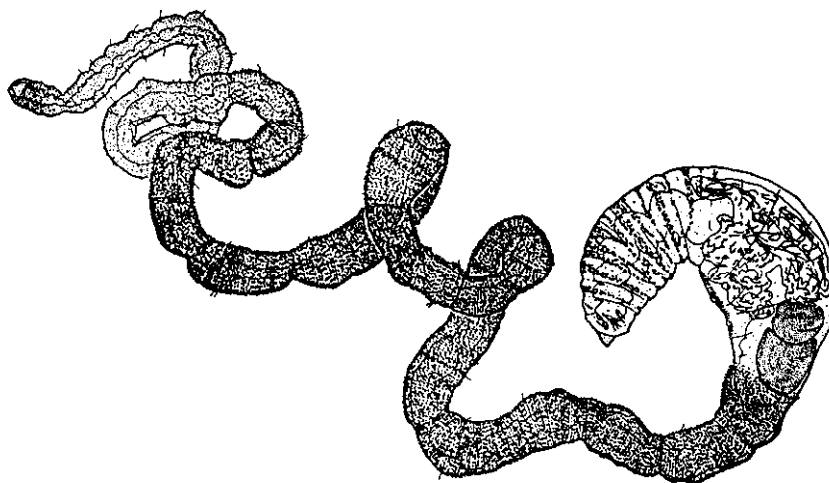


IDENTIFICATION MANUAL
FOR THE
AQUATIC OLIGOCHAETA
OF
FLORIDA
VOLUME II

ESTUARINE AND NEARSHORE MARINE OLIGOCHAETES



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State of Florida
Department of Environmental Protection
Division of Water Facilities
Tallahassee

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ESTUARINE AND NEARSHORE MARINE OLIGOCHAETES**

by

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FIGURE ABBREVIATIONS

a	atrium		seta; giant penial	rs	duct of
aa	atrial ampulla		seta (<i>Adelodrilus</i>)		spermatheca
ad	atrial diverticulum	h	hairs	rsp	pore of
	(<i>Thalassodrilides</i>)	hs	hair-like penial		spermatheca
	atrial duct		seta	s	spermatheca;
ado	atrial duct of other	lm	longitudinal		spermatozeugmata
	side		muscle		(<i>Tubificoides</i>)
apr	anterior prostate	m	muscles	sa	spermathecal
at	atrium	mb	male bursa		ampulla
atd	atrial duct	mf	male funnel	sb	sperm bundle
b	blood vessel	mp	male pore	sd	spermathecal duct
bf	body of foreign	mpa	male papilla	sdi	spermathecal
	particles	mu	muscles		diverticulum
bs	blind sac	nc	nerve cord	se	seta
c	chlorogogen cells	o	ovary	sep	septum in atrial
cg	copulatory gland	od	esophageal diverticulum		ampulla
cl	clitellum	ov	ovary	sf	sperm funnel
cps	cuticular penis	p	penis	sg	spermathecal gland
	sheath	pa	papilla	so	somatic seta
cs	copulatory sac	pl	peritoneal layer	sp	spermathecal
d	diverticulum	pp	pseudopenis		protuberance;
dp	diffuse prostate	ppa	prostatic pad		spermatheca
ds	dorsal seta	ppr	posterior prostate		(<i>Bathydrilus</i>);
dv	dorsal vessel	pr	prostate gland		spermatozeugmata
e	egg	pr1	anterior prostate	sp.th.	spermatheca
ea	epidermal		gland	ss	spermathecal seta;
	appendage	pr2	posterior prostate		spermathecal sac;
ead	entrance of atrial		gland		small penial seta
	duct from other	pra	anterior prostate		(<i>Adelodrilus</i>);
	side	prm	prostomium		shorter penial seta
ec	epidermal crypt	pro	prostate other side		(<i>Inanidrilus</i>)
ed	ejaculatory duct	prp	posterior prostate	st	sperm trap
ep	epidermal pad	ps	penial seta	sv	spermathecal
epi	epithelium	psa	penial sac		vestibule
fb	fold of body wall	pse	penial sac	sz	spermatozeugmata
ff	female funnel	pso	penial seta of	t	testes
fp	flap-like papilla		other side of	vd	vas deferens
g	gut; gland		worm	vdo	vas deferens other side
	(<i>Duridrilus</i>)	ra	rudimentary	vg	ventral gland
gs	gland associated		atrium	vs	ventral seta
	with spermathecal			vv	ventral vessel

DEDICATIONS

This is dedicated to:

The fortunate few who have never forsaken their
childish ways
Who realize the greatest joy is gained through
observation of what is
Not dissection of what might be.

Dr. Ralph Brinkhurst, who has perpetuated the feast;
Dr. Christer Erséus who provided the smörgåsbord,
and
Linda Franklin, without whose assistance this could
not have been produced.

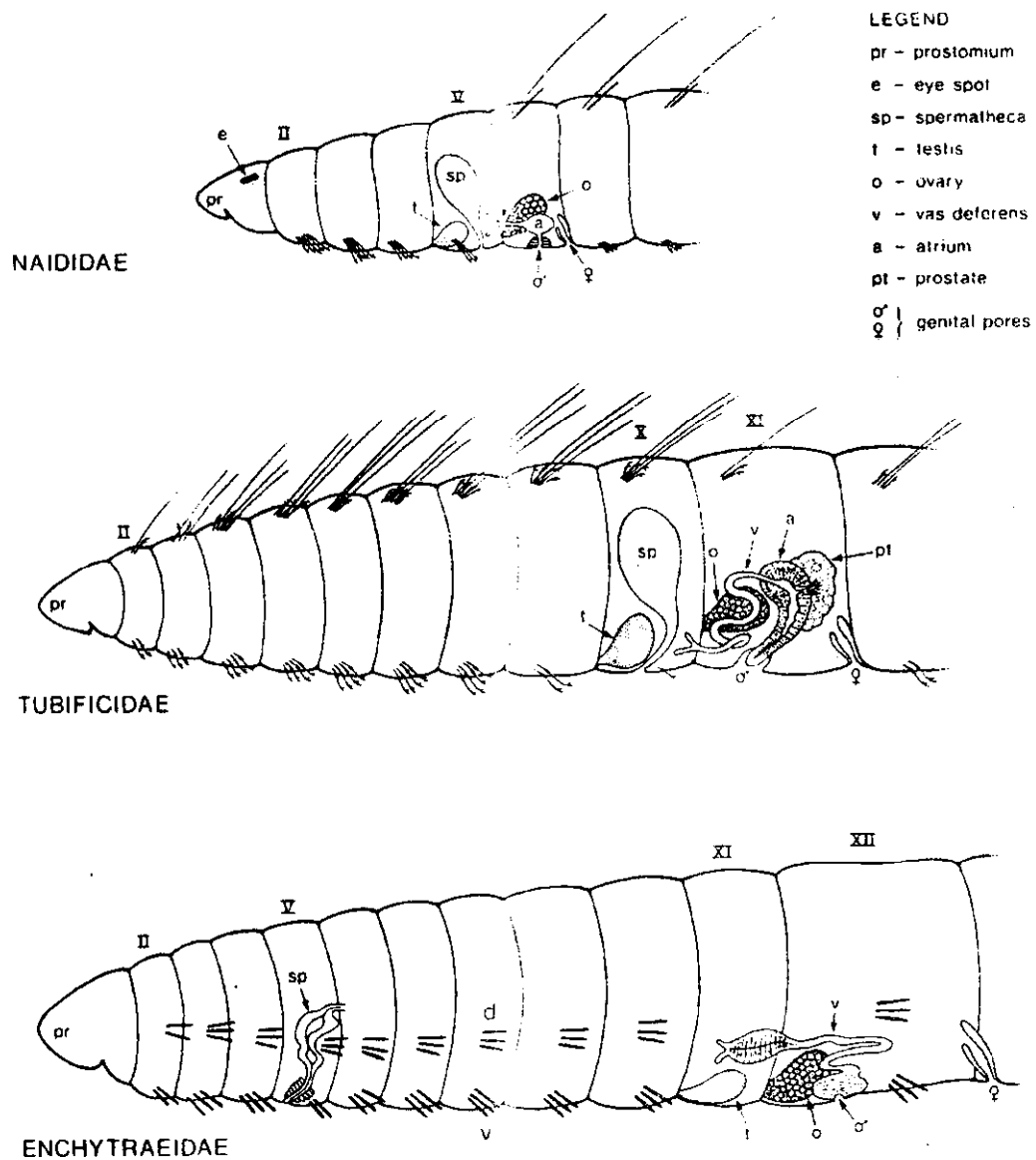


Figure 0-1. (From Brinkhurst, 1986)

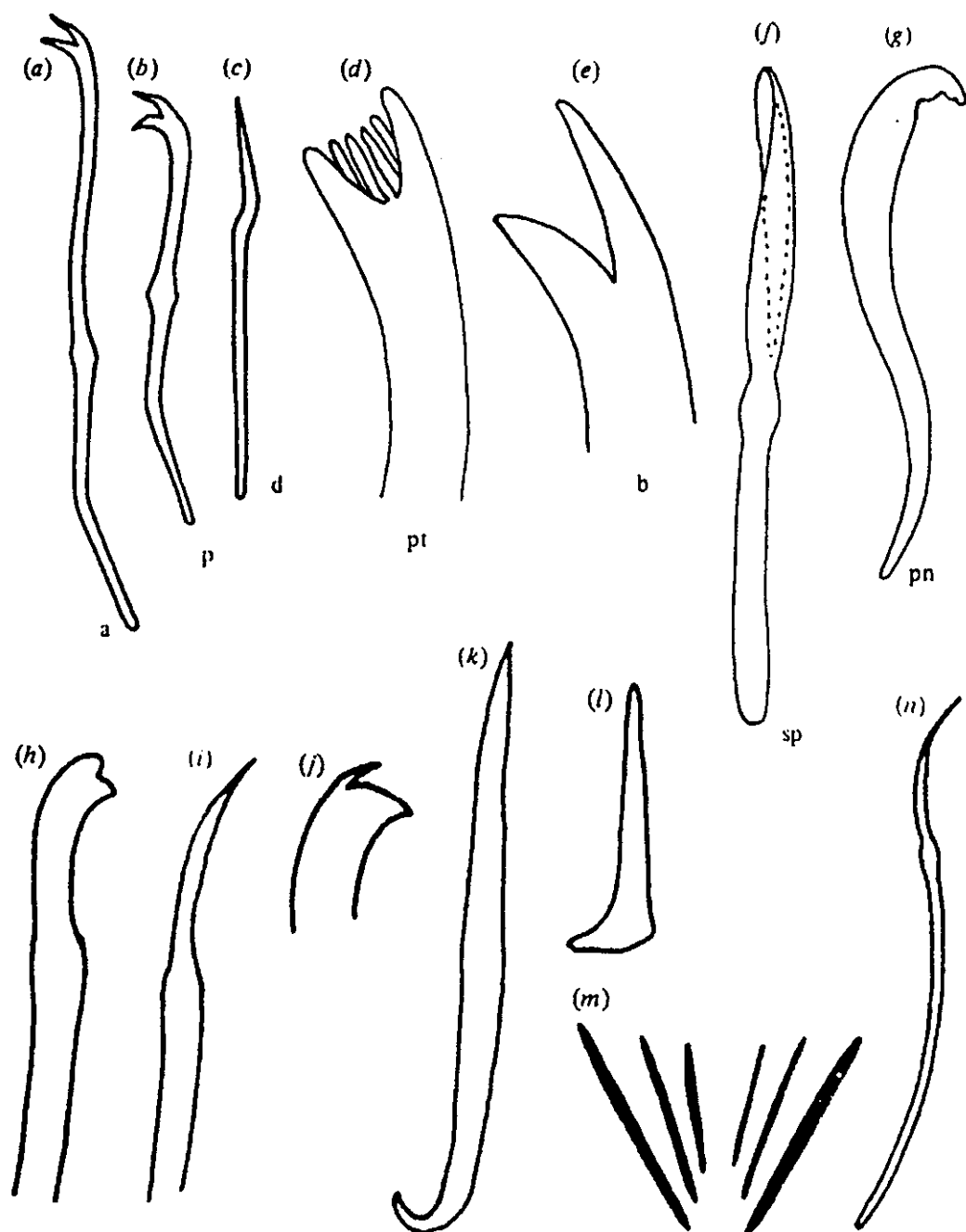


Figure 0-2. (From Brinkhurst, 1982) Oligochaete setae: (a)-(c) Naididae; (d)-(g) Tubificidae; (h)-(j) Lumbriculidae; (k)-(n) Enchytraeidae (k, *Lumbricillus*, l, *Grania*, m, *Fridericia*, n, *Cernosvitoviella*). Key: d = dorsal; a = anterior ventral; p = posterior ventral; b = bifid (present in some form in all ventral bundles of tubificids, and in the dorsals when both hair and pectinate setae absent); pt = pectinate (usually with hair setae in dorsal bundles in tubificids, rarely in naidids); sp = spermathecal (usually the ventrals of X); pn = penials (usually the ventrals of XI) (spermathecae and penials, if present, are the genital setae of mature individuals.).

ARTIFICIAL TAXONOMIC KEY TO THE MAJOR TAXA OF MARINE
AND ESTUARINE TUBIFICIDAE OF FLORIDA

(not applicable to the southern Caribbean,
North American east coast north of
South Carolina, or deep water species)

1. A) Anterior setae trifid, or bifid with parallel
straight teeth in line with the setal shaft and
hair setae absent; penial setae present or
absent.

Heterodrilus
(p. 4, Table 1)

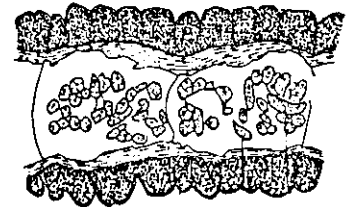


- B) Trifid setae absent; somatic setae with
curved tips, simple or bifid; hair setae may
be present; modified spermathecal and/or
penial setae may be present. 2.



- 2.(1B) A) Mouth, anus, and alimentary canal absent;
body wall very thick, chalky white due to
presence of symbiotic bacteria, secondary
annulations usually conspicuous, 6-8 per
segment; hairs absent; somatic setae all
bifid, frequently with subdental ligament;
modified spermathecal setae absent; highly
modified penial setae usually present.

Olavius/Inanidrilus 3.
(p. 99/78, Table 3)

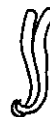


- B) Mouth, anus, and alimentary canal present;
body wall not thickened, but may have
secondary annulations; hairs present or
absent; modified spermathecal and penial
setae present or absent. 4.

- 3.(2A) A) Penial setae two per bundle, at least one of which sickle-shaped seta frequently anismorphic; atria spindle-shaped, erect; copulatory sac absent.

Inanidrilus

(p. 80, Table 3)



- B) Penial setae isomorphic or absent (*O. vacuus*), when present all simple-pointed, straight, with curved tips, not sickle-shaped; atria comma-shaped; copulatory sac present.

Olavius

(p. 99, Table 3)



- 4.(2B) A) Hair setae present. *Tubificoides* (in part)
(p. 210, Table 9)

- B) Hair setae absent. 5.

- 5.(4B) A) Modified genital setae present in XI or X and XI. 6.

- B) Modified genital setae absent or only present in X. 10.

- 6.(5A) A) Modified spermathecal setae in X absent; penial setae in XI include one large spoon-shaped seta and 4-8 smaller, apically hooked setae per bundle. *Adelodrilus magnitheatus*
(p. 72)



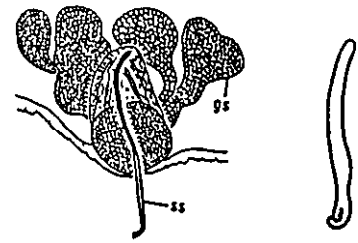
- B) Modified spermathecal setae in X may be present; all penial setae in XI relatively uniform in size. 7.

- 7.(6B) A) Modified spermathecal setae present; modified penial setae also present. 8.

- B) Modified spermathecal setae absent; modified penial setae present. 9.

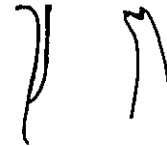
- 8.(7A) A) Spermathecal setae slender, fork-shaped, 1-2 per bundle in X; penial setae in XI, always one per "bundle", slightly sigmoid, simple-pointed, somewhat spoon-shaped.

Milliganius sabulosus
(p. 46)



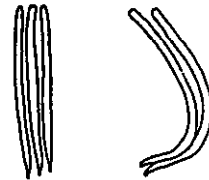
- B) Spermathecal setae simple-pointed, strongly curved entally, 1(2) per bundle; penial setae somewhat curved with chisel-like bifid tips with fine pectinations, 3-4 per bundle.

Bathydrilus notabilis
(p. 126, Table 4)



- 9.(7B) A) Modified penial setae 2-4 per bundle, straight or slightly curved, ectally not hooked or club-shaped (see note for *Pectinodrilus* below).

Pectinodrilus, *Bathydrilus*
(p. 38, 114, Table 4)



- B) Modified penial setae generally 6-25 per bundle usually with strongly hooked or club-shaped ectal tips (*Pectinodrilus* usually has only 4-8 penial setae per bundle which are not ectally hooked).

Coralliodrilus, *Peosidrilus*, *Peosidriloides*, *Bermudrilus*
(p. 31, 53, 63, 67, Table 2)



- 10.(5B) A) Grooved or spoon-shaped spermathecal setae present in X. *Limnodriloides* (in part)

(p. 156, Table 7)



- B) Modified genital setae absent in X and XI.

11.

- 11.(10B) A) Posterior setae with very prolonged (not recurved) lower tooth and needle-like upper tooth; male and spermathecal pores unpaired in XI and IX, respectively.

Uniporodrilus purus
(p. 50)



- B) Posterior setae without prolonged lower tooth, although upper tooth may be reduced or absent. 12.

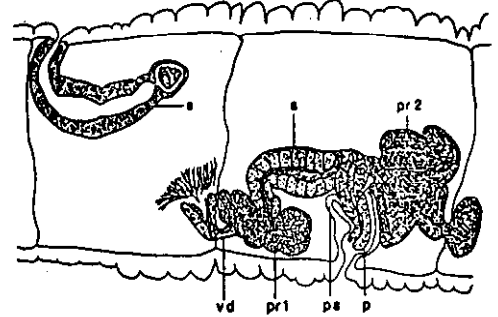
- 12.(11B) A) Cuticular penis sheaths present (except for aberrant *Tubificoides inops*, which is papillated posteriorly and has a subdental ligament on anterior setae); body may be inflated anteriorly, and posterior segments thinner and elongate (*Tubificoides*); body wall papillae present or absent. 13.



- B) Cuticular penis sheaths absent; body not distinctly inflated anteriorly; papillae absent or relatively inconspicuous (see *Duridrilus*, p. 111) (except in *Tectidrilus squalidus* and *T. gabriellae* which have large, leaf-like papillae and are externally indistinguishable from *Tubificoides wasselli*; see remarks for the aforementioned species). 14.

- 13.(12A) A) Very small meiobenthic worms, not inflated anteriorly; no body wall papillae; 3-4 setae per bundle posteriorly; spermatheca unpaired, middorsal in X.

Aktedrilus floridensis
(p. 76)

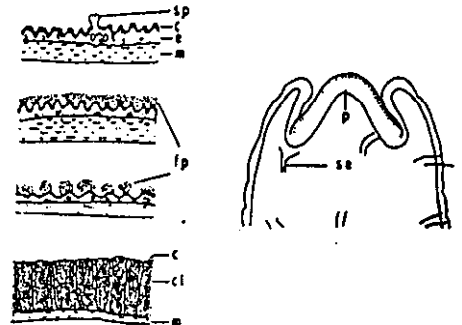


- B) Larger worms, usually distinctly inflated anteriorly; papillations present or absent; one or two setae per bundle posteriorly; spermathecal pores paired ventrally in X.

Tubificoides (in part)
(p. 208, Table 9)

- 14.(12B) A) Cuticle very distinctive, appearing dusted with adherent fine particles and may have scattered papillae; cuticle finely annulated giving it a wavy appearance; prostomium retractable; gut not modified in IX.

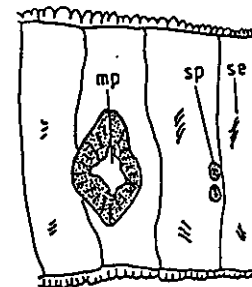
Duridrilus tardus
(p. 111)



- B) Cuticle naked (or heavily papillated in *Tectidrilus squalidus* and *T. gabriellae*), without fine annulations; prostomium not retractable (except *Tectidrilus*). 15.

- 15.(14B) A) Body relatively short and stout, usually comma-shaped when fixed; coelomocytes large, abundant; a large mid-ventral unpaired bursa in XI; gut not modified in IX.

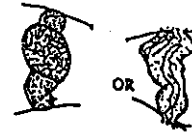
Monopylephorus
(p. 22)



- B) Body shape variable; coelomocytes absent or sparse; not of the rhyacodriline type; gut modified or unmodified in IX. 16.

16.(15B) A) Gut modified in IX.

Limnodriloidinae 17.
(p. 128, Table 5)



B) Gut not modified in IX: unidentifiable immature Tubificidae without hair setae, further identification not possible.

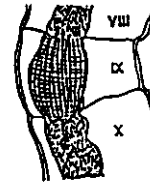
17.(16A) A) A pair of anteriorly directed esophageal diverticula in IX.

Tectidrilus, *Limnodriloides* (in part), *Smithsonidrilus*
18.



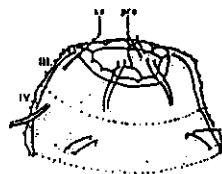
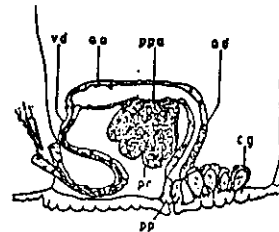
B) Esophagus enlarged in IX, diverticula absent.

Thalassodrilides, *Parakaketio*, *Limnodriloides* (in part)
(p. 131, 145, 156, Tables 5, 6, 7)



18.(17A) A) Body heavily papillate or 4-6 copulatory glands present immediately posterior to male pore; two setae per bundle anteriorly, one seta per "bundle" posteriorly; prostomium generally retractable.

Tectidrilus
(p. 1148)



B) Body not papillate, copulatory glands absent; at least 2-3 setae per bundle anteriorly, usually more than one seta per bundle posteriorly.

Limnodriloides (in part), *Smithsonidrilus*
(p. 156, 186, Table 5)

INTRODUCTION

Identification Manual for the Estuarine and Near Shore Marine Oligochaetes Of Florida, Volume II pertains to the marine and estuarine Tubificidae which have either been collected from coastal Florida waters (less than about 30 meters depth) or reported from more than one isolated location in the Caribbean. Most of the taxa described from the Caribbean may be expected to be found in southern Florida, particularly the reef areas of the Florida Keys. Generally, if a taxon has been reported only from a single location in the Caribbean or Bermuda, that species was excluded. This includes approximately 40 species: four species of *Heterodrilus*, two *Smithsonidrilus*, and the remainder within several genera of Phallodrilinae. An addendum to Volume II describing all species from the Caribbean and incorporating them into the taxonomic keys herein is anticipated.

Seventy-nine species are described in this volume. All but three taxa have been described since 1970. The lack of distinctive discriminating somatic characteristics is primarily responsible for the assumed taxonomic homogeneity of marine oligochaetes. However, within the last two decades, extensive scrutiny of oligochaete reproductive systems, primarily by Dr. C. Erséus, Sweden, has provided the resources for species discrimination. As a result, the distinctions between taxa rely primarily on the variation of size and morphology of the male efferent structures, copulatory apparatuses, and spermathecae. Consequently, the diagnoses contained herein are more extensive than the freshwater counterpart. For the novice oligochaete taxonomist versed in freshwater taxa, which rely primarily on setal or cuticular examination for species discrimination, intensive examination of the internal structures may seem somewhat daunting. However, analysis of whole communities and various populations comprising each community facilitates accurate identification and allows for the association of relatively nondescript external characteristics, such as general body shape, prostomial morphology, and subtle setal variations, enabling species discrimination even for immature specimens.

The author strongly suggests first time users of this volume to take some time to become familiar with the illustrations of the various taxa. "A picture is worth a thousand words". Relying on that principle, the author has incorporated all available published figures for each taxon. This provides insights into intraspecific geographic variation as well as a different perspective in the artistic interpretation by various authors. Of paramount importance to experience the consummate joy of taxonomic fulfillment is patience: before you begin... put your mind at ease.

Subfamily. Rhyacodrilinae Hrabe, 1963

Type Genus. *Rhyacodrilus* Bretscher, 1901

Diagnosis. Freshwater and estuarine taxa. Coelomocytes abundant (not as dense in *Heterodrilus*). Somatic setae include simple-pointed, bifid, trifid and pectinate crotchets and straight or twisted hairs. Genital setae often present in XI as modified penial setae. Spermathecal pore(s) located near septum at anterior of spermathecal segment. Esophagus in IX, not modified. Ciliated vas deferens long or short entering atrium apically or subapically. Atrium highly variable ciliated. Prostate gland diffusely attached to atrium, not pedunculate, or absent. Protrusible pseudopenes often present, true penes rarely present. Sperm random in spermatheca, not arranged in bundles or as spermatzeugmata; spermathecae may be absent and spermatophores attached externally.

Remarks. The primary distinguishing characters of this subfamily as set forth by Hrabe (1963) are the diffuse prostate glands, spermatzeugmata absent, and abundant coelomocytes. Erséus (1981a) defined the subfamily based on Brinkhurst and Jamieson (1971) to include the genera comprising the *Heterodrilus* and *Macquaridrilus* complexes (see Erséus, 1981a, for a complete discussion). Erséus (1992a) provided the most current discussion of Rhyacodriinae and its relationship with Phallodrilinae. He separated the marine Rhyacodrilinae into two unresolved groups: 1) *Ainudrilus* Finogenova, 1982, and *Paupidrilus* Erséus, 1990c, lacking prostate glands, and 2) *Heterodrilus*, *Heronidrilus* Erséus and Jamieson, 1981, and *Monopylephorus*, having long cylindrical atria. The latter group may be included as a separate taxon. Two genera are fairly common in the nearshore and estuaries of Florida. *Monopylephorus* is represented by two species which are exclusively estuarine, and *Heterodrilus* is represented by at least eight shallow water marine taxa which live in sandy habitats.

Genus. *Heterodrilus* Pierantoni, 1902

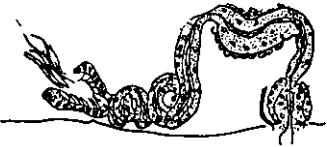
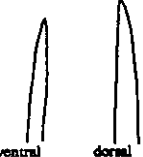
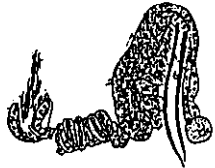
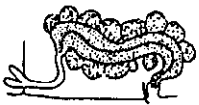
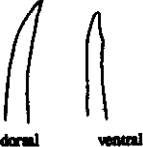
Type Species. *Heterodrilus arenicolus* Pierantoni, 1902.

Diagnosis. (Based on Erséus, 1990a) Tropical or subtropical marine tubificids. Body wall naked. Hair setae absent. At least some anterior setae trifid (third tooth secondarily lost in some species). Posterior setae bifid or simple-pointed. Setae two per bundle in most segments anterior to clitellum, only one seta representing each bundle posterior to clitellum, often large and stout. Penial setae generally present in XI: usually two per bundle, simple-pointed, and relatively straight and stout. Spermathecal setae absent. Male and spermathecal pores paired or unpaired in XI (occasionally in another segment) and X [two pairs in one species, *H. quadrithecatus* (Erséus, 1981a): a normal pair in XII and a rudimentary pair in XI], respectively. Granulated round coelomocytes, generally abundant. Pharyngeal glands present in IV-V, frequently extending into VI. Male genitalia paired in XI (occasionally in another segment): vas deferens ciliated short or long, may be coiled into a tight spiral. Atrium cylindrical, tubular, relatively long in some species: lobed prostate glands broadly attached along most of its length [absent, secondarily lost (?) in some species]; ciliated in all but two species [*H. ersei* (Giere, 1979) and *H. inermis* (Erséus, 1981a)]. Ejaculatory duct absent. Protrusible pseudopenes, without cuticularized lining, present in most species, true pendent penes rare. Spermathecae paired or unpaired: differentiated into an ectal narrow duct and ental sacciform sperm-bearing ampulla. Sperm arranged in loose or compact masses or bundles, often with characteristic granules or secretions.

Remarks. The current definition was revised by Erséus (1990a) to encompass all species with trifid setae (or modified such setae). As such, *Heterodriloides* Erséus, 1981a, and *Giereidrilus* Erséus, 1981a, are now considered junior synonyms of *Heterodrilus*. The bisetal anterior and unisetal posterior bundles, the stout simple-pointed penial setae and tubular atrium with a lobed prostate attached to most of its length are also significant unifying criteria of this genus (as always, there are exceptions).

This genus is a very large, exclusively marine taxon, currently comprised of about 30 species. Although only eight species are included herein, at least four additional species reported from the Caribbean may eventually be recovered, particularly in the subtropical coralline sands associated with the Florida Keys: *H. quadrithecatus*, *H. ersei*, *H. rarus* Erséus, 1990a, and *H. modestus* Erséus, 1990a.

Table 1. Species of *Heterodrilus*.

<i>Heterodrilus</i>	Anterior Setae	Posterior Setae	Male Genitalia
<i>bulbiporus</i>			
<i>flexuosus</i>			
<i>hispidus</i>			
<i>minisetosus</i>			
<i>occidentalis</i>			
<i>paucifascis</i>			
<i>percheffi</i>			
<i>perkinsi</i>			

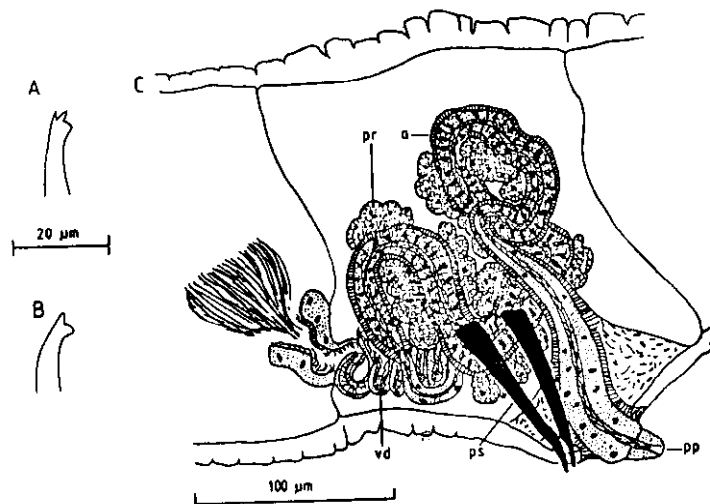
***Heterodrilus bulbiporus* Erséus, 1981**

Heterodrilus bulbiporus Erséus, 1981a:123, Fig. 13.

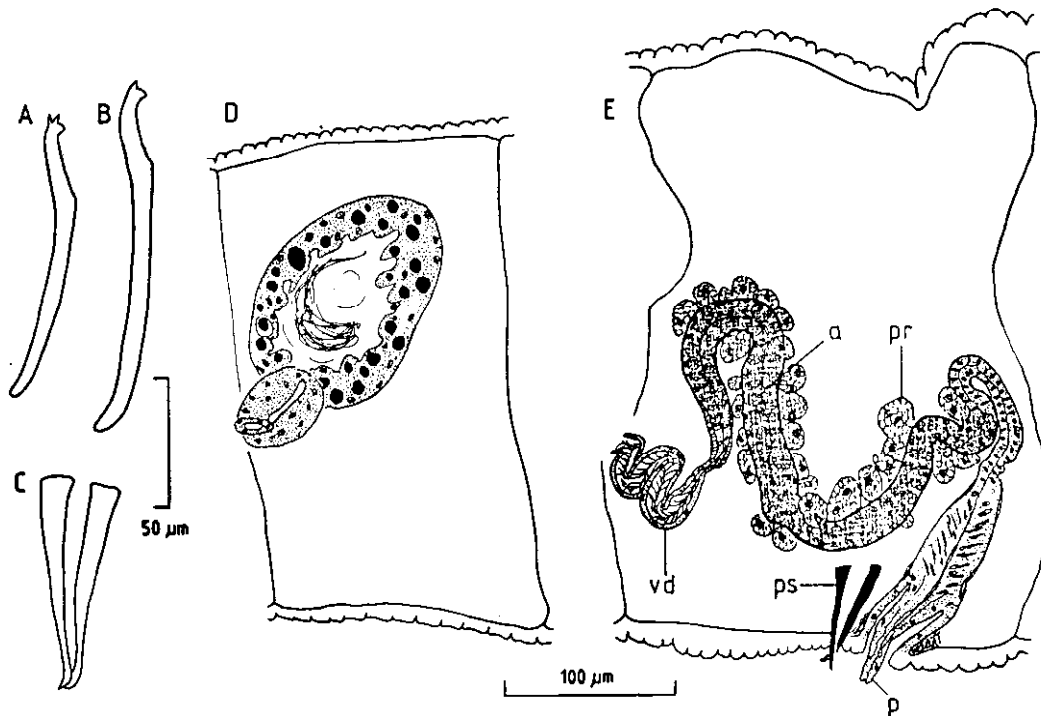
Diagnosis. Length: 5.0-12.0 mm; segments: 38-65. Clitellum extending over $\frac{1}{2}$ X-XII. Anterior setae in II-IX trifid with upper and middle teeth pointed and basally narrow. Lower tooth basally much wider, 40-125 μ m long, two per bundle. Posterior setae from X bifid with upper tooth slightly thinner than lower, both teeth basally wide, 50-140 μ m long, one per "bundle". Penial setae simple-pointed, expanded entally, 80-125 μ m long, 12-13 μ m wide basally. Male and spermathecal pores paired posteriorly in XI, and anteriorly in X, respectively. Granulated coelomocytes abundant. Male genitalia paired: vas deferens long and tightly coiled in a spiral, 7-21 μ m wide. Atrium cylindrical, slender, very long with thick muscular outer layer and granulated inner epithelium, 0.4-1.0 mm long, 18-40 μ m wide; ectal portion narrower, non-granulated; terminating in a bulbous copulatory apparatus. Prostate glands multilobed, attached along most of the length of atrium. Copulatory organ produced as a narrow, tapering, pendant penis (eversible?) enclosed in a copulatory sac. Spermathecae paired, each with a short, broad duct and large, oval, thick-walled ampulla with large bundles of sperm.

Distribution and Habitat. North America (east and west coasts of Florida, North Carolina, New Jersey), Bermuda. Associated with subtidal sands to at least 130 m depth.

Remarks. This species is distinguished from all other *Heterodrilus* by the "proper pendant penis". *Heterodrilus perkinsi* also has well-developed penes, but its vas deferens is much shorter and uncoiled, atria much longer, and penial setae more slender and not expanded basally. *Heterodrilus minisetosus* also has true penes, but are much smaller and less developed than those of *H. bulbiporus*. The morphology of the anterior somatic and penial setae of *H. bulbiporus* is similar to *H. pentcheffi* with which it frequently coexists. These species may be separated based on the configuration of the posterior setae. The lower tooth of the posterior setae of *H. bulbiporus* is fairly well developed, whereas it is very reduced in *H. pentcheffi*.



(from Erőss, 1981a) *Heterodrilus bulbiporus*: A, anterior seta; B, posterior seta; C, lateral view of male duct in segment XI.



(from Erőss, 1986a) *Heterodrilus bulbiporus*: A, anterior trifid seta; B, posterior seta; C, penial seta; D, spermatheca in X; E, lateral view of male genitalia in XI.

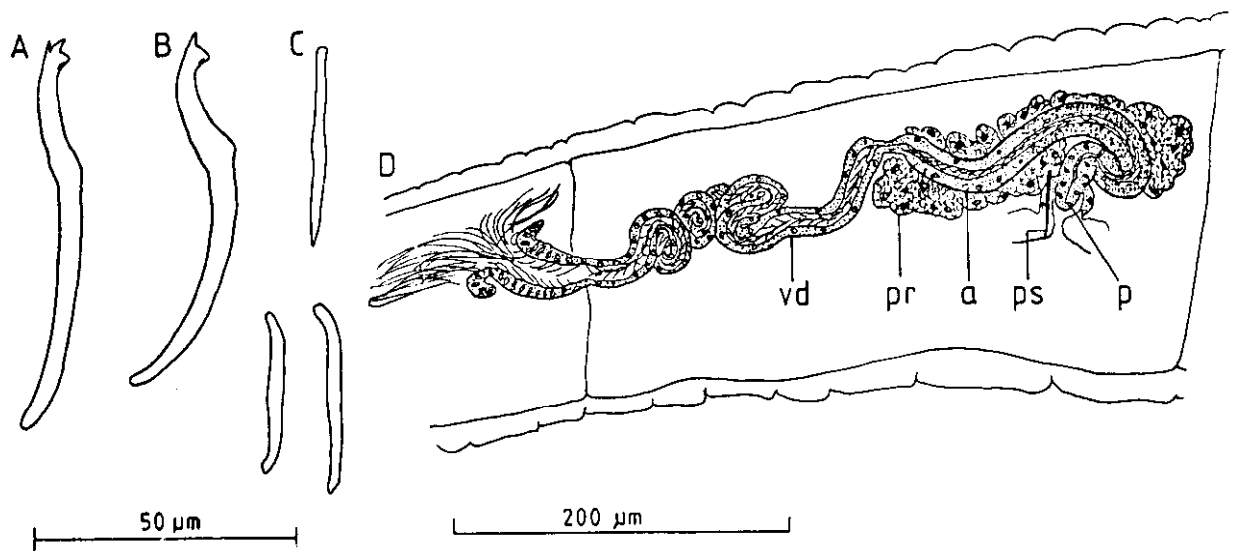
***Heterodrilus flexuosus* Erséus, 1990**

Heterodrilus flexuosus Erséus, 1990a:251-253, Fig. 5A-5D.

Diagnosis. Length: 6.0-9.7 mm; segments: 44-65. Clitellum extending over $\frac{1}{2}$ X-XII. Anterior setae in II-(XI)X(XI) trifold, subdental ligament connecting lower tooth and shaft present, 50-80 μ m long, two per bundle. Posterior setae from about XII bifid with widely diverging broad teeth with subdental ligament, 40-75 μ m long, one per bundle. Penial setae simple-pointed, straight or very slightly curved, not expanded entally, 30-45 μ m long, 2.5-3.5 μ m wide basally, 1(2) per bundle. Male pores paired in posterior in XI. Spermathecal pores absent. Granulated coelomocytes round, abundant. Male genitalia paired: vas deferens much longer than atrium and tightly coiled, 8-19 μ m wide. Atrium cylindrical generally smoothly curved, with thin muscular outer layer, granulated ectally, 140-225 μ m long, 19-23 μ m wide, ectal portion terminating in small, but distinct, penial papilla inside small copulatory sac. Prostate gland multi-lobed, attached to most of the length of the atrium. Copulatory organ produced as a small broad penis. Spermathecae absent.

Distribution and Habitat. Caribbean (Belize), southeast North America (southern Florida Keys). Associated with coarse sands; subtidal to at least 24 m depth.

Remarks. The absence of spermathecae and presence of a subdental ligament distinguishes this species from all other *Heterodrilus* in Florida. This species is uncommon, but immature specimens of *Heterodrilus* collected from off Miami have tentatively been assigned to this species.



(after Erős, 1990a) *Heterodrilus flexuosus*. A, anterior somatic seta; B, posterior somatic seta; C, penial setae of three different specimens; D, lateral view of male genitalia in segment XI.

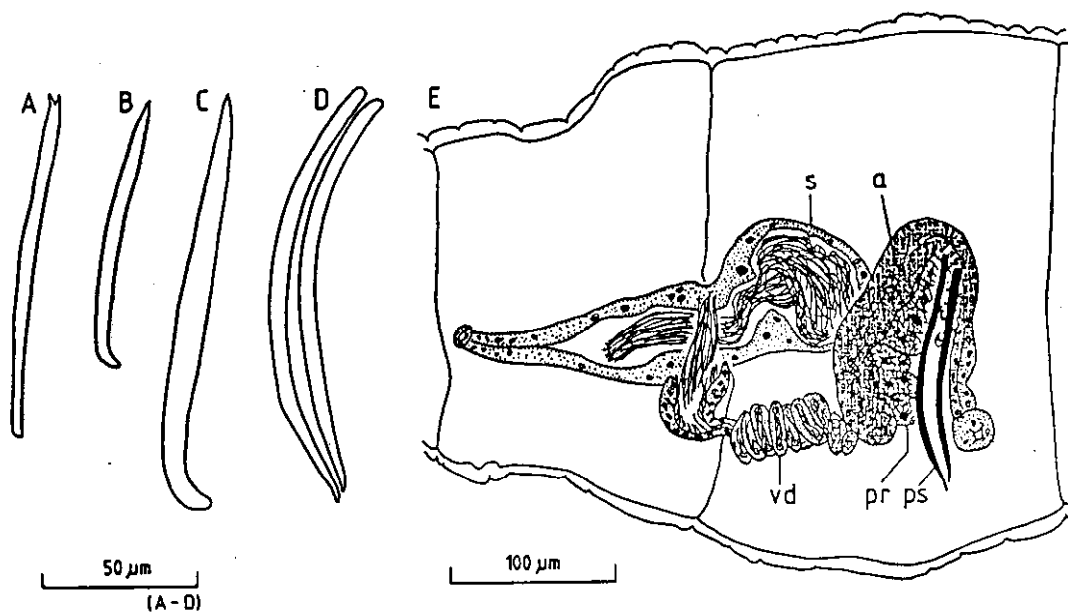
***Heterodrilus hispidus* Erséus, 1986**

Heterodrilus hispidus Erséus, 1986a:291-292, Fig. 2.

Diagnosis. Length: 13.6-13.8 mm; segments: 82-86. Clitellum extending over $\frac{1}{2}$ X-XII. Anterior setae in II-IX bifid with teeth of approximately same length and both oriented along long axis of setae, 60-100 μ m long, two per bundle. Posterior setae from X stout, sharply simple-pointed with curved inner end, one per bundle; dorsal setae much larger (95-135 μ m long) than ventrals (60-95 μ m long). Penial setae simple-pointed, slender, and slightly curved with inner ends generally somewhat tilted over to posterior, 125-135 μ m long, 4.5-5.0 μ m wide medially and basally, two per bundle. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Granulated coelomocytes abundant. Male genitalia paired: vas deferens very long and tightly coiled in a spiral, 9-12 μ m wide. Atrium somewhat C-shaped with thin outer layer, densely granulated, about 300 μ m long, 25-35 μ m wide; ectal portion non-granulated, narrow, terminating in a very simple pseudopenis (?) or simply exiting to the exterior through a simple pore. Prostate glands broadly attaches to ventral surface of atrium. Spermathecae paired, each with slender duct and large ampulla. Sperm in a random mass.

Distribution and Habitat. Southeast North America (east coast of Florida). Associated with shell hash; 10-12 m depth.

Remarks. This species is characterized by the large simple-pointed posterior dorsal and slightly smaller posterior ventral ones. No other species of *Heterodrilus* in Florida has anterior bifids (with secondarily reduced third tooth) and paired slender penial setae.



(after Erséus, 1986a) *Heterodrilus hispidus*: A, anterior bifid seta; B, posterior ventral seta; C, posterior dorsal seta; D, penial seta; E, lateral view of spermatheca and male genitalia in segments X-XI.

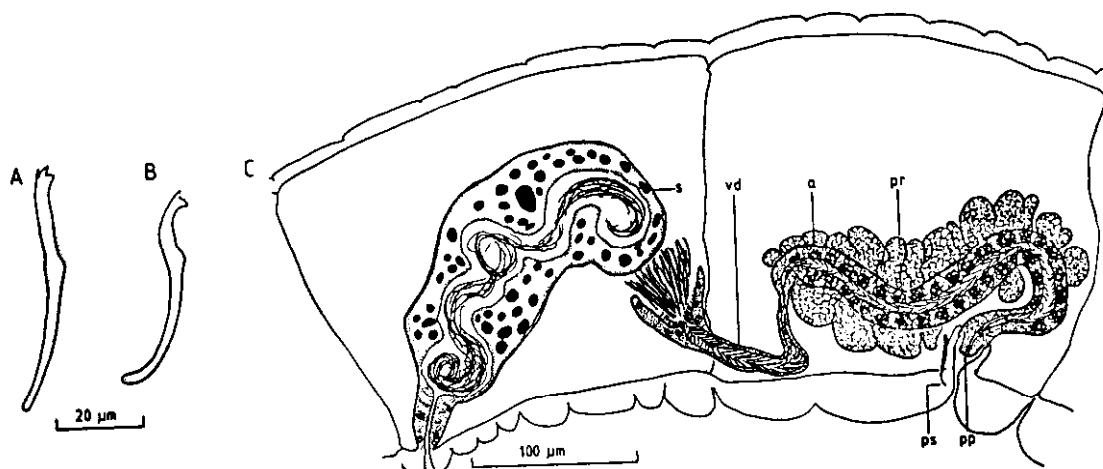
***Heterodrilus minisetosus* Erséus, 1981**

Heterodrilus minisetosus Erséus, 1981a:113-114, Fig. 2.

Diagnosis. Length: 3.8-15.8 mm; segments: 43-111. Clitellum extending over $\frac{1}{2}$ X-XII. Anterior setae in II-IX (X-XV) trifid with upper tooth much thinner and shorter than middle and lower teeth, 45-100 μ m long, two per bundle. Posterior setae from about X bifid with the upper tooth short and thin, lower tooth very broad, 40-85 μ m long, one per bundle. Penial setae frequently absent, when present minute, straight, slightly curved ectally, 15-30 μ m long, 1.5-3.5 μ m wide basally. Male and spermathecal pores paired in XI and anteriorly in X, respectively. Male genitalia paired: vas deferens shorter than atrium, not coiled, 9-14 μ m wide. Atrium more or less M-shaped with slender outer muscular layer, and thicker inner epithelium containing large aggregates of secretion, 160-370 μ m long, 18-35 μ m wide; ectal and ental portions narrow, terminating ectally in small true penis. Prostate glands broadly attached to most of the length of the atrium. Spermathecae paired, each with very short, distinct duct and sacciform ampulla with thick irregular wall containing large granules of secretion. Sperm arranged in long loose bundles.

Distribution and Habitat. Bermuda, Caribbean (Bahamas), east coast of North America (North Carolina, Virginia, east and west coasts of Florida). Associated with muddy, fine sand, medium and coarse coral and shell sand, from barely subtidal to about 33 m depth.

Remarks. Only one other species, *Heterodrilus perkinsi*, included herein has an uncoiled vas deferens. Both species have similar somatic setae, however, in *H. perkinsi* penial setae are usually present and much longer, additionally, it has shorter, wider vas deferentia, much longer atria and well-developed penes. The spermathecal ducts in the latter species are also much longer and the spermathecal ampulla have thinner walls and are smaller.



(after Erasmus, 1981a) *Heterodrilus minisetosus*: A, anterior seta; B, posterior seta; C, lateral view of spermatheca and male duct in segments X-XI.

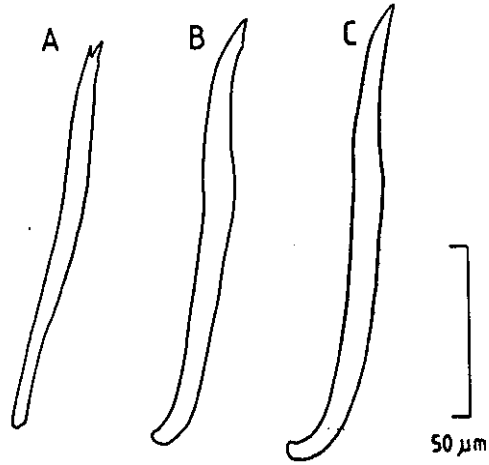
***Heterodrilus occidentalis* Erséus, 1981**

Heterodrilus occidentalis Erséus, 1981a:121, Fig. 11.

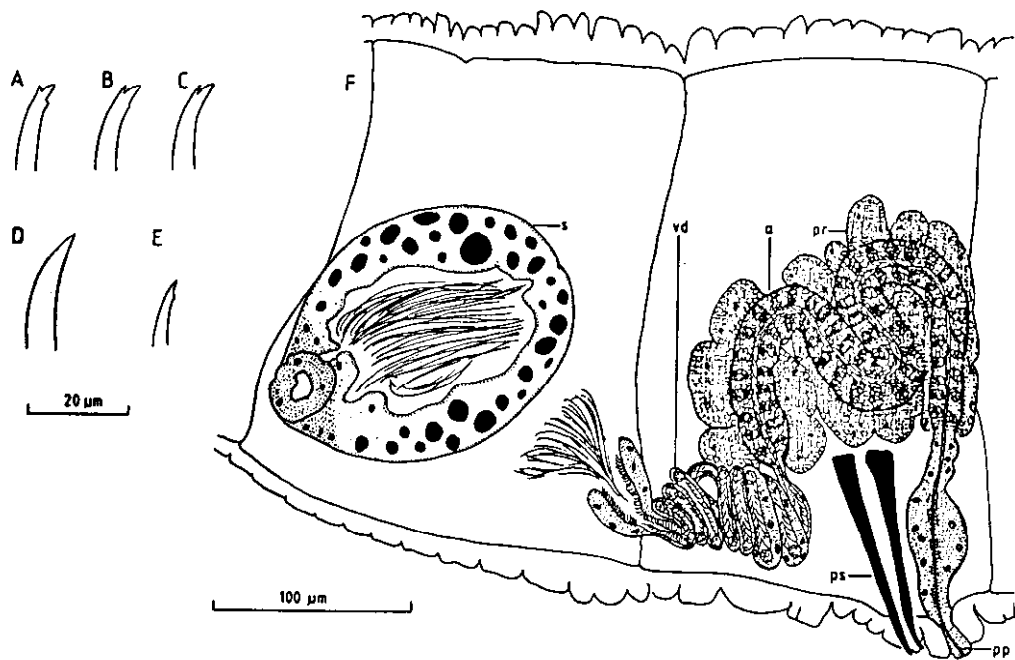
Diagnosis. Length: 5.4-8.1 mm; segments: 60-62. Clitellum extending over $\frac{1}{2}$ X-XII. Anterior setae trifold with middle tooth much larger than the other two, lower tooth gradually diminishing in size to about VIII or IX and is absent in setae thereafter, 50-115 μ m long, two per bundle to IX; simple-pointed setae from about X, but may appear slightly bifid with a faint lower tooth when viewed at certain angles, 125 μ m long, one per bundle from X. Penial setae straight, simple-pointed and erect, expanded entally, 105-115 μ m long, 18 μ m wide basally, two per bundle. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Male genitalia paired: vas deferens very long and tightly coiled in a spiral, narrowing with thinner wall entally, 9-18 μ m wide. Atrium very long and slender, more or less M-shaped with thin outer muscular layer and densely granulated inner epithelium, 395-585 μ m long, 18-32 μ m wide, narrowing ectally, terminating in a wider bulbous portion with a small, terminal pseudopenis. Prostate glands multi-lobed, broadly attached to most of the length of the atrium. Spermathecae paired, each with an indistinct duct and large oval ampulla with thick wall containing large granules of secretion. Sperm arranged in a large bundle.

Distribution and Habitat. East coast of North America (east coast of Florida, North Carolina, New Jersey, Massachusetts). Associated with coarse sand and gravel; subtidally from 4.5-138 m depth.

Remarks. This species is distinguished from other species of *Heterodrilus* in Florida waters by the setal morphology: trifold setae present in anterior most segments and generally simple-pointed or slightly bifid posteriorly. The setae are similar in *H. paucifascis*, but in the latter the atrium is not M-shaped; anterior setae not trifold, and the posterior ventrals are much smaller than the respective dorsals.



(after Erasmus, 1986a) *Heterodrilus occidentalis*, setae: A, from segment VIII; B, from segment XII; C, from posterior segment.



(after Erasmus, 1981a) *Heterodrilus occidentalis*: A, seta from segment IV; B, seta from segment VI; C, seta from segment VIII; D, seta from postclitellar segment; E, seta from posterior end of worm; F, lateral view of spermatheca and male duct in segments X-XI.

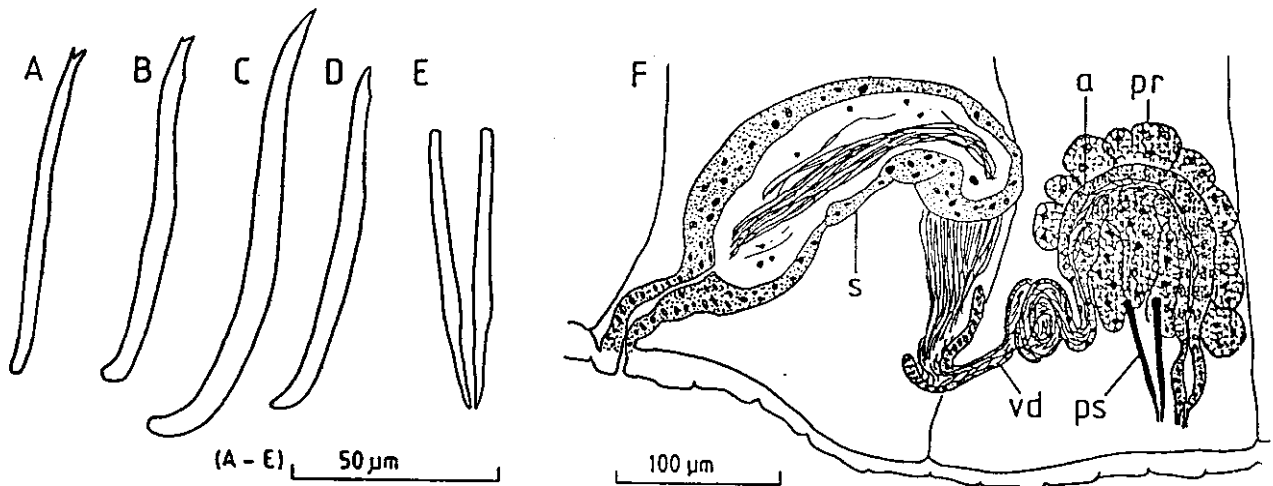
***Heterodrilus paucifascis* Milligan, 1987**

Heterodrilus paucifascis Milligan, 1987:481-482, Fig. 1.

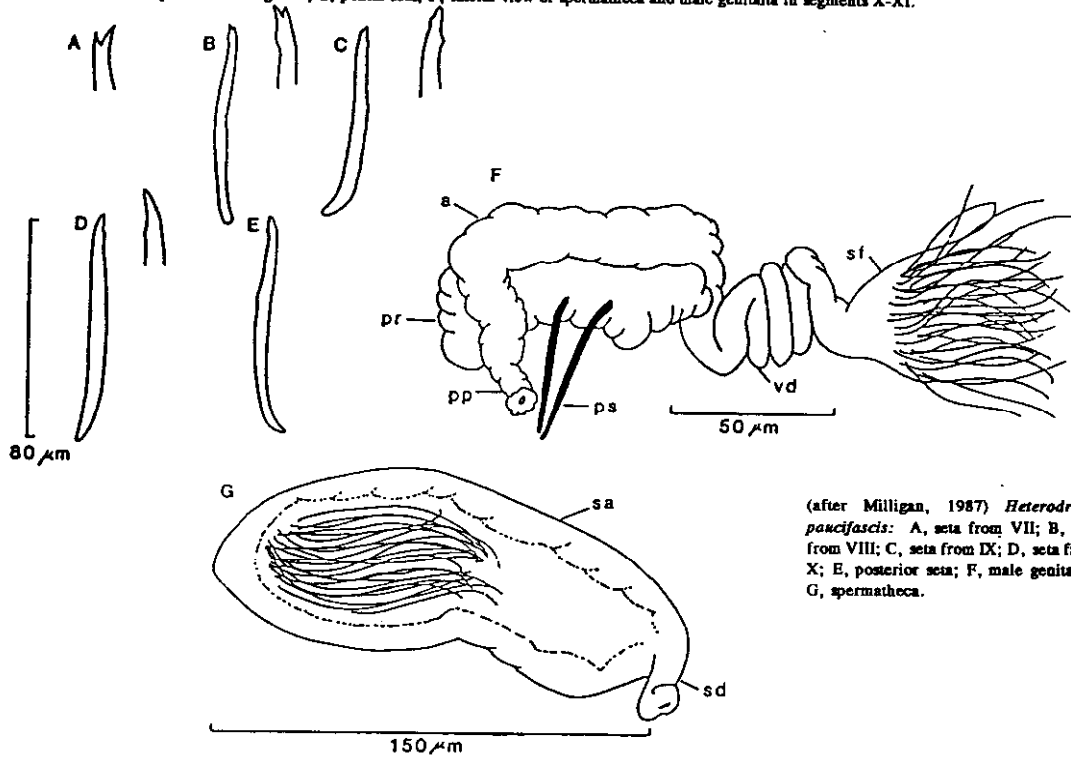
Diagnosis. Length: 3.3-12.3 mm; segments: 56-80. Clitellum extending $\frac{1}{2}$ X-XII. Setae of II-(VIII)IX bifid with upper tooth slightly thinner and shorter than lower, teeth somewhat diverging, 40-105 μm long, two per bundle, one per bundle thereafter. Setae of X-XII following segments with indistinct third tooth (actually more of a swelling than a tooth), developing subdistally and with upper tooth very reduced or rudimentary. Posterior setae simple-pointed or with a very slight swelling representing the lower tooth, usually absent in dorsal setae; posterior dorsal setae distinctly larger (82-115 μm long and 4-7 μm thick) than ventrals (up to 75 μm long and 4-4.5 μm thick). Penial setae simple-pointed and erect, 43-85 μm long, 3-4 μm wide, two per bundle. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Granulated round coelomocytes abundant. Male genitalia paired: vas deferens longer than atrium and tightly coiled, 10-17 μm wide. Atrium cylindrical, C-shaped with thin outer muscular layer and granulated inner epithelium, 135-260 μm long, 20-32 μm wide; ectal part with a bulbous swelling, opening to exterior through a small, simple pore; penial apparatus absent. Prostate glands lobed, broadly attached to most of the length of the atrium. Spermathecae paired, each with short to medium length duct and large, elongate ampulla. Sperm arranged in random masses or a large bundle.

Distribution and Habitat. Caribbean (Belize, Jamaica, Puerto Rico), southeast North America (southeastern Florida). Associated with medium to coarse sand; subtidally to at least 39 m depth.

Remarks. The complete absence of any penial apparatus differentiates *H. paucifascis* from other Florida species. The setal morphology of this species is similar to *H. occidentalis* and *H. hispidus*, also reported from Florida and *H. jamiesoni* Erséus, 1981a, from the South Pacific. It differs from the former by having bifid setae anteriorly, larger dorsal setae than ventrals posteriorly and has a C-shaped, instead of M-shaped, atrium. *Heterodrilus hispidus* also has larger dorsals posteriorly, but lacks trifold setae anteriorly. *Heterodrilus paucifascis* was reexamined and compared to *H. jamiesoni* by Erséus (1990a), who concluded that 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" *H. jamiesoni*. However, the biogeographical differences may warrant maintaining them as separate taxa until additional populations are studied.



(after Erdős, 1990a) *Heterodrilus paucifascis*: A, somatic seta of segment VIII; B, somatic seta of segment X, C-D, Dorsal (C) and ventral (D) somatic setae of the same postclitellar segment; E, penial seta; F, lateral view of spermatheca and male genitalia in segments X-XI.



(after Milligan, 1987) *Heterodrilus paucifascis*: A, seta from VII; B, seta from VIII; C, seta from IX; D, seta from X; E, posterior seta; F, male genitalia, G, spermatheca.

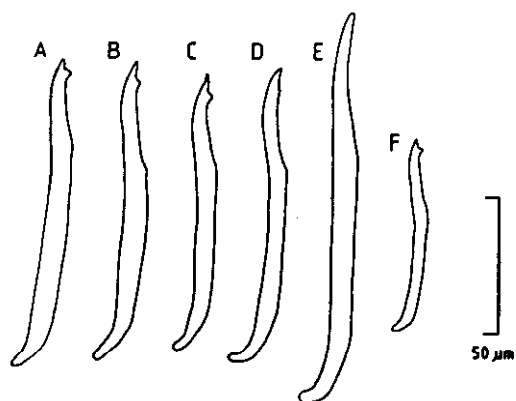
***Heterodrilus pentcheffi* Erséus, 1981**

Heterodrilus pentcheffi Erséus, 1981a:121-123, Fig. 12.

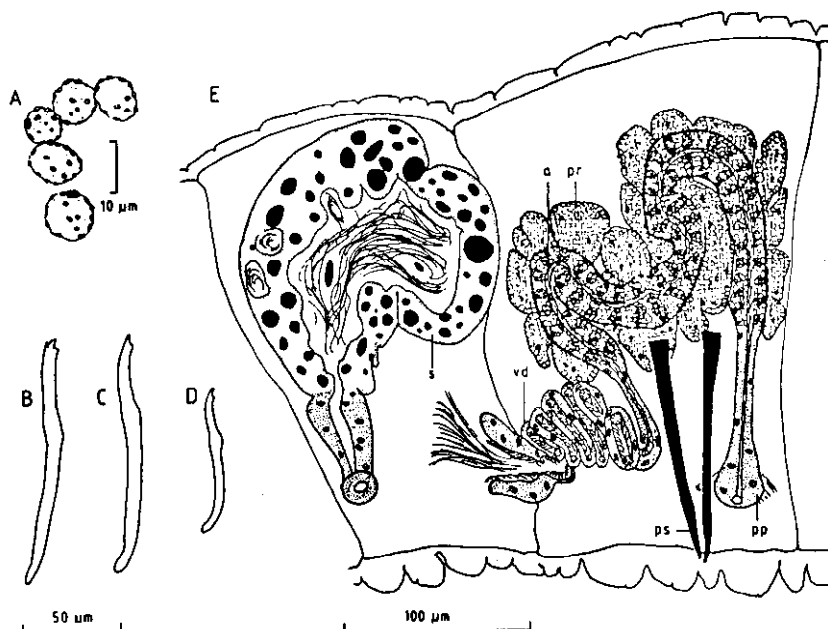
Diagnosis. Length: 4.1-11.3 mm; segments: 43-88. Clitellum extending over $\frac{1}{2}$ X-XII. Setae of II-(VIII)IX(X-XII) trifid with upper tooth thin and short, middle tooth long and basally wide, 55-135 μm long, two per bundle, one per bundle thereafter. Setae bifid in all segments immediately posterior to last segment bearing trifids; lower tooth conspicuous, almost as large as the upper; posteriorly lower tooth generally becomes reduced, so that the setae may appear simple-pointed, 45-145 μm long. At the posterior end, setae becomes smaller and more distinctly bifid, about 45 μm long; dorsal and ventral setae of posterior segments similar. Penial setae simple-pointed, erect, expanded entally, 65-155 μm , 12-14 μm wide basally, 2(3,4) per bundle. Male and spermathecal pores paired in posterior of XI (occasionally in IX, X, XII, or XIII) and anterior of X (occasionally in VIII, IX, XI, or XII), respectively; a small epidermal pad is generally located mid-ventrally between the spermathecal pores. Granulated coelomocytes very abundant. Male genitalia paired: vas deferens very long and tightly coiled in a spiral, narrowing entally, 7-21 μm wide. Atrium very long and slender, generally M-shaped, with slender outer muscular layer and densely granulated inner epithelium, 420-740 μm long, 18-39 μm wide, ectal part tapering considerably before terminating in a small, bulbous pseudopenis. Prostate gland with large lobes broadly attached to most of the length of the atrium. Spermathecae paired, each with narrow, distinct duct and voluminous sacciform ampulla with irregular thick wall containing large granules of secretion. Sperm arranged as large bundles.

Distribution and Habitat. Caribbean (Belize, Panama), east coast of North America (east and west coasts of Florida, North Carolina, New Jersey), Bermuda, Galapagos Islands. Associated with coarse sand; subtidally from 0.5-39 m depth.

Remarks. This species has somatic setae similar to *H. minisetosus*, *H. bulbiporus*, and *H. perkinsi* also common in Florida waters. However, *H. minisetosus* usually lacks penial setae, and, when present, they are very small, the posterior setae are distinctly bifid, and the vas deferens is uncoiled. *Heterodrilus pentcheffi* also differs from *H. bulbiporus* and *H. perkinsi* by the distinctly bifid posterior setae of the latter two. *Heterodrilus pentcheffi* is one of the most common, widespread species of *Heterodrilus* in Florida.



(after Erséus, 1986a) *Heterodrilus pemcheffi*, postclitellar setae: A, from segment immediately posterior to clitellum; B-E, from various segments; F, from posterior end of worm.



(after Erséus, 1981a) *Heterodrilus pemcheffi*: A, coelomocytes; B, anterior seta; C, postclitellar seta; D, seta from most posterior end of worm; E, lateral view of spermatheca and male duct in segments X-XI.

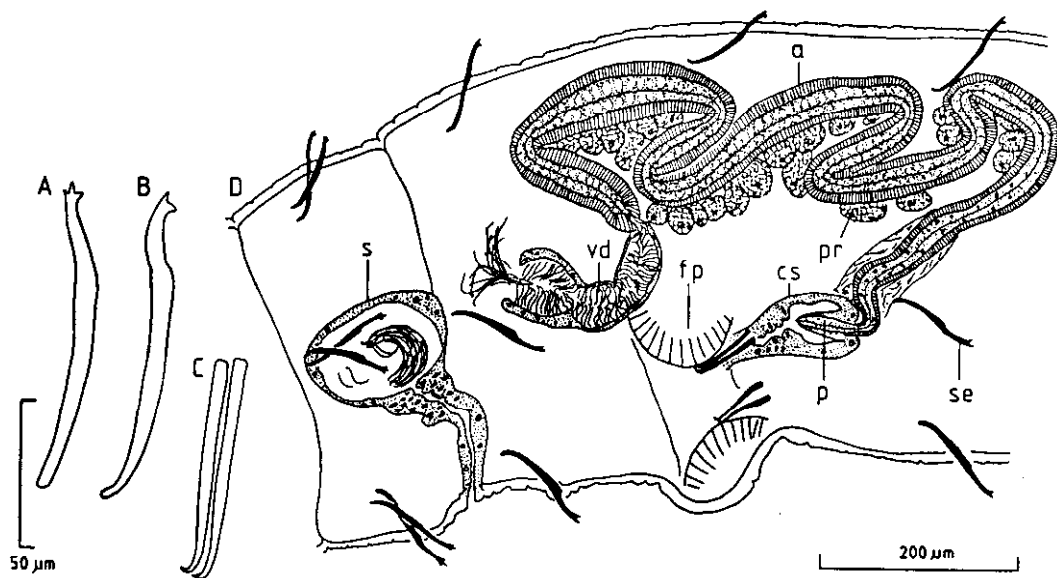
***Heterodrilus perkinsi* Erséus, 1986**

Heterodrilus perkinsi Erséus, 1986a:294-295, Fig. 5.

Diagnosis. Length: (5.7)8.9-11.2 mm; segments: (42)58-72. Clitellum extending over $\frac{1}{2}$ X-XII. Setae of II-(VIII)IX trifold with upper tooth smaller than other two, middle tooth longer than upper and lower teeth, 65-110 μ m long, two per bundle, one per bundle thereafter. Setae from X bifid, with lower tooth slightly larger than upper, both teeth with broad bases, 60-120 μ m long. Penial setae small and straight often retracted into a copulatory sac and inner ends directed obliquely toward posterior; ectal ends simple-pointed and hooked, 60-85 μ m long, 4.5-5.5 μ m wide, (1)2 per bundle. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Male pores located close together in a midventral bursa which is laterally delineated by two flap-like papillae. Granulated coelomocytes present. Male genitalia paired: vas deferens very short and wide with very thin wall, 150-175 μ m long and 34-45 μ m wide, abruptly narrowing at junction of atrium. Atrium very long and slender, somewhat coiled, extending through 2-3 segments, thick outer muscular layer and poorly granulated inner epithelium; 1.4-3.2 mm long and 50-70 μ m wide maximally, ectal part tapering, terminating in a pointed, somewhat conical penis, 45-80 μ m long, 23-37 μ m wide basally. Penis with a thin cuticular lining, located in hollow inner part of deep copulatory sac. Prostate glands scattered along most of the length of the atrium. Spermathecae paired, each with elongate, thick-walled duct and variably shaped ampulla. Sperm arranged in large bundle.

Distribution and Habitat. East coast of North America (east coast of Florida). Associated with shell hash; subtidal, 10-12 m depth.

Remarks. The somatic setae are similar to *H. minisetosus* and *H. bulbiporus*. The penial setae are also small as in *H. minisetosus*. However, the extremely long muscular atrium and very short vas deferens distinguishes this species from all other species of *Heterodrilus*.



(after Erasus, 1986a) *Heterodrilus perkinsi*: A, anterior trifid seta; B, posterior seta (from segment immediately posterior to clitellum); C, penial setae; D, somewhat lateral view of spermatheca and male genitalia in segments X-XII (note that flap-like papillae and penial setae of both sides of worm are shown; the spermatheca and the vas deferens depicted are not from the same side as the atrium in the specimen used).

Genus. *Monopylephorus* Levinsen, 1884

Type Species. *Monopylephorus rubroniveus* Levinsen, 1884.

Diagnosis. (Based on Baker and Brinkhurst, 1981) Marine or brackish water tubificids. Somatic setae include simple-pointed and bifid crotchets, and hair setae (when present, thin, spirally twisted). Modified genital setae rare. Male and spermathecal pores single or paired in XI and near septum of anterior of spermathecal segment, respectively. Coelomocytes abundant. Male genitalia paired: vas deferens rudimentary or absent entering atrium apically. Atrium narrow, tubular, leading to short ejaculatory duct. Prostate gland diffuse, covering almost entire length of atrium. Eversible or protrusible pseudopenes present. Spermathecae single or paired with narrow or bulbous ducts and enlarged ampullae. Sperm in loose masses, sperm heads may be attached to walls of ampulla in some species.

Remarks. The current definition was revised by Baker and Brinkhurst (1981) consequently reclassifying a number of species formerly included in *Monopylephorus*. This genus now consists of a cohesive group containing: 1) *Monopylephorus rubroniveus* complex; lacking hair setae and having a large median copulatory bursa, and including two additional taxa [*M. limosus* (Hatai, 1898) and *M. kermadecensis* (Benham, 1915)] not reported from North America; 2) *M. parvus*, a species with one spermatheca; 3) *M. evertus* Baker and Brinkhurst, 1981, a species similar to *M. parvus*, but with two spermathecae and very large eversion pseudopenes, unlike the *M. rubroniveus* complex, and 4) the *M. irroratus* (Verrill, 1873) complex characterized by thin, spirally-twisted hair setae.

Only *M. rubroniveus* and *M. parvus* occur in Florida and are frequently found coexisting in brackish water mesohaline habitats. They are frequently abundant in saltmarshes.

Key to Species of *Monopylephorus*

1. A) Ventral setae of VII, VIII, IX, and XII usually modified; these setae much larger with upper tooth much longer than lower; posterior setae may be simple-pointed; only one spermatheca present. *M. parvus*
- B) All anterior setae more or less similar; spermathecae paired. *M. rubroniveus*

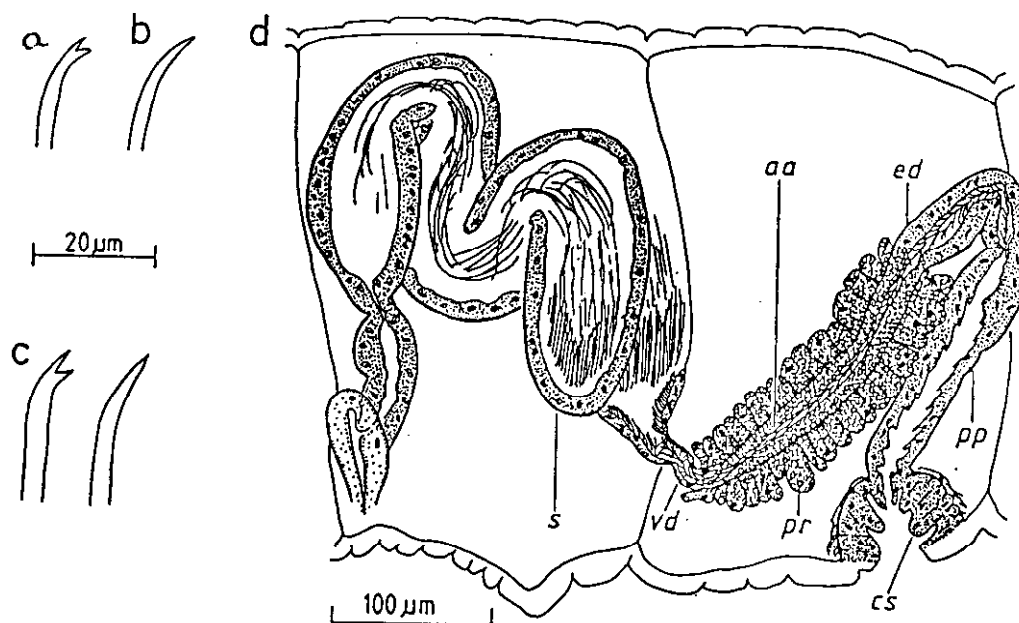
***Monopylephorus parvus* Ditlevsen, 1904**

Monopylephorus parvus Ditlevsen, 1904:427-428, Fig. 25-26.

