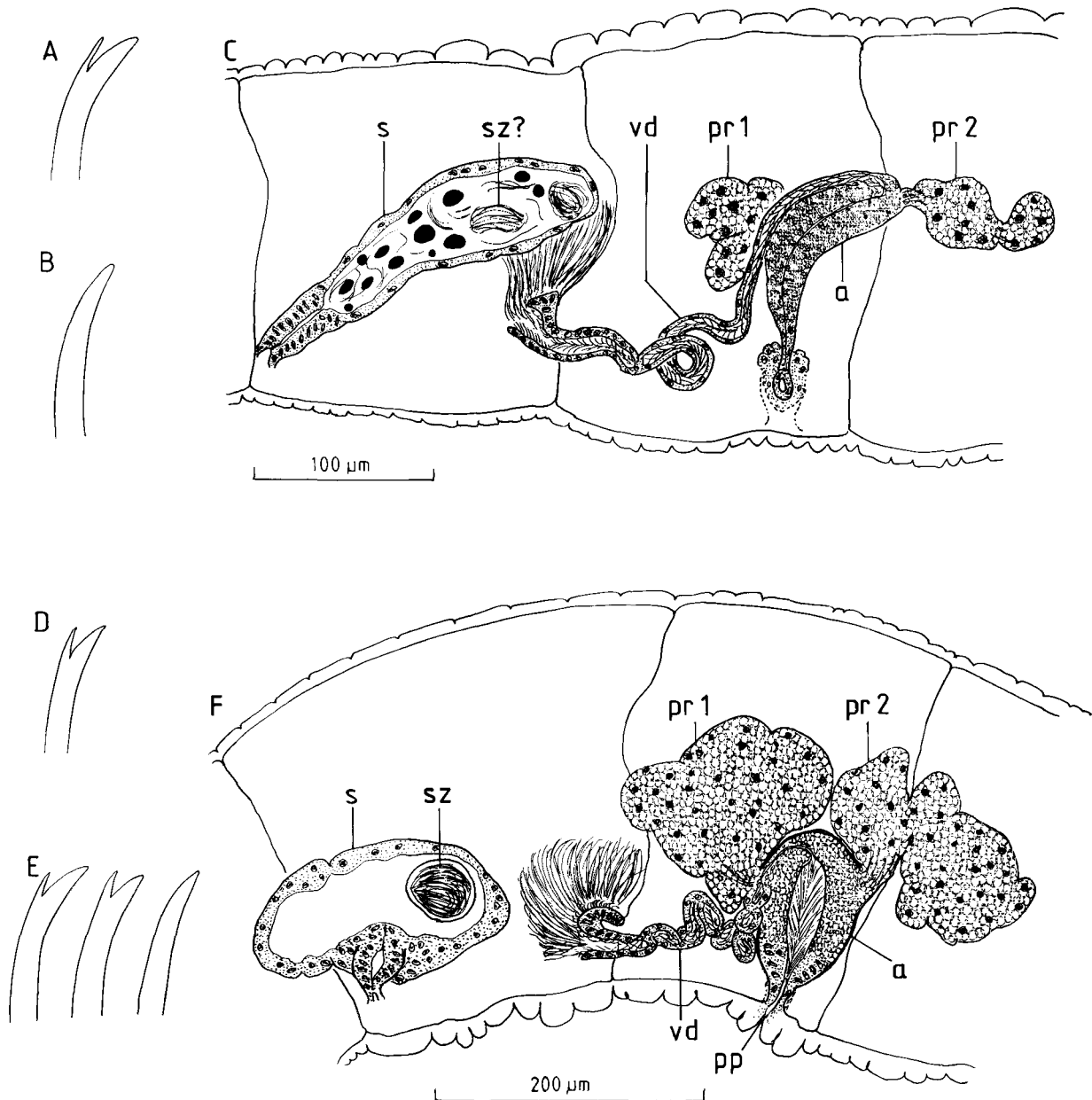


Fig. 24.—A–C. *Bathydriilus vetustus* sp.n.—A. Free-hand drawing of anterior seta.—B. Free-hand drawing of postclitellar seta.—C. Lateral view of spermatheca and male genitalia in segments X–XI.—D–F. *Bathydriilus egenus* sp.n.—D. Free-hand drawing of anterior seta.—E. Free-hand drawing of postclitellar setae.—F. Lateral view of spermatheca and male genitalia in segments X–XI.

### *Bathydriilus egenus* sp.n. (Figs 24D–F)

*Holotype*. USNM 127783.

*Type locality*. About 50 m N of Carrie Bow Cay, Belize, 0.7 m (Station 9).

*Paratypes*. USNM 127784–127786, 3 specimens from type locality.

*Other material* (author's collection). Seven specimens: 5 from type locality; and 2 from near Carrie Bow Cay (exact locality unknown), 1.2–1.8 m, sand with *Halimeda* flakes (16–18 April 1982; coll. H. R. Baker).

*Etymology*. The epithet *egenus* is Latin for 'needy, in want', and alludes here to the species' lack of penial setae.

*Description*. Length (only 1 complete specimen) 20.0 mm, 113 segments. Width at XI 0.30–0.50 mm. Prostomium somewhat elongate. Clitellum extending over X– $\frac{1}{2}$ XIII. Epidermal glands present, arranged in rings, one per segment, at level of setae. Setae 35–55  $\mu$ m long, 2–2.5  $\mu$ m thick, (2)3–4 per bundle anteriorly, 2 per bundle in postclitellar segments. Anterior setae (Fig. 24D) bifid with upper tooth thinner and shorter than lower, pos-

terior setae (Fig. 24E) variable, with upper tooth more or less reduced, some setae being single-pointed. Penial setae absent. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores paired in lateral lines, anteriorly in X.

Pharyngeal glands in IV–VII (VIII). In some specimens, a few round or oval, granulated coelomocytes present. Male genitalia (Fig. 24F) paired. Vas deferens 14–19  $\mu$ m wide, somewhat longer than atrium, entering anterior face of atrium somewhat ental to middle; narrow canal of vas running under atrial lining to join wide lumen of atrium proper at apex of latter. Atrium large and erect, oval, 115–150  $\mu$ m long, 70–95  $\mu$ m wide, with 1–2  $\mu$ m thick outer lining of muscles, and thick, ciliated, and for most parts granulated, inner epithelium. Atrium ectally tapering, ending in very simple (eversible) pseudopenis. Prostate glands large, anterior one attached to middle of anterior face of atrium, posterior one subapically to

posterior face, almost opposite to entrance of anterior prostate. Spermathecae (Fig. 24F, *s*) consisting of short, somewhat triangular ducts, and oval ampullae; latter 140–230  $\mu\text{m}$  long, 95–115  $\mu\text{m}$  wide, with ducts opening into middle, and containing sperm, mostly as skein-like spermatozeugmata.

**Remarks.** As noted for *B. vetustus* above, this new taxon is also one of the few species within *Bathydrilus* that lack penial setae. Among the other species without such setae, *B. edwardsi* is the one most similar to *B. egenus*. However, *B. edwardsi* has bifid (somatic) setae throughout the body, and its vasa deferentia enter a more ectal part of the atria (see Erséus 1984e).

With regard to the arrangement of the vasa deferentia-atria, *B. egenus* rather resembles *B. superiovasatus* Erséus, 1981(c), from the Great Barrier Reef in Queensland, Australia, and *B. munitus* Erséus, 1990(c), recently described from Victoria, Australia. Particularly the latter species, which has single-pointed setae in posterior bundles, may be closely related to *B. egenus*. However, both *B. superiovasatus* and *B. munitus* possess penial setae and are thus readily distinguished from *B. egenus*.

**Distribution and habitat.** Known only from Belize. Subtidal sand, 0.7–1.8 m depth.

### *Bathydrilus adriaticus* (Hrabě, 1971)

*Phallogdrilus adriaticus* Hrabě, 1971a: 220–221, figs 19–25.

*Bathydrilus adriaticus adriaticus*; Erséus 1979c: 145.

*Bathydrilus adriaticus trisetosus* Erséus, 1979c: 145–146, fig. 10.

*Phallogdrilus adriaticus caraibicus* Righi & Kanner, 1979: 62–64, figs 48–51.

*Bathydrilus adriaticus*; Erséus 1985: 134–136, fig. 2; 1987d: 75–76; Erséus & Davis 1989: 76–77, figs 2A–C.

**New material.** ZMA 2855, specimen from sandy beach, 30 m from N shore, Awa di Oostpunt, Curaçao (Lesser Antilles), 0.1–0.3 m, sand on limestone, with scattered *Thalassia* (22 November 1970; coll. P. Wagenaar Hummelinck, station no. 1666). USNM 127787–127791, 5 specimens from northeast (Caribbean) coast of Panama (Archipelago de San Blas), 08°54.7'N, 77°41.0'W, lower intertidal/barely subtidal (29 June 1977; CARIB I. *Alpha Helix* station no. 22-2000). USNM 127792–127794, 3 specimens (1 of which sectioned) from SW of Holetown, Barbados, 6 m, silty sand and coral rubble (25 October 1979; coll. C. Erséus). USNM 127795–127796, 2 specimens from English Bay, Ascension Island (S Atlantic), sand from outer tidepool (12 July 1976; coll. M. L. Jones *et al.*). USNM 127797–127818, 127820–127885, 88 specimens from numerous samples, West Bay, Twin Cays, Belize, 0–0.3 m, mud (various dates, October 1979–May 1984; coll. K. Fauchald *et al.*). USNM 127819, 127886–127887, 3 specimens from W side of middle cay, Blue Ground Range, Belize, 0–0.5 m, mud (November 1979–June 1981; coll. K. Fauchald *et al.*). Author's collection, 10 specimens from Belize: 5 (1 of which sectioned) from Station 16, 2 from Station 74, 1 from each of Stations 52, 85 and 87. Author's collection, 10 specimens from Barbados (all coll. C. Erséus): 1 from Carlisle Bay, at Bridgetown, 7 m, muddy coarse sand (25 October 1979); 1 from same bay and depth, but silty sand (25 October 1979); 5 (1 of which sectioned) from SW of Holetown, 9 m, patch of silty sand and coral rubble (25 October 1979); and 3 from Bellairs Reef, off Coral Reef Club, St James, 13–20 m, coarse sand (29 October and 1 November 1979).

**Remarks.** The Caribbean form of *B. adriaticus* was first described as a separate subspecies *trisetosus*, as the penial setae of all available specimens were three per bundle, a consistent discrepancy *vis-à-vis* the Mediterranean (nominata) form invariably having two penial setae per bundle (Erséus 1979c). The species is, however, now regarded as a single taxon, as material from other areas

(Saudi Arabia and Hawaii) shows variation in this character, the number varying between two and four per bundle, even within the same population (Erséus 1985; Erséus & Davis 1989).

Previous Caribbean records of *B. adriaticus* are from Bermuda, Florida, Bonaire, and possibly Puerto Rico (discussed by Erséus 1979c: 146). The new range extensions for Curaçao and Belize reported here are thus not surprising.

Eighty-three of the 90 (=92%) fully mature specimens from Belize, as well as all individuals from Panama and all but one from Barbados, have three penial setae in both penial bundles. However, in three worms from Twin Cays (Belize), as well as in the single individual from Curaçao, the penial bundle of one side contains only two setae, the bundle of other side being 'normal' with three setae. Finally, in four other specimens from Twin Cays, and in a single worm from Barbados, there are four penial setae on one side, three on the other. This demonstrates that the Caribbean form of *B. adriaticus* also vary somewhat with regard to the number of penial setae.

On the barrier reef off Belize, *Bathydrilus adriaticus* appears particularly common in sediments immediately adjacent to mangrove cays, whereas its congener, *B. formosus* (see below), is a characteristic member of the sand fauna associated with the more exposed, coral-line cays with few or no mangroves.

The two specimens from Ascension Island represent the first record of *B. adriaticus* from the South Atlantic. The worms are rather small (6.6–8.2 mm long, 56–71 segments), with small penial setae (up to about 65  $\mu\text{m}$  long; 3 per bundle) and atria (about 75  $\mu\text{m}$  long, 25  $\mu\text{m}$  wide).

**Distribution and habitat.** Belize, Panama, Curaçao, Barbados, Ascension Island (new records), Bermuda, Florida, (?) Puerto Rico, Bonaire, Mediterranean Sea, Persian Gulf, Hawaii; apparently circumtropical. Intertidal and subtidal, often muddy, sand, to at least 32 m depth.

### *Bathydrilus formosus* Erséus, 1986

*Bathydrilus formosus* Erséus, 1986b: 302–303, fig. 10; Ferraguti *et al.* 1989: 77–79, figs 24–32.

**New material.** USNM 127888–127890, 3 specimens from Ft Pierce, east coast of Florida, 17 m, coarse sand with *Branchiostoma* (4 October 1983; coll. R. P. Higgins). USNM 127891–127896, 6 specimens (1 of which sectioned) from Station 9. Author's collection, 90 specimens: 5 from Station 9; 16 (3 of which sectioned) from Station 2; 9 (2 of which sectioned) from Station 5; 3 from each of Stations 8 (2 specimens sectioned), 31 and 57; 16 from Station 36; 9 from Station 44; 5 from each of Stations 32 and 67; 4 from each of Stations 35 and 39; 2 from Station 77; 1 from each of Stations 23, 26, 28, 40, 80 and 86.

**Remarks.** This species was described by Erséus (1986b) on the basis of material from Belize and Florida. The full description is thus not repeated here, but a few aspects of the morphology of the species deserve attention.

The worm is generally deep red when alive. It is characterized by large, rather stout somatic setae, three per bundle anteriorly, two per bundle in postclitellar segments, and generally bifid [(?) upper tooth not always visible], somewhat curved penial setae. The latter are two per bundle in a majority of the specimens (in 76 of the 88 whole-mounted specimens examined), but occasionally

the bundle of one side contains three (nine specimens) or even four (one specimen) penial setae. Penial setae are completely missing in two specimens, which however do not appear to have reached full sexual maturity.

One feature of *B. formosus* was not noted in the original description: an unpaired epidermal papilla, with a small invagination in the middle, is located mid-ventrally in the anterior end of segment X. Such 'anchoring crypts' (discussed by Giere 1979) are known also from other tubificids with large penial setae [e.g. *Olavius* (*O.*) *pravus* sp.n.: Fig. 23C, *ec*; *O.* (*O.*) *longissimus* (Giere, 1979: fig. 3B); *O.* (*O.*) *alius* Erséus, 1984b: fig. 27B; and *Heterodrilus jamiesoni* Erséus, 1981a: fig. 10D].

The spermatozeugmata are unusually large and conspicuous in this species. The ultrastructure of them was recently described by Ferraguti *et al.* (1989).

*Bathydrius formosus* is apparently the most common species of *Bathydrius* on the barrier reef off Belize. In places, particularly where the sediment consists of coarse, somewhat muddy, sand, it occurs in very high numbers.

*Distribution and habitat.* Belize and Florida (east and west coasts). Subtidal sands, to at least 20 m depth. Erséus (1986b) stated 0.5–11 m depth, but this excluded by mistake the record from 20 m in NE Gulf of Mexico (Erséus 1986b: 302).

### Subfamily Limnodriloidinae

#### Genus *Doliodrilus* Erséus, 1984

*Remarks.* This genus accommodates three species described by Erséus (1984e, 1985) and Erséus & Milligan (1988b). Some details in the definition of *Doliodrilus* as defined by Erséus (1985) were modified by Erséus & Milligan (1988b).

#### *Doliodrilus puertoricensis* Erséus & Milligan, 1988

*Doliodrilus puertoricensis* Erséus & Milligan, 1988b: 12–14, fig. 2.

*New material.* USNM 127897–127908, 12 specimens from West Bay, Twin Cays, Belize, barely subtidal, mud (6–8 April 1981; coll. K. Fauchald *et al.*).

*Brief description of new material.* Length (5 intact specimens) 5.6–8.7 mm, 47–52 segments. Setae bifid, up to about 60  $\mu\text{m}$  long, about 2.5  $\mu\text{m}$  thick, (1)2–4(5) per bundle anteriorly, (1)2–3 per bundle in postclitellar segments. Oesophagus dilated, barrel-shaped in IX. Male ducts paired, small. Vas deferens 7–12  $\mu\text{m}$  wide. Atrium about 105–125  $\mu\text{m}$  long, entally and ectally 9–17  $\mu\text{m}$  wide, at prostatic pad 19–25  $\mu\text{m}$  wide. Spermathecae small, with ducts 21–28  $\mu\text{m}$  long, 14–19  $\mu\text{m}$  wide, and (round) ampullae 21–32  $\mu\text{m}$  in diameter. Sperm as small curved bundles in postcopulatory specimens.

*Remarks.* This species was previously known only from a brackish-water lagoon (Laguna Joyuda) in Puerto Rico (Erséus & Milligan 1988b). The specimens from Belize fit the original description well, even in almost all dimensional features; the atria were, however, somewhat longer (about 165  $\mu\text{m}$ ) in the type material.

*Distribution and habitat.* Belize (new record) and Puerto Rico. Subtidal mud, to at least 2.5 m depth; in Puerto Rico subject to fluctuating salinities.

#### Genus *Thalassodrilides* Brinkhurst & Baker, 1979

*Thalassodrilides* Brinkhurst & Baker, 1979: 1564–1565.

*Curacaodrilus* Righi & Kanner, 1979: 51–52.

*Kaketio* Righi & Kanner, 1979: 55.

*Emended definition* (with assumed synapomorphy in italics). Brackish water or marine tubificids. All setae bifid, hair setae absent. Modified genital setae absent. Male pores paired in segment XI. Spermathecal pores paired in anterior part of X, or absent. Coelomocytes, if present, small and sparse. In segment IX, oesophagus widened and thick-walled, with reticulate blood plexus.

Vasa deferentia wide, ciliated, entering apical end of atria. Atria more or less club-shaped, terminating in *complex, muscular, eversible pseudopenes*. Prostate glands lobed, broadly attached to glandular tissue in ventral part of atrial ampullae; in one species (*ineri*) this glandular part separate from rest of ampulla, forming a large diverticulum. Spermathecae present (paired) or absent; if present, sperm random, or (in *ineri*) aggregated in one large spermatozeugma in each spermatheca.

*Type species.* *Limnodriloides gurwitschi* Hrabě, 1971.

*Other species.* *T. belli* (Cook, 1974)

*T. bruneti* sp.n.

*T. ineri* (Righi & Kanner, 1979) comb.n.

(?)*T. milleri* Brinkhurst & Baker, 1979 sp.dub.

*Remarks.* *Thalassodrilides* was revised once before (Erséus 1981b). At that time the species *ineri* was kept as in its original genus, *Kaketio*, due to its unique traits (see also Erséus 1980b). However, the elaboration of the atria and the copulatory organs of *K. ineri* is very easy to conceive as an apomorphic condition of the basic features of *Thalassodrilides*: (1) the prostate-bearing diverticulum on the atrium most certainly is derived from a single glandular pad in the ventral wall of the atrial ampulla, such as the one present in, for instance, *T. bruneti* (see Fig. 25B; in the atrium of *bruneti* the separation of a prostatic diverticulum appears foreshadowed by the thin septum, *sa*); and (2) the highly complex pseudopenes are not basically different from those of *T. gurwitschi*, *T. belli* and *T. bruneti*, merely larger and with longer ducts inside (cf. Fig. 25B with Righi & Kanner 1979: fig. 43). Moreover, the strange spermatozeugmata of *K. ineri* are as far as known an autapomorphy for this species and do not indicate a relationship to any other species outside *Thalassodrilides*.

Therefore, to render *Thalassodrilides* monophyletic in a cladistic sense, the species *ineri* is now regarded as the most apomorphic member of this genus. *Thalassodrilides* was established in the same year as its two synonyms *Kaketio* and *Curacaodrilus*, but it takes priority as the publication by Brinkhurst & Baker (1979) was circulated a few months before the one by Righi & Kanner (1979).

*Thalassodrilides gurwitschi* (Hrabě, 1971)

*Limnodriloides gurwitschi* Hrabě, 1971b: 33–34, fig. 1.

*Thalassodrilus gurwitschi*; Hrabě 1971a: 224–225, figs 27–35; 1975: 119, fig. 12.

*Thalassodrilides gurwitschi*; Brinkhurst & Baker 1979: 1564; Erséus 1981b: 335–338, fig. 1; 1984e: 157–158, fig. 14; 1985: 143–144, fig. 9 (see *Remarks*); in press: Erséus & Davis 1989: 89.

*Curacaodrilus gurwitschi*; Righi & Kanner 1979: 51–52.

*Curacaodrilus sinus* Righi & Kanner, 1979: 53–54, figs 36–38.

