

Two new species of *Tubificoides* (Annelida: Clitellata: Naididae) from the Blake Ridge methane seep in the northwest Atlantic Ocean

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Abstract.—*Tubificoides blakei* and *T. methanicus*, both new species of oligochaetes, are described from 2156 and 2170 m depth on the Blake Ridge Diapir, near the intersection of the Carolina Rise and the Blake Ridge, off the continental shelf of North and South Carolina (U.S.A. East Coast). *Tubificoides blakei* is characterized by the long, parallel teeth of its bifid crotchets, and its mushroom-shaped, cuticular penis sheaths. It appears most closely related to two other deep-water species reported from the northwest Atlantic Ocean, *T. bruneli* Erséus, 1989 and *T. aculeatus* (Cook, 1969) but differs from these in the detailed morphology of the penis sheaths. *Tubificoides methanicus* lacks hair chaetae but is recognized by its numerous bifid chaetae, which have long, somewhat diverging teeth, the upper teeth often being longer than the lower ones, and its smooth, funnel-shaped penis sheaths. It does not seem to be closely related to any other known deep-sea species of *Tubificoides*, but it resembles the littoral, holarctic, *T. pseudogaster* (Dahl, 1960), differing from the latter mainly by its greater number and larger size of the posterior chaetae.

Tubificoides Lastockin, 1937 (subfamily Tubificinae) is a large, marine oligochaete taxon with about 50 described species worldwide (Milligan 1996), the most recent addition being *T. calvescentis* Erséus et al., 2005. The genus is morphologically confusing since most of the genital structures (e.g., male ducts, spermathecae) are rather similar throughout the species; therefore, nominal taxa are largely discriminated on the basis of unique combinations of minute differences in the structure of the cuticle (some species are heavily papillated), the ap-

pearance and arrangement of the chaetae, and the shape of the cuticular penis sheaths. In many cases, it is easy to identify a particular species as such, but it is difficult to see any clear lines of evolution in these morphological characters (Milligan & Erséus pers. obs.); thus, the phylogenetic relationships within *Tubificoides* are largely unknown.

A high number of specimens of Naididae [formerly Tubificidae; see Erséus et al. (2008); see also International Commission of Zoological Nomenclature (2007)] were collected from two research cruises at the Blake Ridge methane seep at 2156 and 2170 m depth. They represent

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two new species of *Tubificoides*, one with and the other without hair chaetae. Both species are described in the present paper.

Materials and Methods

In 2001, samples were collected during four dives (3709–3712) with the submersible *Alvin* at the Blake Ridge Diapir site, hole 996 of the Ocean Drilling Program, ODP (32°29.633'N, 76°11.454'W), near the intersection of the Carolina Rise and the Blake Ridge, off the continental shelf of North and South Carolina. Collection was by means of mussel bed samplers (26 cm diameter), which are described by Van Dover (2002), and used to sample deep-sea mussel beds and their associated infauna. Oligochaete specimens were just one component of the invertebrate infaunal community associated with the Blake Ridge mussel beds, but most likely residing in the fine, silt-clay sediments under and around the mussels. Additional oligochaete specimens were collected on subsequent dives at the Blake Ridge methane seep in July 2003, at 2170 m depth. Collection was by means of a suction sampler that samples the muddy sediments in and around live clam and mussel beds. For this paper, material was also used from dive 3909 (32°29.772'N, 76°11.125'W). A detailed description of the study site can be found in Van Dover et al., (2003). From ODP studies, it is known that methane and hydrogen sulfide are present in abundance directly below the mussel beds; hydrogen sulfide concentrations were <100 ppm and methane concentrations ranged to as much as 15,600 µL/kg wet sediment in headspace of some samples (Paull et al. 1996).

All samples were fixed in 10% buffered formalin upon collection and transferred to 70% ethanol for long-term storage. The specimens were stained in alcoholic paracarmine, dehydrated in an ethanol-xylene series, and mounted whole in Canada balsam on microscope slides.

Seven specimens of each of the two species were selected for the type series, but several other specimens from the type locality were also examined, and these combined with the type series were used as the basis for the descriptions below.

Types and other reference material are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C. and the Swedish Museum of Natural History (SMNH), Stockholm. Voucher specimens are also lodged at the Duke University Marine Laboratory, Beaufort, North Carolina, in the research collections of Cindy Van Dover.