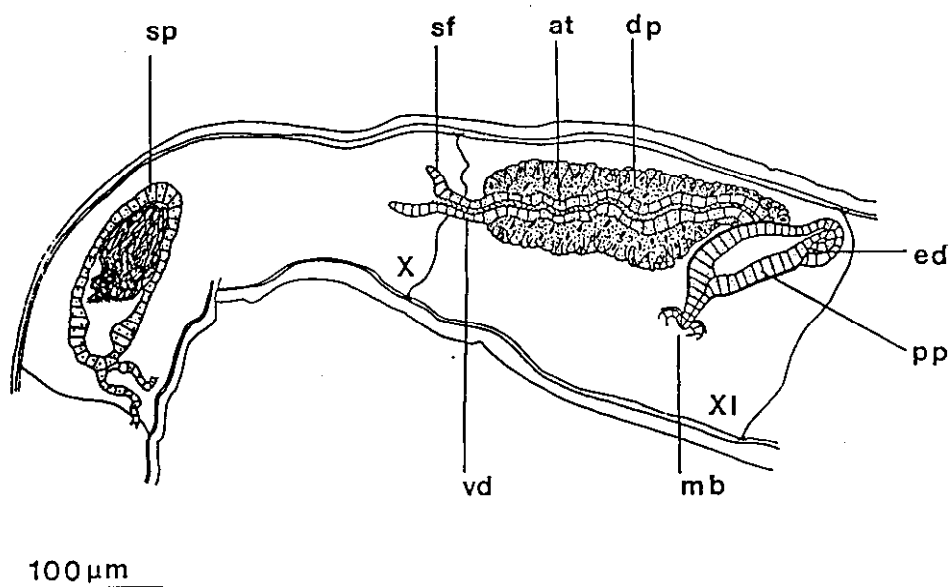
Diagnosis. Length: 5-15 mm; segments: up to 64. Clitellum extending over most posterior part of X and XI-XII. Anterior setae bifid, generally with upper tooth about as thick and long as lower, upper tooth of ventrals may be slightly longer than lower, (2)3-5(6,7) setae per bundle; from mid-body to posterior end setae may be simple-pointed or with upper tooth, as long as, or slightly longer, than lower; simple setae frequently replace all bifids in posterior dorsal bundles, (1)2-5 setae per bundle. Ventrals of VII, VIII, IX, and XII usually slightly modified; setae are larger with upper tooth much longer than lower; ventrals absent in XI. Male efferent ducts open very close together, opening either separately or into a median copulatory sac (bursa) in XI. Spermathecal pore unpaired, median or most anterior part of X (duplicated in IX in one aberrant specimen from the Florida panhandle). Coelomocytes round, very abundant. Male genitalia paired: vas deferens very short, entering long tubular, narrow atrium apically; atrium relatively undifferentiated from vas deferens, both narrowed and internally ciliated, junction distinguished by the diffuse prostate gland ensheathing atrium. Ejaculatory duct short, distinguished by the absence of prostate glands ectally on atrium, thin outer layer of muscles and non-granulated inner epithelium (granulated in atrium, but difficult to determine through prostate glands). Pseudopenis long, non-ciliated and non-granulated inner epithelium, and conspicuous outer layer of circular muscles. Pseudopenes usually open into an unpaired copulatory sac with a folded inner wall. Spermatheca unpaired on the left side with a relatively short duct and elongate, generally twisted, ampulla. Sperm in a random mass with sperm heads oriented toward inner end of ampulla.

Distribution and Habitat. Denmark, North America (Atlantic and Gulf of Mexico coasts of United States, Pacific coast of Canada), India, South Africa, Brazil, southern China. Associated with fine sediments in littoral and estuarine habitats, frequently abundant in intertidal saltmarshes.

Remarks. This species is readily distinguished by the abundant coelomocytes, usually more concentrated anteriorly, median copulatory sac (bursa) in XI, single spermatheca in X, lack of hair setae, modified setae in VII-IX, XII, and simple-pointed setae usually present posteriorly. Details of the morphology of setae and specific dimensions of the male genitalia and spermathecal ampulla are highly variable among populations. Erséus (1984a) suggests that *M. parvus* could be regarded as a polytypic species, with two subspecies.



(after Erasmus, 1984a) *Monopylephorus parvus*: a, anterior dorsal seta; b, posterior dorsal seta; c, ventral setae of segment XII; d, lateral view of spermatheca and male genitalia in segments X-XI.



(after Baker and Brinkhurst, 1981) *Monopylephorus parvus*: Specimen twisted; showing left (and only) spermatheca and left male duct.

***Monopylephorus rubroniveus* Levinsen, 1884**

Monopylephorus rubroniveus Levinsen, 1884:942-944, Fig. 1.

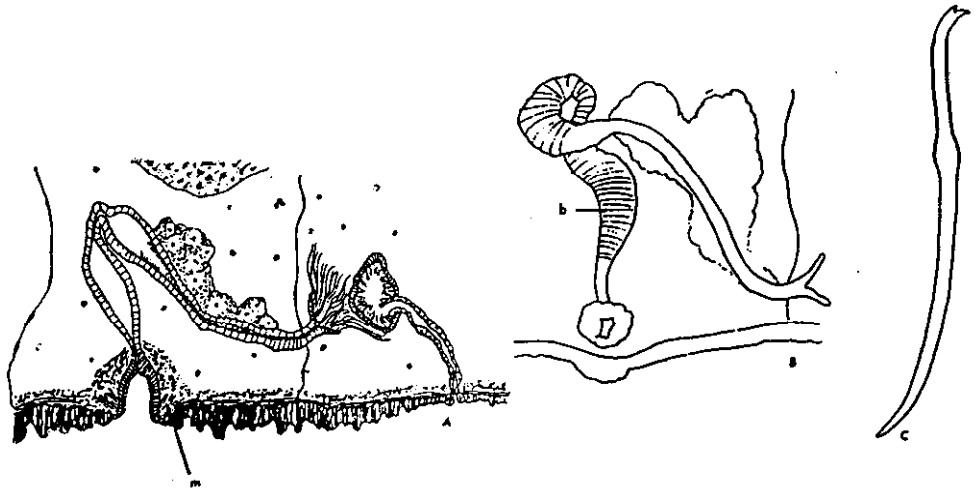
Diagnosis. Length: 6-60 mm; segments: 40-86. Setae bifid with teeth of variable proportions: (1)2-6 setae per bundle anteriorly, (1)2-3 per bundle posteriorly. Male pore unpaired as large mid-ventral copulatory bursa in XI. Spermathecal pores paired, close together or more or less united mid-ventrally in anterior of X. Coelomocytes abundant. Male genitalia paired: vas deferens short, leading directly to narrow tubular atrium. Atrium ensheathed by diffuse prostate glands, with a wider, bulbous portion ectally, immediately prior to junction with short, naked ejaculatory duct which opens into a tall, erect, protrusible pseudopenis. Vas deferens, atrium, and (?)ejaculatory duct ciliated, pseudopenis non-ciliated, entering median copulatory bursa laterally. Spermathecae paired each with a short duct slightly undifferentiated from the small, ovoid ampulla. Sperm in random mass.

Distribution and Habitat. Northwestern Europe (Denmark, Sweden, Britain), France, Brazil, Black Sea, Far East of Russia, northern China, east coast of North America (Atlantic and Gulf of Mexico coasts of United States). Associated with fine sediments, frequently inhabiting organically polluted situations, brackish water, intertidally, and shallow subtidally in estuaries.

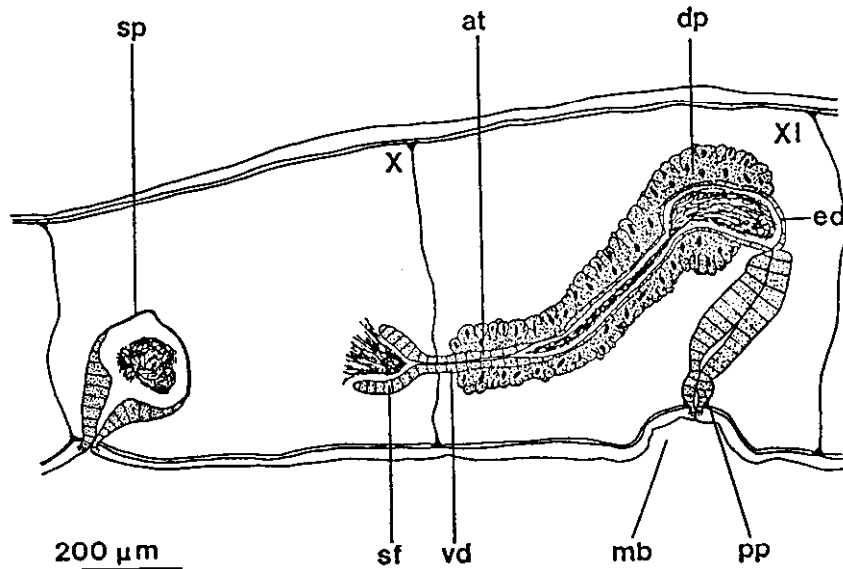
Remarks. This species is highly variable but is distinguished from all other tubificids in North America by the combination of abundant coelomocytes, large, median copulatory (bursa) in XI, paired spermathecae in X, lack of hair setae, and somatic setae all bifid with unmodified ventrals in VII-XII. The very large copulatory bursa, paired spermathecae, and lack of modified anterior ventrals, and simple-pointed posterior setae differentiate this species from the closely related *M. parvus*, with which it co-occurs. Additionally, *M. rubroniveus* is usually stouter and shorter than *M. parvus*.

Baker and Brinkhurst (1981) synonymized seven previously described species with *M. rubroniveus*, one of which, *M. helobius* Loden, 1980, is fairly common in the northern Gulf of Mexico (including the Florida panhandle south to about Tampa Bay). This form of *M. rubroniveus* is distinctive with respect to the much shorter upper tooth of the somatic setae, however, all details of the male genitalia and spermathecae conform well with the description of *M. rubroniveus* by Baker and Brinkhurst (1981).

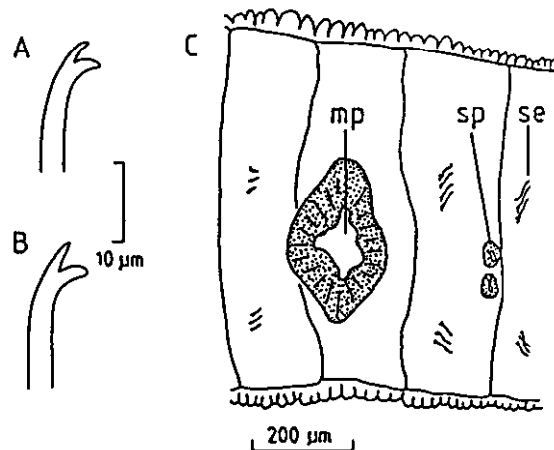
(after Loden, 1980) *Monopylephorus rubroniveus* (as *helobius*): A, male duct; B, male duct during bursal collapse; C, seta, b, banks of circular muscle surrounding the distal part of the male duct; m, muscle fibers apparently utilized for bursal collapse.



(after Baker and Brinkhurst, 1981) *Monopylephorus rubroniveus* (as *glaber*, coastal Massachusetts): Spermatheca and male duct.



(after Eräus, 1990c) *Monopylephorus rubroniveus*: A, anterior seta; B, posterior seta; C, ventral view of genital region, showing unpaired male pore (mp), paired spermathecal pores (sp), and setae (se).



Subfamily. Phallodrilinae Brinkhurst, 1971

Type Genus. *Phallodrilus* Pierantoni, 1902

Diagnosis. (Based on Erséus, 1992a) Primarily marine tubificids. Hair setae absent. Somatic setae include simple-pointed and bifid crotchets; if bifid, teeth may be slender and parallel, or curved with upper tooth variably reduced or equal to lower; a ligament may be present connecting the bases of the teeth, or connecting the lower tooth to the setal shaft (subdental ligament). Genital setae often present, generally as modified penial setae in XI; modified spermathecal setae occasionally present in X and/or XI. Coelomocytes absent (except for a few species) and not of the rhyacodriline type when present. Male genitalia paired: vas deferens generally long, clearly set off from atria and ciliated; modified or reduced in some genera; may be partly or wholly muscular. Atria highly variable (oval, comma-shaped, spindle-shaped, cylindrical, etc.) with ciliated inner epithelium, opening directly to exterior through simple pores or terminating in various types of copulatory structures. Two compact prostate glands attached to each atrium; one to anterior face, another to posterior face (one or both prostate glands may be secondarily lost in some species); attachments may be pedunculate or more broadly connected with inner epithelium of atria or with epithelium of penes or copulatory sacs (in some species of *Aktedrilus*). Spermathecae generally in most anterior part of X, single, paired, dorsal or ventral. Sperm generally as a random mass in spermathecal ampullae, but may be arranged in bundles or as simple spermatozeugmata.

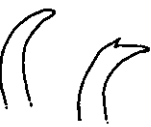
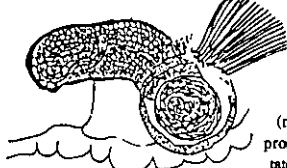
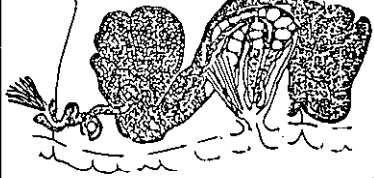
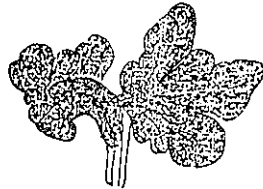
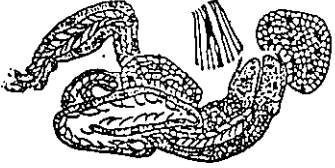
Remarks. The primary diagnostic character for Phallodrilinae, as originally defined by Brinkhurst and Jamieson (1971), is the solid prostate glands "with stalk-like attachments to the male ducts when present". Baker (1982) emended the definition to include two new genera, *Nootkadrilus* and *Discordiprostatus*, which have stalked posterior prostate glands and diffuse prostate glands as well. A subfamily to accommodate these genera was subsequently established by Finogenova (1986) as Nootkadrilinae. The most current disposition (Erséus, 1990a; 1992a) is to recombine them back to Phallodrilinae which now has more than 250 species.

The largest genus, *Phallodrilus*, with more than 70 species, was considered to be a melting pot to include species sharing the basic "phallodriline traits, the biprostate and largely unmodified atria, combined with the lack of the (apomorphic) structures that

characterize the others". As a result, Erséus (1992a) presented a comprehensive phylogenetic analysis according to cladistic principles which resulted in a revision of the generic classification to establish monophyletic groups within the former genus, *Phallodrilus*. This genus has now been reclassified into twenty taxa. As a result, Phallodrilinae now includes 31 genera, eleven of which are expected to occur in Florida waters. More than 30 additional species within a variety of genera have been described from the Caribbean (primarily Belize) and/or Bermuda and may be expected to occur in the Florida. These species will be included in a forthcoming addendum to this manual.

The genera included herein can be divided into two basic categories: 1) the *Inanidrilus/Olavius* group comprised of those species without a mouth, anus, or alimentary canal, and 2) all other taxa with a well-developed mouth, anus, and gut. The majority of species can be identified on the basis of modified penial setae, somatic setae, or a combination of both. However, some species can only be discriminated by the morphology of the atrium and associated prostate glands, copulatory structures, and spermathecae. Close scrutiny of a number of mature individuals within each community is the only reliable method for accurate identification. But once a comprehensive species list is prepared for a given community, secondary somatic characters can then be applied for more rapid determination. Frequently, many species can be readily identified "just by the way they look", what has been termed as "gestalt taxonomy".

Table 2. Phallodrilinae taxa with "*Peosidrilus*-type" penial setae.

Taxon	Anterior Setae #/bundle	Posterior Setae #/bundle	Penial Setae #/bundle	Male Genitalia
<i>Bermudrilus penatus</i>	2-4 teeth equal	(1)2 upper teeth shorter	 (4,5)6-7	 (no posterior prostate)
<i>Coralliodrilus corpulentus</i>	 (2)3	 1-3	 10-12	 (no prostate)
<i>Coralliodrilus priscus</i>	 (2)3(4)	same (1)2(3)	 20-25	 (no prostate)
<i>Peosidrilus acochlearis</i>	 3-5	 (2)3-4(5)	 8-15	
<i>Peosidrilus biprostatatus</i>	 3-4	 3-4	 7-13	
<i>Peosidrilus hirsutus</i>	 2	 dorsal ventral 1	 4-6	
<i>Peosidriloides hornensis</i>	 2-3(4)	 2	 7-12	

Genus. ***Coralliodrilus* Erséus, 1979**

Type Species. *Coralliodrilus leviatriatus* Erséus, 1979.

Diagnosis. (Based on Erséus, 1993) Marine tubificids. Somatic setae bifid or simple-pointed. Penial setae present or absent; when present, from 1-20 per bundle; bifid or simple-pointed with strongly hooked ectal tips. Male and spermathecal pores paired, generally in XI and X, respectively. Coelomocytes, if present, small and sparse, not of the "rhyacodriline type". Male genitalia paired: vas deferens (short in two species) entering atria more or less apically. Atria oval-to-cylindrical, erect or curved toward anterior; may be internally ciliated; often bipartite with ectal part narrower than ental. Prostate glands absent. Atria either opening directly to the anterior through simple pores, or terminating in simple protrusible projections (small penes/pseudopenes). Spermathecae paired, ducts usually short and may have an ectal vestibule, ampullae more or less oval. Sperm in random masses in ampullae.

Remarks. This genus is characterized by the total absence of prostate glands and generally simple-pointed, numerous penial setae with strongly hooked ectal tips. This is a large genus with more than 20 species, only two of which (*C. corpulentus* and *C. priscus*) occur in Florida waters. At least three additional taxa, *C. leviatriatus*, *C. rugosus* Erséus, 1990a, and *C. randyi* Erséus, 1990a, may eventually be found, particularly in the Florida Keys, since they have already been collected either in Bermuda or Belize. The two species from Florida are readily distinguished from each other by the number of penial setae per bundle: about 10-12 in *C. corpulentus*, and 20-25 in *C. priscus*. Additionally, the former species has simple-pointed setae, or setae with an extremely reduced upper tooth.

Key to Species of *Coralliodrilus*

1. A) Penial setae 10-12 per bundle; posterior dorsal setae with very prolonged lower tooth, upper tooth very reduced or absent.. *C. corpulentus*
- B) Penial setae 20-25 per bundle; all somatic setae with upper tooth subequal to lower. *C. priscus*

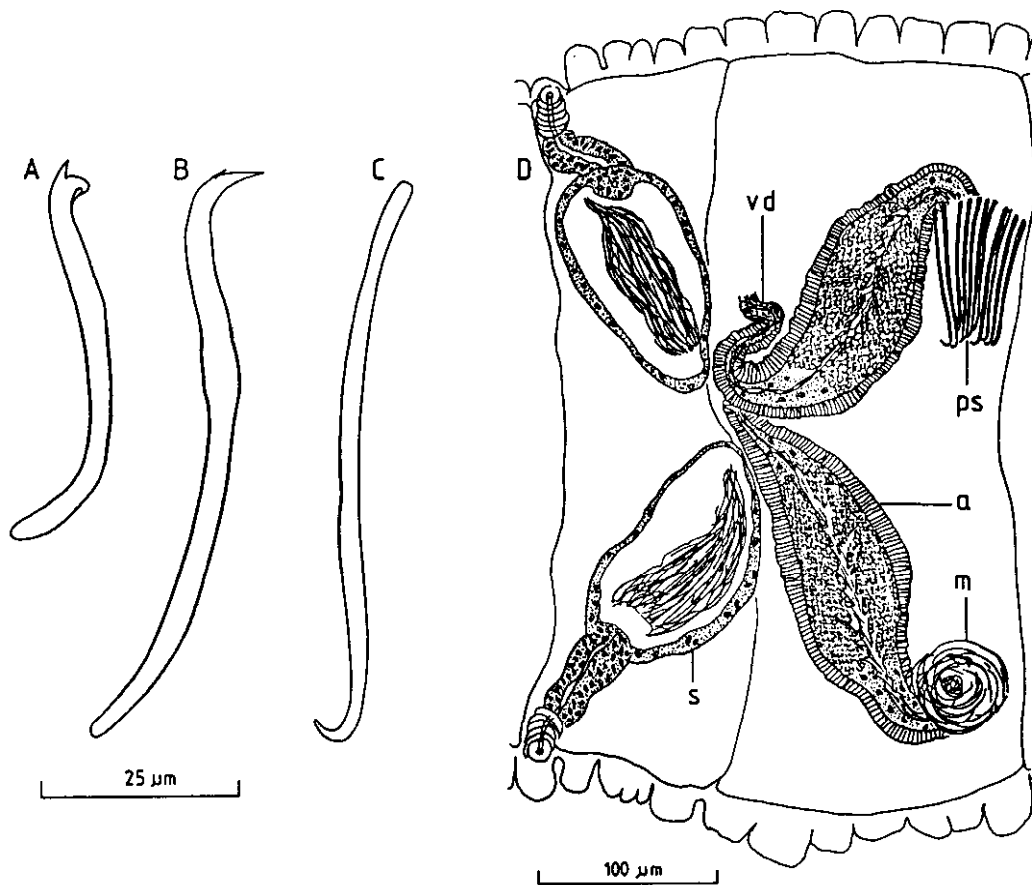
***Coralliodrilus corpulentus* Erséus, 1986**

Coralliodrilus corpulentus Erséus, 1986a:305-307, Fig. 12.

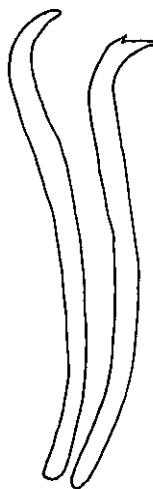
Diagnosis. Length: 4.8-6.0 mm; segments: 54-63. Secondary annulations present, several annuli per segment. Clitellum extending over $\frac{1}{2}$ X-(XI)XII. Anterior somatic setae bifid with upper tooth thinner and slightly shorter than lower; subdental ligament present, setae 55-70 μ m long, 2(3) per bundle; posterior dorsal setae with a much reduced upper tooth and lower tooth prolonged and sharply-pointed, or lacking altogether, appearing bluntly simple-pointed, up to 80 μ m long. Penial setae modified: simple-pointed and strongly hooked ectally; 70-95 μ m long, 10-12 per bundle. Male and spermathecal pores paired in posterior of XI and anterior of X, respectively. Male genitalia paired: vas deferens appears short, difficult to discern exact length, with strong circular muscles, 20 μ m wide ectally. Atrium spindle-shaped, somewhat sigmoid, tapering ectally into short narrow duct surrounded by very strong muscles; 140-290 μ m long, 55-80 μ m wide; inner epithelium ciliated, and, for most parts, granulated. Atrium terminating in simple, minute male pore. Spermathecae paired, each with distinct duct of moderate length and oval, thin-walled ampulla. Sperm in random masses in ampullae.

Distribution and Habitat. Southeast North America (South Carolina and east coast of Florida). Associated with carbonate sands; subtidally to 10-15 m depth.

Remarks. This species is characterized by the absence of prostate glands, numerous ectally-hooked penial setae (about 10-12 per bundle), and strongly modified posterior dorsal setae, with either a very reduced upper tooth and strongly-pointed, prolonged lower tooth, or blunt simple-pointed setae. *Coralliodrilus corpulentus* is a fairly stout worm from which the specific epithet is derived.



(after Eiréus, 1986a) *Coralliodrilus corpulentus*: A, somatic seta; B, posterior dorsal seta; C, penial seta; D, ventral view of spermathecae and male genitalia in segments X-XI (note that musculature is shown at one of the two male openings, penial setae at the other).



(after Eiréus and Milligan, 1992) *Coralliodrilus corpulentus*: posterior dorsal somatic setae.

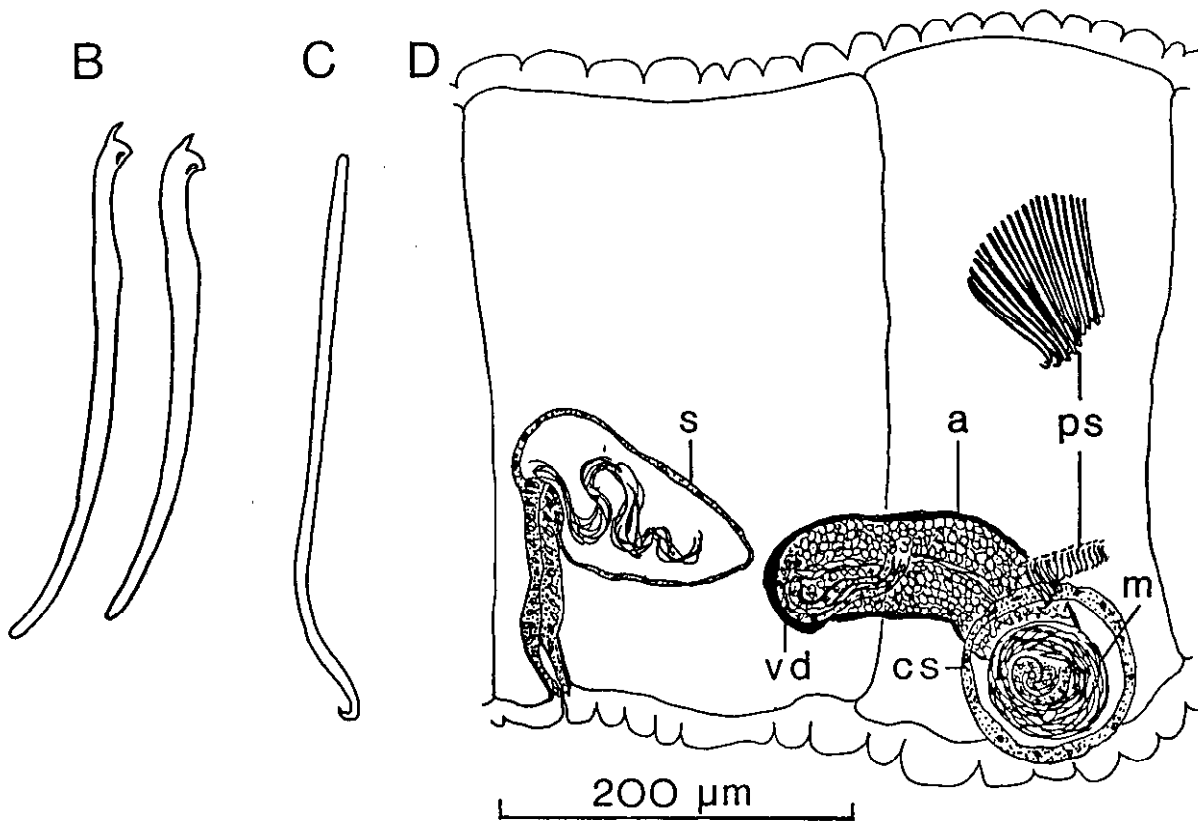
***Coralliodrilus priscus* Erséus and Milligan, 1992**

Coralliodrilus priscus Erséus and Milligan, 1992:587, Fig. 1B-1D.

Diagnosis. Length: 6.2-7.0 mm; segments: 52-55. Secondary annulations present, several annuli per segment. All somatic setae bifid with upper tooth thinner and somewhat shorter than lower, subdental ligament present, setae 40-70 μm long, (2)3(4) per bundle anteriorly, (1)2(3) per bundle posteriorly. Penial setae modified: slender, simple-pointed and strongly-hooked ectally, 80-85 μm long, about 20-25 per bundle. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Male genitalia paired: vas deferens appears very short, difficult to discern exact length or width. Atrium somewhat spindle-shaped extending forward into X, tapering ectally into short, narrow duct surrounded by very strong muscles; 190-220 μm long, 60-70 μm wide; inner epithelium ciliated and granulated; outer layer muscular. Atrium terminating in a very muscular, compact, round bulb, 60 μm wide, at middle of which atrial duct opens to exterior; bulb appears enclosed in round sac. Spermathecae paired, each with narrow, distinct, fairly long duct and somewhat pear-shaped, thin walled ampulla. Sperm arranged in coiled bundles in ampullae.

Distribution and Habitat. Southeast North America (west coast of Florida). Associated with medium sand mixed with silt; subtidally about 24 m depth.

Remarks. This species is very similar to the congener (*C. corpulentus*) also reported from Florida waters, but is distinguished by its lack of modified posterior somatic setae and larger number of penial setae.



(after Erásus and Milligan, 1992) *Coralliodrilus priscus*: B, somatic setae; C, penial seta; D, lateral view of genitalia in segments X-XI. (Penial setae shown in full for one side of worm [upper right in D]. For other side (the other side [the one with spermatheca and male depicted], only tips of penial setae indicated; these setae curved, much distorted, in specimen in question.)

Genus. *Pectinodrilus* Erséus, 1992

Type Species. *Phallodrilus rectisetosus* Erséus, 1979.

Diagnosis. Marine tubificids. Somatic setae simple-pointed or bifid with upper tooth thinner and shorter than lower. Penial setae generally small, straight, simple-pointed with straight or hooked tips; in erect, often fan-shaped bundles, 3-20 per bundle. Male and spermathecal pores generally paired in XI and X, respectively (spermathecal pores generally paired in XI and X, respectively [spermathecal pore unpaired and mid-dorsal in *P. multiplex* (Erséus, 1990b)]). Male genitalia paired: vas deferens entering apical end of atrium; may be modified: partly muscular with a medial ampulla. Atria small, spindle-shaped, more or less erect, each with an anterior prostate gland attached near entrance to vas deferens, and a posterior prostate gland not as closely attached to vas as anterior one. Atria generally opening to exterior through simple pores, or rarely, pseudopenes (*P. multiplex*). Spermathecae paired (single in *P. multiplex*), each with a short duct, which may have an ectal vestibule, and pear-shaped ampulla. Sperm random or arranged in large bundle in ampullae.

Remarks. Species of this genus were formerly included in the very large paraphyletic *Phallodrilus*. Erséus (1992a) established *Pectinodrilus* to accommodate those species with small, spindle-shaped, more or less erect atria, and small, straight, generally numerous penial setae. Previously, many of the species were grouped into the *Phallodrilus rectisetosus* complex (Erséus, 1979b; 1981b; 1988a), the species (previously subspecies) of which could be differentiated on the basis of the number of somatic and penial setae. Currently, there are at least 15 species of *Pectinodrilus* worldwide, but only two have been reported from Florida or the Caribbean: *P. deminutius* and *P. molestus*. These species are readily distinguished from each other by the difference in number of anterior and posterior somatic setae and number of penial setae: *P. molestus* has two somatic setae per bundle both anteriorly and posteriorly, and 3-5 penial setae per bundle; *P. deminutius* has two setae per bundle anteriorly and one per bundle posteriorly, and generally more than five (up to 11) penial setae per bundle.

Key to Species of *Pectinodrilus*

1. A) Two setae per bundle anteriorly, one per bundle posteriorly; generally 4-8(to 11) penial setae per bundle. *P. deminutius*
- B) Two setae per bundle both anteriorly and posteriorly; generally 3-5(6,7) penial setae per bundle. *P. molestus*

***Pectinodrilus deminutius* (Erséus, 1979)**

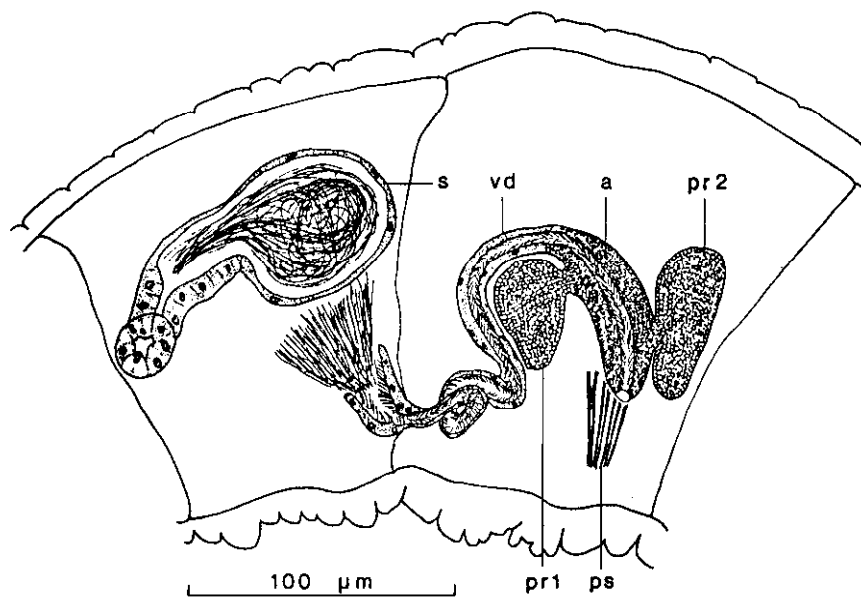
Phallodrilus rectisetosus deminutius Erséus, 1979b:191-192, Fig. 7.

Diagnosis. Length: 3.3-5.9 mm; segments: 36-44. Somatic setae all bifid with upper tooth thinner and shorter, 25-40 μm long, two per bundle anteriorly, one per bundle posteriorly. Penial setae small, straight, simple-pointed with straight or slightly hooked tips, 30-46 μm long, generally 4-8 (up to 11) per bundle. Male and spermathecal pores paired in middle of XI and anterior of X, respectively. Male genitalia paired: vas deferens relatively long and narrow, 7-9 μm wide, entering apical end of atrium. Atrium spindle-shaped, erect, 60-85 μm long, 18-35 μm wide; inner epithelium ciliated and granulated; outer layer thin. Atrium terminating in a small pore opening to the exterior; copulatory structures absent. Anterior prostate gland opening into anterior, ental part of atrium, posterior prostate gland attached to more ectal part of posterior face of atrium. Spermathecae paired, each with relatively short duct and pear-shaped, thin-walled ampulla. Sperm arranged in random masses in ampullae.

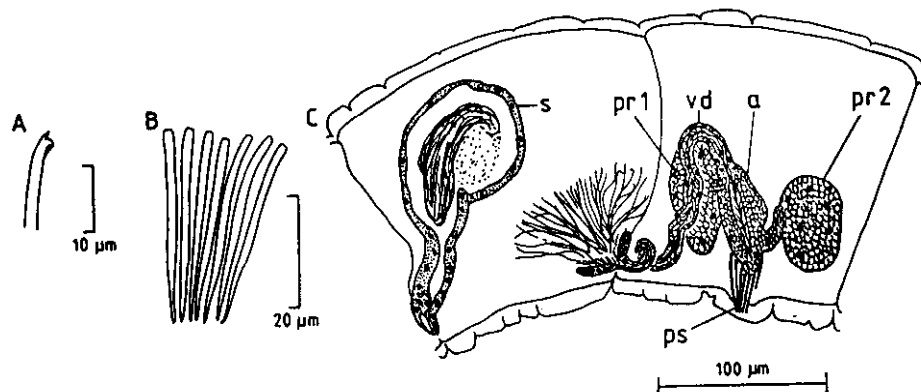
Distribution and Habitat. Caribbean (Belize, Barbados), Bermuda. Associated with coarse to medium sand; subtidally to at least 14 m depth.

Remarks. This species was originally regarded as a subspecies which included *P. molestus* in the *Phallodrilus rectisetosus* complex (Erséus, 1979a). Taxa within this complex all shared the following characteristics: 1) small body size; 2) numerous, straight, sharply simple-pointed penial setae, arranged in tight bundles; 3) small, spindle-shaped atria, each with two compact prostate glands, and 4) pear-shaped, somewhat bipartite spermathecal ampullae. Erséus (1985) later suggested that the complex should be regarded as one taxonomic entity, *P. rectisetosus*. Subsequently, Erséus (1988a) re-evaluated the complex, elevating the previously described subspecies of *P. rectisetosus* to specific status. At the same time, he separated *P. deminutius* into two species based on distribution of somatic setae, number of penial setae per bundle, and, in part, by their biogeography.

Pectinodrilus deminutius is distinguished from its congener, *P. molestus*, the only other representative of *Pectinodrilus* so far reported from Florida or the Caribbean, by: 1) only one seta per bundle posteriorly (two per bundle in *P. molestus*); 2) more penial setae per bundle (less than five in *P. molestus*, and 3) it has so far only been reported from Belize and Bermuda (*P. molestus* is widely distributed throughout the Caribbean, and in Hawaii, Fiji, Australia, and southern China). All specimens of *Pectinodrilus*, so far examined from Florida, have been *P. molestus*, which is fairly common, particularly off southeast Florida.



(after Erasus, 1979b) *Pectinodrilus diminutius*: lateral view of genital organs in segments X and XI.



(after Erasus, 1988a) *Pectinodrilus diminutius*, from Belize: A, somatic seta; B, penial setae; C, lateral view of spermathecae and male genitalia in segments X-XI.

***Pectinodrilus molestus* (Erséus, 1979)**

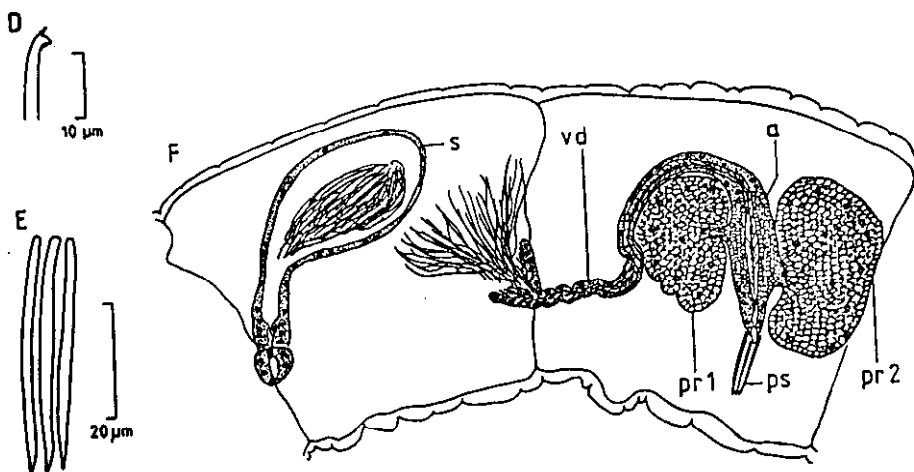
Phallodrilus rectisetosus deminutius (partim) Erséus, 1979b:191-192

Diagnosis. Length: 3.0-6.8 mm; segments: 30-43. Clitellum extending over X-XI. Somatic setae all bifid with upper tooth thinner and shorter than lower, 28-40 μm long, two per bundle anteriorly and posteriorly. Penial setae small, straight, simple-pointed with straight or very slightly hooked tips, 26-47 μm long (2)3-5(6,7) per bundle. Male and spermathecal pores paired in middle of XI and anterior of X, respectively. Male genitalia paired: vas deferens relatively long and narrow, 5-8 μm wide, entering apical end of atrium. Atrium small, spindle-shaped, erect, 35-80 μm long, 14-23 μm wide; inner epithelium ciliated and granulated; outer layer thin. Atrium terminating in a small pore opening to the exterior; copulatory structures absent. Anterior prostate gland opening into anterior ental part of atrium, posterior prostate gland attached to more ectal part of posterior face of atrium. Spermathecae paired, each with relatively short duct and pear-shaped ampulla. Sperm arranged in random masses in ampullae.

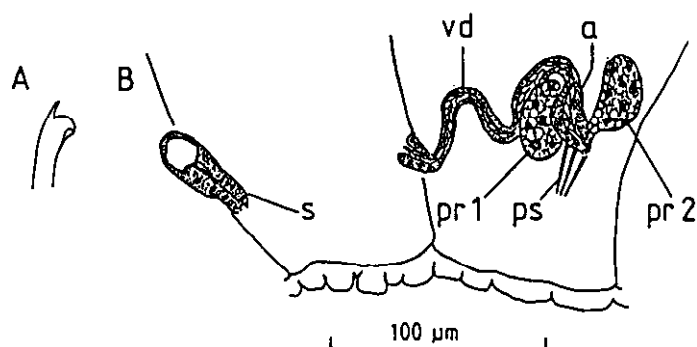
Distribution and Habitat. Caribbean (Belize, Barbados), Bermuda, southeast North America (east and west coasts of Florida), Australia, Hawaii, Fiji, southern China. Associated with intertidal and subtidal sands to at least 70 m depth.

Remarks. The bisetal bundles of somatic setae throughout the body and few penial setae distinguishes this species from *Pectinodrilus deminutius*. *Pectinodrilus molestus* is common throughout Florida. Although *P. deminutius* has not been reported from Florida waters, its presence in the Caribbean suggests that it may eventually be found. (See Remarks for *P. deminutius* for further discussion.)

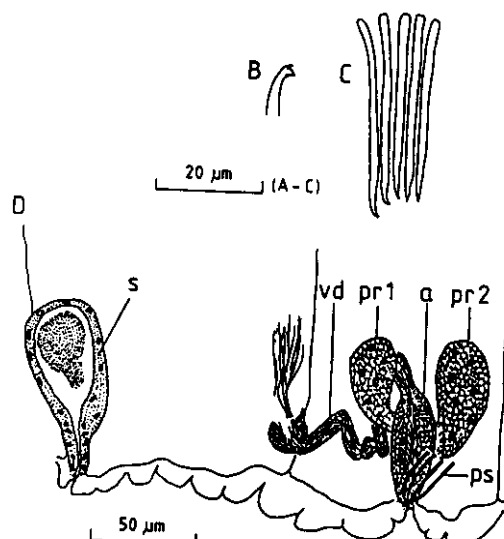
(after Erséus, 1988a)
Pectinodrilus molestus, from
 Belize: D, somatic setae; E,
 penial setae; F, lateral view of
 spermatheca and male genitalia
 in segments X-XI.



(after Erséus, 1992b) *Pectinodrilus molestus*
 from Hong Kong: A, somatic setae; B, lateral
 view of spermatheca and male genitalia in
 segments X-XI.



(after Erséus, 1988a) *Pectinodrilus molestus*, from Hawaii:
 B, somatic seta; C, penial setae; D, lateral view of
 spermatheca and male genitalia in segments X-XI.



Genus. *Milliganius* Erséus, 1992

Type Species. *Phallodrilus sabulosus* Erséus, 1979.

Diagnosis. Marine tubificids. Somatic setae bifid with upper tooth thinner than and either equal to or shorter than lower. Penial setae simple-pointed, erect and stout, may be somewhat spoon-shaped, 1(2) per bundle. Modified spermathecal setae may be present in IX or X (in *M. sabulosus*). Male and spermathecal pores paired in XI and anterior part of X [in XI in *M. compactus* (Erséus, 1990a)], respectively. Male genitalia paired: vas deferens entering apical end of atrium. Atria club or spindle-shaped, more or less erect, each with an anterior prostate gland attached at entrance of vas deferens, and a posterior prostate gland near ectal end. Atria opening to exterior through a simple pore (*M. sabulosus*), into a copulatory chamber (*M. compactus*). Copulatory structures absent. Spermathecae paired slender, each with elongate "vestibule" (long duct), and an ectal ampulla. Sperm in dense mass or loose bundles.

Remarks. This genus was recently established by Erséus (1992a) to accommodate those species previously included in *Phallodrilus* with elongate, slender spermathecae and one stout, simple-pointed, erect penial seta per bundle and lack of penes. Although two species are included in this genus, only one, *M. sabulosus*, commonly occurs in Florida waters. Its only congener, *M. compactus*, has only been reported from one location in the Caribbean (Belize), and consequently, is not included herein. *Milliganius compactus* is readily distinguished by the stout, single penial seta in each bundle of XI and the slender paired spermatheca in the same segment (XI) as the male efferent ducts.

***Milliganius sabulosus* (Erséus, 1979)**

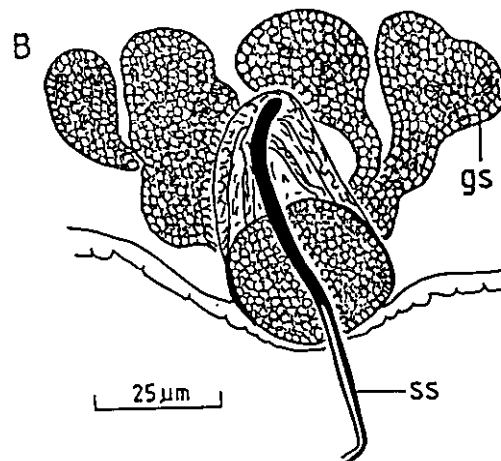
Phallodrilus sabulosus Erséus, 1979b:188-189, Fig. 1-2.

Diagnosis. Length: 2.8-9.0 mm; segments: 22-63. Secondary annulations inconspicuous, about six per segment. Clitellum extending over $\frac{1}{2}$ X-XII. Somatic setae all bifid with upper tooth thinner and shorter or equal to lower, 45-75 μ m long, 2-5 per bundle anteriorly, 2-4(5) posteriorly. Penial setae stout, single-pointed, slightly sigmoid, spoon-shaped, always one per "bundle" and located near the atrial openings in X, 60-80 μ m long. Spermathecal setae more slender than penials, ectally deeply forked either posterior to spermathecal pores in X, or anterior to these pores, posteriorly in IX, 60-100 μ m long, 1-2 per bundle; middle part of each seta enclosed in a glandular body, which bears a few lobes of external glands resembling prostate glands. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Male genitalia paired: vas deferens longer than atrium, 9-13 μ m wide, entering apical end of atrium. Atrium spindle-shaped, almost erect, 60-140 μ m long, 35-45 μ m wide; thick inner epithelium ciliated and granulated; outer layer very slender. Atrium terminating in a small pore opening to the exterior; copulatory structure absent. Anterior prostate gland attached at entrance of vas deferens; posterior prostate gland attached near ectal end of atrium. Spermathecae paired, each with a slender, duct-like ectal portion, and an ental thin-walled, oval ampulla. Sperm in random masses in the dilated outer portion of the ducts.

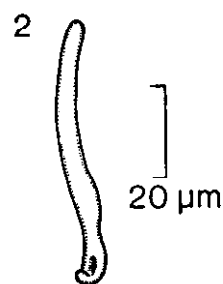
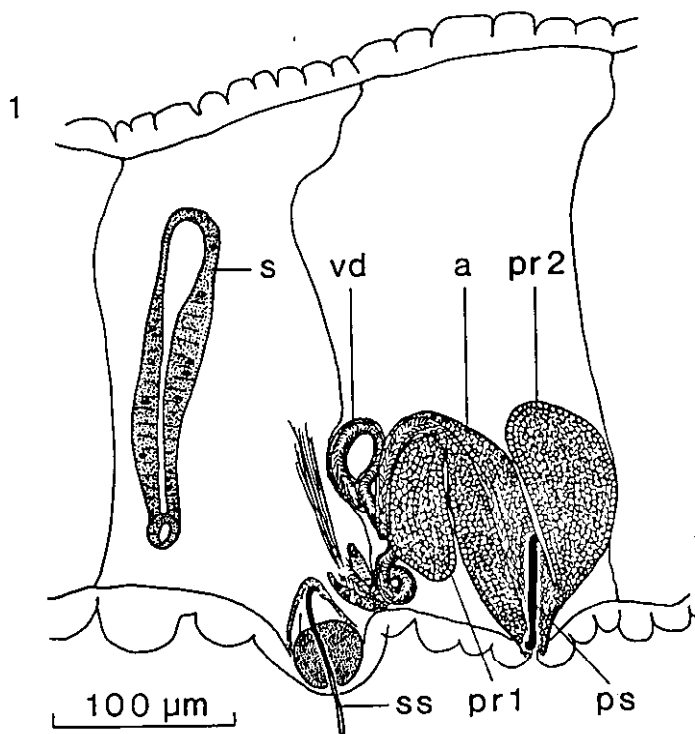
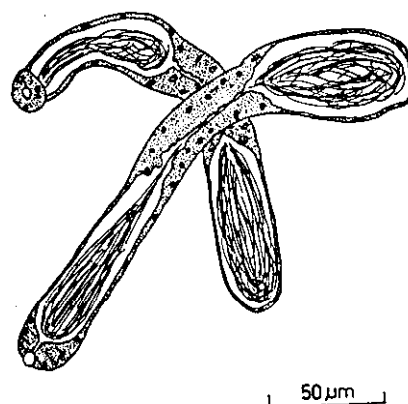
Distribution and Habitat. Eastern North America (east coast and panhandle of Florida, New Jersey). Associated with coarse sand from 3-15.5 m depth.

Remarks. This species is readily distinguished from all other tubificids in Florida water by the characteristic phallodriline morphology of the male genitalia and unique combination of fork-shaped spermathecal setae and single simple-pointed penial seta, one per bundle in XI (not in "X" as mistakenly indicated by Erséus, 1986).

(after Erséus, 1986a) *Milliganius sabulosus*: A, seta from one of posteriormost segments; B, spermathecal seta with associated glands.



(after Erséus and Loden, 1981) *Milliganius sabulosus*: A, spermathecae, as seen in oblique view of a whole-mounted specimen.



(after Erséus, 1979b) *Milliganius sabulosus*: 1, lateral view of genital organs in segments X and XI; 2, penial seta.

Genus. *Uniporodrilus* Erséus, 1979

Uniporodrilus granulothecus Erséus, 1979.

Diagnosis. (Based on Erséus and Milligan, 1993) Small marine tubificids. Prostomium distinctly longer than its width at base; generally well set off from peristomium. Somatic setae generally bifid with upper tooth thinner and shorter than lower [simple-pointed in posterior dorsal bundles of *U. nasutus* (Erséus, 1990a)]. Penial setae absent (*U. purus*) or from 6-22 per bundle arranged in rings or fan-shaped bundles; with simple-pointed or bifid hooked tips. Male pores paired or single in XI. Spermathecal pores paired in X or single in posterior of IX. Pharyngeal cavity large and densely ciliated in some species. All male genitalia structures paired or with single atrium. Vas deferens either entering apical end of or somewhat subapical on atrium. Atrium small, oval, or elongate and curved; when paired, each with two large prostate glands; when single, at least posterior prostate glands present and paired, two pairs may be present (*U. granulothecus*) or only one pair (*U. purus*). Atrium opening into more or less developed copulatory sac. Spermathecae paired or single; generally elongate with thick-walled granulated duct(s) and small ampulla(e).

Remarks. This genus is characterized by small, basically littoral tubificids with the prostomium distinctly longer than wide at base and generally well set off from peristomium, elongate spermathecae with highly granulated ducts and small ampullae, and relatively inconspicuous atria. Although six species are currently included in this relatively aberrant taxon, only *U. purus* has been collected from Florida waters. Two additional species, *U. nasutus* and *U. bipartitus*, were described from the Caribbean (Erséus, 1990a), and may occur in southern Florida. The type species has been reported from North Carolina and New Jersey and may occur in northeastern Florida waters.

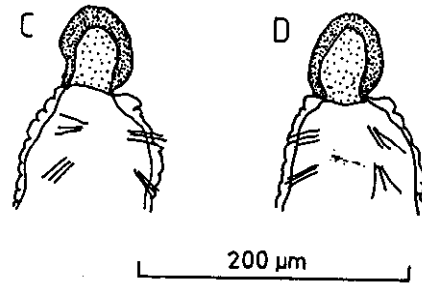
***Uniporodrilus purus* Erséus and Milligan, 1993**

Uniporodrilus purus Erséus and Milligan, 1993:244-247, Fig. 1C-1D, 2.

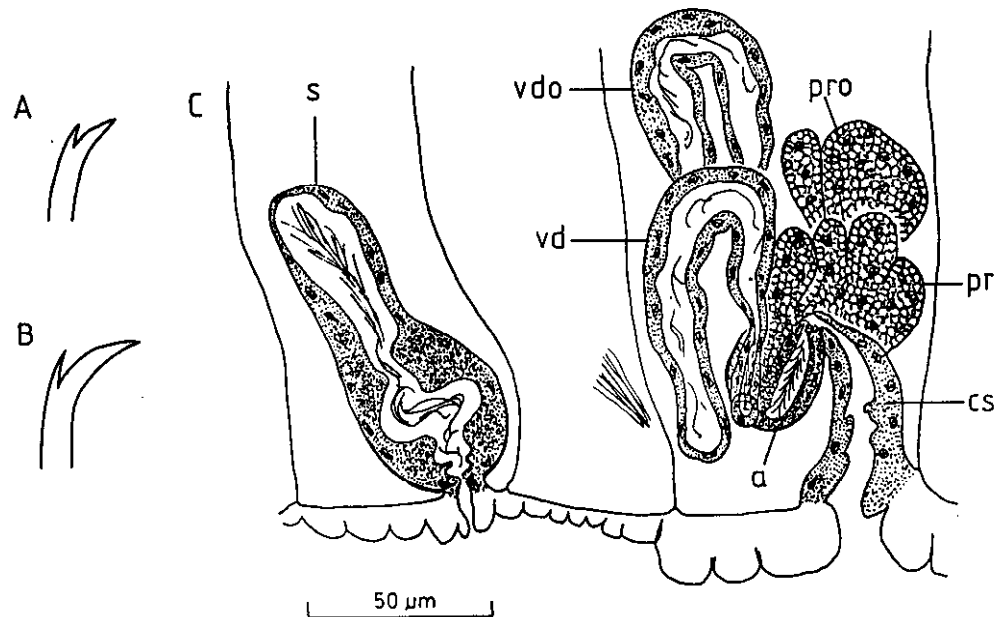
Diagnosis. Length: 1.5-1.9 mm; segments: 25-35. Body very stout. Prostomium clearly longer than its width at base. Clitellum extending over $\frac{1}{2}$ X-XII. Setae bifid with upper tooth much shorter and thinner than lower; lower tooth of posterior setae very prolonged, upper tooth sort and needle-like; all setae 30-45 μm long, three per bundle; ventral (penial) setae absent from XI. Male and spermathecal pores unpaired mid-ventrally in posterior of XI and IX, respectively. Pharyngeal cavity hollow, but not large. All male genital structures not paired: vas deferens paired, thick-walled, longer and wider than atrium, 15-22 μm wide, ciliation sparse, entering unpaired atrium somewhat subapically. Atrium unpaired, oval 30-40 μm long, 27-30 μm wide, inner epithelium ciliated and somewhat granular. Atrium opening into copulatory sac. One pair of multilobed prostate glands broadly attached to posterior of atrium. Spermatheca unpaired, pear-shaped, somewhat differentiated into an elongate, thick-walled ectal duct, and shorter, narrower, thin-walled ampulla. Sperm loosely scattered throughout duct and ampulla.

Distribution and Habitat. Southeast North America (Florida panhandle). Associated with medium-fine sand; subtidally about 6 m.

Remarks. This species is distinguished from the other tubificids expected to occur in Florida waters by the distinctive morphology of the somatic setae: upper tooth thinner and much shorter than lower anteriorly, and the very prolonged (not recurved) lower tooth and needle-like upper tooth of posterior setae; the location of the spermatheca in IX (similar to the congener, *U. granulothecus*) is constant as opposed to a more aberrant pattern exhibited in other species, particularly Rhyacodrilinae; and the absence of penial setae and unpaired male and spermathecal pores also contribute to the uniqueness of this species. *Uniporodrilus purus* is the only species within the genus lacking penial setae.



(after Erséus and Milligan, 1993) *Uniporodrilus purus*: anterior ends of holotype (C) and one paratype (D). Dense shading indicates epidermal lining, light shading (coelomic?) space within promontium.



(after Erséus and Milligan, 1993) *Uniporodrilus purus*: A, free-hand drawing of anterior seta; B, free-hand drawing of posterior seta; C, lateral view of spermatheca and male genitalia in segments X-XI.

Genus. *Peosidrilus* Baker and Erséus, 1979

Type Species. *Peosidrilus biprostatatus* Baker and Erséus, 1979.

Diagnosis. (Based on Erséus and Milligan, 1993) Marine tubificids. Somatic setae bifid with upper tooth thinner and shorter than lower. Penial setae, when present, generally small and straight, with clubbed ectal ends, each bearing an apical hook; however, the "clubs" in some species are indistinct or even absent; many per bundle. Spermathecal pores lateral, or in line with dorsal setae [*P. dorsospermatheca* (Davis, 1985)]. Male genitalia paired: vas deferens ciliated, narrow in all but one species (very dilated in *P. acochlearis*), entering apical end of atrium. Atria elongate, more or less horizontal and curved, or occasionally short and erect; each with an anterior prostate gland attached at entrance of vas deferens, and a posterior prostate gland attached to ectal end of atrium. Atria opening directly to exterior through simple pores, small male projections, or true pendant penes. Copulatory sacs present or absent. Spermathecae paired, of varying shapes; spermathecal vestibules present in a few species.

Remarks. The single unifying character for this genus is the lateral position of the spermathecal pores. Originally, *Peosidrilus* was established for *P. biprostatatus* because of the presence of true pendant, bulbous penes, separated from the atria by constrictions (Baker and Erséus, 1979). However, Erséus (1984b) synonymized it with *Phallogdrilus* because the apically clubbed and hooked penial setae, atria and prostate glands resembled those of other species within that genus. A re-evaluation of *Phallogdrilus* by Erséus (1992a) prompted reestablishment of *Peosidrilus* to accommodate those species with generally lateral spermathecal pores and clubbed, apically-hooked penial setae. Erséus and Milligan (1994) modified the generic diagnosis, restricting *Peosidrilus* to only those species with lateral, or dorsolateral spermathecal pores, thereby naming a new genus, *Peosidriloides*, for *P. flabellifer* (Erséus, 1984b) (because of the ventral position of the pores) and placing a new species, *Peosidriloides hornensis* within it, with the provision that *Peosidrilus* may require further revision when "new information becomes available".

Thirteen species are now included in the genus, *Peosidrilus*; three of which have been reported from Florida and are included herein. These species are readily distinguished from one another based on the morphology of their penial and somatic setae (Table 2). An additional species has been described from the Caribbean (Belize), *P. vicinus* (Erséus, 1990a), and may eventually be recorded from southern Florida.

***Peosidrilus acochlearis* (Erséus and Loden, 1981)**

Adelodrilus acochlearis Erséus and Loden, 1981:821-823, Fig. 1B-1C, 2.

Diagnosis. Length: 2.5-3.9 mm; segments: 27-39. Clitellum extending over $\frac{1}{2}$ X-XII. Somatic setae bifid, 42-62 μm long, anterior dorsal setae and all ventral setae with upper tooth thinner and shorter than lower, 3-5 per bundle; posterior dorsal bundles with "normal" setae and, occasionally, modified setae, lower tooth extremely long, curved downwards and parallel to setal shaft, (2)3-4(5) setae per bundle. Penial setae straight, each with an ectal "club" bearing an apical hook, 30-50 μm long, 8-15 per bundle with ectal ends protruding into small copulatory sac immediately posterior to atrial opening. Male and spermathecal pores paired in posterior of XI and in lateral lines anteriorly in X, respectively. Male genitalia paired: vas deferens thick-walled, very wide, longer than atrium, often convoluted, internally ciliated, but lumen not containing sperm, entering atrium sub-apically. Atrium pear-shaped, 58-82 μm long, 35-43 μm wide with thin outer layer, histologically differentiated into an ental portion with granulated and ciliated inner epithelium, and a non-ciliated, non-granulated eversible ectal portion forming a bulbous pseudopenis with a short, pointed tip when inverted. Anterior prostate gland attached subapically to anterior face of atrium, posterior prostate gland attached opposite to anterior one on posterior of atrium. Spermathecae paired, each with a short, thick-walled duct and slender ampulla. Sperm in random masses in ampullae.

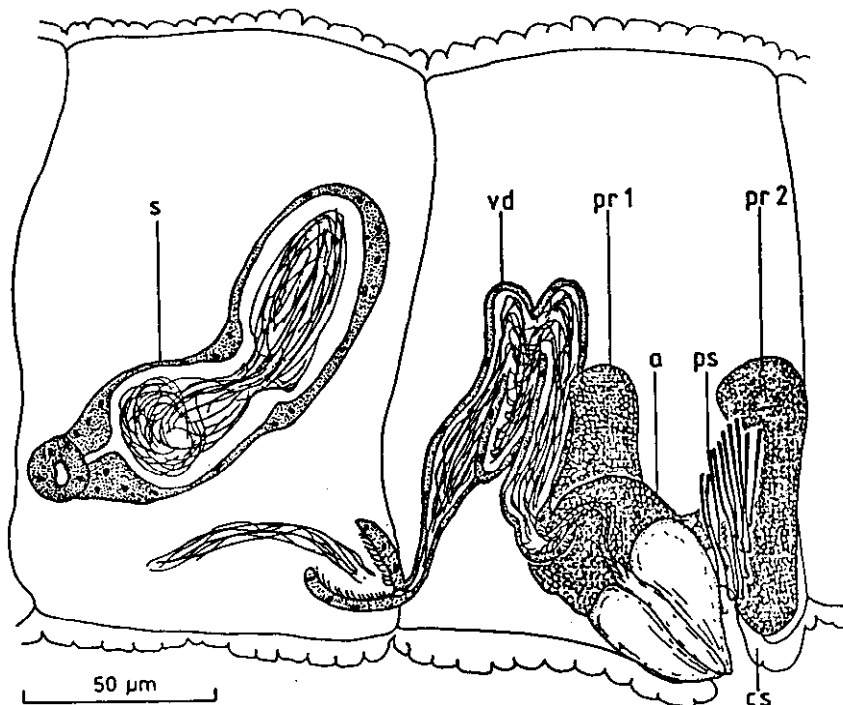
Distribution and Habitat. East coast of North America (North Carolina, east coast of Florida). Associated with very coarse sand with mixed shell in shallow water (< 11 m water), grain size unknown at deeper locations; from 5.5-605 m depth.

Remarks. This species is readily differentiated from all other tubificids in Florida waters by the bipartite atria with a bulbous, non-granular, non-ciliated ectal portion, and the uniquely shaped, posterior dorsal setae: a very prolonged recurved slender lower tooth and very thin, short upper tooth. The numerous, short, club-shaped penial setae is a character shared by many congeners, as well as species of *Bermudrilus* and *Adelodrilus*. *Peosidrilus acochlearis* was originally placed in the genus *Adelodrilus* because Erséus and Loden (1981) thought that the vas deferens "appears filled with sperm". Erséus (1986a) subsequently transferred *A. cochlearis* with *Phallogrilus* after an examination of new material indicated that the original

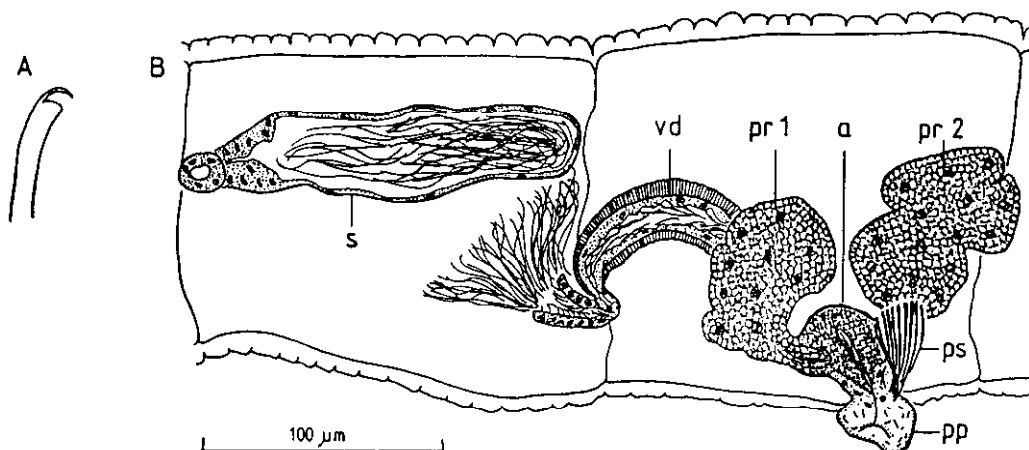
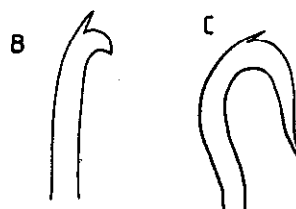
description did not accurately reflect "the true appearance of its vas deferentia", and that they "are ciliated, but they do not store sperm". Upon revising *Phallodrilus*, Erséus (1992a) included *A. acochlearis* with the re-established *Peosidrilus* based on the lateral position of the spermathecal pores (ventral in *Bermudrilus* and *Adelodrilus*), and club-shaped setae.

The shape of the modified posterior dorsal setae and penial setae of *P. acochlearis* is shared by a congener, *P. boeschi* (Erséus, 1984b), also found on the east coast of North America (but not south of Virginia), but the atria of the latter are not bipartite, and the lower tooth of the modified setae are much longer and vas deferens much wider in *P. acochlearis*.

(after Eréus and Loden, 1981) *Peosidrilus acocklearis*: lateral view of genitalia in segments X-XI.



(after Eréus and Loden, 1981) *Peosidrilus acocklearis*: B, free-hand drawing of anterior, somatic seta; C, free-hand drawing of posterior, dorsal, somatic seta.



(after Eréus, 1986a) *Peosidrilus acocklearis*: A, tip of penial seta; B, lateral view of spermatheca and male genitalia in segments X-XI.

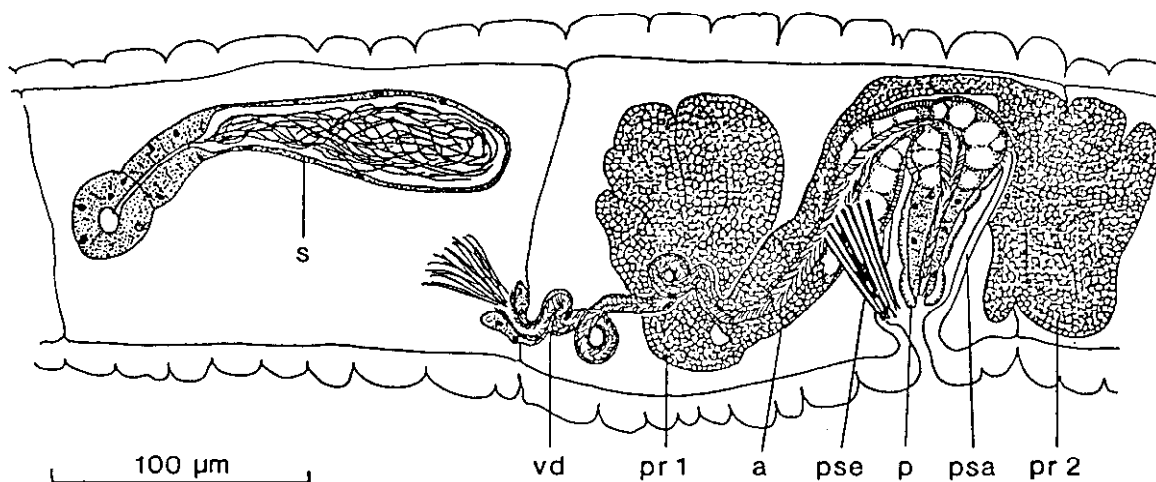
***Peosidrilus biprostatus* Baker and Erséus, 1979**

Peosidrilus biprostatus Baker and Erséus, 1979:506-508, Figs. 1, 2.

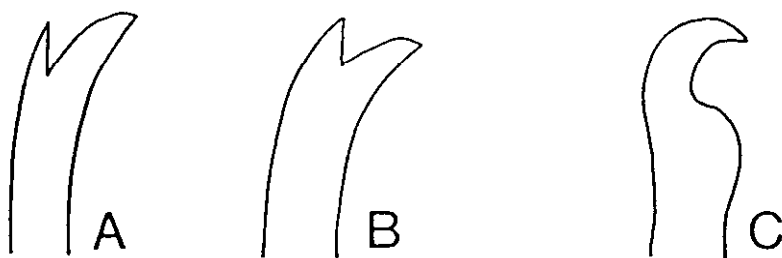
Diagnosis. Length: 4.5-9.5 mm; segments: 38-62. Clitellum extending over $\frac{1}{2}$ X-XII. Somatic setae bifid with upper tooth thinner and shorter than lower, becoming broader posteriorly, about 47 μm long, 3-4 per bundle. Penial setae straight, each with an ectal "club" and an apical strongly curved hook, 30-37 μm long, 7-13 setae per bundle with ectal ends protruding into copulatory sac immediately anterior to atrial opening. Male and spermathecal pores paired in posterior of IX and in lateral lines anteriorly in X, respectively. Male genitalia paired: vas deferens thin-walled, slender, somewhat longer than atrium, internally ciliated, 6-8 μm wide, entering atrium apically. Atrium long, cylindrical, 90-140 μm long, 27-37 μm wide, with thin outer layer; inner epithelium generally densely granulated and ciliated; ventral-middle and ectal parts non-granulated, but with very large vacuolized cells. Anterior prostate gland large attached by narrow stalk subapically on anterior face of atrium near entrance of vas deferens, posterior prostate gland large attached by a very long narrow stalk to middle-to-ectal region of posterior face of atrium. Voluminous pear-shaped penis with a slightly bulbous tip, separated from atrium by a constriction, 30-40 μm long, 12-16 μm wide; inner epithelium of penis ciliated with large vacuolized cells basally; enclosed in deep copulatory (penial) sac. Spermathecae paired, each with a thick-walled duct and thin-walled, somewhat elongate ampulla. Sperm in random masses in ampullae.

Distribution and Habitat. Eastern North America (panhandle and east coast of Florida, North Carolina, New Jersey, Massachusetts). Associated with coarse to medium sand; subtidal, 5.5-605 m depth.

Remarks. The voluminous penes with large vacuoles and typical "*Peosidrilus*-type" club-shaped penial setae with strong apical hooks and unmodified posterior setae characterize *P. biprostatus*. *Peosidrilus* was originally established to separate *P. biprostatus* from similar species of *Phallodrilus* because of its very conspicuous true penes (Baker and Erséus, 1979). Erséus (1984b) concluded that the penis of *P. biprostatus* was simply an "elaboration of the pseudopenial structure found in several *Phallodrilus* forms" and, consequently, transferred it to *Phallodrilus*. When Erséus (1992a) restructured *Phallodrilus*, *Peosidrilus* was resurrected (with *P. biprostatus* as the type species) because of the lateral spermathecal pores and "*Peosidrilus*-type" penial setae.



(after Baker and Brásus, 1979) *Peosidrillus biprostatatus*: lateral view of spermatheca and male genitalia in segments X and XI.



(after Baker and Brásus, 1979) *Peosidrillus biprostatatus*: A, ectal tip of anterior somatic seta; B, ectal tip of posterior somatic seta; C, ectal tip of penial seta.

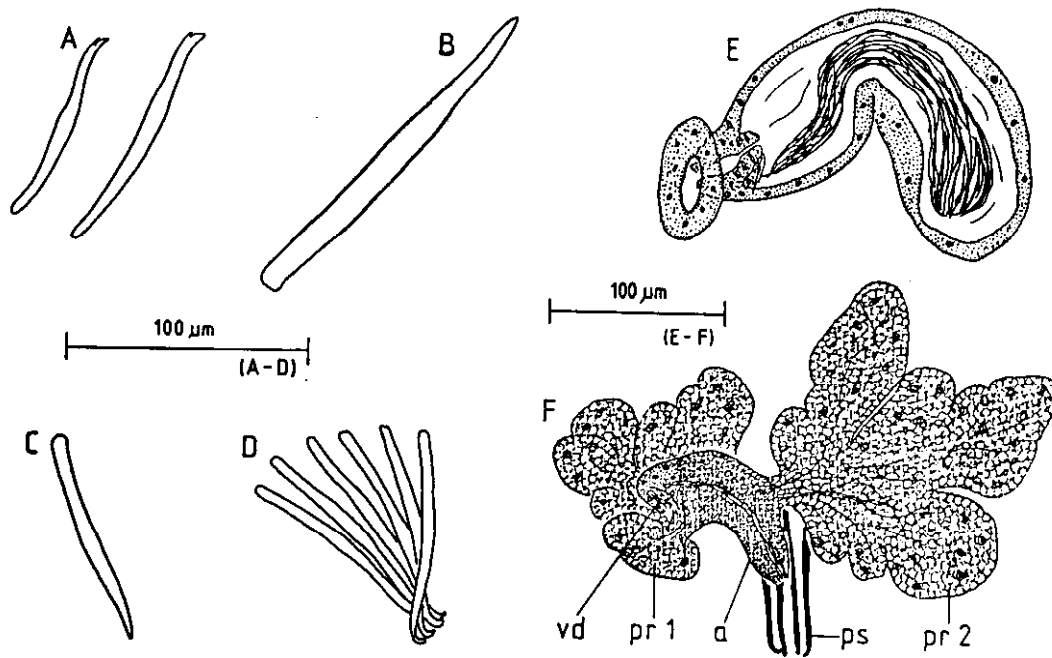
***Peosidrilus hirsutus* (Erséus, 1986)**

Phallodrilus hirsutus Erséus, 1986a:298-299, Fig. 8.

