

REDEFINITION OF *TENERIDRILUS* HOLMQUIST
(OLIGOCHAETA: TUBIFICIDAE), WITH
DESCRIPTION OF TWO NEW SPECIES
FROM NORTH AMERICA

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Abstract.—The tubificid genus *Teneridrilus* Holmquist, 1985 (subfamily Tubificinae) is redefined. The genus was originally monotypic for the type species, formerly classified as *Ilyodrilus mastix* Brinkhurst, 1978. The genus now includes *Teneridrilus columbiensis* (Brinkhurst & Diaz, 1985), a new combination for *Isochaetides columbiensis*, and two new species. The first of these, *Teneridrilus calvus*, is described by Erséus & Brinkhurst, and the second, *Teneridrilus flexus*, by Erséus & Hiltunen. Synapomorphies for the genus are strongly modified chaetae in II and an enlarged eversible pharynx. The genus is distributed from China to British Columbia, Washington, and California in freshwater near the mouths of large rivers, and in the St. Marys River, which connects Lake Superior with Lakes Michigan and Huron.

An aberrant freshwater tubificid with modified chaetae in segment II and greatly enlarged mouth and pharynx was described as *Ilyodrilus mastix* by Brinkhurst (1978) from the Fraser River in British Columbia, and later recorded by Erséus and Qi (1985) from the Pearl River in China. Holmquist (1985:343), who re-examined the type series, challenged the original generic position: "The species *mastix* with its quite differently built male apparatus, its entire lack of spermathecae, and the peculiarly built head region is not compatible with any of the above species, nor with any of the other members of the '*Ilyodrilus*' complex scrutinized, but holds its own position." She accordingly established a monotypic genus, *Teneridrilus*, for *I. mastix*, an action that was supported by the original author (Brinkhurst, pers. comm., in Erséus & Qi 1985:194).

The male efferent duct of *T. mastix* consists of a narrow vas deferens, a stout atrium bearing a small prostate gland, and a small cone-shaped penis without thickened cuti-

cle (see Holmquist 1985 for details and dimensions). All atrial epithelial cells are of one type, unlike those of the tubificine genus *Tubificoides*. Although clearly a member of the Tubificinae, the species has a simple male apparatus atypical of most species in the subfamily. There are large ovaries but no spermathecae—the latter feature usually attributed to self-fertilizing or parthenogenetic species in the Tubificidae (see Brinkhurst 1986a). Species with these characteristics are commonly classified together with species that have normal reproductive systems in genera defined by phylogenetic principles. These involve recognizing shared apomorphies (synapomorphies) that indicate descent from a common ancestor despite more recent adaptations. *Teneridrilus mastix* was originally found in the tidal freshwater part of the Fraser River, British Columbia. *Tubificoides fraseri* Brinkhurst was described from more seaward sites in the same estuary in more saline water (Brinkhurst 1986b). It, too, is a suspected parthenogen with a simplified reproductive

system (spermathecae lacking), but is recognizable as a true *Tubificoides*. Because such an adaptation is not seen as a generic character, we recognize three additional members of the genus *Teneridrilus* that share the peculiar modified chaetae of II and the enlarged pharynx of the type species but which have more elaborate male reproductive systems than that of *T. mastix*. *Teneridrilus columbiensis* and *T. calvus*, n. sp. are both found in tidal freshwaters in the Pacific Rim, but *T. flexus*, n. sp. is known only from the exit channel from Lake Superior.

Material and Methods

Specimens of *Teneridrilus mastix* and *T. calvus*, n. sp. were found during a study in the Sacramento-San Joaquin Delta in California, and were placed at our disposal by Dr. W. C. Fields, Jr. (Newcastle, California). Specimens of *T. flexus*, n. sp. were collected in St. Marys River, the exit channel from Lake Superior, by one of us (D.W.S.). All specimens were mounted whole in Canada balsam and studied with a light microscope.