Systematics

Class Clitellata

Family Naididae

Subfamily Tubificinae

Genus *Tubificoides* Lastockin, 1937

Tubificoides blakei, new species

Figs. 1A–C, 2

Holotype.—USNM 1116918, whole-mounted, sexually mature specimen (collected 25 Sep 2001, *Alvin* dive 3709).

Type locality.—The Blake Ridge Diapir site (ODP Site 996), off the Continental Shelf of North and South Carolina, NW Atlantic Ocean, 32°29.633'N, 76°11.454'W, 2156 m.

Paratypes.—SMNH Type Coll. 7513, sexually mature specimen, from type locality (collected 25 Sep 2001, dive 3709). USNM 1116919, 1116920, two specimens (26 & 28 Sep 2001, dives 3710 & 3712, respectively), and SMNH Type Coll. 7514–7516, three specimens (two from 26 Sep 2001, dive 3710; one from 26 Jul 2003, dive 3909); all more or less fully grown but sexually immature, and all from type locality.

Other material.—SMNH Main Coll. 102207–102217, 19 specimens, and at the Duke University Marine Laboratory in the research collections of Cindy Van

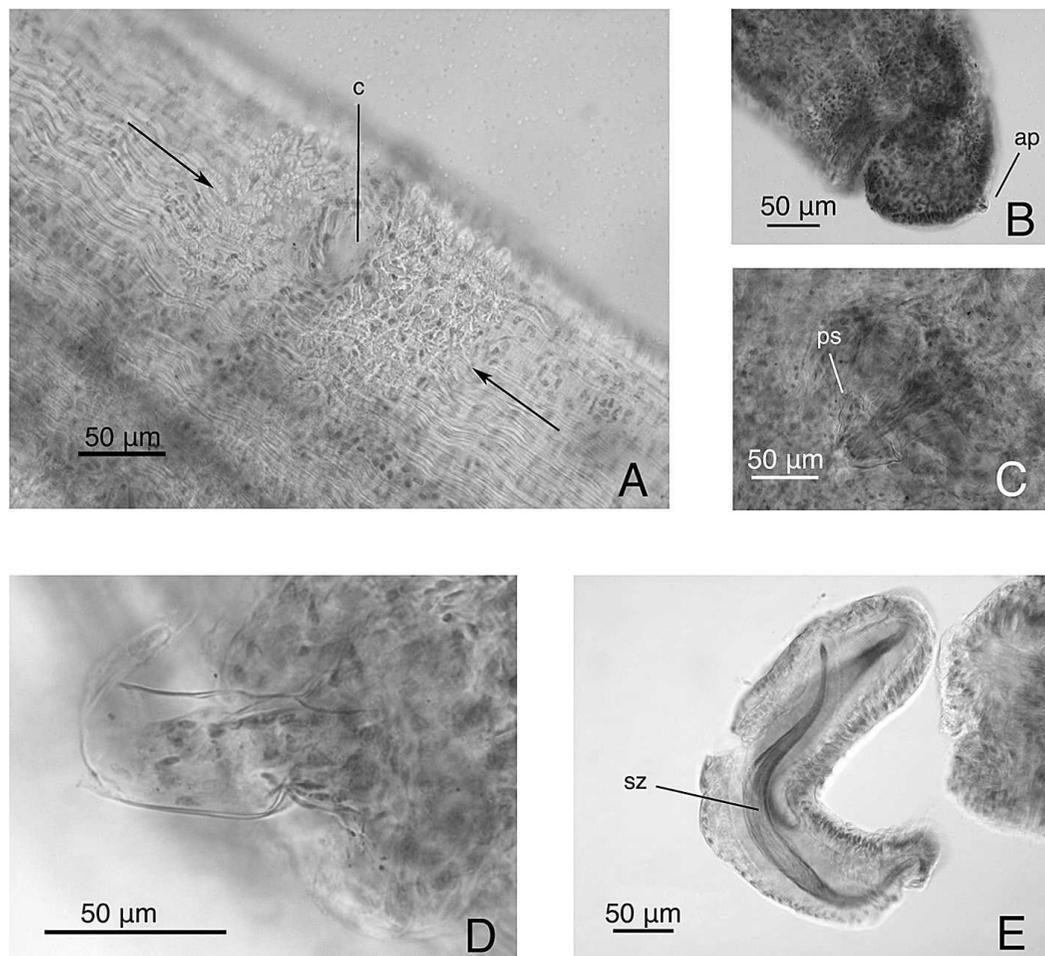


Fig. 1. A–C, *Tubificoides blakei*. A, Epidermal glands; B, Prostomium with apical papilla; C, Penis sheath; D–E, *Tubificoides methanicus*. D, Penis sheath with some protruding soft parts; E, Spermathecal ampulla. Abbreviations: ap, apical papilla; c, chaetae; ps, penis sheath; sz, spermatzeugma.

Dover, six specimens; all immature, from type locality (dives 3709, 3710, 3711, 3712).

Etymology.—Species named after Commodore and Lighthouse Inspector George Smith Blake (1803–71), who also had a U.S. research vessel named after him (the Coast Survey Steamer *Blake*). The Blake Plateau and Blake Ridge (in proximity to each other) also originate from the same name.

Description.—Two immature paratypes complete, 16.9 and 21.8 mm long, with 75 and 84 segments, respectively. Holotype sexually mature; only 6.1 mm long, with

anterior 15 segments; but specimen incomplete, with posterior end missing. Width at XI, 0.5–0.6 mm in sexually mature specimens, 0.35–0.45 mm in immature specimens; all specimens mounted and compressed. Prostomium small, damaged in some specimens; when intact, about as long as (basally) wide, and with a small anterior papilla (Fig. 1B:ap). Cuticle in anterior part of body smooth, in posterior part gradually becoming covered by fine particles, but distinct cuticular papillae nowhere developed. In segments III–X or IV–X of all worms (including immature ones), a band of