Diagnosis. Length: 16.1 mm; segments: 86. Body large. Clitellum extending over $\frac{1}{2}$ X-XII. Anterior somatic setae bifid with very thin, short upper tooth, 70-140 μm long, two per bundle in II-IX(X); posterior from X setae simple-pointed, straight, relatively thick, one per bundle, 140-165 μm long dorsally and 95-95 μm long ventrally. Penial setae more or less straight, ectally pointed and hooked, 4-6 per bundle. Male and spermathecal pores paired in XI and in lateral lines anteriorly in X, respectively. Male genitalia paired: vas deferens relatively wide, longer than atrium, 16-19 μm wide entering atrium apically. Atrium somewhat spindle-shaped and curved, about 105 μm long, 40 μm wide, with thin outer layer; inner epithelium densely granulated. Anterior prostate gland very large, attached subapically on anterior face of atrium, posterior prostate gland very large, attached sub-medially to posterior face. Copulatory sac indistinct, but may be present. Spermathecae paired, elongate each with short thick-walled duct, and thin-walled ampulla, somewhat constricted medially. Sperm arranged as large bundles in ampullae.

Distribution and Habitat. Southeast North America (east coast of Florida). Associated with coarse, clean or somewhat muddy sands; 10-11 m depth.

Remarks. This species has characteristic "*Peosidrilus*-type" penial setae, but has unique somatic setae, more reminiscent of *Heterodrilus* (*H. hispidus*) and *Bathydrielus rarisetis* (Erséus, 1975a) than its congeners: anterior bundles bisetal; postsetal bundles with one stout simple-pointed seta, from which the specific epithet is derived ("shaggy, bristly").



(after Erasus, 1986a) *Peosidrilus hirsutus*: A, anterior setae; B, posterior dorsal seta; C, posterior ventral seta; D, penial setae; E, spermatheca; F, male genitalia.

Genus. *Peosidriloides* Erséus and Milligan, 1994

Type Species. *Phallodrilus flabellifer* Erséus, 1984.

Diagnosis. Marine tubificids. Clitellum short, maximally extending over posterior third of X, all of XI, and anterior two-thirds of XII. Somatic setae bifid with upper tooth thinner and shorter than lower, subdental ligament may be present. Penial setae small, simple-pointed with curved tips (tips may be somewhat club-shaped in *P. flabellifer*), numerous (>10), densely packed in a fan-shape. Male and spermathecal pores paired, ventral in XI and X, respectively. Male genitalia paired: vas deferens ciliated, narrow, several times longer than atrium, entering atrium apically. Atria cylindrical or somewhat spindle-shaped, horizontal, but slightly curved toward male pores. Anterior prostate gland attached near entrance of vas deferens on anterior face of atrium, posterior prostate gland attached ectally on posterior face. Atrium terminating as either a simple pore opening directly to the exterior (*P. flabellifer*) or as a penis-like organ (*P. hornensis*). Spermathecae paired, each with a discrete duct with indistinct ectal vestibule, and thin-walled, elongate ampulla. Sperm as random masses in ampullae.

Remarks. Erséus and Milligan (1994) established this genus in an attempt to make the newly re-established genus, *Peosidrilus* "more monophyletic" by excluding the only species with ventral spermathecal pores and combining it with a new species sharing that character in addition to "*Peosidrilus*-type" penial setae. In addition to the ventral position of the spermathecal pore, the two species now included in *Peosidriloides* are also distinguished from *Peosidrilus* by having vas deferentia several times longer than the atria (about as long or a little longer in *Peosidrilus*), and a shorter clitellum.

Peosidrilus hornensis is the only species expected to be collected in Florida waters since the type location is immediately west of the Florida panhandle on a barrier island in the northern Gulf of Mexico. Its congener, *P. flabellifer*, is unlikely to occur in the shallow Florida waters: it has only been recorded from the deep water of Georges Banks off Massachusetts.

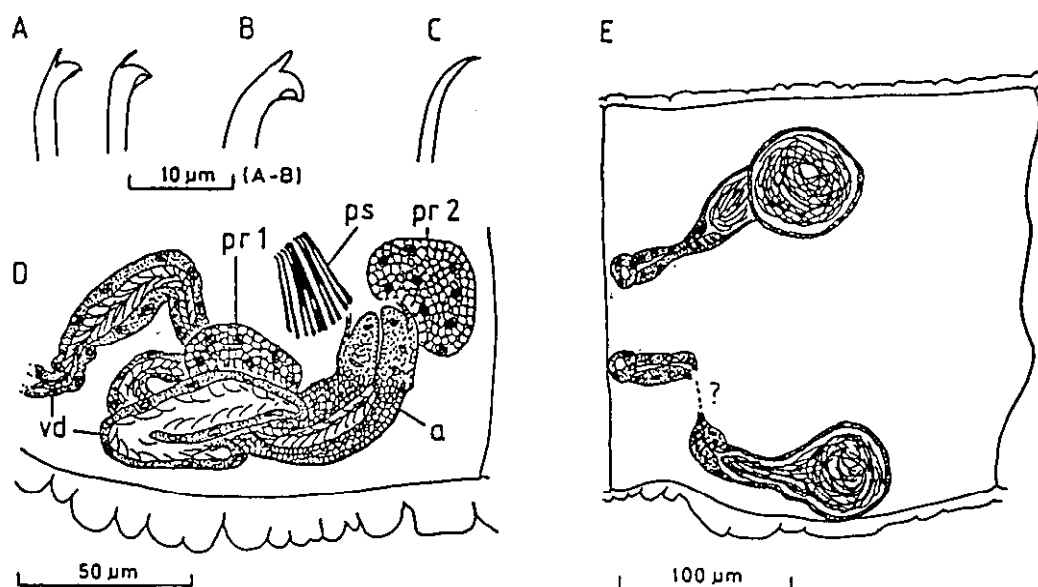
***Peosidriloides hornensis* Erséus and Milligan, 1994**

Peosidriloides hornensis Erséus and Milligan, 1994:637-638, Fig. 1.

Diagnosis. Length: 6.1-8.2 mm; segments: 59-60. Clitellum extending over $\frac{2}{3}$ X- $\frac{2}{3}$ XII. Somatic setae bifid with upper tooth thinner and shorter, subdental ligament present; 35-50 μ m long, 2-3(4) per bundle anteriorly, two per bundle posteriorly. Penial setae simple-pointed with curved, thin tips, 25-35 μ m long, 7-12 per bundle, densely packed close together within each bundle. Male and spermathecal pores paired in posterior of XI and ventrally in anterior of X, respectively. Male genitalia paired: vas deferens relatively wide, coiled, several times longer than atrium, entering atrium apically. Atrium cylindrical, somewhat spindle-shaped, slightly curved; 45-60 μ m long, 20-22 μ m wide, with thin outer layer; inner epithelium granulated and ciliated. Anterior prostate gland small, attached near entrance of va deferens on anterior face of atrium, posterior prostate gland small, attached ectally, near penial organ on posterior margin of atrium. Atrium terminating in a simple copulatory organ (penis?), possibly a fully pendent penis in a copulatory sac. Spermathecae paired, each with a slender duct, somewhat constricted medially and a pear-shaped, thin-walled ampulla. Sperm in random mass in ampullae.

Distribution and Habitat. Eastern North America (northern Gulf of Mexico: Horn Island, a barrier island off Mississippi). Associated with saline intertidal ponds.

Remarks. This species differs from *P. flabellifer*, its only congener, by having more setae per bundle anteriorly (only two per bundle throughout body of *P. flabellifer*), a wider more dilated vas deferens, and a copulatory apparatus (absent in *P. flabellifer*). *Peosidriloides hornensis* differs from most species of *Peosidrilus* by having thin tipped penial setae without an ectal swelling or "club". This species was only collected from small saline ponds on a barrier island in the Gulf of Mexico, which exhibits extreme fluctuations of temperature and salinity.



(after Erséus and Milligan, 1994) *Peosidriloides hornensis*: A, free-hand drawing of anterior somatic setae; B, free-hand drawing of postclitellar somatic seta; C, free-hand drawing of penial seta; D, male genitalia in segment XI; E, spermathecae in segment X (one spermatheca slightly damaged).

Genus. *Bermudrilus* Erséus, 1979

Type Species. *Bermudrilus peniatus* Erséus, 1979.

Diagnosis. (Based on Erséus, 1992a) Marine tubificids. Somatic setae bifid. Penial setae small, numerous, clubbed with apical hooks. Male and spermathecal pores paired in XI and ventrally in X, respectively. Male genitalia paired: vas deferens large, dilated, thin-walled, containing sperm, entering atrium apically. Atria spindle-shaped, bent or coiled. Large anterior prostate gland attached entally on atrium. Posterior prostate gland absent. Cuticularized penis sheath present. Spermathecae paired. Sperm as random masses.

Remarks. This species is characterized by the unique combination of "Peosidrilus-type" penial setae and a cuticularized penis sheath. The lack of the posterior prostate gland is also diagnostic for this genus, shared by very few other phallodriline species, and is differentiated from the very large genus, *Peosidrilus*, which also has small numerous club-shaped penial setae, by having ventral instead of lateral, as in *Peosidrilus*, spermathecal pores. *Bermudrilus* is a monotypic genus which has been reported off the west coast of Florida.

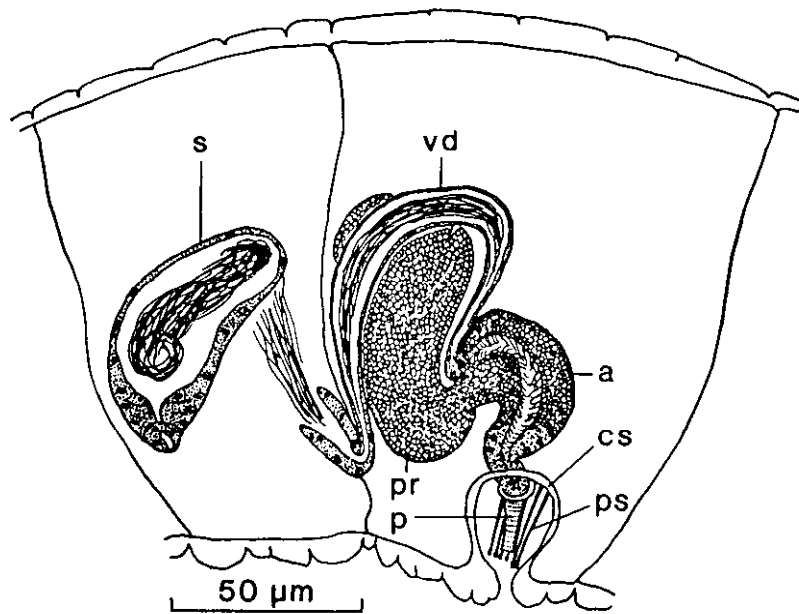
***Bermudrilus peniatus* Erséus, 1979**

Bermudrilus peniatus Erséus, 1979d:425-426, Fig. 4.

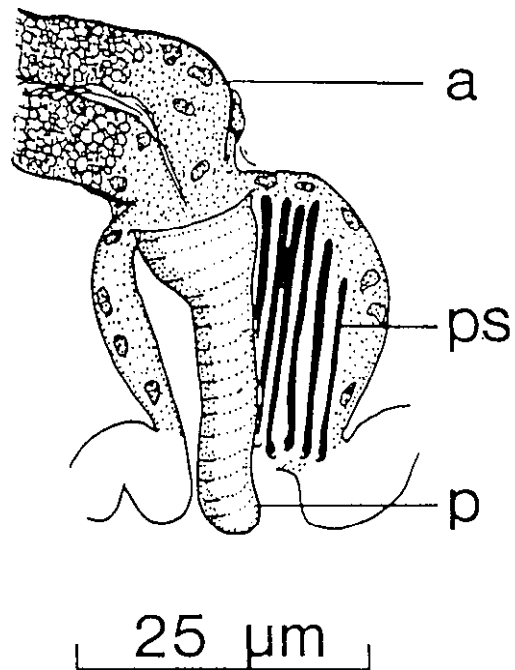
Diagnosis. Length: 3.0-4.1 mm; segments: 39-41. Secondary annulations numerous. Clitellum extending over $\frac{1}{2}$ X(XI)- $\frac{1}{2}$ XII. Somatic setae bifid with upper tooth equal or subequal to lower, 28-35 μ m long, 2-4 per bundle anteriorly and (1)2 posteriorly. Penial setae straight, simple-pointed, club-shaped, with a thin, strongly hooked ectal tooth, 16-25 μ m long, (4,5)6-7 per bundle, located immediately median to penes in copulatory sacs. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Male genitalia paired: vas deferens containing sperm, relatively narrow, somewhat dilated medially, without ciliation, 10 μ m wide, entering atrium apically. Atrium spindle-shaped, bent or coiled, 50-60 μ m long, 20-30 μ m wide; thick inner epithelium ciliated and strongly granulated; outer lining slender. Atrium less granulated ectally, terminating in a funnel-shaped, cuticularized penis, 18-30 μ m long, 8-11 μ m wide basally, located relatively free in a spherical copulatory sac. Large anterior prostate gland attached entally on anterior face of atrium; posterior prostate gland absent. Spermathecae paired, each with indistinct duct and thin-walled oval ampulla. Sperm as random mass.

Distribution and Habitat. Bermuda, southeast North America (west coast of Florida). Associated with medium-coarse sand; subtidal, 10-75 m depth.

Remarks. The "*Peosidrilus*-type" penial setae and cuticular penis sheaths characterize this species. See Remarks for the genus.



(after Ers6us, 1979d) *Bermudrilus peniatus*: lateral view of genital organs in segments X-XI.



(after Ers6us, 1984c) *Bermudrilus peniatus* from off west coast of Florida: showing ectal part of atrium (a), penis (p), and penial setae (ps).

Genus. *Adelodrilus* Cook, 1969

Type Species. *Adelodrilus anisosetosus* Cook, 1969.

Diagnosis. (Based on Erséus, 1992a) Marine tubificids. Somatic setae bifid with upper tooth thinner and shorter (or absent altogether posteriorly) than lower. Penial setae include at least one large, generally spoon-shaped seta and usually a high number of smaller setae. The latter either clubbed with apical hooks, simple-pointed and curved, or with fringed apical tips. Modified genital setae may also be present in X or IX-X. Male and spermathecal pores paired, ventrally in XI and X, respectively. Male genitalia paired: vas deferens large, dilated medially, thin-walled, non-ciliated, containing sperm; entering atrium apically. Atrium generally short with an anterior and posterior prostate gland; generally opening into well-developed copulatory sac. Pseudopenes may be present, true pendant penes absent. Spermathecae paired, slender; ectal vestibules of the spermathecal ducts may be present. Sperm as random masses.

Remarks. The highly modified enlarged spoon-shaped penial seta distinguishes this genus from all other taxa of tubificids in Florida waters. Although many species within this genus occur on the eastern seaboard of North America, only one, *A. magnithecatus*, has been reported south of New Jersey, and has been collected off the west coast of Florida.

Adelodriloides was established by Cook (1970) to accommodate *A. voraginus*, with a giant penial setae and a row of smaller penial setae, characteristics of *Adelodrilus*; however, *A. voraginus* lacks prostate glands. Erséus (1978a) synonymized *Adelodriloides* with *Adelodrilus* because of the similarity with regard to the principal organization of the male genitalia and presence of large penial setae. The lack of prostate glands was considered a secondary reduction.

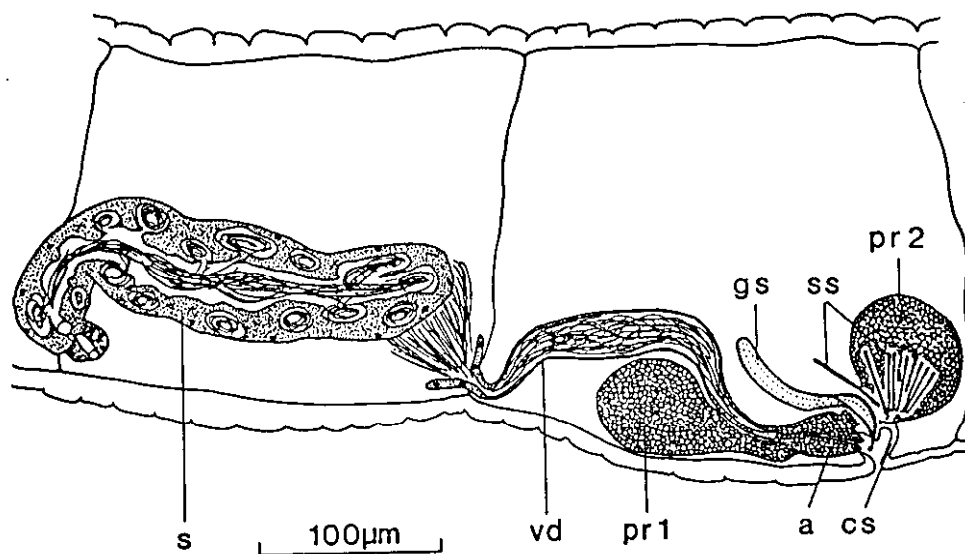
***Adelodrilus magnithecatus* Erséus, 1979**

Adelodrilus magnithecatus Erséus, 1979d:419-321, Fig. 1.

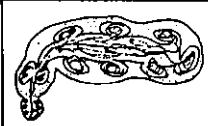
Diagnosis. Length: 2.9-6.5 mm; segments: 26-57. Secondary annulations present, 4-5 per segment. Clitellum extending over $\frac{1}{2}$ X-XII. Somatic setae bifid with upper tooth thinner and shorter than lower anteriorly, 40-50 μ m long, (1)2(3) per bundle throughout body; dorsal setae sharply pointed or with very reduced upper tooth posteriorly. Bundles of penial setae include one giant, sigmoid spoon-shaped setae, 75-115 μ m long, and a row of (4)5-8 smaller apically hooked penial setae, 20-55 μ m long, with thicker ental and ectal ends; projecting, in association with the atrium, into a small copulatory sac. Male and spermathecal pores paired ventrally in posterior of XI and ventrolaterally in anterior of X, respectively. Male genitalia paired: vas deferens large, dilated medially, thin-walled, non-ciliated, containing sperm, 16-37 μ m wide, 250 μ m long, entering atrium apically. Atrium small, 35-60 μ m long, 25-40 μ m wide; thick inner epithelium, granulated, ciliation indistinct (present?); outer layer thin; terminating directly into a small copulatory sac. Anterior prostate gland attached entally to anterior face of atrium; posterior prostate gland attached ectally on atrium at entrance to copulatory sac. Spermathecae paired, each with a short thick-walled distinct duct, and large, oblong, thick-walled ampulla. Sperm arranged as bundles in ampullae, additionally, numerous small balls or rings of sperm are located in cavities within the walls of the ampullae.

Distribution and Habitat. Bermuda, east coast of North America (North Carolina, east coast of Florida). Associated with coarse sand; subtidally 4.5-17 m depth.

Remarks. The large spoon-shaped penial setae and associated smaller club-shaped penials readily distinguish this species from all other tubificids reported from southeast North America. The thick, "spongy", walls of the spermathecae, from which the specific epithet is derived, characterizes this species.



(after Bréthes, 1979d) *Adelodrilus magnihectatus*: lateral view of genital organs in segments X-XI.

Penial setae (whole bundle)	Ectal tip of smaller penial setae	Spermatheca
		

(after Bréthes, 1983c) *Adelodrilus magnihectatus*

Genus. *Aktedrilus* Knöllner, 1935

Type Species. *Aktedrilus monospermathecus* Knöllner, 1935.

Diagnosis. Littoral marine tubificids. Somatic setae bifid, subdental ligament present in some species. Modified penial and spermathecal setae absent. Male pores paired ventrally in posterior of XI. Spermathecal pores unpaired mid-dorsally in anterior of X, or absent. Male genitalia paired: vas deferens variable in length, entering atrium apically. Anterior prostate gland attached entally on atrium; posterior prostate gland either discretely attached to ental end of atrium, or broadly attached to base and/or wall of penial (copulatory) sac. Prominent penes present, with or without cuticular penis sheaths (penes may be reduced to "lips" protruding into a complex, folded copulatory sac). Spermatheca unpaired or absent; when present, ampulla generally shorter than duct. Sperm in loose mass or bundles in ampullae, or attached externally to the body as round spermatophores.

Remarks. This is a speciose genus of littoral, meiobenthic tubificids. Species within this genus are characterized by: 1) absence of penial setae; 2) generally well-developed penes, and 3) mid-dorsal, or absent, unpaired spermatheca with a reduced ampulla. More than 30 species have been described worldwide. Although five species have been reported from Bermuda and the Caribbean, only *A. floridensis* has been reported from Florida waters. Because of the small size and general lack of distinguishing external characteristics, this is a very difficult species to identify. The unique habitat, generally intertidal in clean sand, is, however, very indicative for this genus.

Knöllner (1935) originally established this genus. Hrabe (1973) described a related genus, *Bacescuella*, for a species differentiated from the former taxon by the "structure of the male duct... not provided with a sperm duct" (vas deferens), and absence of spermathecae. Subsequently, Erséus (1978b) refined the definition to include species "with or without a short vas deferens", and species with an unpaired mid-dorsal spermatheca. Erséus (1980) further modified the definition restricting it to species with penes without "cuticular linings" and absent or a small spermathecal ampulla. Baker and Erséus (1982) emended the definition specifying the lack of genital setae, and the atria terminating in "either a protrusible penis, or highly modified lips". Erséus (1987a), recognizing the close relationship of *Bacescuella* and *Aktedrilus*, synonymized them, making the former genus a junior

synonym to *Akteredrilus*. Since 1987, additional species have been described from Hong Kong, Australia, and Spain.

Species which may also occur in Florida waters, primarily in the vicinity of the Keys, are: *A. locyi* Erséus, 1980, *A. monospermathecus*, *A. parvithecatus* Erséus, 1980, and *A. longitubularis* Finogenova and Shurova, 1980.

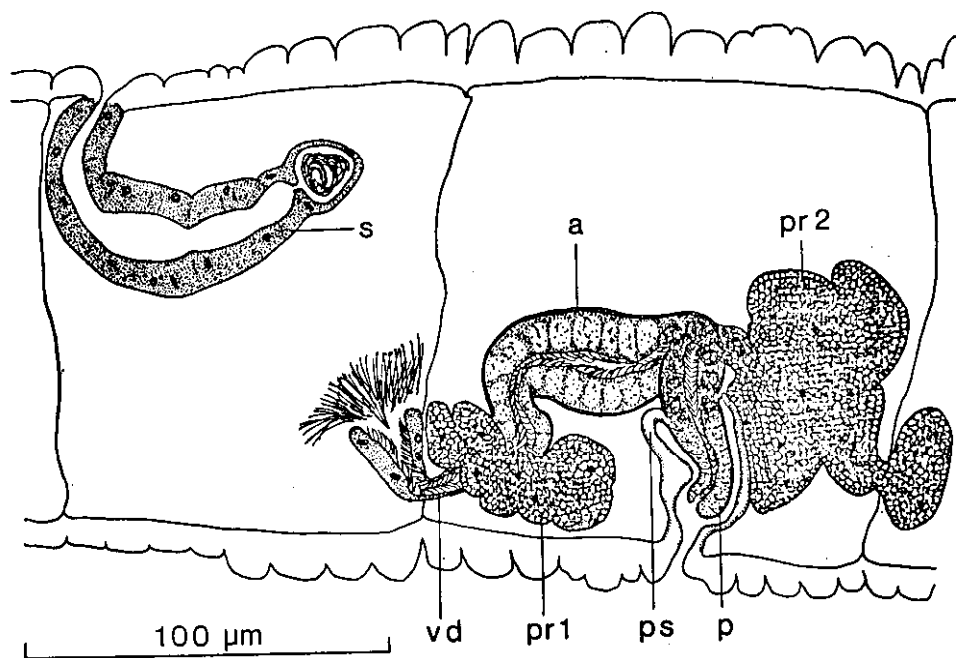
***Akteredrilus floridensis* Erséus, 1980**

Akteredrilus floridensis Erséus, 1980:103-104, Fig. 7.

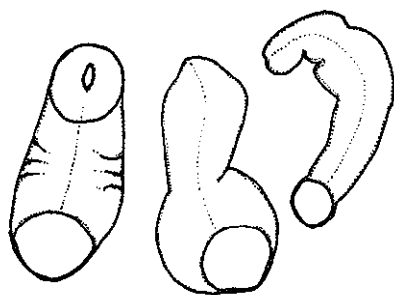
Diagnosis. Length: 1.7-3.0 mm; segments: 27-39. Clitellum extending over $\frac{1}{2}$ X-XII. Somatic setae bifid with upper tooth thinner and slightly shorter than lower, 20-30 μm long, 4-6(7) per bundle anteriorly, (2)3-4(5) per bundle posteriorly. Genital setae absent. Male pores paired, located somewhat posteriorly in XI. Spermathecal pore mid-dorsal, anteriorly in X. Male genitalia paired: vas deferens narrow, shorter than atrium, 7 μm wide, ciliated, entering atrium apically. Atrium cylindrical, 34-55 μm long, 15-20 μm wide, thick inner epithelium, ciliated; conspicuously granulated ectally, outer layer thin. Anterior prostate gland surrounding atrium entally; posterior prostate gland large, attached to ectal part of posterior face of atrium. Penis funnel-shaped, cuticularized, 35-55 μm long, 15-20 μm wide basally. Spermatheca single, with a long duct and small-spherical to pear-shaped ampulla. Sperm as small masses in ampulla.

Distribution and Habitat. Caribbean (Barbados), southeast coast of North America (Keys of Florida), Hong Kong (Erséus, personal communication). Associated with intertidal sand.

Remarks. This is a vary difficult species to identify because of the lack of distinguishing external characters. See Remarks for the genus for more details. In the original description, Erséus (1980) did not specify interspecific distinguishing characteristics, but *A. floridensis* may be separated from its congeners by the funnel-shaped, but not so long, weakly cuticularized penes, and the slender spermatheca, which has a relatively long duct and a very short, but clearly set-off, ampulla. Therefore, until additional specimens are available for review and more distinctive species specific characters are defined, individuals conforming to the specific diagnosis are best left at the generic level.



(after Eršov, 1980) *Akedrilus floridensis*: lateral view of genital organs in segments X and XI.



(after Eršov, 1980) *Akedrilus floridensis*: intraspecific variation of spermathecae (all spermathecal ampulla are directed toward bottom of figure).



(after Eršov, 1980) *Akedrilus floridensis*: somatic seta.

Table 3. Species of gutless tubificids.

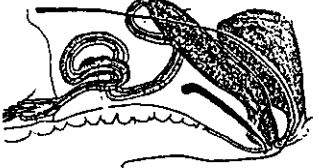
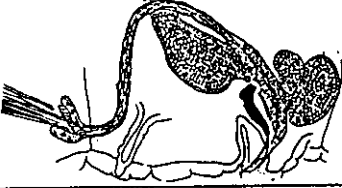
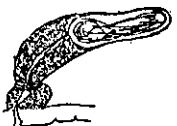
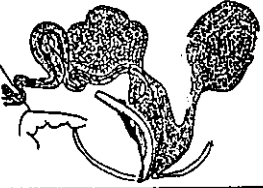
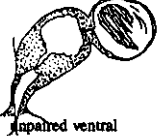
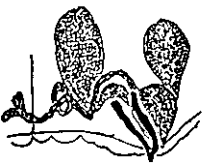
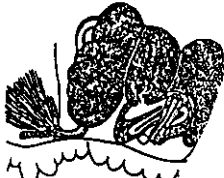
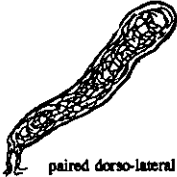
Taxon	Somatic Setae		Penial Setae #/bundle	Spermatheca	Male Genitalia
	Ant.	Post.			
<i>Inanidrilus aduncosetis</i>				 paired ventral	
<i>Inanidrilus bulbosus</i>	Teeth equal No ligament		See Male Genitalia	 unpaired middorsal	
<i>Inanidrilus ernesti</i>				 paired ventral	
<i>Inanidrilus extremus</i>	Upper tooth shorter with ligament			 paired ventral	
<i>Inanidrilus leukodermatus</i>				 paired ventral	
<i>Inanidrilus mexicanus</i>				 paired lateral	
<i>Inanidrilus triangulatus</i>				 paired ventral	
<i>Inanidrilus vacivus</i>				 unpaired ventral	

Table 3. Species of gutless tubificids. Continued.

Taxon	Somatic Setae		Penial Setae #/bundle	Spermatheca	Male Genitalia
	Ant.	Post.			
<i>Olavius caudatus</i>	Upper tooth shorter ligament present 2-5	2-3(4)	1-2(3)	 paired ventral	
<i>Olavius imperfectus</i>	 2-3	(1)2	 (2)3(4)	 paired lateral	
<i>Olavius latus</i>	 3-4	2-3	 5-6	 paired lateral	
<i>Olavius tenuissimus</i>	 3	2(3)	 (0)1(2)	 paired dorso-lateral	
<i>Olavius vocuus</i>	 (2)3(4)	(1)2(3)	0	 paired lateral	

Genus. *Inanidrilus* Erséus, 1979

Type Species. *Inanidrilus bulbosus* Erséus, 1979.

Diagnosis. (Based on Erséus, 1992a) Body white due to subcuticular symbiotic bacteria. Secondary annulation conspicuous, about 4-8 annuli per segment posteriorly. Somatic setae bifid, frequently with subdental ligament. Modified penial setae generally present, two per bundle, basically sickle-shaped, but may be more elaborated and anisomorphic in some species; tips usually simple-pointed (hooked or flattened) but may be bifid or chisel-shaped. Male pores paired, ventral in XI. Spermathecal pores dorsal, ventral, or lateral, paired or single, anteriorly in X. Mouth, gut, and anus absent. Male genitalia paired: vas deferens longer than atrium, usually coiled, and narrow; entering atrium apically or subapically. Atrium erect, small, spindle-shaped, opening directly to exterior, or elongate, more or less folded, opening into sac associated with penial setae. Anterior prostate gland present or absent. Posterior prostate gland attached to posterior face of atrium. Spermathecae paired or single; duct(s) frequently longer than ampulla(e).

Remarks. This genus is one of the two gutless taxa within the Tubificidae. The lack of a mouth, anus, or alimentary canal, and the very thick, chalky-white body wall with about six distinct secondary annulations immediately distinguishes this as either *Olavius* or *Inanidrilus*. Originally, *Inanidrilus* was established to accommodate a unique species of Tubificidae, *I. bulbosus*, characterized by: lack of alimentary canal, highly modified penial setae, an unpaired dorsal spermatheca, and a single posterior prostate gland on each atrium. Erséus and Baker (1982) emended *Inanidrilus* to allow for species with paired spermathecae and sperm as spermatozeugmata. Subsequently, Erséus (1984c) completed a comprehensive survey and phylogenetic analysis of gutless species, modifying the generic criteria specifying conspicuous secondary annulations, bifid somatic setae, lack of spermathecal setae, generally two sickle-shaped penial setae per bundle, and erect, short atria. The emended generic definition was modified to include species with anterior prostate glands. At that time, he also established an additional genus, *Olavius*, to segregate the gutless species with comma-shaped or horizontal atria which open into copulatory sacs, and generally 1-7 basically straight penial setae per bundle. The most current generic diagnosis of *Inanidrilus* is by Erséus (1992a), which is essentially unmodified from his 1984 definition. *Inanidrilus* is a speciose genus with approximately 22 species, primarily restricted to tropical or

subtropical regions of the world. Fourteen species have been reported from the Caribbean. Eight species are included herein, and have been collected from Florida waters (Table 3). The remaining taxa (*I. scalprum* Erséus, 1984c, *I. belizensis* Erséus, 1984c, *I. reginae* Erséus, 1990c, *I. speroi* Erséus, 1984c, *I. gustavsoni* Erséus, 1984c, *I. falcifer* Erséus and Baker, 1982, and *I. renaudae* Erséus, 1984c) may eventually be recovered from the reef areas of the Florida Keys but have only been thus far collected from isolated areas of the Caribbean.

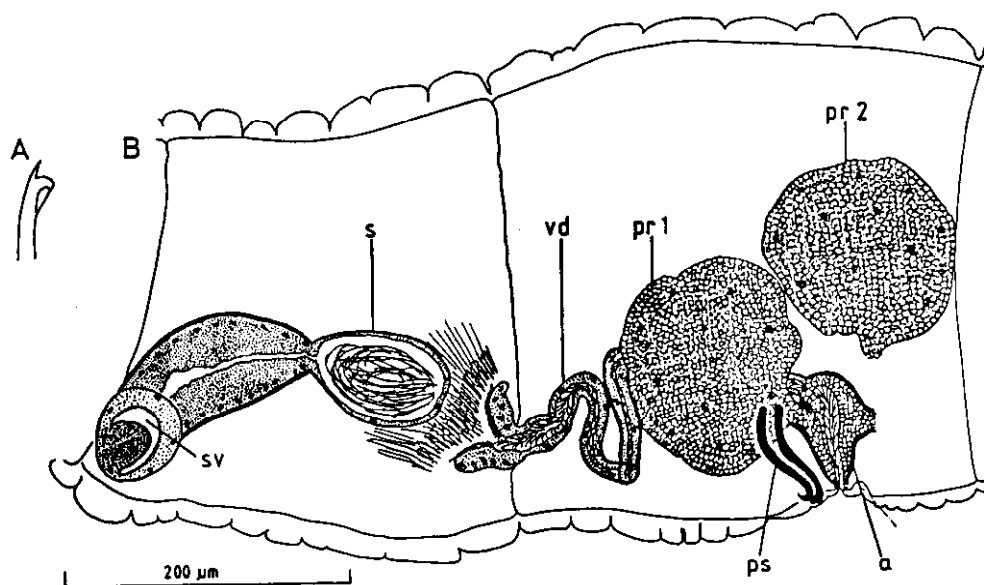
***Inanidrilus aduncosetis* Erséus, 1984**

Inanidrilus aduncosetis Erséus, 1984c:248-249, Fig. 11.

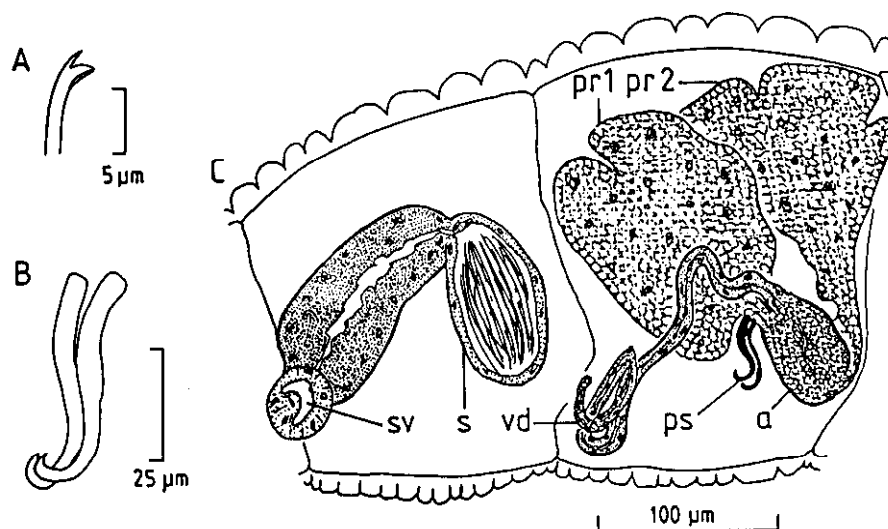
Diagnosis. Length: 10.8-13.4 mm; segments: 81-84. Clitellum extending over $\frac{1}{2}$ X- $\frac{2}{3}$ XII. Secondary annulations 6-7 per segment posteriorly. Somatic setae bifid with upper tooth thinner and shorter than lower and subdental ligament, 30-65 μ m long: (1)2-3 per bundle anteriorly; (1)2 per bundle posteriorly. Penial setae simple-pointed sigmoid, uniformly thick, resembling fishhooks, 50-80 μ m long, two per bundle. Male and spermathecal pores paired ventrally in posterior of XI, and as voluminous vestibules partly occluded by a papilla anteriorly in X, respectively. Male genitalia paired: vas deferens longer than atrium, 7-19 μ m wide; entering atrium subapically. Atrium erect, somewhat pear-shaped, 60-95 μ m long, 35-45 μ m wide; inner epithelium ciliated and granulated; outer lining thick; terminating ectally directly to the exterior through a simple pore. Anterior prostate gland very large, attached by long muscular stalk somewhat entally to anterior face of the atrium; posterior prostate gland very large, attached to posterior face of atrium approximately opposite to anterior gland. Spermathecae paired, each with spindle-shaped or cylindrical thick-walled duct and oval, oblong thin-walled ampulla. Sperm as random masses in spermathecal ampullae.

Distribution and Habitat. Bermuda, Caribbean (Belize). Associated with medium to coarse coral sand; subtidally to at least 8 m depth.

Remarks. The paired, fishhook-shaped (from which this specific epithet is derived), sigmoid penial setae of uniform width distinguish *I. aduncosetis* from most congeners. However, it is included in a complex of *Inanidrilus* species sharing the same morphological characteristics of spermathecae, simple-pointed penial setae, and male efferent ducts. Species included in this complex are *I. leukodermatus* (common throughout the Caribbean and Florida waters), *I. speroi*, *I. fijiensis* Erséus, 1984c, *I. bononii* Erséus, 1984c, and *I. gustavsoni*. See also the description for *I. vacivus* (unpaired spermatheca) for discriminating characteristics. Individuals conforming to the general morphology of any of the aforementioned taxa should be regarded as a member of the *I. leukodermatus* complex until whole communities are scrutinized and compared to the specific diagnosis.



(after Brăeșu, 1984c) *Inanidrilus aduncosetis*: A, free-hand drawing of somatic seta; B, lateral view of genitalia in segments X-XI.



(after Brăeșu, 1990a) *Inanidrilus aduncosetis*: A, somatic seta; B, penial setae; C, lateral view of spermatheca and male genitalia in segments X-XI.

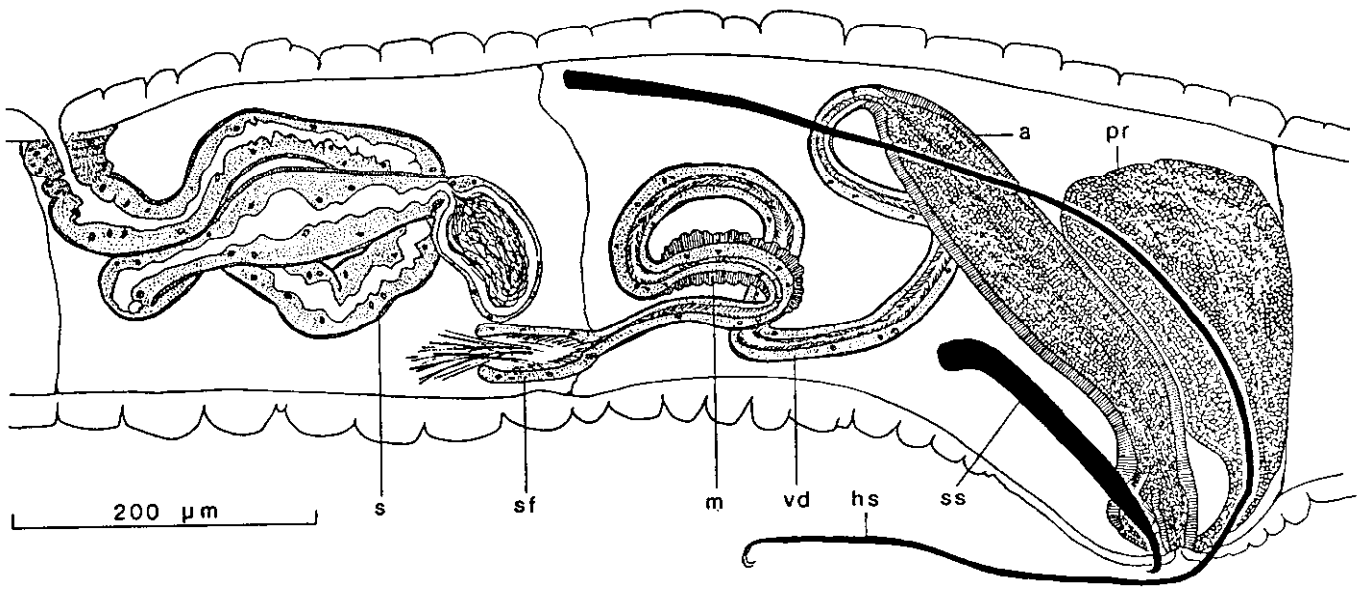
***Inanidrilus bulbosus* Erséus, 1979**

Inanidrilus bulbosus Erséus, 1979e:209-210, Fig. 1.

Diagnosis. Length: 5.7-5.8 mm; segments: 36-42. Clitellum extending over ½ X-XII. Secondary annulations 7-8 per segment posteriorly. Somatic setae bifid with upper tooth thinner but about as long as lower without a subdental ligament, 30-45 µm long, two per bundle throughout; absent dorsally in XI. Penial setae include one very long, simple-pointed hairlike seta, strongly hooked ectally, about 500 µm long; and a shorter, wider simple-pointed setae generally straight but slightly curved entally and slightly hooked ectally, 115-120 µm long. Male pores paired, located in bulbous, large ventral protuberances in posterior of XI. Spermathecal pore unpaired, middorsal in anterior of X. Male genitalia paired: vas deferens long, coiled, 8-13 µm wide; entering atrium apically. Atrium slender, spindle-shaped, 180 µm long, 35 µm wide; inner epithelium ciliated and granulated; outer layer very thick, terminating ectally directly to the exterior through a simple pore. Anterior prostate gland absent; posterior prostate gland large, pedunculate, attached to atrium posteriorly on ectal-most portion. Spermathecae single, with a very long tubular, thick-walled duct and relatively small, oval ampulla. Sperm as a random mass in the spermathecal ampulla.

Distribution and Habitat. Southeast North America (east and west coasts of Florida). Associated with fine to medium sand; subtidally from 2-4 m depth.

Remarks. The unique anisomorphic morphology of the penial setae distinguishes this species from all tubificids. The most closely related taxa are *I. falcifer* from Barbados, and *I. mexicanus*, also from Florida waters. Relative lengths of the penial setae within each bundle differentiate these taxa. Additionally, *I. falcifer* and *I. mexicanus* have paired ventral spermathecae and 2-3 setae per bundle anteriorly (only two in *I. bulbosus*). *I. mexicanus* is also similar to *I. bulbosus* in lacking an anterior prostate gland and subdental ligament on the somatic setae. *I. renaudae*, from the Caribbean, also has anisomorphic penial setae, one being very long, hairlike, and the other being short and sigmoid. The aforementioned species is differentiated from *I. bulbosus* by having generally three setae per bundle anteriorly, an anterior prostate gland, and paired ventral spermathecae; the posterior prostate gland is also located medially on the posterior face of the atrium in *I. renaudae*. A recently described species from southwestern Australia, *I. elaboratus* Erséus, 1990b, also has anisomorphic penial setae similar to *I. bulbosus* and *I. renaudae*, but is more similar to the latter because of the paired ventral spermathecae and presence of an anterior prostate gland. A reexamination of *I. extremus* has indicated that it may also have a small companion penial seta in each bundle (Erséus, personal communication).



(after Bräts, 1979e) *Inanidrilus balborus*: lateral view of genital organs in segments X and XI.

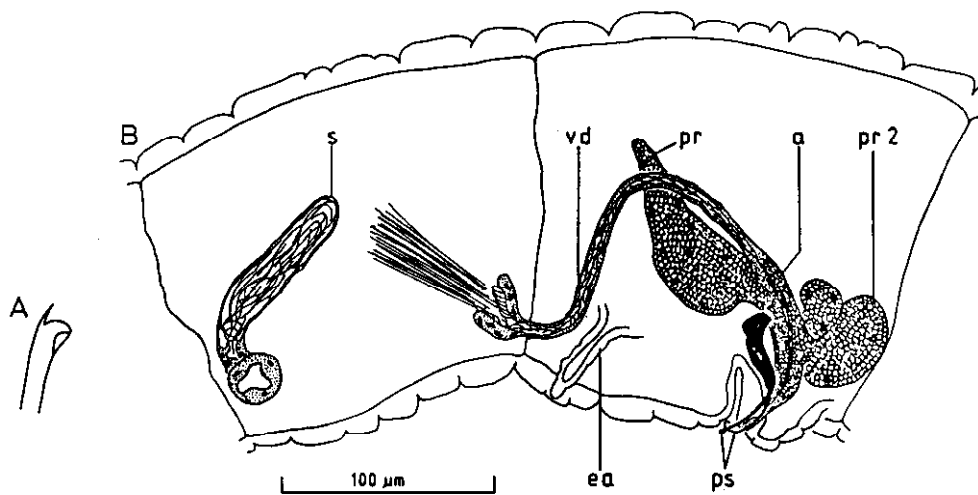
Inanidrilus ernesti Erséus, 1984

Phallodrilus ernesti Erséus, 1984c:251, Fig. 14.

Diagnosis. Length: 3.9-6.7 mm; segments: 34-46. Secondary annulations, six per segment posteriorly. Clitellum extending over $\frac{2}{3}$ X- $\frac{2}{3}$ XII. Somatic setae bifid with upper tooth shorter and thinner than lower, subdental ligament present, 45-60 μ m long, 2-3 per bundle anteriorly; two per bundle posteriorly. Penial setae sickle-shaped, 70-80 μ m long, two per bundle, somewhat anisomorphic; one setae simple-pointed with a very thin, strongly hooked tip, entally expanded; other penial seta with a thicker, blunt tip, also entally expanded. A pair of filiform appendages protrude from ventrum, anteriorly in XI. Male and spermathecal pores paired, posteriorly in XI and anteriorly in X, respectively. Male genitalia paired: vas deferens much longer than atrium and narrow, 5-6 μ m wide; entering atrium apically. Atrium small, slender, tapering ectally, 45-75 μ m long, 12-16 μ m wide; inner epithelium ciliated(?) and granulated; outer layer thin; terminating directly to the exterior, posterior to a slight invagination, into which tips of penial setae protrude. Anterior prostate gland attached immediately ectal to entrance of vas deferens on anterior face of atrium; posterior prostate gland attached to middle-to-ectal posterior face of atrium. Spermathecae paired, each with indistinct duct and thin-walled elongate ampulla. Sperm in random masses in spermathecal ampullae.

Distribution and Habitat. Southeast North America (east coast of Florida). Associated with coarse sand; barely subtidal to 11 m depth.

Remarks. The characteristic shape of the slightly anisomorphic penial setae (one sharp-tipped and one blunt-tipped) and ventral filiform appendages in XI, distinguish this species from all tubificids.



(after Ers6us, 1984c) *Inanidrilus ernesti*: A, free-hand drawing of somatic seta; B, lateral view of genitalia in segments X-XI.

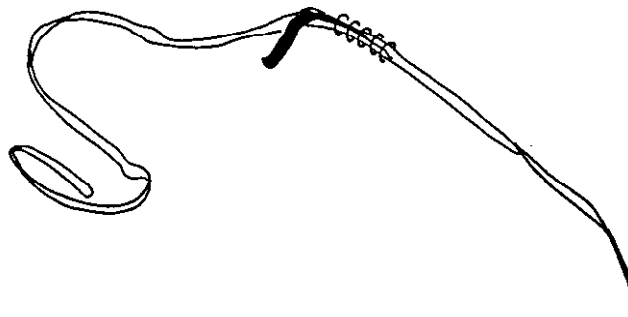
Inanidrilus extremus Erséus, 1979

Inanidrilus extremus Erséus, 1979b:202-203, Fig. 26-27.

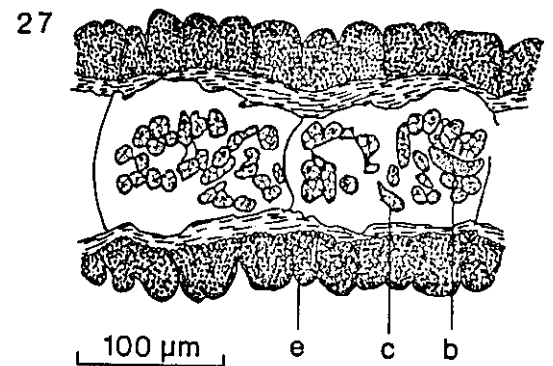
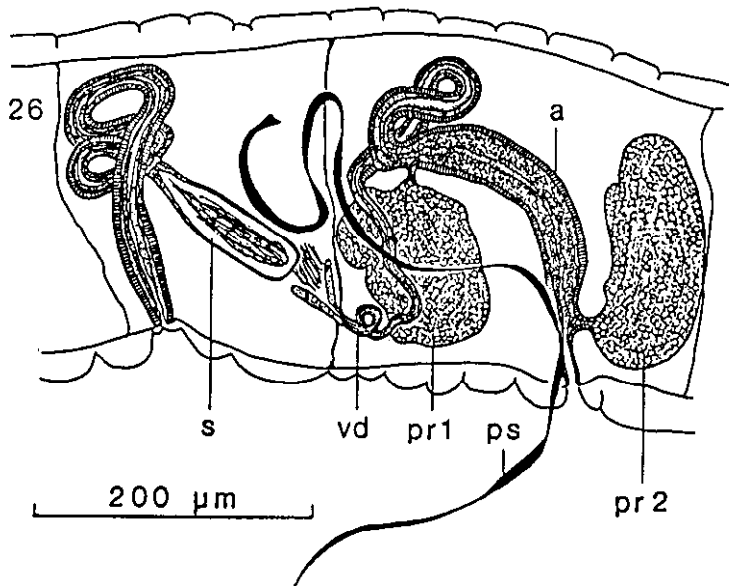
Diagnosis. Length: 4.4-6.9 mm; segments: 34-47. Secondary annulations, 4-6 per segment posteriorly. Clitellum extending over $\frac{1}{2}$ X- $\frac{1}{2}$ XII. Somatic setae bifid, with upper tooth thinner and shorter than lower with subdental ligaments, 45-60 μ m long, 2-3 per bundle anteriorly; two per bundle posteriorly. Penial setae simple-pointed, very thin entally, extremely long, stripe-like and slightly spiral-shaped, 720-870 μ m long, one per bundle, generally ectally protruding through a pore immediately anterior to male opening. Male and spermathecal pores paired posteriorly in XI and anteriorly in X, respectively. Male genitalia paired: vas deferens much longer than atrium, coiled, narrow, 9-12 μ m wide; entering atrium apically. Atrium slender, curved, elongate, "banana-shaped", narrowing ectally; inner epithelium granulated; terminating ectally directly to the exterior through an inconspicuous pore. Anterior prostate gland attached to atrium anteriorly, immediately ectal to junction of vas deferens; posterior prostate gland attached by narrow stalk to posterior face of atrium near male pore. Spermathecae paired, each with long thick-walled ducts and elongate, oblong ampulla. Sperm as random masses in spermathecal ampullae.

Distribution and Habitat. Southeast North America (southeast coast of Florida). Associated with coarse to very coarse sand; subtidally to at least 3 m depth.

Remarks. This species is readily discriminated by the single, slightly spiral, ribbon-like penial seta. This species is unique to the genus by having only one penial seta per bundle, however, reexamination of *I. extremus* by Erséus (personal communication) indicates that there may actually be a small companion seta associated with each giant seta.



(after Erásus, unpublished) *Inanidrilus extremus*: penial setae.



(after Erásus, 1979b) *Inanidrilus extremus*: 26, lateral view of genital organs in segments X and XI; 27, horizontal section through two posterior segments.

***Inanidrilus leukodermatus* (Giere, 1979)**

Phallodrilus leukodermatus Giere, 1979:307-309, Fig. 4.

Diagnosis. Length: 7-11.4 mm (to 25 mm in living material); segments: 53-74. Secondary annulations, six per segment posteriorly. Clitellum extending over $\frac{1}{2}$ X-($\frac{1}{2}$) $\frac{2}{3}$ XII. Somatic setae bifid with upper tooth thinner and about as long as lower, subdental ligament present, about 65 μ m long, three per bundle anteriorly, two per bundle posteriorly. Penial setae simple-pointed, sigmoid, sickle-shaped, ectally strongly hooked and pointed, entally somewhat expanded, 75 μ m long, (1)2 per bundle. Male and spermathecal pores paired posteriorly in XI and anteriorly in X, respectively. Male genitalia paired: vas deferens coiled, much longer than atrium, narrow, 6-7 μ m wide, entering atrium apically. Atrium erect, spindle-shaped, 60 μ m long, about 30 μ m wide; inner epithelium ciliated and granulated; outer layer distinct, but thin; terminating directly to the exterior at the site where the penial setae protrude. Anterior prostate gland attached by a narrow stalk just ectal to the vas deferens on the anterior face of the atrium; posterior prostate gland attached by a short stalk subapically on posterior face of atrium. Spermathecae paired, each with elongate ampulla. Sperm in random masses in spermathecal ampullae.

Distribution and Habitat. Bermuda, Caribbean (Belize). Associated with poorly sorted sand; intertidally and subtidally to 8 m depth.

Remarks. This species is closely related to a complex of species with sickle-shaped, simple-pointed, paired penial setae (*I. speroi*, *I. aduncosetosus*, *I. fijiensis*, *I. bononii*, and *I. gustavsoni*). All species are so morphologically similar that only very close scrutiny of many individuals within each community, and critically evaluating them with the specific diagnoses can provide accurate discrimination. Therefore, taxa conforming to the general morphological criteria of this species are more appropriately designated as the *I. leukodermatus* complex. See Remarks for *I. aduncosetosus* for additional comments.

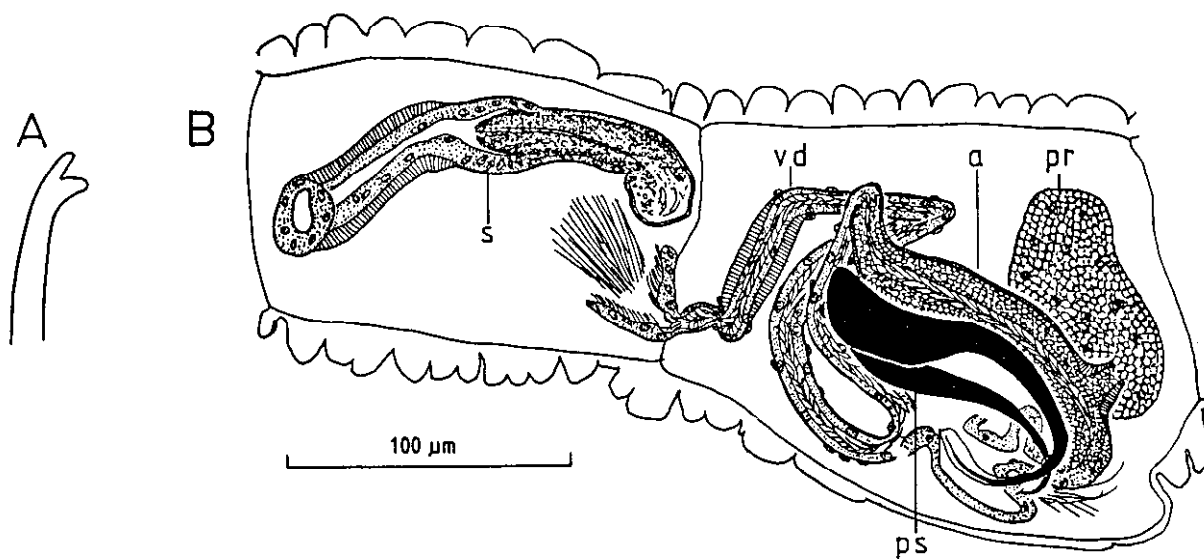
***Inanidrilus mexicanus* Erséus and Baker, 1982**

Inanidrilus mexicanus Erséus and Baker, 1982:3064-3065, Fig. 1.

Diagnosis. Length: 6.8-9.8 mm; segments: 47-52. Secondary annulations 7-9 per segment posteriorly. Somatic setae bifid with upper and lower teeth blunt, equal in length and width, subdental ligament absent; 30 μm long, 2-3 per bundle throughout. Penial setae simple-pointed, sickle-shaped, two anisomorphic setae per bundle: one seta, 150-170 μm long, narrow and strongly curved ectally, with an elongate, leaf-shaped end with thin edges and a thicker central "vein", entally expanded; other penial setae shorter, 105-120 μm long and narrower, strongly curved ectally with a small hook, entally expanded; ectal ends protruding into a complex, thin-walled copulatory sac. Male and spermathecal pores paired on ventral protuberances posteriorly in XI and laterally in anterior of X, respectively. Male genitalia paired: vas deferens coiled, longer than atrium, 9-10 μm wide along most of the length with a thick "muff of circular muscles" entally near sperm funnel; entering atrium apically. Atrium slender, 95-160 μm long, 20-22 μm wide; inner epithelium ciliated and granulated; outer layer distinct; terminating into a thin-walled copulatory sac. Anterior prostate gland absent; posterior prostate gland large, attached by a muscular stalk ectally on posterior face of atrium. Spermathecae paired, slender, each with a long heavily muscular duct; a median bulbous portion separates the duct from the elongate ampulla. Sperm arrangement indiscernible in available material.

Distribution and Habitat. Southeast North America (west coast of Florida). Associated with very fine sand; subtidally 25.9 m depth.

Remarks. The anisomorphic penial setae, somatic setae without subdental ligaments and lack of an anterior prostate gland distinguish *I. mexicanus* from all other species except *I. bulbosus*. However, the paired ventral spermathecae, somatic setae 2-3 per bundle, and distinctive morphology of the penial setae distinguish *I. mexicanus* from the latter. See Remarks for *I. bulbosus* for additional information.



(after Eiras and Baker, 1982) *Inanidrilus mexicanus*: A, free-hand drawing of somatic seta; B, lateral view of spermatheca and male genitalia in segments X-XI.

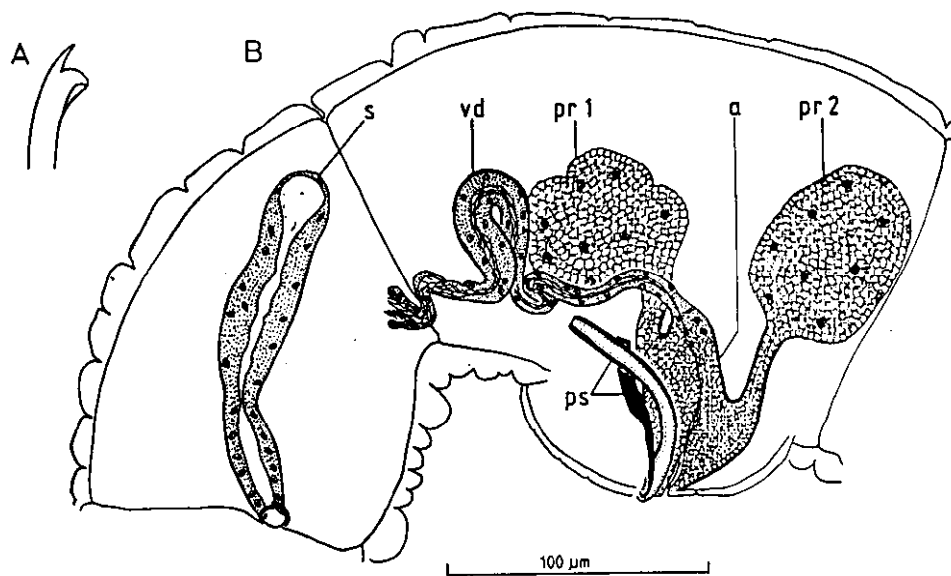
***Inanidrilus triangulatus* Erséus, 1984**

Inanidrilus triangulatus Erséus, 1984c:250-251, Fig. 13.

Diagnosis. Length: 1.5 mm; segments: more than 16. Secondary annulations seven per segment posteriorly. Somatic setae bifid with upper tooth thinner and about as long as lower, subdental ligaments present; 30 μm long, 2-3 per bundle anteriorly, one per bundle dorsally in XI, and two per bundle posteriorly. Penial setae simple-pointed, two anisomorphic setae per bundle: one seta 85 μm long, slightly curved, flat with thickened margins medially and entally, terminating ectally in a thin, somewhat pointed, flattened tip; other penial seta shorter, 55 μm long, somewhat sickle-shaped, with a thin curved tip, ental half wider. Male and spermathecal pores paired on ventral bulbous protuberances posteriorly and ventrally in anterior of X, respectively. Male genitalia paired: vas deferens coiled, much longer than atrium generally narrow, 5-7 μm wide, much wider medial-entally, 15-20 μm wide; entering atrium apically. Atrium erect, somewhat triangular, 80 μm long, 35-40 μm wide; inner epithelium ciliated and granulated; outer layer thin. Anterior prostate gland attached by a stalk immediately ectal to junction of the vas deferens on anterior face of atrium; posterior prostate gland attached by very slender, relatively elongate stalk ectally on posterior face of atrium; terminating to the exterior through a simple pore. Spermathecae paired, slender, each with a long, slender duct and small ampulla. Sperm indiscernible in available material.

Distribution and Habitat. Southeast North America (southeast coast of Florida). Associated with fine coral sand; subtidally to 6 m depth.

Remarks. This species is distinguished by the distinctive morphology of the anisomorphic penial setae and somewhat triangular broadened atrium, from which the specific epithet is derived.



(after Erasmus, 1984c) *Inamidrilus triangularatus*: A, free-hand drawing of somatic seta; B, lateral view of genitalia in segments X-XI.

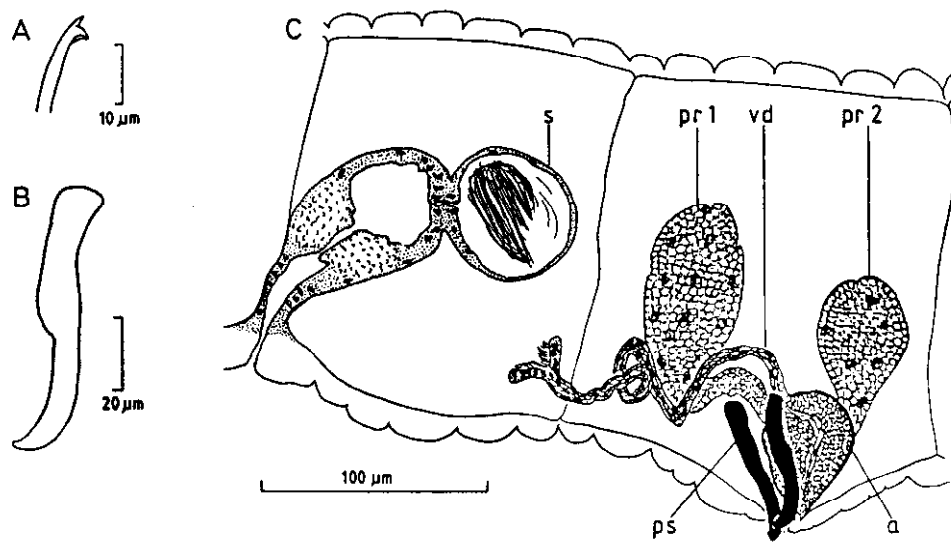
***Inanidrilus vacivus* Erséus, 1984**

Inanidrilus vacivus Erséus, 1984c:249-250, Fig. 12.

Diagnosis. Length: 7.1-8.2 mm; segments: 47-54. Secondary annulations six per segment posteriorly. Clitellum extending $\frac{1}{2}$ X- $\frac{2}{3}$ XII. Somatic setae bifid with upper tooth thinner and shorter than lower, subdental ligament present, 35-50 μ m long, (2)3 per bundle anteriorly, generally two per bundle posteriorly. Penial setae simple-pointed, stout, sickle-shaped, 65-70 μ m long, two isomorphic setae per bundle, ectal tips pointed and slightly curved. Male pores paired posteriorly in XI. Spermathecal pore single in line with ventral setae at one side of worm in anterior-most part of X. Male genitalia paired: vas deferens slightly coiled, much longer than atrium, narrow throughout, 5 μ m wide; entering atrium somewhat apically. Atrium erect, somewhat pear-shaped, 50-60 μ m long, 28-35 μ m wide; inner epithelium ciliated and granulated; outer layer thin but distinct; terminating to the exterior through a small pore. Anterior prostate gland attached by a long stalk immediately ectal to junction of vas deferens on anterior face of atrium; posterior prostate gland attached medially to posterior face of atrium. Spermatheca single with duct-like ectal portion and thin-walled ampulla. Sperm arranged in bundle in spermathecal ampulla.

Distribution and Habitat. Southeast North America (west coast of Florida). Associated with shell hash; subtidally to 10 m depth.

Remarks. The very stout isomorphic penial setae and single spermatheca discriminate this species from the other gutless taxa. This species is somewhat similar to its congeners with isomorphic penial setae. See Remarks for *I. aduncosetus* for additional information.



(after Eiréus, 1984c) *Inanidrilus vacuus*: A, somatic seta; B, penial seta; C, lateral view of genitalia in segments X-XI.

Genus. *Olavius* Erséus, 1984

Type Species. *Phallodrilus longissimus* Giere, 1979.

Diagnosis. (Based on Erséus, 1992a) Marine tubificids. Body white due to subcuticular symbiotic bacteria. Secondary annulations conspicuous, about seven per segment posteriorly. Somatic setae bifid, usually with subdental ligaments. Modified penial setae generally present, 1-7 per bundle, basically simple-pointed straight with curved lips, more elaborate in some species. Male pores paired or as median unpaired male bursa in XI. Spermathecal pores paired, ventral, lateral, or dorsal anteriorly, or occasionally medially in X (erroneously stated as IX by Erséus, 1992a). Mouth, gut, and anus absent. Male genitalia paired: vas deferens generally longer than atrium; entering atrium apically. Atrium oval, comma-shaped, or elongate, more or less horizontal and opening into copulatory sac. Prostate glands absent (in subgenus *Coralliodriloides*), or paired on each atrium. Spermatheca(e) paired or, rarely, single; duct(s) generally short, ampulla(e) slender or oval. Sperm in random masses or as loose bundles in spermathecal ampulla(e).

Remarks. *Olavius* is one of two gutless genera, characterized by the thick, chalky white body wall with conspicuous secondary annulations. This genus was established by Erséus to differentiate the gutless species with generally straight, multiple penial setae and a comma-shaped atrium entering a copulatory sac from those species with generally sickle-shaped penial setae, two per bundle, and an erect, spindle-shaped atrium, usually terminating directly to the exterior. See Remarks for *Inanidrilus* for additional information. Some species of *Olavius* have been designated to two subgenera: *O. (Olavius)* and *O. (Coralliodriloides)*. The former subgenus is composed of those species with a heavily muscular vas deferens, an unpaired male bursa, slender spermathecae, and a dorsal epidermal crypt in X. The latter subgenus is characterized by species lacking both penial setae and prostate glands.

Olavius is a highly speciose genus (composed of about 40 species), well represented throughout the Caribbean, Bermuda, Florida, and the Gulf of Mexico. Twelve species have been reported from the coastal waters of this region. Five species have been collected from coastal Florida and are included herein. An unconfirmed specimen of *O. longissimus* has been reported off Tampa Bay. The remaining taxa [*O. planus* (Erséus, 1979b), *O. finitimus* Erséus, 1990a, *O. tantulus* Erséus, 1984c, *O. pravus* Erséus, 1990a, *O. pellucidus* Erséus, 1984c, and *O. alius* Erséus, 1984c] may eventually be recorded from the reef areas of the Florida Keys, but have thus far been collected only from isolated areas outside coastal Florida waters.

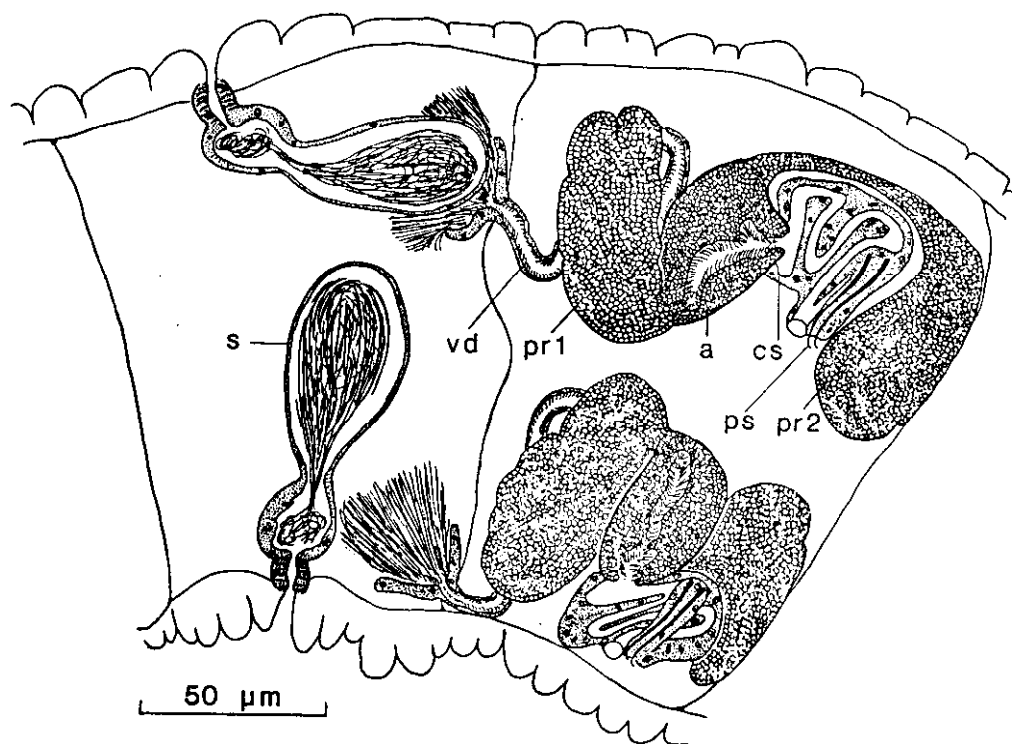
***Olavius caudatus* (Erséus, 1979)**

Phallodrilus caudatus Erséus, 1979b:200-201, Fig. 21.

Diagnosis. Length: 3.0-5.4 mm; segments: 37-61. Body flattened ventrolaterally. Secondary annulations 6-8 per segment posteriorly. Clitellum extending over X-XII. Pygidium prolonged into narrow, very long posterior process. Somatic setae bifid with upper tooth thinner and shorter than lower, subdental ligament present: anteriorly 25-37 μm long, 2-5 per bundle; posteriorly 32-44 μm long, 2-3(4) per bundle. Penial setae simple-pointed, slightly sigmoid, 32-39 μm long, 1-2(3) per bundle. Male and spermathecal pores paired, ventrally in posterior of XI, and laterally in anterior of X, respectively. Male genitalia paired: vas deferens longer than atrium, 8 μm wide; entering atrium apically. Atrium ovoid or roundish, 45-50 μm long, 30 μm wide; inner epithelium ciliated and granulated; outer layer thin; terminating into a voluminous, deeply-folded copulatory sac. Anterior prostate gland attached entally near junction of vas deferens on anterior face of atrium; posterior prostate gland attached by a long "strand" medially or ectally to posterior face of atrium. Spermathecae paired, each with a short duct and a bipartite ampulla with an ectal constriction. Sperm in random masses.

Distribution and Habitat. Southeast North America (east and west coasts of Florida). Associated with sand; subtidally 3 m depth.

Remarks. This species is readily distinguished from all other tubificids in Florida waters by the flat body, filiform caudal process, and 1-3 simple-pointed, sigmoid penial setae. *Olavius planus* from the Caribbean has similar body shape with elongate posterior end but has 5-7 bifid penial setae. *Olavius latus* and *O. vacuus* from Florida also have a similar external morphology, but the former species has 5-6 simple-pointed penials and the latter lacks penial setae altogether. *Olavius imperfectus* from Florida has a relatively similar body, but the caudal process is not as pronounced; the number of penial setae per bundle (2)3(4) is also similar but they are straight instead of sigmoid as in *O. caudatus*. All remaining species of *Olavius* from the Caribbean are readily distinguished by the morphology of the penial setae: either anisomorphic or more stout and less sigmoid.



(after Bråneus, 1979b) *Otarion caudatus*: horizontal view of genital organs in segments X and XI.