The type series of the new species are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Family Tubificidae Subfamily Tubificinae *Teneridrilus* Holmquist, 1985

Definition (emended).—Small tubificids. Prostomium small. Anterior end of worm wide and rather bluntly rounded; pharynx large, eversible, forming a folded diverticulum when withdrawn inside animal. All chaetae of II bifid, but modified: stouter, and with distal tooth thinner and shorter than bifid chaetae of other segments. Hair chaetae present in dorsal bundles (in *T. mastix*) or absent. Modified (grooved) spermathecal chaetae present (in *T. columbiensis*) or absent. Modified penial chaetae absent. Male pores paired in XI. Spermathecal

pores absent (in *T. mastix*) or paired in X. Coelomocytes of the “rhyacodriline-type” absent. Male ducts paired. Vasa deferentia narrow, confined to XI. Atria cylindrical, small, each bearing one small, solid prostate gland (not yet confirmed for *T. flexus*, n. sp.). Penes present, sometimes with thickened cuticular sheath (*T. columbiensis* and *T. calvus*, n. sp.), generally enclosed in muscular sacs. Spermathecae (absent in *T. mastix*) with roundish ampullae and narrow ducts. Sperm as short and broad spermatozeugmata (in *T. columbiensis*), or random, in spermathecae.

Type species.—*Ilyodrilus mastix* Brinkhurst, 1978.

Other species.—*Teneridrilus columbiensis* (Brinkhurst & Diaz, 1985), n. comb., *T. calvus* Erséus & Brinkhurst n. sp., and *T. flexus* Erséus & Hiltunen n. sp.

Remarks.—Monophyly of *Teneridrilus* is indicated by two synapomorphies in the four species of the genus: the large, modified feeding apparatus, and the modified bifid chaetae in segment II. All other features appear homologous to states known also from other Tubificinae. Most of these traits are thus likely to prove to be plesiomorphic and should not be used as a basis for a phylogenetic definition of the genus.

The four species of the genus are all freshwater forms, mostly occurring in riverine habitats.

Teneridrilus mastix (Brinkhurst, 1978)

Ilyodrilus mastix Brinkhurst, 1978:2171–2173, fig. 3.—Erséus & Qi 1985:193–194, fig. 1.

Teneridrilus mastix.—Holmquist 1985:332–334, 336–341, 357–360, figs. 18, 21D–E, 22E, 23K–L, 24P–R, 31A.

New material (studied by, and in collection of, R. O. Brinkhurst).—Several specimens from various sites in the Sacramento-San Joaquin Delta, in fine sediments with slow water flows (collected on several dates since April 1984; W. C. Fields, Jr.).

Remarks.—This species, the type of the genus, is in fact the most atypical member of *Teneridrilus*. Unlike the other three species, it bears both hairs and bifid chaetae in the dorsal bundles. It has very simple penes in penial sacs that are not particularly muscular, and lacks spermathecae.

Teneridrilus mastix is likely to be a reproductive opportunist, not reproducing by normal cross-fertilization.

Distribution and habitat.—British Columbia and California (new record), southern China. Fine sediments of rivers; in freshwater.

Teneridrilus columbiensis
(Brinkhurst and Diaz, 1985),
new combination

Isochaetides columbiensis Brinkhurst & Diaz, 1985:949–952, figs. 1–2.

Remarks.—Originally placed in *Isochaetides* Hrabě, the monophyletic state of which is highly questionable (Brinkhurst 1986a), this species is here transferred to *Teneridrilus* because it has the synapomorphies now recognized for the genus.

Teneridrilus columbiensis is further characterized by lack of hair chaetae, possession of grooved spermathecal chaetae in segment X, and atria appearing as “simple widenings of vasa deferentia, with prostates attached near midpoints” (Brinkhurst and Diaz 1985: 950). Short ejaculatory ducts connect the atria with muscular penial bulbs that bear short, rounded to blunt-ended penis sheaths. The spermathecal ampullae are large and spherical and have short and broad spermatozoegmata.

Distribution and habitat.—Known only from Columbia River, Oregon. Tidal freshwater marsh, muddy sediment.

Teneridrilus calvus Erséus & Brinkhurst,
new species
Fig. 1

Type material.—USNM 123377, holotype, whole-mounted specimen from the

Sacramento-San Joaquin Delta, Sacramento, California, muddy silt and clay (26 February 1987, W. C. Fields, Jr.). USNM 123378–123380, paratypes, 3 whole-mounted specimens from type locality.

Other material.—Several specimens from the type locality, in the collections of R. O. Brinkhurst and C. Erséus.