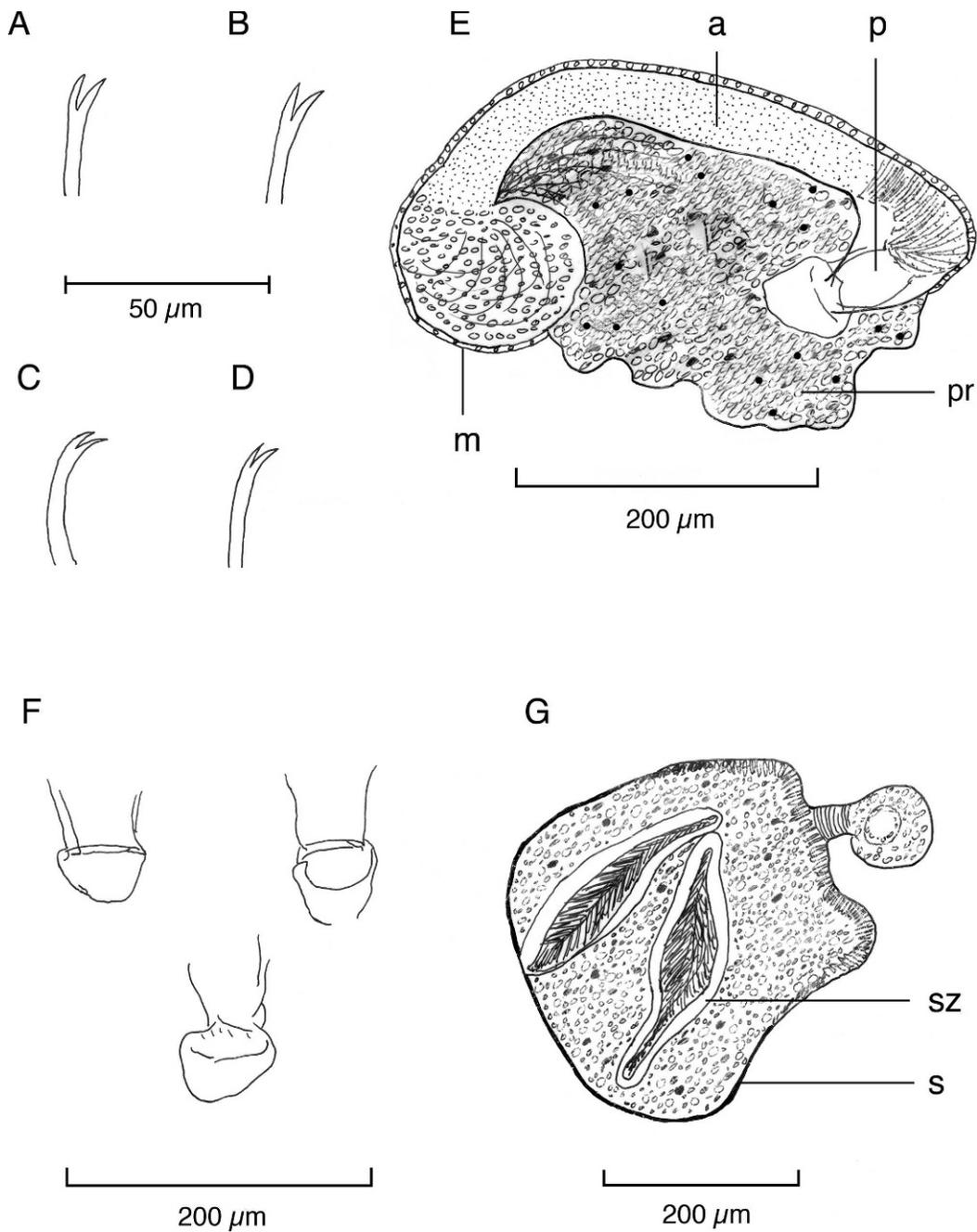


Fig. 2. *Tubificoides blakei*. A, Anterior ventral chaeta; B, Anterior dorsal chaeta; C, Posterior ventral chaeta; D, Posterior dorsal chaeta; E, Male genitalia; F, Penis sheaths; G, Spermatheca. Abbreviations: a, atrium; m, outer muscular layer; p, penis; pr, prostate gland; s, spermatheca; sp, spermathecal pore; sz, spermathecal pore.

epidermal glands surrounding each segment at level of chaetae (Fig. 1A). Clitellum not developed in any of the available specimens. In preclitellar segments, dorsal bundles each with one to three thin hairs (up to about 290 μm long) and one to three bifid crotchets (about 70–75 μm long); latter with slender and almost parallel teeth (Fig. 2B). Postclitellar dorsal chaetae (Fig. 2D) morphologically similar to preclitellar ones, but hairs shorter (about 160 μm long) and each bundle generally with only one hair and one crotchet. Ventral chaetae (Fig. 2A, C) all bifid, one to three per bundle anteriorly and generally one per 'bundle' in postclitellar segments, and with long, parallel teeth. Ventral bifids, however, more sigmoid and distinctly larger (up to 150 μm long) than dorsal ones. In posteriormost segments (of the two complete specimens), teeth of bifid chaetae tend to be shorter than in anterior and mid-body segments, and occasionally, ventral bundles with two instead of only one bifid chaeta. Nodus hard to detect in anterior bundles, occurring medially in posterior bundles. Male pores paired, located in line with ventral chaetae, in middle of segment XI. Spermathecal pores paired, located immediately anterior to ventral chaetae, in middle of segment X.