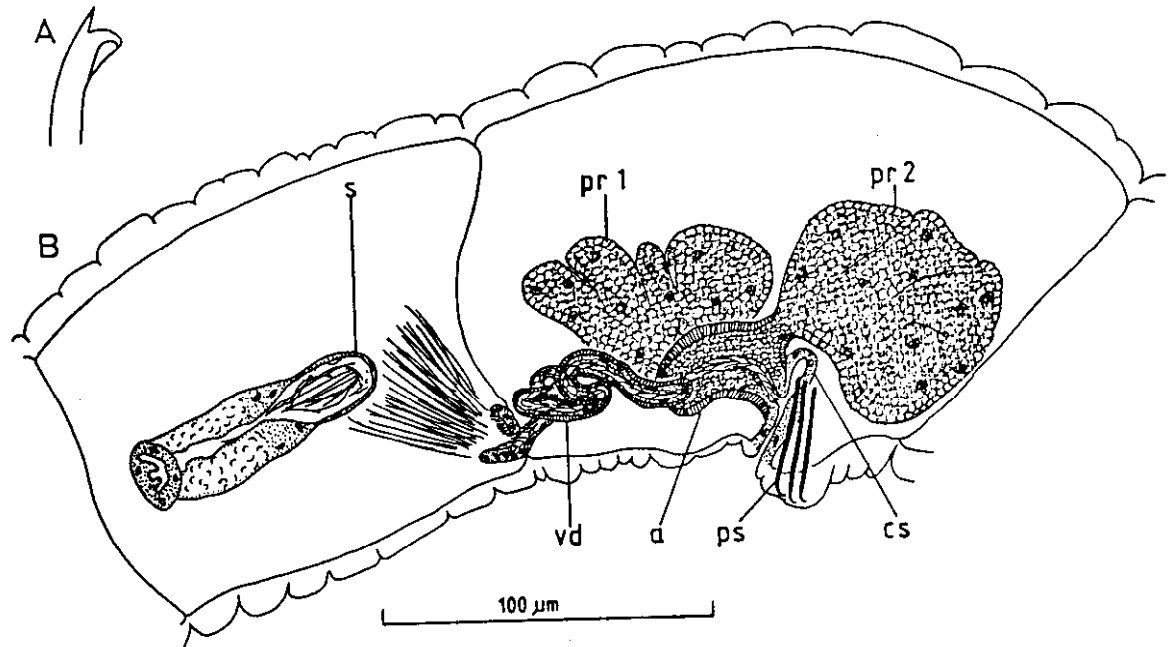
Olavius imperfectus Erséus, 1984

Olavius imperfectus Erséus, 1984c:255-256, Fig. 18.

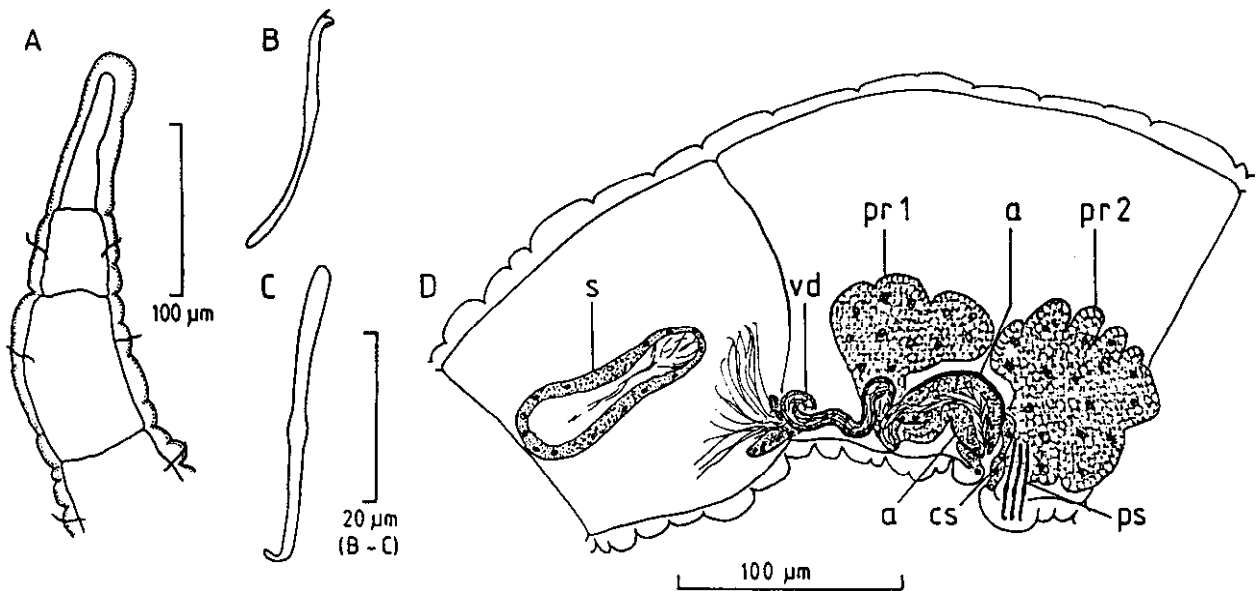
Diagnosis. Length: 5.6-8.6 mm; segments: 42-57. Secondary annulations seven per segment posteriorly. Clitellum extending $\frac{1}{2}$ X-XII. Pygidium slender, longer than wide. Somatic setae bifid with upper tooth thinner and shorter than lower, subdental ligament present, 30-35 μ m long, 2-3 per bundle anteriorly; (1)2 per bundle posteriorly. Penial setae simple-pointed, straight with strongly hooked tips, 30-45 μ m long; (2)3(4) per bundle. Male and spermathecal pores paired posteriorly in XI and laterally in anterior of X, respectively. Male genitalia paired: vas deferens coiled, longer than atrium, 5-9 μ m wide; entering atrium apically. Atrium elongate, oval, somewhat curved, 40-52 μ m long, 25-35 μ m wide; inner epithelium ciliated and granulated; outer layer thick, distinct; terminating into a small, somewhat folded copulatory sac. Anterior prostate gland large attached entally near junction of vas deferens on anterior face of atrium; posterior prostate gland attached by distinct stalk ectally to posterior face of atrium. Spermathecae elongate, paired, each with ectal, duct-like granular portion and ental, oval, thin-walled ampulla. Sperm scattered throughout spermathecae, often partly embedded in ampullar walls.

Distribution and Habitat. Southeast North America (east coast of Florida), Caribbean (Belize). Associated with coarse sand and shell hash; subtidally to 8 m depth.

Remarks. This species is distinguished from other species of *Olavius* from Florida by the morphology and number of penial setae. No other species from Florida or the Caribbean have about three straight, isomorphic penial setae per bundle, with strongly hooked tips. See Remarks for *O. caudatus* for additional information.



(after Eiras, 1984c) *Olavius imperfectus*: A, free-hand drawing of somatic seta; B, lateral view of genitalia in segments X-XI.



(after Eiras, 1990a) *Olavius imperfectus*: 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.

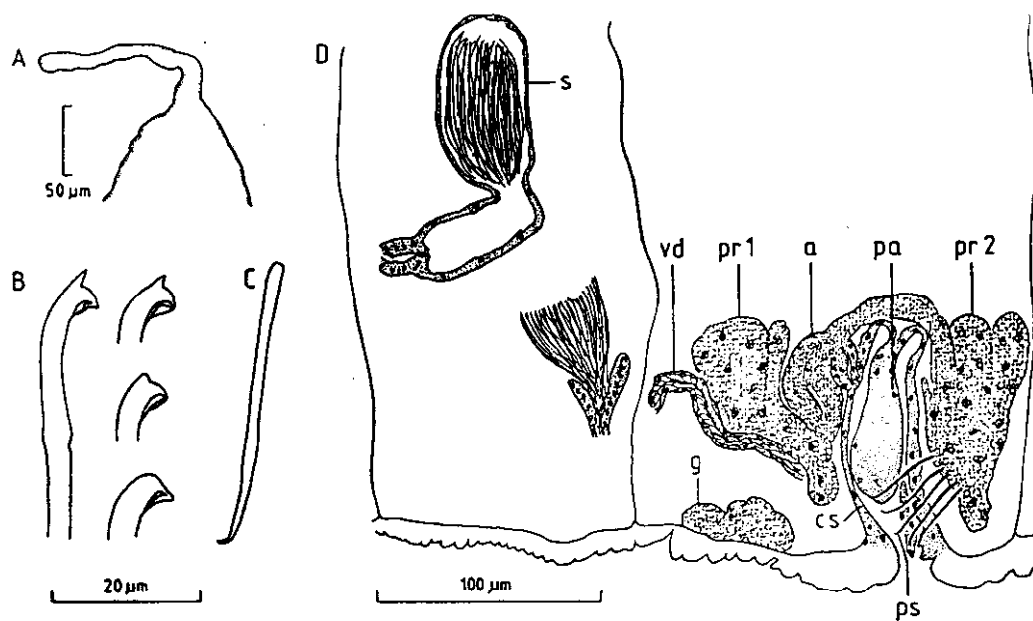
***Olavius latus* Erséus, 1986**

Olavius latus Erséus, 1986a:307-308, Fig. 13.

Diagnosis. Length: 9.5 mm; segments: 80. Secondary annulations indistinct. Clitellum extending over $\frac{1}{2}$ X-XII. Pygidium formed into a long, filiform caudal process. Somatic setae bifid with upper tooth thinner and shorter than lower, subdental ligaments present: 3-4 per bundle anteriorly; 2-3 per bundle posteriorly. Penial setae simple-pointed, ectally thin with curved tips, 35 μ m long, 5-6 per bundle. Male and spermathecal pores paired, ventral in posterior of XI and laterally in anterior of X, respectively. Male genitalia paired: vas deferens longer than atrium, about 10 μ m wide, entering atrium apically(?). Atrium somewhat comma-shaped, 50-60 μ m long, 25 μ m wide; inner epithelium thick; outer layer thin; terminating into a short "duct" opening at the inner end of a very complex, folded, deep penial sac, one fold appearing as a somewhat "pendant(?) papilla". Anterior prostate gland large, apparently attached ectally to anterior face of atrium; posterior prostate gland large, attached by a long stalk ectally to the posterior face of atrium. Glandular bodies located anterior to male pores near body wall. Spermathecae paired, each with an indistinct duct and bipartite ampulla with a medial constriction. Sperm arranged in bundles in ental portion of ampullae.

Distribution and Habitat. Southeast North America (east coast of Florida). Associated with shell hash; subtidally to 11 m depth.

Remarks. This species is distinguished from all other species of *Olavius* from Florida or the Caribbean by the elongated filiform pygidial process and 5-6 simple-pointed, straight, isomorphic penial setae per bundle with ectal hooks. See Remarks for *O. caudatus* for additional information. See also Remarks for *O. vacuus*. Considering the near identical morphology of the pygidium and male genitalia, this species should be identified conclusively with caution. Erséus (1990a) cites a greater number of setae anteriorly and posteriorly and larger bipartite spermathecal ampullae as species discriminating criteria. However, a variation of only plus or minus one setae per bundle is a relatively normal variation within this genus, and the bipartite condition and disparity in size of the spermathecal ampullae could be attributable to the degree of post-copulatory response. This taxon appears to be part of a complex of closely related species that could be referred to as the "*O. latus* complex".



(after Bråbø, 1986a) *Olavius latus*: A, pygidium with caudal process; B, somatic setae; C, penial seta; D, lateral view of spermatheca and male genitalia in segments X-XI.

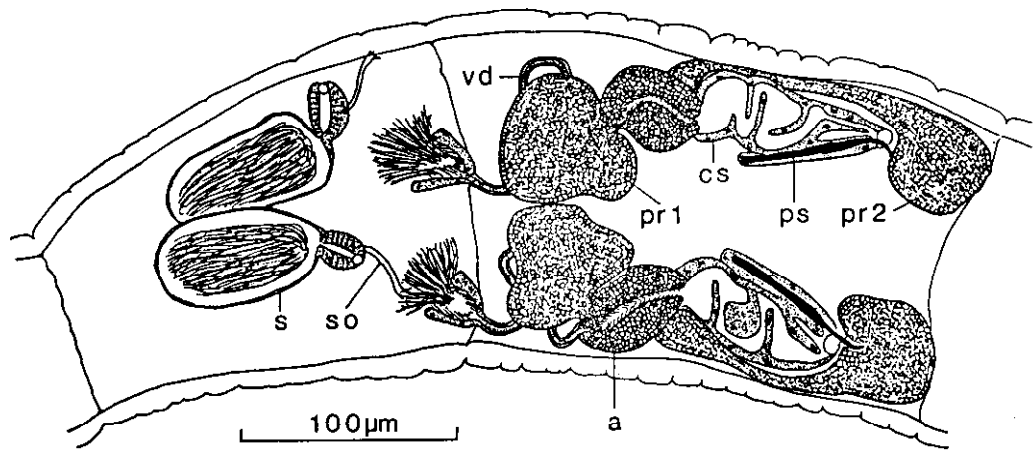
***Olavius tenuissimus* (Erséus, 1979)**

Phallodrilus tenuissimus Erséus, 1979b:199-200, Fig. 20.

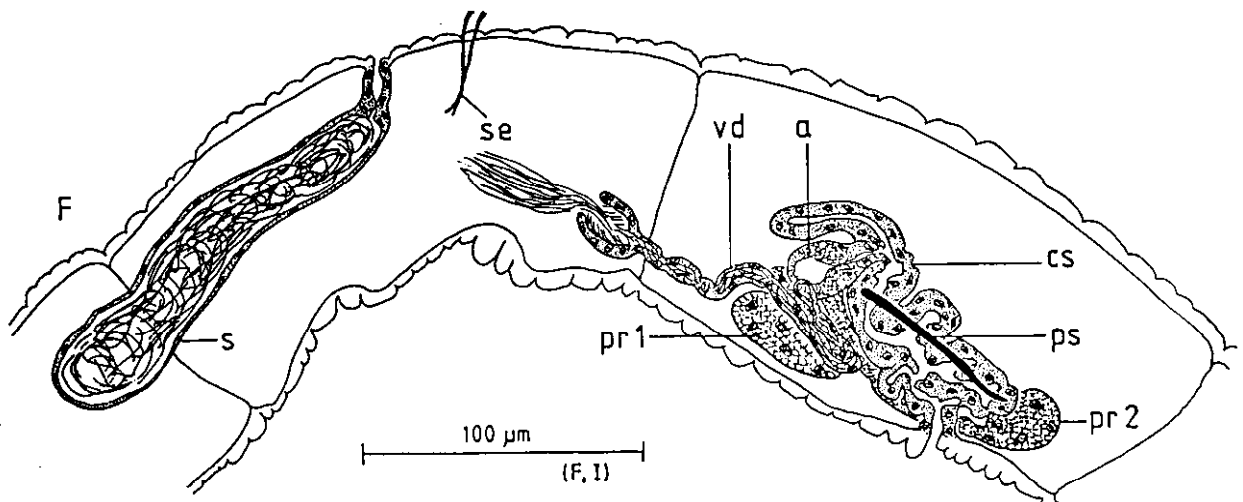
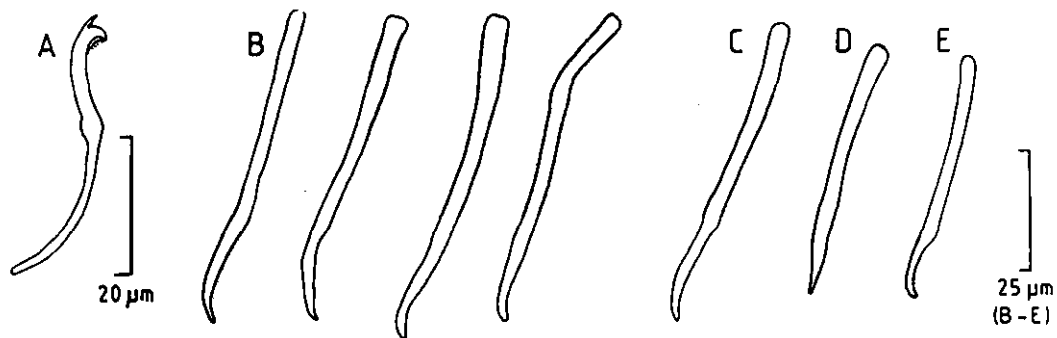
Diagnosis. Length: 2.5-9.5 mm; segments: 20-47. Secondary annulations 6-7 per segment, occasionally inconspicuous. Clitellum extending over ($\frac{1}{2}$ X)X-XII. Pygidium somewhat elongate, terminally rounded. Somatic setae bifid with upper tooth thinner and shorter than lower, subdental ligament present: 35-50 μ m long, 3 per bundle anteriorly; 2(3) per bundle posteriorly. Penial setae simple-pointed, generally straight, narrowing ectally with slightly curved ends, 45-74 μ m long, (0)1(2) per bundle. Male and spermathecal pores paired, ventrally in posterior of XI and dorso-laterally in anterior of X, respectively. Male genitalia paired: vas deferens much longer than atrium, 5-7 μ m wide; entering atrium apically. Atrium small, oval, pear-shaped, 30-60 μ m long, 20-35 μ m wide; inner epithelium ciliated and granulated; outer layer thin; terminating into a voluminous, deeply folded copulatory sac. Anterior prostate gland attached entally near junction of vas deferens to anterior face of atrium; posterior prostate gland attached by a long stalk to middle-to-ectal part of posterior face of atrium. Spermathecae paired, each with short, thick-walled discrete duct and thin-walled oval to elongate ampulla. Sperm arranged in large bundles or random masses in spermathecal ampullae.

Distribution and Habitat. Southern and eastern North America [Massachusetts, New Jersey, North Carolina, Florida (west coast)], Caribbean (Belize), Bermuda. Associated with fine to coarse sand; subtidally to 141 m depth.

Remarks. This species is distinguished from all other *Olavius* expected to occur in Florida waters by the usually single, straight, strong, penial seta per "bundle", with a slightly hooked ectal end. See Remarks for *O. caudatus* for additional information. This species has been misidentified from various regions in Florida and Caribbean [see Erséus (1990a) for a complete discussion], and should be regarded with caution and is part of a complex of closely related species which may be referred to as the "*O. tenuissimus* complex".



(after Eiras, 1979b) *Ollawus tenuissimus*: horizontal view of genital organs in segment X and XI.



(after Eiras, 1990a) *Ollawus tenuissimus*: A, somatic seta; B-E, penial setae of specimens from Belize (B), Gulf of Mexico (C), New Jersey (D), and Bermuda; F, lateral view of spermatheca and male genitalia in segments X-XI.

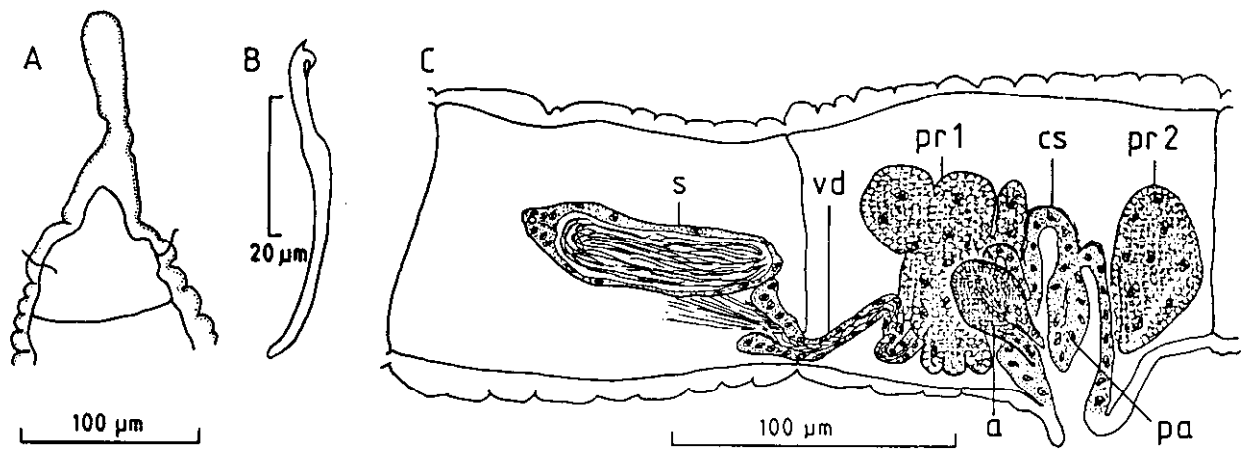
***Olavius vacuus* Erséus, 1990.**

Olavius vacuus Erséus, 1990a:271-272, Fig. 22.

Diagnosis. Length: 3.6-20.4 mm; segments: 53-132. Secondary annulations 4-7 per segment. Clitellum extending $\frac{1}{2}$ X-XII. Pygidium with a long filiform process. Somatic setae bifid with upper tooth thinner and shorter than lower, subdental ligament present: 30-60 μ m long, (2)3(4) per bundle anteriorly; (1)2(3) per bundle posteriorly. Penial setae absent. Male and spermathecal pores paired, ventral in posterior of XI and laterally in anterior of X, respectively. Male genitalia paired: vas deferens longer than atrium, 7-14 μ m wide; entering atrium more or less apically. Atrium somewhat oval, tapering ectally, 30-60 μ m long, 15-28 μ m wide; inner epithelium granulated; outer layer thin; ectally narrowing (forming a short duct?) opening into the anterior face of a large convoluted copulatory sac, one "fold" often appearing as a "pendant papilla". Anterior prostate gland large, attachment indiscernible; posterior prostate gland attachment indiscernible. Spermathecae paired, each with a short duct and slender, elongate ampulla. Sperm arranged in a large bundle in spermathecal ampullae.

Distribution and Habitat. Eastern North America (Virginia, east and west coasts of Florida). Associated with fine to coarse sand and shell hash; subtidally to 58.5 m depth.

Remarks. The lack of penial setae and presence of the long filiform caudal process characterizes this species of *Olavius* from all other congeners identified from the Gulf of Mexico, east coast of North America, Bermuda, or the Caribbean. However, its similarity to *O. latus* was discussed by Erséus (1990a) and should be considered. The lack of penial setae may be a result of intraspecific morphological variability. See Remarks for *O. latus* for additional information.



(after Erasmus, 1990a) *Olavius vacuus*: A, posterior end of worm with prolonged pygidium; B, seta; C, lateral view of spermatheca and male genitalia in segments X-XI.

Genus. *Duridrilus* Erséus, 1983

Type Species. *Duridrilus tardus* Erséus, 1983.

Diagnosis. (Based on Erséus, 1992a; 1993) Marine tubificids. Worms generally rather stiff and sluggish. Prostomium retractable. Cuticle usually with fine adherent particles forming discrete minute papillae scattered over body surface (body wall smooth, not covered with particles or papillae in *D. kimi* Erséus, 1993). Somatic setae bifid with upper tooth reduced, or modified, single-pointed; maximally three per bundle anteriorly, generally only one per "bundle" posteriorly. Modified genital setae absent. Male and spermathecal pores paired in XI and X, respectively. Male genitalia paired: vas deferens narrow, much longer than atrium and convoluted, internally ciliated with thin walls; entering atrium apically. Atria cylindrical to club-shaped; erect or with apical end tilted over to posterior; narrowing ectally. Anterior prostate gland attached to the anterior face of the atrium by distinct stalk at some distance from the apical end on the anterior face; posterior prostate gland attached generally opposite the anterior gland, on posterior face of atrium (almost apical in *D. pastoralis* Erséus, 1990b). True penes absent; eversible pseudopenes may be present. Spermathecae paired, each with distinct, relatively long duct and round-to-oval ampulla. Sperm arranged as simple spermatzeugmata, skein-like balls, or random masses in spermathecal ampullae.

Remarks. This genus is differentiated from other species of Phallodrilinae by the retractable prostomium, cuticular papillae (however, a species without papillae or thickened cuticle, from which the original generic epithet is derived, was recently described from western Australia), and the long, narrow vas deferens. This genus also lacks penial setae, frequently found in phallodrilines. Body wall papillation also occurs in some species of *Tubificoides* and *Tectidrilus* recorded from Florida waters. *Duridrilus* is distinguished from both by the phallodriline-type biprostate atrium, specifically it can be readily discriminated from *Tubificoides* by the lack of a well-developed cuticular penis sheath, and from *Tectidrilus* by the unmodified gut in IX.

Of the six species currently included in *Duridrilus*, only *D. tardus* has been reported throughout the Caribbean and expected to occur in Florida waters. None of the other species have been reported from North America.

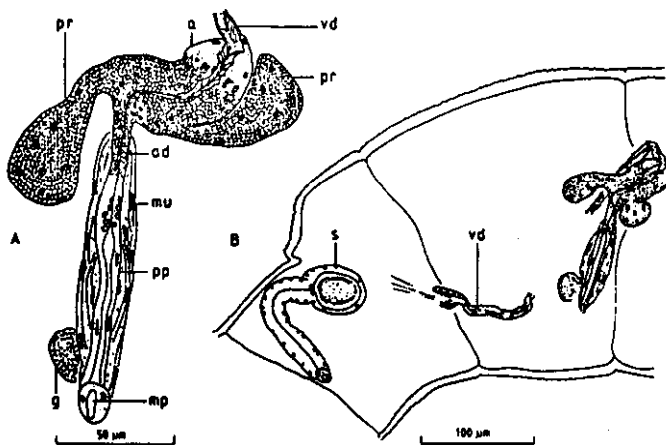
***Duridrilus tardus* Erséus, 1983**

Duridrilus tardus Erséus, 1983a:29-31, Fig. 1-2.

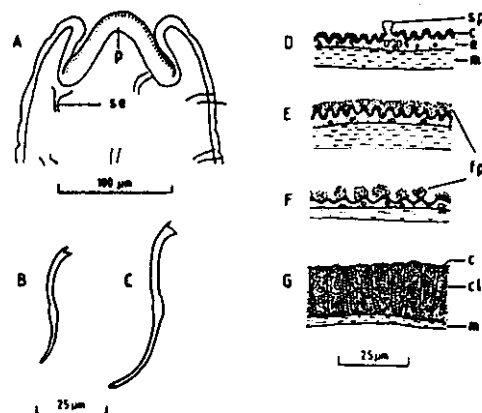
Diagnosis. Length: 8.9-15.7 mm; segments: 47-82. Prostomium retractable. Cuticle thick, "dusted" with small adherent particles or scattered papillae may be absent anteriorly; posterior segments with about 30-35 fine annulations producing a "wavy" appearance. Clitellum extending over $\frac{1}{2}$ X-XII. Somatic setae bifid with upper tooth thinner and shorter than lower: 40-75 μ m long, two per bundle in II-VIII, one per "bundle" thereafter; setae absent from XI. Male and spermathecal pores paired in posterior of XI and anteriorly in X, respectively. Male genitalia paired: vas deferens longer than atrium, narrow, 5.5-7.5 μ m wide; entering atrium apically. Atrium composed of an ental oval ampulla, 55-75 μ m long, 28-40 μ m wide; inner epithelium granulated and ciliated, outer muscular layer thin; and an ectal duct, 30-50 μ m long and 10-14 μ m wide, entally granulated; terminating ectally in long, slender pseudopenis with complex system of muscles, 60-95 μ m long, 15-28 μ m wide. Anterior prostate gland attached approximately medially on anterior face of atrium; posterior prostate gland attached opposite to anterior gland on posterior face of atrium. A discrete glandular body located immediately anterior to ectal part of pseudopenial sac. Spermathecae paired, each with a long duct and oval ampulla. Sperm arranged as random masses or ring of spermatozoa surrounding a core of secretory products in the spermathecal ampullae.

Distribution and Habitat. Bermuda, Caribbean (Barbados, Puerto Rico, Belize), southern China. Associated with coarse sand; subtidally, 7-39 m depth.

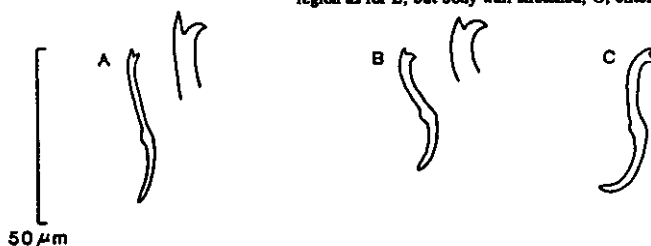
Remarks. This species is readily distinguished from other tubificids in Florida water by its distinctive-looking cuticle with fine particles and/or papillae and posterior segments finely annulated, giving it a "wavy" appearance. The bisetal anterior bundles, unisetal posterior bundles, and papillation are similar to those of *Tectidrilus*, but the papillae are not nearly as well-developed or pronounced in *D. tardus*. See Remarks for genus for additional information.



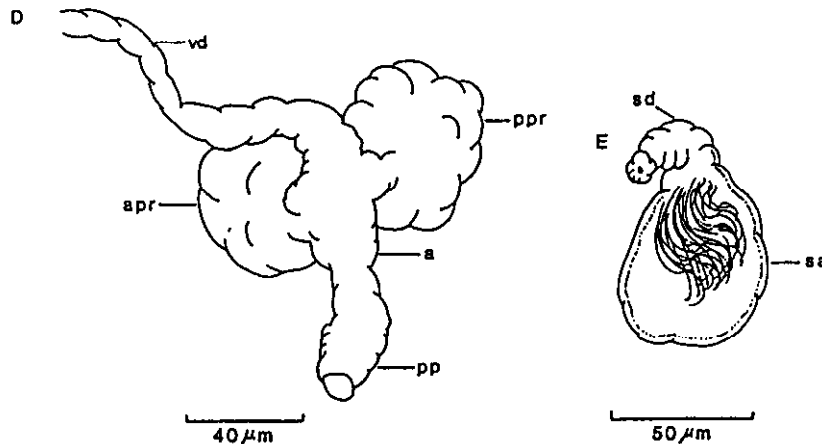
(after Erős, 1983a) *Duridrilus tardus*: A, ectal parts of male efferent duct; B, lateral view of spermatheca and male efferent duct.



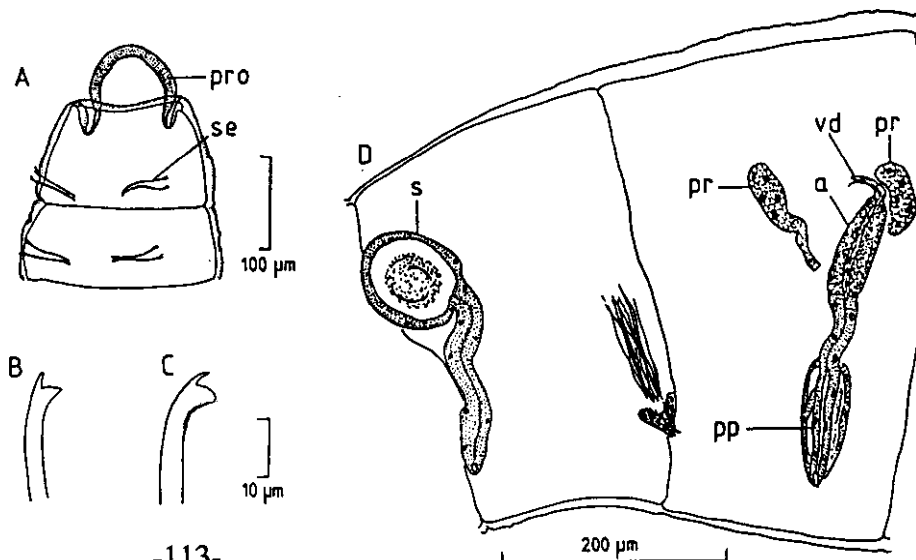
(after Erős, 1983a) *Duridrilus tardus*: A, anterior end of worm; p, prostomium, se seta; B, seta from segment II; C, seta from segment IX; D-G, optical sections through body wall in different regions; D, most anterior part of worm; E, posterior part of worm (body wall not stretched); F, same region as for E, but body wall stretched; G, clitellum.



(after Milligan, 1987) *Duridrilus tardus*: A, seta from V; B, seta from X; C, posterior seta; D, male genitalia; E, spermatheca.



(after Erős, 1990) *Duridrilus tardus*: A, anterior end of worm showing partly retracted prostomium and setae of segments II-III; B, anterior seta; C, posterior seta; D, lateral view of spermatheca and male genitalia in segments X-XI.



Genus. *Bathydrilus* Cook, 1970

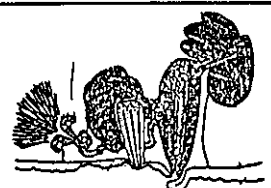
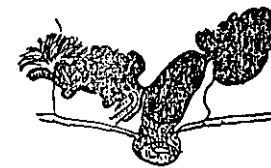
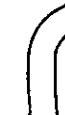
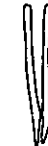
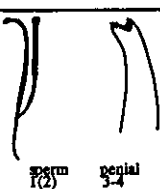
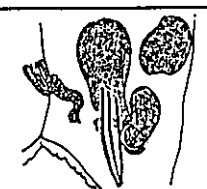
Type Species. *Bathydrilus asymmetricus* Cook, 1970.

Diagnosis. (Based on Erséus, 1992a) Marine tubificids. Somatic setae bifid in some species with upper tooth of posterior setae absent. Modified genital setae present or absent; penial setae, when present, generally 2-4 per bundle, straight or curved, simple-pointed, rarely bifid, or minutely pectinate (*B. notabilis*); modified spermathecal setae may be present in XI or X. Male and spermathecal pores paired in XI and ventral, lateral or dorsal in X, respectively. Male genitalia paired: vas deferens internally ciliated, narrow, relatively long, entering atrium subapically or ectally but in most species still running inside atrial walls to reach atrial apices, and there entering lumina of atria. Atrium oval, spindle-shaped, or cylindrical; erect or posteriorly directed; terminating into a copulatory sac or opening directly to the exterior through a simple pore. Anterior prostate gland attached to middle-to-ectal face of atrium; posterior prostate gland, attached to atrium apically or, rarely, medially. True pendant penes absent, but pseudopenes may be present. Spermathecae paired, each with a short duct (possibly long in *B. torosus* Baker, 1983) and ampulla of variable shape. Sperm arranged in "skein-like" spermatozeugmata, short, compact bundles, or as random masses in spermathecal ampullae.

Remarks. All species of *Bathydrilus* included herein from Florida waters have at least two modified penial setae in each ventral bundle of XI. As the generic epithet indicates many taxa within this genus are from deep water. Currently, about 30 species are included in *Bathydrilus*. The five species reported from Florida waters are shallow water forms. Two additional species, *B. vestustus* and *B. egenus*, have recently been described from the Caribbean (Erséus, 1990a) and may be expected to occur in the Florida Keys, but they are distinctive in lacking penial setae and have simple-pointed setae posteriorly.

This genus has undergone a variety of emendations since Cook (1970) originally described the type species. The most comprehensive discussion of *Bathydrilus* was by Erséus (1979f) in which *Macroseta* Erséus, 1975, was designated as a junior synonym upon re-examination of the type of *Bathydrilus* and finding paired prostate glands attached to the atrium. Erséus (1981b) slightly modified the generic definition to include species with "prespermathecal setae". The most current definition, accompanied by a brief phylogenetic synopsis of the species, is by Erséus (1992a).

Table 4. *Bathydrilus* and *Pectinodrilus* species.

Taxa	Anterior Setae #/bundle	Posterior Setae #/bundle	Penial Setae #/bundle	Male Genitalia
<i>Bathydrilus adriaticus</i>	 (1,2)3(4)	 (1)2(3)	 2-3	
<i>Bathydrilus formosus</i>	 3	 2	 2(3)	
<i>Bathydrilus ingens</i>	 2-3(4)	 2	 3	
<i>Bathydrilus macroprostus</i>	 2-3(4)	 2	 2	
<i>Bathydrilus notabilis</i>	 (2)3-4	 (1)2	 sperm penial 1(2) 3-4	
<i>Pectinodrilus deminutus</i>	 2	 1	 4-8(-11)	
<i>Pectinodrilus molestus</i>	 2	 2	 (2)3-5(6,7)	

***Bathydrilus adriaticus* (Hrabe, 1971)**

Phallodrilus adriaticus Hrabe, 1971a:220-221, Fig. 19-25.

Diagnosis. Length: 5.4-11.2 mm; segments: 40-86. Clitellum extending over $\frac{1}{2}$ X-($\frac{1}{2}$ XII)XII. Somatic setae bifid with upper tooth thinner and shorter than lower: 40-50 μ m, (1,2)3(4) per bundle anteriorly, (1)2(3) per bundle posteriorly. Modified penial setae straight, single-pointed with tips close together, 60-115 μ m long, 2-3 per bundle. Male and spermathecal pores paired posteriorly in XI and anteriorly in X, respectively. Male genitalia paired: vas deferens internally ciliated, longer than atrium, coiled, narrow, 5-10 μ m wide; entering ectal portion of atrium. Atria erect, more or less cylindrical, narrowing ectally, 75-150 μ m long, 20-50 μ m wide; inner epithelium granulated and ciliated (?); outer layer relatively thin; terminating in a pseudopenis opening into a complex invagination of the body wall. Anterior prostate gland attached to atrium approximately medially, at the junction of the vas deferens; posterior prostate gland attached near ental apex of atrium. Spermathecae paired, each with an inconspicuous duct and sacciform ampulla. Sperm arranged as roundish, or rhomboid spermatozeugmata.

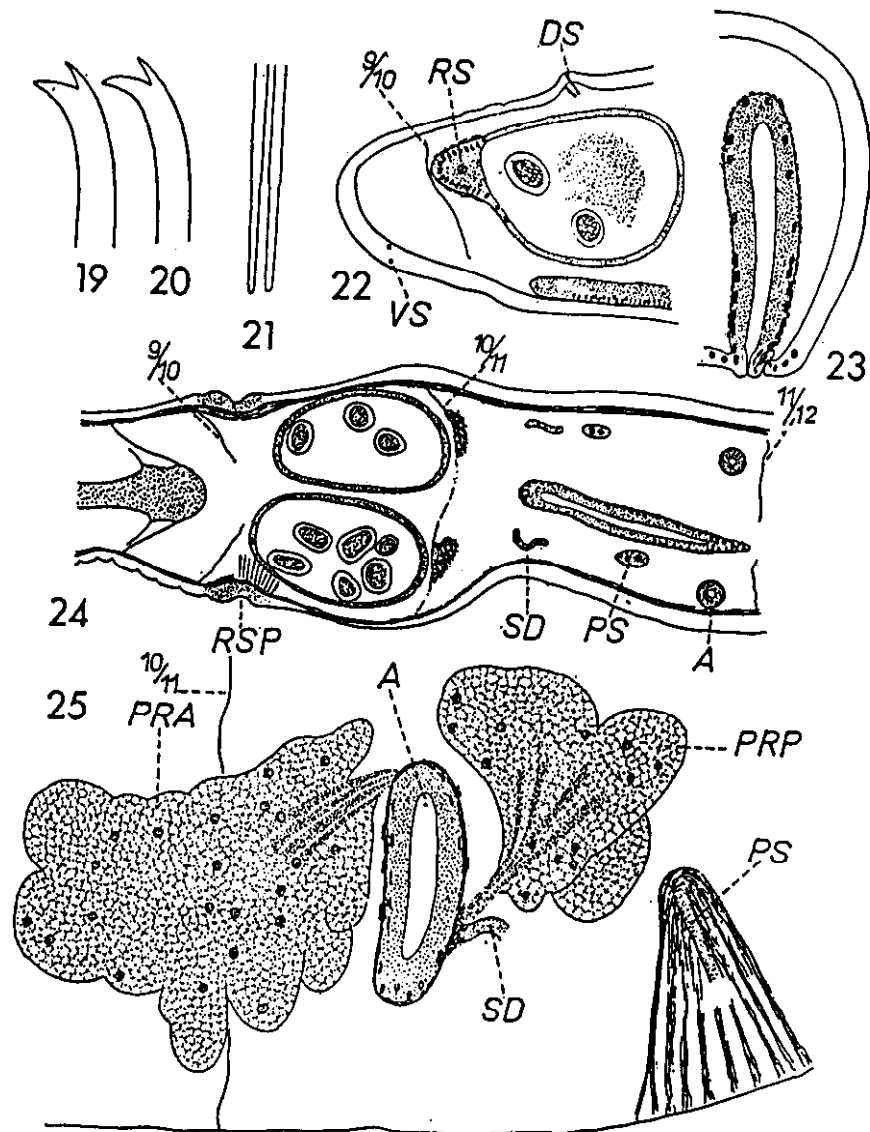
Distribution and Habitat. Caribbean [Bonaire, ?Puerto Rico (as *Spiridion insigne* Knöllner, 1935), Belize, Panama, Caracas, Barbados], southern Atlantic (Ascension Islands), Mediterranean Sea (former Yugoslavia), Persian Gulf (Saudi Arabia), Hawaii, southeast North America (Keys of Florida), Bermuda. Associated with muddy, silty-sand to at least 32 m depth.

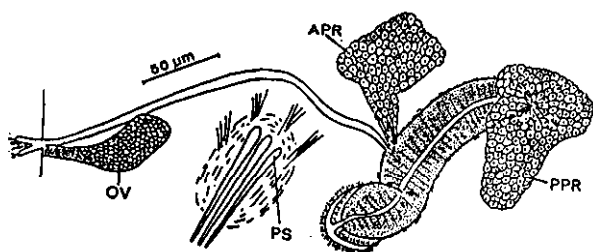
Remarks. This species is distinguished by the straight simple-pointed setae, arranged in 2-3 per bundle with the tips close together. *Bathydrilus adriaticus* has been described from tropical regions throughout the world. Originally included with *Phallodrilus*, it was subsequently combined with *Bathydrilus* (Erséus, 1979f). Two subspecies [*trisetosus* Erséus, 1979 = *caraibicus* Righi and Kanner, 1979, and *adriaticus* (Hrabe, 1971)] were subsequently invalidated as specific variations of *B. adriaticus* (Erséus, 1985; Erséus and Davis, 1989).

This species is almost identical with *B. ingens* with respect to the morphology of the spermathecae, male genitalia, and penial setae. The latter has slightly curved tips; however, this character was also described for *Phallodrilus adriaticus caraibicus*, as well as the rhomboid spermatozeugmata. The presence of "single-pointed and

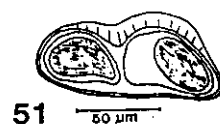
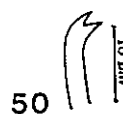
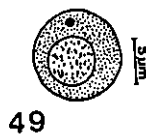
rhomboid spermatzeugmata. The presence of "single-pointed and somewhat enlarged" setae in some of the dorsal bundles of *B. ingens* appears to be the primary differentiating criterion. The latter species has been collected throughout Florida, and, upon further scrutiny, may prove to be a synonym of the circumtropical *B. adriaticus*. *Bathydrilus longus*, Erséus, 1979f, described from the continental shelf off New Jersey, shares many of the similar characteristics of both aforementioned species. However, the sperm in *B. longus* are in random masses. Variations regarding patterns of dorsal epidermal glands and the degree of invaginations of the male pores have also been cited as specific criteria distinguishing all aforementioned taxa. These species comprise a complex of closely related taxa herein referred to as the "*B. adriaticus* complex".

(after Hrabě, 1971a)
Bathydrilus adriaticus:
 19-20, ventral setae of VII;
 21, penial setae; 22, longitudinal
 section of X; 23, longitudinal
 section of airium; 24, horizontal
 section of VIII-IX; 25,
 longitudinal section of XI.



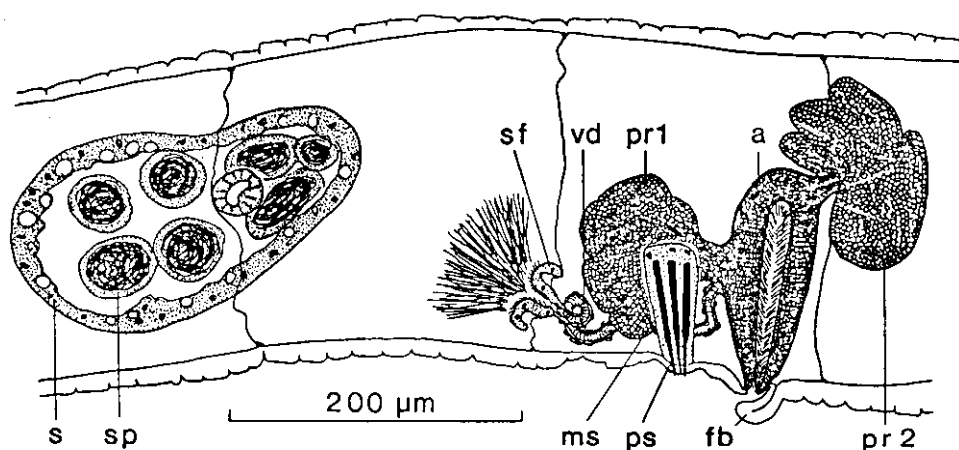


(after Righi and Kanner, 1979) *Bathydrius adriaticus* as *Phallo-drius adriaticus caralibicus*: male duct.

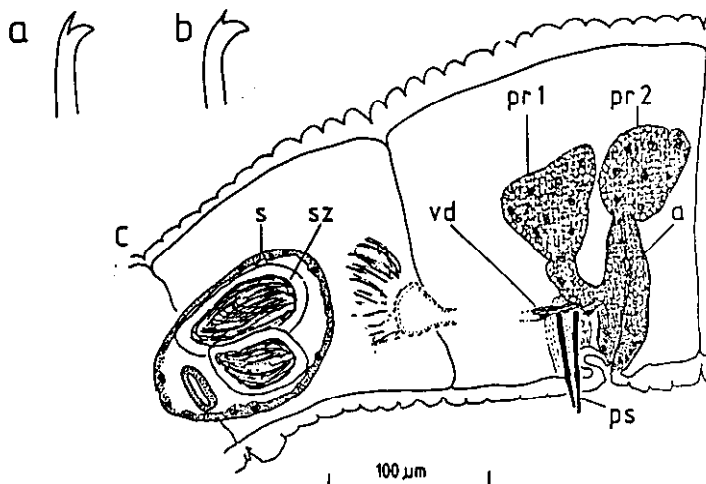
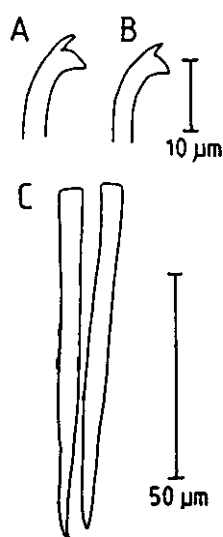


(after Righi and Kanner, 1979) *Bathydrius adriaticus* and *Phallo-drius adriaticus caralibicus*: 49, coelomocyte; 50, seta; 51, spermathecal ampulla with two spermatozoa.

(after Erasus, 1979f) *Bathydrius adriaticus*: lateral view of genital organs in segments X and XI.



(after Erasus and Davis, 1989) *Bathydrius adriaticus*: A, anterior somatic seta; B, posterior somatic seta; C, penial setae.



(after Erasus, 1985) *Bathydrius adriaticus*: a, free-hand drawing of anterior seta; b, free-hand drawing of posterior seta; c, lateral view of spermatheca and male duct in segments X-XI.

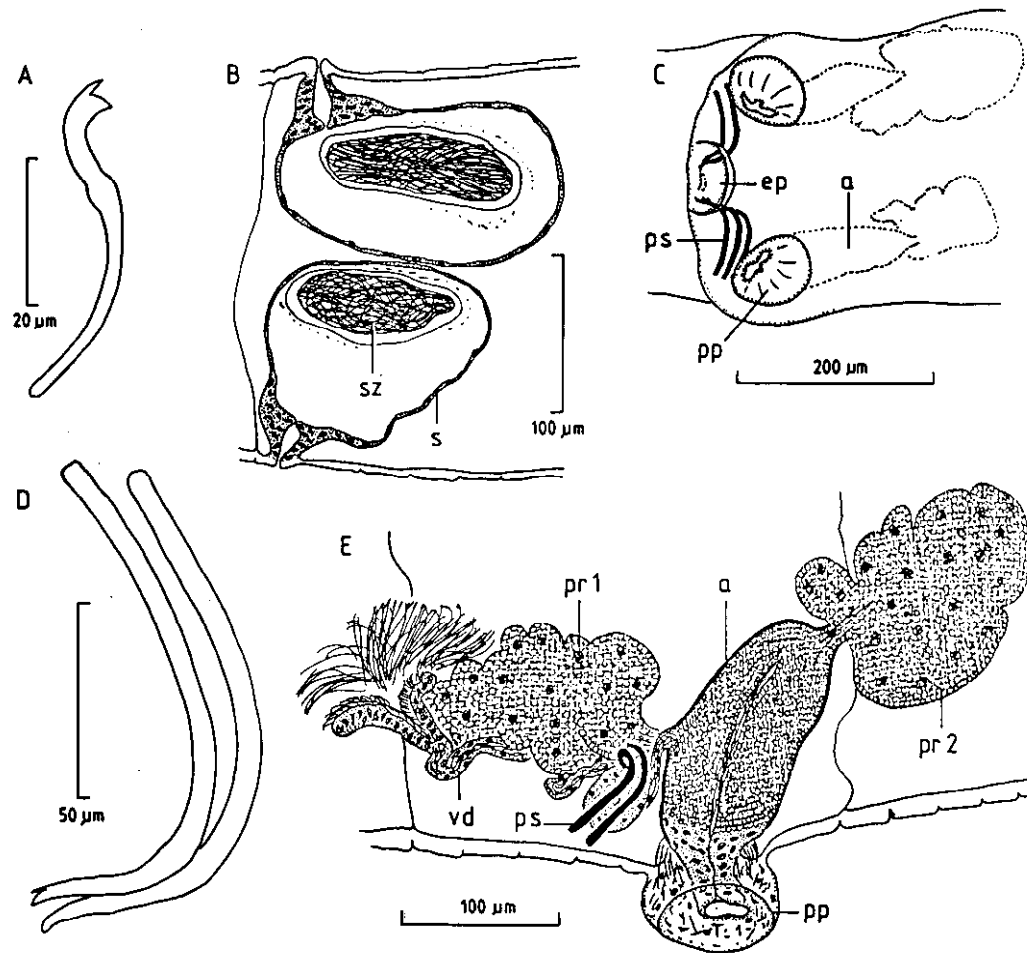
***Bathydrilus formosus* Erséus, 1986**

Bathydrilus formosus Erséus, 1986a:302-303, Fig. 10.

Diagnosis. Length: 15.9-18.0 mm; segments: 84-108. Epidermal glands as continuous dorsal band in many posterior segments. Clitellum extending over $\frac{1}{3}$ X-XII. Somatic setae bifid, sigmoid with upper tooth thinner and shorter than lower: 45-55 μm long, three per bundle anteriorly, two per bundle posteriorly. Penial setae strongly curved, slightly bifid with upper tooth much thinner than lower, not always discernable, 2(3) per bundle, 100-155 μm long; emerging near mid-ventral line at summit of oval epidermal pad medially in XI. An unpaired epidermal papilla, with a small invagination in the middle is present, midventrally in anterior of X. Male and spermathecal pores paired posteriorly in XI and laterally in anterior of X, respectively. Male genitalia paired: vas deferens longer than atrium, 9-12 μm wide; entering atrium medially on anterior face. Atrium pear or spindle-shaped, 150-235 μm long, 50-80 μm wide; inner epithelium densely granulated and ciliated; outer layer distinct; ectal portion less granulated terminating into bulbous muscular pseudopenis. Anterior prostate gland attached to anterior face of atrium at junction of vas deferens; posterior prostate gland attached to atrium apically. Spermathecae paired, each with a short triangular duct and large, thin-walled ampulla. Sperm arranged as roundish, rhomboidal or elongate spermatzeugmata in spermathecal ampullae.

Distribution and Habitat. Caribbean (Belize), southeast North America (east and west coasts of Florida). Associated with generally coral sand; subtidally 0.5-11 m depth.

Remarks. The unique bifid smoothly curved "finely formed, beautiful... aesthetically pleasing" (Erséus, 1986a) penial setae from which the specific epithet is derived, is the principal diagnostic characteristic discriminating this species from all other tubificids in Florida waters.



(after Hrabša, 1986a) *Bathydrius formosus*: A, somatic seta; B, spermathecae in segment X; C, ventral view of penial setae and male pores in segment XI; D, penial setae; E, lateral view of male genitalia in segment XI.

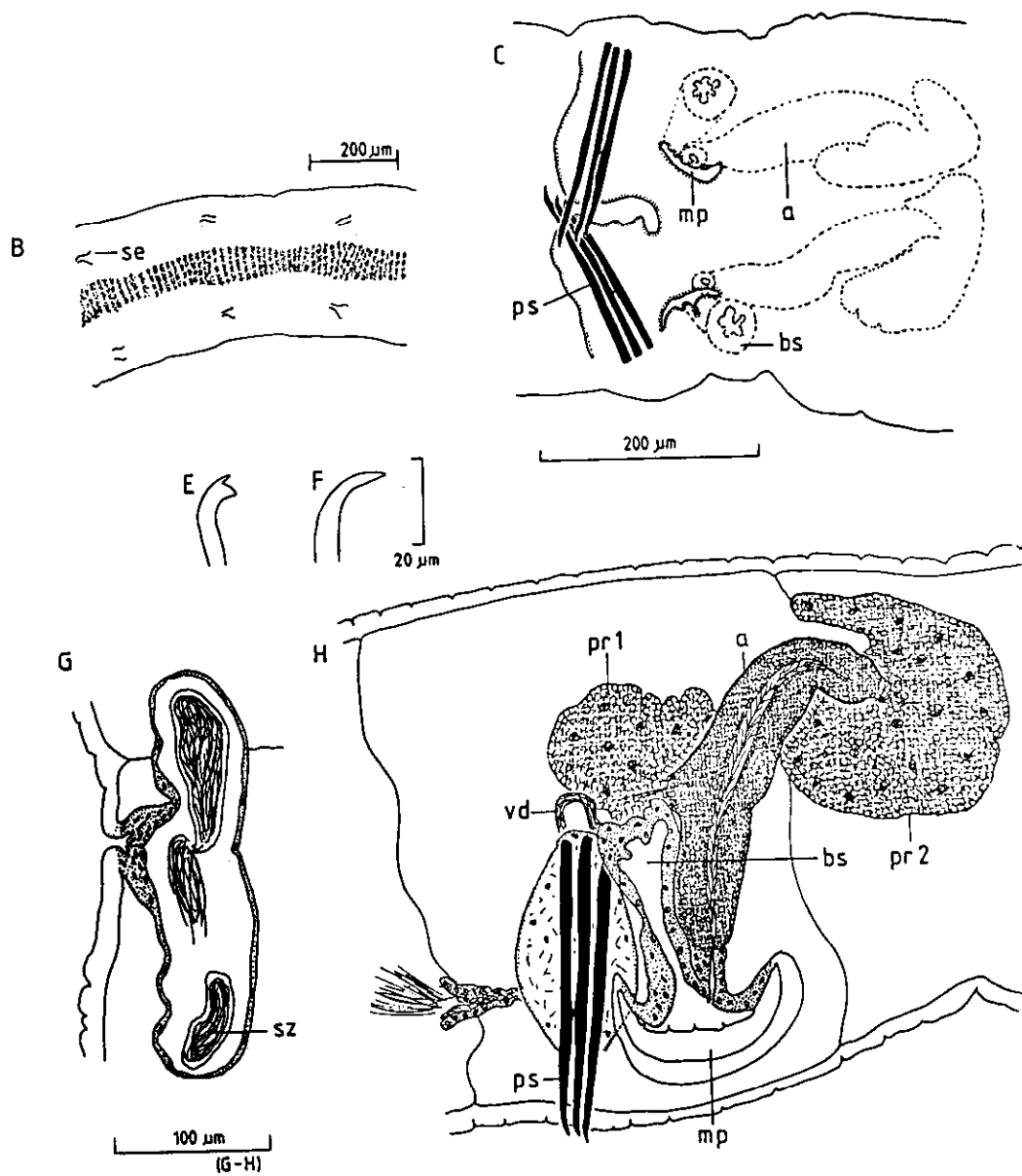
***Bathyrilus ingens* Erséus, 1986**

Bathyrilus ingens Erséus, 1986a:300-302, Fig. 9B, 9C, 9E-9G.

Diagnosis. Length: 25.6-27.0 mm; segments: 127-139. Epidermal glands as continuous dorsal band in segments from just anterior to clitellum to posterior most segments. Clitellum extending over $\frac{1}{3}$ X-XII. Somatic setae bifid, with upper tooth thinner and shorter than lower: 35-85 μm long, 2-3(4) per bundle anteriorly, two per bundle posteriorly; posterior bundles may include simple-pointed, somewhat enlarged setae. Penial setae straight with slightly curved simple-pointed tips, (80)150-200 μm long, three per bundle; tips of bundles often crossing each other, exiting at summits of two large papillae. Male and spermathecal pores paired in posterior of XI and laterally in anterior of X, respectively. Male genitalia paired: vas deferens longer (?) than atrium (complete length not always discernable), narrow, 7 μm wide; entering atrium on ectal-to-middle anterior face. Atrium elongate spindle-shaped, 220-270 μm long, 30-90 μm wide; inner epithelium granulated and ciliated; outer layer distinct; terminating ectally in the outer end of a deep blind sac forming a complex, elaborate pseudopenis. Anterior prostate gland attached to anterior face of atrium at junction of vas deferens; posterior prostate gland large, attached to atrium apically. Spermathecae paired, each with a short triangular duct and large, elongate, somewhat bilobed, thin-walled ampulla. Sperm arranged as rhomboid or elongate spermatozeugmata, as bundles, or as random masses in spermathecal ampullae.

Distribution and Habitat. East coast North America (North Carolina, east and west coasts of Florida), Bermuda. Associated with coarse sands; subtidally 4.5-17 m depth.

Remarks. This species is very similar to the closely related *B. adriaticus* with respect to the general number and morphology of the penial setae and male efferent ducts. The larger size, from which the specific epithet of *B. ingens* is derived, simple-pointed, enlarged posterior setae, and complex male copulatory apparatus are distinctive. However, unless large numbers of fully mature individuals within each community are analyzed, designation of this taxon should simply be referred to as the "*B. adriaticus* complex". See Remarks for the *B. adriaticus* for additional information.



(after Erőss, 1986a) *Bathydrilus ingens*: B, pattern of dorsal epidermal glands (shown for a few successive segments in postclitellar part of body); C, ventral view of penial setae and male pores in segment XI; E, anterior seta; F, posterior dorsal seta; G, spermatheca; H, lateral view of male genitalia in segment XI.

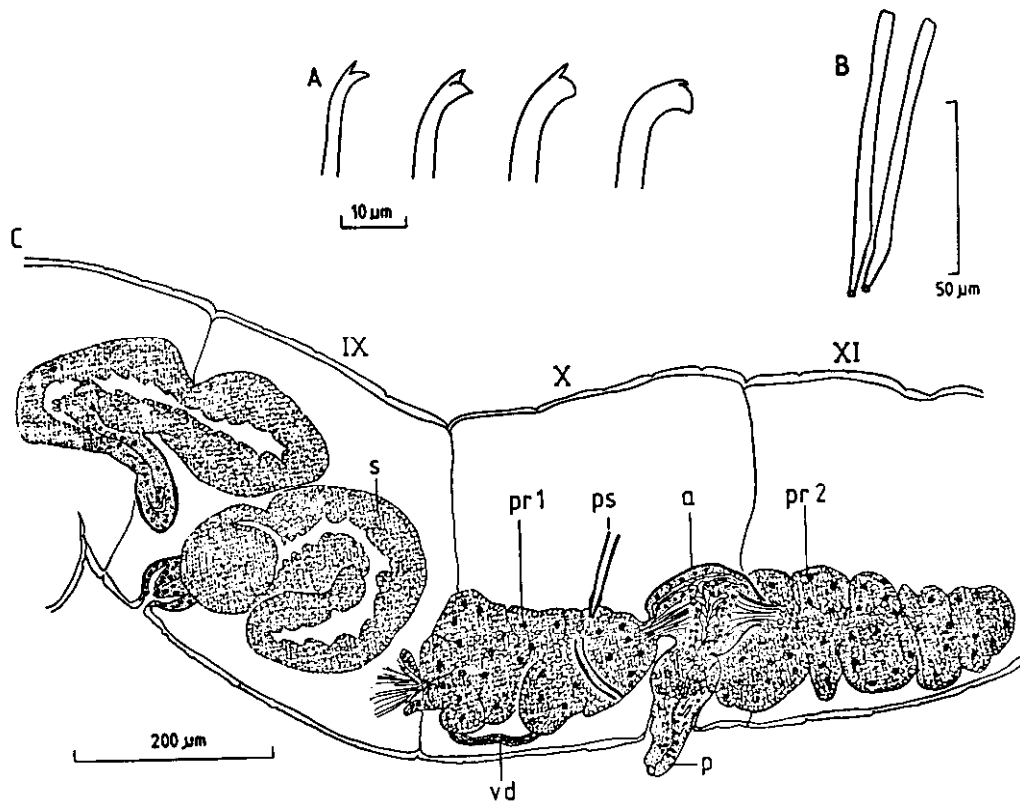
***Bathyrilus macroprostatus* Erséus, 1986**

Bathyrilus macroprostatus Erséus, 1986a:303-305, Fig. 11.

Diagnosis. Length: greater than 4.7 mm; segments: greater than 25. Clitellum extending over $\frac{1}{2}$ X-XII. Somatic setae bifid: anteriorly 50-55 μm long, 2-3(4) per bundle, with upper tooth thinner and shorter than lower; posterior setae larger, 70-85 μm long, two per bundle, with upper tooth much smaller than lower. Penial setae straight to somewhat curved with ectal swelling and flat, hooked tips, 70-90 μm long, two per bundle. Male and spermathecal pores paired posteriorly in XI and in anterior of X, respectively. Male genitalia paired: vas deferens longer than atrium, narrow, 8-9 μm wide; entering atrium entally on anterior face. Atrium erect or somewhat spindle-shaped, tilted over the posterior, 230-245 μm long, 115-140 μm wide; bipartite, separated by a constriction; inner epithelium granulated (granulations of ental portion may not be developed), ciliated; thick outer layer, terminating in elongate pseudo(?)penis without cuticular sheath. Anterior prostate gland large, attached to anterior face of atrium ental to medial constriction at junction of vas deferens; posterior prostate gland large attached opposite anterior gland on posterior face of atrium. Spermathecae paired, each with short, muscular duct and elongate, thick-walled ampulla. Sperm arrangement unknown.

Distribution and Habitat. Southeast coast of North America (east coast of Florida).

Remarks. The characteristic diminutive flat-tipped penial setae with sub-apical swellings distinguish this species from other tubificids from Florida waters. The very large prostate glands and permanently pendant(?), well-developed penes differentiate *B. macroprostatus* from its congeners.



(after Eiréus, 1986a) *Bathydrius macroprostataz*: A, somatic setae; B, penial setae; C, somewhat lateral view of asirium (of one side only), penial setae, and spermathecae in segments IX-XI (note that this location is an anomaly, characterizing the holotype only).

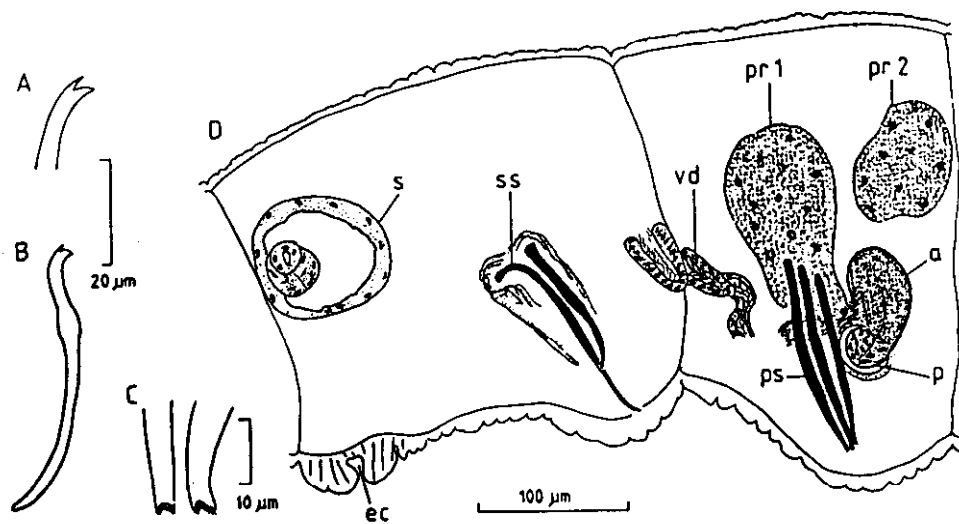
***Bathyrilus notabilis* Erséus and Milligan, 1988**

Bathyrilus notabilis Erséus and Milligan, 1988:292-294, Fig. 1-2.

Diagnosis. Length: 10.6-11.6 mm; segments: 64-66. Clitellum extending over X-XII. Somatic setae bifid, sigmoid, 45-65 μm long: anterior setae with upper tooth shorter and thinner than lower: (2)3-4 per bundle; posterior setae with upper tooth very reduced, (1)2 per bundle. Penial setae in XI somewhat curved with chisel-like bifid tips with fine pectinations, 120-200 μm long, 3-4 per bundle; exiting at summits of flap-like epidermal lobes. Spermathecal setae in X, simple-pointed, strongly curved entally, 120-165 μm long, 1(2) per bundle. Male and spermathecal pores paired in posterior of XI and laterally in anterior of X, respectively. A midventral "epidermal crypt" is present anteriorly in X. Male genitalia paired: vas deferens longer than atrium, 14 μm wide; entering atrium medially on anterior face. Atrium oblong to comma-shaped, erect, 85-135 μm long, 35-55 μm wide; inner epithelium granulated, ciliation not apparent; outer layer distinct, terminating ectally in discrete papilla enclosed in a small sac. Anterior prostate gland attached to anterior face of atrium at junction of vas deferens; posterior prostate gland attached to atrium apically. Spermathecae paired, each with a short triangular duct and oval ampulla. Sperm arranged in loose bundles in spermathecal ampullae.

Distribution and Habitat. Southeast North America (west coast of Florida). Associated with fine to coarse sediments; subtidally, 4-58.5 m depth.

Remarks. The species is "notable" for having modified simple-pointed spermathecal setae and slightly bifid penial setae with finely pectinate tips, which distinguish it from all other tubificids in Florida waters.



(after Ertesus and Milligan, 1968) *Bathydrilus notabilis*: A, anterior somatic seta; B, posterior somatic seta; C, tips of penial setae; D, lateral view of genitalia in segments X-XI.

Subfamily. Limnodriloidinae Erséus, 1982

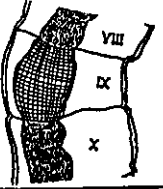
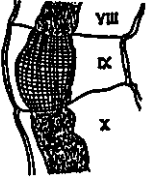
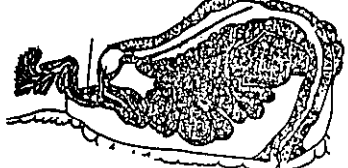
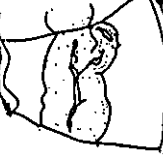
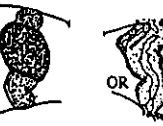
Type Genus. *Limnodriloides* Pierantoni, 1903.

Diagnosis. Almost exclusively marine. Somatic setae (when present; absent in *Tectidrilus achaetus* Erséus and Qi, 1985), all bifid, hairs absent. Modified genital setae occasionally present; if present, usually associated with the spermathecae in X and ectally grooved or spoon-shaped. Esophagus modified in IX, either enlarged and barrel-shaped with reticulate blood plexus or bearing an anteriorly directed pair of lateral finger-shaped diverticula (only one diverticulum present in *Doliodrilus diverticulatus* Erséus, 1985). Ciliated vas deferens enters well differentiated atrium apically or subapically. Each atrium composed of two morphologically distinct regions: 1) entally, an enlarged tubular ampulla with a broadly attached lobed prostate gland connected via a "prostatic pad" either within the lining of the atrium or as a granulated diverticulum bulging ventrally from the atrium, and 2) an ectal duct of variable length opening to the exterior as a simple pore or through a modified penial apparatus without a cuticular penis sheath. Spermathecae may be single or paired, dorsal, ventral, or ventrolateral, or absent altogether. Sperm generally arranged in compact spindle or torch-shaped bundles (spermatozeugmata) within the spermathecae of mated individuals.

Remarks. This subfamily was established by Erséus (1982a) to accommodate species previously considered Aulodrilinae. The primary distinguishing characters of these species are the modified gut (either as a diverticulum or swollen glandular region) in IX, and a lobed prostate gland broadly attached to the atrium by a modified "prostatic pad". Additionally, almost all the species of this subfamily are marine.

Currently, this subfamily comprises 92 species within six genera: *Limnodriloides*, *Thalassodrilides*, *Parakaketio*, *Doliodrilus*, *Tectidrilus*, and *Smithsonidrilus*. *Thalassodrilides*, *Doliodrilus*, and *Parakaketio* include only species with an enlarged gut plexus in IX instead of paired diverticula. All species currently included in *Smithsonidrilus*, which was recently combined with *Marcusaedrilus* (Erséus, 1990a), possess paired gut diverticula in IX. Species of *Limnodriloides* and *Tectidrilus* include those taxa with either modification. Representatives of all genera have been collected from Florida waters or the Caribbean.

Table 5. Limnodriloidinae genera.

Taxa	Somatic Setae #/bundle Ant. Post.	Esophagus in IX	Male Genitalia
<i>Thalassodrilus</i>	(1)2-5(6) 1-3(4)		
<i>Parakakelio</i>	2(3-5) (1)2-3		
<i>Tecidrilus</i>	2 1		
<i>Limnodrilioides</i>	2-4(5) 1-3		
<i>Smithsonidrilus</i>	(1)2-3(4) (1)2		

Genus. *Thalassodrilides* Brinkhurst and Baker, 1979

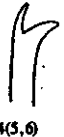
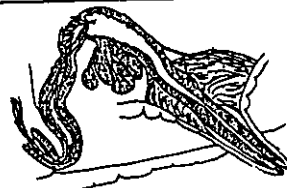
Type Species. *Limnodriloides gurwitschi* Hrabě, 1971b.

Diagnosis. (Based on Erséus, 1990a). Brackish water or marine tubificids. All setae bifid, hair setae and modified genital setae absent. Male pores paired in segment XI. Spermathecal pores paired or absent in segment X. Esophagus in IX greatly dilated with thickened walls and reticulate blood plexus. Vasa deferentia wide, ciliated, entering atria apically. Atria terminating in complex, muscular, eversible pseudopenes. Prostate glands compact, broadly connected by glandular tissue to ventral surface of atria. Spermathecae paired or absent. Sperm if present, random or tightly bundled.

Remarks. The history of this genus is interesting, but somewhat confusing. Following is a brief synopsis. *Rhyacodrilus prostatus* was described by Knöllner (1935). Brinkhurst (1963) established a new genus, *Thalassodrilus* (from the Latin "thalassa" meaning "of bays, gulfs, or inland seas") for *R. prostatus* since its placement in *Rhyacodrilus* was clearly incorrect based on Hrabě's (1960) and Brinkhurst's (1963) reexaminations. Hrabě (1967) disagreed with Brinkhurst's (1963) decision and resurrected *Limnodriloides* and included *T. prostatus* in that genus. Hrabě (1971b) then described *Limnodriloides gurwitschi*. Later that year, Hrabě redefined the genus *Thalassodrilus* and transferred into it *L. gurwitschi*, *L. prostatus*, *Limnodriloides roseus* Pierantoni, 1904, and *L. pectinatus* Pierantoni, 1904. However, Cook (1970, 1974) regarded the latter two taxa as "species dubiae" of *Spiridion*. Based on Erséus (1975b) reexamination of *T. prostatus*, it was transferred into *Phallodrilus*. Since *P. prostatus* was originally the type species of *Thalassodrilus*, the species previously included in that genus were subsequently left without generic position. As a result, Brinkhurst and Baker (1979) established the genus *Thalassodrilides* to accommodate those species and a new species, *T. milleri*, but also included *T. roseus* and *T. pectinatus* based on Hrabě's (1971b) decision. Also in 1979, Erséus revised the genus *Phallodrilus* and declared *T. pectinatus* as a probable synonym of *Phallodrilus rectisetosus*. Erséus (1981c) subsequently reviewed *Thalassodrilides* and declared *Curacaodrilus sinus* Righi and Kanner, 1979, from the Caribbean as a junior synonym of *T. gurwitschi*. In 1990, Erséus emended the generic definition of *Thalassodrilides* to include *Kaketio ineri* Righi and Kanner, 1979, and a new species, *T. bruneti*. At that time, he listed three additional taxa in that genus, *T. belli* (Cook, 1974), *T. gurwitschi*, and (?) *T. milleri*. However, *L. roseus* was not included. This species has apparently not been

However, *L. roseus* was not included. This species has apparently not been seen since it was described and its description is inadequate for a definitive generic position. It should, therefore, be considered a "species dubia". With the exception of the questionable *T. milleri* and *T. briani* Erséus, 1992b, all species of *Thalassodrilides* are expected to occur in Florida waters.

Table 6. *Thalassodrilides* species.