Etymology.—The epithet “*calvus*” is Latin for “bald, without hair,” and refers to the lack of hair chaetae in this species.

Description.—Holotype 6.9 mm long, but not complete, consisting of the first 29 anterior segments. Paratypes 4.6–5.3 mm long, with 22–33 segments. Width at XI (compressed specimens) 0.21–0.31 mm. Prostomium (Fig. 1A, pro) triangular, small. Body wall with scattered particles on surface. Clitellum extending over XI–XII. Chaetae all bifid, those of II (Fig. 1B) stout, 30–35 μ m long, about 2.5 μ m thick, 2–3 per bundle; with distal tooth distinctly thinner and shorter than proximal. Chaetae of other anteclitellar segments (Fig. 1C) about 50 μ m long, 2.0–2.5 μ m thick, up to 5(6) per bundle, with distal tooth almost as thick as, but longer than, proximal. Postclitellar chaetae up to about 40 μ m long, about 2 μ m thick, 2 per bundle, with teeth about equal in length and thickness. Chaetae absent ventrally in XI. Male pores paired in line with ventral chaetae in XI. Spermathecal pores immediately anterolateral to ventral chaetae in X.

Mouth and pharynx (Fig. 1A) enlarged and complexly folded (semi-schematic in drawing), apparently forming a massive, eversible feeding apparatus. In all specimens studied, esophagus and gut filled (and distended) with sediment and detritus along most of worm, indicating that large amounts are engulfed. Pharyngeal glands not observed. Male genitalia (Fig. 1D) paired. Vas deferens 6–9 μ m wide, much longer than atrium, entering apical end of latter. Atrium 45–60 μ m long, 20–28 μ m wide, somewhat comma-shaped or spindle-shaped, with apical end tilted over to posterior. Atrium with ventral bulge bearing (somewhat broadly at-

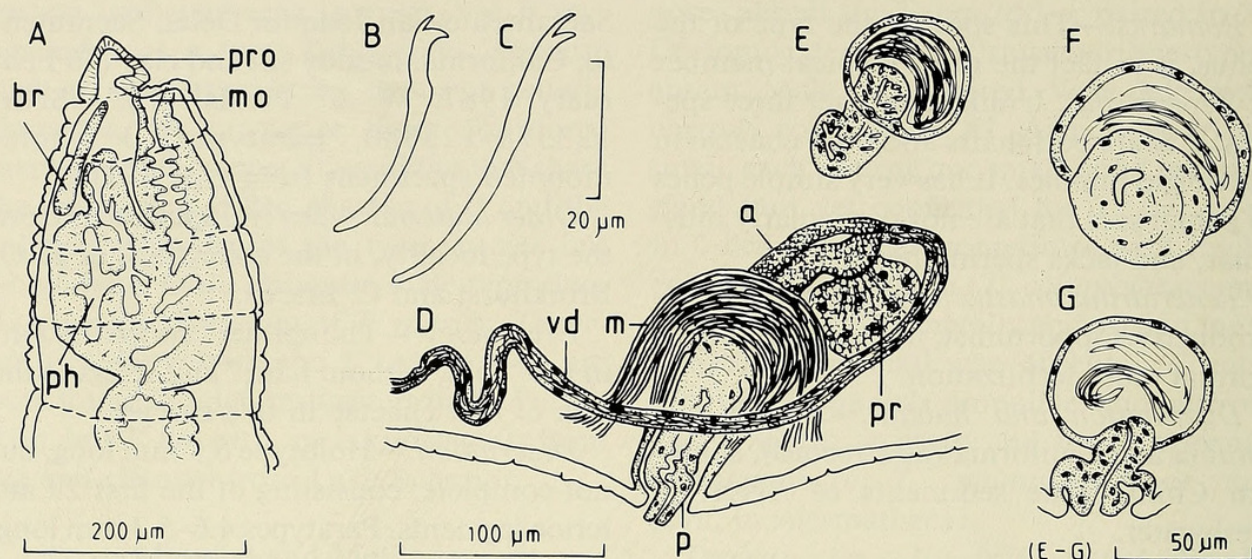


Fig. 1. *Teneridrilus calvus* Erséus & Brinkhurst, n. sp.: A, Anterior end of worm, with folding of pharynx semi-schematically drawn; B, Chaeta of segment II; C, Chaeta of segment IV; D, Male genitalia; E, Spermatheca from one specimen; F–G, Spermathecae from another specimen. Abbreviations: a atrium; br brain; m muscular bulb; mo mouth; p penis; ph pharynx; pr prostate gland; pro prostomium; vd vas deferens.