Pharyngeal glands in segments (III)IV–V. Esophagus not modified in IX. Male genitalia (Fig. 2E) paired. Vas deferens 25–30 μm wide, thin-walled and densely ciliated; exact length unknown, but vas much coiled and appears several times longer than atrium. Entrance of vas deferens and prostate gland (pr) into atrium not observed. Atrium (a) about 400 μm long, about 65–100 μm wide, with thin (3–4 μm), but distinct, outer muscular layer (m). Atrium bipartite with thick, granulated inner epithelium in elongate portion, and coarser cellular structure in distal, cap-like portion (Fig. 2E). Atrium terminating in penis (p) enclosed in rather complex penial sac;

penis with somewhat mushroom-shaped cuticular sheath (Figs. 1C:ps, 2F), 90–100 μm long, 60–75 μm wide at inner base, 50–60 μm wide at flared tip; except for the flared tip, penis sheath smooth. Spermathecae (Fig. 2G:s) large, each consisting of three parts: a muscular, spherical bulb at orifice (diameter about 90 μm), a short narrow duct proper (50–85 μm long, 35–40 μm wide), and, clearly set off from this duct, a voluminous more or less oval ampulla; base of ampulla thick, with tall lining of epithelial cells, inner part of ampulla thin-walled. In holotype, each ampulla containing a few broad, spindle-shaped (i.e., tapering at both ends), spermatozeugmata (Fig. 2G:sz), 300–370 μm long, 75–90 μm wide at middle.