<i>Thalassodrilides</i>	Anterior Setae #/bundle	Posterior Setae #/bundle	Spermatheca	Male Genitalia
<i>belli</i>	 3-6	 (1)2(3)		
<i>bruneti</i>	 (1)2-4	 1-2(3)	absent	
<i>gurwitschi</i>	 (1)2-4(5,6)	 (1)2(3,4)	absent	
<i>ineri</i>	 3-5	 1-3		

***Thalassodrilides belli* (Cook, 1974)**

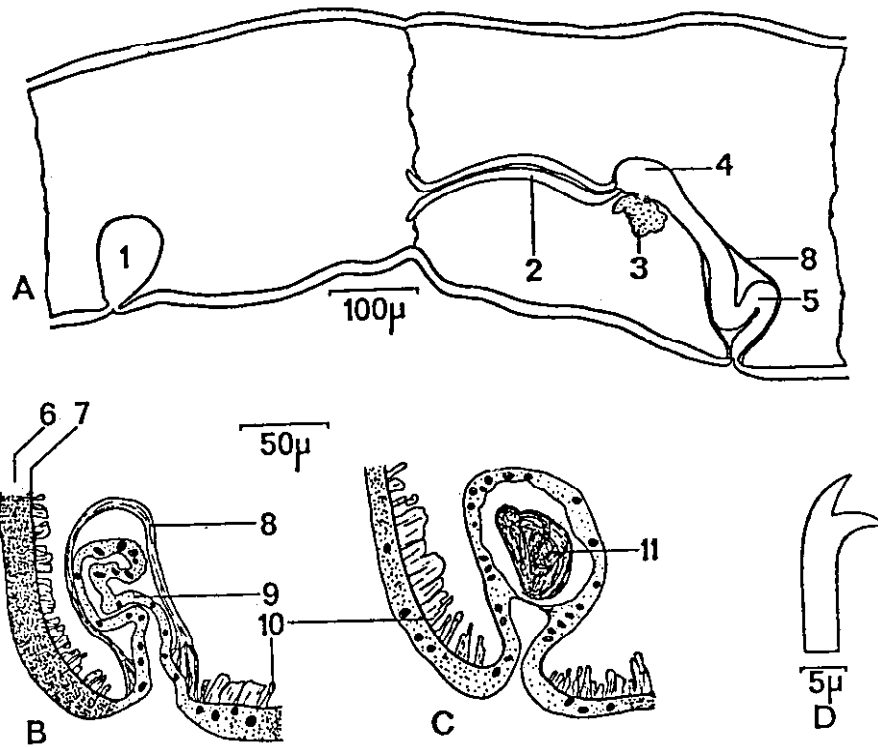
Thalassodrilus belli Cook, 1974:129, Fig. 2.

Diagnosis. Length: up to 17 mm; segments: up to 66. Clitellum extending over XI-½ XII. Setae all bifid, upper tooth thinner but as long as lower: 69-105 µm long, anteriorly 3-6 per bundle; posteriorly (1)2(3) per bundle; ventral setae absent in XI. Male pores not on bulbous projections. Spermathecal pores open anteriorly in the ventrum of X. Conspicuous blood plexus present in thickened esophageal wall in IX. Male genitalia paired: vas deferens relatively short and wide entering atrium apically; atrium about as long or longer than vas deferens with a small prostate gland attached on a glandular ventral region entally, ectal portion of atrium forms a convoluted duct folded inside a muscular sac, terminating in an eversible pseudopenis. Paired spermathecae small, pear-shaped, sperm arranged as a compact, random mass.

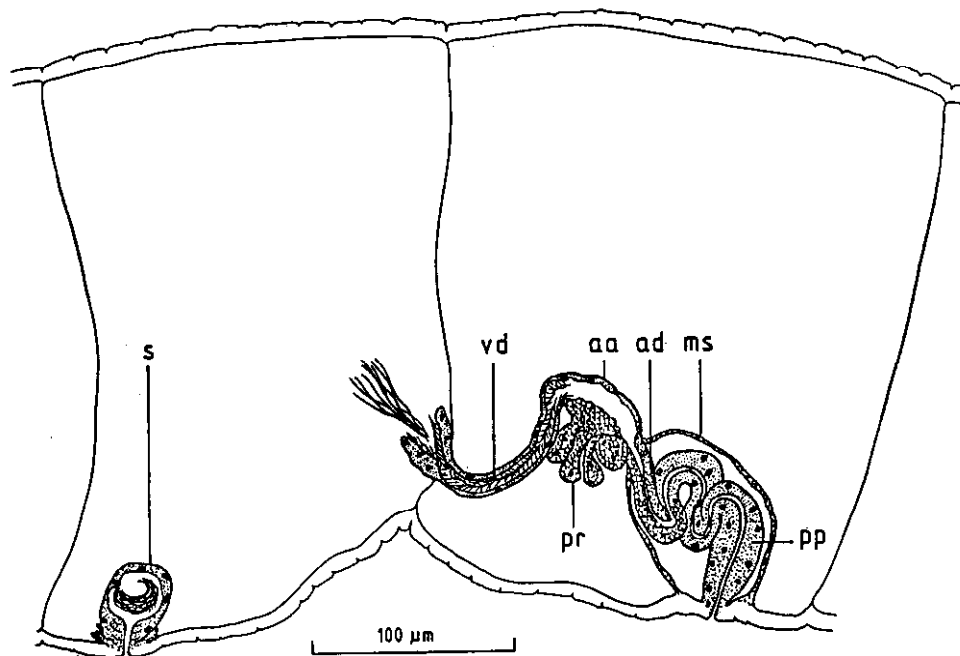
Distribution and Habitat. North America (Virginia, Louisiana, Texas, Mississippi, Florida, Pacific coast of Mexico), Caribbean (Trinidad and Puerto Rico), Bermuda. Found in brackish water in shallow mud, clay, silt sediments.

Remarks. The enlarged esophagus in IX with the thicker wall and conspicuous blood plexus is characteristic for *Thalassodrilides*. The presence of spermathecae distinguishes *T. belli* from *T. gurwitschi* and *T. bruneti*. The morphology of the somatic setae further distinguishes *T. belli* from its congeners: the upper and lower teeth are approximately the same length and have the same basal width in *T. belli*, whereas the upper tooth is shorter and thinner in all other taxa of *Thalassodrilides*.

Erséus (1981c) states that there is a distinction in the position of the spermathecal pores between the Pacific and Atlantic populations: the pores are more lateral in position in the Pacific form.



(after Cook, 1974) *Thalassodrilus belli*: A, longitudinal view of genital segments; B, transverse section of male pore; C, transverse section of spermatheca; D, seta (segment VIII); 1, spermatheca; 2, vas deferens; 3, prostate gland; 4, atrial ampulla; 5, penial complex; 6, epithelium of clitellum; 7, circular muscle; 8, muscle sac surrounding penis; 9, lining epithelium of penial duct; 10, longitudinal muscle; 11, sperm mass.



(after Bräus, 1981c) *Thalassodrilus belli*: lateral view of genital organs in segments X-XI (specimen from Texas).

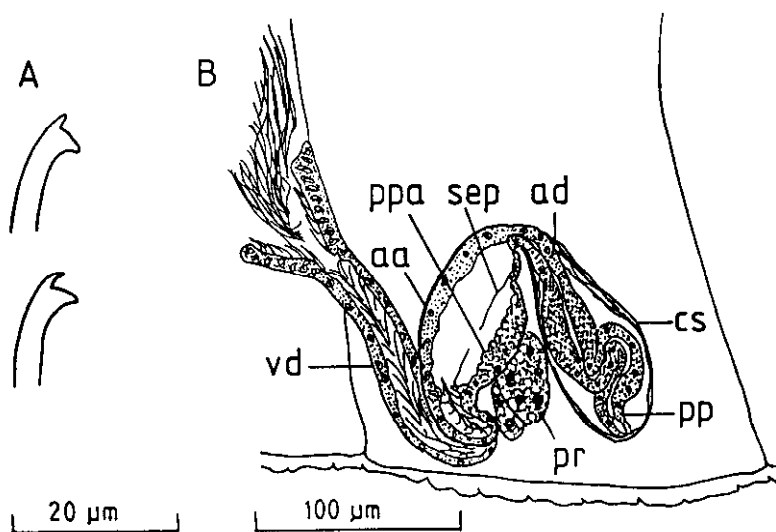
***Thalassodrilides bruneti* Erséus, 1990**

Thalassodrilides bruneti Erséus, 1990a:278-279, Fig. 25.

Diagnosis. Length: 4.6-5.3 mm; segments: 33-44. Clitellum extending over XI-XII. Setae all bifid with upper tooth shorter and narrower than lower, 35-70 μm long: (1)2-4 per bundle anteriorly and 1-2(3) posteriorly. Ventral setae absent from XI. Male pores paired in XI. Spermathecal pores absent. Esophageal wall in IX greatly thickened with conspicuous blood plexus. Male genitalia paired: vas deferens wide, entering atrium apically. Atrium about as long as vas deferens, 55-80 μm long, 25-50 μm wide, with thin horizontal septum internally and a small prostate attached to a ventral glandular pad; terminating in a slender atrial duct with a distal pseudopenis inside a pear-shaped muscular copulatory sac. Male pores not on protuberances when pseudopenes are withdrawn. Spermathecae absent.

Distribution and Habitat. Caribbean (Belize, Curacao). Associated with muddy sediments intertidally and subtidally.

Remarks. This species is "virtually identical to *T. gurwitschi*" (Erséus, 1990a). The characters Erséus relies on for separation of the two species are size (*T. bruneti* is smaller with fewer segments), and the male protuberances are generally lacking in *T. bruneti*. Curiously, these are the same reasons Righi and Kanner (1979) used to separate *Curacaodrilus sinus* from *T. gurwitschi* which Erséus (1981c) did not consider justifiable reasons for species discrimination, and that the more conspicuous male projections in *T. gurwitschi* are simply a function of size. The horizontal atrial septum present in *T. bruneti* is relatively indistinct and may have been overlooked in *T. gurwitschi*. Since *T. bruneti* has not been reported from Florida (it is only known from Belize in the Caribbean) individuals lacking spermathecae may be more appropriately considered as *T. gurwitschi*.



(after Erasmus, 1990a) *Thalassodrilus bruneti*: A, setae, showing variation in teeth; B, somewhat lateral view of male genitalia in segment XI.

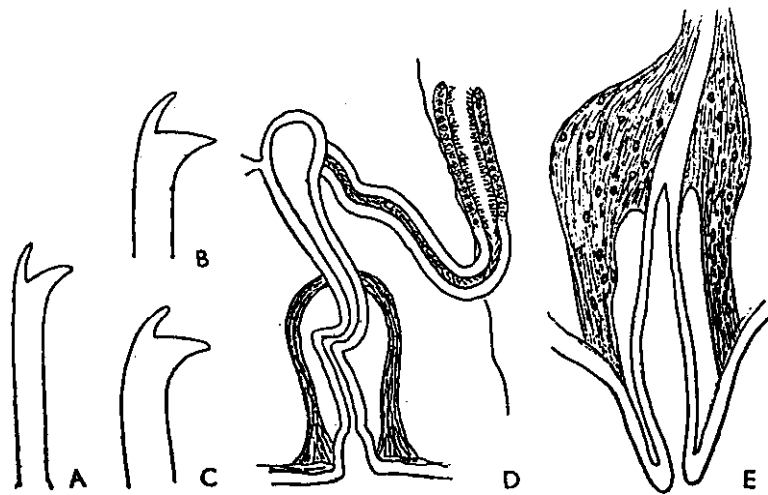
***Thalassodrilides gurwitschi* (Hrabe, 1971)**

Limnodriloides gurwitschi Hrabe, 1971b:33-35, Fig. 1.

Diagnosis. Length: 6-20 mm; segments: up to 64. Clitellum extending over XI-($\frac{1}{2}$ XII)XII. Setae all bifid to about 85 μ m long; upper tooth shorter and narrower than lower; (1)2-4(5,6) per bundles anteriorly; (1)2(3,4) posteriorly. Ventral setae absent from XI. Male pores on bulbous projections, which may or may not be introverted into the body. Spermathecal pores absent. Conspicuous blood plexus present in thickened esophageal wall in IX. Male genitalia paired: vas deferens 17-25 μ m wide and short, entering atrium apically. Atrium about as long as vas deferens, 80-100 μ m long, 30-35 μ m wide, with a small prostate gland attached entally, terminating in pseudopenes which are generally everted and protrude from projections of the body wall. Spermathecae absent.

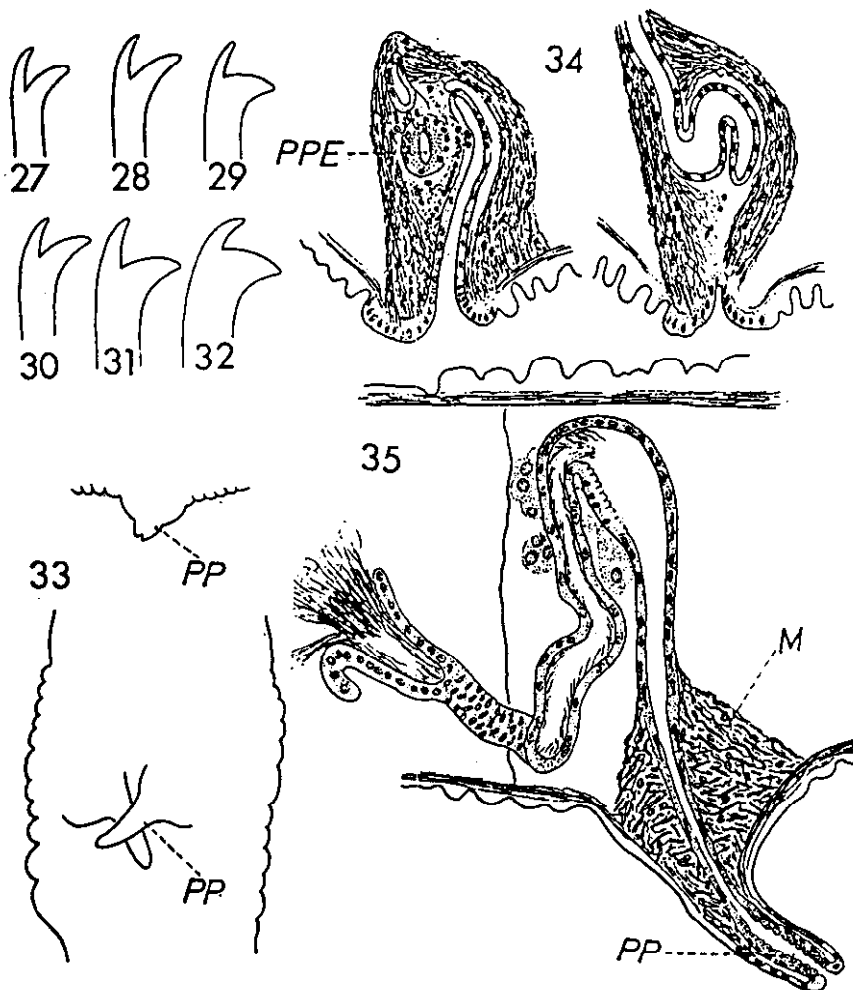
Distribution and Habitat. Widespread throughout the Caribbean and Gulf of Mexico, also the Black Sea, Mediterranean Sea, Persian Gulf, southern China, Hawaii, western Australia. Found inter- and subtidally, generally associated with muddy sediments in marine and brackish water.

Remarks. This is a relatively large species which requires fully mature individuals for accurate specific determination. This species is readily recognized, even immature specimens, as a member of *Thalassodrilides* by the enlarged thick-walled esophagus in IX. Although species within other genera of Limnodriloidinae may have a dilated esophagus in IX, none are as thick-walled as in *Thalassodrilides*. In fully mature specimens collected from the Caribbean the protuberances on the body wall of XI are almost always everted, even when the pseudopenes are inverted. This character and the complete lack of spermathecae distinguish it from the other species within this genus. Another distinction between *T. gurwitschi* and the closely related *T. belli* is that the basal width of the upper tooth is much narrower in the former whereas they are equal in the latter. Also see Remarks for *T. bruneti*.

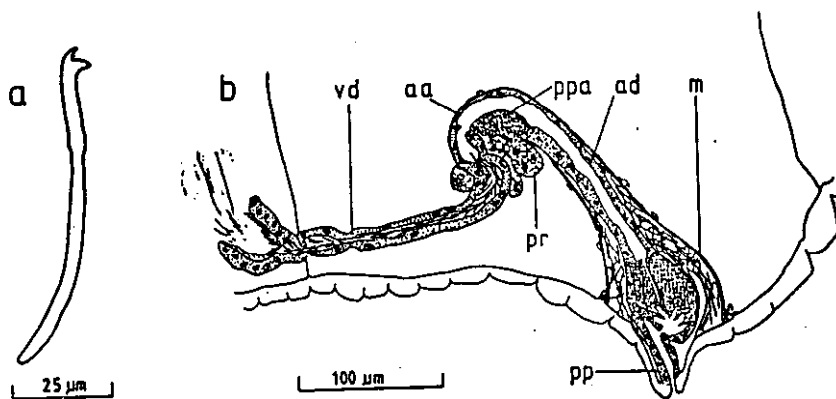


(after Hrabě, 1971b) *Thalassodrilus gurwitschi*: ventral seta of A, segment 3, distal end; B, segment 25; C, segment 45; D, male duct (half schematically); E, non quite protruded distal part of male duct.

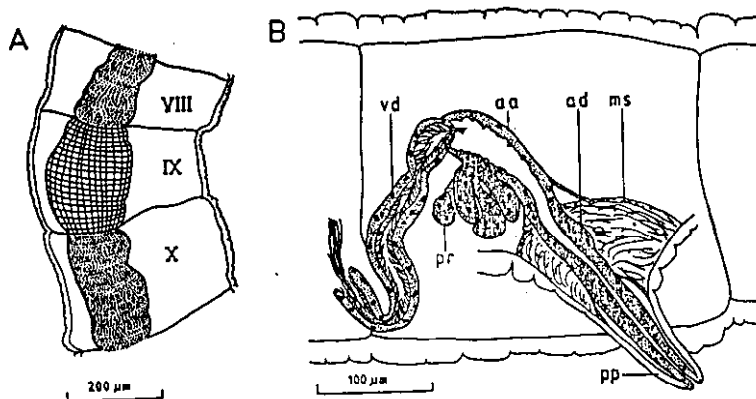
(after Hrabě, 1971a)
Thalassodrilus gurwitschi: 27-32, ectal
 "end of dorsal setae
 from segments 2, 4, 45,
 ventral setae of segments
 2, 7, 10 x 1535; 33,
 contracted and protruded
 pseudopenes (PP) x 67;
 34, two sections through
 contracted pseudopenis,
 PPE; end of pseudopenis
 with glandular epitheli-
 um x 235; 35; longitu-
 dinal section of male
 duct; M, muscle fibres;
 PP, end of protruded
 pseudopenis with gland-
 ular epithelium x 255.



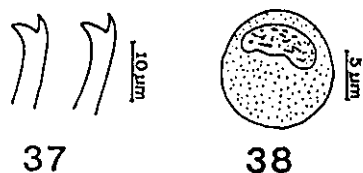
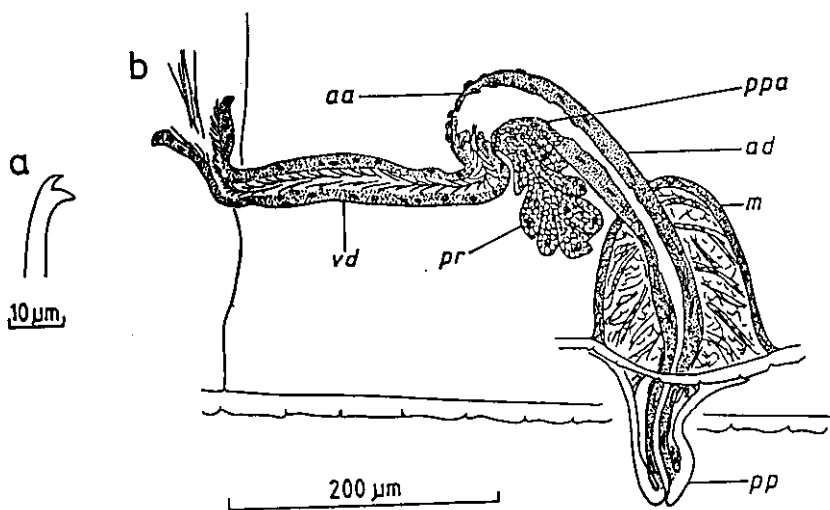
(after Erasus, 1985) *Thalassodrilides garwitschi* from Saudi Arabia: a, seta; b, lateral view of male duct in segment XI.



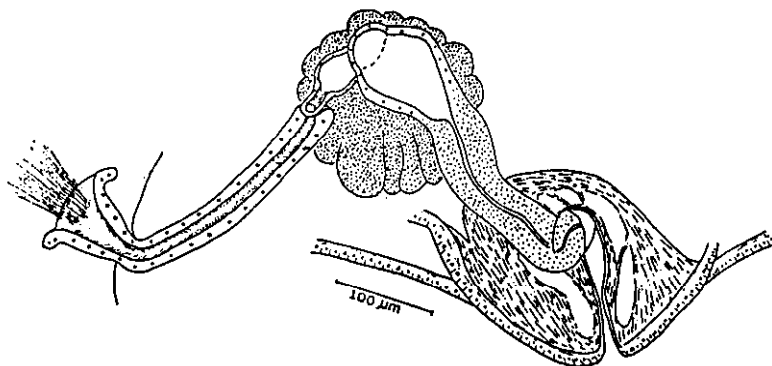
(after Erasus, 1981c) *Thalassodrilides garwitschi*: A, semi-schematic drawing showing position and shape of the barrel-shaped, thick-walled portion of the esophagus in segment IX; B, lateral view of male efferent duct in segment XI (specimen from Puerto Rico).



(after Erasus, 1984a) *Thalassodrilides garwitschi* from Hong Kong: a, seta; b, lateral view of male genitalia.



(after Righi and Kanner, 1979) *Thalassodrilides garwitschi*, as *Curacaodrilus sinas*: 37, setae; 38, coelomocyte.



(after Righi and Kanner, 1979) *Thalassodrilides garwitschi*, as *Curacaodrilus sinas*: male duct.

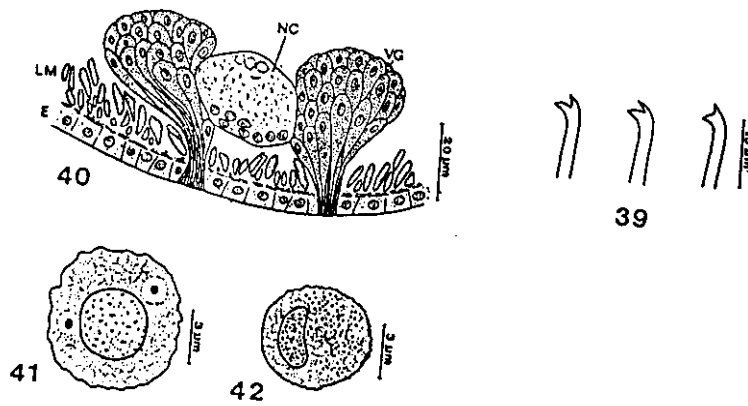
***Thalassodrilides ineri* (Righi and Kanner, 1979)**

Kaketio ineri Righi and Kanner, 1979:55-62, Fig. 39-47.

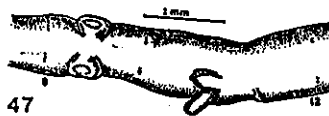
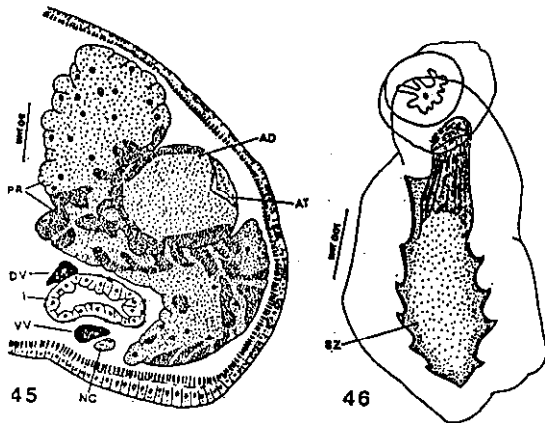
Diagnosis. Length: 25 mm; segments: 52-90. All setae bifid, upper tooth thinner and somewhat shorter than the lower: anteriorly 3-5 per bundle; posteriorly, 1-3 per bundle; ventral setae absent in XI. Male pore mid-ventral in XI. Spermathecal pores open anteriorly on ventrum of X. Esophagus in IX dilated and thick-walled devoid of chlorogogen cells. Male genitalia paired: vas deferens relatively wide and shorter than remaining male ducts, entering atrium apically. Atrium more or less cylindrical, divided into two parallel structures: a proper atrium which is thin-walled and narrow, and a compact body which covers the ventrolateral surface of the atrium proper, and to the full length of which the prostate glands are attached; terminating in a glandular atrial duct which is continued into a long ejaculatory duct ending in folded eversible pseudopenes enclosed in a large muscular sac. The muscular sacs open into an unpaired copulatory chamber which opens to the body surface mid-ventrally. Spermathecae paired anteriorly in X each, comprised of a voluminous egg-shaped ampulla containing a hyaline structure with six pairs of lateral denticles bent toward the spermathecal pore, and a short duct opening outside the body through a small pore. Sperm as loose bundles.

Distribution and Habitat. Caribbean (Belize, St. Martin, Barbados, Curacao, Bonaire), southeast North America (Florida Keys). Lower intertidal and subtidal and to 2 m depth. Specimens have also been collected from a shallow *Halimeda* reef.

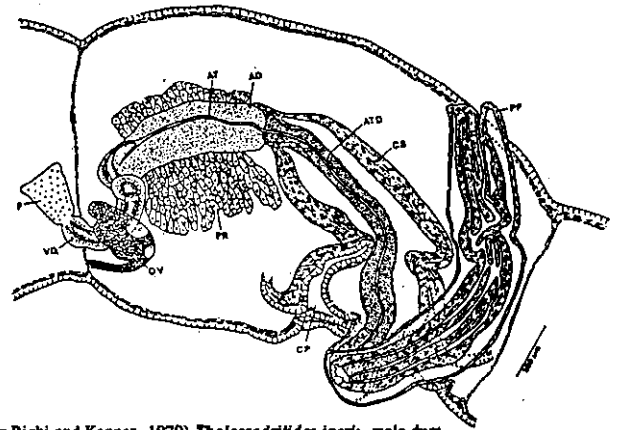
Remarks. This is a very large, stout tubificid characterized by the unique male genitalia with the glandular atrial diverticula terminating in a single horseshoe-shaped pore mid-ventrally in XI, and the peculiar internal morphology of the spermathecae which contain a unique hyaline structure (a kind of spermatozeugmata) with six pairs of denticles, somewhat reminiscent of a Christmas tree. The very prominent nipple-like papillae on which the spermathecal pores are located also characterize this taxon. This species originally formed the monotypic genus *Kaketio* Righi and Kanner, 1979, until Erséus (1990a) transferred it to *Thalassodrilides* based on the assumption that the prostate gland bearing atrial diverticulum was derived from a glandular pad as is present in *T. bruneti*, and the complex copulatory apparatus is basically similar to the congeners.



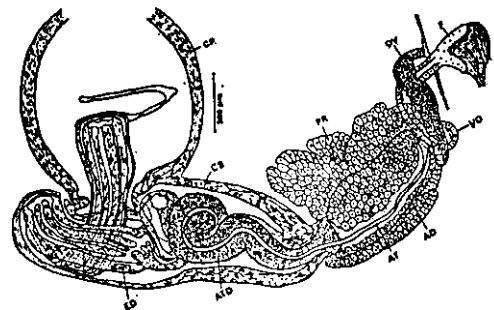
(after Righi and Kanner, 1979) *Thalassodrilus inerti*: 39, setae of segments V, VII, and XI; 40, transverse section of segment VII; 41-42, coelomocytes.



(after Righi and Kanner, 1979) *Thalassodrilus inerti*: 45, transverse section of segment XI; 46, spermatheca; 47, ventral view of segments IX-XII.



(after Righi and Kanner, 1979) *Thalassodrilus inerti*: male duct.



(after Righi and Kanner, 1979) *Thalassodrilus inerti*: male duct.

Genus. *Parakaketio* Erséus, 1982

Type Species. *Parakaketio longiprostatum* Erséus, 1982.

Diagnosis. Hairs absent. Modified genital setae absent. Male and spermathecal pores paired in XI and anterior portion of X, respectively. Esophagus in IX dilated, thick-walled, with reticulate blood plexus. Male and spermathecal pores paired in XI and X, respectively. Male genitalia paired: vas deferens wide, enters atrium apically, atrium long, cylindrical, terminating in a simple pore. Copulatory structures are absent. Ental portion of atrium elongate, divided by a longitudinal septum into a dorsal lumen and ventral diverticulum largely filled with secretory granules. Prostate gland broadly attached to a conspicuous prostatic pad on the ventral surface of the atrial diverticulum. Spermathecae paired. Sperm arranged as coiled bundles.

Remarks. This genus is most similar to *Thalassodrilides*, particularly *T. ineri* representing the junior synonym, *Kaketio*, for which *Parakaketio* derives its name. The enlarged thick-walled esophagus in IX is most similar to *Thalassodrilides* than any other Limnodriloidinae genera. The differentiated atrium is somewhat intermediate between *T. ineri* and *T. bruneti*. However, the very simple, only slightly muscular pseudopenis clearly distinguishes the two genera.

Parakaketio is a monotypic genus which has not been recorded outside the type locality of southeast Florida.

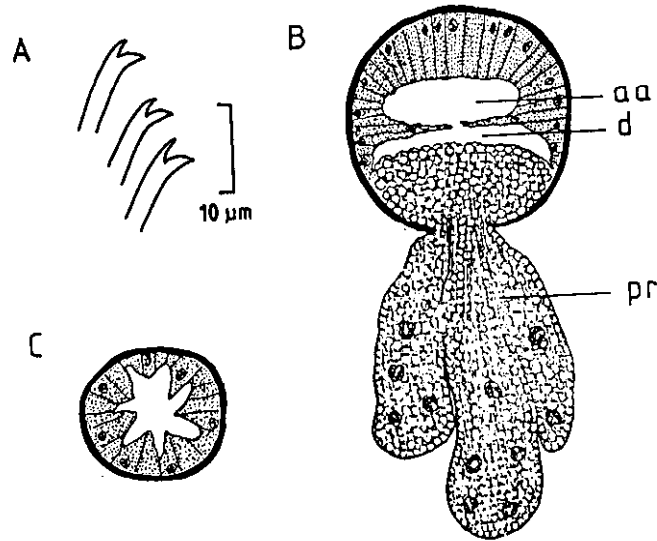
***Parakaketio longiprostatus* Erséus, 1982**

Parakaketio longiprostatus Erséus, 1982c:195-196, Fig. 1-2.

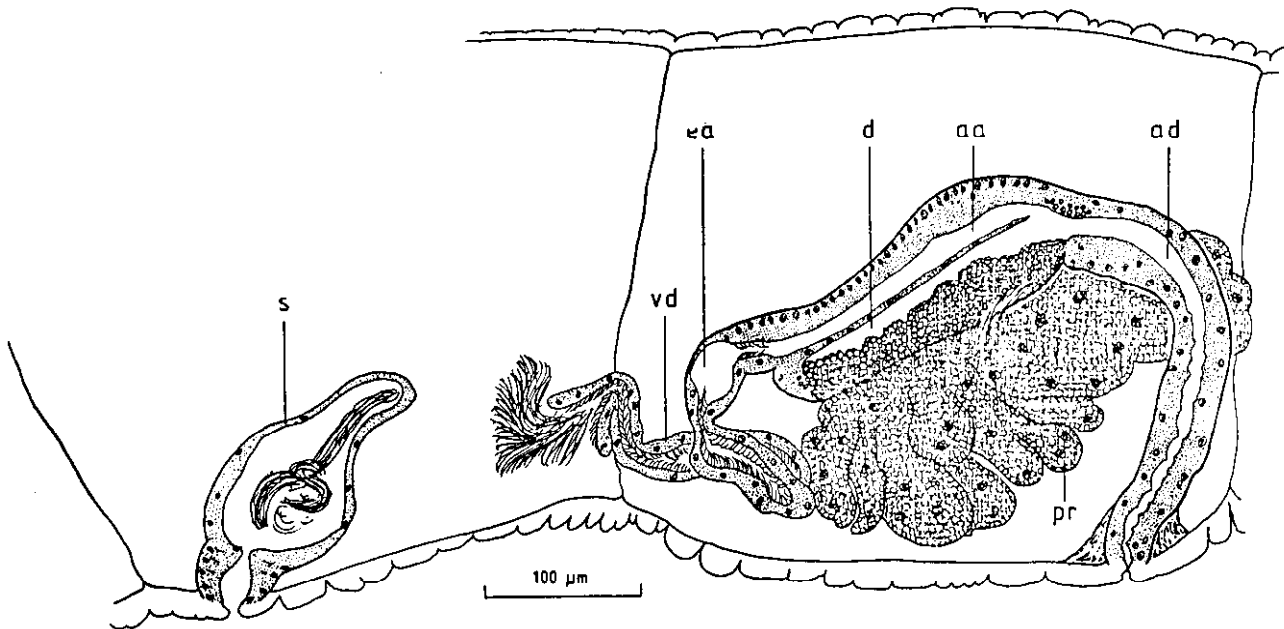
Diagnosis. Length: 12.8 mm; segments: 62. Clitellum extending over XI-XII. All setae bifid, upper tooth thinner and shorter than lower: 40-55 μm long anteriorly (2)3-5 per bundle, posteriorly (1)2-3 per bundle; ventral setae absent in XI. Male and spermathecal pores paired in posterior part of XI and anterior part of X, respectively. Esophagus in IX enlarged, thick-walled with reticulate blood plexus. Male genitalia paired: vas deferens short; 25-33 μm wide, entering atrium apically. Atrium longer than vas deferens, 450-575 μm long, divided into three main sections: 1) a short non-ciliated, thin-walled ental region, 30-35 μm wide, 2) a longer, longitudinally differentiated mid-region, 40-70 μm wide, with a prostate gland broadly attached to the glandular ventral portion, and 3) a long ectal duct, 30-45 μm wide, 250 μm long, exiting the body wall through a simple pore. No penial apparatus present. Spermathecae paired in anterior part of X, each comprised of a pear-shaped ampulla and short thick-walled duct.

Distribution and Habitat. Known only from the Miami area in Florida. Associated with sand and shell substrates of 3 m depth.

Remarks. This species superficially resembles *Thalassodrilides belli*, but differs because of the absence of a complex copulatory apparatus of the former. *Parakaketio longiprostatus* is very similar to *Limnodriloides rubicundus* which also possesses an enlarged esophagus in IX and lacks well-developed pseudopenes. The size of the various structures of the male genitalia can be used to differentiate the taxa. In *P. longiprostatus* the vas deferens is 25-33 μm wide and the atrial duct is about 250 μm long, whereas they are 9-13 μm and 40-55 μm in *L. rubicundus*, respectively. Additionally, the esophageal enlargement is very short in *rubicundus* and the spermathecal pores are in the middle of segment X in *rubicundus*.



(after Bråtus, 1982c) *Parakakelio longiprostatus*: A, setae; B, transverse section (semi-schematic) through the atrium, showing the proper atrial ampulla (aa), the atrial diverticulum (d), and the prostate gland (pr); C, transverse section (semi-schematic) through the atrial duct.



(after Bråtus, 1982c) *Parakakelio longiprostatus*: lateral view of spermatheca and male duct in segments X-XI.

Genus. *Tectidrilus* Erséus, 1982

Type Species. *Tectidrilus squalidus* Erséus, 1982.

Diagnosis. Body wall generally papillate or with cuticular particles. Prostomium retractable in some heavily papillate species. Clitellum short extending over XI and small portions of X and/or XII. Somatic setae all bifid (absent in *T. achaetus*), two (very rarely 3) per bundle in a variable number of preclitellar segments; one per bundle in remaining segments. Modified genital setae generally absent (small simple-pointed setae associated with male and spermathecal pores in *T. achaetus*). Male and spermathecal pores paired ventrally in XI and X, respectively. Esophageal diverticula in IX present or absent. Male genitalia paired: vas deferens enters atrium apically or subapically; atrium comprised of an ental non-ciliated ampulla with a broadly attached prostate gland connected to a ventral prostatic pad, and a granulated ectal duct usually terminating in a small pseudopenial papilla inside a copulatory sac, when pseudopenial papilla is absent, the duct opens directly on the body surface. Spermathecae paired with round or oval ampulla and distinct ducts which may have an ectal bulbous vestibule. Sperm organized as slender spermatozeugmata, bundles, or random masses.

Remarks. Two of the three species of *Tectidrilus* (*T. squalidus* and *T. gabriellae*) in Florida are readily distinguished by the dense papillation, retractable prostomium, and bisetal bundles anteriorly and unisetal bundles posteriorly. These species may be confused with *Tubificoides wasselli*, which is virtually identical with regard to somatic characters. The third taxon, *T. bori*, lacks papillae, but is readily discriminated by the bisetal anterior bundles and unisetal posterior bundles. Additionally, distinct ventral copulatory glands are present in mature individuals of *T. bori*.

Since Erséus (1982a) established this genus, the "definition" has undergone considerable modification (Erséus and Qi, 1985; Erséus, 1990c; 1991). Currently, the three characters defining this genus are: 1) the short clitellum, 2) bisetal bundles in a few, most anterior segments and unisetal postclitellar bundles (except in *T. achaetus* which lacks somatic setae), and 3) a tendency toward body wall papillation [except *T. bori*, *T. pictoni* (Erséus, 1984a), and *T. intermixus* Finogeneva, 1986].

Key to Species of *Tectidrilus*

- | | | | |
|----|----|--|----------------------|
| 1. | A) | Body wall heavily papillate. | 2. |
| | B) | Body wall naked; copulatory glands present. | <i>T. bori</i> |
| 2 | A) | Two setae per bundle to VII; prostate glands small, southeast Florida. | <i>T. gabriellae</i> |
| | B) | Two setae per bundle to VI; prostate gland large, east and west coasts of Florida. | <i>T. squalidus</i> |

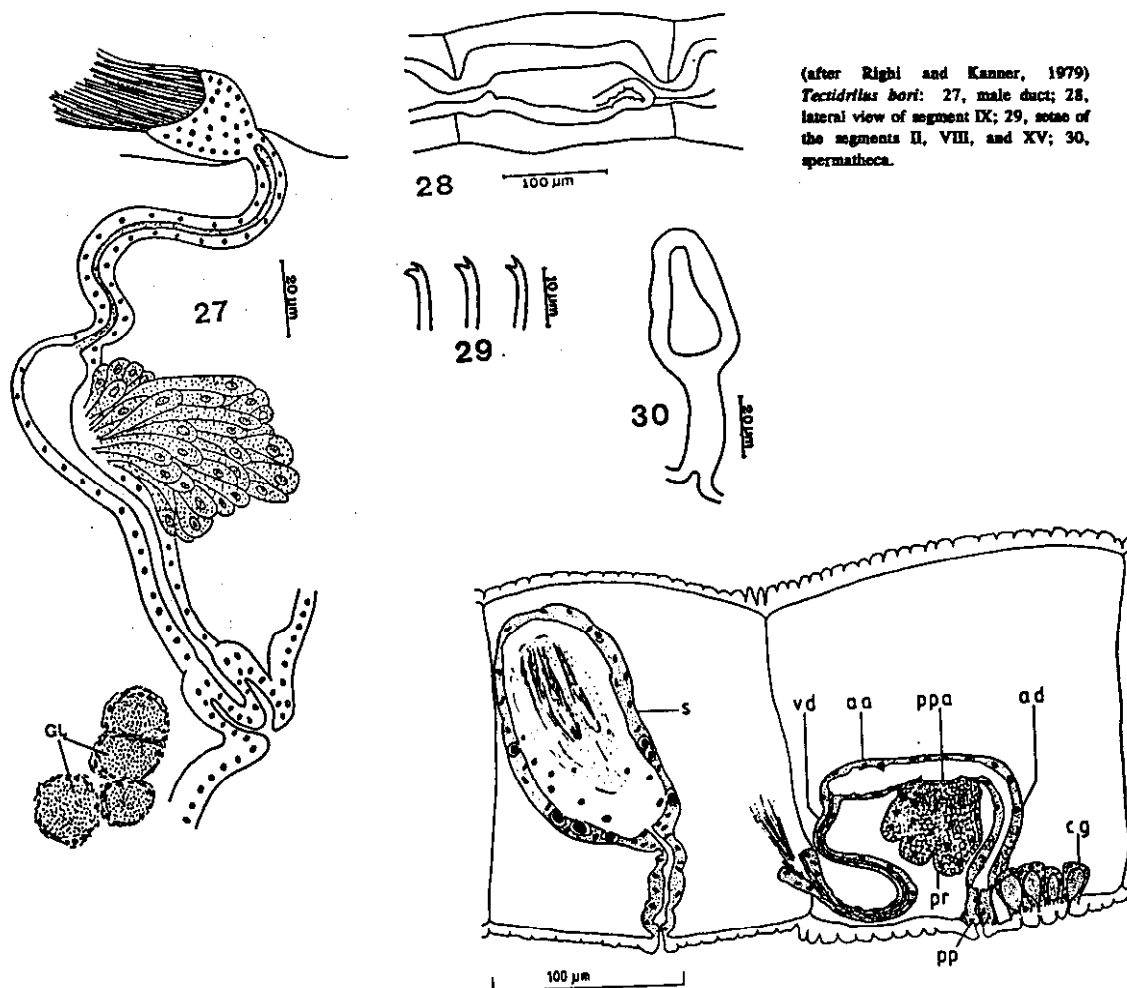
***Tectidrilus bori* (Righi and Kanner, 1979)**

Limnodriloides bori Righi and Kanner, 1979:47-49, Fig. 27-30.

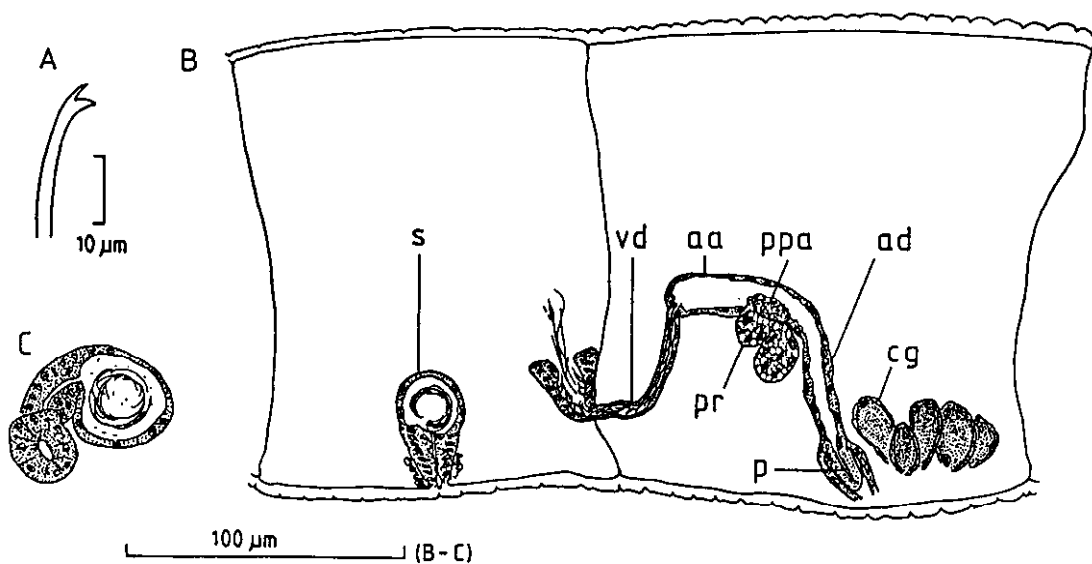
Diagnosis. Length: 4.4-11.0 mm; segments: 24-58. First five segments contractile, prostomium not retractable. Papillae absent. Clitellum extending over XI-½ XII. All setae bifid, upper tooth thinner, but as long as lower, 40-55 µm long: two per bundle in II-VII, one per bundle thereafter; setae arising from the middle of segments II-VIII, from IX setae originate from the posterior third of each segment. Ventral setae absent in X and XI (X and XII in original description). Male and spermathecal pores paired in XI and X, respectively. Esophageal diverticula directed anteriorly in anterior of IX. Male genitalia paired: vas deferens narrow, 5-9 µm wide, but about as long as atrium, entering atrium apically. Atrium differentiated into an ental ampulla, 35-55 µm long, 12-26 µm wide, with a broadly attached prostate gland connected to a ventral cup-shaped prostatic pad ectally, and a narrower duct, 35-60 µm long, 6-20 µm wide, with inconspicuous granulation terminating at the summit of a more or less discrete pseudopenial papilla [originally described as a "conical penis... with thin cuticular sheat [sic]" by Righi and Kanner (1979)] in a pseudopenial sac; a row of (3)4-5(6) voluminous copulatory glands located immediately posterior to each male pore. Spermathecae paired with well-defined oval ampullae and slender ducts. Sperm loosely arranged as spermatozuogmata but tending toward a random organization.

Distribution and Habitat. Caribbean (Belize, Barbados, Curacao), southeast North America (east and west coasts of Florida), Hawaii. Associated with muddy and fine sands; subtidal to 70 m depth.

Remarks. This species is fairly unique within the genus by lacking papillae (a character shared by only two other species of *Tectidrilus* not reported in the western hemisphere) and possessing conspicuous copulatory glands. These glands are easily distinguished and frequently present in not fully mature specimens. The bisetal bundles of II-VII and unisetal "bundles" thereafter and lack of papillae readily discriminate this species.



(after Erasus, 1982a) *Tectidrilus bori*: lateral view of spermatheca and male genitalia in segments X-XI.



(after Erasus and Davis, 1989) *Tectidrilus bori*: A, seta; B, lateral view of spermatheca and male genitalia in segments X-XI; C, spermatheca of another specimen.

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

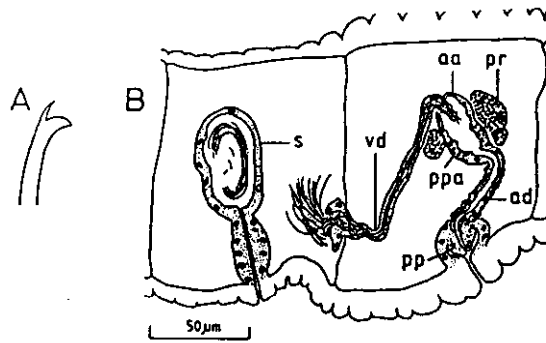
Peloscolex gabriellae Marcus, 1950:1-3, Fig. 1-4.

Diagnosis. Length: 4.0-12.6 mm; segments: 29-54. Prostomium retractable. Body wall densely coated with leaf-like papillae. Clitellum extending over XI and margins of X and XII. All setae bifid 50-70 μm long with upper tooth thinner and shorter than lower: two per bundle in II-VII, one per bundle thereafter. Ventral setae absent from X and XI. Male and spermathecal pores paired in XI and X, respectively. Esophageal diverticula present in IX. Male genitalia paired: vas deferens narrower, 6-12 μm wide, but as long as atrium, entering atrium subapically. Atrium differentiated into an oval ampulla entally, 40-60 μm long, 19-28 μm wide, with a small prostate gland attached to an inconspicuous prostatic pad; and an ectal non-granulated atrial duct, 45-70 μm long, 8-14 μm wide, terminating at the summit of a small cone-shaped papilla in a round pseudopenial sac. Spermathecae paired with well-defined oval ampulla and relatively wide duct. Sperm arranged in loose bundles or random masses.

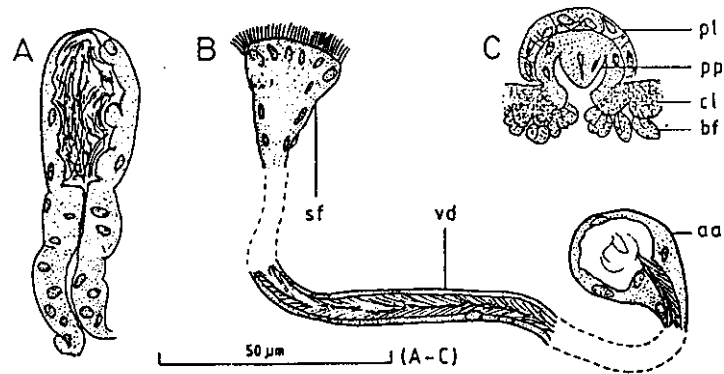
Distribution and Habitat. Caribbean (Belize, Panama, Bonaire, Aruba, Curacao, Barbados), (?)southeast North America (southeast coast of Florida), Brazil, Bermuda. Associated with muddy silt and sand; subtidally to at least 9 m depth.

Remarks. This species is very similar to *Tectidrilus squalidus* and *Tubificoides wasselli*. Both taxa are densely papillated, have a retractable prostomium and bisetal bundles in II-VI or VII and unisetal bundles thereafter. The presence of gut diverticula in IX and absence of a cuticular penis sheath separates *T. gabriellae* from *T. wasselli*. The atrial ducts opening at the summits of distinct pseudopenial papillae in small copulatory sacs, and the smaller prostate glands, distinguishes it from *T. squalidus* in which the ducts open directly on the body surface as a simple pore. Additionally, *T. gabriellae* generally has two setae per bundle to VII, whereas *T. squalidus* usually has two per bundle only to VI.

This species was originally described as *Peloscolex*. It was subsequently transferred to *Tubificoides* by Brinkhurst and Baker (1979) and finally redescribed by Erséus (1982a). Most of the papillate specimens resembling this species collected in Florida waters are generally *T. squalidus*. However, *T. gabriellae* has reportedly been collected from southeast Florida.



(after Erséus, 1982a) *Tectidrilus gabriellae*: A, free-hand drawing of seta; B, lateral view of spermatheca and male genitalia in segments X-XI.



(after Erséus, 1982a) *Tectidrilus gabriellae*: details from a sectioned type specimen, all from one particular, very thick, section; A, spermatheca; B, fragments of the male efferent duct; C, pseudopenis and male pores.

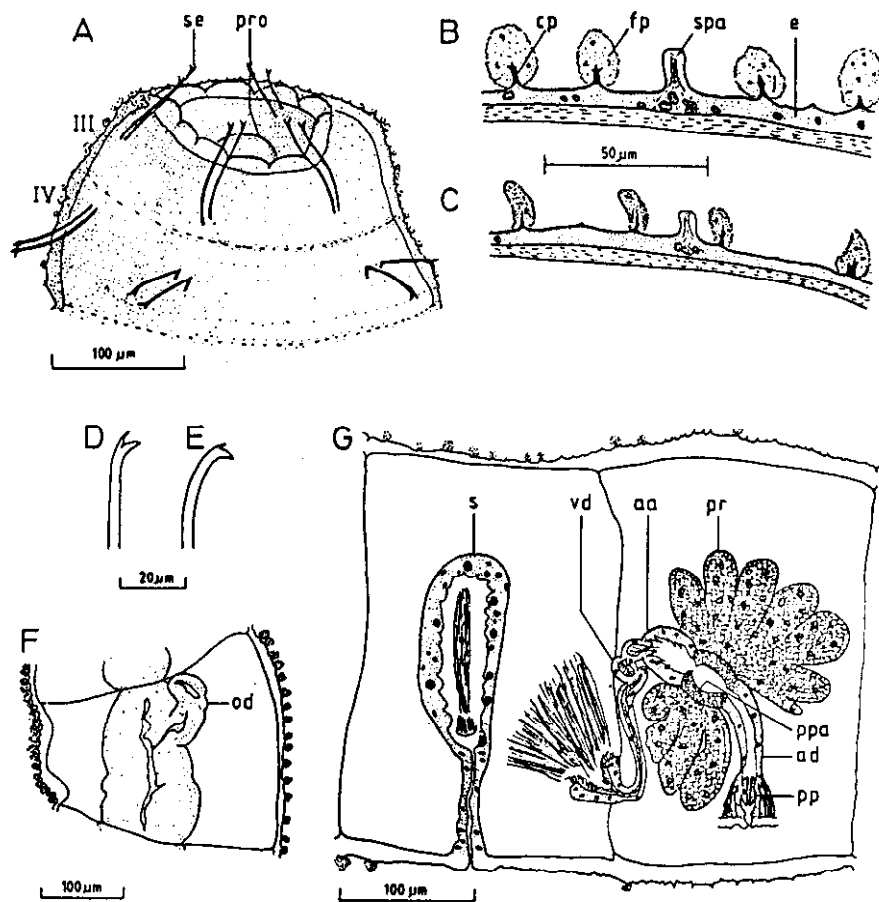
***Tectidrilus squalidus* Erséus, 1982**

Tectidrilus squalidus Erséus, 1982a: 253-255, Fig. 30.

Diagnosis. Length: 4.0-12.6 mm; segments: 34-43. Prostomium retractable. Body wall densely coated with leaf-like papillae. Clitellum extending over XI and margins of X and XII. All setae bifid, relatively slender, 55-100 μm long: two setae per bundle in II-VI, one seta per "bundle" thereafter; anteriorly upper tooth thinner and about as long as lower, posterior setae with upper tooth very reduced. Male and spermathecal pores paired in XI and X, respectively. Esophageal diverticula present in IX. Male genitalia paired: vas deferens narrower, 12-23 μm wide, but about as long as atrium, entering atrium apically. Atrium differentiated into an ental ampulla which is divided into an ental compartment, 60-80 μm long, 20-35 μm wide, which contains a cup-shaped granulated prostatic pad to which a large multi-lobed prostate gland is attached; and an ectal atrial cylindrical duct, 60-85 μm long, 14-20 μm wide, without granulation opening directly on the body surface through a simple pore. Spermathecae paired each with an oval ampulla and slender duct. Sperm organized as torch-shaped spermatozeugmata.

Distribution and Habitat. Barbados and Bermuda; widely scattered along the east and west coast of Florida. Associated with muddy silt and sand to at least 5 m depth.

Remarks. This species is distinguished from the closely related *T. gabriellae* by the absence of a discrete pseudopenial papillae, large prostate glands, and more organized arrangement of sperm. See Remarks for *T. gabriellae* for additional information.



(after Eiréna, 1962a) *Tectidrilus squalidus*: A, anterior end with prothorax and first two segments retracted; B, optic section through body wall (specimen from Miami area); C, optic section through body wall (specimen from Indian River); D, seta from an anterior segment; E, seta from a posterior segment; F, oesophagus in segment IX; G, lateral view of spermatheca and male genitalia in segments X-XI.

Genus. *Limnodriloides* Pierantoni, 1903

Type Species. *Limnodriloides appendiculatus* Pierantoni, 1903.

Diagnosis. (Based on Erséus, 1982a) Marine tubificids. Hair setae absent, somatic setae all bifid, generally more than two per bundle anteriorly. Modified spermathecal setae may be present in X. Clitellum generally extending over XI and XII. Body wall without papillae or adherent foreign particles. Male and spermathecal pores paired or unpaired in XI and X, respectively. Esophagus in IX modified, either dilated and glandular or with a pair of anteriorly directed diverticula. Male genitalia paired: vas deferens enters atrium apically or slightly subapically; atrium without cilia, comprised of: 1) an ental ampulla with a broadly attached prostate gland connected with a prostatic pad within the inner atrial epithelium; and 2) an atrial duct of variable length, with granulations. Pseudopenes or true penes present, lacking cuticular sheaths. Spermathecae single or paired, dorsal or ventral-lateral. Sperm arranged in loose bundles or as slender spermatozeugmata.

Remarks. This genus may be considered as a "melting pot" for species of Limnodriloidinae with a modified esophagus in IX, broadly attached prostate connected to a prostatic pad on the atrium, and not sharing any of the autopomorphies of the other genera within this subfamily. This genus is currently being revised by Erséus (in preparation), and is expected to be separated into several new genera. Until the revision is published, three species groups can be recognized based on Erséus' (1982a; 1990a) suggestions. The species from Florida waters are therefore separated into the following three groups as modified by Erséus (1990a) for the species expected to occur in Florida: 1) the "*monothecus* group", characterized by the tendency toward a very long atrial duct and dorsal position of a single spermathecal pore (*L. monothecus*, *L. anxius*, *L. major*, *L. sacculus*, *L. uniampullatus*); 2) the "*barnardi* group", characterized by modified genital setae (ectally grooved spermathecal setae) (*L. barnardi*, *L. baculatus*, *L. adversus*, *L. hastatus*), and 3) the "*rubicundus* group", characterize by the "less derived species within the genus" (Erséus, 1990a) which lack genital setae and have poorly developed copulatory structures (*L. rubicundus*, *L. pierantonii*, *L. vespertinus*). The first species is differentiated from the latter two by its absence of esophageal diverticula in IX and copulatory sac.

Hrabe (1971a) established the genus *Bohadschia* to distinguish species of *Limnodriloides* with true penes from those with pseudopenes. Cook (1974) and Erséus (1982a) recognized the difficulties in adhering to this distinction due to the presence of intermediate forms. Additionally, this genus was preoccupied by a holothurian genus. As a result, *Bohadschia* is no longer considered valid.

The date *Limnodriloides* was established has been reported as 1903 and 1904 by various authors — the article in which the genus was defined and type species designated. Although the manuscript was received in 1903, the actual date of publication has not, as yet, been conclusively established.

Table 7. *Limnodriloides* species.

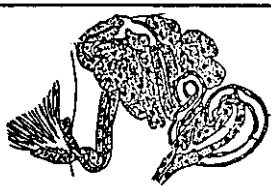
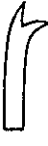
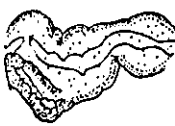
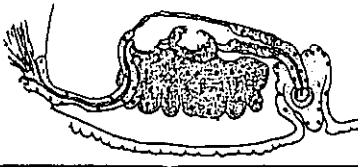
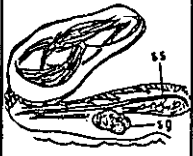
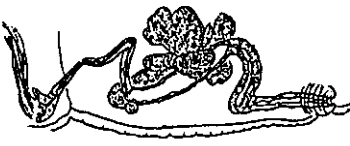
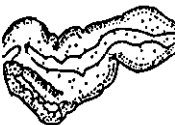
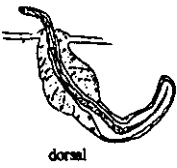
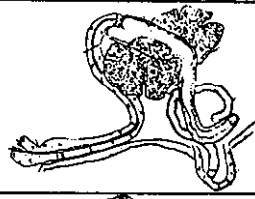
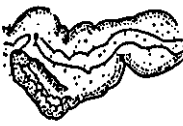
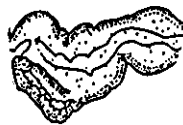
<i>Limno- driloides</i>	Somatic Setae #/bundle Ant. Post.	Esophagus in IX	Spermatheca	Male Genitalia
<i>adversus</i>	 2-3 2			
<i>anxius</i>	 (1)2-4 (1)2(3)		 dorsal	
<i>baculatus</i>	 2-3 2			
<i>barnardi</i>	 2-4 (1)2			
<i>hastatus</i>	 2-3 (1)2		 ss ls	
<i>major</i>	 2(3) 1		 dorsal	
<i>monotheus</i>	 (1)2-4 1-2		 dorsal	
<i>pietramontii</i>	 2-4(5) (1)2			

Table 7. *Limnodriloides* species. Continued.

<i>Limno- driloides</i>	Somatic Setae #/bundle Ant. Post.	Esophagus in IX	Spermatheca	Male Genitalia
<i>rubicundus</i>	 (1)2-3 (1)2(3)			
<i>sacculus</i>	 (1)2-3 (1)2		 dorsal	
<i>unilampulatus</i>	 (1)2-3 (1)2		 dorsal	
<i>vespertinus</i>	 (2)3(4) 2			

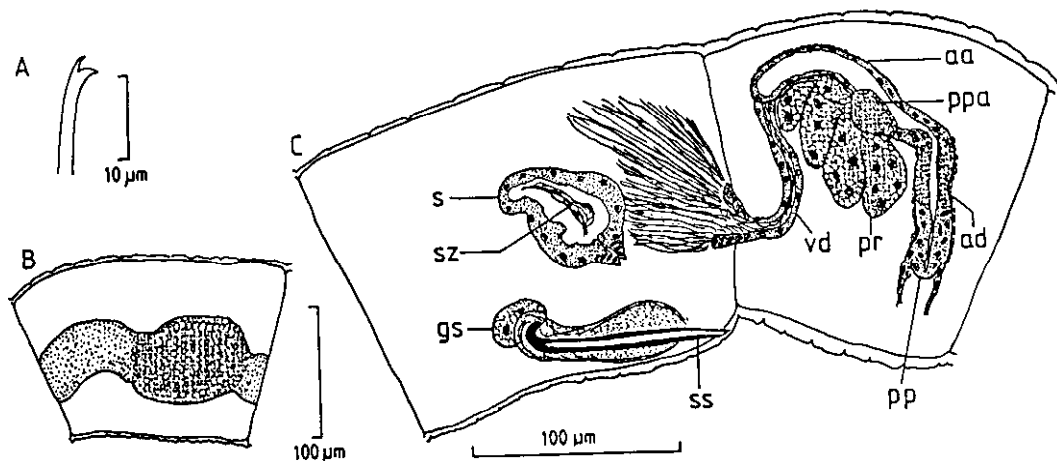
***Limnodriloides adversus* Erséus, 1990**

Limnodriloides adversus Erséus, 1990a:286-287, Fig. 29.

Diagnosis. Length: 4 mm; segments: 41. Clitellum extending over XI and most of XII. Somatic setae bifid, upper tooth thinner but almost as long as lower, 35-47 μm long: 2-3 per bundle anteriorly, absent in XI, dorsal setae absent in X, two per bundle posteriorly. Large, posteriorly directed spermathecal seta, strongly curved entally, and a long groove along most of the length, enclosed in a deep muscular sac present ventrally in X. Male and spermathecal pores paired in XI and X, respectively. Esophagus thick-walled and glandular in posterior of X, without diverticula. Male genitalia paired: vas deferens narrower, 14-16 μm wide, and shorter than atrium, entering atrium more or less apically. Atrial ampulla elongate, 75-85 μm long, up to 25 μm wide, with a distinct prostatic pad ectally to which a moderately large prostate gland is attached. Atrial duct 50-70 μm long, 18-21 μm wide, with granulated mid-region, terminating in simple pseudopenis. Spermathecae paired, each with oval-to-pear shaped ampulla and short triangular duct. Sperm arranged in spindle-shaped bundles.

Distribution and Habitat. Caribbean (Panama, Belize). Associated with mud from barely subtidal to 5 m depth.

Remarks. The lack of gut diverticula in IX and the posteriorly directed large spermathecal seta in X distinguishes this species from other Limnodriloidinae. This species is closely related to *L. hastatus* from Florida, however, the spermathecal setae are paired and directed anteriorly in the latter contrary the posteriorly directed single seta of X in *L. adversus* which also has the groove extending almost the entire length of this seta.



(after Bráns, 1990a) *Limnodriloides adversus*: 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.

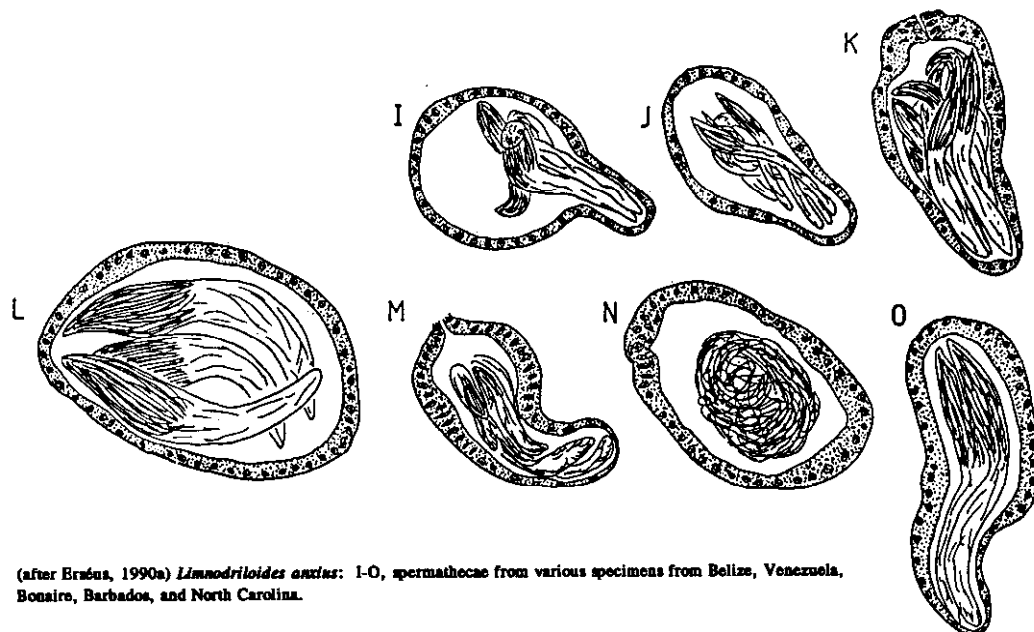
***Limnodriloides anxius* Erséus, 1990**

Limnodriloides anxius Erséus, 1990a:282-284, Fig. 26I-26O, 27A-27D.

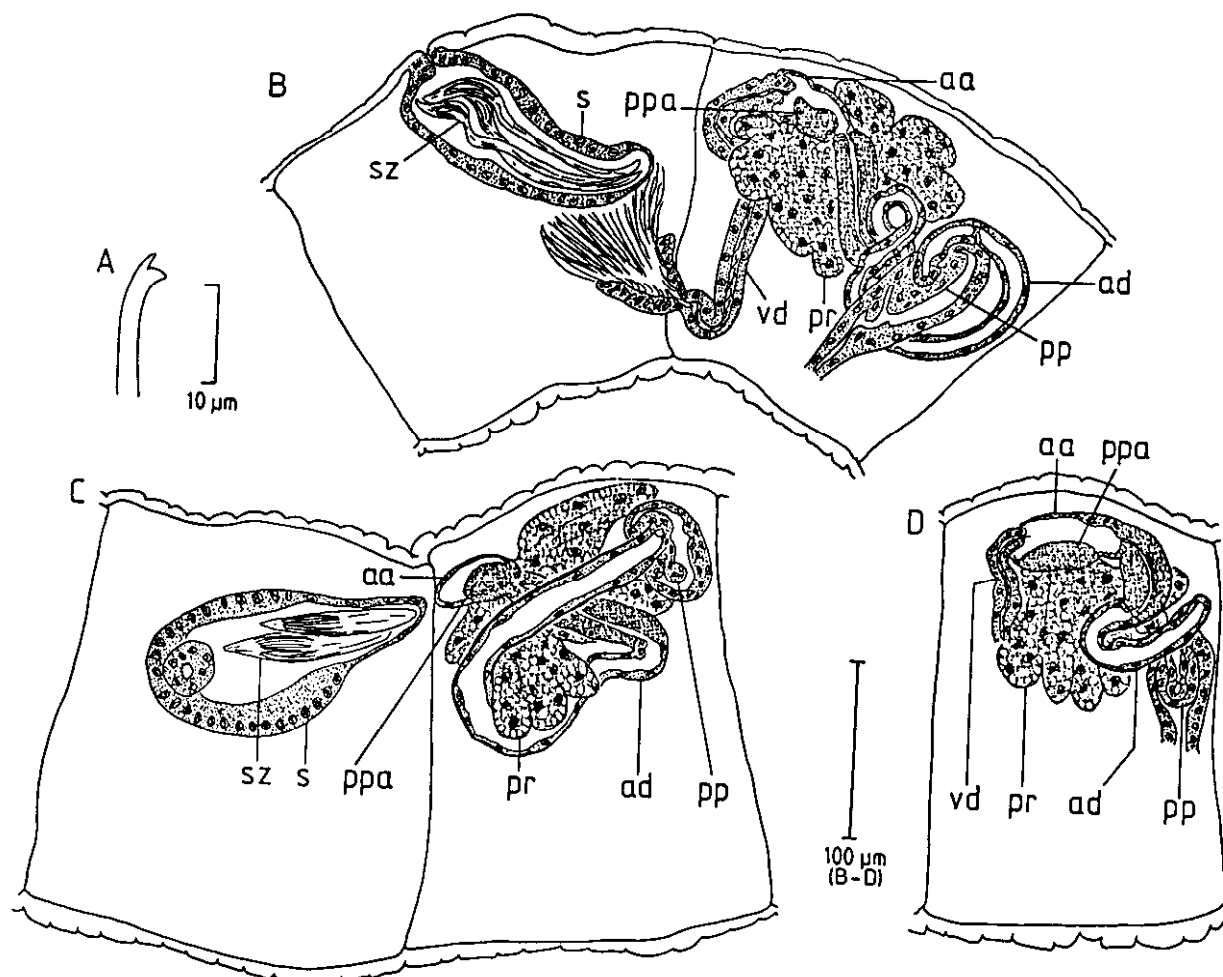
Diagnosis. Length: 7.8-8.8 mm; segments: 69-70. Clitellum poorly developed. All setae bifid with upper tooth thinner and shorter than lower, 28-60 μm long: (1)2-4 per bundle anteriorly, absent from (X) XI, (1)2(3) per bundle posteriorly. Male pores paired in XI. Spermathecal pore unpaired, middorsal medially in X. Esophagus with a pair of diverticula in IX. Male genitalia paired: vas deferens 14-19 μm wide, appearing shorter than atrium entering latter subapically. Atrial ampulla oblong, 60-70 μm long, large prostate gland attached to prostatic pad on ental portion of atrial ampulla. Atrial duct elongate, slender, 220-330 μm long, convoluted, 23-26 μm wide entally with thick inner epithelium, 16-20 μm wide ectally with thinner inner epithelium. Duct terminating in pseudopenial papilla inside copulatory sac; sac 60-75 μm long, 37-50 μm wide. Spermatheca single, with elongate pear-shaped ampulla and indistinct duct. Sperm arranged as spindle-shaped spermatozeugmata.

Distribution and Habitat. Caribbean (Belize, Bonaire, Venezuela, Barbados), east coast of North America (Florida through Virginia). Associated with muddy sand; lower intertidal to at least 20 m.

Remarks. This is one of the five species very similar to *Limnodriloides monotheucus*. Based upon a reappraisal of *L. monotheucus* by Erséus (1990a), five closely related species with a single middorsal spermatheca and elongate atrial duct are now recognized: *L. monotheucus* s. str., *L. anxius*, *L. major*, *L. uniampullatus*, and *L. sacculus*. The distinctions among these species are based primarily on the shape of the spermatheca. The setal distribution and morphology of the male genitalia are highly variable, rendering them of little value for taxonomic distinctions within this complex.



(after Erős, 1990a) *Limnodriloides anxius*: I-O, spermathecae from various specimens from Belize, Venezuela, Bonaire, Barbados, and North Carolina.



(after Erős, 1990a) *Limnodriloides anxius*: A, seta; B-C, lateral view of genitalia in X-XI; D, lateral view of genitalia in XI.

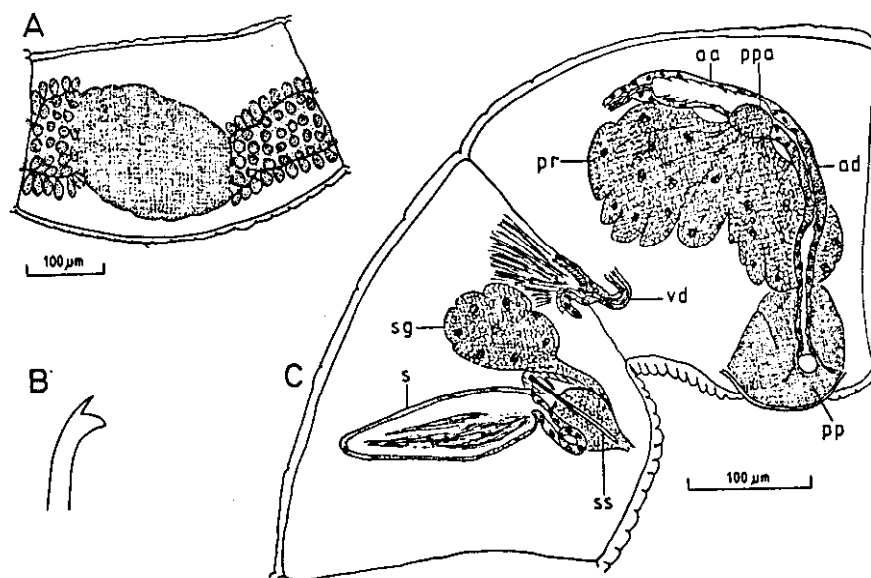
***Limnodriloides baculatus* Erséus, 1982**

Limnodriloides baculatus Erséus, 1982a:240-242, Fig. 20.