tached?) discrete prostate gland. Atrium entering heavily muscular bulb, interior to which is a hollow sac with a cylindrical or somewhat tapering penis. Penis 60–95 μm long, 18–30 μm wide, with thin but distinct cuticular lining (= a cylindrical sheath) along most of its length, but with ‘soft’ and somewhat pointed tip, protruding from opening of sheath. Spermathecae (Fig. 1E–G) with wide and distinct ducts, and spherical or oval ampullae; body wall thickened and somewhat folded at pore, often with a circular groove surrounding pore (but details not clear in available material); ampullae 30–60 μm long, 25–70 μm wide; sperm random or as loose bundles in ampullae.

Remarks.—This species is distinguished from *T. mastix* and *T. columbiensis* by its characteristic, slender penes (Fig. 1D), which, however, are not as long as those of *T. flexus*, n. sp. (see below).

The complex spermathecal pores of *T. calvus* (Fig. 1G) are unique within the genus. The corresponding pores are inconspicuous in *T. columbiensis* and *T. flexus*, and absent in *T. mastix*.

Distribution and habitat.—Known only from the Sacramento-San Joaquin Delta in

California, where it is commonly associated with the following invertebrates (W. C. Fields, Jr., pers. comm.): *Corbicula fluminea*, *Corophium stimpsoni*, *Anisogammarus ramellus*, *Limnodrilus angustipenis*, *L. hoffmeisteri*, *Bothrioneurum vej dovskyanum*, *Aulodrilus limnobius*, *Nereis limnicola*, and *Prostoma graecense*. Freshwater muddy sediments.

Teneridrilus flexus Erséus & Hiltunen,
new species

Fig. 2

Type material.—USNM 123381, holotype, whole-mounted specimen from St. Marys River, exit channel from Lake Superior, Chippewa Co., Michigan, U.S.A. (June 1985, D. W. Schloesser). USNM 123382–123383, paratypes, 2 whole-mounted specimens (one represented by fragments only) from type locality.

Etymology.—The epithet “*flexus*” is Latin for “winding” and refers to the flexible shape of the penes in this species.

Description.—Length of holotype 4.1 mm, about 32 segments (worm coiled and distorted), paratypes not complete. Width at