Remarks.—*Tubificoides blakei* is yet another species with a unique combination of characters (cf. Introduction), and its exact systematic position in relation to its congeners is not obvious. Its mushroom-shaped penis sheaths are virtually identical to those of two other species with hair chaetae: *T. insularis* (Stephenson, 1922), a papillated, intertidal-estuarine, North Atlantic form (Stephenson 1922, Brinkhurst 1985), and *T. palacoleus* Baker, 1983, a non-papillated, subtidal, Arctic species (Baker 1983). However, none of these taxa have the bifid chaetae with the long teeth that are characteristic of *T. blakei* (particularly, in its preclitellar chaetae). In *T. insularis*, most bifids have a reduced upper tooth (see Brinkhurst 1985:401, fig. 1), while in *T. palacoleus*, the bifids have symmetrical but short teeth, and all postclitellar crotchets are single-pointed.

In the deep waters of the northwest Atlantic Ocean, however, there are four previously known species that have hair chaetae as well as bifid chaetae resembling those of *T. blakei*, i.e., bifids with slender parallel teeth. These taxa are *T. aculeatus* (Cook, 1969a), from abyssal depths off Delaware and Massachusetts

[1330–2946 m depth; see Erséus & Rota (2003)], *T. bruneli* Erséus, 1989, from the St. Lawrence estuary in Canada (242 m depth), *T. crinitus* Erséus, 1989 and *T. paracrinitus* Erséus & Milligan, 1989, both from the continental slope of the northern Gulf of Mexico (320–582 m depth). The first two of these other species have penis sheaths with modified tips. The sheaths of *T. bruneli* are terminally curved with distended tips and subapical openings (Erséus 1989:883, fig. 3D), while those of *T. aculeatus* are straight and not terminally curved but instead bear a series of lateral cuticular hooks near their terminal ends (Cook 1969a:494, fig. 2B, C). These penial features alone discriminate these two species from *T. blakei*, but they share with the latter a smooth body cuticle anteriorly and a covering of fine cuticular particles posteriorly, long and coiled vasa deferentia, and unusually broad spermatozeugmata; albeit the latter structures are distinctly stouter in *T. bruneli* and *T. aculeatus* (see Cook 1969a:494, fig. 2D; Erséus 1989:883, fig. 3E) than in *T. blakei* (Fig. 2G). Further, *T. bruneli* has spermathecae (Erséus 1989:883, fig. 3E) that are similar to those of the new species, and *T. aculeatus* has a prostomium with “a very small papilla anteriorly” (Cook 1969a:494), just as noted for *T. blakei* above. Despite the discrepancies (including also differences in the detailed morphology of the bifid chaetae), it is thus likely that *T. blakei* is most closely related to *T. bruneli* or *T. aculeatus*.

Tubificoides crinitus and *T. paracrinitus*, on the other hand, while also having ventral, bifid chaetae with slender parallel teeth, and long coiled vasa deferentia, show less morphological affinity to the new species. First, all their dorsal crotchets are single-pointed instead of bifid. Second, their penis sheaths are thimble-shaped, without distended tips. Third, their spermatozeugmata are slender, as is typical of most species of *Tubificoides*, and not as broad as those of *T. blakei*.

Distribution and habitat.—Known only from the Blake Ridge Diapir methane seep, NW Atlantic, found in and around mussel and clam beds in silt-clay sediments, 2156 m depth.

Tubificoides methanicus, new species

Figs. 1D–E, 3

Holotype.—USNM 1116921, whole-mounted, sexually mature specimen (collected 26 Sep 2001, *Alvin* dive 3710).

Type locality.—The Blake Ridge Diapir site (ODP Site 996), off the Continental Shelf of North and South Carolina, NW Atlantic Ocean, 32°29.633'N, 76°11.454'W, 2156 m.