**New material.** USNM 127909–127912, 4 specimens (1 of which sectioned) from Station 61. USNM 127913–127914, 2 specimens from West Bay, Twin Cays, Belize, barely subtidal, mud (8 April 1981; coll. K. Fauchald *et al.*). Author's collection, 16 specimens: 3 (1 of which sectioned) from Station 21; 9 (2 of which sectioned) from Station 75; 2 from Station 61; 1 from Station 17; and 1 (sectioned) from Station 83.

**Brief description of new material.** Length (5 specimens) 6.3–7.5 mm, 41–49 segments. Width at XI 0.48–0.65 mm. Setae up to about 75  $\mu\text{m}$  long, 3.5  $\mu\text{m}$  thick, (1)2–4(5) per bundle anteriorly, (1)2(3) per bundle in postclitellar segments. Atrial ampullae at least about 100  $\mu\text{m}$  long, about 35  $\mu\text{m}$  wide. Copulatory sac heavily muscular, 140–160  $\mu\text{m}$  long, about 120  $\mu\text{m}$  wide. Pseudopenes everted and protruding from male protuberances on body wall in most (preserved) specimens. Male protuberances still present when pseudopenes are withdrawn. Spermathecae absent.

**Remarks.** This circumtropical species has been recorded from many parts of the world. A very similar form, but with smaller body size and with less developed musculature around the pseudopenes, is overlapping in distribution with *T. gurwitschi* in the area studied in Belize. It is described as a new species, *T. bruneti*, below.

Material from the Persian Gulf coast of Saudi Arabia was identified as *T. gurwitschi* by Erséus (1985). It has somewhat intermediate pseudopenes and possibly belongs to *T. bruneti* too (see *Remarks* for *bruneti* below).

**Distribution and habitat.** Widespread in the Caribbean (Aruba, Curaçao, Bonaire, Panama, Puerto Rico, Florida; new record from Belize); also Black Sea, Mediterranean Sea, (?) Persian Gulf (see *Remarks*), southern China, Hawaii, Western Australia; apparently circumtropical. Intertidal and subtidal, generally muddy sediments. Marine and brackish-water.

*Thalassodrilides bruneti* sp.n. (Fig. 25)

**Holotype.** USNM 127915.

**Type locality.** E side of South Point, Twin Cays, Belize, 0.1 m (Station 61).

**Paratypes.** USNM 127916–127920, 5 specimens (1 of which sectioned) from type locality.

**Other material.** ZMA 2856, 2 specimens from sandy beach, 30 m from N shore, Awa di Oostpunt, Curaçao (Lesser Antilles), 0.1–0.3 m, sand on limestone, with scattered *Thalassia* (22 November 1970; coll. P. Wagenaar Hummelinck, station no. 1666). USNM 127921, specimen from southern part of barrier reef, Belize, 16°43.8'N, 87°52.0'W, lower intertidal, sediment unknown (15 July 1977; CARIB I. *Alpha Helix* station no. MS-54-500). Author's collection, 54 specimens: 46 (1 of which sectioned) from type locality; 6 (2 of which sectioned) from Station 17; 1 from Station 43; and 1 (sectioned) from Station 75.

**Etymology.** Named for Dr Carlos Brunet (University of Houston, Texas), who collected the sediment sample from the type locality, and who in many other ways assisted me during the field work at Carrie Bow Cay.

**Description of material from type locality.** Length (6 specimens) 4.6–5.3 mm, 33–44 segments. Width at XI 0.46–0.56 mm. Prostomium somewhat triangular. Clitellum extending over XI–XII. Setae (Fig. 25A) bifid, with upper tooth thinner and shorter than lower. Setae 35–60  $\mu\text{m}$  long, 2.5–3  $\mu\text{m}$  thick, (1)2–4 per bundle anteriorly, 1–2(3) per bundle in postclitellar segments, but absent ventrally from XI. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pores absent.

Pharyngeal glands in IV–V. Oesophagus in IX enlarged, thick-walled and with conspicuous blood plexus. Male genitalia (Fig. 25B) paired. Vas deferens 19–25  $\mu\text{m}$  wide, about as long as, and entering apical end of atrium. Atrial ampulla somewhat spindle-shaped, 55–80  $\mu\text{m}$  long, 25–50  $\mu\text{m}$  wide, with thin outer lining and rather wide lumen, latter partly divided by thin, horizontal septum, into dorsal and ventral compartments. Prostatic pad inconspicuous, but extending along most of length of atrial ampulla. Prostate gland small, lobed. Atrial duct slender, slightly longer than ampulla, running inside somewhat pear-shaped, moderately muscular, copulatory sac; inner part of duct granulated, outer part forming eversible pseudopenis. Male pores not on protuberances when pseudopenes are withdrawn. Spermathecae absent.

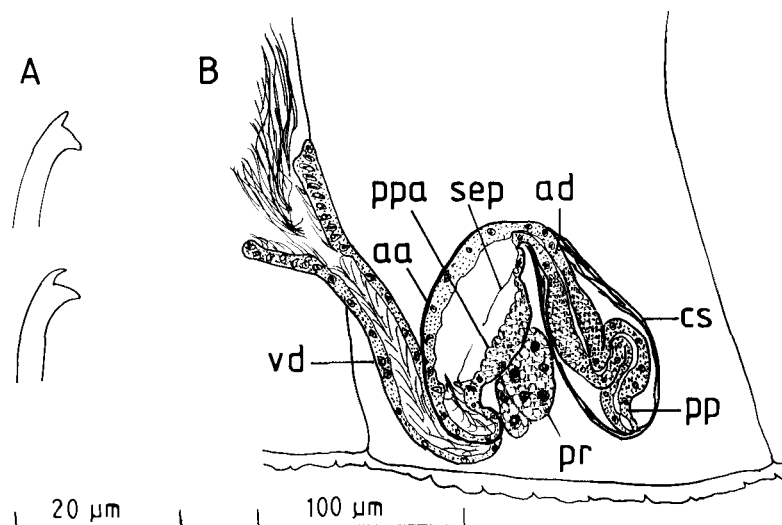


Fig. 25. *Thalassodrilides bruneti* sp.n.—A. Setae, showing variation in teeth.—B. Somewhat lateral view of male genitalia in segment XI.

**Brief description of material from Curaçao.** Length (1 intact specimen) 9.0 mm, about 33 segments, width at XI 0.30–0.37 mm; worms thus less contracted than those from Belize. Setae up to 70  $\mu\text{m}$  long, 3  $\mu\text{m}$  thick, 2–5 per bundle anteriorly, 2(3) per bundle in postclitellar segments. Atrial ampullae about 80  $\mu\text{m}$  long, 33  $\mu\text{m}$  wide. Copulatory sac 105–130  $\mu\text{m}$  long, 55–65  $\mu\text{m}$  wide.

**Remarks.** This species is virtually identical to *T. gurwitschi* in terms of somatic characters, and also in most features of the male ducts. The copulatory sacs of *T. bruneti* are, however, not as heavily muscular as those of *T. gurwitschi*, and *T. bruneti* lacks the male protuberances that generally are prominent in the other species.

The specific separation of *T. gurwitschi* and *T. bruneti* is supported by the fact that they occur at the same localities in Belize (Stations 17, 61 and 75) and still are two distinct forms. *Thalassodrilides bruneti* is smaller than *T. gurwitschi* (cf. brief description of latter above), but it is not likely to be a younger stage of that species, as most of the specimens examined are clitellate and bear well developed eggs.

However, when comparing with material from other parts of the world, the discrimination of *T. bruneti* may appear less clear. Both the body size and the copulatory sacs of *T. gurwitschi* show considerable geographic variation. For instance, the material identified as *T. gurwitschi* from Saudi Arabia (Erséus 1985) has copulatory organs that are intermediate in comparison with those of the two species in Belize. The Arabian form may in fact be *T. bruneti*, or possibly a third species.

**Distribution and habitat.** Belize and Curaçao. Intertidal or barely subtidal, muddy sediments.

### *Thalassodrilides ineri* (Righi & Kanner, 1979) comb.n.

*Kaketio ineri* Righi & Kanner, 1979: 55–62, figs 39–47; Erséus 1980b: 1220–1222; Ferraguti *et al.* 1989: 76–77, figs 14–23.

**New material.** ZMA 2857, 4 specimens from sandy beach, 30 m from N shore, Awa di Oostpunt, Curaçao (Lesser Antilles), 0.1–0.3 m, sand on limestone, with scattered *Thalassia* (22 November 1970; coll. P. Wagenaar Hummelinck, station no. 1666). ZMA 2858, specimen from W shore of Flamingo Pond, Simson Bay Lagoon, St Martin, Leeward Islands (Lesser Antilles), lower intertidal, sand and soft mud with celgrass (8 June 1949; coll. P. Wagenaar Hummelinck, station no. 1132A). ZMA 2859–2860, 5 specimens from N of Castle Landing, Great Lagoon, Barbuda, Leeward Islands (Lesser Antilles), 0–0.5 m, soft mud with *Rhizophora* (24 July 1967; coll. P. Wagenaar Hummelinck, station nos. 1539, 1539A). USNM 127922–127923, 2 specimens (1 of which sectioned) from Station 17. USNM 127924–127929, 6 specimens from West Bay, Twin Cays, Belize, barely subtidal, mud (various dates, October 1979–December 1980; coll. K. Fauchald *et al.*). USNM 127930–127939, 10 specimens from W side of middle cay, Blue Ground Range, Belize, 0.2–0.5 m, mud (9–11 November 1979; coll. K. Fauchald *et al.*). Author's collection, 7 specimens: 3 (2 of which sectioned) from Station 74; and 4 (1 sectioned, 3 dissected) from Station 83.

**Remarks.** As discussed in *Remarks* for *Thalassodrilides* above, *Kaketio ineri* is herewith transferred to that genus.

*Thalassodrilides ineri* is a large and rather stout marine tubificid; the largest intact specimen from Belize is 17.3 mm long, 0.75 mm wide at clitellum, and consists of 90 segments. The species has complex male genitalia, including large, eversible pseudopores (see Righi & Kanner

1979), and in mated specimens the spermathecae contain conspicuous spermatozoogmata of a kind unique for the Tubificidae. The ultrastructure of these sperm aggregates was recently described by Ferraguti *et al.* (1989).

As discussed by Erséus (1981b), *Thalassodrilides milleri* Brinkhurst & Baker, 1979, from Delaware (eastern U.S.A.), is very similar, possibly identical, to *T. ineri*. However, whether the two are the same species cannot be settled until new material of the former (preferably from the type locality) becomes available. If they prove to be a single taxon, the specific epithet *milleri* will take precedence as it was published a few months before the publication of *Kaketio ineri* (see Erséus 1981b: 333).

Originally described from Bonaire in the southern Caribbean Sea (Righi & Kanner 1979), *T. ineri* has also been reported from Florida and Bermuda by Erséus (1980b), who concluded that the species can be expected to occur throughout the Caribbean area. The new records strongly support this.

**Distribution and habitat.** Belize, St. Martin, Barbuda, Curaçao (new records), Bonaire, Florida and Bermuda. Lower intertidal and subtidal mud, to at least about 2 m depth.

### Genus *Tectidrilus* Erséus, 1982

**Remarks.** *Tectidrilus* Erséus, 1982(b) is a coherent, probably monophyletic taxon; its members show at least a tendency towards body wall papillation (not always true for *T. bori*) and a shortening of the clitellum, both assumed apomorphic traits. The definition of the genus was recently modified (Erséus 1989b).

### *Tectidrilus gabriellae* (Marcus, 1950)

*Pelosclex gabriellae* Marcus, 1950: 1–3, figs 1–4; Righi & Kanner 1979: 46.

*Pelosclex gabriellae* ("uncertain position"); Holmquist 1979: 56.

*Pelosclex gabriellae* (*partim*); Brinkhurst 1965: 133, not figs 5L–I; Cook 1970: 980–981.

*Tubificoides gabriellae* (*partim*); Brinkhurst & Baker 1979: 1556.

*Tectidrilus gabriellae*; Erséus 1982b: 255–258, figs 31–32.

**New material.** USNM 127940, specimen from West Bay, Twin Cays, Belize, depth and sediment unknown (date unknown; coll. K. Fauchald *et al.*). USNM 127941–127942, 2 specimens from north (Caribbean) coast of Panama: 1 from 08°54.7'N, 77°41.0'W, intertidal (29 June 1977; CARIB I. *Alpha Helix* station no. MS-21-500); and 1 from 09°32.8'N, 78°59.5'W, 5 m (30 June 1977; CARIB I. *Alpha Helix* station no. ND-24-500). ZMA 2861, 2 specimens from S part of Lagoen, Bonaire (Lesser Antilles), 0.5–2 m, sandy sediment, near *Rhizophora* (19 September 1967; coll. P. Wagenaar Hummelinck, station no. 1559).

**Remarks.** *Pelosclex gabriellae* Marcus was long confused with various papillate species of the genus *Tubificoides* (subfamily Tubificinae), but it was redescribed and selected as the type species of the limnodriloidine genus *Tectidrilus* (Erséus 1982b).

The new material from Belize, Panama and Bonaire fits the re-description of *T. gabriellae* (which was based on material from Barbados and Bermuda; see Erséus 1982b) in all respects, even in dimensional terms. Righi & Kanner (1979) found specimens agreeing with Marcus' (1950) original description in material from Aruba and Curaçao; that record from the Netherlands Antilles is now corro-

borated by my specimens from Bonaire, the third island in the group.

*Distribution and habitat.* Belize, Panama, Bonaire (new records), Aruba, Curaçao, Barbados, Bermuda and Brazil. Subtidal muddy silt and sand, to at least 9 m depth.

### *Tectidrilus bori* (Righi & Kanner, 1979)

*Limnodriloides bori* Righi & Kanner, 1979: 47–49, figs 27–30.

*Tectidrilus bori*; Erséus 1982b: 258–260, fig. 33; Erséus & Davis 1989: 94–95, fig. 14.

*New material.* USNM 127943, specimen from Station 17. USNM 127944–127945, 2 specimens from West Bay, Twin Cays, Belize, depth and sediment unknown (date unknown; coll. K. Fauchald *et al.*). Author's collection, 2 specimens: 1 from Station 55; and 1 (sexually immature) from Station 81.

*Remarks.* This species has very characteristic copulatory glands located immediately posterior to the male pores. Originally described from Bonaire by Righi & Kanner (1979), *T. bori* is known from several parts of the Caribbean area (Erséus 1982b), as well as from Hawaii (Erséus & Davis 1989).

*Distribution and habitat.* Belize (new record), Bermuda, Florida, Barbados, Curaçao and Hawaii. Intertidal and subtidal, generally muddy sands, to at least about 70 m depth.

### Genus *Limnodriloides* Pierantoni, 1903

*Remarks.* This large, probably paraphyletic (see Erséus in press), genus was re-defined by Erséus (1982b). I then recognized three different species-groups within *Limnodriloides*, for diagnostic rather than phylogenetic purposes. Of the species treated in the present paper, *L. monotheucus*, *L. anxius* sp.n., *L. major* sp.n., *L. sacculus* sp.n., and *L. uniampullatus* may be regarded as members within the “*L. agnes*-group” (characterized by a strong tendency towards very long atrial ducts, and a dorsal location of the spermathecal pores), *L. adversus* sp.n. and *L. barnardi* within the “*L. winkelmanni*-group” (characterized by modified genital setae), and, finally, *L. rubicundus* and *L. pierantonii* within the “*L. appendiculatus*-group” (which contains the less derived species within the genus).

### *Limnodriloides monotheucus* Cook, 1974 (Figs 26A–H)

*Limnodriloides monotheucus* Cook, 1974: 131–132, fig. 3; Brinkhurst & Baker 1979: 1564; Erséus 1988c: 67.

*Bohadschia monotheuca* Hrabě, 1975: 112–114, figs 1–3 (but status uncertain).

*Limnodriloides monotheucus* (*partim*); Erséus 1982b: 250–253, figs 28–29; 1986b: 309.

*Nec Limnodriloides monotheucus*; Erséus 1987b: 274 (= *L. anxius* sp.n. described below).

*Type material and type locality.* USNM 45285 (holotype), USNM 45286 (six paratypes), and National Museum of Natural Sciences, Ottawa, NMC 3475 (one paratype); all from Bahia de San Quintin, Baja California, Pacific coast of Mexico (Cook 1974). The USNM material was examined by Erséus (1982b).

*Material re-examined.* IRCZM 51:004–51:005, 2 specimens from Indian River, Florida (see Erséus 1982b). FSBC I 331875, specimen from Hutchinson Island, Florida (see Erséus 1986b). USNM 96823–96831, 15 specimens from Ardtoe Fish Farm, Ardtoe, Scotland (2 June

1978; coll. H. R. Baker). Author's collection: specimens from California (Santa Barbara), from Gulf of Mexico, Bermuda, off Florida (190 m depth), North Carolina, Maryland, and New Jersey (see Erséus 1982b); specimens from near Miami, Florida (listed by Erséus 1982b), except single specimen from Bear Cut (now identified as *L. anxius* sp.n.; see below); specimen from Hutchinson Island, Florida (Erséus 1986b); and single specimen from Newport River (W of Gallant Point), near Beaufort, North Carolina [most other specimens from North Carolina listed by Erséus (1982b) are precopulatory, with poorly developed spermathecae; they may be either *L. monotheucus* or *L. anxius*; see also material under latter].

*New material.* USNM 127946–127949, 4 specimens from W side of middle cay, Blue Ground Range, Belize, 0.2 m, mud (9 November 1979; coll. K. Fauchald *et al.*). USNM 127950, specimen from West Bay, Twin Cays, Belize, barely subtidal, *Thalassia* roots and *Halimeda* rubble (7 December 1980; coll. K. Fauchald *et al.*). Author's collection: 2 specimens (1 of which sectioned) from Station 49 (Belize); 6 specimens from Victoria, British Columbia (further data unknown; coll. H. R. Baker); and specimen from off North Carolina, 583 m depth (date unknown; courtesy D. Davis).

*Brief description of material from Belize.* Length (2 complete specimens) 6.5–9.2 mm, 53–62 segments. Setae bifid, 35–62  $\mu\text{m}$  long, 2–3  $\mu\text{m}$  thick, (1)2–4 per bundle anteriorly, absent from (X)XI, 1–2 per bundle thereafter. Spermathecal pore unpaired, mid-dorsal in X. Vas deferens 16–21  $\mu\text{m}$  wide. Atrial ampulla 60–80  $\mu\text{m}$  long, 21–35  $\mu\text{m}$  wide. Atrial duct long and slender, ental part somewhat granulated, 16–25  $\mu\text{m}$  wide; ectal part 12–16  $\mu\text{m}$  wide, not granulated, but with thin outer lining of muscles. Pseudopenial sac 105–120  $\mu\text{m}$  long, 40–55  $\mu\text{m}$  wide. Spermatheca (Fig. 26A) an unpaired, very slender, ampulla, 315–450  $\mu\text{m}$  long, maximally 35–60  $\mu\text{m}$  wide; inner end much narrower. Ratio length/width of spermatheca 6.2–11.4 ( $X = 8.8$ ; coefficient of variation = 25%;  $n = 5$ ). Spermatozeugmata a few to (at least) 9 in number, about 205–230  $\mu\text{m}$  long; length 20–30 $\times$  width.

*Remarks.* *Limnodriloides monotheucus* was originally described from the Pacific coast of Mexico (Cook 1974). It was subsequently reported from many geographical areas on both sides of North and Central America, and the Mediterranean taxon *Bohadschia monotheuca* by Hrabě (1975) was regarded as both a synonym and a homonym for Cook's form (Erséus 1982b).

In my previous study of this complex (Erséus 1982b), with access to a large amount of material, I noted considerable geographical variation in the morphology of the male ducts (granulation and width of ental part of atrial duct), spermatheca and spermatozeugmata. I also put forward the possibility that specimens from Barbados may belong to a species separate from *L. monotheucus* *s.str.*

In the present study of material from Belize, several *Limnodriloides* specimens with unpaired, dorsal spermathecae were found. This time the variation, particularly in the size and shape of the spermathecae, proved to be even greater than noted before. This initiated a re-appraisal of the taxonomy of *L. monotheucus*, and no less than five different species belonging to this complex were recognized in the material from Belize: *L. monotheucus* *s.str.*, *L. anxius* sp.n., *L. major* sp.n., *L. uniampullatus* Erséus, 1982, and *L. sacculus* sp.n.