Diagnosis. Length: 7.2-12.7 mm; segments: 42-70. Clitellum extending over XI- $\frac{2}{3}$ XII. All somatic setae bifid, upper tooth thinner and slightly shorter than lower, 35-45 μ m long: 2-3 per bundle anteriorly, two per bundle posteriorly. Ventral setae absent from XI. Ventral setae of X modified; single-pointed; ectal half-grooved; 85-95 μ m long; one at each side embedded in a glandular sac immediately posterior to the paired spermathecal pores in the middle of X. Male pores paired in posterior of XI. A part of the esophagus in IX thick-walled and glandular; diverticula absent. Male genitalia paired: vas deferens narrow, 8-16 μ m wide, length undetermined, entering atrium apically or just subapically. Atrial ampulla cylindrical about 120-130 μ m long, 35-42 μ m wide at prostatic pad, large prostate gland attached to prostatic pad on ectal portion of atrial ampulla. Atrial duct about as long as atrial ampulla but narrower, 19-27 μ m wide, opening directly to the surface of the body; ectal part of duct enclosed in an amorphous mass, no discrete pseudopenial sac. Spermathecae paired, each with pear-to-spindle shaped thin-walled ampullae and short ducts. Sperm arranged in spindle-shaped bundles.

Distribution and Habitat. Eastern North America (Florida and North Carolina). Associated with sandy substrates; subtidally, 1.5-11.5 m depth.

Remarks. The lack of esophageal diverticula and discrete pseudopenial sac, and the relatively small grooved spermathecal setae in X distinguish this species from all other Limnodriloidinae. It is similar to *L. hastatus* but the spermathecal setae of the former lies more perpendicular to the body wall and is smaller. The spermathecal setae of *L. baculatus* are also smaller and more perpendicular than those of *L. adversus* as well as only being grooved in the ectal half. The disposition and morphology of the spermathecal setae of *L. baculatus* are most similar to those of *L. barnardi*, however, the latter has esophageal diverticula in IX and a well-developed pseudopenis in a muscular sac.



(after Bråhus, 1982a) *Limnodriloides baculatus*: A, oesophagus in segment IX; B, free-hand drawing of somatic seta; C, lateral view of spermatheca and male genitalia in segments X-XI.

***Limnodriloides barnardi* Cook, 1974**

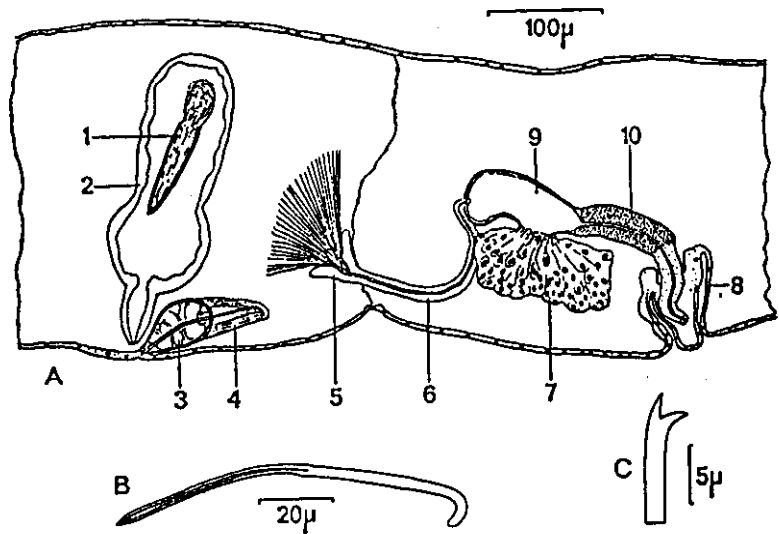
Limnodriloides barnardi Cook, 1974:134-135, Fig. 5.

Diagnosis. Length: 3.8-10 mm; segments: 31-54. Clitellum extending over XI and XII. All somatic setae bifid, upper tooth slightly sub-equal to lower, 35-60 μm long: 2-4 per bundle anteriorly, (1)2 per bundle posteriorly, ventral setae absent from XI. Ventral setae of X modified, each "bundle" contains one straight or curved elongate walking stick-shaped spermathecal seta, 55-120 μm with a groove extending from the node to the ectal end; ectal half embedded in a pear-shaped sac immediately posterior (occasionally anterior) to the paired spermathecal pores. Male pores paired in posterior of XI. Esophageal diverticula present in IX. Male genitalia paired: vas deferens narrow, 9-14 μm , about 180 μm long, entering atrium apically. Atrial ampulla ovoid to elongate, 60-110 μm long, 35-60 μm wide, large prostate gland attached to cup-shaped prostatic pad on the ectal half of the atrial ampulla. Atrial duct 75-160 μm long, 20-35 μm wide, granulated medially, terminating in a lateral papilla in the wall of a pseudopenial sac. Spermathecae paired, each with a round-to-pear shaped ampulla and short, but distinct duct. Sperm arranged in long, narrow bundles.

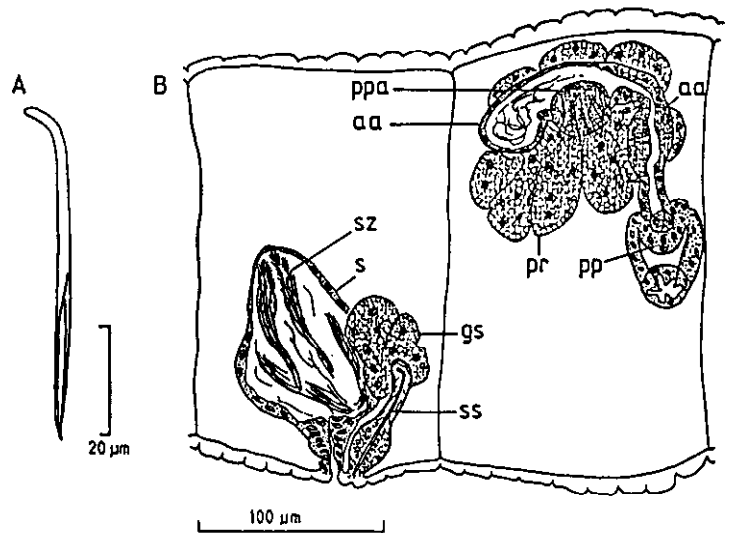
Distribution and Habitat. Caribbean (Bahamas, Belize, Guadeloupe, Panama), Bermuda, east coast of North America (Florida through Massachusetts), Pacific coast of Mexico. Associated with sand; subtidal to 150 m depth.

Remarks. The esophageal diverticula, spermathecal setae, and well-developed pseudopenis differentiates this species from all other Limnodriloidinae. See Remarks for *L. baculatus* for additional information. This species is one of the most common, widespread *Limnodriloides* species in Florida. The smaller size of the spermathecal setae and its more angular displacement with relation to the body wall separates *L. barnardi* from *L. hastatus* and *L. adversus*, the other species composing the *L. barnardi* complex.

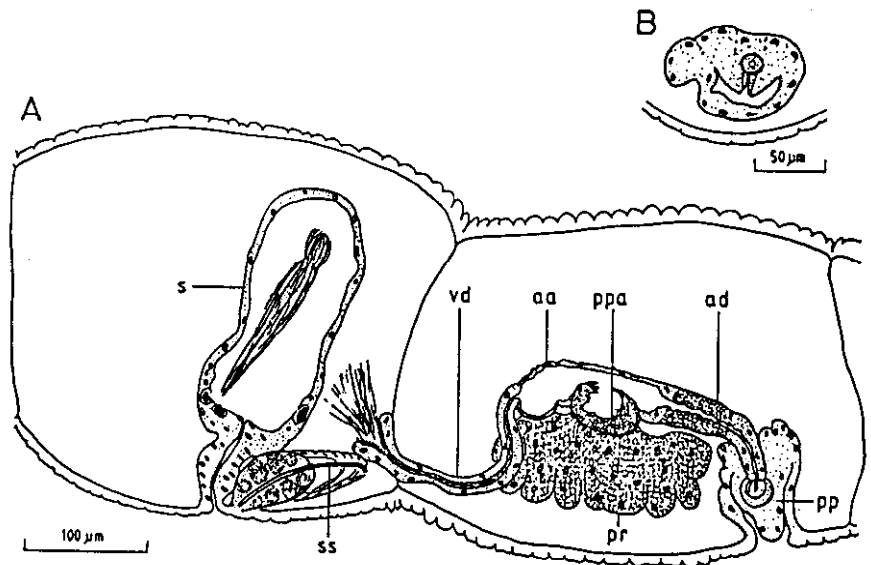
(after Cook, 1974) *Limnodriloides barnardi* from Baja California; A, longitudinal view of genital segments; B, spermathecal seta; C, somatic seta; 1, sperm bundle; 2, spermathecal ampulla; 3, vacuolated muscular sac surrounding spermathecal seta; 4, protractor muscles of spermathecal seta; 5, male funnel; 6, vas deferens; 7, prostate gland; 8, penial sac; 9, atrial ampulla; 10, glandular part of atrial duct.



(after Erasus, 1990a) *Limnodriloides barnardi* from Belize: A, spermathecal seta; B, oblique view of spermatheca, spermathecal seta, and male genitalia in segments X-XI.



(after Erasus, 1982a) *Limnodriloides barnardi* from Baja California: A, lateral view of spermatheca and male genitalia in segments X-XI (paratype); B, optic section through pseudopenis, from a ventral view (another paratype).



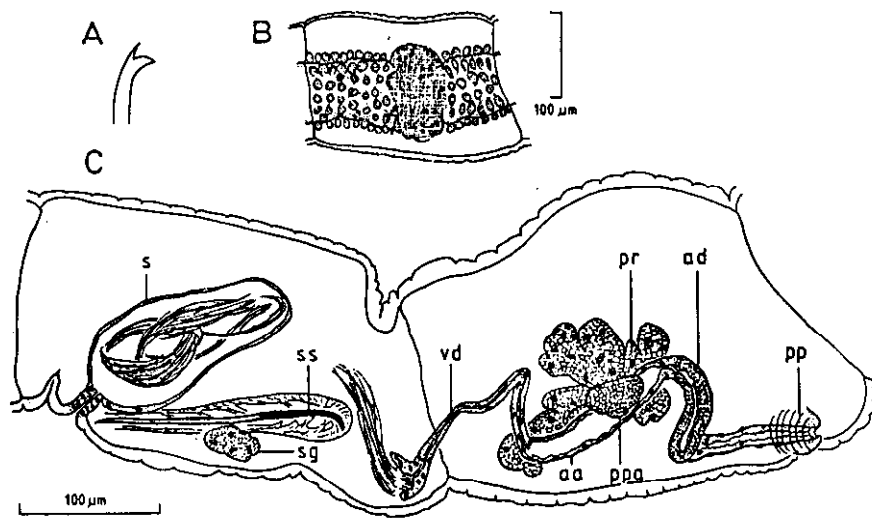
***Limnodriloides hastatus* Erséus, 1982**

Limnodriloides hastatus Erséus, 1982a:242-243, Fig. 21.

Diagnosis. Length: 7.7-10.2 mm; segments: 41-54. Clitellum extending over XI- $\frac{2}{3}$ XII. All somatic setae bifid, upper tooth thinner and shorter than lower, 30 μ m long: 2-3 per bundle anteriorly, (1)2 per bundle posteriorly, ventral setae absent from XI. Ventral setae of X modified, each "bundle" contains a simple-pointed, elongate spermathecal seta; about 180 μ m long; ental end curved; ectal $\frac{2}{3}$ grooved; directed anteriorly lying parallel to body wall; surrounded by elaborate muscles along entire length; ectal tip protruding at spermathecal pore. Male and spermathecal pores paired in posterior of XI, and anterior of X, respectively. A short part of esophagus thick-walled and glandular in IX; diverticula absent. Male genitalia paired: vas deferens narrow, shorter than atrium, entering atrium apically. Atrial ampulla cylindrical, 120-130 μ m long, 29-33 μ m wide, large prostate gland attached to roundish-to-oval prostatic pad on ectal-most part of ampulla. Atrial duct about 200 μ m long and 10-30 μ m wide, entally granulated, terminating in a simple pseudopenis. Spermathecae paired, each with a pear-shaped, thin-walled ampulla and small, distinct duct. Sperm arranged in spindle-shaped, slightly curved bundles.

Distribution and Habitat. West coast of Florida; subtidal to 40 m depth.

Remarks. This species is distinguished by the partly enlarged esophagus in IX, and long, anteriorly directed spermathecal setae. This species is very similar to *L. adversus*, however, the spermathecal setae is directed posteriorly in the latter, and there is only one in X instead of two. The size and disposition of the spermathecal setae of *L. hastatus* distinguishes it from *L. barnardi* and *L. baculatus*, the other taxa comprising the *L. barnardi* complex.



(after Bráňa, 1962a) *Limnodriloides hastatus*: A, free-hand drawing of somatic seta; B, oesophagus in segment XI; C, lateral view of spermatheca and male genitalia in segments X-XI.

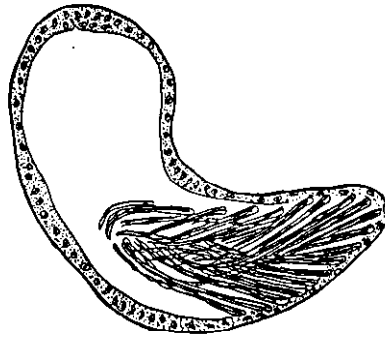
***Limnodriloides major* Erséus, 1990**

Limnodriloides major Erséus, 1990a:284-285, Fig. 26P, 27E-27F.

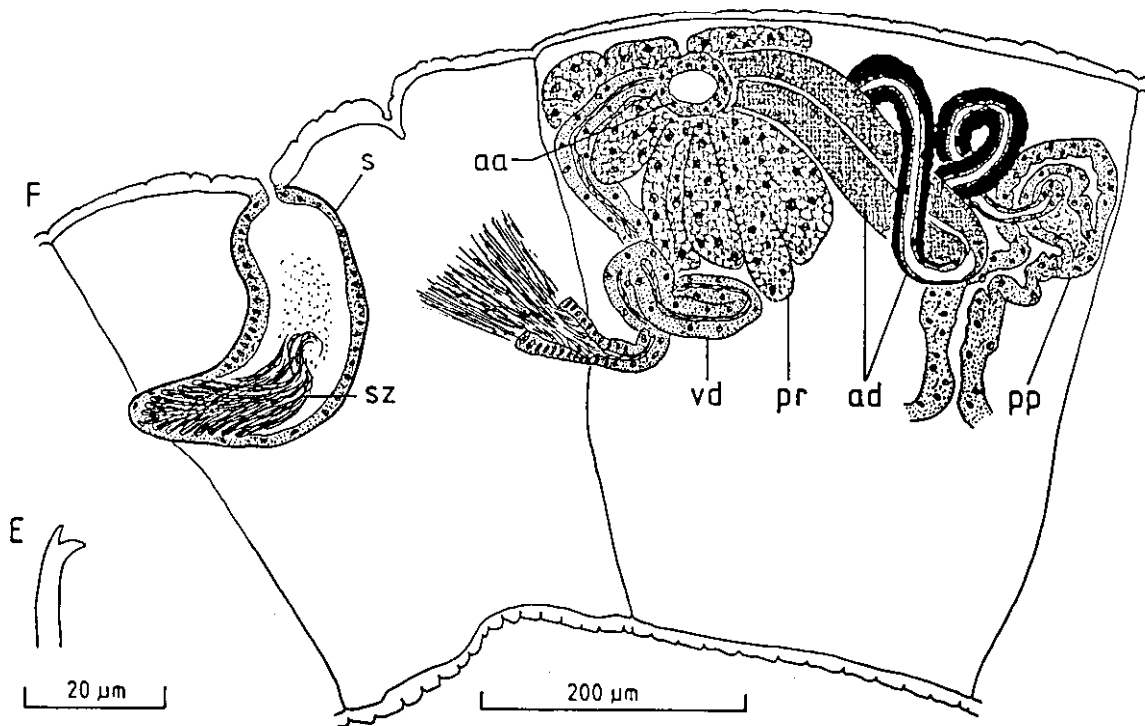
Diagnosis. Length: more than 7.8 mm; segments: more than 37. All somatic setae bifid, upper tooth thinner and shorter than lower, 37-62 μm long: 2(3) per bundle anteriorly, one per "bundle" posteriorly, absent from X-XI. Modified genital setae absent. Spermathecal pore single, middorsal, in middle of X. Male pores paired in posterior of XI. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia paired: vas deferens relatively wide, 23-30 μm , length undetermined; entrance to atrium undetermined. Atrial ampulla small, oval, about 60 μm long, 45 μm wide, prostate gland large attachment to atrium not observed. Atrial duct very long (0.9 mm) and convoluted. Ental part of atrial duct very wide, 65-70 μm , about 215 μm long with thin outer muscular layer and thick granulated inner epithelium. Ectal part of atrial duct thinner, 28-43 μm , nongranulated with thick muscular layer, up to 12 μm thick, becoming thinner ectally, terminating in a large pseudopenial papilla inside a voluminous copulatory sac; sac 160 μm long, about 60 μm wide. Spermatheca unpaired with an oblong, somewhat curved ampulla about three times longer than wide with thin but distinct muscular layer. Sperm arranged as slender spermatozeugmata (up to 20 in number) in inner end of ampulla

Distribution and Habitat. Caribbean (Belize). As yet, only found in barely subtidal sand.

Remarks. This species was based on the description of a single individual. Erséus (1990a) determined that the inordinately large size from which it derives its specific epithet, was sufficiently distinctive to warrant establishing it as a separate taxon. Additionally, the great length and thickness of the atrial duct, and high number of spermatozeugmata further distinguishes *L. major* from other species within the *L. monothecus* complex.



(after Erséus, 1990a) *Limnodriloides major*: spermatheca.



(after Erséus, 1990a) *Limnodriloides major*: E, seta; F, lateral view of spermatheca and male genitalia in X-XI.

***Limnodriloides monotheucus* Cook, 1974**

Limnodriloides monotheucus Cook, 1974:131-132, Fig. 3.

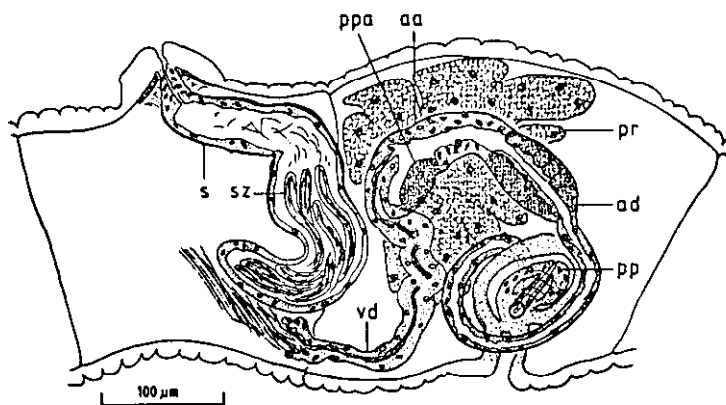
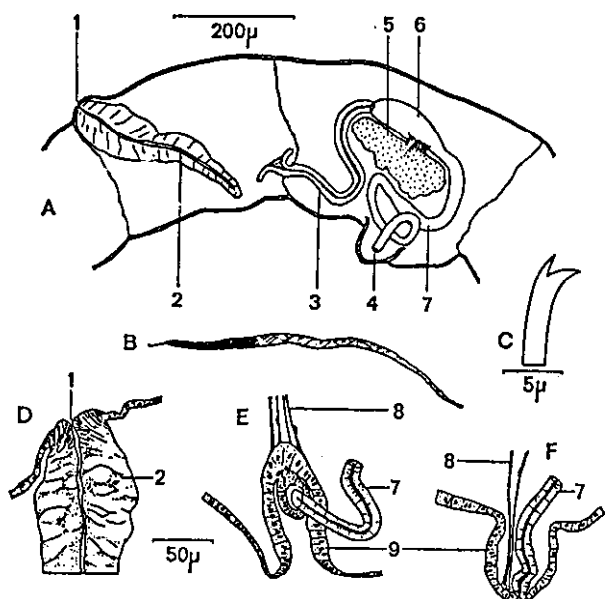
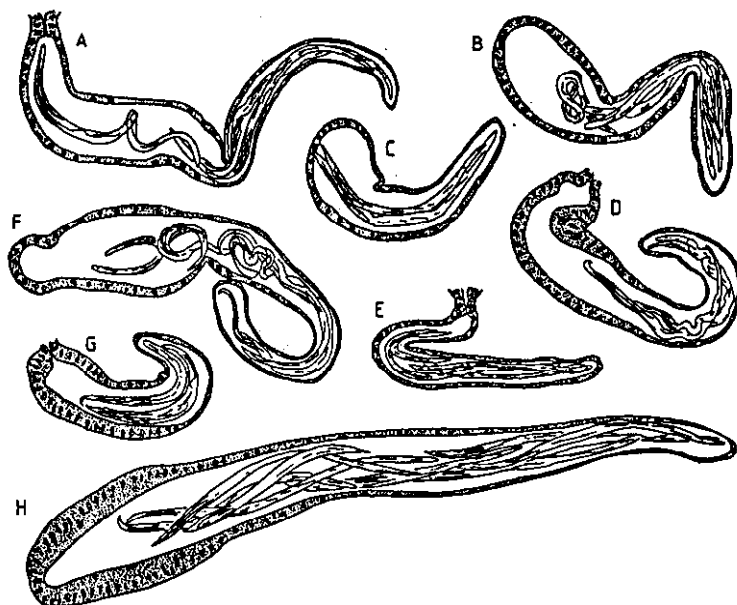
Diagnosis. Length: 6.5-9.5 mm; segments: 46-62. All somatic setae bifid, upper tooth thinner and shorter than lower, 35-62 μm long: (1)2-4 per bundle anteriorly, 1-2 posteriorly, absent in X and XI. Modified genital setae absent. Spermathecal pore single, middorsal in anterior of X; male pores paired in XI. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia paired: vas deferens relatively thick, 16-34 μm wide, shorter than atrium, 245-300 μm long, entering atrium more or less apically. Atrial ampulla somewhat ovoid, 60-130 μm long, 21-50 μm wide, moderately large prostate gland attached to elongated prostatic pad on ectal portion of atrial ampulla. Atrial duct tubular elongate and convoluted, 450-550 μm long, 12-27 μm wide, somewhat granulated entally. Pseudopenial sac 90-120 μm long, 40-77 μm wide. Spermatheca unpaired with a very slender ampulla. Sperm arranged in long narrow bundles, from a few to at least nine in number.

Distribution and Habitat. North America (western coast from Mexico to British Columbia; eastern coast, Gulf of Mexico, Florida through New Jersey), Caribbean (Belize), Bermuda, Scotland, Yugoslavia. Associated with sand and mud to at least 583 m depth; also brackish water.

Remarks. This species is distinguished by the esophageal diverticula in IX, single, middorsal elongate spermatheca and elongate, convoluted atrial duct. Five closely related species with a single mid-dorsal spermatheca form a complex, herein referred to as the "*L. monotheucus* complex", and may be separated by morphology of the spermatheca and spermatozeugmata. See *L. anxius* for a more detailed discussion.

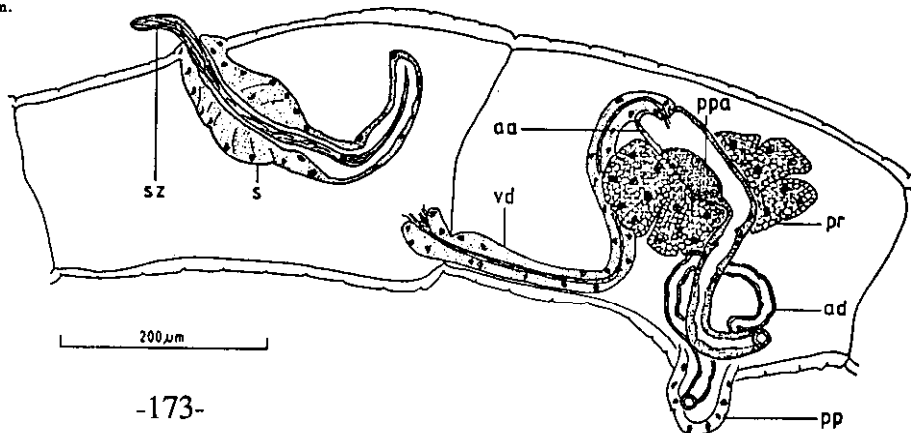
All species which now compose the *L. monotheucus* complex are included in this guide because they are so closely related and all have been found in the Caribbean.

(after Erséus, 1990a) *Limnodriloides monotheclus*: A-H, spermathecae of various specimens from Belize, Bermuda, and both coasts of North America.



(after Erséus, 1982a) *Limnodriloides monotheclus*: lateral view of spermatheca and male genitalia in segments X-XI (holotype of *Bohadschia monotheclus* HRABE).

(after Cook, 1974) *Limnodriloides monotheclus*: A, longitudinal view of genital segments; B, sperm bundle; C, somatic seta; D, proximal end of spermatheca; E, penis sac (resting position); F, penis sac (everted position). 1, spermathecal pore; 2, spermatheca; 3, vas deferens; 4, male pore; 5, prostate gland; 6, atrial ampulla; 7, atrial duct; 8, penis retractor muscles; 9, penis sac epithelium.



(after Erséus, 1982a) *Limnodriloides monotheclus*: lateral view of spermatheca and male genitalia in segments X-XI (paratype).

***Limnodriloides pierantonii* (Hrabe, 1971)**

Bohadschia pierantonii Hrabe, 1971a:217-220, Fig. 1-6.

Diagnosis. Length: about 5 mm; segments: about 40. Clitellum extending over XI-XII. All somatic setae bifid, upper tooth thinner and shorter than lower, 35-65 μm long: 2-4(5) per bundle anteriorly, (1)2 per bundle posteriorly, ventral setae absent in XI, variable in X. Modified genital setae absent. Male and spermathecal pores paired in posterior of XI and middle of X, respectively. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia paired: vas deferens narrow, 12-19 μm wide, about as long as atrium, entering atrium subapically. Atrium club-shaped, more or less erect. Atrial ampulla spindle-shaped, 60-80 μm long, 30-35 μm wide with thin muscular layer, large prostate gland attached to well developed prostatic pad extending over median portion of ampulla. Atrial duct straight, 60-95 μm long and 20-25 μm wide, granulated along most of its length, terminating in lateral papilla within a copulatory sac. Spermathecae paired, each with a more or less pear-shaped ampulla and well-defined short duct. Sperm arranged as torch-shaped spermatozeugmata with very narrow ectally directed "shafts".

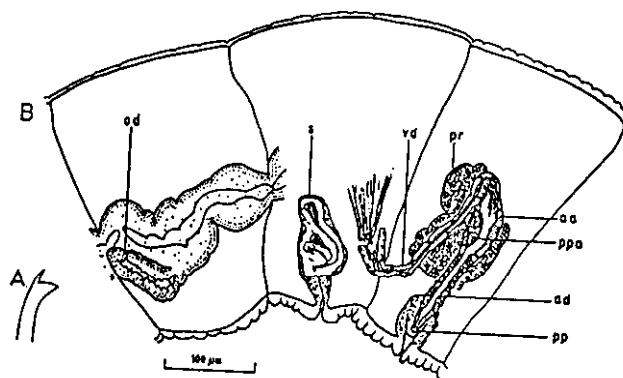
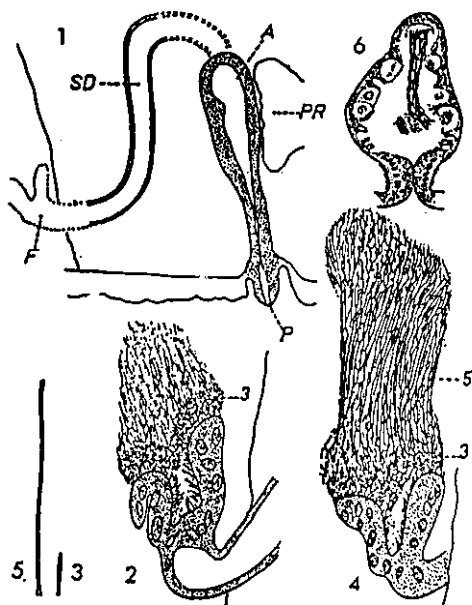
Distribution and Habitat. Caribbean (Barbados, Venezuela), Yugoslavia, Turkey, Romania, Hong Kong (Erséus, personal communication). Associated with muddy sands to a depth of at least 200 m.

Remarks. This species is distinguished primarily by the lack of definitive characters. The presence of esophageal diverticula, lack of modified genital setae, and uncomplicated male genitalia characterize this species. *Limnodriloides pierantonii* was originally included in the genus *Bohadschia* by Hrabe (1971) because of presence of true penes (now determined to be "pseudopenes" by Erséus [1982a]). Subsequently, *Bohadschia* became a junior synonym of *Limnodriloides* (Cook, 1974; Erséus, 1982a). Upon further examination of specimens of *L. claviger* Erséus, 1982a, by Erséus (1990a), the material from the Caribbean is now regarded as *L. pierantonii* because of the club-shaped atrium, torch-shaped spermatozeugmata and clearly developed pseudopenes. Specimens of *L. claviger* described from Bermuda (Erséus, 1982a) and Hawaii (Erséus and Davis, 1989) are now regarded as *Smithsonidrilus minusculus* (Erséus, 1983b).

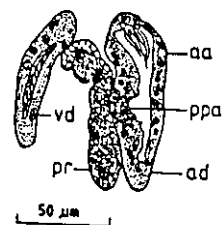
This is a relatively nondescript species which superficially resembles *L. barnardi* which is very common throughout Florida and occasionally lacks the modified spermathecal setae which characterize it. Identification of specimens as *L. pierantonii* from Florida should be regarded tentatively.

This species differs from the other species in the *L. rubicundus* complex by having a much smaller prostate gland and thin-walled spermathecae, which separate it from *L. vespertinus*, and having a pair of gut diverticula, which separates it from *L. rubicundus*.

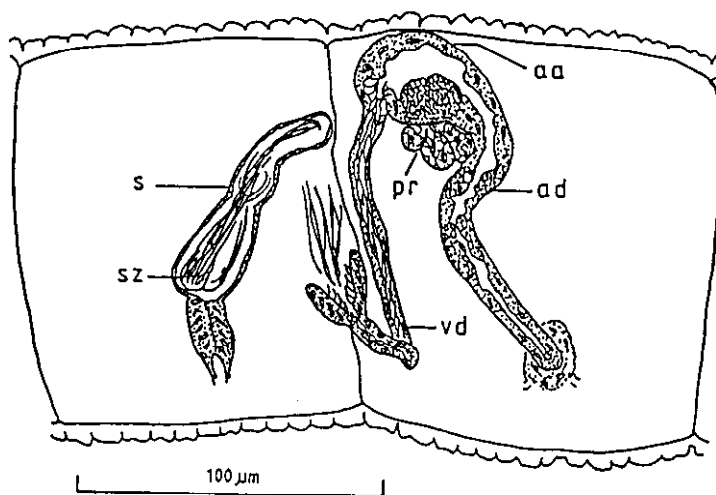
(after Hrabě, 1971a) *Limnodriloides pieramonii* from the Adriatic Sea: 1, male duct; a, atrium; f, male funnel; p, penis; pr, prostate gland; ad, sperm duct, x 400; 2, male funnel with one layer of spermatozoa (3), x 890; 3, head of spermatozoon from the funnel shown in #2 (schematically); 4, male funnel with two layers of spermatozoa (3 and 5), x 890; 5, head of spermatozoon on upper layer (schematically); 6, spermatheca x 385.



(after Erőss, 1982a) *Limnodriloides pieramonii* from Italy: A, free-hand drawing of seta; B, lateral view of oesophageal diverticulum, spermatheca, and male genitalia in segments IX-XI.



(after Erőss, 1987c) *Limnodriloides pieramonii* from Italy: section of parts of male duct.



(after Erőss, 1987b) *Limnodriloides pieramonii* as claviger, specimen from Bahía de Amuay, Venezuela: lateral view of spermatheca and male duct.

Limnodriloides rubicundus Erséus, 1982

Limnodriloides rubicundus Erséus, 1982a:226-228, Fig. 10.

Diagnosis. Length: 3.2-15.7 mm; segments: 39-79. Clitellum extending over XI-XII. All setae bifid, upper tooth thinner and slightly shorter than lower, 25-55 μm long: (1)2-3(4-7) per bundle anteriorly, (1)2(3) per bundle posteriorly, ventral (and rarely dorsal) setae absent from X and XI. Male and spermathecal pores paired in posterior of XI and X, respectively. A part of the esophagus in IX thick-walled and glandular; diverticula absent. Male genitalia paired: vas deferens narrow, 6-20 μm wide, and as long as or slightly shorter than atrium, entering atrium more or less apically. Atrial ampulla cylindrical, 55-175 μm long, 16-47 μm wide, with thin outer muscular lining, large prostate gland attached to a small cup-shaped prostatic pad on ectal portion of atrial ampulla. Atrial duct straight, 60-135 μm long, 10-27 μm wide, with granulated inner epithelium along most of its length, terminating in simple pseudopenis. Spermathecae paired, each with an oval or oblong ampulla and short, distinct duct. Sperm arranged in slender or loose bundles or random.

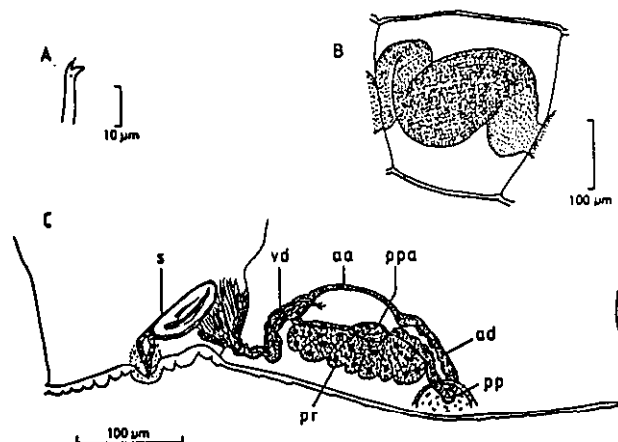
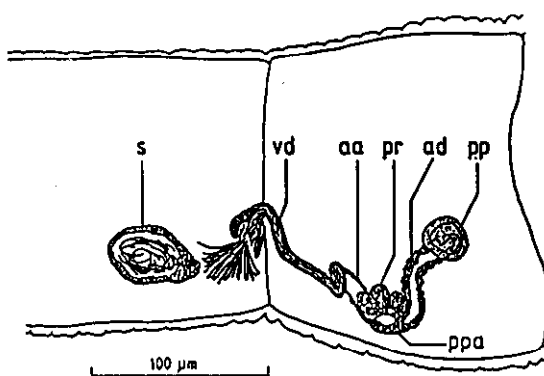
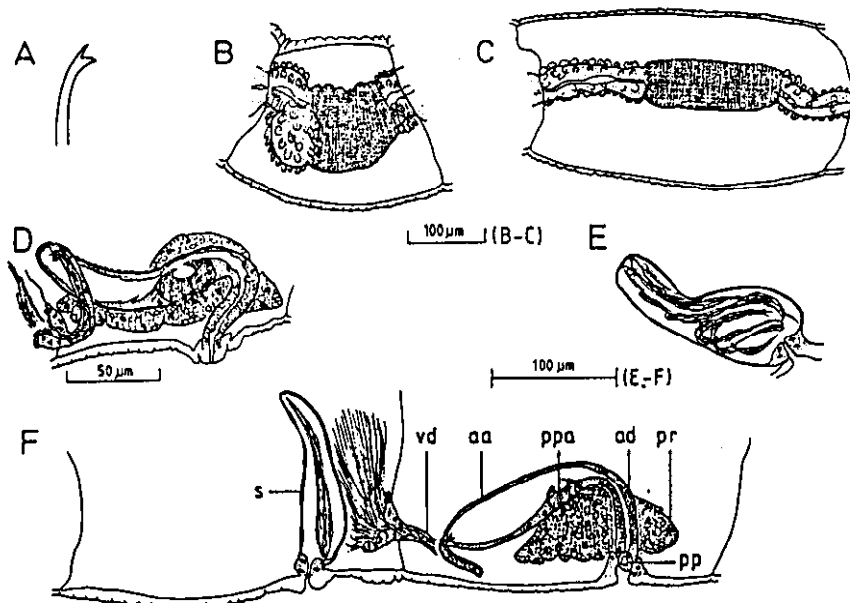
Distribution and Habitat. Indo-Pacific (Australia, Fiji, Hawaii), Caribbean (Barbados, Bahamas, Belize, Venezuela), east coast of North America (Florida through Delaware). Usually associated with muddy and or fine sand sediments; intertidal to at least 75 m depth.

Remarks. This is a widely distributed circumtropic species which is distinguished by the thick-walled glandular part of the esophagus in IX, without esophageal diverticula, lack of modified spermathecal setae, and fairly short atrial ducts which terminate in simple pseudopenes. There is considerable intraspecific geographic variation regarding the size of the male genitalia. The size of the atrial ampullae and ducts were smallest in the Hawaiian populations (Erséus and Davis, 1989) and Hong Kong populations (Erséus, 1992b), largest in the western Australian populations (Erséus, 1993a) and intermediate in the Caribbean populations. Additionally, the Australian specimens had a larger number of anterior setae per bundle (up to 7). The arrangement of sperm in the spermathecae is also variable between geographic populations, ranging from "random" (Hong Kong), to "somewhat bundled" (western Australia), to "slender bundles" (northern territories of Australia). Based on the aforementioned variations, which have been the basis for specific criteria in other species, this species is quite possibly a

complex of more than one species, as suggested by Erséus (in press).

This species is superficially similar to *Parakaketio longiprostatus* from Florida which also has a thick-walled glandular esophageal region in IX, lacks modified spermathecal setae and has simple pseudopenes. However, even allowing for the great deal of intraspecific geographic morphological variation of *L. rubicundus*, the atrium of *P. longiprostatus* is significantly larger (atrial ampulla: 450-575 μm vs. 115-210) and morphologically dissimilar (atrium with a longitudinal septum and much larger, more broadly attached prostate) and the spermathecal pores are anterior in *P. longiprostatus* and posterior in *L. rubicundus*. *Limnodriloides rubicundus* differs from the other species in the *L. rubicundus* complex by lacking gut diverticula.

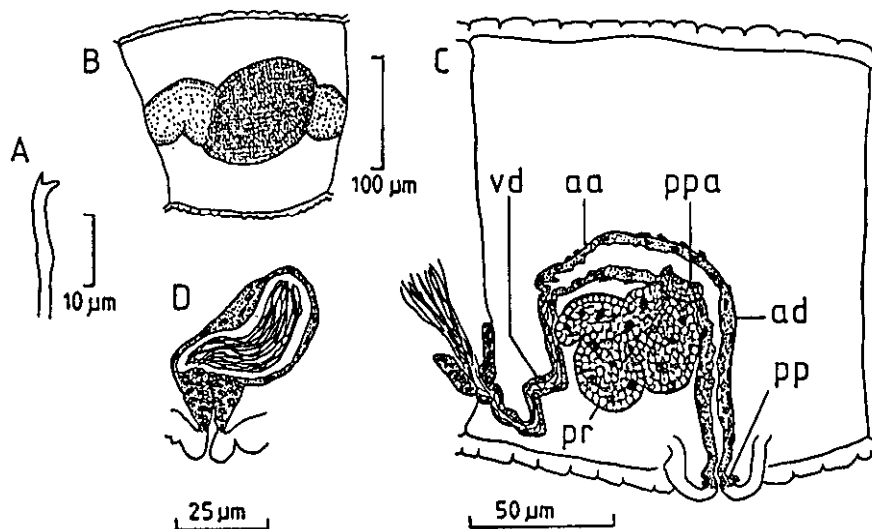
(after Br  us, 1982a) *Limnodriloides rubicundus*: A, free-hand drawing of seta; B, oesophagus in segment IX (contracted specimen); C, oesophagus in segment IX (relaxed, stretched specimen); D, male genitalia, with atrial muscles contracted; E, spermatheca; F, lateral view of spermatheca and male genitalia in segments IX-X (specimen with distended atrial ampulla; atrial muscles not contracted).



(after Br  us, 1992b) *Limnodriloides rubicundus* from Hong Kong: genitalia in X-XI.

(after Br  us, 1993a) *Limnodriloides rubicundus* from Rottnest Island, Australia: A, seta; B, modified part of oesophagus in segment IX; C, lateral view of spermatheca and male genitalia in segments X-XI.

(after Br  us and Davis, 1989) *Limnodriloides rubicundus* from Hawaii: A, seta; B, glandular thickening of oesophagus in segment IX; C, lateral view of male genitalia in segment XI; D, spermatheca.



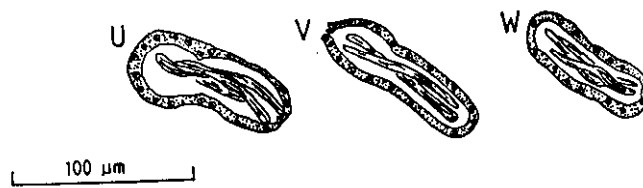
***Limnodriloides sacculus* Erséus, 1990**

Limnodriloides sacculus Erséus, 1990a:285-286, Fig. 26U-26W, 28.

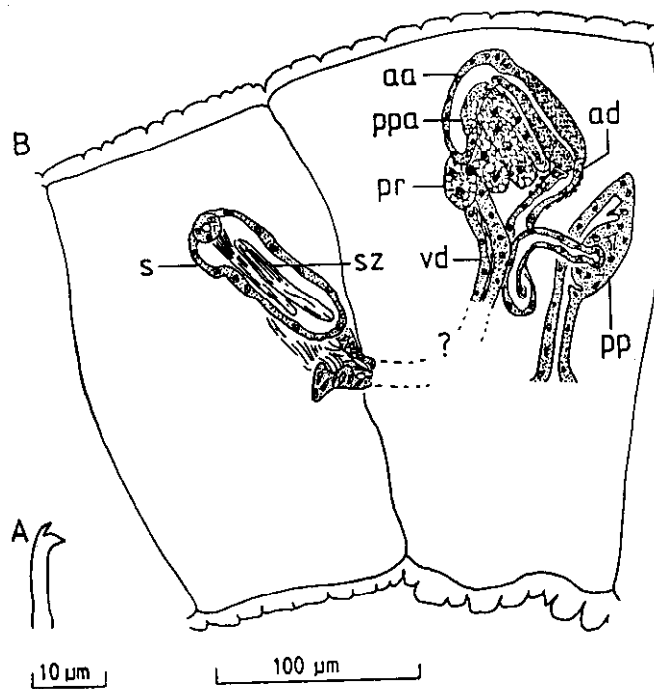
Diagnosis. Length: 3.9-4.8 mm; segments: 40-46. Clitellum extending over XI-XII. All setae bifid, upper tooth thinner and shorter than the lower, 32-47 μm long: (1)2-3 per bundle anteriorly, (1)2 per bundle posteriorly, absent from X-XI. Spermathecal pore single, middorsal in middle of X. Male pores paired in posterior of XI. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia paired: vas deferens about 10 μm wide appearing shorter than atrium, entering atrium subapically. Atrial ampulla oblong, about 55-60 μm long, 19-26 μm wide, small lobed prostate gland attached to elongate prostatic pad ventral in ampulla. Atrial duct long and slender, about 215 μm long; ental part, 55-60 μm long, 19-27 μm wide with granulated inner epithelium; ectal part thinner, 155-160 μm long and 7-11 μm wide, moderately convoluted, terminating in a pseudopenial papilla inside a voluminous copulatory sac; sac 65-100 μm long, 25-40 μm wide. Spermatheca unpaired, ampulla elongate, about 2-3.6 times longer than wide, duct indistinct. Sperm arranged as straight, slender spermatozeugmata, 2-4 in number.

Distribution and Habitat. Caribbean (Belize). Associated with muddy, fine to medium sands; subtidally to a depth of 0.2-1 m depth.

Remarks. This species is a member of the *L. monothecus* complex, having a middorsal spermatheca, gut diverticula in IX, and an elongate atrial duct. It is most similar to *Limnodriloides uniampullatus*, but differs with respect to the spermatheca, which is much more elongate in *L. sacculus* (named for the sac-like small spermatheca), but not as much as *L. monothecus*. Additionally, it differs from *L. anxius*, which has a more spherical, larger spermatheca.



(after Brásus, 1990a) *Limnodriloides sacculus*: U-W, spermathecae of various specimens from Belize.



(after Brásus, 1990a) *Limnodriloides sacculus*: A, seta; B, oblique view of spermatheca and male genitalia in segments X-XI.

***Limnodriloides uniampullatus* Erséus, 1982**

Limnodriloides uniampullatus Erséus, 1982a:248-250, Fig. 27.

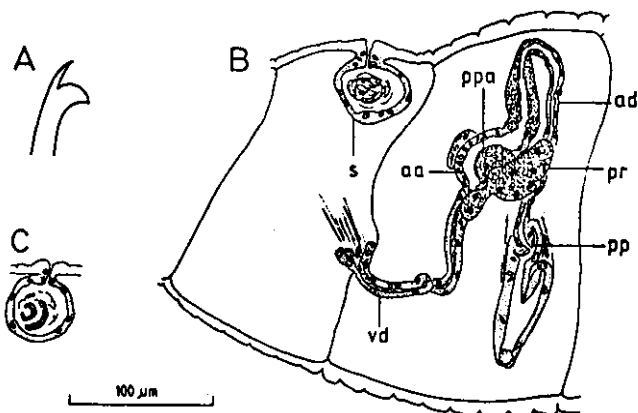
Diagnosis. Length: 3.3-6.2 mm; segments: 31-44. Clitellum extending over XI-XII. All setae bifid, upper tooth much thinner and shorter than lower, 28-50 μm long: (1)2-3 per bundle anteriorly, (1)2 per bundle posteriorly, absent from XI (and rarely X). Spermathecal pore single, middorsal in posterior of X. Male pores paired in posterior of XI. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia paired: vas deferens narrow, 9-16 μm wide, shorter than atrium. Atrial ampulla 35-50 μm long, 14-26 μm wide, small prostate gland attached to well developed prostatic pad in middle of ampulla. Atrial duct long and slender, about 150-250 μm long, differentiated ental part 12-28 μm wide, heavily granulated; ectal part thin, 6-12 μm wide not granulated, terminating in a very small pseudopenial papilla at inner end of a deep pseudopenial sac with thin, folded walls; sac 35-105 μm long, 22-30 μm wide. Spermatheca unpaired which small, globular ampulla, duct indistinct. Sperm arranged as random mass or (more often) as short simple spermatozeugmata, few in number.

Distribution and Habitat. Caribbean (Bonaire, Belize), western Pacific (Great Barrier Reef of Australia, southern China). Associated with subtidal coralline sands; subtidally to at least 6 m depth.

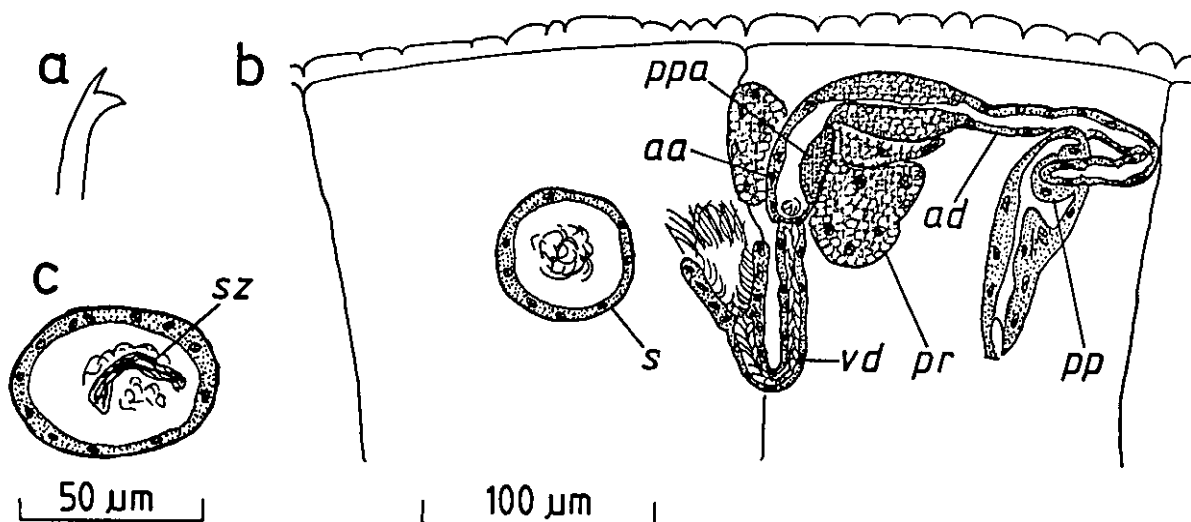
Remarks. This species is part of the *L. monotheucus* complex, having a middorsal spermatheca, gut diverticula in IX, and an elongate atrial duct. However, it differs from all congeners by the diminutive, spherical (never elongate) spermatheca. This species is most similar to *L. sacculus* which has a larger, elongate spermatheca.



(after Erős, 1990a) *Limnodriloides unilampullatus*: Q-T, spermathecae of various specimens from Belize and Bonaire.



(after Erős, 1982a) *Limnodriloides unilampullatus* from Australia: A, free-hand drawing of seta; B, lateral view of spermatheca and male genitalia in segments X-XI (holotype); C, spermatheca (paratype).



(after Erős, 1984a) *Limnodriloides unilampullatus* from Hong Kong: a, free-hand drawing of seta; b, ventral, somewhat oblique view of spermatheca and male genitalia in segments X-XI; c, spermatheca of another specimen.

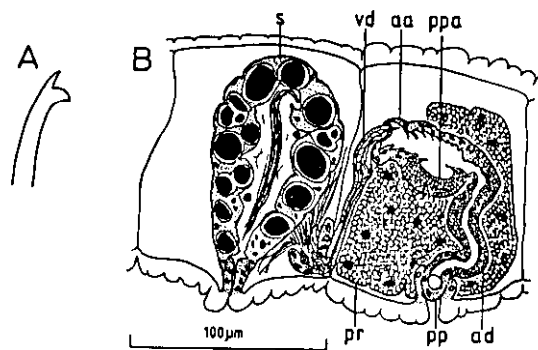
***Limnodriloides vespertinus* Erséus, 1982**

Limnodriloides vespertinus Erséus, 1982a:215-216, Fig. 2.

Diagnosis. Length: 4.4-5.5 mm; segments: 37-46. Clitellum extending over XI to $\frac{1}{2}$ XII. All setae bifid, upper tooth thinner and shorter than lower, 25-47 μ m long: (2)3(4) per bundle anteriorly, two per bundle posteriorly, ventral setae absent from X and XI. Male and spermathecal pores paired in posterior of XI and middle of X, respectively. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia paired: vas deferens very narrow, 5-14 μ m wide, shorter than atrium, entering atrium subapically. Atrial ampulla stout, 45-70 μ m long, 28-47 μ m wide; very large voluminous prostate gland broadly attached to conspicuous, cup-shaped prostatic pad on ectal part of ampulla. Atrial duct cylindrical and sinuous, 80-130 μ m long, 14-20 μ m wide, granulated most of its length, terminating in a simple pseudopenis within a small pseudopenial sac. Spermathecae paired, each with a large thick-walled oval ampulla and shorter distinct duct; walls of ampulla with numerous cavities containing secretory granules. Sperm arranged in spindle-shaped, slender bundles.

Distribution and Habitat. East coast of North America (southeast Florida, Bahamas). Associated with shallow, muddy bottoms; subtidal to at least 3 m depth.

Remarks. This species is part of the *L. rubicundus* group having less derived characters, such as no modified spermathecal setae or a single middorsal spermathecal pore. It is differentiated from *L. rubicundus* by having a gut diverticula in IX. It differs from both *L. rubicundus* and *L. pierantonii* (the other species comprising the *L. rubicundus* complex) by having a large, voluminous prostate gland and thick-walled spermathecae, the walls of which are invested with granular filled large cavities. Additionally, the prostatic pad is more developed (bulging) and the duct is longer and heavily granulated throughout *L. vespertinus*.



(after Eræus, 1982a) *Limnodriloides vespertinus*: A, free-hand drawing of seta; B, lateral view of spermatheca and male genitalia in segments X-XI.

Genus. ***Smithsonidrilus* Brinkhurst, 1966**

Type Species. *Smithsonidrilus marinus* Brinkhurst, 1966.

Diagnosis. (Based on Erséus, 1990a) Marine tropical and subtropical tubificids. Somatic setae all bifid, hair setae and modified genital setae absent. Male and spermathecal pores paired or unpaired in XI and middle of X, respectively. Body wall smooth without papillae or adherent foreign particles. Pharyngeal glands generally well developed in IV or V. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia paired or variably united: vas deferens enters atrium apically or slightly subapically. Each atrium differentiated into 1) an ental atrial ampulla, ciliated entally (ciliation may be inconspicuous in some species) with a broadly attached lobed prostate gland attached to a heavily granulated distinct ventral prostatic pad within the inner atrial epithelium; the pad may be modified into an elongate diverticula in some species; and 2) an ectal slender atrial duct which is variably granulated and may be ectally united to form an unpaired ejaculatory duct. Pseudopenes present, paired or unpaired; when paired, often elaborate (with many folds) and occasionally bearing large compact copulatory glands. Spermathecae single or paired, ampulla with sperm arranged as loose balls, rings, bundles, or slender spermatozeugmata; ducts usually differentiated into two parts: the outer part either tubular and duct-like, or dilated and appearing as a secondary invagination of the body wall (a vestibule).

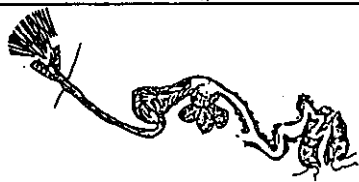
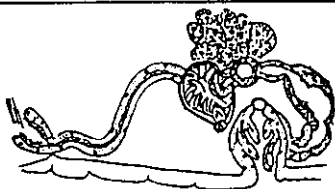
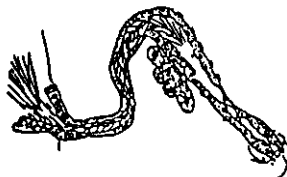
Remarks. The definition of *Smithsonidrilus* was recently emended (Erséus, 1990a) to accommodate species previously assigned to *Marcusaedrilus*, which is now considered a junior synonym of *Smithsonidrilus*. The primary character unifying all species, now within the genus *Smithsonidrilus*, is the entally ciliated atrial duct which is considered as a synapomorphic character, but not conspicuous in some species. This is the only genus in which all species have paired esophageal diverticula in IX. With the exception of *Smithsonidrilus peruanus* (Finogenova, 1986) and *S. minusculus*, all species share a second synapomorphy: a spermathecal vestibule (ectal chamber of the spermathecal duct).

The species within this genus expected to occur in Florida waters can be divided into two general groups: 1) the "*S. marinus*" group in which all species have an atrial prostatic pad developed into an atrial diverticulum and an unpaired ejaculatory duct which has an elaborate complex copulatory sac generally with copulatory glands

(copulatory glands not present in *S. hummelincki*) and an unpaired spermatheca with a filiform diverticulum attached to the inner end of the ampulla (filiform diverticulum not well developed in *S. hummelincki*): *S. exspectatus*, *S. hummelincki*, *S. marinus*, *S. westoni*, and *S. multiglandularis*; and 2) the "*S. luteolus*" group which has less elaborate paired copulatory sacs without copulatory glands, and the spermathecae are paired without filiform diverticula: *S. luteolus* and *S. minusculus*.

Twenty species are currently included in *Smithsonidrilus*. In addition to the seven aforementioned species, two taxa have also been collected from a single location in the Caribbean and may occur in the Florida Keys: *S. appositus* Erséus, 1990a (a member of the *S. luteolus* group), and *S. involutus* Erséus, 1990a (a member of the *S. marinus* group).

Table 8. *Smithsonidrillus* species.

<i>Smithsoni- drillus</i>	Somatic Setae #/bundle Ant. Post.	Spermatheca	Male Genitalia
<i>expectatus</i>	 (1)2-3 (1)2		
<i>hummelinki</i>	 2-3(4) (1)2		
<i>luteolus</i>	 (1)2-4(5) (1)2		
<i>marinus</i>	 2-3(4) 2		
<i>minusculus</i>	 (1)2-3(4) (1)2		
<i>multiglandularis</i>	 2-3(4) (1)2		
<i>westoni</i>	 (1)2-3(4) 2		

***Smithsonidrilus expectatus* Erséus, 1993**

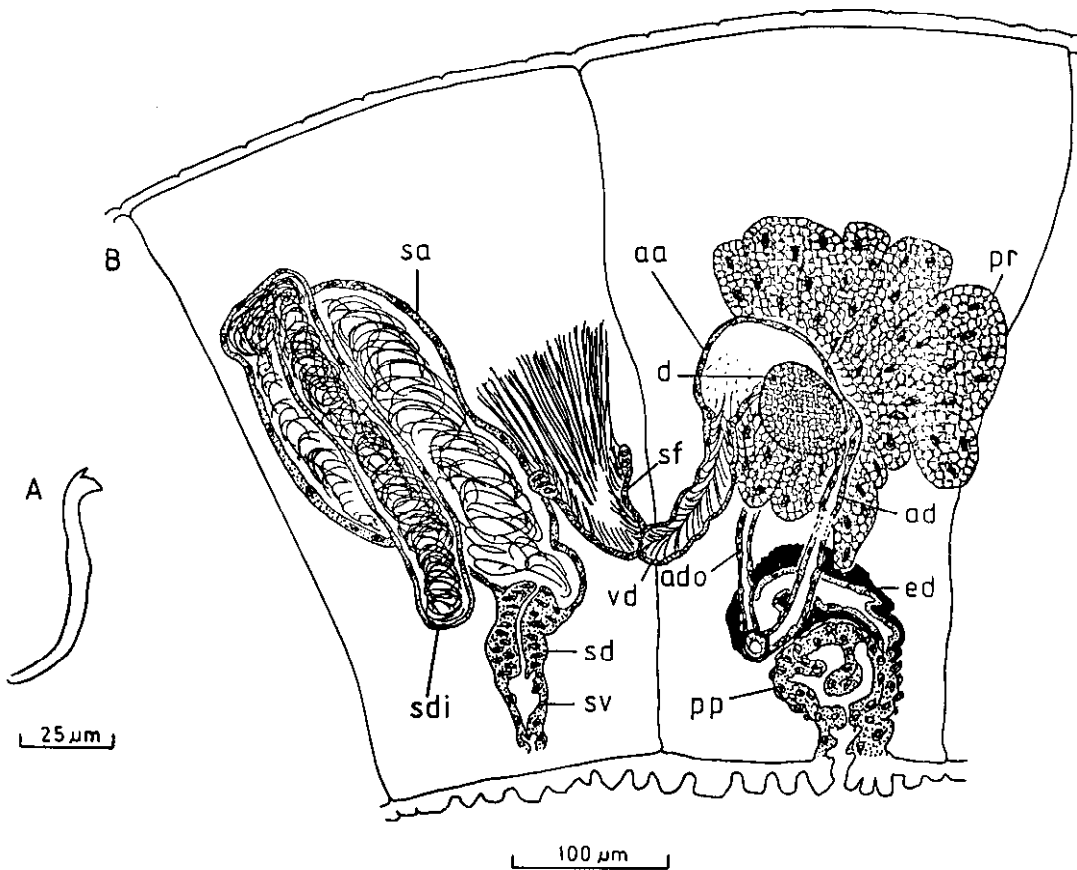
Smithsonidrilus expectatus Erséus, 1993:587-559, Fig. 1.

Diagnosis. Length: 10.4-16.5 mm; segments: 54-87. Clitellum extending over $\frac{2}{3}$ X- $\frac{2}{3}$ XII. All somatic setae bifid, upper tooth much thinner and shorter than lower, 45-80 μ m: (1)2-3 per bundle anteriorly, (1)2 per bundle posteriorly, absent from XI. Male and spermathecal pores unpaired located mid-ventrally in posterior of XI and middle of X, respectively. Esophagus in IX with a pair of anteriorly directed slender diverticula. Male genitalia complex, paired for most parts; ejaculatory duct and pseudopenis (copulatory sac) unpaired. Vas deferens thin-walled but relatively thick and short, 25-35 μ m wide and about as long as atrial ampulla which is fairly wide entally, 25-55 μ m, and narrower ectally, about 100-175 μ m long; large lobed prostate gland attached to a well developed, heavily granulated ventral prostatic pad forming a diverticulum extending about half the length of the atrial ampulla. Cilia was not observed in the atrial ampulla which terminates ectally in a slender, non-granulated atrial duct, 115-140 μ m long, 13-19 μ m wide. Atrial ducts from both sides join to form a conspicuous, unpaired ejaculatory duct, 100-165 μ m long, 45-90 μ m wide with thick, folded muscle layer 5-15 μ m wide. Ejaculatory duct enters a complex folded copulatory sac subapically on posterior side. The sac acts as an eversible pseudopenis 75-80 μ m deep, 65-75 μ m wide; and may bear a small copulatory gland. Spermatheca single with an oval ampulla having a long filiform diverticulum attached to the inner end, and a relatively short duct with an ectal inconspicuous vestibule. Sperm not in an organized arrangement, but as a random mass throughout the ampulla and associated diverticulum.

Distribution and Habitat. Southeast North America (Florida Keys). Associated with medium to coarse sand in very shallow water; 0.1-0.6 m depth.

Remarks. This species is part of the *S. marinus* complex having unpaired male and spermathecal pores, an atrial diverticulum developed from the prostatic pad, and usually a filiform diverticulum of the spermatheca. It is differentiated from *S. hummelincki* by the presence of the spermathecal diverticulum and poorly ciliated (if at all) atrial ampulla. The latter character also separates *S. expectatus* from *S. marinus*, *S. westoni*, and *S. multiglandularis*. It is further

distinguished from the latter three taxa by the shorter, heavily muscular ejaculatory duct, less complex copulatory sac, and the absence of well developed copulatory glands. The specific epithet of *S. exspectatus* was derived by providing the expected link, with regard to the morphology of the male genitalia, between *S. hummelincki* and the other species of the *S. marinus* complex with unpaired male and spermathecal pores.



(after Erséus, 1993b) *Smithsonidrilus exspectatus*: A, neta; B, lateral view of spermatheca and male genitalia in segments X-XI.

***Smithsonidrilus hummelincki* (Righi and Kanner, 1979)**

Marcusaedrilus hummelincki Righi and Kanner, 1979:49-57, Fig. 31-35.

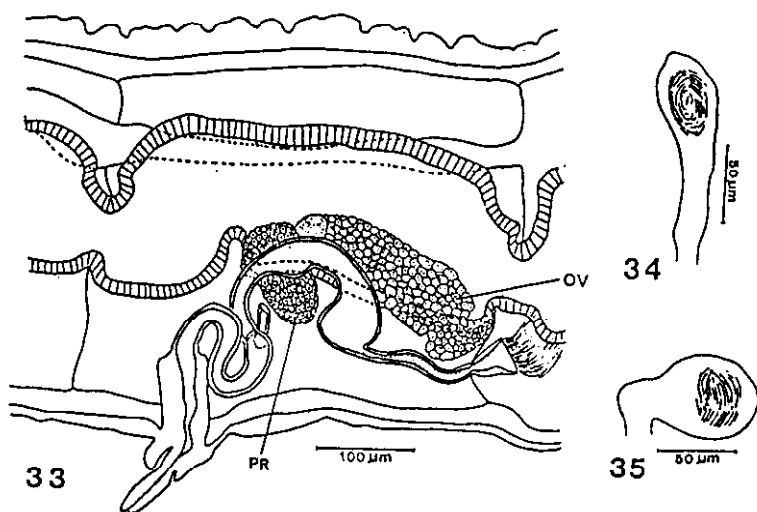
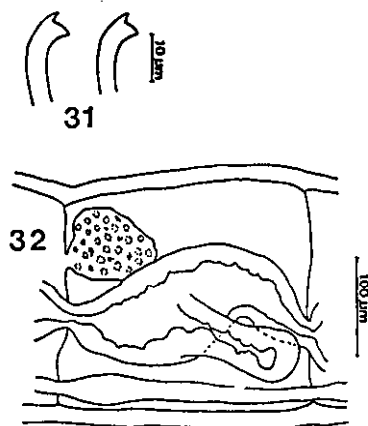
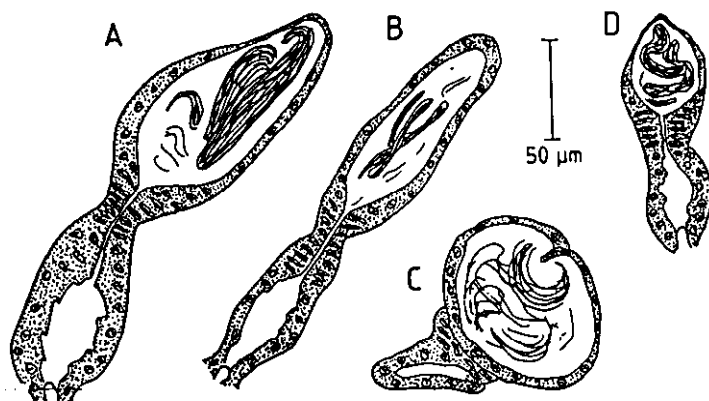
Diagnosis. (Based on Erséus, in press) Length: 5.8-14.0 mm; segments: 33-65. Clitellum extending over XI- $\frac{2}{3}$ XII. All somatic setae bifid, upper tooth much thinner and shorter than lower, 50-75 μ m long: 2-3(4) per bundle anteriorly, (1)2 per bundle posteriorly, absent from XI. Male and spermathecal pores unpaired, mid-ventrally, in posterior of XI and middle of X, respectively. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia complex, but not very large and conspicuous, paired for most parts; ejaculatory duct and pseudopenis (copulatory sac) unpaired. Vas deferens narrow and relatively long, about as long as combined length of atrial ampulla and duct; entering atrial ampulla apically or slightly subapically. Atrial ampulla club-shaped, ciliated in the ental half, 100-150 μ m long, 30-50 μ m wide, lobed prostate gland broadly attached to roundish, well defined prostatic pad (atrial diverticulum) in ectal half of atrial ampulla which terminates ectally into a narrow, poorly granulated atrial duct, about 100 μ m long. Atrial ducts from both sides join to form a muscular and wavy unpaired ejaculatory duct, about as long as atrium, and 25-50 μ m wide. Ejaculatory duct leads to a compact pseudopenial bulb consisting of: 1) an outer very elaborate muscular layer; 2) an inner slightly winding duct, the wall of which forms the actual pseudopenis when everted, and 3) an intermediate diffuse layer of cells. When everted, the pseudopenis is cylindrical and slender. Spermatheca single, tripartite: 1) an ental oval, pear or spindle-shaped, thin-walled ampulla; 2) a middle thick-walled, narrow duct, and 3) an ectal oval swelling forming a vestibule. Sperm generally forming a loose ball or bundle in the ampulla, but may be arranged as small spermatozeugmata (Erséus, 1990a).

Distribution and Habitat. Caribbean (Guadeloupe, Bonaire, Aruba, Panama, Belize, Bahamas, Puerto Rico, Virgin Islands, Barbados, Curacao), southwest North America (southern Florida), Bermuda. Associated with mud and sand; intertidal to at least 21 m depth.

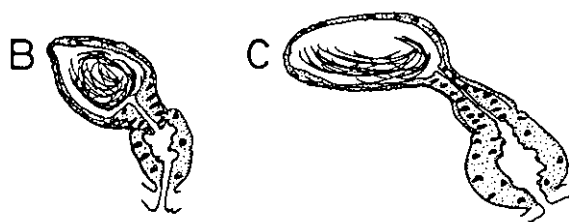
Remarks. This species is part of the *S. marinus* complex having unpaired male and spermathecal pores. It differs from the other species within this group by lacking a distinct filiform diverticulum on the inner end of the spermathecal ampulla, and by possessing a much simpler, yet still fairly complex, copulatory apparatus.

Smithsonidrilus hummelincki is the type species of *Marcusaedrilus* which is now a junior synonym of *Smithsonidrilus*. This species is one of the most common marine tubificids throughout the Caribbean and southern Florida. The immature specimens can usually be differentiated from other species of tubificids comprising a benthic community by the much larger, more robust somatic setae, with a very stout recurved lower tooth and much reduced upper tooth, particularly in the postclitellar segments.

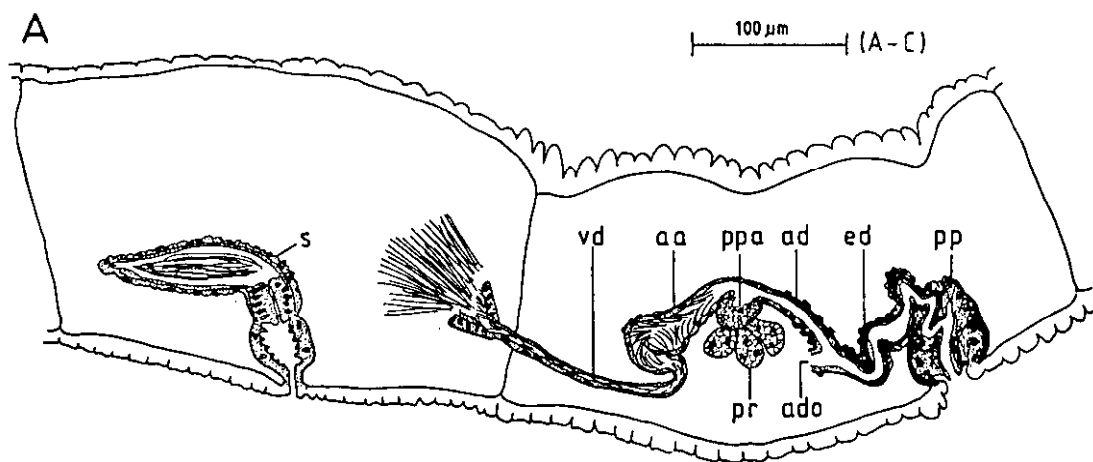
(after Erasus, 1990a) *Smithsonidrilus hummelincki*, spermatheca: A-C, specimens from Belize; D, specimen from Panama.



(after Righi and Kanner, 1979) *Smithsonidrilus hummelincki*: 31, setae; 32, gut diverticula in IX; 33, lateral view of XI; 34-35, spermatheca.



(after Erasus, 1983b) *Smithsonidrilus hummelincki*: A, lateral view of spermatheca and male duct in segments X-XI (specimen from Bahamas); B, spermatheca (specimen from Bahamas); C, spermatheca (specimen from St. Croix, Virgin Islands).



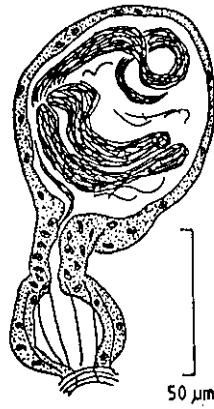
***Smithsonidrilus luteolus* (Erséus, 1983)**

Marcusaedrilus luteolus Erséus, 1983b:27-29, Fig. 3.

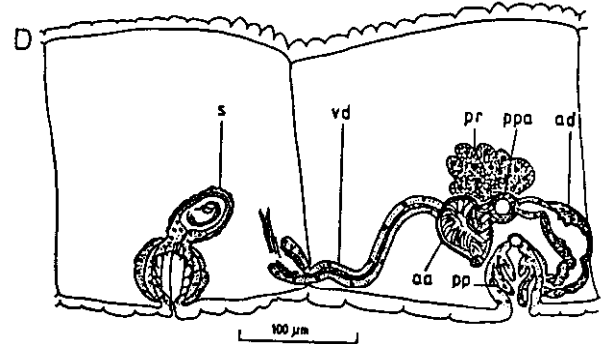
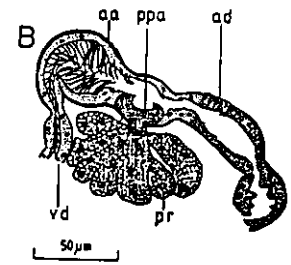
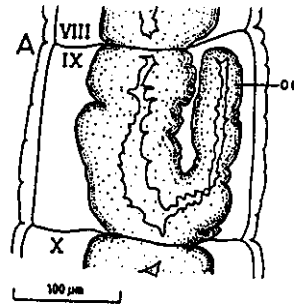
Diagnosis. Length: 6.1-15.7 mm; segments: 53-88. Clitellum extending over $\frac{2}{3}$ X-XII. All somatic setae bifid with upper tooth thinner and shorter than lower, and with an inconspicuous subdental ligament connecting tip of lower tooth with setal shaft, 45-70 μm long: (1)2-4(5) per bundle anteriorly, (1)2 per bundle posteriorly, ventral setae absent from XI. Male and spermathecal pores paired in posterior of XI and middle of X, respectively. Esophagus in IX with a large pair of anteriorly directed diverticula. Male genitalia paired: vas deferens 14-22 μm wide about as long as rest of male duct, entering atrial ampulla subapically. Atrial ampulla globular, heavily ciliated entally, 70-145 μm long, 30-80 μm wide; large, lobed prostate gland broadly attached to distinct, cup-shaped prostatic pad (not forming an atrial diverticulum) in ectal half of atrial ampulla which terminates in a heavily granulated atrial duct 150-225 μm long, 15-47 μm wide. Atrial duct opens at apical end of pseudopenial sac with folded inner wall which may be everted completely during copulation. Spermathecae paired, tripartite, each comprised of: 1) an ental roundish ampulla; 2) a middle narrower duct, and 3) an ectal globular selling forming a vestibule. Sperm arranged as somewhat spindle-shaped spermatzeugmata or loose curved bundles.