Paratypes.—USNM 1116922, 1116923, two specimens (26 Jul 2003, dive 3909), and SMNH Type coll. 7517–7520, four specimens (one from 25 Sep 2001, dive 3709; three from 26 Jul 2003, dive 3909); all specimens sexually mature. Thus, one SMNH paratype from type locality, all other paratypes from 32°29.772'N, 76°11.125'W, 2170 m.

Other material.—SMNH Main coll 102218–102227, 12 specimens, and at the Duke University Marine Laboratory in the research collections of Cindy Van Dover, six specimens; a mixture of mature and immature specimens, all from type locality (dives 3709, 3711, 3712) and near type locality (dive 3909).

Etymology.—Named after the Blake Ridge methane gas seep where the specimens were collected.

Description.—Holotype 9.9 mm long, sexually mature with 54 anterior segments; longest paratype, 9.2 mm, with 53 anterior segments; all specimens in type series with posterior ends missing. Width at XI, 0.5–0.8 mm in mounted, compressed specimens. Holotype and two paratypes with short prostomium, (basally) wider than long; other paratypes with prostomium about as wide as long. Prostomium lacking anterior papilla (cf. *T. blakei* above). Cuticle covered by fine particles throughout body but cuticular

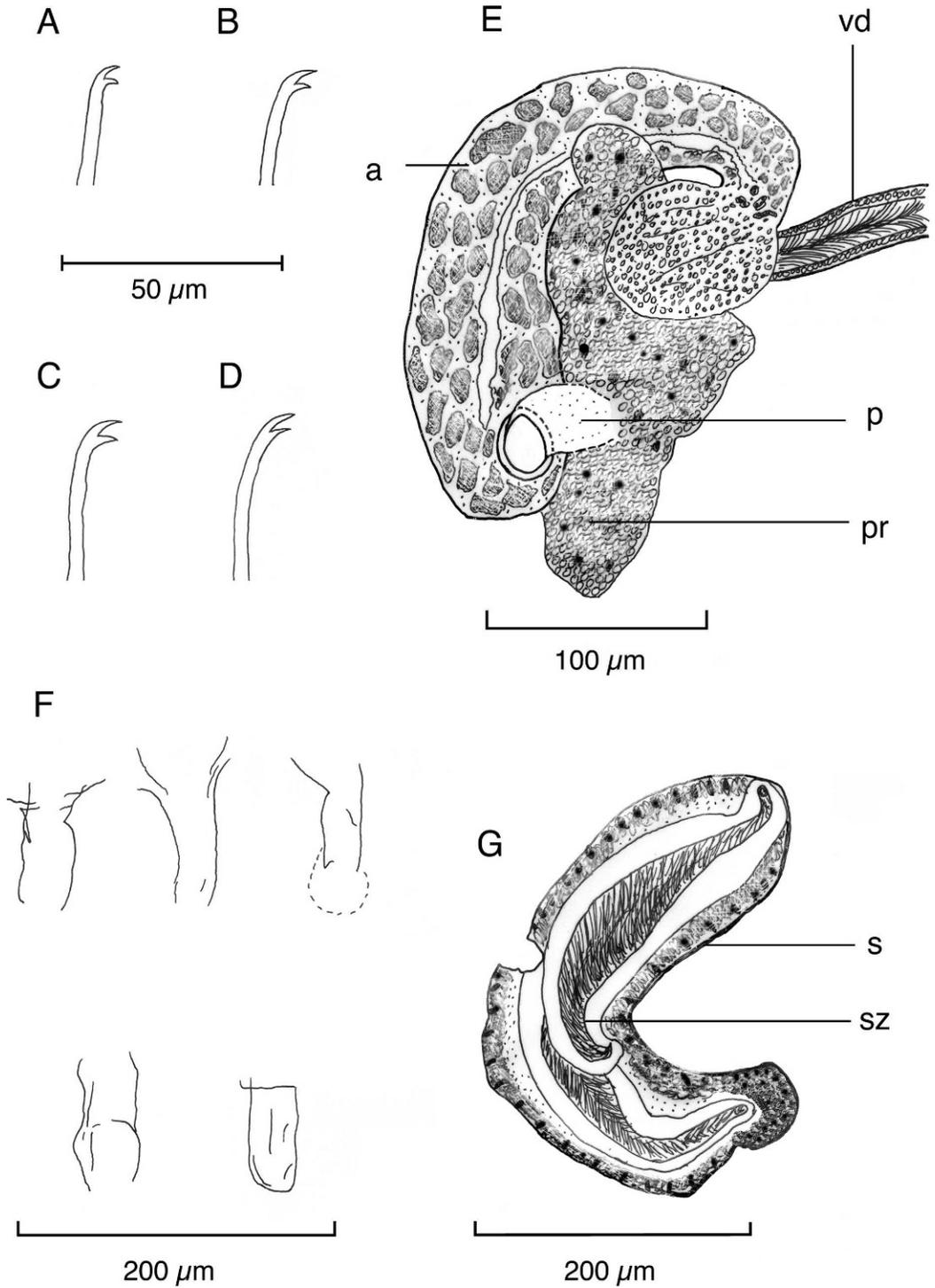


Fig. 3. *Tubificoides methanicus*. A, Anterior ventral chaeta; B, Anterior dorsal chaeta; C, Posterior ventral chaeta; D, Posterior dorsal chaeta; E, Male genitalia; F, Penis sheaths; G, Spermathecal ampulla (detached); duct and spherical, muscular bulb not shown. Abbreviations: vd, vas deferens; others as in Fig. 2.

papillae nowhere developed. Segments II–III of some specimens very short; also, in some specimens, mid-body segments elongated. Clitellum not developed in any specimen. Throughout worm, dorsal chaetal bundles each with (two) three or four bifid crotchets (40–110 μm long, Fig. 3B, D) with upper tooth slightly longer than or equal to lower tooth, both teeth somewhat curved. Dorsal chaetae gradually increasing in length in postclitellar segments; also, in posteriormost segments, with upper tooth becoming markedly longer and thinner than lower. Preclitellar ventral bundles with two or three chaetae (Fig. 3A), about 50–75 μm long, with appearance similar to that of dorsals. Postclitellar ventral bundles with two or three, sometimes four, chaetae, up to 80 μm long with upper teeth slightly longer than lower (Fig. 3C). Nodulus occurs medially in chaetae, when present. Male pores in middle of XI, located in line with ventral chaetae. Spermathecal pores paired, in lateral lines, and in middle of X.