Cook's original material of *L. monotheucus* has very slender spermathecae and spermatozeugmata, as have all other East Pacific and a majority of the West Atlantic

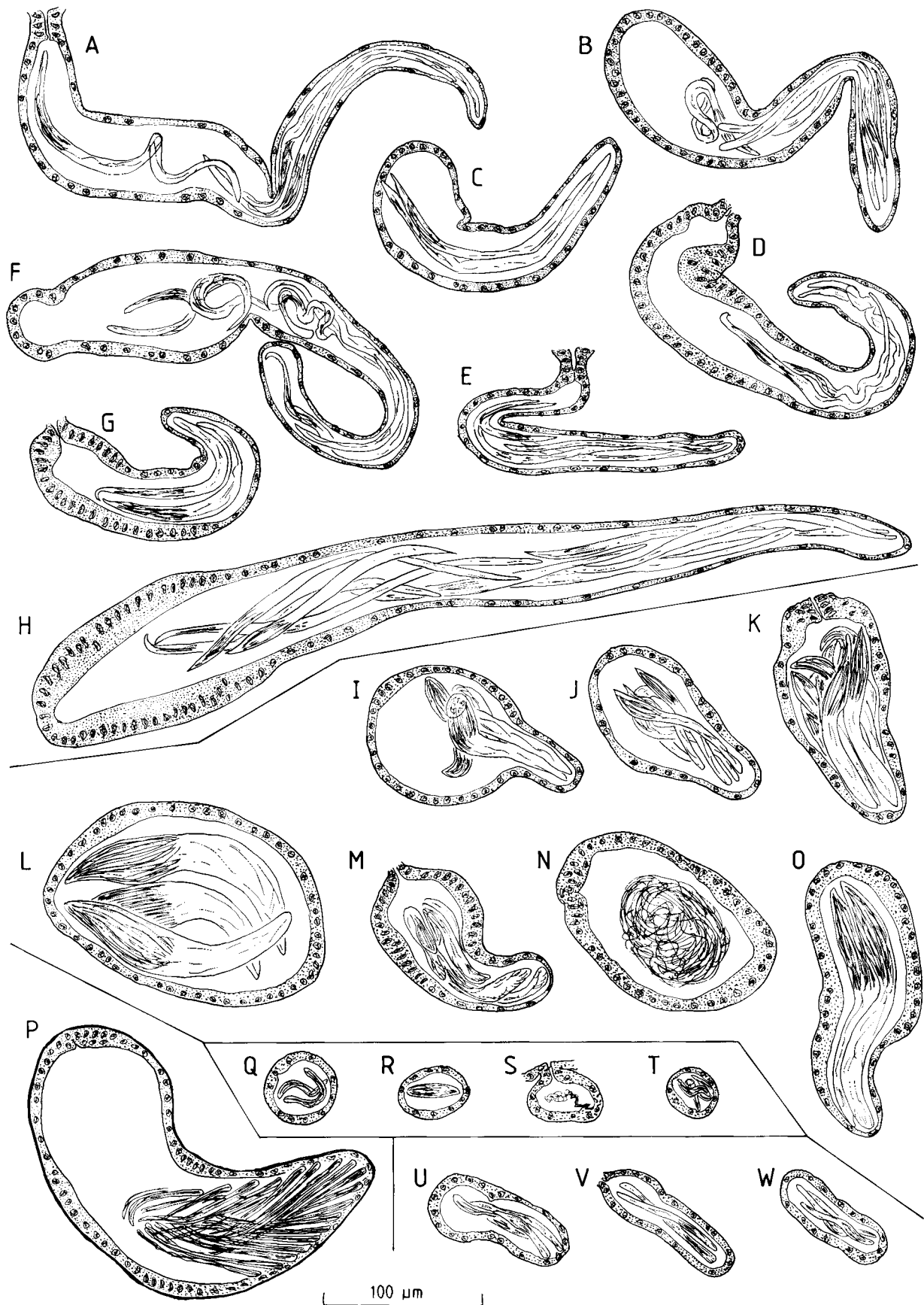


Fig. 26. Spermathecae of various specimens belonging to the *Limnodriloides monotheucus*-complex, all drawn to the same scale.—A–H. *Limnodriloides monotheucus* Cook, specimens from Twin Cays, Belize (A); Biscayne Bay, Florida (B); Hutchinson Island, Florida (C); off New Jersey, 174 m depth (D); off North Carolina, 583 m depth (E); Bermuda (F); California (G); and British Columbia (H).—I–O. *Limnodriloides anxius* sp.n., specimens from Carrie Bow Cay, Belize (I); Twin Cays, Belize (J); Venezuela (K); Bonaire, Lesser Antilles (L); Barbados (M–N); and North Carolina (O).—P. *Limnodriloides major* sp.n., holotype (Belize).—Q–T. *Limnodriloides uniampullaeus* Erséus, specimens from Belize (Q–S); and Bonaire, Lesser Antilles (T).—U–W. *Limnodriloides sacculus* sp.n., specimens from Belize, Stations 16 (U) and 78 (V–W).

specimens previously identified as this species by me. These worms are therefore all considered as the same species (*monothecus s.str.*), at least for the time being, although there is some variation in size and extension of the spermathecae when worms from different geographical areas are compared (Figs 26A–H). Specimens with other kinds of spermathecae and spermatozeugmata (Figs 26I–W) are recognized as other taxa.

In most of the American individuals of *L. monothecus s.str.*, the ental part of the atrial duct appears to be only moderately granulated and swollen; this may be an additional character discriminating *L. monothecus* from other species within the complex (see below), particularly *L. anxius* sp.n. and *L. major* sp.n. described below. A complication here is that Hrabě's taxon *Bohadschia monotheca*, described on the basis of a single specimen from Yugoslavia (examined and depicted by Erséus 1982b), has slender spermathecae as well as heavily granulated atrial ducts. The status of Hrabě's European form *vis-à-vis* the American *L. monothecus* is thus not settled.

Other European material of *L. monothecus*, from Scotland, collected by the late Dr H. R. Baker (Victoria, B. C., Canada) is deposited at the USNM (see material above). The specimens, which never have been reported in the literature before, were examined by me while at this museum. Fifteen of the 18 individuals initially identified (by Baker) as *L. monothecus* are morphologically very similar to the material from the west coast of North America (e.g. spermatheca very slender, similar to those shown in Figs 26G–H). Baker's record from Scotland is thus reported here. [The three remaining worms on Baker's slides are representatives of other tubificid species; one is a *Limnodriloides* with modified spermathecal setae (possibly *L. scandinavicus* Erséus, 1982b), the other two are *Tubificoides* spp., one with and one without hair setae.]

*Distribution and habitat.* East Pacific: Mexico through British Columbia. West Atlantic: Belize (new record), Gulf of Mexico, Bermuda, Florida through New Jersey. NE Atlantic: Scotland (new record). (?)Mediterranean Sea: Yugoslavia. Subtidal sand and mud, to at least 583 m depth; also brackish water.

### *Limnodriloides anxius* sp.n. (Figs 26I–O, 27A–D)

*Limnodriloides monothecus* (*partim*); Erséus 1982b: 250–253 (*nec* figs 28–29); 1986b: 309; *nec sensu* Cook 1974.

*Limnodriloides monothecus*; Erséus 1987b: 274.

*Holotype.* USNM 127951.

*Type locality.* West Bay, Twin Cays, Belize, barely subtidal, *Thalassia* and *Halimeda* rubble (6 December 1980; coll. K. Fauchald *et al.*).

*Paratypes.* USNM 127952–127954, 3 specimens from type locality (but various dates, November 1979–April 1981; coll. K. Fauchald *et al.*).

*Other new material.* USNM 127955–127957, 3 specimens from type locality (October 1979). ZMA 2862, specimen from Puito, northeast part of Lac, Bonaire, Lesser Antilles, 0.5 m, mudflat with *Thalassia* and *Codakia* (11 March 1979; P. Wagenaar Hummelinck, station no. 1577Aa). Author's collection: 11 specimens from Belize (2 from Station 52; 6 from Station 61; 1 from Station 84; and 2 from W of S end of Carrie Bow Cay, 0.3 m, heterogeneous, poorly oxygenated sand (4 April 1982, coll. H. R. Baker); and 1 sectioned specimen from River Bay (inner end of bay at river mouth), NE part of Barbados, lower intertidal, probably with frequent brackish conditions, coarse sand (27 October 1979; coll. C. Erséus).

*Material re-examined, previously identified as* *L. monothecus* by Erséus (1982b, 1986b, 1987b). FSBC 1 37861, specimen from off

Hutchinson Island, east coast of Florida, 27°21.6'N, 80°13.1'W, 10.9 m, shell hash (Station 2 in Erséus 1986b) (4 January 1973; coll. R. Gallagher *et al.*). Author's collection: 6 specimens from Chesapeake Bay, Virginia, U.S.A. (3 from eastern shore, 3 from York River); 1 specimen from Newport River (N of Gallant Point), near Beaufort, North Carolina; 1 specimen from Bear Cut, Miami, Florida; 7 specimens (plus some precopulatory individuals probably of the same species) from Barbados (different stations); and 1 specimen from Bahia de Amuay, Venezuela.

*Etymology.* Named *anxius* (Latin for 'troublesome'), to indicate the taxonomic confusion caused by the great variation in some characters of this species.

*Description of type material* (Figs 27A, C–D). Length (3 complete specimens) 7.8–8.8 mm, 69–70 segments. Width at XI 0.21–0.27 mm. Prostomium variable in shape. Clitellum poorly developed. Setae (Fig. 27A) bifid, with upper tooth thinner and shorter than lower. Setae 28–60  $\mu\text{m}$  long, 1–2.5  $\mu\text{m}$  thick, (1)2–4 per bundle anteriorly, absent from (X)XI, (1)2(3) per bundle thereafter, except for some segments at posterior end, in which 'bundles' are unisetal. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pore unpaired, mid-dorsal in middle of X.

Pharyngeal glands in IV–V. Oesophageal diverticula present in IX. Male genitalia (Figs 27C–D) paired. Vas deferens 14–19  $\mu\text{m}$  wide, appearing shorter than atrium, entering atrium subapically (see Fig. 27D). Atrial ampulla oblong, 60–70  $\mu\text{m}$  long, 26–35  $\mu\text{m}$  wide; prostatic pad elongate, ventral in ampulla. Prostate gland lobed, large. Atrial duct slender, totally 220–330  $\mu\text{m}$  long, convoluted. Ental part of atrial duct 50–75  $\mu\text{m}$  long, 23–26  $\mu\text{m}$  wide, with thick inner epithelium. Ectal part of atrial duct 160–260  $\mu\text{m}$  long, 16–20  $\mu\text{m}$  wide, with distinct muscular lining, 1–3  $\mu\text{m}$  thick, but thin and not granulated inner epithelium. Duct terminating in pseudopenial papilla inside copulatory sac; sac 60–75  $\mu\text{m}$  long, 37–50  $\mu\text{m}$  wide. Spermatheca (Fig. 27C, s) elongate pear-shaped, 100–160  $\mu\text{m}$  long, maximally 40–85  $\mu\text{m}$  wide (i.e. about 2–3 $\times$  longer than wide), with inner epithelium thicker in ectal than in ental part. Sperm arranged as 1–2 spindle-shaped spermatozeugmata in spermatheca. Spermatozeugmata 80–90  $\mu\text{m}$  long, 11–16  $\mu\text{m}$  wide; length thus about 6–8 $\times$  width.

*Notes on other material* (Figs 26I–O, 27B). The total material identified as *L. anxius* comprises 37 specimens, from several different geographical areas. The worms exhibit a great morphological variation (summarized for some characters in Table V), and some of the non-type individuals are only tentatively regarded as members of *L. anxius*. The type material has been restricted to four specimens from basically the same locality. They are so similar to each other (but clearly different from the other known species of the *L. monothecus*-complex) that it is unlikely that future studies will have to challenge the status of the paratypes *vis-à-vis* the holotype.

Most of the other specimens from Belize are smaller (five complete specimens: 5.4–6.1 mm long, 44–61 segments) than the individuals of the type series. The single worm from Station 84 is, however, exceptionally large (12.2 mm, 81 segments). The specimens from Station 52 and 61 have maximally two setae per bundle in anterior segments, lack setae completely in both segments X and XI, and have unisetal 'bundles' in all postclitellar seg-

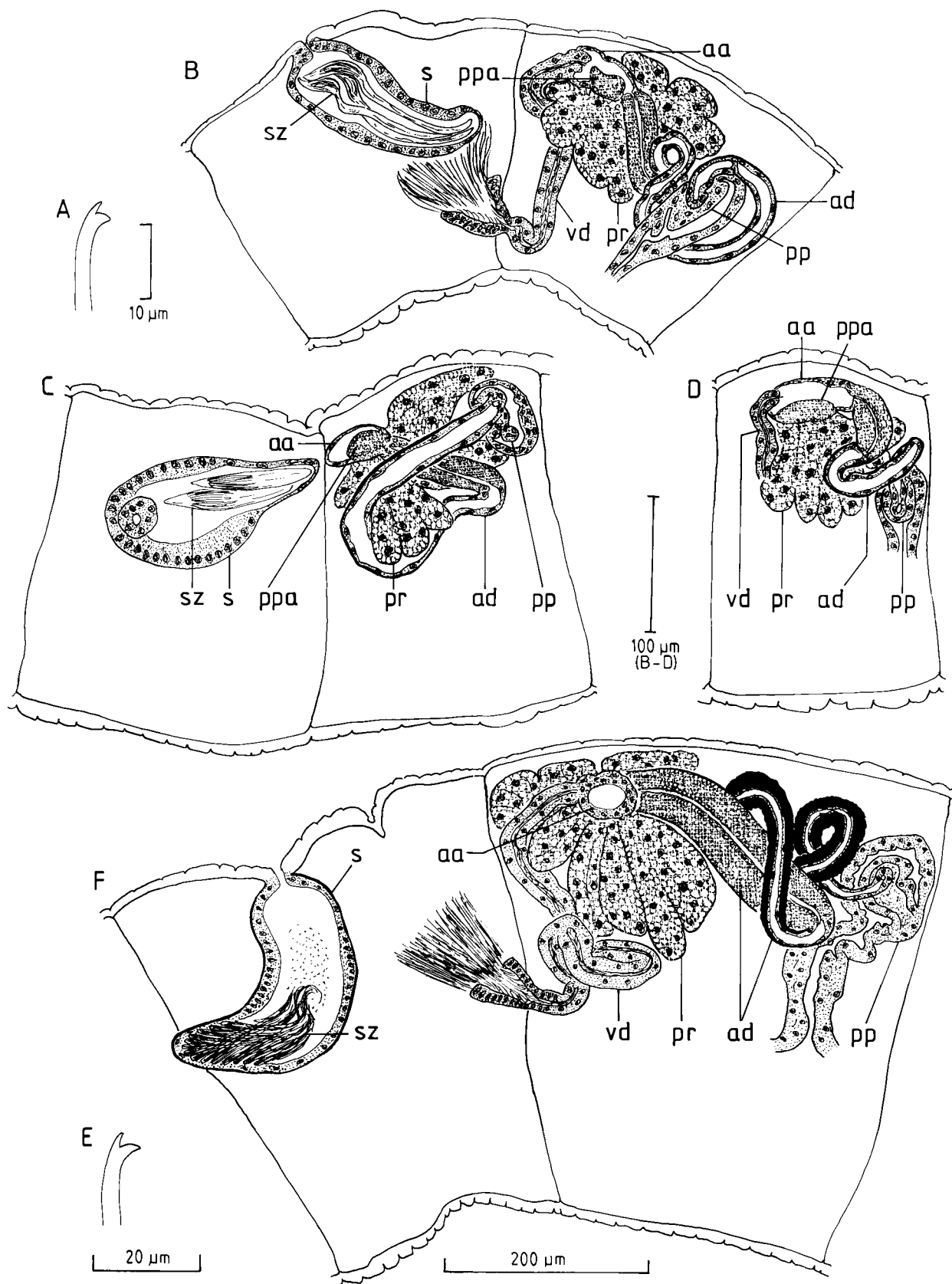


Fig. 27.—A–D. *Limnodriloides anxius* sp.n.—A. Seta.—B. Lateral view of spermatheca and male genitalia in segments X–XI, specimen from Station 61.—C. Oblique view of spermatheca and male genitalia (in X–XI), holotype.—D. Lateral view of male genitalia (in XI), paratype.—E–F. *Limnodriloides major* sp.n.—E. Seta.—F. Lateral view of spermatheca and male genitalia in X–XI.

ments, whereas specimens from other localities in Belize resemble the types with regard to the setal numbers. Some worms (particularly those from Station 61; see Fig. 27B) have more slender atrial ducts than those of the type series. The spermathecae are generally somewhat elongate, pear-shaped (Figs 26I–J, 27B), as in the type series (Fig. 27C), but the spermatozuigmata vary in slenderness.

The very large worm from Station 84 (mentioned above) differs from all other Belizean specimens in that its spermatheca is oval (length only 1.2× width), with the sperm not forming spermatozuigmata, but randomly arranged in ampulla. The same applies to the specimen from River Bay, Barbados (Fig. 26N). The spermathecae of the individual from Bonaire (Fig. 26L) is also oval, but contains very large, spindle-shaped spermatozuigmata.

All specimens previously recorded as *L. monotheucus* from Chesapeake Bay (Erséus 1982b), Barbados (Erséus 1982b), and Venezuela (Erséus 1987b), are now regarded as *L. anxius* (Figs 26K, M). In the old material from Florida (Erséus 1982b, 1986b) and Beaufort, North Carolina (Erséus 1982b), both *L. monotheucus* and *L. anxius* are present (Figs 26B–C, O).

**Remarks.** The setal arrangement and male genitalia are both highly variable characters in *L. monotheucus* and *L. anxius*, and it appears very difficult to use them for a specific discrimination of the taxa. However, the spermathecae, which are never as slender in *L. anxius* (Figs 26I–O) as they are in *L. monotheucus* (Figs 26A–H), clearly distinguish the two species.

**Distribution and habitat.** As far as known restricted to the west Atlantic: Belize, Bonaire, Venezuela, Barbados, Florida through Virginia. Lower intertidal and subtidal, generally muddy, sand, to at least 20 m depth; also in brackish-water(?).

#### *Limnodriloides major* sp.n. (Figs 26P, 27E–F)

**Holotype.** USNM 127958.

**Type locality.** E side of South Point, Twin Cays, Belize, barely subtidal(?), somewhat muddy, heterogeneous coral sand (exposed to waves from NE) (9 April 1982; coll. H. R. Baker).

**Etymology.** Named *major* (Latin for 'larger') as it appears larger than the other taxa within the *L. monotheucus*-complex.

**Description.** Length more than 7.8 mm, more than 37 segments (holotype not complete). Width at XI 0.51 mm. Prostomium somewhat triangular. Clitellum poorly developed. Setae (Fig. 27E) bifid, with upper tooth thinner and shorter than lower. Setae 37–62 µm long, 2.5–3.5

µm thick, 2(3) per bundle anteriorly, totally absent from X–XI, 1 per 'bundle' thereafter. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pore unpaired, mid-dorsal in middle of X.

Pharyngeal glands in IV–V. Oesophageal diverticula present in IX. Male genitalia (Fig. 27F) paired. Vas deferens 23–30 µm wide, about  $\frac{2}{3}$ × length of atrium; entrance into atrium not observed. Atrial ampulla small, oval, about 60 µm long, 45 µm wide; prostatic pad not observed. Prostate gland large, lobed. Atrial duct very long, about 0.9 mm, convoluted. Ental part of atrial duct about 215 µm long, 65–70 µm wide, with very thin outer lining, and thick, granulated inner epithelium. Granulated part abruptly terminating in slender ectal part; latter 28–43 µm wide, with up to 12 µm thick muscular lining. Muscular lining thinning towards end of duct, which terminates in large pseudopenial papilla inside voluminous copulatory sac; sac 160 µm long, about 60 µm wide. Spermatheca (Figs 26P; 27F, s) an oblong, somewhat curved ampulla, 260 µm long, 90 µm wide (about 3× longer than wide), with thin, but distinct outer muscular lining; inner epithelium evenly thick. Sperm arranged as slender spermatozuigmata in inner end of ampulla. Spermatozuigmata about 20 in number, up to about 150 µm long; up to about 30× longer than wide.

**Remarks.** This large form is very distinct in comparison to all other members of the *L. monotheucus*-complex; this is the reason why a single specimen has been assigned to a separate taxon with confidence. It is distinguished from its closely related congeners by the great length of the granulated parts of its atrial ducts, and by the high number of spermatozuigmata in its spermatheca. The thickness of the atrial duct musculature varies in the other taxa, and is sometimes great also in specimens of *L. monotheucus* and *L. anxius*. The muscle layer is, however, nowhere as thick (12 µm) as in the specimen of *L. major* described here.