Distribution and Habitat. Caribbean (Barbados), southeast North America (southern Florida). Associated with subtidal muds and sands to at least 21 m.

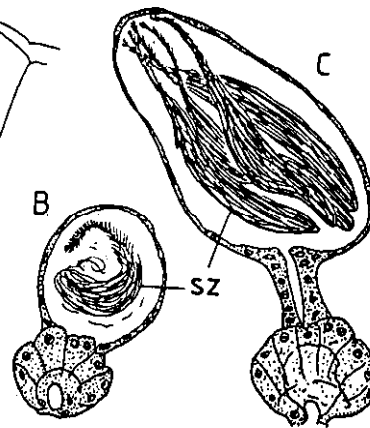
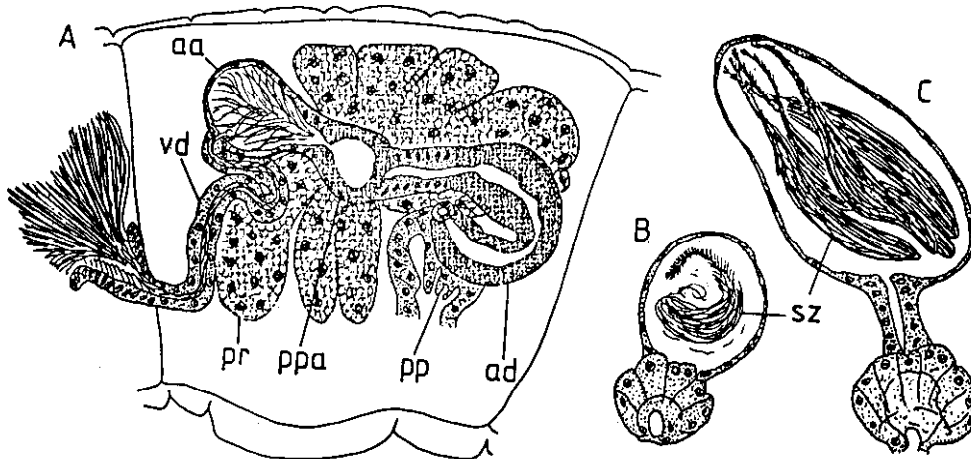
Remarks. This species is part of the *S. luteolus* complex, having paired male and spermathecal pores, lacking a filiform diverticulum on the inner end of the spermatheca, and the prostatic pad is not developed into an atrial diverticulum. *Smithsonidrilus luteolus* is distinguished from the other species of the *S. luteolus* complex (*S. minusculus*) by the much larger, folded copulatory sac of the former, whereas it is very simple in the latter. Specimens of this species collected from Hutchinson Island, Florida, were much larger than the Barbados or Miami material. It is further distinguished from all other species of Limnodriloidinae listed herein by the unique subdental ligament of the somatic setae. This structure is common in species of Phallodrilinae and some, mostly Indo-Pacific species of *Heterodrilus*, but is found in only one other Limnodriloidinae species, *Smithsonidrilus appositus* from Belize in the Caribbean.



(after Erásus, 1986a) *Smithsonidrilus luteolus* from Hutchinson Island: spermatheca.



(after Erásus, 1983b) *Smithsonidrilus luteolus*: A, lateral view of oesophagus in segment IX; B, lateral view of atrium; C, seta; D, lateral view of spermatheca and male duct in segments X-XI (holotype).



(after Erásus, 1990a) *Smithsonidrilus luteolus* from Belize: A, lateral view of male genitalia in segment X; B-C, spermathecae.

***Smithsonidrilus marinus* Brinkhurst, 1966**

Smithsonidrilus marinus Brinkhurst, 1966:300-302, Fig. 2.

Diagnosis. Length: 9.6 mm; segments: about 56. Clitellum extending over XI- $\frac{1}{3}$ XII. All somatic setae bifid with upper tooth thinner and shorter than lower, 55-80 μ m long: 2-3(4) per bundle anteriorly, two per bundle posteriorly, ventral setae absent from XI. Male and spermathecal pore unpaired in middle of XI and X, respectively. Esophagus in IX with a pair of anteriorly directed diverticula. Male genitalia complex occupying most of coelom in XI; paired for most of the parts; ejaculatory duct and pseudopenes (copulatory sac) unpaired. Vas deferens 10-15 μ m wide, shorter than atrium, opening subapically into a club-shaped atrial ampulla which is heavily ciliated in the ental half, about 200 μ m long and 35-55 μ m wide; large, lobed prostate gland broadly attached to a heavily granulated atrial diverticulum (modified prostatic pad) about half the length of the atrial ampulla on the ectal part of the atrial ampulla which terminates in a thick heavily granulated atrial duct about as long as the atrial diverticulum and 22-30 μ m wide. Atrial ducts from both sides join to form a very long (probably longer than the vas deferens and atrium combined), coiled, unpaired ejaculatory duct; width approximately equal to the individual atrial ducts. Ejaculatory duct enters asymmetrically into the posterior of a complex folded copulatory sac. A large compact pear-shaped copulatory gland, 60-110 μ m wide, is attached to each lateral side of the sac. When the sac is everted, a large asymmetrical pseudopenis is formed. Spermatheca single with a round, ball-shaped ampulla having a long filiform diverticulum attached to the inner end, a large (glandular?) mass surrounding the ectal part of the spermathecae ampulla, and a very wide short duct [also termed the spermathecal sac by Erséus (1982b), or "spermathecal vestibule" (Erséus, 1990a)]. A "proper duct" appears poorly developed. Two small glandular bodies may be attached to the "vestibule". Sperm arranged in large spindle-shaped bundles.

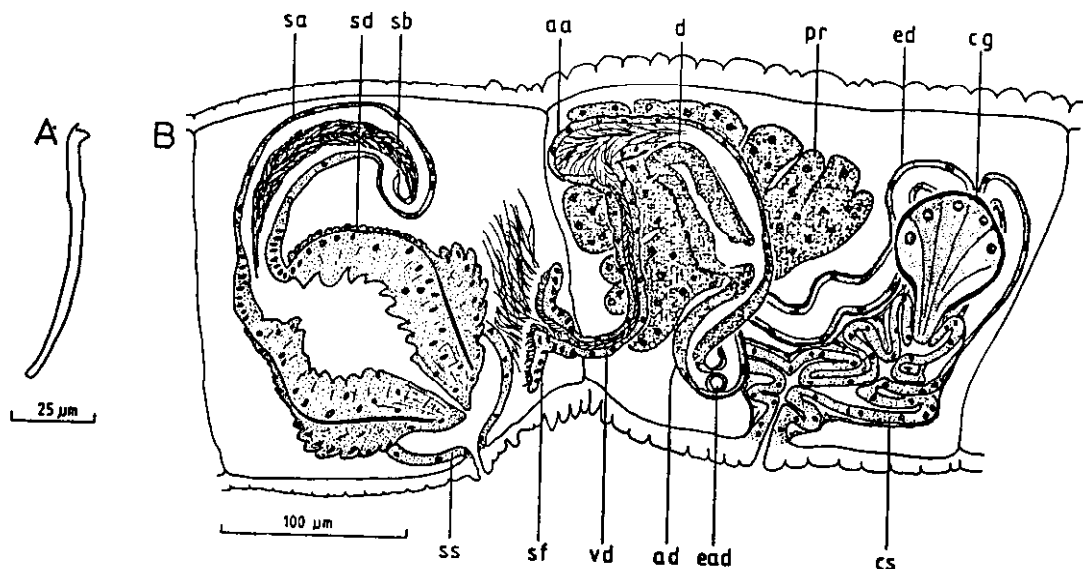
Distribution and Habitat. Southeast North America (central and southern Florida). Associated with subtidal sand to at least 3 m depth.

Remarks. *Smithsonidrilus marinus* is the type species of the genus, and is part of a complex of closely related species which have an unpaired ejaculatory duct and an unpaired mid-ventral spermatheca with a filiform spermathecal diverticulum on the inner end. It differs from the other species in this group (except *S. westoni*) by having a pair of large copulatory glands associated with the copulatory sac. It is most similar

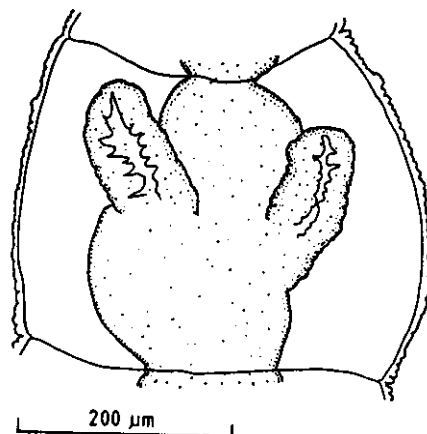
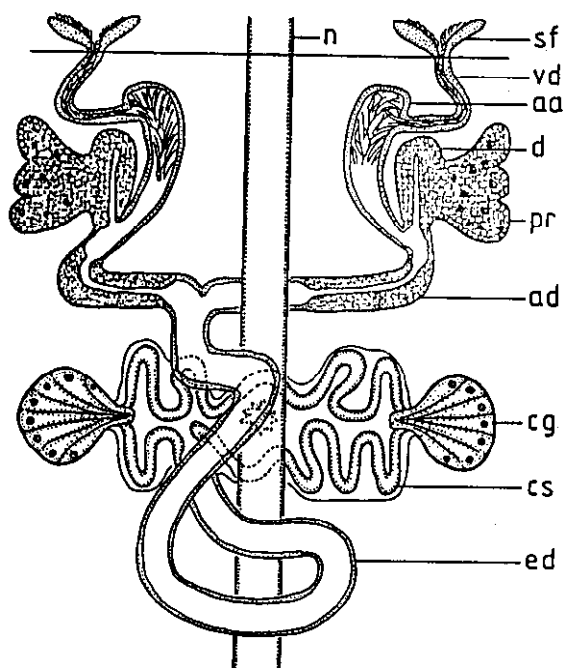
to *Smithsonidrilus westoni*, which was a subspecies of *S. marinus* until recently (Erséus, 1990a), but differs from the latter by three primary features: 1) *S. westoni* lacks the large mass of cells surrounding the ectal part of the spermathecal ampulla; 2) the sperm "bundles" are more slender in *S. westoni*, and 3) the spermathecal vestibule is more developed and complex in *S. westoni*. Otherwise, the principal organization of the male genitalia of both species are identical.

Note: In the redescription of *S. marinus* (Erséus, 1982b), the "Spermathecal ampulla, spermathecal duct, and spermathecal sac" are herein referred to as spermathecal diverticulum, spermathecal ampulla, and spermathecal vestibule, respectively.

(after Bråhus, 1982b)
Smithsonidrilus marinus:
 A, seta; B, lateral view of
 spermatheca and male
 genitalia in segments X and
 XI.

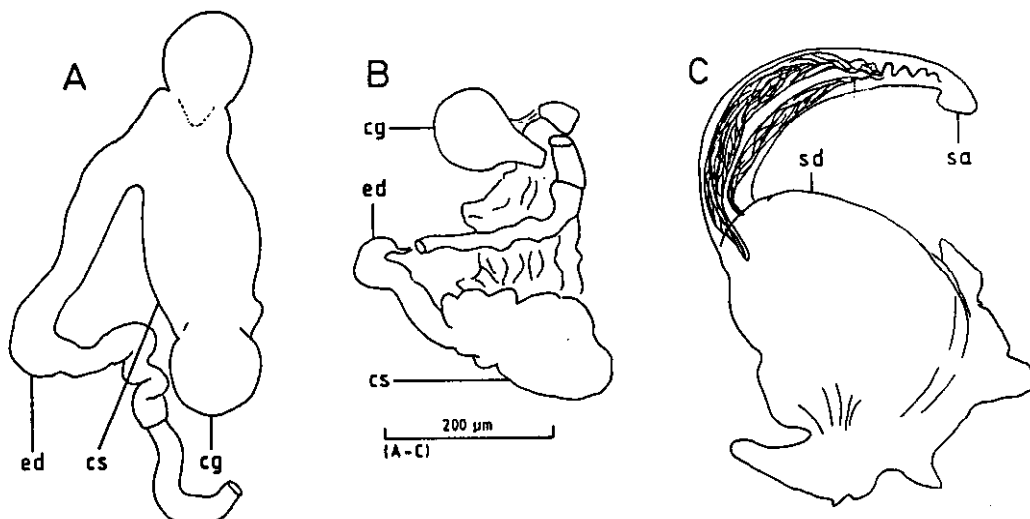


(after Bråhus, 1982b)
Smithsonidrilus marinus:
 dorsal, schematic view of
 male genitalia.



(after Bråhus, 1982b) *Smithsonidrilus marinus*:
 ventral view of segment IX showing oesophagus
 with diverticula.

(after Bråhus, 1982b)
Smithsonidrilus mari-
nus, dissected fragments
 of the type material: A,
 ectal parts of male effer-
 ent duct of the holotype;
 B, parts of male duct of
 paratype; C, spermathe-
 ca of paratype (same as
 in B).



***Smithsonidrilus minusculus* (Erséus, 1983)**

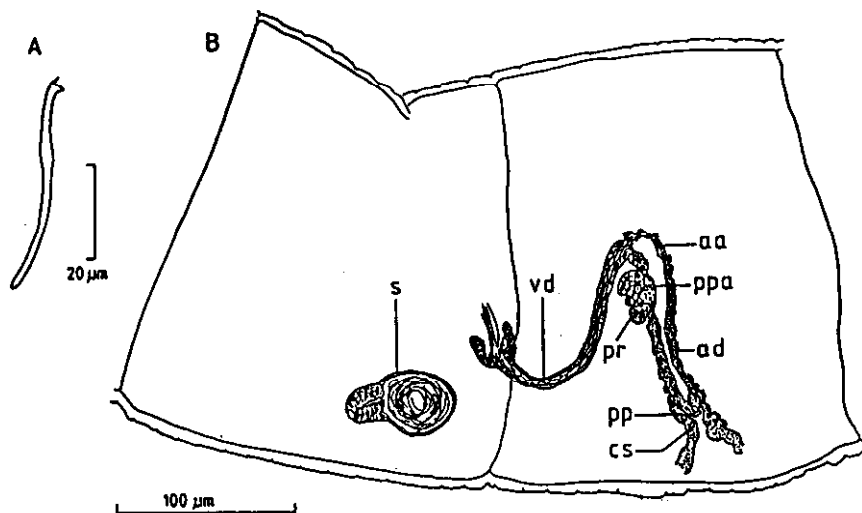
Marcusaedrilus minusculus Erséus, 1983b:30-31, Fig. 5.

Diagnosis. Length: 3.8-6.9 mm; segments: 24-52. Clitellum extending over XI-XII. All somatic setae bifid with upper tooth thinner and shorter than lower, 25-51 μm long: (1)2-3(4) per bundle anteriorly, (1)2 per bundle posteriorly, ventral setae absent from X and XI (rarely present in X). Male and spermathecal pores paired in middle or posterior of XI and X, respectively. Esophagus in IX with a pair of small anteriorly directed diverticula. Male genitalia paired: vas deferens 6-17 μm wide, about as long as or slightly longer than atrium, entering atrial ampulla apically or slightly subapically. Atrium club-shaped; atrial ampulla elongate, ciliated in ental half, 28-63 μm long [up to 110 μm long in Australian specimens (Erséus, 1993a)], 14-46 μm wide; very small, lobed prostate gland attached to a very small, inconspicuous prostatic pad in ectal half of atrial ampulla which enters a partially granulated atrial duct, 45-100 μm long, 12-23 μm wide. Atrial duct terminates at the inner end of a small and simple pseudopenial sac. Spermathecae paired, shape is variable but generally each is very small with a spherical to pear-shaped ampulla and short duct which may or may not be medially constricted so that a small vestibule is formed. Sperm arranged in small to large rings or loose, broad bundles, or in a random mass.

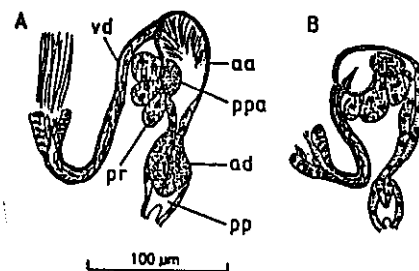
Distribution and Habitat. Australia (Northern Territories, Queensland, western Australia), southern China, Hawaii, Bermuda, Caribbean (Belize). Associated with intertidal and subtidal sands to at least 15 m depth.

Remarks. This species is a member of the *S. luteolus* group which has paired male and spermathecal pores and lacks an atrial diverticulum and spermathecal diverticulum. This species is distinguished from all congeners by its very diminutive size, inconspicuous atria, very small prostate glands, inconspicuous prostatic pads, small, simple pseudopenes, and very small, generally spherical spermathecae. It has a worldwide distribution and was previously confused with *Limnodriloides claviger*. Species originally described as *L. claviger* from Bermuda, Queensland, western Australia, and Hawaii are now considered to be *S. minusculus*.

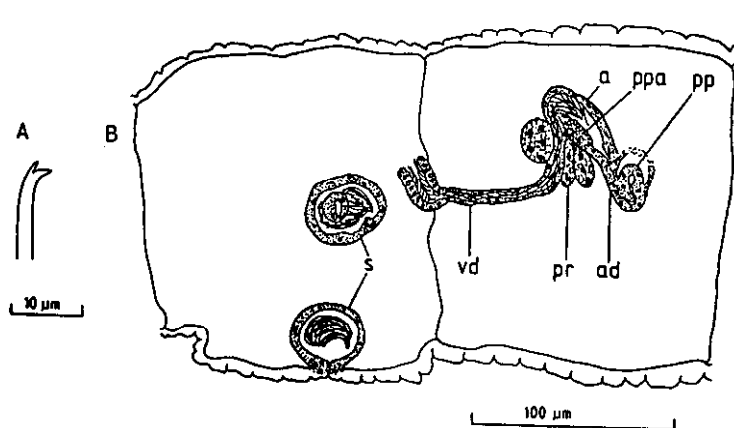
Although this species has not been reported from Florida as yet, its worldwide distribution and presence in the Caribbean suggest that it is likely to occur. Its small size may have made it easy to overlook in previous investigations.



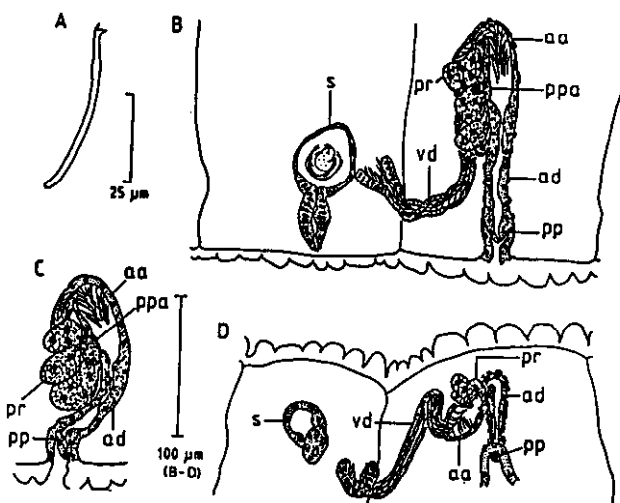
(after Erőss and Davis, 1989) *Smithsonidrilus minusculus*, as *Limnodriloides claviger*: A, seta; B, lateral view of spermatheca and male genitalia in segments X-XI.



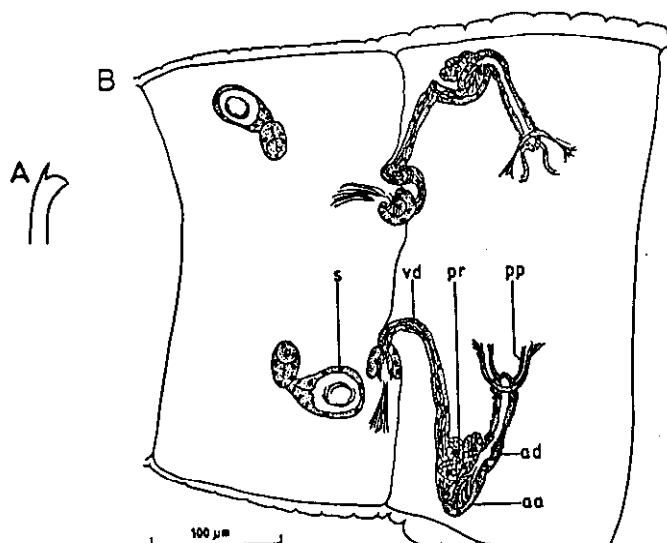
(after Erőss, 1993a) *Smithsonidrilus minusculus* from Australia: A-B, male genitalia.



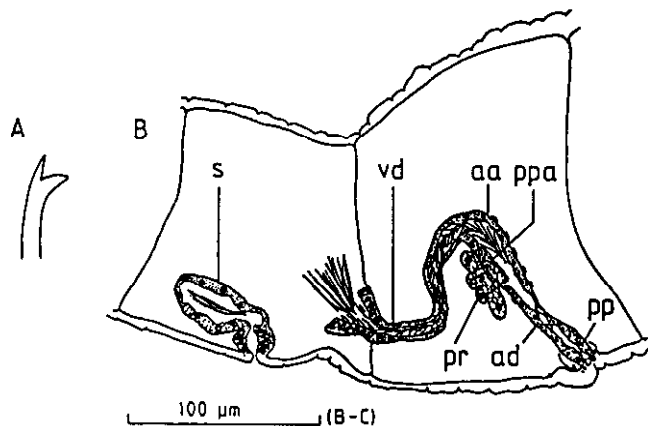
(after Erőss, 1990a) *Smithsonidrilus minusculus* from Belize: A, seta; B, oblique view of spermathecae (of both sides) and male genitalia (of one side) in segments X-XI.



(from Erőss, 1990b) *Smithsonidrilus minusculus*: A, seta; B, lateral view of spermatheca and male genitalia in segments X-XI; C, atrium from another specimen; D, lateral view of spermatheca and male genitalia.



(after Erőss, 1983b) *Smithsonidrilus minusculus* from Australia: A, free-hand drawing of seta; B, ventral view of spermathecae and male ducts in segments X-XI.



(after Erőss, 1992b) *Smithsonidrilus minusculus* as *Limnodriloides minusculus* from Hong Kong: A, seta; B, genitalia in X-XI.

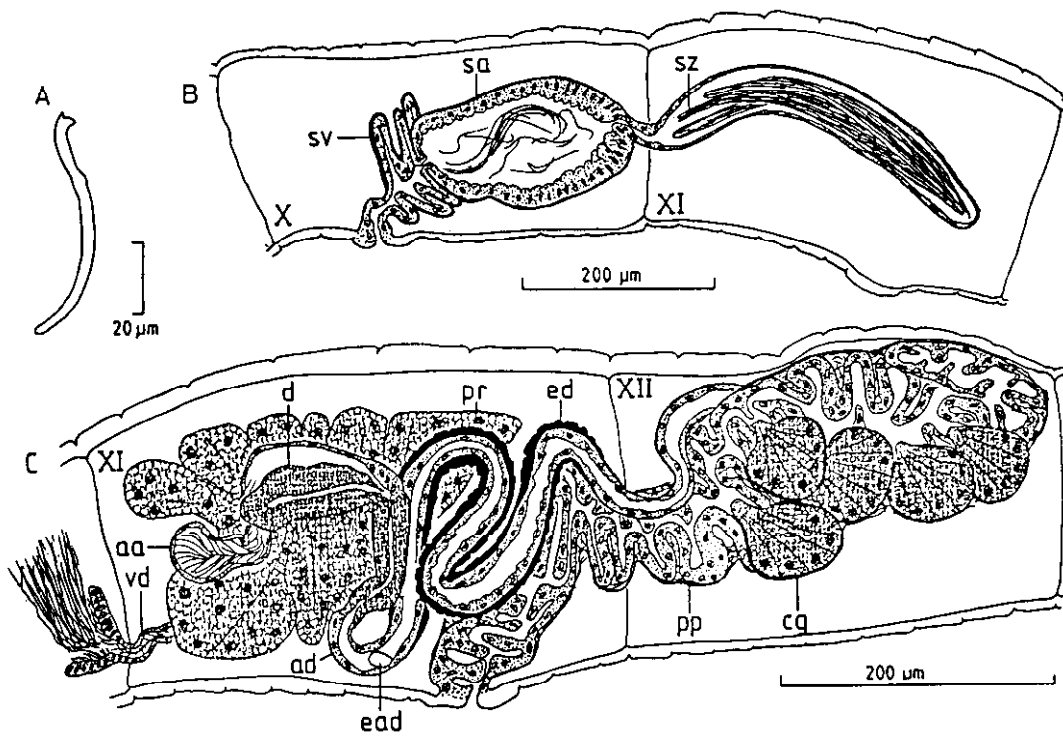
***Smithsonidrilus multiglandularis* Erséus, 1990**

Smithsonidrilus multiglandularis Erséus, 1990a:295, Fig. 36A-36C.

Diagnosis. Length 15.6-20.5 mm; segments: 72-83. Clitellum extending over XI- $\frac{2}{3}$ XII. All somatic setae bifid with upper tooth thinner and shorter than lower, 45-70 μ m long: 2-3(4) per bundle anteriorly, (1)2 per bundle posteriorly, absent from XI. Male and spermathecal pore unpaired posteriorly in XI and medially in X, respectively. Esophagus in IX with a large pair of anteriorly directed diverticula. Male genitalia complex, occupying most of the coelom in XI and part of XII; paired for most of the parts; ejaculatory duct and pseudopenis (copulatory sac) unpaired. Vas deferens appears shorter than atrium. Atrial ampulla somewhat club-shaped ciliated entally, 190-210 μ m long, 30-40 μ m wide; large, lobed prostatic gland attached to atrial diverticulum (modified prostatic pad) on the ectal part of the atrial ampulla which leads to a heavily granulated atrial duct, about as long as atrial ampulla. Atrial ducts from both sides join to form a very long, convoluted ejaculatory duct, 30-42 μ m wide. Ejaculatory duct enters a very large, complex pseudopenis (copulatory sac), generally extending into XII. Pseudopenis with much folded inner wall. (4)5(6) large compact round to pear-shaped copulatory glands, 55-80 μ m long are attached to the inner part of the pseudopenis. Spermatheca single, complex, with a large oval spermathecal ampulla having a slender diverticulum extending into XI, and large spermathecal sac (vestibule) with folded somewhat muscular wall. Sperm arranged as numerous, very long spermatozuogmata.

Distribution and Habitat. Southeast North America (southern Florida), Caribbean (Puerto Rico). Associated with sand; subtidal to at least 90.8 m depth.

Remarks. This species is a member of the *S. marinus* complex, and appears to be the most advanced species having very elaborate male ducts with a single ejaculatory duct, a very complex pseudopenis with multiple copulatory glands, and a unique unpaired spermatheca with a slender diverticulum and highly folded enlarged vestibule. It is most similar to *S. marinus* and *S. westoni*, having very large distinct copulatory glands associated with the pseudopenial sac: the large number, generally five in the former instead of two, serve to distinguish these species.



(after Ercéus, 1990a) *Smithsonidrilus multiglandularis*: A, meta; B, lateral view of spermatheca in segments X-XI (male genitalia not drawn in XI); C, lateral view of male genitalia in XI-XII.

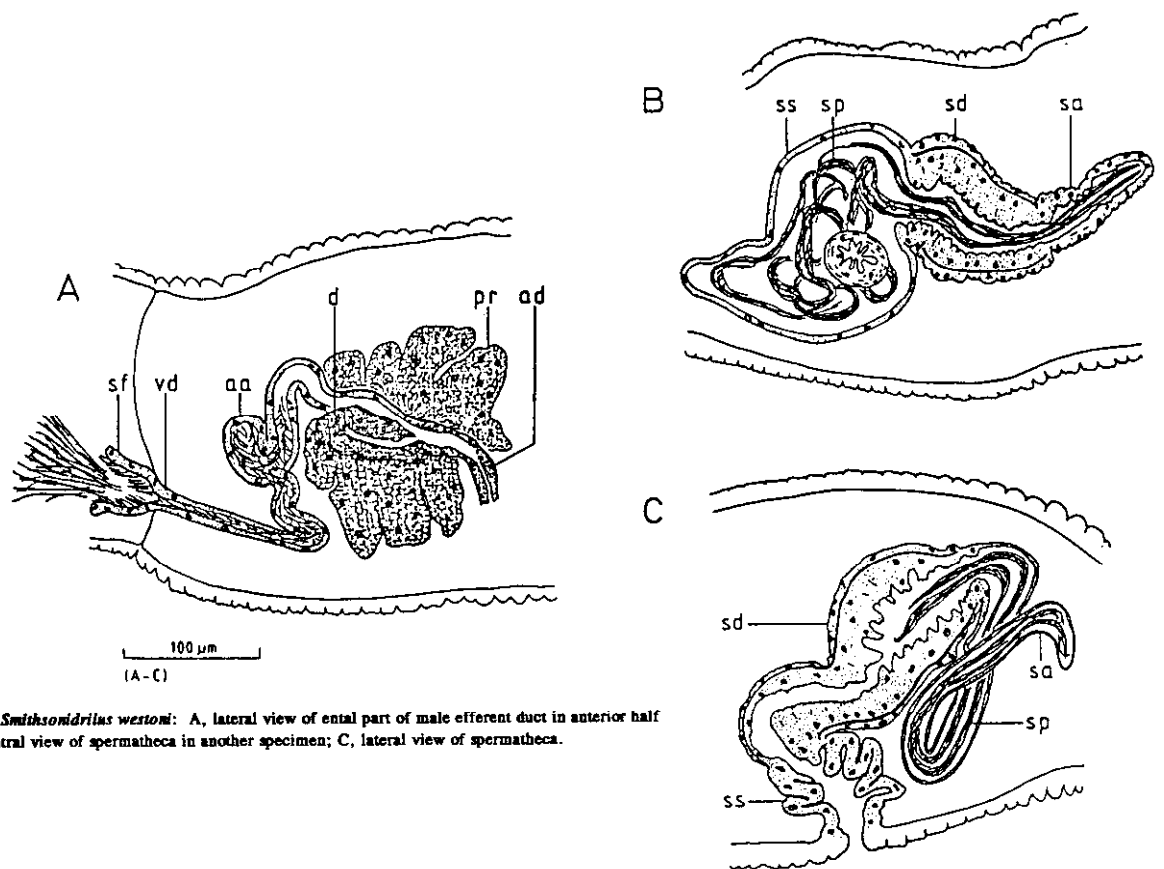
***Smithsonidrilus westoni* Erséus, 1982**

Smithsonidrilus marinus westoni Erséus, 1982b:52-53, Fig. 5.

Diagnosis. Length: 9.9-19.4 mm; segments: 50-82. Clitellum extending over XI- $\frac{2}{3}$ XII. All somatic setae bifid with upper tooth thinner and shorter than lower, 45-75 μ m long: (1)2-3(4) per bundle anteriorly, two per bundle posteriorly, ventral setae absent from XI. Male and spermathecal pores unpaired, slightly posterior to middle of XI and middle of X, respectively. Esophagus in IX with a pair of anteriorly directed diverticula. Vas deferens 12-14 μ m wide; atrial ampulla heavily ciliated in the ental half generally 200-250 μ m long and 20-40 μ m wide; large lobed prostate gland broadly attached to a heavily granulated atrial diverticulum (modified prostatic pad), slightly less than half the length of the atrial ampulla, on the ectal part of the atrial ampulla which terminates in a short atrial duct, much shorter than the atrial ampulla. Atrial ducts from both sides join to form a very long coiled, unpaired ejaculatory duct, longer than the vas deferens and atrium combined, 25-60 μ m wide. Ejaculatory duct enters asymmetrically in the posterior of a complex, folded copulatory sac. A large compact pear-shaped copulatory gland 40-75 μ m wide, is attached to each lateral side of the sac. Spermatheca single with a round-to-oval ampulla having a slender diverticulum attached to the inner end; ectal end of ampulla not surrounded by large mass of glandular cells (as in *S. marinus*), and joins with a very short, wide, folded duct or vestibule. Sperm arranged in very slender elongate bundles.

Distribution and Habitat. Eastern North America (New Jersey through North Carolina), Caribbean (Bahamas), Bermuda. Associated with sand; subtidal to at least 200 m depth.

Remarks. The organization of the male genitalia is virtually identical to that of *S. marinus*. The only differences are with respect to size of specific structures, and the atrial diverticulum is only about one-third the length of the atrial ampulla in *S. westoni* as opposed to one-half the length in *S. marinus*. The most significant difference is that the mass of glandular cells enveloping the ectal portion of the spermatheca in *S. marinus* is absent in *S. westoni*, and the spermathecal vestibule is more folded and complex in the latter. Erséus (1990a) cites the more compact arrangement of sperm in *S. westoni* as a specific distinction. However, the variability in the arrangement of sperm in other species of *Smithsonidrilus* is considerable and should be viewed with caution as a specific criterion. Until recently, this species was considered a subspecies of *S. marinus*, but was elevated to specific rank following a comprehensive phylogenetic revision of the genus by Erséus (1990a). (See Remarks for *S. marinus* for further discussion).



(after Erséus, 1982b) *Smithsonidrilus westoni*: A, lateral view of ental part of male efferent duct in anterior half of segment XI; B, ventral view of spermatheca in another specimen; C, lateral view of spermatheca.

Subfamily. Tubificinae Eisen, 1879

Type Genus. *Tubifex* Lamarck, 1816.

Diagnosis. Mostly freshwater. Coelomocytes not abundant (of the rhyacodriline form). Somatic setae include simple-pointed, bifid, and pectinate crotchets and hairs. Genital setae occasionally present as a single hollow-ended spermathecal setae in each ventral bundle of X, and rarely XI. Spermathecal pore located in middle of segment X. Esophagus not modified (or only slightly dilated) in IX. Ciliated vas deferens either of uniform width, or differentiated into narrow and wide sections; enters atrium apically or subapically. Atrium highly variable: may be relatively wide and comma-shaped, long and slender, or an intermediate form. Single, stalked prostate gland attached to atrium. Atrium generally leads to a long or short ejaculatory duct which usually terminates in true penes (permanent, pendant) frequently with thickened cuticular penis sheaths. Sperm arranged as slender spermatzeugmata consisting of two types of sperm.

Remarks. The primary distinguishing characters of this subfamily are the absence of abundant, coelomocytes, the single stalked compact prostate glands, the permanent, pendant true penes, and sperm as spermatzeugmata comprised of two types of sperm. The majority of genera within this subfamily are freshwater. Currently, there are about seven genera which have brackish water or marine representatives. Except for one cave dwelling species described from Spain (*Tubificoides galarzai* Giani and Rodriguez, 1988), *Tubificoides* is exclusively found in estuarine or marine environments and is the only genus of Tubificinae occurring in the coastal regions of southeast North America.

Genus. *Tubificoides* Lastockin, 1937

Type Species. *Tubificoides heterochaetus* Lastockin, 1937 = *T. swirencowi* Jaroschenko, 1948 [non *T. heterochaetus* (Michaelson, 1926)].

Diagnosis. (Based on Erséus, 1989) Exclusively marine and brackish water species. Body wall naked or with fine particles adhering to cuticle, often forming distinct papillae. Prostomium may be retractable in heavily papillated species. Hair setae absent or present in dorsal bundles; dorsal setae may also include simple-pointed, bifid, or pectinate crotchets; ventral setae all bifid, lower tooth may be very reduced making setae appear simple; modified genital setae absent. Male and spermathecal pores paired in posterior of XI and middle of X, respectively. Coelomocytes, if present, not of the "rhyacodriline type". Male genitalia paired in XI. Vas deferens ciliated, thin-walled, entering atrium subapically, generally opposite to large stalked prostate gland. Rounded inner end of atrium cap-like, very heavily granulated and histologically different from the rest of atrium. Main body of atrium cylindrical, generally curved or comma-shaped; ectal portion often histologically distinct. Atrium terminating in a copulatory sac, which, in all but one species, contains a pendant (true) penis bearing a thickened cuticular penis sheath (in *T. inops* the copulatory organ is modified into a complex, probably eversible pseudopenis). Ejaculatory duct not well developed or absent. Spermathecae comprised of a cylindrical duct which frequently forms a distinct swelling (vestibule) near the ectal pore, and round to oval to pear-shaped ampulla. A distinct "sperm trap" is generally present at the junction of the duct and ampulla. Sperm arranged in the ampulla as spindle-shaped, often very slender spermatozeugmata in postcopulatory specimens.

Remarks. The aforementioned diagnosis is based on the most current previous definition by Brinkhurst and Baker, 1979 and was emended by Erséus (1989). The diagnosis required emendation when a new species, *Tubificoides inops*, was discovered. Although this species has a pseudopenis, opposed to a true, pendant penis with a thickened cuticular penis sheath, the shape of the atrium, with the cap-like apical portion and subapical entrance of the vas deferens, was considered as the single most significant criterion on which to recognize the genus, therefore, regarding the configuration of the copulatory organ as a secondary character.

Tubificoides was reestablished by Holmquist (1978) and extended by Brinkhurst and Baker (1979) to include previously described *Tubifex*

and *Peloscolex* species with male efferent ducts "of characteristic form, a tendency toward simple-pointed setae posteriorly, more or less papillate body walls, and a saltwater habitat". See Brinkhurst and Baker (1979) for a more complete discussion.

The genus now includes more than 50 species, with many as yet undescribed. Ten species are included herein, however, many additional species have been described from deep water in the Gulf of Mexico and off the Atlantic coast of North America.

Table 9. *Tubificoides* species.

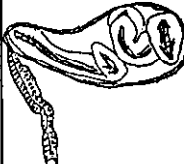
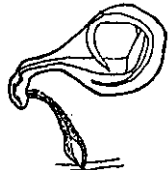
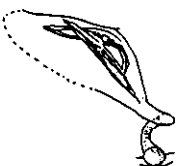
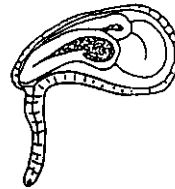
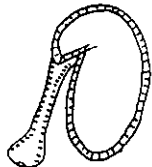
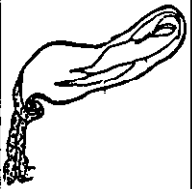
<i>Tubificoides</i>	Dorsal Setae #/bundle Anterior		Dorsal Setae #/bundle Posterior		Spermatheca	Body Wall Penis Sheath
	Hairs	Bifid	Hairs	Bifid		
<i>armatus</i>	 (simple)					naked 
	1-2	1-2	0	1		
<i>brownae</i>						naked 
	0	3-5	0	1		
<i>bermudae</i>						posterior papillae 
	0	2-3	0	1-2		
<i>heterochaetus</i>						posterior papillae 
	0	2-4	0	1-2(3)*		
<i>inops</i>						posterior papillae  penis sheaths absent
	0	2-5	0	1-3		
<i>lunatus</i>						naked 
	0	3-4	0	1-2		
<i>moset</i>						naked 
	0	2-4	0	2(3)		
<i>parviductus</i>						naked 
	2	2	1	1		

Table 9. *Tubificoides* species. Continued.

<i>Tubificoides</i>	Dorsal Setae #/bundle Anterior Hairs Bifid	Dorsal Setae #/bundle Posterior Hairs Bifid	Spermatheca	Penis Sheath
<i>pollux</i>	 1-2 2-3	 0 2-3		posterior papillae 
<i>wasselli</i>	 0 2	 0 1		papillae 

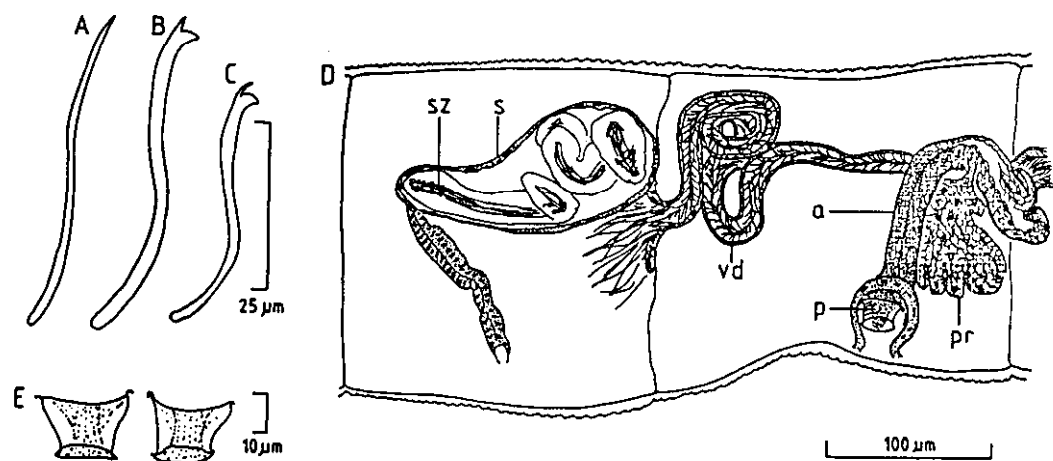
***Tubificoides annulus* Erséus, 1986**

Tubificoides annulus Erséus, 1986a:310, Fig. 15.

Diagnosis. Length: 7-8 mm; segments: about 47. Prostomium appearing somewhat retractable. Body smooth, without cuticular adherent particles or papillae, but cuticle thick and finely ridged. Clitellum extending over XI-½ XII. Anterior dorsal bundles comprised of 1-2 simple-pointed setae (possibly bifid with teeth very close together) 35-55 μm long, and 1-2 hairs, 85-150 μm long. Anterior ventral setae bifid, upper tooth thinner and shorter than lower, 40-50 μm long; absent in XI. Dorsal and ventral posterior setae all bifid, one per bundle. Male and spermathecal pores paired, posterior in XI and immediately anterior to ventral setae in X, respectively. Esophagus in IX somewhat enlarged and glandular. Male genitalia paired: vas deferens 11-18 μm wide, at least five times as long as atrium entering atrium subapically. Atrium long, cylindrical, curved ventrally, 200 μm long, maximally about 30 μm wide, with thick outer layer of muscle arranged in circles around long axis. Prostate gland attached by short stalk to atrium opposite to, but more ectal than the entrance of vas deferens. Penis sheath somewhat ring-shaped, slightly wider ventrally, 15 μm long, 20 μm wide. Spermathecae paired, each with a slender duct and oblong ampulla; sperm trap indistinct. Sperm arranged as slender spermatozeugmata with rounded tips.

Distribution and Habitat. Southeast North America (east coast of Florida). Associated with coarse, clean or muddy sands; subtidal, 10-11.5 m depth.

Remarks. This species is distinguished from all congeners by the unique combination of: 1) body wall naked; 2) anterior dorsal bundles comprised of 1-2 hairs and 1-2 simple-pointed setae, and posterior dorsal and ventral bundles with one bifid seta, and 3) the unique ring-shaped penis sheath, from which the specific epithet is derived.



(after Ereskus, 1986a) *Tubificoides annulus*: A, anterior, single-pointed, dorsal seta; B, anterior ventral seta; C, posterior seta; D, lateral view of spermatheca and male genitalia in segments X-XI; E, penis sheaths.

***Tubificoides bermudae* Råsmark and Erséus, 1986**

Tubificoides bermudae, Råsmark and Erséus, 1986:612-615, Fig. 1-2.

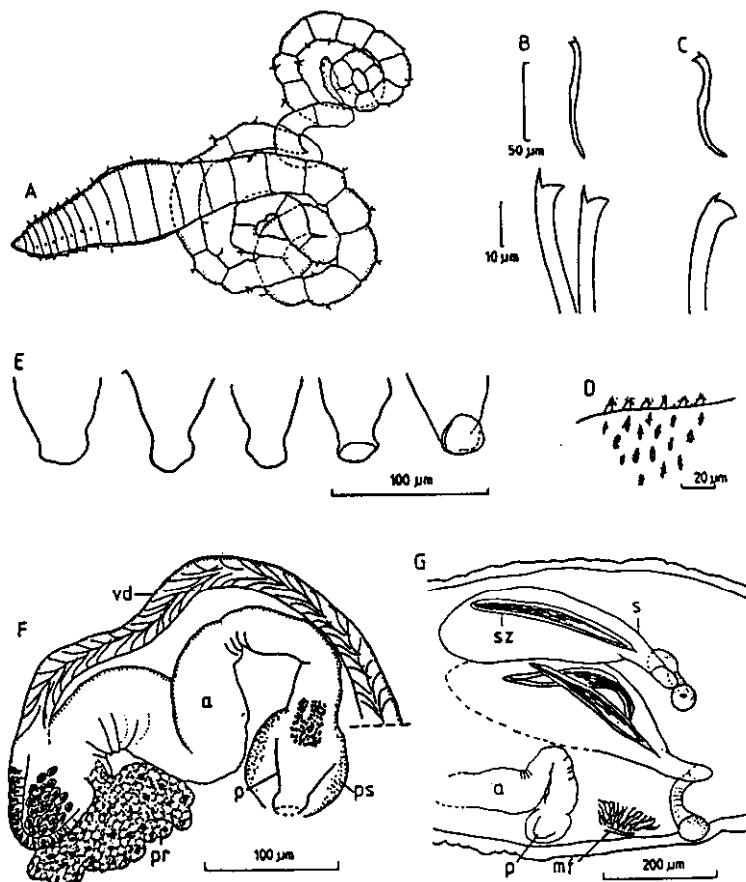
Diagnosis. Length: 6.4-12.3 mm; segments: 50-60. Prostomium retractable. Body wall in postclitellar region with small, leaf-shaped papillae, encrusted with adherent particles. Clitellum extending over XI- $\frac{1}{2}$ XII. All somatic setae bifid, upper tooth thinner and shorter than lower, 50-95 μ m long: 2-3 per bundle anteriorly, one seta per bundle in X-XII. Posterior setae with upper tooth very reduced and lower tooth much stouter, 55-75 μ m long, 1-2 per bundle. Male and spermathecal pores paired, in middle of XI and X, respectively. Esophagus in IX somewhat enlarged. Male genitalia paired: vas deferens 22-26 μ m wide, about as long as atrium, entering atrium subapically. Atrium tubular, about 440 μ m long, 33-62 μ m wide, with muscles arranged in circles around long axis. Prostate gland moderately large, attached by short stalk to atrium opposite to entrance of vas deferens. Penis sheath conical, slightly distended ectally with a terminal opening, 51-61 μ m long, 44-59 μ m wide at base. Spermathecae paired, each with a slender, somewhat coiled, duct with bulbous swelling ectally, and oblong, sac-like ampulla; sperm trap present. Sperm arranged as slender, spindle-shaped spermatozeugmata with one end pointed, the other blunt.

Distribution and Habitat. Caribbean (Bahamas, Belize), southeast North America (southern Florida), Bermuda. Associated with muddy sands; lower intertidal to at least 15 m depth.

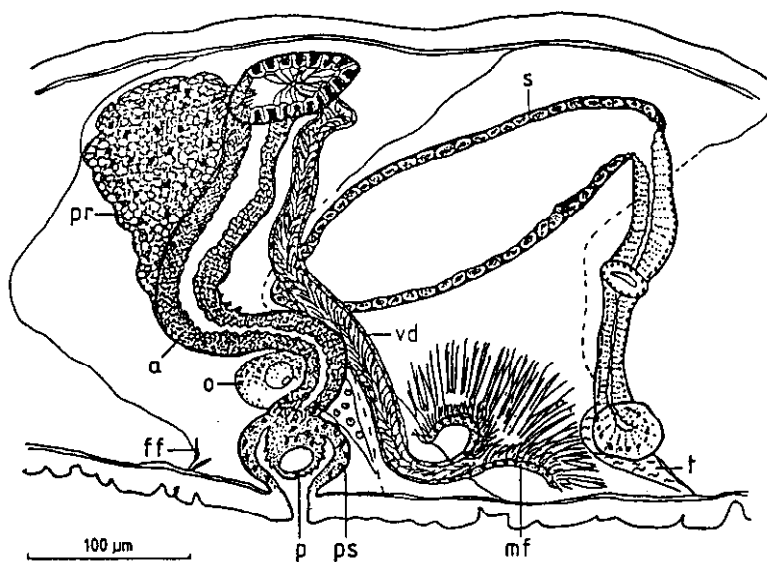
Remarks. This species is distinguished from all congeners by the unique combination of: 1) papillate body wall of postclitellar region; 2) hair setae absent, all setae bifid, 2-3 per bundle anteriorly, and 1-2 per bundle posteriorly, and 3) the conical penis sheath, slightly distended ectally. This species is superficially similar to *Tubificoides wasselli* and *Tectidrilus* spp. which also have papillations, a retractable prostomium, and lack hair setae. However, those taxa are all papillated anteriorly and posteriorly, and they only have one seta maximally per bundle posteriorly (among other differences). *Tubificoides panamensis* Erséus, 1989, is also papillated posteriorly and naked anteriorly, and lacks hairs; however, it has 2-3 setae per bundle posteriorly and the penis sheath is sharply conical without a distended ectal end, and the opening is more laterally displaced.

It is similar to *T. motei*, which also has a conical penis sheath and lacks hairs, but the latter generally has 3-4 setae per bundle anteriorly and postclitellar papillae are lacking.

(after Råsmark and Erséus, 1986) *Tubificoides bermudae*:
 A, general outline of whole-mounted, fixed specimen; B, anterior setae; C, posterior setae; D, body wall papillae; E, penis sheaths from different specimens; F, male duct from a dissected specimen; G, spermathecae and parts of male duct, whole-mounted specimen.



(after Råsmark and Erséus, 1986) *Tubificoides bermudae*: lateral view of male duct and spermatheca; reconstruction from a few longitudinal sections.



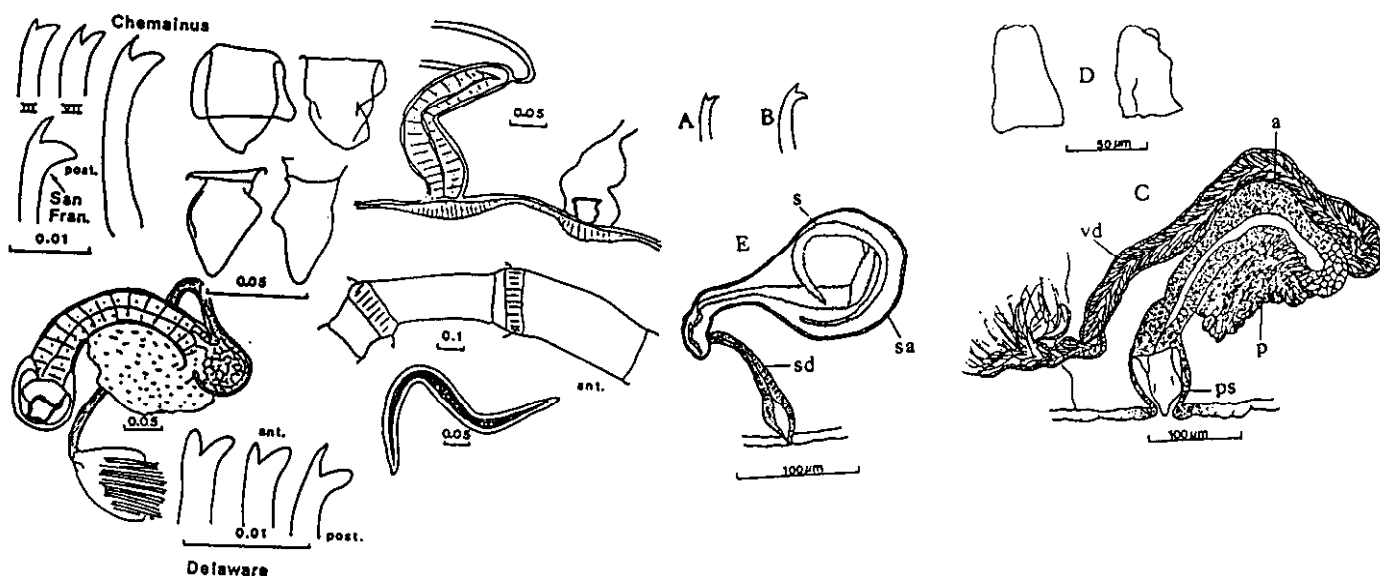
***Tubificoides brownae* Brinkhurst and Baker, 1979**

Tubificoides brownae Brinkhurst and Baker, 1979:1557, Fig. 3.

Diagnosis. Length: 9-20 mm; segments: 38-43. Prostomium not retractable. Body wall without papillae or adherent cuticular particles, but may have ringlike annulations in posterior part of segments. Body somewhat inflated to about XIII-XIV, after which segments become narrower and more elongate. Clitellum extending over IX-½ XI, but indistinct and difficult to determine exact posterior limit. All somatic setae bifid, upper tooth thinner and shorter than lower, 45-60 µm long: 3-5 per bundle anteriorly, one per bundle posteriorly. Male and spermathecal pores paired in XI and X, respectively. Male genitalia paired: vas deferens fairly thick walled, long and convoluted, 13-21 µm wide, about 1½-2 times larger than atrium, entering atrium subapically. Atrium elongate, tubular, bent over ventally, or comma-shaped, 230-430 µm long, 65-90 µm wide maximally. Prostate gland relatively large, attached by short stalk to atrium opposite to entrance of vas deferens. Penis sheath often crumpled in appearance, somewhat conical slightly longer than wide, 70 µm long, 60 µm wide at base. Spermathecae paired, each with an elongate duct with a bulbous swelling ectally, and oblong, sac-like ampulla; conspicuous sperm trap present. Sperm arranged as elongate, spindle-shaped spermatozeugmata.

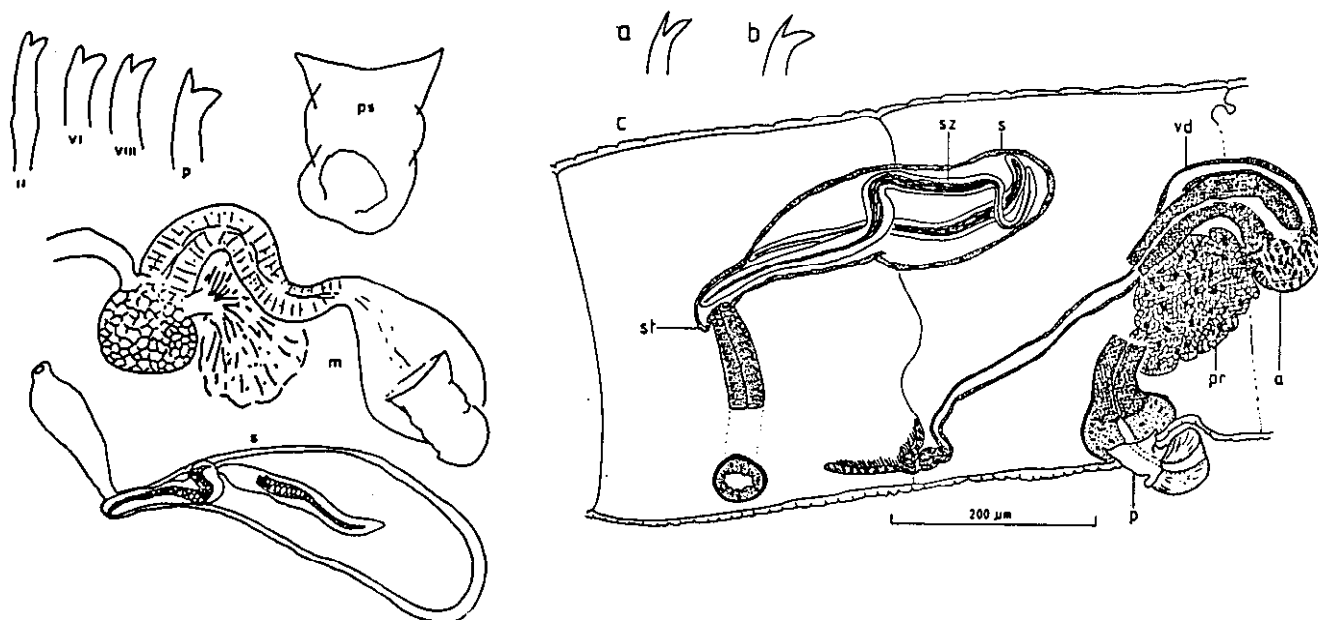
Distribution and Habitat. North America (Pacific coast: British Columbia to California, Atlantic coast: Massachusetts to Florida including Gulf of Mexico), Saudi Arabia, England. Associated with silt and sand; subtidal to at least 25 m depth.

Remarks. This species is distinguished from all congeners by the unique combination of: 1) body wall naked; 2) hair setae absent, all setae bifid, 3-5 per bundle anteriorly and one per bundle posteriorly, and 3) the slightly conical, relatively broad, crumpled penis sheaths, about 1½ times longer than wide. The inflated anterior segments, elongate posterior segments, and the number of setae per bundle in anterior and posterior segments are very consistent among populations and distinguishes this species from all other oligochaetes in the southeast North America, even immature specimens. *Tubificoides brownae* is frequently found with *Tubificoides motei*. Both species are superficially very similar, however, they are readily separated by: 1) the more conical, elongate penis sheaths of *T. motei*, and 2) *T. motei* consistently has two setae per bundle posteriorly as opposed to one per bundle for *T. brownae*. This is one of the most common species of *Tubificoides* in Florida waters.



(after Milligan, 1991) *Tubificoides brownae*: A, anterior seta; B, posterior seta; C, male genitalia; D, penis sheaths; E, spermatheca.

(after Brinkhurst, 1986) *Tubificoides brownae*: setae of specimens from Chemainus, British Columbia, Delaware, and San Francisco; penis sheaths, spermathecal duct with sperm trap showing position relative to male pore and enlarged body wall by pores, elongate postclitellar segments, spermatozeugma, and male duct. Scale bar units, mm.



(after Brinkhurst and Baker, 1979) *Tubificoides brownae* from Delaware: setae, penis sheath, male genitalia, and spermatheca.

(after Bråneus, 1985) *Tubificoides brownae* from Saudi Arabia: a, free-hand drawing of anterior seta; b, free-hand drawing of postclitellar seta; c, lateral view of spermatheca and male duct in segments X-XI.

***Tubificoides heterochaetus* (Michaelsen, 1926)**

Limnodrilus heterochaetus Michaelsen, 1926:22-28, Fig. A.

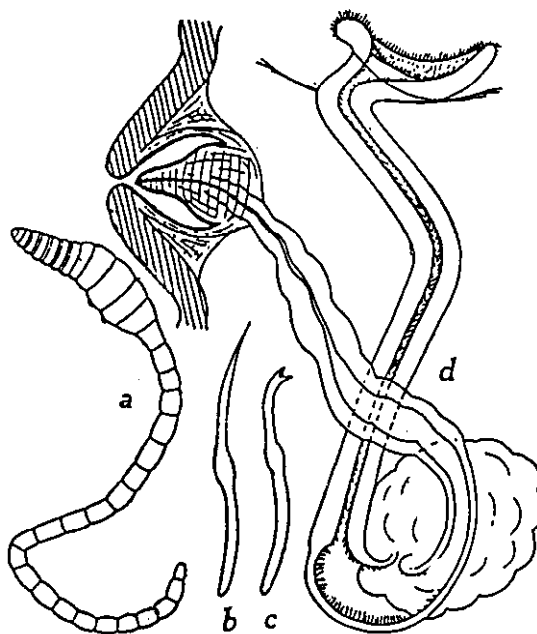
Diagnosis. Length: 7-9 mm; segments: 46. Prostomium not retractable. Body wall naked anteriorly, papillate posteriorly: papillae generally small, sharp-pointed, and not dense. Body inflated anteriorly to about XIII-XV, after which segments become narrower and more elongate. Clitellum extending over $\frac{1}{2}$ X- $\frac{1}{2}$ XII. Anterior somatic setae bifid, upper tooth about as thick and long as lower, 50 μ m long: 2-4 per bundle dorsally, 3-5 per bundle ventrally; generally one seta per ventral bundle in X and absent ventrally in XI; lower tooth very reduced, or setae simple-pointed in posterior dorsal and ventral bundles, 60 μ m long, 1-2(3) per bundle. Male and spermathecal pores paired in XI and X, respectively. Esophagus somewhat enlarged in IX. Male genitalia paired: vas deferens 35.5 μ m wide, about as long as atrium, entering atrium subapically. Atrium elongate, somewhat comma-shaped, about 300 μ m long. Prostate gland small, attached by short stalk to atrium opposite to entrance of vas deferens. Penis sheath indistinct, crumpled, slightly conical, 46 μ m long, 36 μ m wide. Spermathecae paired, each with short duct with bulbous swelling ectally, and an elongate ampulla; sperm trap present. Sperm arranged as slender spermatozeugmata.

Distribution and Habitat. North America (Virginia, North Carolina, Louisiana, Florida (panhandle and east coast to Port St. Lucie), Europe (North Sea, Danube estuary). Associated with silty mud, generally in areas with extreme salinity fluctuations ($\sim 2^{\circ}/\text{oo}$ - $17^{\circ}/\text{oo}$) in a very short time; subtidal to at least 4 m depth.

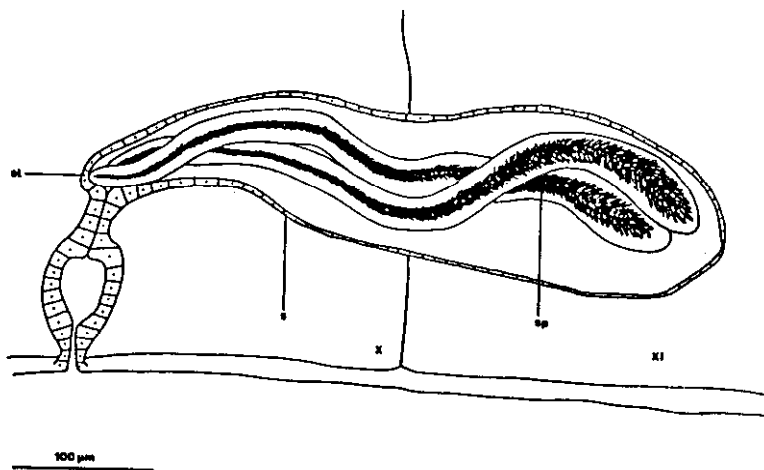
Remarks. This species is distinguished by lacking papillae and hair setae and having the lower tooth reduced in the dorsal and ventral posterior bundles, tending toward a simple-pointed condition. The sharp-pointed papillae of the posterior segments are distinctive. Although the papillae may be lacking (shed), sharp cuticular projections are still evident.

Although *T. heterochaetus* was originally described with a cuticular penis sheath (Michaelsen, 1926), Brinkhurst and Jamieson (1971) and Brinkhurst and Baker (1979) described *T. heterochaetus* as lacking them. Subsequently, Baker (1981) redescribed this species and corrected the oversight. *Tubificoides heterochaetus* is a very common species in the northern Gulf of Mexico and in the vicinity of Chesapeake Bay south to about Port St. Lucie, Florida.

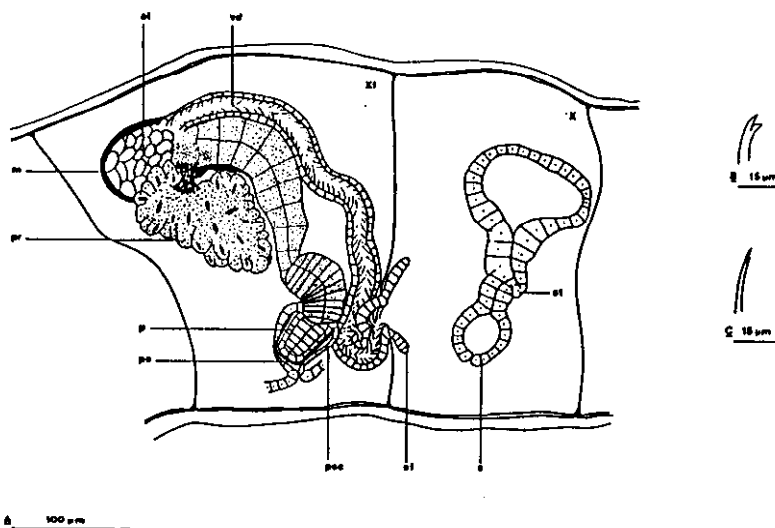
(after Michaelsen, 1926) *Tubificoides heterochaetus*: a, body; b, simple dorsal seta; c, ventral seta; d, male genitalia.



(after Baker, 1981) *Tubificoides heterochaetus*: spermathecae of a North Carolina specimen, sperm trap clearly present, basal portion of spermathecal duct bulbous with distinct lumen.



(after Baker, 1981) *Tubificoides heterochaetus*: A, male duct and spermatheca of lectotype, penis sheath thickened slightly to show form; B, dorsal anterior bifid seta; C, dorsal posterior bifid seta.



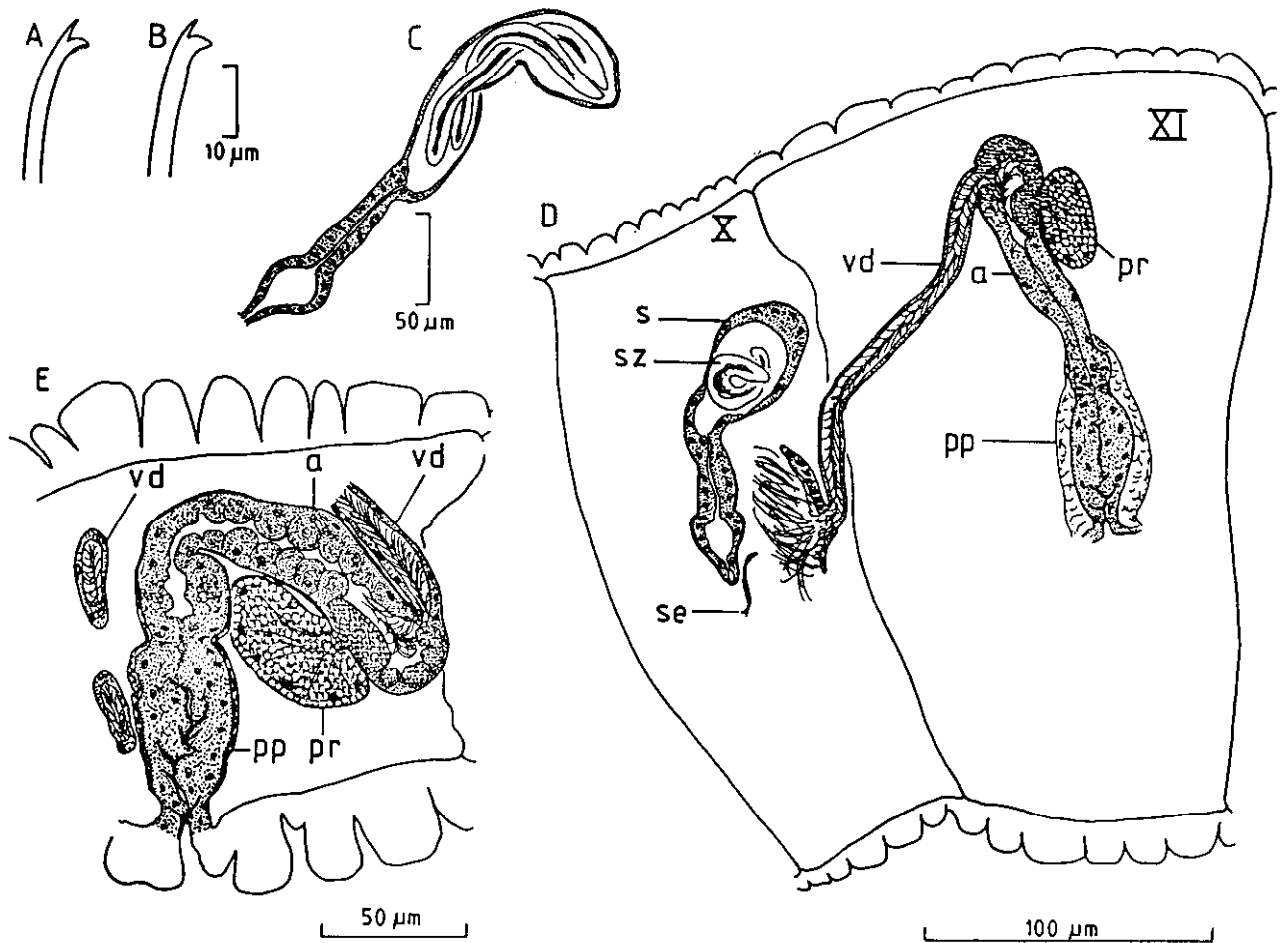
***Tubificoides inops* Erséus, 1989**

Tubificoides inops Erséus, 1989:880-882, Fig. 2.

Diagnosis. Length: 3.1-6.6 mm; segments: 24-45. Body wall naked anteriorly; fine particles aggregated into discrete, pointed papillae in postclitellar segments. Clitellum extending over XI-½ XII. All somatic setae bifid, upper tooth thinner and somewhat longer than lower; lower tooth bearing indistinct subdental ligament in anterior setae, 50-75 µm long: 2-5 per bundle anteriorly; upper tooth reduced posteriorly, 1-3 per bundle; ventral setae of XI sometimes absent. Male and spermathecal pores paired in middle of XI and X, respectively. Esophagus somewhat enlarged in IX. Male genitalia paired: vas deferens thin-walled, 8-13 µm wide, about 1½ times longer than atrium, entering atrium subapically. Atrium erect, curved ventrally, 80-145 µm long, 23-40 µm wide maximally. Prostate gland compact, small with smooth outline, attached by short stalk opposite entrance of vas deferens. True penis absent. Copulatory sac, 35-65 µm long, 33-45 µm wide, folded inner surface lined with cuticle forming eversible (?) pseudopenis. Spermatheca paired, each with elongate duct with a bulbous swelling ectally, and elongate ampulla; sperm trap present. Sperm arranged as slender spermatozeugmata.

Distribution and Habitat. Caribbean (Panama, Barbados), Gulf of Mexico (Mississippi). Associated with muddy silt and sand; subtidal to at least 13 m depth.

Remarks. The lack of true pendant penes with thickened cuticular penis sheaths distinguishes *T. inops* from all other species of *Tubificoides*. No other species of Tubificinae has setae with a subdental ligament.



(after Erséus, 1989) *Tubificoides inops*: A, anterior seta; B, posterior seta; C, spermatheca, specimen from Barbados; D, lateral view of spermatheca and male genitalia in segments X-XI, whole-mounted specimen from Panama; E, lateral section through male genitalia in segment XI, sectioned specimen from Barbados.

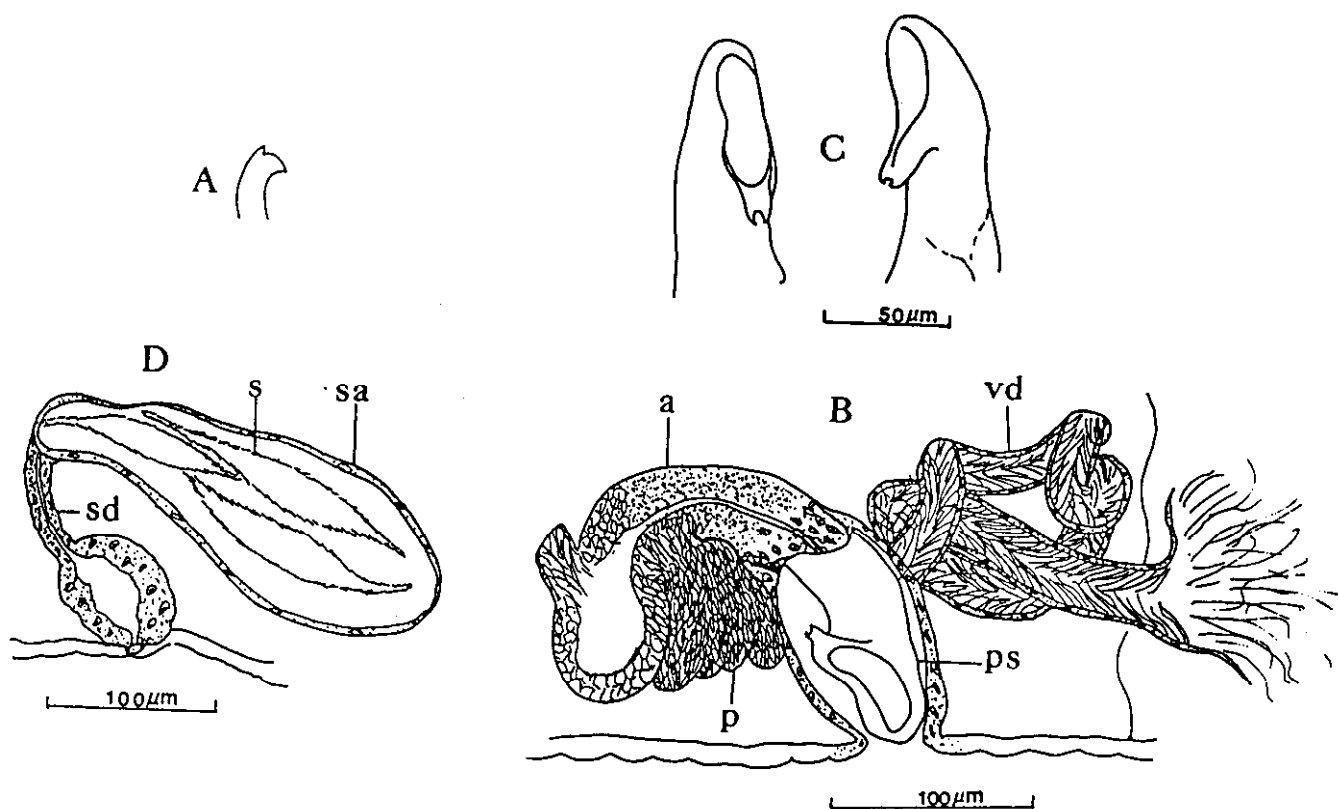
***Tubificoides lunatus* Milligan, 1991**

Tubificoides lunatus Milligan, 1991:341-342, Fig. 2.