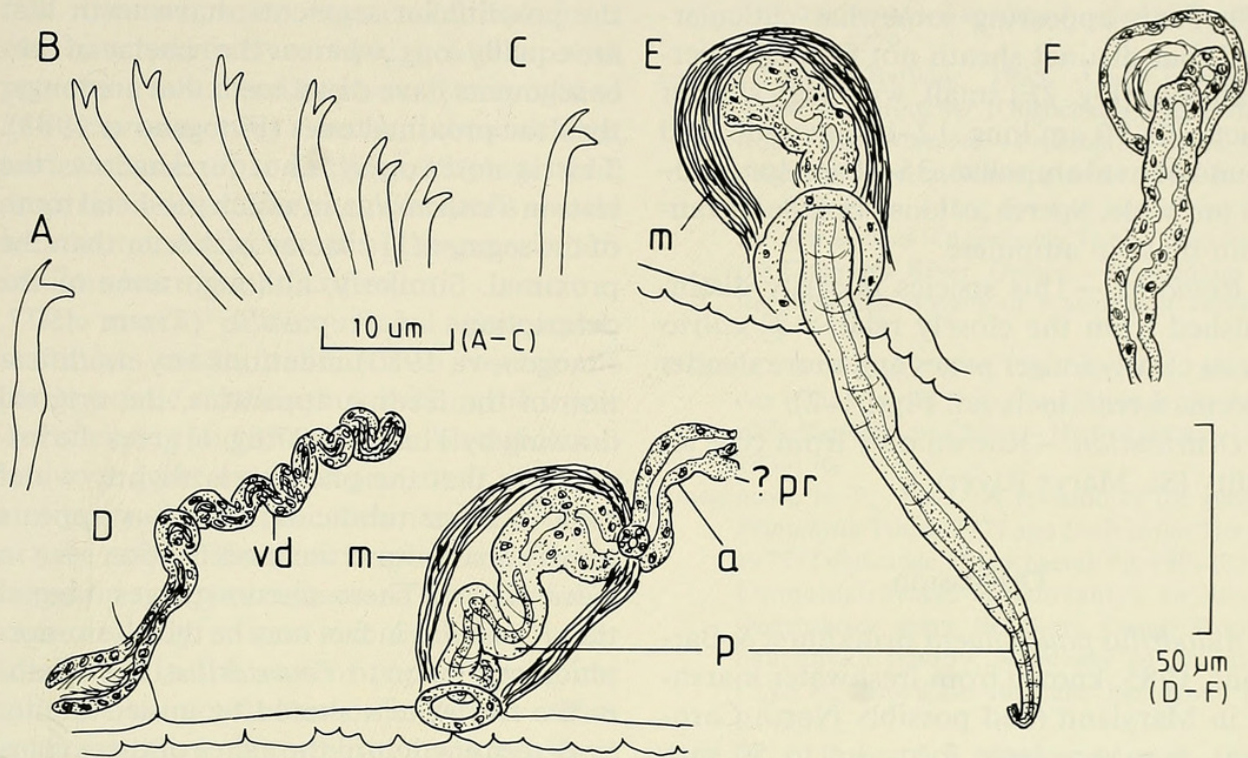


Fig. 2. *Teneridrilus flexus* Erséus & Hiltunen, n. sp.: A, Chaeta from segment II; B, Bundle of chaetae from segment V; C, Chaeta from postclitellar segment; D, Male genitalia from one side of much distorted specimen (paratype), with prostate gland (if present at all?) and vas deferens detached from atrium; E, Copulatory organ of other paratype, with penis protruded; F, Spermatheca. Abbreviations: a atrium; m muscular bulb; p penis; ?pr possible attachment of prostate gland; vd vas deferens.

XI (compressed specimens) 0.24–0.25 mm. Prostomium somewhat triangular, small. Body wall without adhering particles. Clitellum extending over XI–XII. Chaetae all bifid, those of II (Fig. 2A) stout, about 30 μ m long, about 2 μ m thick, 2–3 per bundle, with distal tooth distinctly thinner and shorter than proximal. Chaetae of segments III through VII or thereabouts (Fig. 2B) clearly longer than those of II, 40–47 μ m long, 2.0–2.5 μ m thick, 4–6 per bundle, with distal tooth about as thick as the proximal, but clearly longer. Chaetae of mid-body and posterior part of worm (Fig. 2C) about 35 μ m long, about 1.5 μ m thick, 1–3 per bundle (bundles sometimes missing?), somewhat similar in shape to those of II. Chaetae absent ventrally in XI. Male and spermathecal pores paired, ventrally in XI and X, respectively, but exact position in relation to chaetal lines difficult to see in available material.

Mouth and pharynx modified as in *T. calvus* (see Fig. 1A); esophagus and gut filled with sediment along most of worm. Pharyngeal glands not observed. Male genitalia (Fig. 2D–E) paired. Vas deferens about 5–7 μ m wide, longer than atrium, but detached from atrium in the paratype, where it is best visible (Fig. 2D). Atrium inconspicuous (visible only in one paratype; Fig. 2D), slender, about 40 μ m long, 9–11 μ m wide, with non-muscular outer lining and virtually non-granulated inner epithelium. Prostate gland not observed, but a small structure may be remains of a prostate stalk in (much distorted) paratype (Fig. 2D: ?pr). Atrium entering heavily muscular bulb, interior of which is a hollow sac with a very long, tapering, flexible penis. Penis about 150–200 μ m long, 15–20 μ m wide at base, only about 5 μ m wide at tip, either coiled and retained within sac (Fig. 2D) or protruding through male pore, reaching far out from worm (Fig.

2E). Penis appearing somewhat cuticularized, but distinct sheath not formed. Spermathecae (Fig. 2F) small, with very slender ducts, 80–90 μm long, 12–15 μm wide, and round or oval ampullae, 35–40 μm long, 30–35 μm wide. Sperm as loose bundle or random mass in ampullae.