**Distribution and habitat.** Known only from Twin Cays, Belize. Barely subtidal sand.

#### *Limnodriloides uniampullatus* Erséus, 1982 (Figs 26Q–T)

*Limnodriloides uniampullatus* Erséus, 1982b: 248–250, fig. 27; 1984e: 169, fig. 23; 1990b: 302.

**New material.** USNM 127959–127960, 2 specimens from W side of middle cay, Blue Ground Range, Belize, barely subtidal (9 June 1981; coll. K. Fauchald *et al.*). USNM 127961, specimen from West Bay, Twin

Table V. Mean value (X), coefficient of variation (CV), minimum (min) and maximum (max) values of nine characters in *L. anxius* sp.n. n = number of specimens where the character could be measured

Character	X	CV	min	max	n
Body length of fixed, complete worms (mm)	6.18	34%	3.7	12.2	17
Number of segments	53.9	25%	35	81	17
Atrial ampulla, length/width	2.35	23%	1.59	3.33	15
Granulated part of atrial duct, length/width	3.15	33%	2.04	5.65	13
Non-granulated part of atrial duct, length/width	13.0	31%	8.9	25.0	15
Muscular layer of ditto, thickness (µm)	2.43	65%	0.5	7.0	35
Spermatheca, length/maximum width	1.95	27%	1.07	3.17	26
Number of spermatozuigmata in spermatheca	3.97	49%	1.0	8.0	33
Spermatozuigmata, length/width	7.60	43%	3.92	16.7	28

Cays, Belize, 0.1 m, mud (14 May 1984; coll. K. Fauchald *et al.*). Author's collection: 1 specimen from each of Stations 61 and 75. ZMA 2865, specimen from S part of Lagoen, Bonaire (Lesser Antilles), 0.5–2 m, sandy sediment, near *Rhizophora* (19 September 1967; coll. P. Wagenaar Hummelinck, station no. 1559).

**Brief description of new material.** Length (3 complete specimens) 3.3–4.0 mm, 31–40 segments. Setae bifid, 28–50  $\mu\text{m}$  long, 1.5–2.5  $\mu\text{m}$  wide, (1)2–3 per bundle anteriorly, absent from XI, or (in 1 specimen) from X–XI, (1)2 per bundle thereafter, except for some segments of posterior end, in which 'bundles' are unisetal. Spermathecal pore unpaired, mid-dorsal in X. Vas deferens 9–16  $\mu\text{m}$  wide. Atrial ampulla 35–40  $\mu\text{m}$  long, 14–23  $\mu\text{m}$  wide. Atrial duct long and slender, ental part (30–70  $\mu\text{m}$  long) granulated, 12–24  $\mu\text{m}$  wide; ectal part, 7–12  $\mu\text{m}$  wide, not granulated but with thin lining of muscles. Pseudopenial sac 35–105  $\mu\text{m}$  long, 22–30  $\mu\text{m}$  wide. Spermatheca (Figs 26Q–T) unpaired, small, globular or somewhat oval, 34–47  $\mu\text{m}$  long, 26–44  $\mu\text{m}$  wide; containing a few simple, curved spermatozuogmata, about 35–40  $\mu\text{m}$  long, in post-copulatory specimens.

**Remarks.** This species was previously known only from the Indo-west Pacific region (Queensland and Hong Kong), and its presence in the Caribbean is thus somewhat surprising. Still, however, the new material fits the original description (Erséus 1982*b*) well, even in dimensional features.

The male ducts of *L. uniampullatus* are very similar to those of *L. sacculus* sp.n. (see Fig. 28B). However, the spermatheca of *L. uniampullatus* (Figs 26Q–T) is more or less spherical and very small, never elongate as in the other species (Figs 26U–W).

**Distribution and habitat.** West Atlantic: Belize, Bonaire (new records); west Pacific: Great Barrier Reef, southern China, Subtidal sands, to at least 6 m depth.

#### *Limnodriloides sacculus* sp.n. (Figs 26U–W, 28)

**Holotype.** USNM 127963.

**Type locality.** Near sandy beach, W side of Wee Wee Cay, Belize, 0.3 m (Station 21).

**Paratypes.** USNM 127964–127965, 2 specimens from Station 78. USNM 127966, specimen from West Bay, Twin Cays, Belize, 0.3 m, mud (6 December 1980; coll. K. Fauchald *et al.*).

**Other material** (author's collection). One specimen from each of Stations 16 and 49.

**Etymology.** The species is named for the shape of its spermatheca; *sacculus* is Latin for 'small sack, bag'.

**Description.** Length (3 complete specimens) 3.9–4.8 mm, 40–46 segments. Width at XI 0.20–0.29 mm. Prostomium generally triangular; rounded in 1 specimen. Clitellum extending over XI–XII. Setae (Fig. 28A) bifid, with upper tooth thinner and shorter than lower. Setae 32–47  $\mu\text{m}$  long, 2–2.5  $\mu\text{m}$  thick, (1)2–3 per bundle anteriorly, totally absent from X–XI, (1)2 per bundle thereafter, except for some segments at posterior end, in which 'bundles' are unisetal. Male pores paired in line with ventral setae, posteriorly in XI. Spermathecal pore unpaired, mid-dorsal in middle of X.

Pharyngeal glands in IV–V. Oesophageal diverticula present in IX. Male genitalia (Fig. 28B) paired. Vas deferens about 10  $\mu\text{m}$  wide, appearing slightly shorter than atrium, entering atrium subapically. Atrial ampulla oblong, about 55–60  $\mu\text{m}$  long, 19–26  $\mu\text{m}$  wide; prostatic pad elongate, ventral in ampulla. Prostate gland lobed, small. Atrial duct slender, about 215  $\mu\text{m}$  long (measured

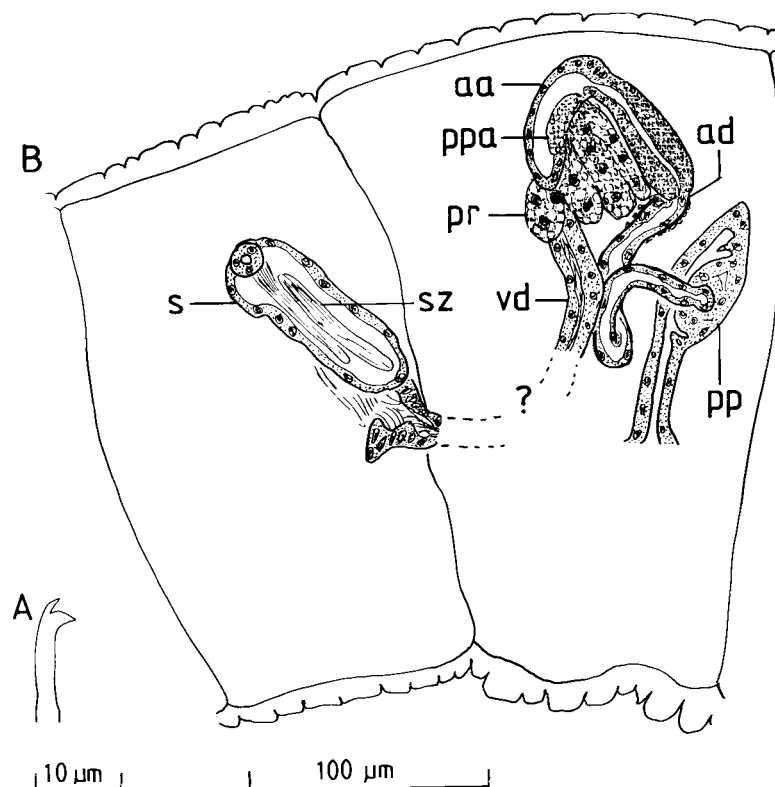


Fig. 28. *Limnodriloides sacculus* sp.n.—A. Seta.—B. Oblique view of spermatheca and male genitalia in segments X–XI.

in 2 specimens), convoluted. Ental part of atrial duct 55–60  $\mu\text{m}$  long, 19–27  $\mu\text{m}$  wide, with thick, granulated inner epithelium. Ectal part of atrial duct 155–160  $\mu\text{m}$  long, only 7–11 wide, with very thin, but distinct muscular lining. Duct terminating in pseudopenial papilla inside voluminous copulatory sac; sac 65–100  $\mu\text{m}$  long, 25–40  $\mu\text{m}$  wide. Spermatheca (Figs 26U–W; 28B, *s*) an elongate ampulla (duct absent), 80–95  $\mu\text{m}$  long, 26–47  $\mu\text{m}$  wide (i.e. 2.0–3.6 $\times$  longer than wide); inner epithelium evenly thick. Sperm arranged as straight, slender spermatozeugmata in spermatheca. Spermatozeugmata 2–4 in number, about 50–60  $\mu\text{m}$  long; about 7–12 $\times$  longer than wide.

**Remarks.** The male ducts of this new species are virtually identical to those of *L. uniampullatus* reported above; both taxa are small forms within the *L. monotheucus*-complex. The spermatheca of *L. sacculus* (Figs 26U–W), however, is clearly more elongate than that of *L. uniampullatus* (Figs 26Q–T), although it is not as long and slender as the one in *L. monotheucus* (Figs 26A–H). Moreover, it is distinguished from *L. anxius* by the size and shape of its spermatheca; in *L. anxius* the spermatheca is larger, and spherical to pear-shaped (Figs 26I–O).

**Distribution and habitat.** Known only from Belize. Subtidal, often muddy, fine to medium sands, 0.2–1 m depth.

#### *Limnodriloides adversus* sp.n. (Fig. 29)

**Holotype.** USNM 127967, whole-mounted specimen.

**Type locality.** N (Caribbean) coast of Panama, 09°32.8'N, 78°59.5'W, 5 m (30 June 1977; CARIB I. *Alpha Helix* station no. ND-24-1000).

**Paratype.** USNM 127968, specimen from West Bay, Twin Cays, Belize, 0.2 m, mud (27 October 1979; coll. K. Fauchald *et al.*).

**Etymology.** The species epithet *adversus* is Latin for 'turned towards', 'opposite', which refers to the direction of the spermathecal seta; in this species the large seta is directed against the posterior, which is contrary to the situation in the closely related *L. hastatus* and *L. parahastatus* (see below).

**Description.** Length of paratype 4.0 mm, 41 segments (holotype not complete). Width at XI 0.14–1.17 mm. Prostomium somewhat clongate, well set off from peris-

tomium. Clitellum extending over XI and most of XII in paratype, poorly developed in holotype. Somatic setae (Fig. 29A) bifid, with upper tooth almost as long as, but clearly thinner than lower. Setae 35–47  $\mu\text{m}$  long, 1–2  $\mu\text{m}$  thick, 2–3 per bundle anteriorly, 2 per bundle in postclitellar bundles. Setae totally absent from XI, absent dorsally from X. One large spermathecal seta (Fig. 29C, *ss*) present ventrally in X; at one side only, in holotype with tip near mid-ventral line of worm. This seta 77–98  $\mu\text{m}$  long, about 7  $\mu\text{m}$  wide, with inner end curved, and with long groove along most of its length; seta almost parallel with long axis of worm, tip pointing towards posterior. Spermathecal seta enclosed in deep muscular sac, outer part of which glandular, inner part bearing small glandular body on its outside (Fig. 29C, *gs*) (in paratype, such a glandular body also present on side of worm which is devoid of spermathecal seta). Male pores paired, in line with ventral setae, posteriorly in XI. Spermathecal pores paired, in line with ventral somatic setae, somewhat posterior to middle of X.

Pharyngeal glands conspicuous in IV–V. In IX, a posterior, short portion of oesophagus thick-walled and glandular (Fig. 29B); diverticula absent. Male genitalia (Fig. 29C) paired. Vas deferens up to 14–16  $\mu\text{m}$  wide, shorter than atrium, entering latter more or less apically (difficult to see in available material). Atrial ampulla slender, 75–85  $\mu\text{m}$  long, up to about 25  $\mu\text{m}$  wide (at prostatic pad), for most parts with thin inner epithelium, and thin, but distinct outer lining of circular muscles; prostatic pad distinct, in ventral lump in most ectal part of ampulla. Prostate glands moderately large, lobed. Atrial duct 50–70  $\mu\text{m}$  long, 18–21  $\mu\text{m}$  wide, with granulated middle part; muscular lining very thin, indistinct. Atrial duct terminating in simple pseudopenis. Spermathecae (Fig. 29C, *s*) with very short, triangular ducts, and oval-to-pear-shaped ampullae, 60–65  $\mu\text{m}$  long, 40–57  $\mu\text{m}$  wide; latter containing one or a few spindle-shaped bundles of sperm (=poorly preserved spermatozeugmata?).

**Remarks.** *Limnodriloides adversus* is closely related to *L. hastatus* Erséus, 1982(b), from the Gulf of Mexico coast

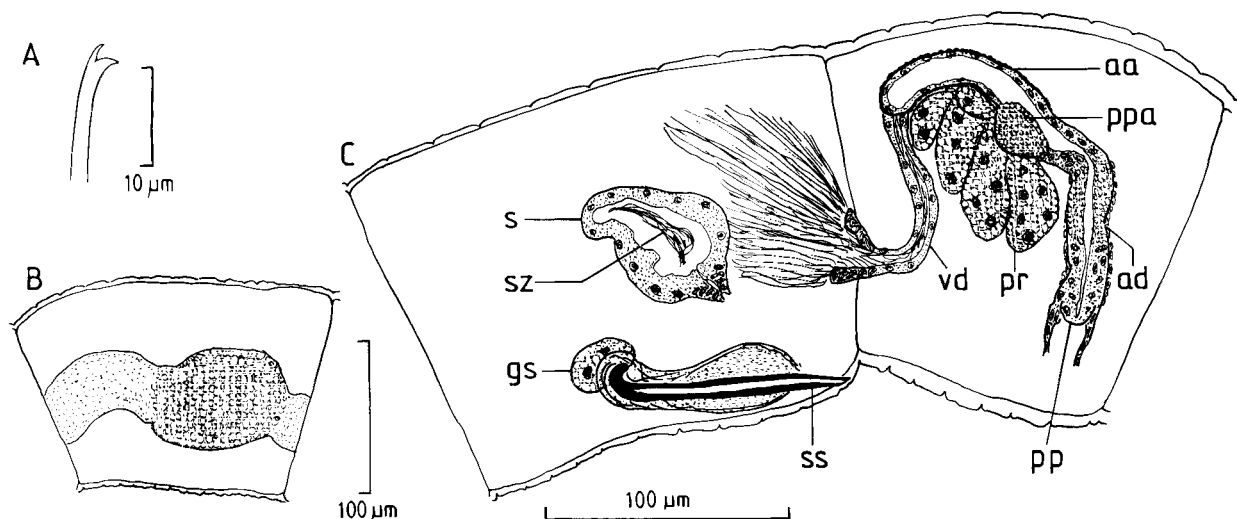


Fig. 29. *Limnodriloides adversus* sp.n.—A. Seta.—B. Oesophagus in segment IX, showing thickened, glandular, posterior part.—C. Lateral view of spermatheca, spermathecal seta and male genitalia in segments X–XI.

of Florida, and *L. parahastatus* Erséus, 1985 from the Persian Gulf coast of Saudi Arabia; all three species have short glandular portions in segment IX (instead of oesophageal diverticula, which otherwise characterize *Limnodriloides*), and very large, grooved, spermathecal setae in segment X. The spermathecal setae are, however, paired (one at each side of worm) and directed towards the anterior in *L. hastatus* and *L. parahastatus*; in both specimens of the new form, the spermathecal seta is single (but whether this is invariably so in this species needs to be corroborated by additional material), with its tip facing the opposite direction. Moreover, in neither of the other two taxa is the groove extending along such a long part of the seta as in *L. adversus*.

*Distribution and habitat.* Caribbean coast of Panama and Belize. Subtidal, to at least 5 m depth.

### *Limnodriloides barnardi* Cook, 1974 (Fig. 30)

*Limnodriloides barnardi* Cook, 1974: 134–135, fig. 5; Erséus 1982b: 232–234, fig. 13; Davis 1985: 171–172.

*Limnodriloides barnardi* (partim); Erséus 1976: 32–33, nec fig. 3.

*Limnodriloides winkelmanni* Michaelsen, 1914 (partim); Jamieson 1977: 338, nec fig. 2; Brinkhurst & Baker 1979: 1564.

*New material.* USNM 127969, specimen from N (Caribbean) coast of Panama, 09°34.6'N, 78°43.2'W, 0.4 m (30 June 1977; CARIB 1. *Alpha Helix* station no. 23-333/149). USNM 127970–127972, 3 specimens from same area, 09°32.9'N, 78°59.5'W, 5 m (30 June 1977; CARIB 1. *Alpha Helix* station no. ND-24-500/1000). USNM 127973–127976, 4 specimens from Belize, Station 52. MNHN MA 3, specimen from Les Raisins clairs (lagoon), Grand-Terre, Guadeloupe, 1.5 m, reduced fine sand (date unknown; coll. G. Boucher & N. Goubault). Author's collection, 14 specimens: 2 from Station 67; 3 (1 of which sectioned) from Station 38; 4 from Station 52; and 1 from each of Stations 40, 46, 61, 64 and 65.

*Brief description of material from Belize.* Length (5 complete specimens) 3.8–6.2 mm, 39–52 segments. Setae bifid, 35–50  $\mu\text{m}$  long, 1.5–2.5  $\mu\text{m}$  thick, 2–4 per bundle anteriorly, (1)2 per bundle in postclitellar segments. Bifid setae absent from X–XI. Ventral setae of X (when pres-

ent), one at each spermathecal pore, modified into slender, walking-stick-shaped spermathecal setae (Figs 30A; B, *ss*); these setae 55–70  $\mu\text{m}$  long, 2–2.5  $\mu\text{m}$  thick, with groove extending along about ectal half of seta. Spermathecal and male pores paired, in line with ventral setae. Oesophageal diverticula in IX. Male genitalia (Fig. 30B) paired. Vas deferens about 14  $\mu\text{m}$  wide in one specimen (not visible in other specimens), entering atrium more or less apically. Atrial ampulla 60–82  $\mu\text{m}$  long, 35–47  $\mu\text{m}$  wide (at prostatic pad); ental half thin-walled with spacious lumen (containing sperm in specimen depicted in Fig. 30B), ectal half with large, round prostatic pad; pad generally bulging considerably. Prostate gland large, lobed. Atrial duct 75–160  $\mu\text{m}$  long, 20–33  $\mu\text{m}$  wide at middle (granulated) part. Duct terminating in lateral papilla in wall of pseudopenial sac. Spermathecae (Fig. 30B, *s*) with short, but distinct, ducts, and round-to-pear-shaped ampulla; latter with several spermatozeugmata in postcopulatory specimens.

*Brief description of material from Panama.* No complete specimen. Setae 30–45  $\mu\text{m}$  long, 1.5–2  $\mu\text{m}$  thick, 2–3 per bundle anteriorly, 1–2 per bundle in postclitellar segments. Spermathecal setae 66–68  $\mu\text{m}$  long, 2–3  $\mu\text{m}$  thick; groove of varying length, in two specimens extending over about  $\frac{2}{3}$  of seta. Atria as in Fig. 30B, but slightly smaller (ampullae 63–77  $\mu\text{m}$  long, ducts about 70  $\mu\text{m}$  long). Spermathecae slender, smaller than those of Belizean specimens.

*Remarks.* The single worm from Guadeloupe conforms well to the other material, but it has somewhat larger spermathecal setae (96–98  $\mu\text{m}$  long, 3  $\mu\text{m}$  thick).

In some of the present specimens, the atrial ducts are more slender than in the original (type) material, but as there is much variation in this feature even within the populations, this difference is regarded as intra-specific.

In this species, the spermathecal setae are occasionally located anterior to the spermathecal pores (normally,

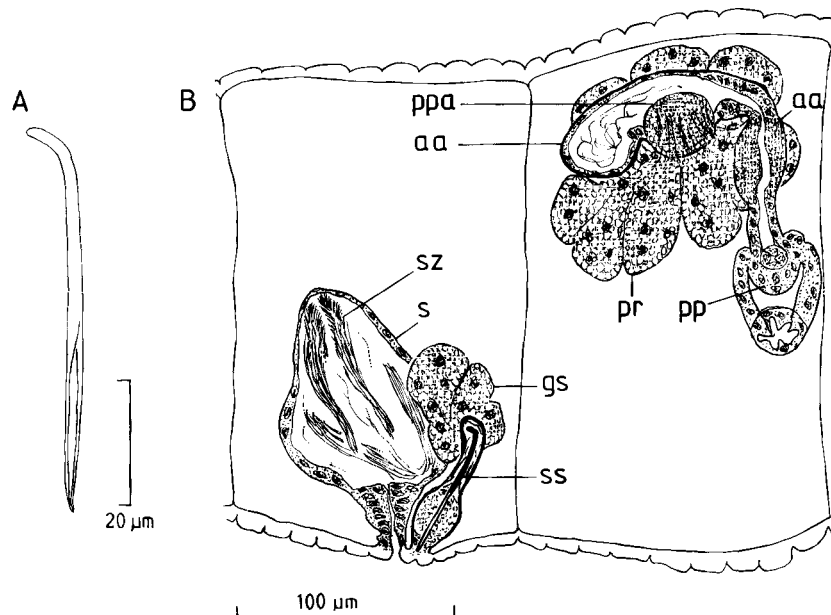


Fig. 30. *Limnodriloides barnardi* Cook.—A. Spermathecal seta.—B. Oblique view of spermatheca, spermathecal seta and male genitalia in segments X–XI.

posterior to the pores; as in Fig. 30B), or absent at one or both sides of the worm.