Pharyngeal glands in segments (III)IV–V. Esophagus not modified in IX. Male genitalia (Fig. 3E) paired. Vas deferens (vd) 20–25 μm wide, rather thick-walled; exact length unknown, but vas much coiled and appears several times longer than atrium. Vas entering atrium subapically, more or less opposite prostate gland (pr). Atrium (a) elongate with distinct voluminous cap at distal end; atrium about 70 μm wide, 350–415 μm long (atrial length measurable in only two specimens). Atrium bipartite with finely granular distal cap-like portion, and coarser cellular structure in elongate portion (Fig. 3E). Atrium terminating in penis (p) enclosed in a simple penial sac; penis with somewhat funnel-shaped penis sheath (Figs. 1D, 3F), 85–90 μm long, 35–40 μm wide at base, with wide terminal opening. Spermathecae (Figs. 1E, 3G:s) each with muscular, oval bulb at orifice (diameter about 25 μm), followed

by an about 300 μm long, narrow (25–35 μm wide) duct proper, and, innermost, voluminous, sausage-shaped (i.e., curved, cylindrical with rounded ends) ampulla. All type specimens post-copulatory with spermatozeugmata (Figs. 1E:sz, 3G:sz), sometimes as many as five or six in each spermatheca. Spermatozeugmata slender, 240–400 μm long, narrow at both ends and with slightly thickened, 15–40 μm wide, mid-part.

Remarks.—The phylogenetic status of *Tubificoides methanicus* within the genus is hard to determine on morphological grounds. It is clearly separated from previously described deep-sea species of *Tubificoides*, inasmuch as all such species possess hair chaetae, whereas *T. methanicus* does not. On the other hand, the funnel-shaped, smooth penis sheath is not unique for this species but is reminiscent of that of several congeners. The intertidal *Tubificoides pseudogaster* (Dahl, 1960) lacks hair chaetae, and was originally described from Kysing Fjord, Denmark, and later reported from both the Pacific and Atlantic coasts of North America, as well as several sites in northern Europe (Dahl 1960, Brinkhurst & Baker 1979, Baker 1980). It has a penis sheath of much the same shape as in *T. methanicus* (see Brinkhurst 1965:164, fig. 2i, Brinkhurst & Baker 1979:1555, fig. 5, Baker 1980:338, fig. 1). For instance, judging from these figures, it seems that the penis sheath of *T. pseudogaster* has a terminal opening as noted for *T. methanicus* above. At the same time, however, discrepancies in the shape of the chaetae as well as the shape of the male genitalia are apparent when comparing the different descriptions of *T. pseudogaster*. Regardless of this, *T. pseudogaster*, as re-described by Baker (1980), strongly resembles our new species with regard to the teeth of the bifid chaetae, and the shape of the penis sheath. *Tubificoides methanicus*, however, differs by the numerous bifid crotchets throughout its body (posterior bundles