Remarks.—This species is easily distinguished from the closely related *T. calvus* by its clearly longer penes and more slender spermathecal ducts (cf. Figs. 1–2).

Distribution.—Known only from type locality (St. Marys River).

Discussion

Aulodrilus paucichaeta Brinkhurst & Barbour, 1985, known from freshwater marshes in Maryland (and possibly North Carolina), is a very large form, up to 50 mm long, which has some features in common with these smaller *Teneridrilus* species. The small atria, intimately associated with large, spherical, muscular penial bulbs, the wedge to spherical shaped penes, and the bundled sperm in the spermathecae make *A. paucichaeta* similar to the taxa treated here. However, in *A. paucichaeta* the chaetae of segment II are not much different from those of the following segments, and the pharynx does not appear to be modified in the *Teneridrilus* manner (observations on some of the original specimens of *A. paucichaeta* in Brinkhurst's collection). Therefore, the species is excluded from *Teneridrilus*.

The European *Peipsidrilus*, established by Timm (1977) for *P. pusillus* Timm, 1977, later revised by Finogenova (1983) to include *Umbadrilus saamicus* Timm, 1978 (described in Timm & Popchenko 1978), and further revised by Giani et al. (1984) to include *Neoaulodrilus libanus* Giani et al., 1982, is probably closely related to *Teneridrilus*. The three species of *Peipsidrilus* are also small freshwater forms (length 6–8 mm), with simple atria and small penes enclosed in muscular sacs. In *P. pusillus*, the chaetae of segment II, as well as those of

the postclitellar segments, have teeth that are equally long, whereas the chaetae of other segments have distal teeth that are longer than the proximal ones (Finogenova 1983). This is noteworthy, as it foreshadows the state in *Teneridrilus*, in which the distal tooth of the segment II chaetae is shorter than the proximal. Similarly, although none of the descriptions of *P. pusillus* (Timm 1977, Finogenova 1983) mentions any modification of the feeding apparatus, the original drawing by Timm (1977:fig. 1) gives the impression that the pharynx is slightly wider than in other tubificids, and thus appears transitional toward the modification seen in *Teneridrilus*. These circumstances suggest that *P. pusillus* in fact may be the plesiomorphic sister taxon to *Teneridrilus*, but whether the two genera should be united cannot be determined until the states of these characters (chaetae of II and feeding apparatus) in all species of *Peipsidrilus* have been carefully reexamined.

The taxa discussed so far are only a part of a whole complex within the Tubificinae characterized by rather simple atria and penes, and by a tendency toward bearing random sperm instead of spermatozeugmata in the spermathecae. Some loose sperm were observed in the spermathecae of *T. columbiensis* by one of us (C.E.) but the significance of this is unclear until tubificines with the same feature are examined. Genera involved in this complex are *Aulodrilus* Bretscher (Giani et al. 1984), *Isochaetides* Hrabě emend., Brinkhurst (Brinkhurst 1984, 1986a), *Peipsidrilus* Timm (1977), *Krenedrilus* Dumnicka (Giani et al. 1990), and *Sketodrilus* Karaman, 1976. The morphological features of these often appear to be plesiomorphic and the species in question are thus likely to be less derived Tubificinae. However, some of the species may be advanced members of the subfamily; i.e., their lack of genital complexity is due to regression linked with reduction in body size or modification in reproductive strategy (see comments on *T. mastix* in Introduction).

For instance, some species of *Aulodrilus* combine relatively simple genitalia with presumed advanced traits such as modified and very numerous chaetae, tube-dwelling, and asexual reproduction. Phylogenetic analysis to determine such questions should be attempted after some of the generic definitions have been clarified.

The scarcity of unequivocal apomorphic states has made it difficult to resolve the phylogenetic relationships within the lower Tubificinae, and the generic classification has to a great extent represented phenetic similarity and unique combinations of characters rather than monophyletic groups based on synapomorphies—a statement that unfortunately is true also for many other tubificids. In the present paper, we do not attempt to rectify this difficulty for other genera, but we claim that there is evidence that the four *Teneridrilus* species constitute a true monophyly.

Acknowledgments

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