*Limnodriloides barnardi* was originally described from the Pacific coast of Mexico (Cook 1974), and subsequently recorded from a number of areas in the North-west Atlantic (Erséus 1982b; Davis 1985).

*Distribution and habitat.* Belize, Panama, Guadeloupe (all new records). Bahamas, Bermuda, east coast of the U.S. (Florida through Massachusetts). Pacific coast of Mexico. Subtidal sand, to at least 150 m depth.

### *Limnodriloides rubicundus* Erséus, 1982

*Limnodriloides rubicundus* Erséus, 1982b: 226–228, fig. 10; 1987b: 273–274; Erséus & Davis 1989: 93–94, fig. 13.

*New material.* USNM 127977–127979, 127981–127990, 13 specimens from West Bay, Twin Cays, Belize, barely subtidal, mud (various dates, October 1979–November 1983; coll. K. Fauchald *et al.*). USNM 127980, 127991–127993, 4 specimens from W side of middle cay, Blue Ground Range, Belize, barely subtidal, mud (November 1979, June 1981; coll. K. Fauchald *et al.*). Author's collection, 40 specimens from Belize: 5 (1 of which sectioned) from Station 56; 12 from Station 83; 7 from Station 75; 11 from Station 61; 2 from each of Stations 17 and 52; and 1 from Station 21. Author's collection, 3 specimens from Barbados (all coll. C. Erséus): 1 from Carlisle Bay, mouth of Carenage, Bridgetown, estuary of Constitution River, 4 m, organically polluted, muddy silt (24 October 1979); 1 from Bellairs Reef, St James, 4.5 m, muddy silt (24 October 1979); and 1 from SW of Holetown, 9 m, silt (25 October 1979).

*Remarks.* This species was described on the basis of a large material from Eastern U.S.A., Bahamas and Bermuda (Erséus 1982b), and was recently found also in Hawaii (Erséus & Davis 1989). It resembles *L. adversus* sp.n. described above by having a short glandular portion of the oesophagus in segment IX, and very slender atrial ampullae with ectally located prostatic pads; *L. rubicundus*, however, lacks spermathecal setae. The new material conforms well to the original description.

*Distribution and habitat.* Belize, Barbados (new records), Venezuela, Bahamas, Bermuda, east coast of the U.S. (Florida through Delaware), Hawaii. Intertidal and subtidal, muddy, generally fine, sediment, to at least 74 m depth.

### *Limnodriloides pierantonii* (Hrabě, 1971)

*Bohadschia pierantonii* Hrabě, 1971a: 217–220, figs 1–6; 1973: 36–37, fig. 7; 1975: 114–115, fig. 11.

*Limnodriloides fragosus* Finogenova, 1972: 98–101, figs 6–15; *nec sensu* Hrabě 1975 (= *L. appendiculatus* Pierantoni and *L. hrabetovae* Erséus; discussed by Erséus 1987e).

*Limnodriloides pierantonii*; Cook 1974: 131; Erséus 1982b: 219–221, fig. 5; 1987e: 161, fig. 2A.

(?) *Limnodriloides claviger* (*partim*?) Erséus, 1982b: 221–223, fig. 6. "*Limnodriloides claviger*"; Erséus 1987b: 272–273, fig. 1.

*Material re-examined.* Author's collection: specimens from Italy (see Erséus 1987e) and Venezuela (see Erséus 1987b). USNM 73930, holotype of *Limnodriloides claviger*, from Barbados (see Erséus 1982b).

*Remarks.* To date, *L. pierantonii* has only been recorded from the Mediterranean and Black Seas (Erséus 1987e). However, the discovery of ciliation in the atria of some type specimens of *L. claviger* initiated a re-appraisal of this species' identity. [Bermudian specimens of "*claviger*" with ciliated and very narrow atrial ampullae (all paratypes plus a single specimen in author's collection) are

now identified as *Smithsonidrilus minusculus* (Erséus 1983a) comb.n. (see below).]

The holotype of *L. claviger*, from Barbados, has clearly club-shaped atria and lacks cilia on the inner epithelium of the atrial ampullae (although a few cilia extends into the lumen from the ends of the vasa deferentia). Moreover, in this worm the sperm in the spermathecae are aggregated in somewhat torch-shaped spermatozeugmata, not bundled or random as in the individuals from Bermuda. These features (ciliated, club-shaped atria, and spermatozeugmata) also characterize the European *L. pierantonii*, which was previously distinguished from *L. claviger* primarily on the basis of its possession of pseudopenes (cf. Erséus 1982b: figs 5–6). Upon re-examination, the *claviger* holotype now also appears to have pseudopenes, although they are not as elaborate as in the European form. It therefore seems likely that *L. claviger* (*s.str.*) in fact is a junior synonym to *L. pierantonii*.

The presence of *L. pierantonii* in the Caribbean area is supported by a single specimen from Venezuela, recorded as *L. claviger* by Erséus (1987b): it is now identified as *L. pierantonii* too. As shown already in my illustration of that specimen (Erséus 1987b: fig. 1), it has both pseudopenes and spermatozeugmata.

Specimens from Hawaii, tentatively identified as *L. claviger* by Erséus & Davis (1989), are now regarded as *S. minusculus* (see Erséus in press), which further demonstrates how confused the taxonomy of these species has been.

*Distribution and habitat.* Barbados, Venezuela (new records), Yugoslavia, Italy, Turkey and Roumania. Subtidal, muddy sands, to at least 200 m depth.

### Genus *Smithsonidrilus* Brinkhurst, 1966

*Smithsonidrilus* Brinkhurst, 1966: 300; Erséus 1982a: 48.

*Marcusaedrilus* Righi & Kanner, 1979: 49; Erséus 1983a: 25–26; in press.

*Emended definition* (combined after Erséus 1982a: *Smithsonidrilus*; and Erséus in press: *Marcusaedrilus*) (with assumed synapomorphy in italics). Marine tropical and subtropical tubificids. All setae bifid; hair setae and modified genital setae absent. Male pores, paired or unpaired, in segment XI. Spermathecal pores, paired or unpaired, in middle of X. Coelomocytes, if present, small and sparse. Pharyngeal glands generally well developed in IV–V. A pair of oesophageal diverticula present anteriorly in IX.

Vasa deferentia ciliated, entering atria apically or slightly subapically. Each atrium consists of (1) an atrial ampulla, which is entally ciliated (ciliation inconspicuous in some species), and which ectally bears a lobed, broadly attached, ventral prostate gland connected with a distinct, heavily granulate 'prostatic pad' within the inner atrial epithelium, storing the secretory products of the prostate (in some apomorphic species, prostatic pad modified into elongate diverticulum); (2) a slender atrial duct, at least partly granulated. In some species, atrial ducts ectally united to form unpaired ejaculatory duct. Pseudopenes present, paired or unpaired; when unpaired, often elab-

orate (with many internal folds) and sometimes bearing large, compact, copulatory glands. Spermathecae paired or unpaired; ampullae with sperm in loose balls, rings, bundles or slender spermatozeugmata; ducts in most species divided into two parts, of which outer part often appearing as a secondary invagination of body wall (a 'vestibule').

*Type species.* *Smithsonidrilus marinus* Brinkhurst, 1966, emend. Erséus, 1982(a).

*Other species.* *S. peruanus* (Finogenova, 1986) comb.n.  
*S. minusculus* (Erséus, 1983a) comb.n.  
*S. tuber* (Erséus, 1983a) comb.n.  
*S. luteolus* (Erséus, 1983a) comb.n.  
*S. appositus* sp.n.  
*S. grandiculus* (Erséus, 1983a) comb.n.  
*S. assimilis* (Erséus, 1990e) comb.n.  
*S. vesiculatus* (Erséus, 1984e) comb.n.  
*S. pauper* sp.n.  
*S. capricornae* (Erséus, 1983a) comb.n.  
*S. irregularis* (Erséus, 1983a) comb.n.  
*S. sacculatus* (Erséus, 1983a) comb.n.  
*S. hummelincki* (Righi & Kanner, 1979) comb.n.  
*S. westoni* (Erséus, 1982a) stat.n.  
*S. multiglandularis* sp.n.  
*S. involutus* sp.n.

*Remarks.* The definition of the genus *Marcusaedrilus sensu* Erséus (1983a) was recently modified to accommodate *M. peruanus* (Erséus in press). It was pointed out in these previous accounts, however, that the highly derived *Smithsonidrilus* probably has evolved from an ancestor which would have been classified as a *Marcusaedrilus*, and that the latter genus (if excluding *Smithsonidrilus*) may be paraphyletic.

The present study approaches the phylogenetic relationships of *Marcusaedrilus* and *Smithsonidrilus* more specifically again (Tables VI–VII, Fig. 31). This time parsimony is applied to establish a hypothesis (Fig. 31), which indeed suggests that *Smithsonidrilus* is an apomorphic lineage within *Marcusaedrilus*. Thus, to keep the two as separate taxa would be to accept paraphyly of the latter. Consequently, the two genera are herewith united into one, which by priority will be named *Smithsonidrilus*. The ciliation of the atrial ampullae is regarded as the synapomorphy of all species included (character 2 in Fig. 31), whereas the spermathecal vestibules constitute a second synapomorphy for all species except *S. peruanus* and *S. minusculus* (character 9 in Fig. 31).

### *Smithsonidrilus minusculus* (Erséus, 1983) comb.n. (Fig. 32)

*Limnodriloides claviger* (partim, nec holotype); Erséus 1982b: 221–222, nec fig. 6 [holotype, *L. claviger* s.str. = *L. pierantonii* (Hrabě, 1971a)]; Erséus & Davis 1989: 92–93, fig. 12.

*Marcusaedrilus minusculus* Erséus, 1983a: 30–31, fig. 5; in press: fig. 17.

*Material re-examined.* USNM 73931–73933, paratypes of *Limnodriloides claviger*, from Bermuda (see Erséus 1982b). Author's collection: additional specimen of "*L. claviger*" from Bermuda (Erséus 1982b); and specimens from Queensland, Western Australia and Hawaii (see Erséus 1983a, in press; Erséus & Davis 1989).

*New material.* USNM 127994, specimen from West Bay, Twin Cays, Belize, barely subtidal, dense *Halimeda* with *Halimeda* rubble (8 December 1980; coll. K. Fauchald *et al.*).

*Description of specimen from Belize.* Length more than 2.3 mm, more than 28 segments (specimen not intact, lacking both anterior and posterior ends). Width at XI 0.18 mm. Clitellum extending over XI–XII, poorly developed. Setae (Fig. 32A) bifid, with upper tooth thinner and shorter than lower. Setae 30–50  $\mu\text{m}$  long, 1.5–2  $\mu\text{m}$  thick, 3 per bundle immediately anterior to clitellum, 2 per bundle in postclitellar segments. Ventral setae absent from X–XI. Male and spermathecal pores paired in line with ventral setae, posterior to middle of XI and X, respectively.

Oesophageal diverticula in anterior part of IX. Male genitalia (Fig. 32B) paired. Vas deferens 5–8  $\mu\text{m}$  wide, slightly longer than atrium, entering latter somewhat subapically. Atrium slender, club-shaped, totally about 80  $\mu\text{m}$  long, ampulla about 20  $\mu\text{m}$  wide, duct 12  $\mu\text{m}$  wide. Atrial ampulla with thin outer lining and entally ciliated inner epithelium; prostatic pad ventral, inconspicuous. Atrial duct partially granulated, ending in small pseudopenial papilla. Prostate gland small, with a few lobes. Spermathecae (Fig. 32B, s) small, round, 35–37  $\mu\text{m}$  in diameter, with very short, indistinct ducts; sperm as broad bundle in each spermatheca.

*Remarks.* The segmental numbers used to indicate the position of clitellum, genital pores and oesophageal diverticula in this description are based on the assumption that

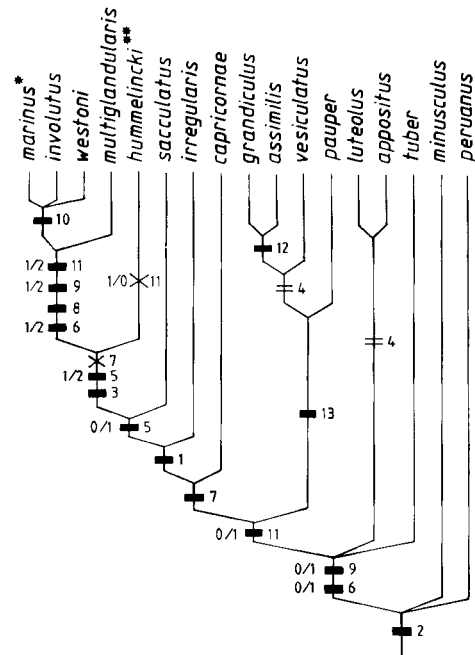


Fig. 31. The most parsimonious cladogram obtained with the PAUP program for the 17 ingroup taxa of *Smithsonidrilus* (Table VII) and their 13 characters (Table VI). All character transformations are of unity weight. Length of tree 20 steps, consistency index 0.85. Rooting at the hypothetical ancestor (see head of Table VII). The type species of *Smithsonidrilus* is marked with one asterisk (\*; *S. marinus*), the one of the junior synonym *Marcusaedrilus* with two asterisks (\*\*; *S. hummelincki*). Numbers to the right of the symbols refer to characters (Table VI), numbers to the left indicate transformations of character states (e.g. 1/2 means 'going from state 1 to state 2'). Filled rectangle represents autapomorphy; two parallel lines, convergence; cross, reversal of character state.

The following options were selected for the execution of the PAUP program: ADDSEQ=CLOSEST, SWAP=ALT, MULPARS, OPT=FARRIS.

Table VI. Characters and character states used for Wagner analysis of the species of *Smithsonidrilus* (including the former members of *Marcusadrilus*). All multistate characters are considered as ordered (0–1–2); state 2 is assumed to be apomorphic vis-à-vis state 1

Character	Character states
1.	Male and spermathecal pores paired (0); unpaired (1)
2.	Atrial ampulla without cilia (0); with ciliated inner epithelium, at least in most ental part (1)
3.	Prostatic pad located inside atrial ampulla proper (0); bulging out from ampulla as a diverticulum (1)
4.	Granulated part of atrial duct short (0); long (1)
5.	Non-granulated part of atrial duct short (0); long, paired (1); long, unpaired (2)
6.	(Primary) copulatory sac simple (0); bulbous, complex (1); very large, with many folds (2)
7.	Secondary copulatory sac absent (0); present (1)
8.	Copulatory glands absent (0); present (1)
9.	Spermathecal vestibule absent (0); present, but simple (1); present, large, folded (2)
10.	Spermathecal glands (associated with vestibule) absent (0); present
11.	Spermathecal ampulla round or oval (0); slender, but not bipartite (1); bipartite, inner part much narrower than outer part (2)
12.	Wall of spermathecal ampulla not granulated (0); with numerous granules of secretion (1)
13.	Copulatory apparatus without penis (0); with true penis (1)

Table VII. Data matrix for Wagner analysis of the species of *Smithsonidrilus* (including the former members of *Marcusadrilus*). For characters and character states, see Table VI. The outgroup is a hypothetical ancestor, resembling species of the genus *Limnodriloides*. ? missing value

Taxa	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
outgroup	0	0	0	0	0	0	0	0	0	0	?	0	0
<i>marinus</i> Brinkhurst	1	1	1	0	2	2	0	1	2	1	2	0	0
<i>involutus</i> sp.n.	1	1	1	0	2	2	0	1	2	1	2	0	0
<i>westoni</i> Erséus, stat.n.	1	1	1	0	2	2	0	1	2	1	2	0	0
<i>multiglandularis</i> sp.n.	1	1	1	0	2	2	0	1	2	0	2	0	0
<i>hummelincki</i> (Righi & Kanner) comb.n.	1	1	1	0	2	1	0	0	1	0	0	0	0
<i>luteolus</i> (Erséus) comb.n.	0	1	0	1	0	1	0	0	1	0	0	0	0
<i>grandiculus</i> (Erséus) comb.n.	0	1	0	1	0	1	0	0	?	0	1	1	1
<i>minusculus</i> (Erséus) comb.n.	0	1	0	0	0	0	0	0	0	0	0	0	?
<i>tuber</i> (Erséus) comb.n.	0	1	0	0	0	1	0	0	1	0	0	0	0
<i>capricornae</i> (Erséus) comb.n.	0	1	0	0	0	1	1	0	1	0	1	0	0
<i>sacculatus</i> (Erséus) comb.n.	1	1	0	0	1	1	1	0	1	0	1	0	0
<i>irregularis</i> (Erséus) comb.n.	1	1	0	0	0	1	1	0	1	0	1	0	0
<i>vesiculatus</i> (Erséus) comb.n.	0	1	0	1	0	1	0	0	1	0	1	0	1
<i>peruanus</i> (Finogcnova) comb.n.	0	1	0	0	0	0	0	0	0	0	0	0	?
<i>assimilis</i> (Erséus) comb.n.	0	1	0	1	0	1	0	0	1	0	1	1	1
<i>appositus</i> sp.n.	0	1	0	1	0	1	0	0	1	0	0	0	0
<i>pauper</i> sp.n.	0	?	0	0	0	1	0	0	1	0	1	0	1

the specimen is a normal tubificid with regard to these features; if so, the individual lacks the prostomium, the first seven segments, and the posterior end (beyond segment XXVIII).

As discussed in *Remarks* for *Limnodriloides pierantonii* above, the taxonomy of *S. minusculus* and *Limnodriloides claviger* has been much confused. A re-examination of old as well as new material revealed that two different species appear to have been identified as *L. claviger*, and that both can be attributed to other names. The paratypes of the original, Caribbean, material of *L. claviger* (see Erséus 1982b) are difficult to distinguish from what was subsequently described as *Marcusaedrillus minusculus* from the South Pacific (Erséus 1983a), whereas *L. claviger s. str.* (holotype and a worm from Venezuela) is likely to be a junior synonym of *L. pierantonii* (see above).

The spermathecal ducts of *S. minusculus* are somewhat variable in shape. In the Australian material the ducts are slender, with a constriction near middle (Erséus 1983a: fig. 5B; in press: fig. 17B), whereas the Hawaiian and Caribbean specimens have shorter ducts and seem to lack this constriction. The new specimen from Belize appear to have the shortest ducts of all (see Fig. 32B). The shape of the spermathecal ampullae vary too, from spherical to pear-shaped, with the sperm arranged as bundles, rings or random masses inside.

*Distribution and habitat.* Bermuda, Belize (new records), Great Barrier Reef, Western Australia, Hawaii. Intertidal and subtidal sand, to at least 15 m depth.

***Smithsonidrilus luteolus* (Erséus, 1983) comb.n.** (Figs 33A–C)

*Marcusaedrillus luteolus* Erséus, 1983a: 27–29, fig. 3; 1986b: 309–310, fig. 14.

*New material.* USNM 127995, 1 specimen from barrier reef off Belize, 17°10.0'N, 87°56.1'W, 20 m, sediment unknown (15 June 1977; CARIB I. *Alpha Helix* station no. PD-61-500). USNM 127996–127997, 2 specimens from Station 82. Author's collection, 40 specimens: 1 from each of Stations 1, 10, 14, 26, 27, 48, 62, 70 and 82; 2 each of Stations 6, 66 and 67; 3 from each of Stations 9, 12 and 34; 5 from each of Stations 79 and 86; and 6 from Station 23.