with lower number of chaetae in *T. pseudogaster*), and the increasing size of the chaetae in posterior segments, and evidently, also in its adaptation to the deep sea.

Distribution and habitat.—Known only from the Blake Ridge Diapir methane seep, NW Atlantic, found in and around mussel and clam beds in silt-clay sediments, 2156 and 2170 m depth.

Discussion

Tubificoides paracrinitus, and two other naidids (*T. pequegnatae* Erséus & Milligan, 1989, and *Limnodriloides olearius* Erséus & Milligan, 1989; the latter within the subfamily Limnodriloidinae), were described from an oil seepage area in the Gulf of Mexico (see Erséus & Milligan 1989), i.e., from a habitat that probably is comparable in some respect to the Blake Ridge methane seeps. As with the three species from the Gulf of Mexico, it is possible that *Tubificoides blakei* and *T. methanicus* are endemic to hydrocarbon seeps, but there is yet no morphological or other evidence that the worms benefit nutritionally (and specifically) from the bacterial mats of the seeps.

Two morphological features of *T. blakei* and one of *T. methanicus* deserve some further comment. First, the rings of epidermal glands present in most preclitellar segments of *T. blakei* are reminiscent of the transverse, elongated patches of epidermal glands present ventrally in the corresponding segments of *Limnodriloides olearius* (see Erséus & Milligan 1989:888, fig. 1A). Such patches/rings are not commonplace among marine naidids, but they appear to be convergently evolved in *T. blakei* and *L. olearius*, simply judging from the fact that the genera *Tubificoides* and *Limnodriloides* are not closely related. For *L. olearius*, Erséus and Milligan hypothesized that the patches are associated with reproduction, as they were not seen in sexually imma-

ture specimens. For *T. blakei*, the glandular rings are present in all specimens studied, so their function is probably not sexual.

Second, a small papilla at the apical end of the prostomium, as mentioned above for *Tubificoides blakei*, is also reported for several other deep-sea Naididae, e.g., *T. aculeatus* (Cook, 1969a), *Bathydriulus asymmetricus* Cook, 1970, and *B. sandersi* Erséus, 1983 (both in the subfamily Phalodrilinae), as well as deep-sea Enchytraeidae, e.g. *Grania torosa* Rota & Erséus, 2003 and *G. papillinasus* Rota & Erséus, 2003. It is noteworthy that these three distantly related groups all possess a similar, small prostomial papilla. It is thus likely that this feature is convergently evolved for these deep-sea species, and correlated, in some way, to their habitat. On the other hand, an apical, prostomial papilla also appears in the shallow-water species *Tubificoides intermedius* (Cook, 1969b), described from Cape Cod Bay, Massachusetts. In this case, the feature may be a synapomorphy for *T. blakei*, *T. intermedius* and possibly some other species of *Tubificoides*; because of its minute nature, the papilla may have been overlooked in earlier descriptions of *Tubificoides*.

Finally, the gradually increasing length of the posterior chaetal bundles of *T. methanicus* seems to be a unique character within *Tubificoides*.

Acknowledgments

We are indebted to Ylva Lilliemarck (Swedish Museum of Natural History) for mounting the slides. Financial support was provided to CE by the Swedish Research Council (grant # 621-2001-2788). Sample collection was supported by National Oceanic & Atmospheric Administration's National Undersea Research Program (University of North Carolina, NC-Wilmington National Undersea Research Center) and Ocean Ex-

ploration Program grants to Cindy Lee Van Dover.

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Associate Editor: Rick Hochberg.