Diagnosis. Length: 8.7-9.0 mm; segments: 43-45. Prostomium not retractable. Body wall naked. Clitellum extending over XI-½ XII. All somatic setae bifid, upper tooth shorter and thinner than very broad lower tooth, 25-37 µm long: 3-4 per bundle anteriorly, 1-2 per bundle posteriorly; ventral setae of X and XI absent; dorsal setae absent in XI. Male and spermathecal pores paired in XI and anterior of X, respectively. Male genitalia paired: vas deferens 25-30 µm wide, long and convoluted, about three times longer than atrium, entering atrium subapically. Atrium sharply bent-over ventally, 200 µm long, 60 µm wide maximally. Prostate gland moderate in size, attached by short stalk to atrium opposite to entrance of vas deferens. Penis sheaths cylindrical, each with a large oval disto-lateral opening with a flap-like projection on the proximal margin with a crescent-shaped margin; 100-125 µm long, 25-32 µm wide basally. Spermathecae paired, each with a slender duct with distinct ectal swelling and a large oval ampulla; very distinct sperm trap present. Sperm arranged as spindle-shaped spermatozeugmata.

Distribution and Habitat. Southeast North America (off Tampa Bay, west coast of Florida). Associated with sand and silt; subtidally to 22 m depth.

Remarks. *Tubificoides lunatus* is distinguished from all other *Tubificoides* by: 1) lacking papillae; 2) lacking hair setae, and 3) having a characteristic cone-shaped penis sheath with a crescent-shaped lower margin with a disto-lateral projection. This species is very rare and has only been recovered for deeper (about 22 m) water.



(after Milligan, 1991) *Tubificoides lunatus*: A, somatic seta; B, male genitalia; C, penis sheath; D, spermatheca.

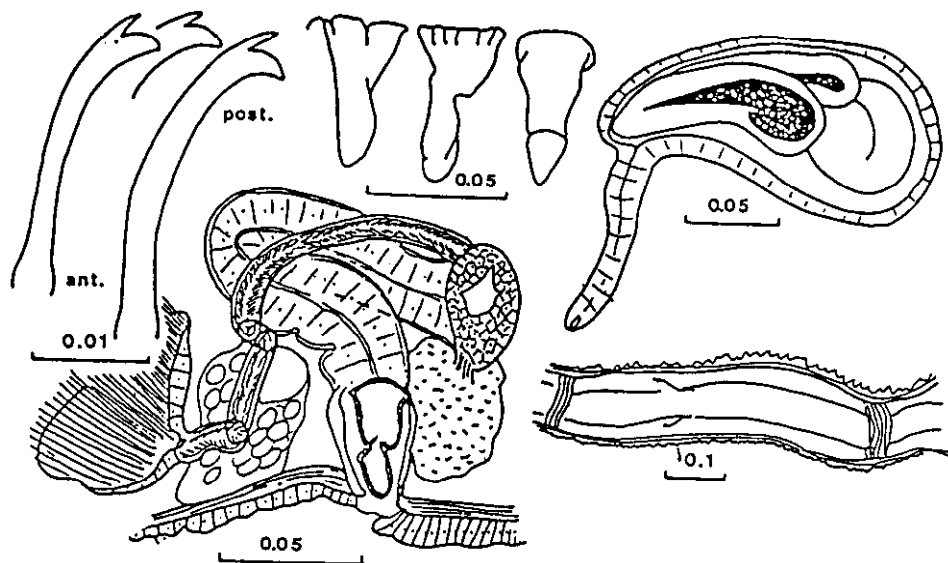
***Tubificoides motei* Brinkhurst, 1986**

Tubificoides motei Brinkhurst, 1986:1,274-1,275, Fig. 3.

Diagnosis. Length: 5-6 mm; segments: to 40. Prostomium not retractable. Body wall naked. Body somewhat inflated to about XIII-XIV, after which segments become narrower and much more elongate. All somatic setae bifid with upper tooth thinner and shorter than lower, 2-4 setae per bundle anteriorly, 2(3) per bundle posteriorly. Male and spermathecal pores paired in XI and laterally in X, respectively. Male genitalia paired: vas deferens 10 μ m wide, about as long as atrium, entering atrium subapically. Atrium elongate and slender, bent-over ventrally, 190 μ m long, 30 μ m wide. Prostate gland of moderate size, attached by short stalk to atrium opposite to entrance of vas deferens. Penis sheaths sharply conical, well defined, each tapering to narrow distal end with oblique opening, 50 μ m long, 26 μ m wide. Spermathecae paired, each with distinct narrow duct without ectal swelling, and oval ampulla; conspicuous sperm trap present. Sperm arranged as fairly broad spermatozeugmata

Distribution and Habitat. North America (British Columbia, east and west coasts of Florida). Associated with sand to at least 35 m depth.

Remarks. This species is characterized by: 1) lack of papillae; 2) lack of hair setae, 2-4 bifid setae anteriorly and, almost without exception, two bifid setae per bundle posteriorly, and 3) a distinctly sharply-conical penis sheath. This species is very similar to *Tubificoides brownae*, with which *T. motei* frequently coexists. However, the latter can be readily discriminated even as immature individuals by the bisetal posterior bundles, as opposed to the unisetal posterior bundles of *T. brownae*.



(after Brinkhurst, 1986) *Tubificoides motet*: setae, penis sheaths, spermatheca with spermatozeugmata, male duct, elongate postclitellar segments with furrowed wall. Scale bar units, mm.

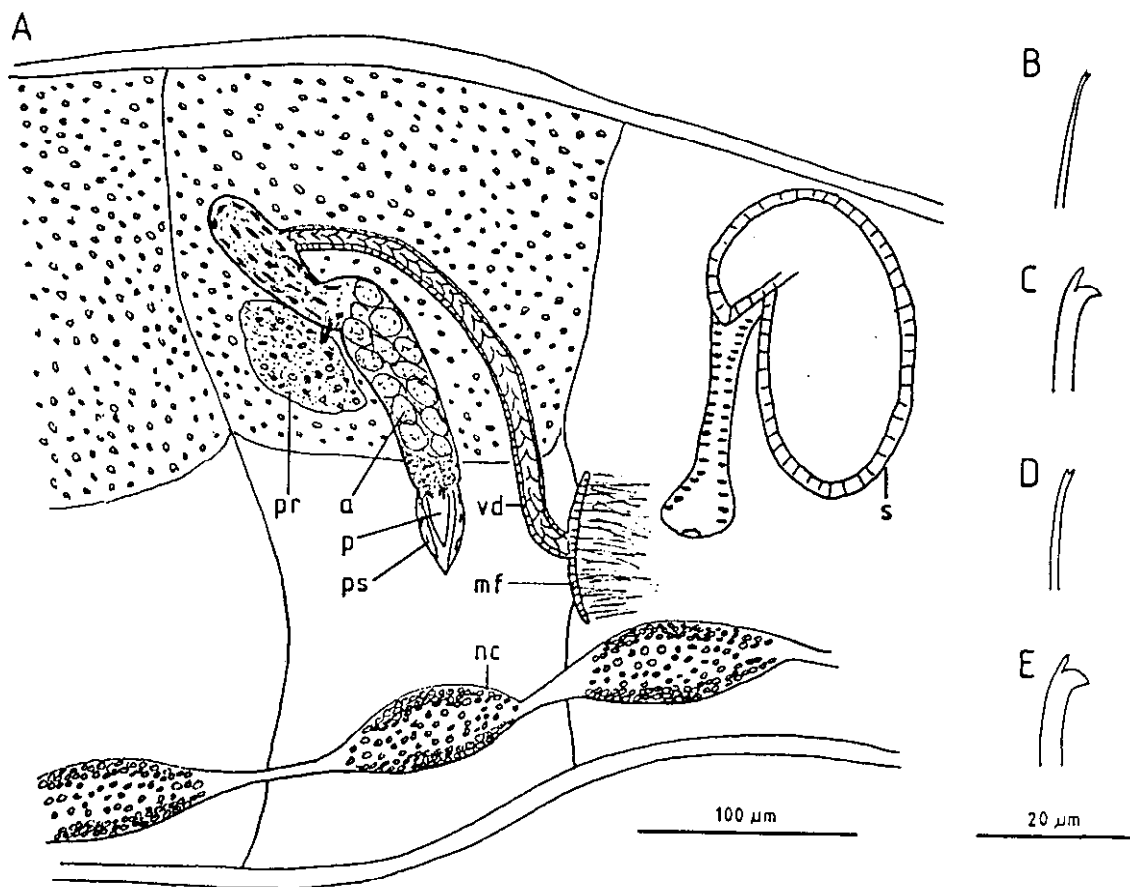
***Tubificoides parviductus* Helgason and Erséus, 1987**

Tubificoides parviductus Helgason and Erséus, 1987:164-165, Fig. 4.

Diagnosis. Length: 3.3-9.0 mm; segments: 30-47. Prostomium not retractable. Body wall naked, however, encrusted with some granular material. Clitellum extending over XI-½ XII. Dorsal bundles with two hair setae, 133-196 µm long, and two bifid setae with very small, subequal, somewhat parallel teeth, which may appear simple-pointed, 62 µm long anteriorly, one hair seta, 60-92 µm long, and one bifid seta, 37-48 µm long, posteriorly. Ventral setae all bifid with upper tooth thinner and shorter than lower, 55-62 µm long, 2-3 per bundle anteriorly, 34-48 µm long, two per bundle posteriorly; ventral setae of XI absent. Male and spermathecal pores in middle of XI and immediately anterior to ventral setae in X, respectively. Esophagus in IX, somewhat enlarged. Male genitalia paired: vas deferens thin-walled, 9-14 µm wide, about 1-1½ times longer than atrium, entering atrium subapically. Atrium short and cylindrical, 147-240 µm long, 17-40 µm wide, fairly uniform in width. Prostate gland small, attached by short stalk to atrium opposite to, but more ectally located to entrance of vas deferens. Penis sheaths thin-walled, variable in shape, conical to thimble-shaped, 32-43 µm long, 13-23 µm wide. Spermathecae paired, each with elongate duct with a hollow swelling ectally, and elongate, wide ampulla; sperm trap present. Sperm arranged in stout spermatzeugmata, one end somewhat truncate, the other pointed.

Distribution and Habitat. Caribbean (Barbados), Bermuda, southeast North America (southwest coast of Florida). Associated with coarse, more or less, muddy sand; subtidal to at least 21 m depth.

Remarks. The distinctive dorsal setae with very small teeth and lack of hair setae differentiates this taxon from other species of *Tubificoides* in Florida. Additionally, the very small atrium of fairly uniform width, from which the specific epithet is derived, and the prostate gland located ectally to the entrance of the vas deferens, also serve to discriminate *T. parviductus* from other *Tubificoides*. Other than the small size, the configuration of the penis sheath is not distinctive.



(after Helgason and Bråhus, 1987) *Tubificoides parviductus*: A, lateral-to-ventral view of male duct and spermatheca; B, anterior dorsal bifid seta; C, anterior ventral seta; D, posterior dorsal bifid seta; E, posterior ventral seta.

***Tubificoides pollex* Milligan, 1991**

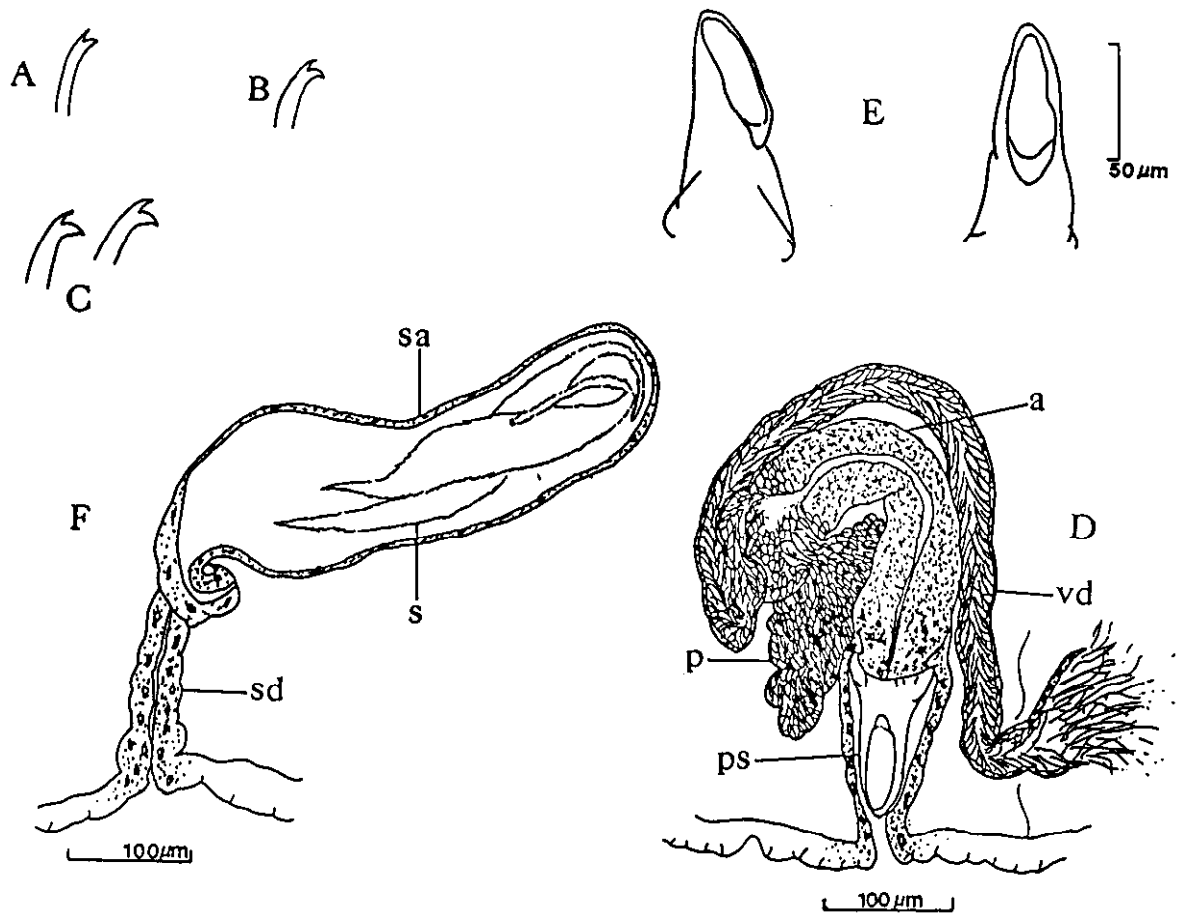
Tubificoides pollex Milligan, 1991:340-341, Fig. 1.

Diagnosis. Length: 4.7-7.8 mm; segments: 28-48. Prostomium not retractable. Body wall naked anteriorly covered with very fine, pointed papillae posteriorly. Anterior segments compressed, posterior segments narrower and more elongate. Clitellum extending over X-XII. Dorsal bundles anteriorly with 1-2 hair setae, 92-112 μm long, to VIII, and 2-3 bifid setae with upper tooth thinner but as long as lower, 50-68 μm long; posteriorly hair setae absent, bifid setae with upper tooth much thinner and shorter than lower, 70 μm long, 2-3 per bundle. Ventral setae all bifid, upper tooth thinner and shorter than lower, 53-73 μm long throughout, 3-4 per bundle anteriorly, two per bundle posteriorly; ventral setae of XI absent. Male and spermathecal pores in middle of XI, and anterior and lateral to ventral setae of X, respectively. Esophagus in IX somewhat enlarged. Male genitalia paired: vas deferens thin-walled, convoluted entally, 20-25 μm wide, about two times longer than atrium, entering atrium subapically. Atrium elongate, bent-over entally, comma-shaped, 210-237 μm long, 50-62 μm wide maximally. Penis sheaths thumb-shaped, each with large, lateral opening bearing flap-like projection on the proximal margin, 83-100 μm long, 38-45 μm wide basally. Spermathecae paired, each with a narrow, elongate duct with bulbous vestibule ectally, and large, oval ampulla. Sperm arranged in vermiform spermatozeugmata; sperm trap not well developed.

Distribution and Habitat. Southeast North America (west-central coast of Florida). Associated with silty, calcareous sand; subtidal to 25 m depth.

Remarks. The thumb-shaped penis sheath, for which this species is named, with a large lateral opening bearing a proximal flap-like projection characterizes this species from all other *Tubificoides*. Only one congener, *T. bakeri* Brinkhurst, 1985, reported only from west coast of North America, shares a similar setal distribution: hairs and bifids anteriorly and only bifids posteriorly. However, *T. bakeri* lacks posterior papillae and the penis sheaths are much smaller without a lateral projections.

The penis sheath of *Tubificoides lunatus* is similar to that of *T. pollex*, but the lateral projection in the former has a crescent-shaped lower margin, and hair setae are absent. *T. lunatus* is very rare and has only been recovered from deeper (about 25 m) water.



(after Milligan, 1991) *Tubificoides pollex*: A, anterior dorsal bifid setae; B, posterior dorsal setae; C, anterior ventral setae; D, male genitalia; E, penis sheaths; F, spermatheca.

***Tubificoides wasselli* Brinkhurst and Baker, 1979**

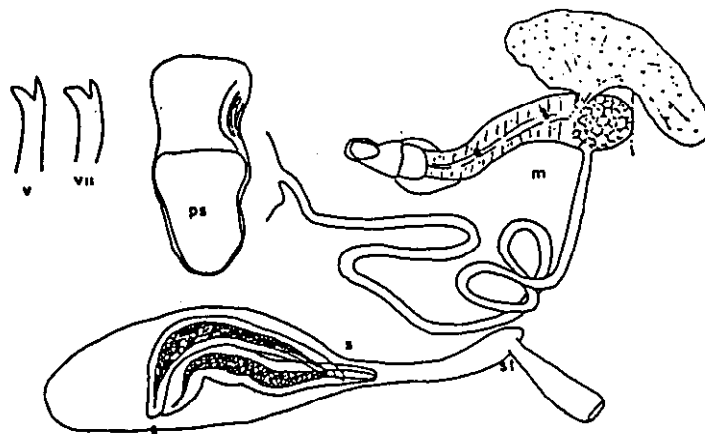
Tubificoides wasselli Brinkhurst and Baker, 1979:1556, Fig. 1.

Diagnosis. Length: 8-11 mm; segments: about 51. Prostomium retractable. Body wall densely covered with large papillae: posterior segments elongate. All somatic setae bifid with upper tooth thinner and shorter than lower, 45-55 μm long, two per bundle to VI-VIII, thereafter upper tooth becomes very reduced and lower tooth broader and recurved, one per bundle. Ventral setae may be absent in X and XI; dorsal setae may also be absent in X. Male and spermathecal pores paired in XI and X, respectively. Male genitalia paired: vas deferens thin-walled, 15 μm wide, about 2-3(5) times longer than atrium, entering atrium subapically. Atrium comma-shaped, 170-380 μm long, about 29 μm wide maximally. Prostate gland large, attached by short stalk to atrium opposite to entrance of vas deferens. Penis sheaths conical, thimble-shaped, 40-50 μm long, 30-40 μm wide basally, each with shovel-shaped disto-lateral opening. Spermathecae paired, each with elongate duct and long oval ampulla; sperm trap distinct. Sperm arranged as elongate spermatzeugmata.

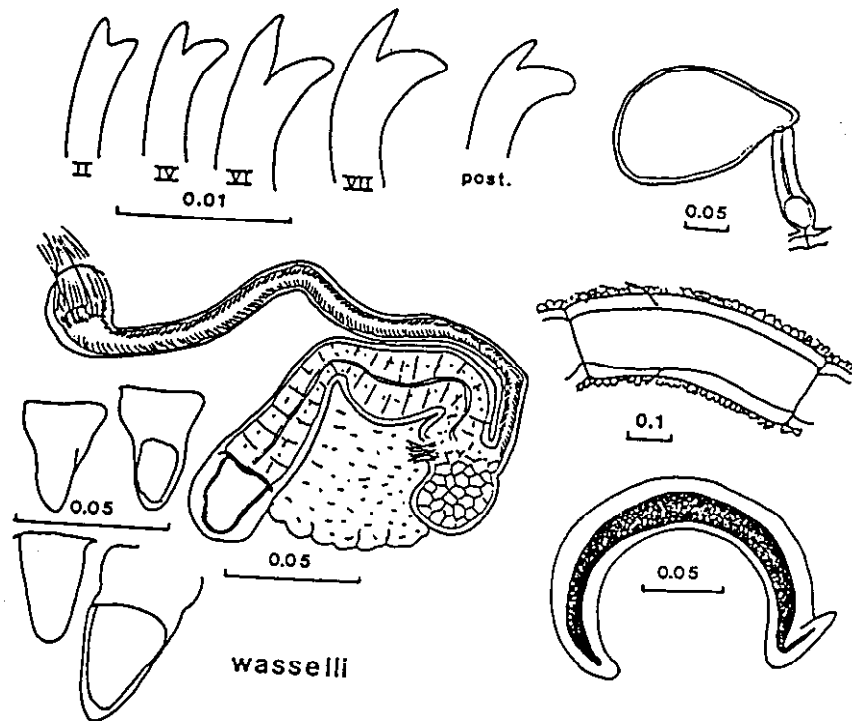
Distribution and Habitat. North America (Atlantic Coast: Delaware to Florida, Gulf of Mexico; Pacific Coast: British Columbia to California), Puerto Rico. Associated with sand and mud in estuaries and nearshore from intertidal to 60 m depth.

Remarks. This species is readily distinguished by the dense papillation, retractable head, lack of hair setae and two bifid setae per bundle to about VII or VIII and one thereafter. Superficially, this species is identical with *Tectidrilus gabriellae* and *T. squalidus*. It is distinguished, however, by its lack of esophageal diverticula in IX and the presence of cuticular penis sheaths. Additionally, the sperm in the ampullae of *T. wasselli* are arranged in very compact, elongate spermatzeugmata, whereas they are random or in loose bundles in *Tectidrilus* spp.

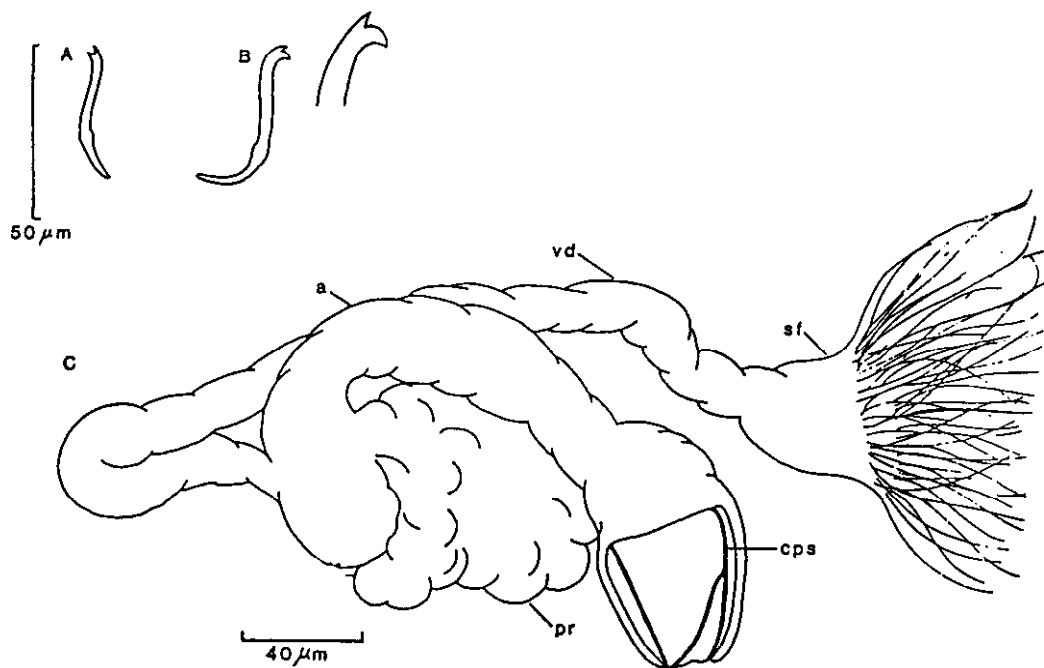
(after Brinkhurst and Baker, 1979) *Tubificoides wasselli*: setae, penis sheath, male genitalia, spermatheca.



(after Brinkhurst, 1986) *Tubificoides wasselli*: setae, spermatheca (unmated), penis sheaths, male duct, elongate papillate postciltellar segment, spermatoneugma. Scale bar units, mm.



(after Milligan, 1987) *Tubificoides wasselli*: A, seta from VII; B, seta from VIII; C, male genitalia.



LITERATURE CITED

- Baker, H.R. 1981. A re-description of *Tubificoides heterochaetus* (Michaelsen) (Oligochaeta, Tubificidae). *Proc. Biol. Soc. Wash.* 94:564-568.
- Baker, H.R. 1982. Two new Phallodriline genera of marine Oligochaeta (Annelida: Tubificidae) from the Pacific Northeast. *Can. J. Zool.* 60:2487-2500.
- Baker, H.R. 1983. New species of *Bathydrilus* Cook (Oligochaeta: Tubificidae) from British Columbia. *Can. J. Zool.* 61:2162-2167.
- Baker, H.R. and C. Erséus. 1982. A new species of *Bacescuella* Hrabe (Oligochaeta, Tubificidae) from the Pacific coast of Canada. *Can. J. Zool.* 60:1951-1954.
- Baker, H.R. and C. Erséus. 1979. *Peosidrilus biprostatus* n. g., n. sp., a marine tubificid (Oligochaeta) from the eastern United States. *Proc. Biol. Soc. Wash.* 92:505-509.
- Baker, H.R. and R.O. Brinkhurst. 1981. A revision of the genus *Monopylephorus* and redefinition of the subfamilies Rhyacodrilinae and Branchiurinae (Tubificidae: Oligochaeta). *Can. J. Zool.* 59:939-965.
- Benham, W.B. 1915. Oligochaeta from the Kermadec Island. *Trans. Proc. N.Z. Inst.* 47:174-195.
- Brinkhurst, R.O. 1963. Notes on the brackish water and marine species of Tubificidae (Annelida, Oligochaeta). *J. Mar. Biol. Assoc. UK.* 43:709-715.
- Brinkhurst, R.O. 1966. A contribution to the systematics of the marine Tubificidae (Annelida, Oligochaeta). *Biol. Bull.* 130:297-303.
- Brinkhurst, R.O. 1985. A further contribution to the taxonomy of the genus *Tubificoides* Lastockin (Oligochaeta: Tubificidae). *Can. J. Zool.* 63:400-410.
- Brinkhurst, R.O. 1986. Taxonomy of the genus *Tubificoides* Lastockin (Oligochaeta, Tubificidae): species with bifid setae. *Can. J. Zool.* 64:1270-1279.
- Brinkhurst, R.O. and B.G.M. Jamieson (eds.). 1971. *Aquatic Oligochaeta of the World*. Oliver & Boyd, Edinburgh, Scotland. 860 p.
- Brinkhurst, R.O. and H.R. Baker. 1979. A review of the marine Tubificidae (Oligochaeta) of North America. *Can. J. Zool.* 67:1553-1569.

- Cook, D.G. 1969. The Tubificidae (Annelida, Oligochaeta) of Cape Cod Bay with a taxonomic revision of the genera *Phallodrilus* Pierantoni, 1902, *Limnodriloides* Pierantoni, 1903, and *Spiridion* Knöllner, 1935. *Biol. Bull.* 136:9-27.
- Cook, D.G. 1970. Bathyal and abyssal Tubificidae (Annelida, Oligochaeta) from the Gay Head-Bermuda transect, with descriptions of new genera and species. *Deep Sea Res.* 17:973-981.
- Cook, D.G. 1974. The systematics and distribution of marine Tubificidae (Annelida: Oligochaeta) in the Bahia de San Quintin, Baja California, with descriptions of five new species. *Bull. S. Calif. Acad. Sci.* 73:126-140.
- Davis, D. 1985. The Oligochaeta of Georges Bank (NW Atlantic), with descriptions of four new species. *Proc. Biol. Soc. Wash.* 98:158-176.
- Ditlevsen, A. 1904. Studien an Oligochaeten. *Z. Wiss. Zool.* 77:398-480.
- Erséus, C. 1975a. *Peloscolex amplivasatus* sp.n. and *Macroseta rarisetis* gen. et sp.n. (Oligochaeta, Tubificidae) from the west coast of Norway. *Sarsia.* 58:1-8.
- Erséus, C. 1975b. On the systematic position of *Rhyacodrilus prostatus* Knöllner (Oligochaeta, Tubificidae). *Zool. Scr.* 4:33-35.
- Erséus, C. 1976. Marine subtidal Tubificidae and Enchytraeidae (Oligochaeta) of the Bergen area, western Norway. *Sarsia.* 62:25-48.
- Erséus, C. 1978a. New species of *Adelodrilus* and a revision of the genera *Adelodrilus* and *Adelodriloides* (Oligochaeta, Tubificidae). *Sarsia.* 63:135-144.
- Erséus, C. 1978b. Two new species of the little-known genus *Bacescuella* Hrabe (Oligochaeta, Tubificidae) from the North Atlantic. *Zool. Scr.* 7:263-267.
- Erséus, C. 1979a. *Coralliodrilus leviatriatus* gen. et sp.n., a marine tubificid (Oligochaeta) from Bermuda. *Sarsia.* 64:179-182.
- Erséus, C. 1979b. Taxonomic revision of the marine genus *Phallodrilus* Pierantoni (Oligochaeta, Tubificidae), with descriptions of thirteen new species. *Zool. Scr.* 8:187-208.
- Erséus, C. 1979c. *Uniporodrilus granulothecatus* n. g., n. sp., a marine tubificid (Oligochaeta) from eastern United States. *Trans. Amer. Microsc. Soc.* 98:414-418.

- Erséus, C. 1979d. *Bermudrilus peniatus* n.g., n. sp. (Oligochaeta, Tubificidae) and two new species of *Adelodrilus* from the Northwest Atlantic. *Trans. Amer. Microsc. Soc.* 98:418-427.
- Erséus, C. 1979e. *Inanidrilus bulbosus* gen. et sp.n., a new marine tubificid (Oligochaeta) from Florida (USA). *Zool. Scr.* 8:209-210.
- Erséus, C. 1979f. Taxonomic revision of the marine genera *Bathydrilus* Cook and *Macroseta* Erséus (Oligochaeta, Tubificidae), with descriptions of six new species and subspecies. *Zool. Scr.* 8:139-151.
- Erséus, C. 1980. Taxonomic studies on the marine genera *Aktedrilus* Knöllner and *Bacescuella* Hrabě (Oligochaeta, Tubificidae), with descriptions of seven new species. *Zool. Scr.* 9:97-111.
- Erséus, C. 1981a. Taxonomic revision of the marine genus *Heterodrilus* Pierantoni (Oligochaeta, Tubificidae). *Zool. Scr.* 10:111-132.
- Erséus, C. 1981b. Taxonomic studies of Phallophila (Oligochaeta, Tubificidae) from the Great Barrier Reef and the Comoro Islands, with descriptions of ten new species and one new genus. *Zool. Scr.* 10:15-31.
- Erséus, C. 1981c. Taxonomy of the marine genus *Thalassodrilus* (Oligochaeta, Tubificidae). *Trans. Amer. Microsc. Soc.* 100:333-344.
- Erséus, C. 1982a. Taxonomic revision of the marine genus *Limnodriloides* (Oligochaeta, Tubificidae). *Verh. Naturwiss. Ver. Hamburg (NF)*. 25:207-277.
- Erséus, C. 1982b. Revision of the marine genus *Smithsonidrilus* Brinkhurst (Oligochaeta, Tubificidae). *Sarsia*. 67:47-54.
- Erséus, C. 1982c. *Parakakatio longiprostatum* gen. et sp.n., a new marine tubificid (Oligochaeta) from Florida, U.S.A. *Zool. Scr.* 11:195-197.
- Erséus, C. 1983a. *Duridrilus tardus* gen. et sp.n., a marine tubificid (Oligochaeta) from Bermuda and Barbados. *Sarsia*. 68:29-32.
- Erséus, C. 1983b. Taxonomic studies of the marine genus *Marcusaedrilus* Righi and Kanner (Oligochaeta, Tubificidae), with descriptions of seven new species from the Caribbean area and Australia. *Zool. Scr.* 12:25-36.
- Erséus, C. 1983c. New records of *Adelodrilus* (Oligochaeta, Tubificidae), with descriptions of two new species from the Northwest Atlantic. *Hydrobiologia*. 106:73-83.

- Erséus, C. 1984a. The marine Tubificidae (Oligochaeta) of Hong Kong and southern China. *Asian Mar. Biol.* 1:135-175.
- Erséus, C. 1984b. Taxonomy of some species of *Phallodrilus* (Oligochaeta: Tubificidae) from the Northwest Atlantic, with description of four new species. *Proc. Biol. Soc. Wash.* 97:812-826.
- Erséus, C. 1984c. Taxonomy and phylogeny of the gutless Phallodrilinae (Oligochaeta, Tubificidae), with description of one new genus and twenty-two new species. *Zool. Scr.* 13:239-272.
- Erséus, C. 1984d. A record of *Bermudrilus peniatus* (Oligochaeta: Tubificidae) from the Gulf of Mexico. *Gulf. Res. Rep.* 7:381.
- Erséus, C. 1985. Annelida of Saudi Arabia. Marine Tubificidae (Oligochaeta) of the Arabian Gulf coast of Saudi Arabia. *Fauna Saudi Arabia.* 6:130-154.
- Erséus, C. 1986. Marine Tubificidae (Oligochaeta) at Hutchinson Island, Florida. *Proc. Biol. Soc. Wash.* 99:286-315.
- Erséus, C. 1987a. Taxonomic revision of the marine interstitial genus *Aktedrilus* (Oligochaeta, Tubificidae), with description of three new species. *Stygologia.* 3:107-124.
- Erséus, C. 1987b. Records of *Limnodriloides* (Oligochaeta, Tubificidae) from Venezuela. *Proc. Biol. Soc. Wash.* 100:272-274.
- Erséus, C. 1987c. Marine Limnodriloidinae (Oligochaeta, Tubificidae) from Italy, with descriptions of two new species. *Boll. Zool.* 54:159-164.
- Erséus, C. 1988. Taxonomic revision of the *Phallodrilus rectisetosus* complex (Oligochaeta: Tubificidae). *Proc. Biol. Soc. Wash.* 101:784-793.
- Erséus, C. 1989. Four new west Atlantic species of *Tubificoides* (Oligochaeta, Tubificidae). *Pro. Biol. Soc. Wash.* 102:878-886.
- Erséus, C. 1990a. 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*. *Zool. Scr.* 19:243-303.
- Erséus, C. 1990b. The marine Tubificidae and Naididae (Oligochaeta) of southwestern Australia. p. 43-88. In: *Proceedings of the Third International marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia*

- (eds. F.E. Wells, D.I. Walker, H. Kirkman, and R. Lethbridge). Vol. 1. Western Australian Museum, Perth, Australia.
- Erséus, C. 1990c. Marine Oligochaeta of Hong Kong. p. 259-335. In: *Proceedings of the Second International Marine Biological Workshop: The marine Flora and fauna of Hong Kong and Southern China*, Hong Kong, 1986 (ed., B. Morton). Vol. 1. Hong Kong University Press, Hong Kong.
- Erséus, C. 1991. Two new species and a phylogenetic analysis of the genus *Tectidrilus* (Oligochaeta, Tubificidae). *Zool. Scr.* 20:333-338.
- Erséus, C. 1992a. A generic revision of the Phallodrilinae (Oligochaeta, Tubificidae). *Zool. Scr.* 21:5-48.
- Erséus, C. 1992b. Hong Kong's marine Oligochaeta: a supplement. p. 157-180. In: *The Marine Flora and Fauna of Hong Kong and Southern China III*. Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong. April 11-29, 1989 (ed., B. Morton). Hong Kong University Press, Hong Kong.
- Erséus, C. 1993a. The marine Tubificidae (Oligochaeta) of Rottnest Island, Western Australia. In: *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia*. (eds., F.E. Wells, D.I. Walker, H. Kirkman, and R. Lethbridge). Western Australian Museum, Perth, Australia.
- Erséus, C. 1993b. A new marine species of *Smithsonidrilus* (Oligochaeta: Tubificidae) from the Florida Keys. *Proc. Biol. Soc. Wash.* 106(3):587-590.
- Erséus, C. In press. The marine Tubificidae (Oligochaeta) of Darwin Harbour, Northern Territory, Australia, with descriptions of fifteen new species. Sixth International Biological Workshop. *The Marine Flora and Fauna of Darwin Harbour, Northern Territory, Australia*.
- Erséus, C. and B.G.M. Jamieson. 1981. Two new genera of marine Tubificidae (Oligochaeta) from Australia's Great Barrier Reef. *Zool. Scr.* 10:105-110.
- Erséus, C. and D. Davis. 1989. The marine Tubificidae (Oligochaeta) of Hawaii. *Asian Mar. Biol.* 6:73-100.
- Erséus, C. and H.R. Baker. 1982. New species of the gutless marine genus *Inanidrilus* (Oligochaeta, Tubificidae) from the Gulf of Mexico and Barbados. *Can. J. Zool.* 60:3063-3067.

- Erséus, C. and M.R. Milligan. 1994. *Peosidriloides*, a new genus, and new records of *Peosidrilus* (Oligochaeta: Tubificidae) from the United States, with the description of a new species from the Gulf of Mexico. *Proc. Biol. Soc. Wash.* 107(4):634-640.
- Erséus, C. and M.R. Milligan. 1993. A new species of *Uniporodrilus* (Oligochaeta, Tubificidae) from the Gulf of Mexico coast of Florida, and a phylogenetic analysis of the genus. *Proc. Biol. Soc. Wash.* 106:243-250.
- Erséus, C. and M.R. Milligan. 1988. A new *Bathydrius* (Oligochaeta: Tubificidae) from the eastern Gulf of Mexico. *Bull. Mar. Sci.* 42:292-295.
- Erséus, C. and M.R. Milligan. 1992. A new species of *Coralliodrilus* (Oligochaeta: Tubificidae) from the eastern Gulf of Mexico, and a new record of *C. corpulentus* from South Carolina. *Proc. Biol. Soc. Wash.* 105:585-588.
- Erséus, C. and M.S. Loden. 1981. Phallodrilinae (Oligochaeta, Tubificidae) from the east coast of Florida, with description of a new species of *Adelodrilus*. *Proc. Biol. Soc. Wash.* 94:819-825.
- Erséus, C. and Qi Sang. 1985. Two aberrant Tubificidae (Oligochaeta) from Pearl River in the People's Republic of China. *Hydrobiologia.* 127:193-196.
- Finogenova, N.P. 1982. *Ainudrilus oceanicus* - new genus and species of the family Tubificidae (Oligochaeta). *Zool. Zh.* 61:1255-1258.
- Finogenova, N.P. 1986. Six new species of Marine Tubificidae (Oligochaeta) from the continental shelf off Peru. *Zool. Scr.* 115:45-51.
- Finogenova, N.P. and N.M. Shurova. 1980. A new species of the genus *Aktedrilus* (Oligochaeta, Tubificidae) of the littoral zone of the Sea of Japan. p. 65-69. In: *Pribrezhnyi Plankton I Bentos Severnoi Chasti Yaponskogo Morya*. Akademia Nauk SSSR, Valdivostok. [In Russian]
- Giana, N. and P. Rodriguez. 1988. Description de quelques espèces nouvelles de Tubificidae (Oligochaeta) de grottes et de sources karstiques de la peninsule Ibérique. *Stylogia.* 4:121-137.
- Giere, O. 1979. Studies on marine Oligochaeta from Bermuda, with emphasis on new *Phallodrilus* species (Tubificidae). *Cah. Biol. Mar.* 20:301-314.
- Hatai, S. 1898. On *Vermiculus limosus*, a new species of Aquatic Oligochaeta. *Annot. Zool. Jpn.* 2:103-111.

- Helgason, G.V. and C. Erséus. 1987. Three new species of *Tubificoides* (Oligochaeta, Tubificidae) from the Northwest Atlantic and notes on geographic variation in the circumpolar *T. kozloffii*. *Sarsia*. 72:159-169.
- Holmquist, C. 1978. Revision of the genus *Peloscolex* (Oligochaeta, Tubificidae). 1. Morphological and anatomical scrutiny; with discussion on the generic level. *Zool. Scr.* 7:187-208.
- Hrabe, S. 1960. Oligochaeta limicola from the collection of Dr. S. Husmann. *Publ. Fac. Sci. Univ. Brno*. (415):245-277.
- Hrabe, S. 1963. On *Rhyacodrilus lindbergi* n. sp. A new cavernicolous species of the family Tubificidae (Oligochaeta) from Portugal. *Bolm. Soc. Port. Cienc. Nat.* 10:52-56.
- Hrabe, S. 1967. Two new species of the family Tubificidae from the Black Sea, with remarks about various species of the subfamily Tubificidae. *Spisy Prir. Fak. Univ. Brne*. 485:331-356.
- Hrabe, S. 1971a. On new marine Tubificidae of the Adriatic Sea. *Scr. Fac. Sci. Nat. Univ. Brno* (Biol. 3). 1:215-216.
- Hrabe, S. 1971b. A note on the Oligochaeta of the Black Sea. *Vest. Cs. Spol. Zool.* 35:32-34.
- Hrabe, S. 1973. A contribution to the knowledge of marine Oligochaeta, mainly from the Black Sea. *Trav. Mus. Histo. Nat. Gr. Antipa*. 13:27-38.
- Knöllner, F.H. 1935. Ökologische und systematische Untersuchungen über litorale und marine Oligochäten der Kieler Bucht. *Zool. Jb. Syst.* 66:425-512.
- Levinsen, G.M.R. 1884. Systematisk - geografisk Oversight over de nordiske Annulata. Vidensk. Medd. Dan. Naturhist. Foren. Khobenhaven. 4(1883):92-350.
- Loden, M. 1980. A new euryhaline species of *Monopylephorus* (Oligochaeta: Tubificidae) from the southern United States. *Bull. Mar. Sci.* 30:600-603.
- Marcus, E. du Bois-Reymond. 1950. A marine tubificid from Brazil. *Comun. Zool. Mus. Hist. Nat. Montevideo*. 3:1-6.
- Michaelson, W. 1926. Oligochaeten aus dem Ryck bei Greifswald und von benachbarten Meeresgebieten. *Mitt. Hamb. Zool. Mus. Inst.* 42:21-29.

- Milligan, M.R. 1987. Marine Tubificidae (Oligochaeta) from Puerto Rico with descriptions of two new species, *Tubificoides aguadillensis* and *Heterodrilus paucifascis*. *Proc. Biol. Soc. Wash.* 100:480-489.
- Milligan, M.R. 1991. Two new species *Tubificoides* (Oligochaeta, Tubificidae) and new records of *T. brownae* and *T. imajimai* from the Gulf of Mexico and Caribbean, with a redescription of *T. bakeri*. *Zool. Scr.* 20(4):339-345.
- Pierantoni, U. 1902. Due nuovi generi de Oligochaeti marini rinvenuti nel Golfo di Napoli. *Boll. Soc. Nat. Napoli.* 16:113-117.
- Pierantoni, U. 1903. Altri nuovi oligochaeti del Golfo di Napoli (*Limnodriloides* n. gen.). *Boll. Soc. Nat. Napoli.* 17:185-192.
- Råsmark, B. and C. Erséus. 1986. A new species of *Tubificoides* (Oligochaeta: Tubificidae) from Bermuda and Bahamas. *Proc. Biol. Soc. Wash.* 99:612-615.
- Righi, G. and E. Kanner. 1979. Marine Oligochaeta (Tubificidae and Enchytraeidae) from the Caribbean Sea. *Stud. Fauna Curacao.* 58:44-68.
- Verrill, A.E. 1873. Report on the invertebrate animals of Vineyard Sound. *Rep. U.S. Comm. Fish.* 324:622-624.

APPENDIX A

**IDENTIFICATION MANUAL FOR THE FRESHWATER, ESTUARINE,
AND NEAR SHORE MARINE OLIGOCHAETES OF FLORIDA
VOLUME I. SECTIONS I-VII.**

State of Florida
Department of Environmental Protection
Division of Water Facilities
Tallahassee

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**"IDENTIFICATION MANUAL FOR THE
FRESHWATER, ESTUARINE, AND NEAR SHORE
MARINE OLIGOCHAETES OF FLORIDA"**

VOLUME I

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I. INTRODUCTION

Accurate identification of oligochaetes is imperative to any environmental bioassessment project. Oligochaetes generally comprise in excess of 50% of the macroinvertebrate communities in Florida lakes, rivers and streams, and at least 10% of the benthic community in estuaries and near shore coastal areas.

Unfortunately, they have developed a reputation for being a taxonomically difficult group because they must be mounted on microscope slides for examination, and frequently require fully mature individuals for specific determination. While it is true that oligochaetes must be examined under a compound microscope necessitating preparation on microscope slides, the majority of the species in Florida may be identified based on somatic characters. The remainder, generally tubificids and lumbriculids, can be identified based on the associated mature individuals within the community, relating their somatic characters with those of the immature forms.

Both freshwater and marine oligochaetes form an integral component of aquatic communities throughout Florida, largely contributing to the diet of bottom feeding omnivores. Many environmental studies have focussed on the use of freshwater oligochaetes as indicators of trophic conditions. As a result, a great deal of information concerning the taxonomy and ecology of freshwater taxa has been compiled since the first Oligochaetae were formally identified by Linneus in the 18th century. Currently, there are approximately 80 species of freshwater oligochaetes, represented by two major families, Tubificidae and Naididae, recorded from Florida or expected to occur. Less than one-quarter account for the majority of the taxa commonly encountered.

The complexity of the taxonomy and ecology of estuarine and marine oligochaetes has only recently been recognized. In the last two decades, the number of described saltwater tubificids has increased from 40 species known worldwide, to more than 600. More than half have been recorded from the eastern seaboard of North America, with the majority inhabiting the subtropical and tropical waters of the Gulf of Mexico and Caribbean.

Few comprehensive taxonomic treatises have been prepared concerning aquatic oligochaetes. Stephenson (1930) authored one of the earlier major reviews of Oligochaeta, but this was primarily meant as an overview of the zoology of the group, not to be used as a taxonomic reference. More recently, Christina Sperber published the most comprehensive contribution to the taxonomy of Naididae in 1948. Not until Brinkhurst and Jamieson (1971) compiled an all-encompassing treatise on the systematics and taxonomy of aquatic oligochaetes throughout the world could the frustration of non-taxonomists attempting to identify oligochaetes be somewhat alleviated. This monograph provided a broad general base establishing uniformity in nomenclature up to that time.

Since the publication of *Aquatic Oligochaeta of the World* in 1971, the nomenclature and systematics of Oligochaeta have undergone numerous revisions and modifications. In an effort to remain current, Brinkhurst and Wetzel (1984) produced a supplement to the 1971 global review providing an annotated list of freshwater oligochaetes described or revised between 1971 and 1984.

Shortly thereafter, Brinkhurst (1986) published the *Guide to the Freshwater Aquatic Microdile Oligochaetes of North America*. This publication is a necessary supplement to the library of any biologist dealing with freshwater oligochaete taxonomy. However, the more serious student of systematics should make every attempt to obtain a copy of the Brinkhurst and Jamieson (1971) classic for comprehensive background information regarding the biology, morphology and systematics of the aquatic Oligochaeta.

As previously noted, the literature regarding freshwater oligochaetes of North America has been effectively compiled into a single cohesive publication (Brinkhurst, 1986). Albeit a decade old and an update should be considered, the taxonomic and distributional information contained therein is invaluable. However, the novice marine or estuarine biologist is not as fortunate to have the same guidance through the taxonomic labyrinth created by their saltwater cousins. Many regional publications pertaining to marine oligochaete taxonomy have been produced. Brinkhurst was most instrumental in recognizing the potential diversity of marine oligochaetes and wrote numerous publications in the '60s concerning marine Oligochaeta in Great Britain. Brinkhurst in the '60s, '70s, and '80s contributed to the knowledge of the fauna associated with coastal regions of North America (Brinkhurst and Baker, 1979; Brinkhurst, 1985, 1986; Baker and Brinkhurst, 1981). However, up until the early '70s, marine Oligochaeta were considered a relatively insignificant taxonomic component of the benthic community. Cook and Brinkhurst (1973) listed only two species of truly marine Naididae, 21 marine Tubificidae, 13 marine Enchytraeidae, and two megascolecid taxa for a total of 38 marine species listed for the east coast of North America. Since then a taxonomic "Big Bang" has occurred along the eastern seaboard, with approximately 300 species presently described from that region. Dr. C. Erséus of Sweden is primarily responsible for this diversification. Although he has written more than 100 manuscripts regarding the taxonomy of marine oligochaetes, the vast majority are restricted to a single taxonomic entity or isolated geographic region. The most comprehensive publications pertaining to the Florida waters are his works on the fauna of the U. S. barrier reef in Belize (Erséus, 1990), and that on oligochaetes of Hutchinson Island on the east coast of Florida (Erséus, 1986). However, neither of those publications provide taxonomic guides, and are simply checklists with descriptions.

The purpose of this manual is to provide a guide for the non-taxonomist to rapidly identify oligochaetes expected to be encountered throughout Florida waters utilizing, in most cases, the most discriminating readily observable somatic characters. The manual is divided into two volumes. The first volume concentrates on freshwater taxa; whereas, Volume II concerns the estuarine and near shore marine fauna.

The vast majority of oligochaetes inhabiting aquatic ecosystems of Florida will be in one of two families: Naididae or Tubificidae; additionally, two species of Opistocystidae may occasionally occur. Although species of the families Lumbriculidae and Enchytraeidae are frequently encountered in the course of an aquatic investigation, many taxa within those families are not truly aquatic. Sixty-five years ago when oligochaete taxonomy was still in a relative state of infancy, Stephenson (1930) suggested that no single author could do justice to a review of Oligochaeta as a whole, and the taxa were becoming so numerous serious investigators may have more than they can handle concentrating on one family. Brinkhurst (1971) reinforced this opinion a quarter of a century ago, and that was before the more than tenfold increase in the descriptions of marine species.

Unfortunately, the "explosion" of knowledge regarding the taxonomy of this group has resulted in an accumulation of uncompiled species descriptions. Recently, the number of new taxa being described has reached a relatively steady state. The time is now appropriate to produce a cohesive compilation of the literature, collating the taxonomic and ecological information into a single volume. Currently, approximately 80 saltwater species have been recorded from estuaries and near shore coastal regions of Florida. An additional forty taxa, which have been recorded from the Caribbean, can also be expected to be encountered in the tropical waters off southern Florida.

This identification manual will enable environmental specialists saddled with the responsibility of identifying macroinvertebrates to recognize accurately the oligochaete fauna associated with Florida lakes, streams, estuaries and near shore marine waters. This can be accomplished with minimal sample preparation, relying primarily on somatic characters or cuticularized genital structures.

II. ECOLOGY

The diversity of habitats oligochaetes inhabit is immeasurable. Oligochaeta have successfully exploited virtually every habitable niche from submerged caves and the anaerobic sulfur-rich thiobiotic sediments off the coast of Florida to the icefields of Alaska. Most aquatic oligochaetes are free-burrowing deposit feeders, ingesting sediment. Some species, however, lack a mouth, anus and alimentary canal. This small group of phallodriline tubificids inhabit the thiobiotic marine sediments, existing off the metabolic by-products of subcuticular symbiotic bacteria.

Ecology of specific taxa is presented in the text with more detailed information available throughout the literature (Brinkhurst and Jamieson, 1971; Brinkhurst and Cook, 1979; Pfannkuche, 1978; Diaz and Erséus, 1994), but is primarily restricted to the freshwater fauna. Since the vast majority of marine and estuarine species have been described only in the last two decades, and very few ecologists identify them beyond class, detailed ecological requirements are largely unknown. However, recent taxonomic studies by Dr. C. Erséus and me from the Gulf of Mexico, Caribbean and east coast of Florida have provided significant insight regarding the diversity, ecological associations and habitat preferences of the more cosmopolitan taxa. For instance, saltmarshes with silty sediment, and salinities ranging from about 10‰ to 27‰ are generally dominated by the subfamily Limnodriloidinae, with three to four species of Limnodriloidinae frequently co-occurring. Whereas fine coralline sands with a small percentage of silt at depths from two to four meters harbor an extremely diverse community of phallodriline tubificids. In a recent study by Erséus (1986) twenty-five species of Tubificidae were identified from just two adjacent collecting areas in coralline sands just off Hutchinson Island on the east coast of Florida. Diaz and Erséus (1994) have recently correlated environmental relationships with marine species associated with the barrier reef off Belize in the Caribbean. Details regarding specific taxa will be provided in Volume II.

Freshwater families can be more easily be generalized with respect to their individual habitat preferences. Naididae are common in the sediments of streams, ponds and slow moving rivers. Although they coexist with Tubificidae, Naididae occur in highest concentrations where tubificid densities are low. Naidids are commonly associated with aquatic vegetation and in the coarse sediments of fast flowing streams. Many species appear to be herbivorous, grazing on algae, diatoms and plant fragments. However, at least one genus, *Chaetogaster*, is carnivorous. Almost all the species of this family are entirely freshwater inhabitants, although many species can tolerate short periods of saline exposure, only one species in Florida is truly estuarine: *Paranais litoralis*. This worm will frequently establish dense populations in the lower oligo- to meso-saline stretches of estuaries. Many species are capable of swimming, enabling them to enter the water column, enhancing their distributional capabilities and allowing them to colonize submerged substrates. As a result, they are able to rapidly colonize artificial

substrate sampling devices (e.g., Hester-Dendys) commonly utilized for ecological investigations throughout Florida. Naididae primarily reproduce asexually, forming long chains of zooids enabling them to form large populations in a very short time period. A high diversity of naidids is frequently associated with pristine conditions. Many species are easily recognized by their anal gills, proboscis, or ocular pigmentation, and anterior setal distribution and morphology.

Tubificidae are commonly referred to as "sludge worms" because they often form dense mats or writhing balls in the very fine sediments associated with organically polluted waters. The explanation for the extremely high densities of tubificids in organically polluted situations may be correlated to an increase of food and living space created by the exclusion of competitors due to prolonged anaerobic conditions. Providing there is sufficient water flow for the elimination of metabolic wastes, and there is a periodic replenishment of oxygen, population increases may be dramatic in the absence of competitors. Tubificids generally exist in fine sediments such as muds and silts, where they graze on the microflora associated with the sediment they ingest. They less frequently occur in association with naidids where aquatic vegetation is abundant, in the stagnant water of ponds and pools with high algae concentrations.

From middle to lower peninsular Florida, the vast majority of tubificids encountered will be one of four taxa: *Limnodrilus hoffmeisteri*, *Aulodrilus pigueti*, *Haber speciosus*, and *Psammoryctides convolutus*. The last two taxa frequently co-occur inhabiting lotic waters with sediments composed primarily of fine sand with little organics. This is in contrast to the two former species, which are associated with larger rivers and lakes with a mud and silt substrate. However, there may be substantial overlap among the four aforementioned taxa.

The Panhandle of Florida is frequently designated as part of the Carolinian zoogeographic province, harboring temperate communities. As a result, the diversity and species composition of tubificids is more variable than in the West-Indian province associated with lower peninsular Florida.

Enchytraeids are primarily terrestrial, generally comprising less than 1% of the annelid community in aquatic environments. Identification of most taxa requires detailed examination of the internal anatomy. For the most part, this is beyond the scope of non-taxonomists and their presence may be considered incidental in the overall environmental evaluation. Additionally, the lack of recent taxonomic reviews of North American taxa hinders the identification of enchytraeids beyond family level. One notable exception is the *Grania* complex. The setae of *Grania* spp. are of sufficient distinction to separate this marine assemblage from all related taxa. Consequently, until a comprehensive review of the aquatic Enchytraeidae of North America is complete, the extent of their involvement in this manual will be to family level.

Lumbriculidae are normally infrequently encountered, but their large size makes them difficult to overlook. Of the twenty species recorded from North America, the two species occurring in Florida are for the most part restricted to the littoral margins of lakes and rivers where they are associated with detritus, stones and rooted vegetation.

The only other oligochaete family likely to be encountered in Florida waters is Opistocystidae. A single taxon, *Crustipellis tribranchiata* has been reported, but uncommon, throughout Florida. This species has the same habitat requirements of Naididae, with which it is sympatric, existing in shallow, relatively "clean" habitats with some degree of aquatic vegetation. Its distribution throughout Florida may be significantly underestimated because it is frequently confused with other species of Naididae if their posterior end is lacking. A closely related species, *Trieminentia corderoi*, is also included in this manual since I have identified it from various regions from Florida, but is otherwise unknown from North America.

One final note worth mentioning is the systematic placement of Aeolosomatidae. Historically, this family has been included with Oligochaeta. However, aeolosomatids are now generally considered to be Aphanoneura and will not be discussed.

III. COLLECTION AND PREPARATION

Many environmental investigations require amassing a large number of substrate samples in a very short period with the organisms to be sorted from the debris and identified at a later time. The most common method of collecting sediment is with either a grab sampler (*i.e.*, a PONAR or Ekman) or hand core. Epsom salts or $MgCl_2$ may be added to the sample for 15 to 30 minutes to narcotize the organisms. The sediment is then washed through a 0.5 mm or less screen. The residue is then fixed with a 10% formalin solution stained with rose bengal to facilitate separation of the worms from the sediment. After a minimum of 48 to 72 hours, the formalin is decanted off the residue and replaced with 70% ethyl- or isopropyl alcohol. Samples may remain in this condition indefinitely, providing the alcohol level is periodically checked for deterioration. Sorting the worms from the residue is accomplished using a dissecting microscope.

If the purpose of the collection is strictly for finding oligochaetes and quantification is not a factor, an alternate method may be employed: elutriation. For elutriation, a bucket is filled about one-third to one-half full with sediment. The sediment is passed through a 1 cm to 2 cm screen to remove the rocks, coarse gravel, detritus and vegetation. Water is added to the sediment and swirled to suspend the organisms, the supernatant is decanted into a 0.25 mm screen and the resulting organisms rinsed into an appropriately labelled container. The sediment should be elutriated an additional two or three times to ensure removal of the majority of worms from the sediment. Live worms are then sorted from the sediment within 12 hours and fixed in a 10% formalin solution for at least 48 to 72 hours, and transferred to 70% alcohol.

For routinely examining large collections, the fastest method is to mount the worms on microscope slides in Amman's lactophenol. This is a temporary medium composed of phenol (carbolic acid), lactic acid, glycerol and water in a ratio of 1:1:2:1. Two drops of mounting media are placed on each slide. One to five worms (depending on their size) are arranged in a row within each drop, and a cover slip is placed over the worms. Placement of the worms in a single row with their heads pointing in the same direction facilitates identification of large numbers of specimens simply by moving the stage left to right without having to look away from the microscope trying to locate each specimen. Tubificids may be fairly long and have a tendency to coil up upon fixation, frequently obscuring taxonomically important characters. To straighten when mounting, grab one end with the forceps and drag it on the dry part of the slide into the drop of Amman's. This usually removes the kinks. The slides are placed on slide trays, which can be stacked and are available through scientific supply distributors. Metal cookie sheets can be an inexpensive alternative, gluing thin spacers at 2.5 cm intervals to keep the slides separate. After each tray is mounted, examine the slides to ensure there are no air bubbles. If necessary, add a drop of mounting media next to the cover slip. Capillary action will draw the fluid in to eliminate air spaces.

Identification of freshwater material requires examination of setae and/or cuticular structures, such as penis sheaths. For this purpose, chemical maceration of the internal structures facilitates these observations. Gentle heating in a drying oven set at approximately 90°C (or on top of an electric range with burner control set at 3-1/4) for about 15 to 30 minutes, depending on the size of the worms. Since temperature controls vary for each unit, experimentation and continuous examination of the specimens is initially required to prevent melting the worms, leaving only a scattered mass of setae.

If permanent (semi-permanent) mounts are required, Hydramount or CMC-10 may be used. The specimens may be mounted directly into these media from water or alcohol (or Amman's) as described previously for temporary mounts. Both media will also clear the specimens after a day or two.

Identification of marine oligochaetes frequently requires the examination of internal structures. Generally, mount all specimens temporarily in Amman's lactophenol for preliminary examination. Specimens which need to be maintained for reference are carefully removed from the slide, stained in paracarmine stain, destained to the appropriate tint in acidified alcohol, dehydrated through an alcohol series, cleared in terpeneol (xylene works well, but renders the material brittle), and mounted in Canada Balsam.

Dissection of the male genitalia of large specimens such as *Thalassodrilides* is recommended for accurate identification. The dorsum of segments VII through XIII is teased open to expose the spermathecae and male genitalia. The lateral portions of the body wall are teased away, leaving only the ventral section containing the male and female pores and associated genital structures. Care may be taken to then remove the alimentary canal. The dissection may either be accomplished in the final mounting medium or completed in alcohol, dehydrated and mounted in Canada Balsam. Care must be exercised in the latter method to avoid loss of or damage to the specimen.

IV. MORPHOLOGY

Oligochaetes are segmented, bilaterally symmetrical, vermiform organisms. Aquatic oligochaetes are generally much smaller than their terrestrial counterparts. Usually they possess a subterminal anterior mouth and a terminal anus. However, these are absent in two genera of marine tubificids which are common in the coastal waters of Florida (*Olavius* and *Inanidrilus*). Each segment is separated by an "intersegmental groove" and designated by a roman numeral (Fig. 0-1). The first segment (I) is the peristomium immediately posterior to the terminal prostomium which is produced into an elongate proboscis in some genera of naidids and lumbriculids. Additionally, paired purple pigment spots (eyes) may be present in some species of naidids. This segment is always devoid of setae. Generally setae first appear on segment II and are arranged in four discrete bundles, two dorso-lateral and two ventro-lateral. The dorsal bundles of setae of most naidids begin posterior to II. However, since this family reproduces primarily by asexual fission, with the anterior-most segments developing last, confusion frequently results when attempting to identify species based solely on setal placement. Examination of whole communities containing parent specimens alleviates this problem by associating the setal morphology of newly budded individuals with mature specimens examined from the community.

The most obvious character useful in the identification of oligochaetes is setal morphology. First, a discussion of the use of setae v. chaetae is appropriate. A great deal of emphasis has been placed on replacing setae with "chaetae" as the correct term of the hair-like extensions from the body wall to conform with the suffix of the class name. Traditionally, "setae" has been used in reference to these structures for more than a century. Being a traditionalist, and not wishing to introduce more confusion into the preexisting quagmire of taxonomic verbiage, I will use "setae" throughout this manual. At any rate, by whatever term, the reader will know to what is referred.

Setae may be divided into two basic forms: hairs and crotchets (Fig. 0-2, 0-3). Hairs are elongate, slender, terminate in a distally acute point, and lack a nodulus or intermediate swelling along the shaft. However they may have lateral hairs or serrations occasionally appearing hispid. This type of setae is present only in the dorsal bundles and occurs in the majority of Naididae, many of the Tubificidae and the Opistocystidae. Hairs are not present in Lumbriculidae or Enchytraeidae.

Crotchets may be either bifid, with or without intermediate teeth between the two main laterals, or they may be simple, in which case the term crotchet is somewhat of a misnomer. These setae are characteristically stouter, have a characteristically sigmoid configuration and possess a nodulus which is a swelling of the setal shaft at the point of emergence through the body wall. The crotchets of Naididae are usually more slender or, at the risk of sounding chauvinistic, more effeminate than those of tubificids. The dorsal simple "crotchets" of naidids, which are frequently associated with hair setae, are referred to as needle setae, and may be minutely bifid.

Crotchets with intermediate teeth are called pectinate and, in many species, can only be discerned at 1,000x magnification, although with experience pectinate setae may be determined at a lower power by the configuration of the lateral teeth. Pectinate setae are normally restricted to the dorsal bundles and are only found in tubificids and naidids. Except for a few species of Tubificidae, in the genus *Tubificoides*, pectinate setae in marine taxa are rare. The anterior ventral bundles of some tubificids occasionally exhibit small intermediate teeth, however this character appears to exhibit a great deal of intraspecific variation and may be a result of environmental conditions.

Two additional setal variations with respect to their distal termination only occur in marine taxa. Most species of *Heterodrilus* have trifid setae. This is the only genus found in Florida waters possessing this aberration. The other variation pertaining to dorsal crotchets is the presence of a subdental ligament extending from the shaft to the distal end of the lower tooth. This type of aberrant setae is species specific for many taxa in all subfamilies of tubificids, but is most prevalent in the species of Phallodrilinae and absent in all other families.

Modified ventral setae associated with genital pores occur in mature individuals of many taxa. These can be diagnostic characters for many species of Tubificidae, but are of incidental importance in Naididae. The latter family reproduces primarily asexually. Mature individuals are infrequent.

In Tubificidae, modified setae associated with the spermathecal pore, usually on segment X, are called "spermathecal setae" and usually have a characteristic elongate spoon shape. As a general rule, there is only one seta per "bundle". Modified setae associated with the male pore, usually on segment XI, are referred to as "penial setae". These setae exhibit considerable interspecific variation, with generally more than one per bundle, and may be arranged in a fan-shaped configuration.

The reproductive structures are the primary distinguishing characteristic among oligochaete taxa. Oligochaetes are hermaphrodites, possessing both fully developed male and female organs simultaneously within a single mature individual. Although self-fertilization has not definitively been demonstrated, parthenogenic reproduction is suspected in a few taxa lacking spermathecae. Cross fertilization with the exchange of sperm between concopulants is generally the rule. A mucoid cocoon forms around the genital segments with the sperm from the concopulant and the eggs from the individual released into the cocoon, resulting in fertilization which is therefore considered to be external. Sperm may aggregate into loose bundles, compact bundles (spermatozeugmata), or randomly distributed within the spermathecae. The arrangement of sperm is a taxonomically significant character in Tubificidae, particularly the marine Limnodriloidinae. The position of the spermathecal pores may be dorsal, ventral, lateral, anterior or posterior, single or paired, and is also species specific.

The morphology of the spermathecae and male organs are particularly significant in the identification of marine oligochaetes. The spermatheca is generally formed by an ectal vestibule, an intermediate spermathecal duct and an ental spermathecal ampulla where the sperm is stored. The male reproductive structures are formed by an ental sperm funnel leading into a ciliated vas deferens, which empties into an atrium. The atrium customarily has a prostate gland associated with it. This gland may be diffusely attached to the atrium as in the Rhyacodrilinae, broadly attached as in the Limnodriloidinae, or attached by a short stalk as in the Tubificidae. Ectally, the atrium may form an ejaculatory duct terminating simply as a pore, or forming a penis or pseudopenis which may be ensheathed in cuticle, the shape of which is highly diagnostic, particularly in the freshwater *Limnodrilus* and the marine *Tubificoides*. The cuticularized penis sheath is most easily distinguished in cleared specimens. The penis may be withdrawn into a copulatory sac, or it may have copulatory glands, as in *Tectidrilus bori*, associated with it. Although the male organs may be paired, they occasionally unite ectally or discharge through a common bursa. The male pores are always ventral or ventro-lateral in position in Tubificinae.

Three additional somatic characters are significant in the identification of oligochaetes. Papillae may be distributed along the body wall, apparently serve an excretory function, and are occasionally sloughed off. Therefore, care must be exercised using this character. This cuticular ornamentation is only present in tubificids and some species of naidids. A modification of the gut on segment IX characterizes the subfamily Limnodriloidinae. This modification may be in the form of an enlarged gut plexus or having two anterior projecting digitiform processes. The final character having taxonomic significance with reference to this manual is the presence of coelomocytes. These are small to large nucleated cells which float free in the coelomic fluid. They are derived from the chlorogogen tissue associated with the alimentary canal, and presumably aid in the distribution of nutrients throughout the body. Although they are present to some degree in all taxa, they are particularly abundant and conspicuous (albeit very small) in most Rhyacodrilinae, with some species of *Heterodrilus* being notable exceptions.

V. USE OF KEYS

Following is an artificial key enabling the user to utilize the most easily observable characters to separate the taxa. This is only a regional key for taxa which have been reported or may logically be expected to occur in Florida waters. The freshwater taxa are fairly well documented based on the large number of environmental studies conducted by the state and various consulting companies in compliance with state regulations. Estuarine and marine taxa have not been analyzed to the extent of their freshwater counterparts. Even so, the coastal oligochaete fauna of Florida has been investigated more thoroughly in recent years than any state on the eastern seaboard. The diversity is also far greater due to the tropical biogeography, therefore the list of taxa included herein is considered to be fairly comprehensive. This list omits species expected to occur in depths greater than 30 meters, or which have been described only from isolated locations on Caribbean reefs and not expected to be found in Florida waters. When a decision between two taxa is very close, distributional and ecological information may facilitate the choice.

The taxonomic keys in Volume I contain primarily freshwater taxa, but include euryhaline species likely to be encountered in extreme oligohaline environments. Conversely, tolerant freshwater taxa may occur in saline waters.

In many instances specimens are not completely intact, *i.e.*, the majority of setae may be broken off, the posterior end may be lacking or, in the case of naidids, the anterior end may be regenerating, giving a false representation of which segment the dorsal setae first appear. Therefore examination of large populations is frequently necessary for accurate identification. For the most part, the keys in this manual are dichotomous, providing only two choices. The keys in Volume II, estuarine and marine species, may terminate in a "species group" of closely related taxa. Species within each group requires closer scrutiny than the inexperienced biologist is able to provide. In these instances, an illustrated table is provided for comparison of species specific distinguishing characters. In most cases, once a taxon has been determined to fit into a specific group, distributional information will provide insight toward a specific determination.

One final note: Always compare the specimen with the complete diagnosis provided in the text, rather than just relying on "key" characters. The taxonomy of oligochaetes, especially the marine fauna, is a dynamic science. Taxa are continuously being synonymized and split. In fact, the genus *Limnodriloides* is currently being revised by Dr. Erséus and may be split into a number of new genera. This revision is under review and will be published shortly. The user is advised to keep abreast of all current literature.

VI. KEY TO FAMILIES OF FLORIDA MICRODILE OLIGOCHAETES

1. A) Hair setae present in dorsal and ventral bundles. (not included in this key) Class Aphanoneura (Aeolosomatidae)
 B) Hair setae restricted to dorsal bundles, if present. Class Oligochaeta; 2.
2. A) Two sigmoid shaped setae per bundle, generally unidentate, but may be bifid with reduced lower tooth; hair setae absent; proboscis may be present; relatively large worms. (Fig. 35-1) Lumbriculidae
 B) Smaller worms usually more than two setae per bundle, if bundles are bisetal the setae are usually straight or boot-shaped without a nodule (Enchytraeidae in part); (if worms are very elongated, thread-like with a single large sickle-shaped seta per bundle, they are probably groundwater species unlikely to occur in Florida and are not included in this key: *Haplotaxis*). (Fig. 0-2). Hair setae present or absent. 3.
- 3.(2) A) Dorsal bundles composed of 1-2 hairs and 1-2 simple-pointed needles; ventral setae generally bifid; posterior end terminates in three digitiform processes (not gills). (Fig. 1-2) Opistocystidae
 B) If caudal processes present (gills), they are paired, ciliated, and recessed in a terminal branchial fossa; dorsal bundles with or without hairs, needles may be simple-pointed, bifid, pectinate, or palmate. 4.
- 4.(3) A) Setae all simple-pointed, two or more per bundle, straight, sigmoid, or boot-shaped; worms generally small; hairs absent; genital setae absent. (Fig. 0-2) Enchytraeidae
 B) Ventral setae generally bifid, usually more than two per bundle; dorsal bundles may include hairs and needles of various shapes; genital setae may be present. 5.
- 5.(4) A) Dorsal setae generally begin behind II; ventral setae of II-V frequently differentiated from the rest, generally bifid; eyes, proboscis and posterior gills may be present, cuticularized penis sheaths absent. (Fig. 0-1) Naididae

- B) Dorsal setae begin in II, ventral bundles with numerous bifid setae, or occasionally simple setae; genital setae may be present in ventrals of IX, X, or XI; cuticularized penis sheaths may be present in XI; no eyes, no proboscis, no terminal gills. Tubificidae