*Brief description of new material.* Length (3 complete specimens) 8.3–8.6 mm, 67–76 segments. Setae bifid, 45–70  $\mu\text{m}$  long, 2–3.5  $\mu\text{m}$  thick, (1)2–4 per bundle anteriorly, (1)2 per bundle in postclitellar segments. Ventral setae absent from XI. Male genitalia (Fig. 33A) paired. Vas deferens 14–22  $\mu\text{m}$  wide, entering atrial ampulla subapically. Atrial ampulla 70–145  $\mu\text{m}$  long, with ental (heavily ciliated) half 30–80  $\mu\text{m}$  wide; muscular lining of this part distinct, but thin. Prostate gland large, lobed. Atrial duct about 190–225  $\mu\text{m}$  long, 28–47  $\mu\text{m}$  wide. Pseudopenial sac with folded wall. Spermathecae (Figs 33B–C) variable in shape and size, totally 130–270  $\mu\text{m}$  long, with ectal swelling 55–75  $\mu\text{m}$  wide, duct (sometimes present merely as a constriction) 19–33  $\mu\text{m}$  wide, ampulla 65–95  $\mu\text{m}$  wide; sperm as somewhat spindle-shaped spermatozeugmata (with one end narrower than the other).

*Remarks.* Most of the specimens examined have well developed seminal vesicles, sometimes reaching a few segments behind clitellar region; sperm production thus is high in this species, contrary to the situation in *M. appositus* sp.n. (described below).

Originally described from Florida and Barbados, *M. luteolus* was expected to occur throughout the Caribbean (Erséus 1983a). The new record corroborates this.

*Distribution and habitat.* Belize (new record), Barbados, Florida. Subtidal mud and sand, to at least 24 m depth; in present study common at stations with medium to coarse sand.

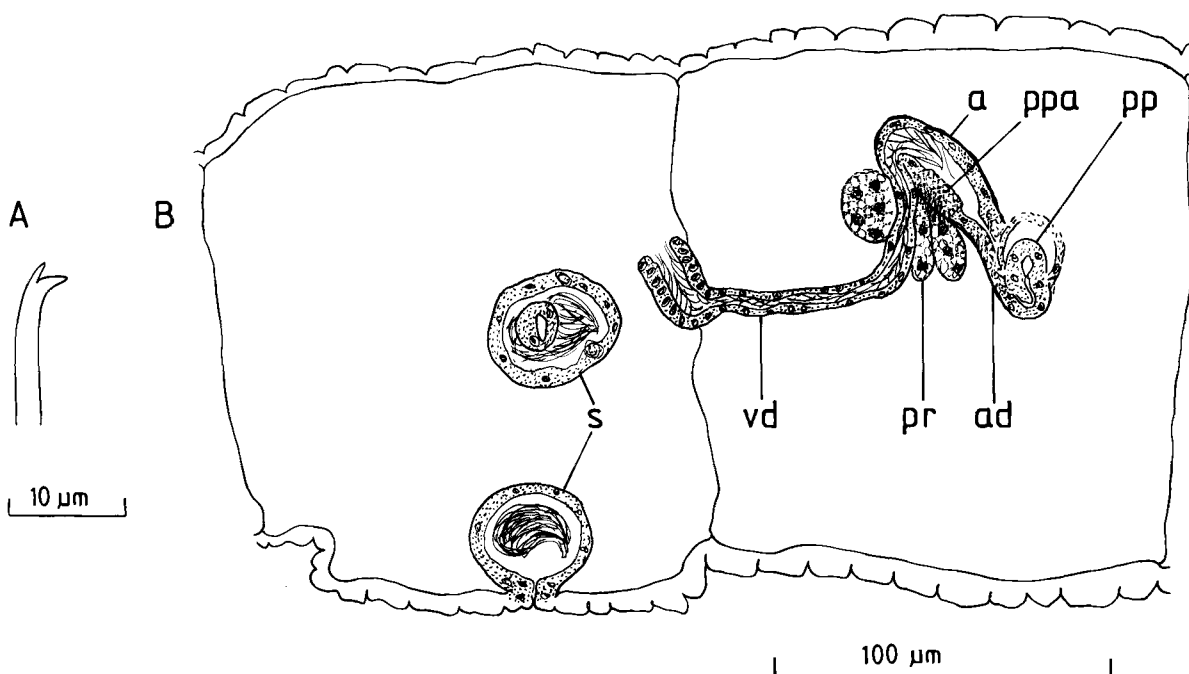


Fig. 32. *Smithsonidrilus minusculus* (Erséus) comb.n.—A. Seta.—B. Oblique view of spermathecae (of both sides) and male genitalia (of one side) in segments X–XI.

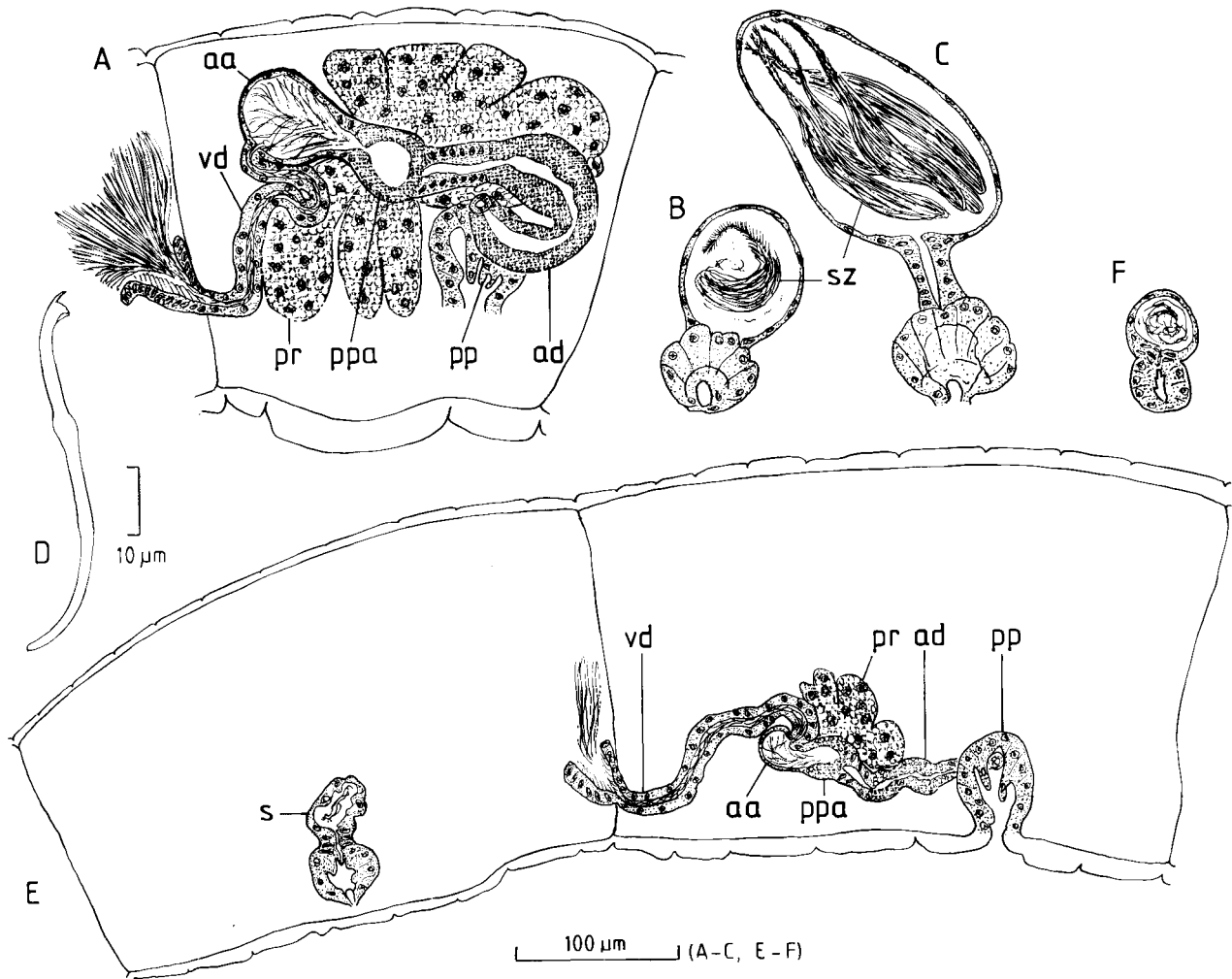


Fig. 33.—A–C. *Smithsonianidrilus luteolus* (Erséus) comb.n.—A. Lateral view of male genitalia in segment X.—B–C. Spermathecae of specimens from Stations 82 (B) and 6 (C).—D–F. *Smithsonianidrilus appositus* sp.n.—D. Seta.—E. Lateral view of spermatheca and male genitalia in segments X–XI, holotype.—F. Spermatheca of paratype from Station 50.

### *Smithsonianidrilus appositus* sp.n. (Figs 33D–F)

*Holotype*. USNM 127998.

*Type locality*. Inside reef crest SE of laboratory, Carrie Bow Cay, Belize, 0.5 m (Station 39).

*Paratypes*. USNM 127999, sectioned specimen from Station 51. USNM 128000–128003, 4 specimens, from Stations 2, 8, 19 and 50, respectively.

*Other material* (author's collection). Seventeen specimens: 1 from each of Stations 1, 2, 8, 9, 36, 37, 50, 51, 65, 67, 78 and 79; 2 from Station 55; and 3 from Station 19.

*Description*. Length (2 complete specimens) 5.3–5.9 mm, 52–58 segments. Width at XI 0.19–0.31 mm. Prostomium short, rounded. Clitellum extending over  $\frac{2}{3}$ X–XII. Setae (Fig. 33D) bifid, with subdental ligament, and upper tooth thinner and shorter than lower. Setae 35–57  $\mu$ m long, 2–3.5  $\mu$ m thick, 2–4(5) per bundle anteriorly, 2(3) per bundle in postclitellar segments. Ventral setae of XI absent. Male pores paired, in line with ventral setae, posterior to middle of XI. Spermathecal pores paired, in line with ventral setae, in middle of X.

Pharyngeal glands in IV–V. Oesophageal diverticula in IX, very large. Male genitalia and spermathecae small (see Fig. 33E), paired. Vas deferens 11–14  $\mu$ m wide, about as long as atrium, entering latter subapically. Atrial ampulla slender, 55–70  $\mu$ m long, entally 21–26  $\mu$ m wide,

with ciliation in ental half, and somewhat cup-shaped prostatic pad, 19–26  $\mu$ m long, in ectal half. Prostate gland small, lobed. Atrial duct 65–105  $\mu$ m long, 19–28  $\mu$ m wide, with indistinct granulation along most of its length. Muscular lining of atrium thin throughout. Atrial duct opening at inner end of round-to-oval pseudopenial sac; latter with somewhat folded inner wall. Spermathecae (Figs 33E, s; 33F) totally 73–80  $\mu$ m long, consisting of (1) round-to-oval ectal swelling (vestibule), 30–43  $\mu$ m wide, (2) very short duct (in many specimens merely a constriction at middle of spermatheca), and (3) small, round-to-oval ampulla, 30–41  $\mu$ m wide; latter with a few spermatozoa in postcopulatory specimens.

*Remarks*. Most of the specimens examined are clitellate and contain several mature eggs. Sperm, however, developing stages in the coelomic cavity as well as mature cells at the sperm funnel and in the spermathecae, are not numerous. This is a striking feature, especially when comparing *S. appositus* with the closely related *S. luteolus* (see above). It probably indicates that the two species have different reproduction strategies, the new species possibly being a parthenogenetic form.

*Smithsonianidrilus appositus* is further distinguished from *S. luteolus* by its clearly smaller genital organs (see Figs

33A, E, in which male ducts and spermathecae of both species are drawn to the same scale), and the less developed ental ciliated part of its atrial ampullae (this part is distended and somewhat muscular in *luteolus*).

*Distribution and habitat.* Known only from Belize. Subtidal medium to coarse sand, to at least 3 m depth.

***Smithsonidrilus pauper* sp.n.** (Fig. 34)

*Holotype.* SMNH 4163.

*Type locality.* Bahía Independencia, Peru, 14°10'40"S, 76°14'20"W, 37.5 m, sand (31 August 1986; coll. E. Canahuire & D. Iparraguirre).

*Paratype.* SMNH 4164, specimen from type locality.

*Etymology.* The epithet *pauper*, Latin for 'poor', alludes to the low number of setae in this species.

*Description.* Length more than 5.6–7.4 mm, more than 28–33 segments (specimens not complete). Width at XI 0.27–0.29 mm, anterior part of worm even wider. Prostomium narrow, slightly longer than broad, clearly set off from peristomium. Clitellum not developed in available specimens. Setae (Figs 34A–C) bifid, with somewhat variable tips, but upper tooth generally slightly narrower and shorter than lower. Teeth tend to be more divergent in anterior setae than in posterior ones (cf. Figs 34A, C). Setae 40–55  $\mu\text{m}$  long, about 2.5  $\mu\text{m}$  thick, (1)2 per bundle in segments II–VIII, 1 (occasionally 2) per 'bundle' thereafter. Ventral setae absent from X–XI. Male and spermathecal pores paired in line with ventral setae, in posterior parts of XI and X, respectively.

Pharyngeal glands present in IV–V. Oesophageal diverticula present anteriorly in IX, but much distorted in available specimens. Male genitalia (Fig. 34D) paired. Vas deferens 12–20  $\mu\text{m}$  wide, shorter than atrium, entering apical end of latter. Atrium elongated club-shaped, with ampulla heavily muscular (muscular lining 3–4  $\mu\text{m}$  thick). Atrial ampulla 95–110  $\mu\text{m}$  long, 40–60  $\mu\text{m}$  wide, entally with a few long cilia around entrance of vas deferens, ectally with a part of inner epithelium devel-

oped into a prostatic pad. Latter communicating with very large, lobed prostate gland. Atrial duct slender, 120–140  $\mu\text{m}$  long, maximally 28–40  $\mu\text{m}$  wide, for most parts with thick, heavily granulated inner epithelium, ectally tapering and ending in a small penis-like papilla inside a bulbous, muscular(?), round and rather conspicuous copulatory sac. Spermathecae (Fig. 34E) with short, but distinct ducts opening into small roundish vestibules, and (when fully developed) pear-shaped ampullae, latter up to 170  $\mu\text{m}$  long, up to 80  $\mu\text{m}$  wide, and with wall much thicker in ectal (wide) part than in ental (narrow) part. In one of spermathecae of holotype, sperm arranged in (at least one) large spermatozeugma; otherwise spermathecae poorly developed and devoid of sperm in available material.

*Remarks.* This species appears closely related to the South Pacific *S. grandiculus* (Erséus, 1983) comb.n., as indicated by the similarities in setae (shape as well as numbers), atria (few cilia in ampullae and long, granulated ducts), copulatory organs (penis-like papillae in conspicuous, roundish copulatory sacs), and spermathecae (ampullae with wide, thick-walled outer part, and narrow, thin-walled inner part) (see Erséus 1983a). *Smithsonidrilus vesiculatus* (Erséus, 1984) comb.n., from Hong Kong, belongs to the same assemblage, although it has a greater number of setae (up to 3, sometimes 4, per bundle anteriorly, generally 2 per bundle posteriorly) (see Erséus 1984e). The new species is easily distinguished from the other two by its heavily muscular atrial ampullae, from *S. grandiculus* also by its less filiform inner part of the spermathecal ampulla.

*Smithsonidrilus peruanus* (Finogenova, 1986) comb.n., described on the basis of a single individual from 50 m depth off the Peruvian coast, is clearly different from *S. pauper*; it has up to three setae per bundle, its atrial ampullae are not muscular, its atrial ducts not granulated, its copulatory organs very small and inconspicuous, and its spermathecal ampullae are ovoid and thin-walled.

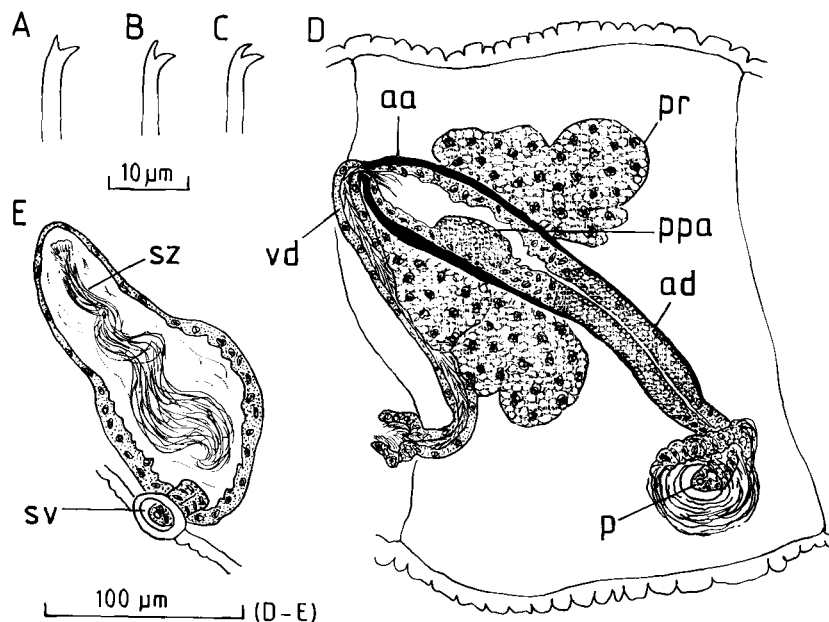


Fig. 34. *Smithsonidrilus pauper* sp.n.—A. Seta of most anterior part of body.—B. Seta of segment VIII.—C. Postelitelar seta.—D. Lateral view of male genitalia in segment XI.—E. Spermatheca.

*Distribution and habitat.* Known only from Bahia Independencia in Peru. Subtidal sand, 37.5 m depth.

***Smithsonidrilus hummelincki* (Righi & Kanner, 1979) comb.n. (Fig. 35)**

*Marcusaedrilus hummelincki* Righi & Kanner, 1979: 49–51, figs 31–35; Erséus 1983a: 26–27, fig 1.

*New material.* MNHN MA 4, specimen from SW point, Îlot Fajou, Grand Cul-de-Sac, Guadeloupe, 16°20.7'N, 61°35.5'W, barely subtidal, medium coralline sand with ripple marks (3 April 1979; coll. J. Renaud-Mornant & N. Gourbault). ZMA 2863, specimen from Puito, northeast part of Lac, Bonaire, Lesser Antilles, 0.5 m, mudflat with *Thalassia* and *Codakia* (11 March 1979; coll. P. Wagenaar Hummelinck, station no. 1577Aa). USNM 128004, specimen from Aruba, Lesser Antilles, 12°30.3'N, 70°02.7'W, at low-water line, sediment unknown (26 June 1977; CARIB I. *Alpha Helix* station no. MS-17-500). USNM 128005, specimen from N (Caribbean) coast of Panama, 09°34.6'N, 78°43.2'W, 0–4 m, sediment unknown (30 June 1977; CARIB I. *Alpha Helix* station no. 23-333/149). USNM 128006, specimen from barrier reef off Belize, 17°10.0'N, 87°56.1'W, 20 m, sediment unknown (15 July 1977; CARIB I. *Alpha Helix* station no. MS-60-500). USNM 128007–128054, 49 specimens from West Bay, Twin Cays, Belize, barely subtidal, mud (various dates, October 1979–March 1981; coll. K. Fauchald *et al.*). USNM 128055–128058, 4 specimens from W side of middle cay, Blue Ground Range, Belize, barely subtidal, mud (various dates, November 1979–August 1980; coll. K. Fauchald *et al.*). Author's collection, 66 specimens: 1 from each of Stations 2 (specimen sectioned), 30, 32, 49, 57, 61, 73, 74, 77 and 78; 2 from each of Stations 26, 65 and 67; 3 from each of Stations 9 and 52; 11 (2 of which sectioned) from Station 5; 8 (1 of which sectioned) from each of Stations 23 and 40; 8 from Station 43; 5 (1 of which sectioned) from Station 37; and 4 from Station 45.

*Remarks.* This common Caribbean tubificid was thoroughly described by Righi & Kanner (1979) and Erséus (1983a). It is the type species of *Marcusaedrilus*, now a junior synonym of *Smithsonidrilus* (see *Remarks* for genus above).

*Smithsonidrilus hummelincki* has an unpaired, rather complex, pseudopenial apparatus, and an unpaired, ventral, spermatheca. The latter (Fig. 35) is tripartite, generally slender, and with sperm loose (Fig. 35C), or, more often, as (rather small) spermatozeugmata (Figs 35A, B, D).

*Distribution and habitat.* Guadeloupe, Bonaire, Aruba, Panama, Belize (all new records), Bermuda, Florida, Bahamas, Puerto Rico, Virgin Islands, Barbados and Curaçao. Intertidal and subtidal mud and sand, to at least 21 m depth.

***Smithsonidrilus marinus* Brinkhurst, 1966**

*Smithsonidrilus marinus* Brinkhurst, 1966: 300–302, fig. 2 (*partim*); Brinkhurst 1971: 571, fig. 8.40A–E (*partim*).  
*Smithsonidrilus marinus marinus*; Erséus 1982a: 48–51, figs 1–4.

*Material re-examined* (see Erséus 1982a). USNM 68663–68666, 10 specimens from St Petersburg and Miami areas, Florida. Author's collection, 8 specimens from Miami.

*Remarks.* A re-examination of the material of the nominate form of *S. marinus* showed that the walls of the spermathecal vestibule (at least in some specimens) in fact bears one, possibly two, glandular bodies, similar to the gland described for *S. involutus* sp.n. below (see Fig. 36F, *sg*). The homologies of the various parts of the spermatheca should also be re-interpreted: what was called the spermathecal duct in *S. marinus* (Erséus 1982a: fig. 2B, *sd*) is probably for most parts the basal end of the spermathecal ampulla, the “ampulla” in the earlier account (Erséus 1982a: fig. 2B, *sa*) being homologous to the diverticulum described for *S. multiglandularis* sp.n. and *S. involutus* below (see Figs 36B, F). A proper duct appears poorly developed in all these highly derived species, but it is discernible in *S. involutus* (Fig. 36F, *sd*).

When *S. marinus* was redescribed (Erséus 1982a), two subspecies were recognized, *S. marinus marinus* and *S. marinus westoni*. The two were distinguished from each other with regard to three features: (1) *westoni* lacks the large (glandular?) mass surrounding the ectal part of the spermathecal “duct” (now re-interpreted as a part of the ampulla) in *marinus*; (2) the sperm “bundles” (they appear in fact to be proper spermatozeugmata) are slenderer in *westoni* than in the nominate form; and (3) the spermathecal vestibule is more developed in *westoni* than in *marinus*. As there now are additional species in this complex (*multiglandularis* and *involutus*), it is more consistent to regard *S. westoni* as a taxon of the same rank.

*Distribution and habitat.* Western and southern Florida. Subtidal sand, to at least 3 m depth.

***Smithsonidrilus westoni* Erséus, 1982, new rank**

*Smithsonidrilus marinus westoni* Erséus, 1982a: 52–53, fig. 5.

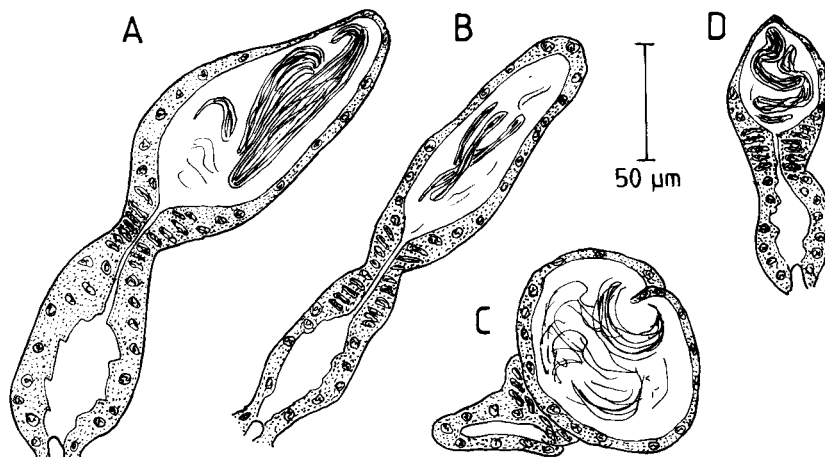


Fig. 35. *Smithsonidrilus hummelincki* (Righi & Kanner) comb.n., spermathecae.—A–C. Specimens from Belize.—D. Specimen from Panama.

*Material re-examined.* Material in the USNM and author's collection, from Bermuda, Bahamas and east coast of the United States (see Erséus 1982a).

*Remarks.* As discussed in *Remarks* for *S. marinus* above, this form is now regarded as a separate species.

A sectioned specimen of *S. westoni* from Bermuda (USNM 89661) has a gland attached to the spermathecal vestibule, as described for *S. involutus* below (see Fig. 36F, *sg*) and noted for *S. marinus* above; this feature thus appears to characterize all three species. Moreover, the various parts of the spermathecal ampulla are now interpreted in the same way for *S. westoni* as for *S. marinus* (see *Remarks* for *marinus*).

*Distribution and habitat.* New Jersey through North Carolina (east coast of the U.S.), Bahamas and Bermuda. Subtidal sand, to at least 200 m depth.

### *Smithsonidrilus multiglandularis* sp.n. (Figs 36A–C)

*Holotype.* USNM 128059.

*Type locality.* Southwest shelf of Florida, 26°45'50"N, 82°45'11"W, 24.4 m, fine sand (November 1980; coll. for Bureau of Land Management; courtesy M. R. Milligan).

*Paratypes.* USNM 128060, 2 specimens from type locality (mounted on same slide as holotype). USNM 128061, specimen from near type locality, but 26°45'42"N, 84°00'08"W, 90.8 m, coarse sand (same date and source as other type specimens).

*Other material.* M. R. Milligan collection, 3 specimens: 1 from type locality; 1 from same area, but 25°46'01"N, 82°23'49"W, 26 m, very fine sand (same date and source as for types); and 1 from 2 km offshore, Aguadilla Bay, west coast of Puerto Rico, 38.8 m, coarse sand and shell (18 April 1985; coll. A. Stoner, for Center for Energy and Environmental Research at the University of Puerto Rico).

*Etymology.* Named *multiglandularis* for its many conspicuous copulatory glands (see Fig. 36C, *cg*).

*Description.* Length (4 complete specimens) 15.6–20.5 mm, 72–83 segments. Width at XI 0.23–0.36 mm. Prostomium elongate. Clitellum extending over XI– $\frac{2}{3}$ XII. Setae (Fig. 36A) bifid, with upper tooth thinner and much shorter than lower. Setae 45–70  $\mu$ m long, 3–5  $\mu$ m thick, 2–3(4) per bundle anteriorly, totally absent from XI, (1)2 per bundle thereafter. Male pore unpaired, located mid-ventrally and posteriorly in XI. Spermathecal pore unpaired, mid-ventral, near middle of X.

Pharyngeal glands in (IV)V. Oesophageal diverticula, in IX, large. Male ducts (Fig. 36C) complex, filling a great part of XI, and generally also extending into XII. Vasa deferentia through granulated part of atrial ducts paired, ejaculatory duct (non-granulated part of atrial duct) and pseudopenis (copulatory sac) unpaired. Vas deferens not clearly visible in available material, but appearing shorter than atrium; entrance into atrium not seen. Atrial ampulla somewhat club-shaped, thin-walled, about 190–210  $\mu$ m long, entally 30–40  $\mu$ m wide, with ciliated inner epithelium; muscular lining of ampulla thin. Prostatic pad modified into elongate diverticulum, 75–100  $\mu$ m long, attached to most ectal part of atrial duct. This diverticulum bearing large, lobed prostate gland. Ental (paired) part of atrial duct shorter than atrial ampulla, 23–32  $\mu$ m wide, with very thin outer muscular lining, and thick, granulated inner epithelium. Ectal to union of granulated ducts of both sides of worm (Fig. 36C, *ead*), atrial duct modified into an unpaired, very long, convoluted, 30–42

$\mu$ m wide, ejaculatory duct; ental part of this duct generally heavily muscular. Ejaculatory duct opening into very large, complex, pseudopenis (copulatory sac). Latter sometimes confined to segment XI, but generally extending into XII (as shown in Fig. 36C). Pseudopenis with much folded inner wall. (4)5(6) large, compact copulatory glands attached to inner part of pseudopenis; these glands round-to-pear-shaped, 55–80  $\mu$ m long, with distinct outer muscular lining. Spermatheca (Fig. 36B) unpaired, complex, consisting of (1) large spermathecal sac (vestibule), with folded, somewhat muscular, wall; (2) a large oval spermathecal ampulla, 165–280  $\mu$ m long, 105–230  $\mu$ m wide, with inner lining of rather tall epithelial cells, particularly tall in inner end of ampulla (this ampulla confined to segment X); and (3) a slender diverticulum, 260–450  $\mu$ m long, 55–95  $\mu$ m wide, with thin wall and containing numerous, very long spermatozeugmata (this diverticulum, which tends to attach somewhat subapically on ampulla proper, situated within segment XI).

*Remarks.* This remarkable tubificid appears to be the most advanced member of the *S. marinus*-complex, having very elaborate male ducts and spermatheca. The copulatory glands of *S. multiglandularis* are very similar in shape and size to those of *S. marinus* and *S. westoni*, but they generally are five in number, not two as in the other two species.

*Distribution and habitat.* West coast of Florida, Puerto Rico. Subtidal sand, to at least 90.8 m depth.

### *Smithsonidrilus involutus* sp.n. (Figs 36D–F)

*Holotype.* USNM 128062.

*Type locality.* Immediately behind breakers, about 2 km N of South Water Cay, Tobacco Reef, Belize, 0.7–1 m (Station 78).

*Paratypes.* USNM 128063–128065, 3 specimens from type locality. USNM 128066, specimen from Station 60.

*Other material.* ZMA 2864, specimen from Drunkemans Key, Jamaica, 0–0.5 m, sandy debris (15 June 1973; coll. P. Wagenaar Hummelink, station no. 1683). Author's collection, 2 specimens from Station 19.

*Etymology.* The genitalia in this species, as well as in the closely related *S. marinus*, *S. westoni* and *S. multiglandularis*, are very 'intricate' (Latin, *involutus*).

*Description of material from Belize.* Length (4 complete specimens) 6.2–10.1 mm, 45–58 segments. Width at XI 0.32–0.52 mm. Prostomium pointed or rounded triangular. Clitellum extending over XI– $\frac{2}{3}$ XII. Setae (Fig. 36D) bifid, with upper tooth thinner and (more or less) shorter than lower. Setae 50–70  $\mu$ m long, 3–5  $\mu$ m thick, 2–3(4) per bundle anteriorly, totally absent from XI, (1)2 per bundle thereafter. Male pore unpaired, located mid-ventrally and posteriorly in XI. Spermathecal pore unpaired, mid-ventral, near middle of X.

Pharyngeal glands in (III)IV–V. Oesophageal diverticula, in IX, large. Male ducts (Fig. 36E) complex, filling a great part of XI. Vasa deferentia through granulated part of atrial ducts paired, ejaculatory duct (non-granulated part of atrial duct) and pseudopenis (copulatory sac) unpaired. Vas deferens 16–21  $\mu$ m wide, shorter than atrium, entering latter subapically. Atrial ampulla somewhat club-shaped, thin-walled, 155–210  $\mu$ m long, entally

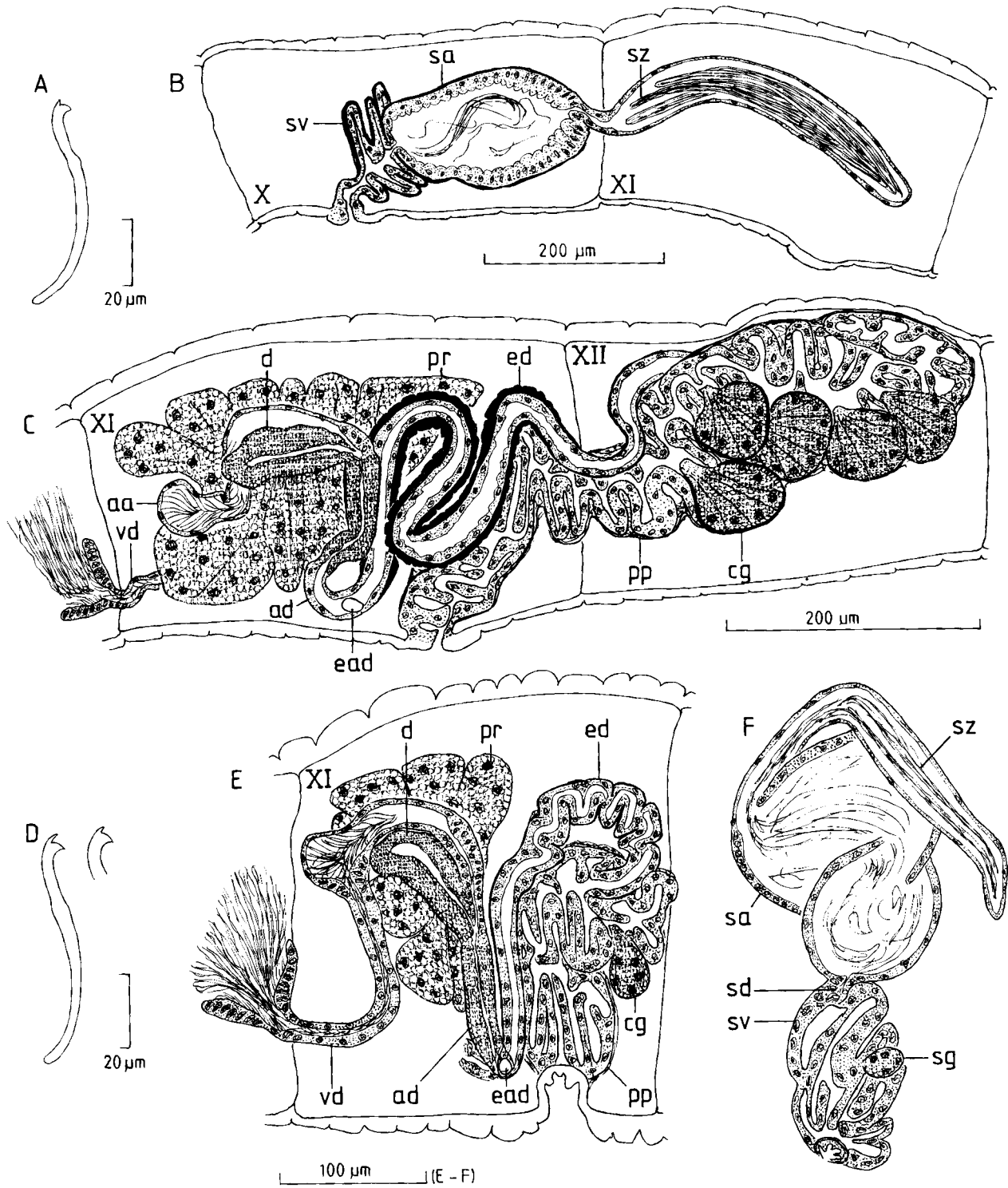


Fig. 36.—A-C. *Smithsonianidrilus multiglandularis* sp.n.—A. Seta.—B. Lateral view of spermatheca in segments X-XI (male genitalia not drawn in XI).—C. Lateral view of male genitalia in XI-XII.—D-F. *Smithsonianidrilus involutus* sp.n.—D. Setae.—E. Lateral view of male genitalia in XI.—F. Spermatheca.

35–70  $\mu\text{m}$  wide, with ciliated inner epithelium; muscular lining of ampulla thin. Prostatic pad modified into elongate diverticulum, 55–105  $\mu\text{m}$  long, attached to most ectal part of atrial duct. This diverticulum bearing large, lobed prostate gland. Ental (paired) part of atrial duct shorter than atrial ampulla, 21–30  $\mu\text{m}$  wide, with very thin outer muscular lining, and thick, granulated inner epithelium. Ectal to union of granulated ducts of both sides of worm (Fig. 36E, *ead*), atrial duct modified into an unpaired, very long, convoluted, somewhat muscular, ejaculatory duct; width approximately same as that of

granulated duct. Ejaculatory duct opening into large, complex, pseudopenis (copulatory sac). Latter generally erect in segment XI, 210–280  $\mu\text{m}$  tall, 85–115  $\mu\text{m}$  wide, with much folded inner wall. At least one small, oval copulatory gland, 25–35  $\mu\text{m}$  long, appears to be attached to pseudopenis in most specimens examined, but glands probably easy to overlook; in one paratype (at least), a second such gland present. Spermatheca (Fig. 36F) unpaired, complex, consisting of (1) large spermathecal sac (vestibule), with folded wall and with a distinct, 26–59  $\mu\text{m}$  long, oval-to-round glandular body (similar to gland

attached to pseudopenis), attached to approximately middle of vestibule (see Fig. 36F); (2) a very short duct-like part, generally merely a constriction between vestibule and ampulla; and (3) a large bipartite, thin-walled ampulla. Ectal part of ampulla 80–145  $\mu\text{m}$  wide, round or elongated oval, often somewhat twisted (indicated in Fig. 36F); this part generally containing loosely arranged sperm. Inner end of ampulla, a long finger-like diverticulum, 16–49  $\mu\text{m}$  wide, somewhat sub-apically attached to wide part of ampulla, generally containing sperm arranged in very slender spermatozeugmata; spermathecal diverticulum observed in all but one specimen (occasionally missing?).

*Specimen from Jamaica.* Length 6.6 mm, 39 segments. Conforms in essential parts to description above, but male genitalia and spermatheca smaller; for instance, pseudopenis only 115  $\mu\text{m}$  tall. Spermathecal diverticulum not observed, but spermathecal segment damaged.

*Remarks.* This new species from Belize and Jamaica appears morphologically intermediate between *S. hummelincki* and the other members of the *S. marinus*-complex (*marinus*, *westoni* and *multiglandularis*) (see cladogram in Fig. 31). *Smithsonidrilus involutus* has the atria, ejaculatory duct and pseudopenis also characteristic of the three last-mentioned species, but it has less developed copulatory glands and a more thin-walled spermathecal ampulla (ectal part of ampulla very thick in *marinus*, *westoni* and *multiglandularis*; erroneously interpreted as the spermathecal duct in *marinus* and *westoni* by Erséus 1982a).

*Distribution and habitat.* Belize and Jamaica. Subtidal sand, to at least 1 m depth.

### Subfamily Tubificinae

#### Genus *Tubificoides* Lastockin, 1937

*Remarks.* The majority of the brackish-water and marine species of the subfamily Tubificinae belong to this genus, the most recent definition of which was provided by Erséus (1989a).

#### *Tubificoides bermudae* Råsmark & Erséus, 1986 (Fig. 37A)

*Tubificoides bermudae* Råsmark & Erséus, 1986: 612–615, figs 1–2.

*New material.* USNM 128067–128071, 5 specimens from Station 80. Author's collection, 87 specimens: 20 (3 of which sectioned) from Station 2; 4 (1 of which sectioned) from Station 5; 1 from Station 38; 2 from each of Stations 33, 37, 40, 46 and 55; 3 from each of Stations 41 and 59; 5 from Station 51; 6 from Station 26; 7 from each of Stations 9 and 79, 10 from Station 80; and 11 from Station 45.

*Remarks.* This species appears common in muddy sand bottoms on the barrier reef off Belize. It was originally reported from similar habitats in Bermuda and Bahamas (Råsmark & Erséus 1986). Five of the new specimens were more closely examined than the rest; they conform well to the original description, even in dimensional

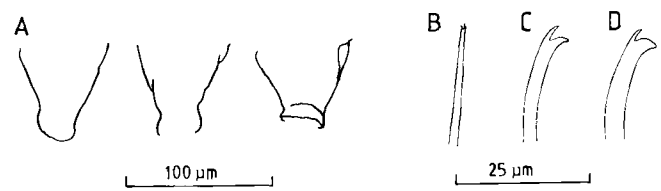


Fig. 37.—A. *Tubificoides bermudae* Råsmark & Erséus, penis sheaths of three different specimens.—B–D. *Tubificoides parviductus* Helgason & Erséus.—B. Dorsal seta of segment VI.—C. Ventral seta of VI.—D. Ventral seta of XIII.

features. They are 11.1–14.6 mm long, consist of up to at least 63 segments (posterior end not fully differentiated), and have two or three bifid setae per bundle in anterior segments, one or two (similar) setae per bundle in post-clitellar segments.

The characteristic, cuticular, penis sheaths (Fig. 37A) are, in the new material, 50–75  $\mu\text{m}$  long, basally 60–65  $\mu\text{m}$  wide, distally 25–35  $\mu\text{m}$  wide.

*Distribution and habitat.* Belize (new record), Bermuda and Bahamas. Intertidal and subtidal, often muddy, sand, to at least 15 m depth.

#### *Tubificoides parviductus* Helgason & Erséus, 1987 (Figs 37B–D)

*Tubificoides parviductus* Helgason & Erséus, 1987: 164–165, figs 4–5.

*New material.* USNM 128072, sexually immature specimen from Station 82.

*Remarks.* Although this single specimen is not sexually mature, the morphology and arrangement of its setae strongly suggest that it is identical to *T. parviductus*, previously known from Bermuda and Barbados (Helgason & Erséus 1987).

In the dorsal bundles of segments II–VIII, there are two long hair setae and two (occasionally one) bifid setae (Fig. 37B), the latter with very small, more or less parallel teeth that almost make the tip appear single-pointed. From segment XI, the dorsal setae are smaller, and from X, each bundle generally contains only one hair and one bifid seta. The ventral setae are more normal bifids (Figs 37C–D), three per bundle in segments II–VII, thereafter two per bundle (except for X and XII, in which ventral ‘bundles’ are unisetal and absent, respectively). The upper tooth of the ventral setae is larger (in relation to lower tooth) in anterior segments (Fig. 37C) than in post-clitellar segments (Fig. 37D).

*Distribution and habitat.* Belize (new record), Bermuda and Barbados. Medium to coarse, often muddy, sand, 6–21 m depth.

### Ecological notes on the Tubificidae of the barrier reef off Belize

Although the author's samples from Belize were not quantitative, and the stations not randomly distributed, the present study gives an indication of at least three subgroups within the marine tubificid fauna of the area studied, each recognized with reference to the habitat preferences of its constituent species.

Six species, all meiobenthic members of the subfamily Phallodrilinae, were exclusively found in high intertidal habitats (Stations 7, 20, 25 and 54) or in saline ground-water at some distance from the shore (Stations 18 and 29). These species are: *Coralliodrilus rugosus*, *Phallodrilus nasutus*, *P. biparis*, *Aktedrilus longitubularis*, *A. parvithecatus* and *Jamiesoniella athecata*.

A second group comprises species largely restricted to sediments with a high organic content, in particular the bottoms associated with mangrove cays (Stations 17, 37, 38, 52, 55, 56, 61, 83 and 87; plus the stations at Twin Cays and Blue Grange Range intensively sampled by K. Fauchald *et al.*). Most species in this group belong to the Limnodriloidinae: *Doliodrillus puertoricensis*, *Thalassodrilides* spp., *Tectidrillus* spp., *Limnodriloides* spp., and some *Smithsonidrillus* spp., especially *S. hummelincki* (latter species euryoecious, occurring also in less muddy sediments). However, *Ainudrilus geminus* (Rhyacodrilinae), *Bathydriilus adriaticus* and probably *B. vetustus* (Phallodrilinae) were also characteristic of these organically enriched habitats.

The remaining taxa, the majority of species treated in this paper, form the third group. With regard to habitat it is more difficult to define. It includes *Heronidrillus gravidus*, *Heterodrilus* spp., most of the Phallodrilinae including all gutless forms, *Smithsonidrillus* spp. and *Tubificoides* spp., which occurred in varying combinations in the sandy sites on the barrier reef proper. Further subdivision of these habitats is difficult to make, as the collecting procedure was not designed for obtaining quantitative ecological data. In the list of the 87 stations above, the sediments are merely described in a qualitative way, based on field observations of grain size, content of mud, associated plants, etc. Thirteen species in this group occurred at ten or more of the stations. This, however,

does not necessarily imply they are the commonest species in the area; the selection of sampling sites was not randomized. In Table VIII, the co-occurrences of these thirteen species are tabulated in a two-dimensional way; the number of stations at which any particular species is co-occurring with any other is given. For instance, it is shown that the four species that are most frequent in the collection, *Heterodrilus flexuosus* (36 stations), *Phallodrilus molestus* (33 stations), *Inanidrillus leukodermatus* (30 stations), and *Bathydriilus formosus* (19 stations), also commonly occur together. All four were found at seven different stations: east, north, west and south of Carrie Bow Cay (Stations 5, 9, 23 and 32), and back reefs of Columbus Reef (Station 57) and Tobacco Reef (Stations 77 and 80). At another six stations, the three first-mentioned species were present together (i.e. without *B. formosus*). Although not quantitatively conclusive, it seems possible that these species are the most characteristic tubificids of the barrier reef off Belize.

### Biogeography and faunal diversity

The present material has increased the taxonomic and distributional information about the marine shallow-water Tubificidae in the Caribbean area considerably. [The area referred to here is the 'Caribbean province' in a broad sense (Valentine 1973); other authors (e.g. Briggs 1974) divide it further into the Caribbean (*sensu stricto*), West Indian and Brazilian provinces.] Fifty-nine species of marine Tubificidae are now recorded from Belize, a high diversity in comparison with the results of similar studies elsewhere in the Caribbean (Table IX).

Bermuda is a satellite group of islands in relation to the tropical west Atlantic. Although located at 32° North, it is

Table VIII. The thirteen commonest tubificid species at the eighty-seven stations on the barrier reef off Belize sampled by the author in November 1985, and the number of stations at which they co-occurred with each other

	<i>Heterodrilus flexuosus</i>	<i>Heterodrilus paucifascis</i>	<i>Heterodrilus modestus</i>	<i>Heterodrilus pentcheffi</i>	<i>Phallodrilus molestus</i>	<i>Inanidrillus leukodermatus</i>	<i>Inanidrillus scalprum</i>	<i>Duridrillus tardus</i>	<i>Bathydriilus formosus</i>	<i>Smithsonidrillus luteolus</i>	<i>Smithsonidrillus appositus</i>	<i>Smithsonidrillus hummelincki</i>	<i>Tubificoides bermudae</i>
<i>Heterodrilus flexuosus</i>	■												
<i>Heterodrilus paucifascis</i>	5	■											
<i>Heterodrilus modestus</i>	8	5	■										
<i>Heterodrilus pentcheffi</i>	14	2	4	■									
<i>Phallodrilus molestus</i>	18	2	5	10	■								
<i>Inanidrillus leukodermatus</i>	18	3	5	11	23	■							
<i>Inanidrillus scalprum</i>	7	—	1	4	8	10	■						
<i>Duridrillus tardus</i>	9	3	1	9	7	7	1	■					
<i>Bathydriilus formosus</i>	14	—	3	9	12	11	3	4	■				
<i>Smithsonidrillus luteolus</i>	13	5	1	5	10	8	4	7	5	■			
<i>Smithsonidrillus appositus</i>	8	1	—	3	7	6	2	3	6	4	■		
<i>Smithsonidrillus hummelincki</i>	11	—	3	4	10	10	2	1	10	4	4	■	
<i>Tubificoides bermudae</i>	5	—	—	2	9	9	3	2	6	3	6	7	■
Total no. stations	36	10	11	17	33	30	12	13	19	18	15	21	16

Table IX. Faunal composition of marine Caribbean Tubificidae, a comparison of four restricted geographical areas sampled by author, in Bermuda, near Miami (southeast Florida), in Belize (present study) and Barbados. For each area, the sampling effort is two or three weeks field work (including sorting in laboratory), but additional specimens from other sources are included. Species not known from Miami, but from other parts of Florida, are indicated in Remarks. E. = Erséus

Taxa	Bermuda	Miami	Belize	Barbados	(Remarks)
<b>Rhyacodrilinae:</b>					
<i>Heterodrilus minisetosus</i> E., 1981a	×	×			
<i>H. bulbiporus</i> E., 1981a	×				Florida
<i>H. pentcheffi</i> E., 1981a	×	×	×		
<i>H. quadrithecatus</i> (E., 1981a)	×		×		
<i>H. ersei</i> (Giere, 1979)	×		×		
<i>H. paucifascis</i> Milligan, 1987			×		Florida
<i>H. flexuosus</i> sp.n.			×		
<i>H. rarus</i> sp.n.			×		
<i>H. modestus</i> sp.n.			×		
<i>Ainudrilus geminus</i> sp.n.			×		
<i>Heronidrilus gravidus</i> sp.n.			×	×	
<b>Phallodrilinae:</b>					
<i>Coralliodrilus leviatriatus</i> E., 1979a	×				
<i>C. rugosus</i> sp.n.			×		
<i>C. randyi</i> sp.n.			×		
<i>Phallodrilus molestus</i> E., 1988a	×	×	×	×	
<i>P. deminutius</i> E., 1979d	×		×	×	
<i>P. exiguus</i> E., 1979d	×				
<i>P. macmasterae</i> E., 1986a	×				
<i>P. sabulosus</i> E., 1979d		×			
<i>P. compactus</i> sp.n.			×		
<i>P. singularis</i> sp.n.			×		
<i>P. vicinus</i> sp.n.			×		
<i>P. nasutus</i> sp.n.			×		
<i>P. bipartitus</i> sp.n.			×		
<i>P. caviatriatus</i> E., 1984a				×	
<i>Adelodrilus magnithecaus</i> E., 1979b	×				
<i>Bermudrilus peniatus</i> E., 1979b	×				Florida
<i>Aktedrilus locyi</i> E., 1980a	×				
<i>A. monospermathecus</i> Knöllner, 1935	×				
<i>A. parvithecatus</i> (E., 1978)	×		×		
<i>A. floridensis</i> E., 1980a		×		×	
<i>A. longitubularis</i> Finogenova & Shurova, 1980			×		
<i>Jamiesoniella athecata</i> E., 1981c			×		
<i>Inanidrilus leukodermatus</i> (Giere, 1979)	×		×		
<i>I. aduncosetis</i> E., 1984b	×		×		
<i>I. triangulatus</i> E., 1984b		×			
<i>I. extremus</i> (E., 1979d)		×			
<i>I. bulbosus</i> E., 1979e		×			
<i>I. scalprum</i> E., 1984b			×		
<i>I. belizensis</i> E., 1984b			×		
<i>I. reginae</i> sp.n.			×		
<i>I. speroi</i> E., 1984b				×	
<i>I. gustavsoni</i> E., 1984b				×	
<i>I. falcifer</i> E. & Baker, 1982				×	
<i>Olavius planus</i> (E., 1979d)	×				
<i>O. (O.) alius</i> E., 1984b	×				
<i>O. tenuissimus</i> (E., 1979d)	×	×	×		
<i>O. (O.) longissimus</i> (Giere, 1979)	×		×		
<i>O. caudatus</i> (E., 1979d)		×			
<i>O. vacuus</i> sp.n.			×		Florida
<i>O. imperfectus</i> E., 1984b			×		Florida
<i>O. finitimus</i> sp.n.			×		
<i>O. tantulus</i> E., 1984b			×		
<i>O. (O.) pravus</i> sp.n.			×		
<i>O. pellucidus</i> E., 1984b				×	
<i>Duridrilus tardus</i> E., 1983b	×		×	×	
<i>Bathydrilus adriaticus</i> (Hrabě, 1971a)	×	×	×	×	
<i>B. formosus</i> E., 1986b			×		Florida
<i>B. egenus</i> sp.n.			×		
<i>B. vetustus</i> sp.n.			×	×	
<b>Limnodriloidinae:</b>					
<i>Thalassodrilides belli</i> (Cook, 1974)	×				
<i>T. ineri</i> (Righi & Kanner, 1979)	×	×	×		
<i>T. gurwitschi</i> (Hrabě, 1971b)			×		Florida
<i>T. bruneti</i> sp.n.			×		
<i>Parakakettio longiprostatas</i> E., 1982c		×			
<i>Doliodrilus puertoricensis</i> E. & Milligan, 1988b			×		
<i>Tectidrilus bori</i> (Righi & Kanner, 1979)	×	×	×	×	

Table IX. Continued

Table IX. *Continued*

<i>T. gabriellae</i> (Marcus, 1950)	×		×	×
<i>T. squalidus</i> E., 1982b		×		
<i>Limnodriloides barnardi</i> Cook, 1974	×	×	×	
<i>L. monotheucus</i> Cook, 1974	×	×	×	
<i>L. rubicundus</i> E., 1982b	×	×	×	×
<i>L. vespertinus</i> E., 1982b		×		
<i>L. baculatus</i> E., 1982b		×		
<i>L. anxius</i> sp.n.		×	×	×
<i>L. major</i> sp.n.			×	
<i>L. uniampullatus</i> E., 1982b			×	
<i>L. sacculus</i> sp.n.			×	
<i>L. adversus</i> sp.n.			×	
<i>L. pierantonii</i> (Hrabě, 1971a) (= <i>L. claviger</i> )				×
<i>Smithsonidrilus westoni</i> E., 1982a	×			
<i>S. hummelincki</i> (Righi & Kanner, 1979)	×	×	×	×
<i>S. minusculus</i> E., 1983a	×		×	
<i>S. marinus</i> Brinkhurst, 1966		×		
<i>S. luteolus</i> E., 1983a		×	×	×
<i>S. appositus</i> sp.n.			×	
<i>S. involutus</i> sp.n.			×	
Tubificinae:				
<i>Tubificoides bermudae</i> Råsmark & E., 1986	×		×	
<i>T. parviductus</i> Helgason & E., 1987	×		×	×
<i>T. motei</i> Brinkhurst, 1986		×		
<i>T. wasselli</i> Brinkhurst & Baker, 1979		×		
<i>T. inops</i> E., 1989a				×
Total no. of species per area (all areas, 92 species)	35	26	59	21

strongly influenced by the warm Gulf Stream, and many marine species present in the West Indies proper are also found in Bermuda (Briggs 1974; Sterrer 1986). Bermuda may thus be used as a reference area for (primarily) the northeastern fauna of the Caribbean region. The marine Tubificidae of Bermuda have been treated in several papers (Erséus 1978, 1979a–d, 1980a, 1981a–b, 1982a–b, 1983a–b, 1984b, 1986a, 1988a; Giere 1979; Helgason & Erséus 1987; Lasserre & Erséus 1976; Råsmark & Erséus 1986), which include records of totally 35 different species (Table IX). A majority of these were collected by me, while visiting Bermuda twice in 1977, during a total of three weeks. Although involving only 46 stations, the sampling effort in Bermuda is thus somewhat comparable with that in Belize (present paper). Moreover, the Bermuda and Belize studies involved approximately the same range of habitats, with the slight discrepancy that some species, found in very shallow bottoms near the mangrove cays in Belize, were instead collected in muddy sand at 4–6 m depth in protected areas of the Bermudian archipelago (Erséus 1982b, 1983a).

Two other collection endeavours by the present author, each with a duration of two weeks, were undertaken in the Biscayne Bay area, at Miami, Florida (1977; 17 stations), and in Barbados (1979; 23 stations). They did not cover as much habitat variety as the Bermudian and Belizean studies, which may partly explain why fewer taxa were recorded (Table IX). Twenty-six species were found in Miami (Erséus 1979c–e, 1980a–b, 1981a, 1982a–c, 1983a, 1984b, 1988a, present paper; Brinkhurst 1986), 21 in Barbados (Erséus 1982b, 1983a–b, 1984a–b, 1987a, 1988a, 1989a, present paper; Erséus & Baker 1982).

The data in Table IX are not conclusive with regard to biogeographical patterns; much more information from the Caribbean region as a whole is needed. Unless a very careful search has been undertaken, a negative 'score' from one area sampled does not at all tell that a species is

not there. In addition, the 92 species listed exclude others that have been described from Florida (most of which listed by Erséus 1986b), the Gulf of Mexico, Puerto Rico, Martinique, Guadeloupe and Panama (Erséus 1982b, 1983e, 1984b, 1988c, 1989a, c; Erséus & Milligan 1988a–b, 1989; Shirley & Loden 1982), which are members of largely the same fauna. Nevertheless, some aspects of the comparative data in Table IX deserve attention.

Returning to those four areas investigated more closely by the author, it shows that the barrier reef off Belize harbours no less than 64% of the total number of species for all areas, and probably has a good representation of the Caribbean marine turbificid fauna as a whole. Belize and Bermuda show the greatest overlap in species composition of any possible comparison between two of the areas: 22 species (31%) of the combined number of species in Belize and Bermuda. This relatively high degree of overlap may have been biased by the similarity in habitat variation that was noted for these two areas (see above), but at the same time it still may be an underestimation of the true overlap. In the other comparisons, the overlap ranges between 16% (Belize versus Miami) and 22% (Bermuda versus Miami).

Five species have been found in all four areas: *Phalldrilus molestus*, *Bathydrilus adriaticus*, *Tectidrilus bori*, *Limnodriloides rubicundus* and *Smithsonidrilus hummelincki*. The four first-mentioned have been recorded from other oceans as well and may be circumtropically distributed (see e.g. Erséus 1988a; Erséus & Davis 1989). Other species, not recorded from all areas considered here, but known also from the Pacific Ocean, Indian Ocean, or the east Atlantic (including the Mediterranean), are *Jamiesoniella athecata*, *Duridrilus tardus*, *Thalassodriloides gurtwitschi*, *Limnodriloides monotheucus*, *L. uniampullatus*, *L. pierantonii*, *S. minusculus*, and all *Aktedrilus* except *A. floridensis*. They appear to be additional members of the large group of species that tend to turn up anywhere in the

tropical or subtropical waters of the world. *Heterodrilus pentcheffi*, *Thalassodrilides belli*, *Limnodriloides barnardi*, *Tubificoides motei* and *T. wasselli* have so far only been found on both sides of the isthmus of Panama, also including temperate regions on both sides of North America (see Brinkhurst 1986; Cook 1974; Erséus 1984d), and it is still possible that they are restricted to the Americas.

Nine species (*Heterodrilus minisetosus*, *H. bulbiporus*, *Phallogdrilus sabulosus*, *Adelodrilus magnithecatus*, *Olavius tenuissimus*, *O. vacuus*, *Limnodriloides baculatus*, *L. anxius* and *Smithsonidrilus westoni*) appear restricted to the west Atlantic, but they extend their ranges northwards into the temperate zone along the east coast of the United States. For instance, *Olavius tenuissimus* has been collected as far north as Georges Bank, off Massachusetts (Davis 1985).

The remaining 62 species in Table IX, plus *Smithsonidrilus hummelincki* that was mentioned above, have to date only been recorded from within the Caribbean area. They are thus the candidates for the true Caribbean elements in the fauna considered here. Some indeed seem to be present throughout the Caribbean (*Phallogdrilus deminutius*, *Tectidrilus gabriellae*, *Smithsonidrilus luteolus*, *S. hummelincki*, *Tubificoides parviductus*), but most of them are known only from one or two areas, and much more information is required to establish their full geographical ranges.

*Phallogdrilus deminutius* has been regarded as more endemic than its close relatives, *P. molestus*, *P. rectisetosus* Erséus, 1979, and *P. heronensis* Erséus, 1981 (Erséus 1988a). *Tectidrilus gabriellae* is the only species of the present study that also is known from the most southern part of the 'Caribbean province', the State of Sao Paulo, Brazil (Marcus 1950).

A Caribbean origin of the most apomorphic group within *Smithsonidrilus* (*S. marinus* through *S. multiglandularis* in the cladogram; Fig. 31) is highly probable, considering that they appear to constitute the sister group of *S. hummelincki* and that none of them have been found outside the west Atlantic.

As noted in *Remarks for Olavius finitimus* in the taxonomic section above, the barrier reef of Belize may represent an overlap zone between southern and northern species in Central America. In Belize, *O. finitimus* co-occurs with the exceedingly similar *O. tenuissimus*, but it has not been found anywhere else within the distribution of the latter. *Olavius tenuissimus* is the Caribbean gutless species that extends the farthest to the north (mentioned above); *O. finitimus* may be its southern counterpart.

Otherwise, the degree of regional endemism within the Caribbean province is difficult to establish on basis of the present information. One pattern is, however, emerging with regard to the many gutless species within the Phallogdrilinae (genera *Inanidrilus* and *Olavius*). In Table IX, 22 gutless species are included, but if other species of this group from Florida and Guadeloupe (but not found in Bermuda, Miami, Belize or Barbados) are added (*I. vacivus* Erséus, 1984b, *I. ernesti* Erséus, 1984b, *I. renaudae* Erséus, 1984b, *I. mexicanus* Erséus & Baker, 1982, *O. latus* Erséus, 1986b, *O. macer* Erséus, 1984b), a total of 28 species are known from the Caribbean. A few of these gutless forms are evidently more widely distributed

(*I. leukodermatus*, *I. aduncosetis*, *O. tenuissimus*, *O. (O.) longissimus*, *O. vacuus*, *O. imperfectus*, *O. pellucidus*), but each of the rest is so far only known from one restricted area: two species are unique to Bermuda, nine to Florida, six to Belize, three to Barbados, and one to Guadeloupe. This strongly suggests that the gutless Tubificidae have undergone a (recent?) radiative evolution in the tropical west Atlantic (as well as in other parts of the world; see Erséus 1984b), perhaps more so than any other group of marine Tubificidae. One reason for this probably relates to the unusual ecophysiological adaptation of these curious animals. Due to the nutritional requirements of the worms' symbiotic, subcuticular bacteria, the population maxima of *Inanidrilus* and *Olavius* are generally located at oligoxic or anoxic depths around the redox discontinuity layer in the mostly carbonate sediments (Giere *et al.* 1982, 1984). This may make gutless tubificids more sessile than other marine oligochaetes, restricting the possibilities of dispersal by currents, rafting, other animals, etc. Furthermore, the Caribbean offers many gaps of deep water between the patches of shallow bottoms around islands and land masses, acting as geographic barriers that reduce the gene flow between different populations. Some of the gutless species that are known from only one area to date will certainly prove to have wider distributions, but it can also be predicted that many additional new taxa will be discovered in various parts of the Caribbean in the future.

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