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ORIGINAL ARTICLE

Free-living nematode species (Nematoda) dwelling in hydrothermal sites of the North Mid-Atlantic Ridge

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Abstract Morphological descriptions of seven free-living nematode species from hydrothermal sites of the Mid-Atlantic Ridge are presented. Four of them are new for science: *Paracanthonchus olgae* sp. n. (Chromadorida, Cyatholaimidae), *Prochromadora helenae* sp. n. (Chromadorida, Chromadoridae), *Prochaetosoma ventriverruca* sp. n. (Desmodorida, Draconematidae) and *Leptolaimus hydrothermalis* sp. n. (Plectida, Leptolaimidae). Two species have been previously recorded in hydrothermal habitats, and one species is recorded for the first time in such an environment. *Oncholaimus scanicus* (Enoplida, Oncholaimidae) was formerly known from only the type locality in non-hydrothermal shallow milieu of the Norway Sea. *O. scanicus* is a very abundant species in Menez Gwen, Lucky Strike and Lost City hydrothermal sites, and population of the last locality differs from other two in some morphometric characteristics. *Desmodora marci* (Desmodorida, Desmodoridae) was previously known from other remote deep-sea hydrothermal localities in south-western and north-eastern Pacific. *Halomonhystera vandoverae* (Monhysterida, Monhysteridae) was described and repeatedly found in mass in Snake Pit hydrothermal site. The whole hydrothermal nematode assemblages are featured by low diversity in comparison with either shelf or deep-sea non-hydrothermal communities. The nematode species list of the Atlantic hydrothermal vents consists of representatives of common shallow-water genera; the new species are also related to some shelf species. On the average, the hydrothermal species differ from those of slope and abyssal plains of comparable depths by larger sizes, diversity of buccal structures, presence of food content in the gut and ripe eggs in uteri.

Keywords Descriptions · Hydrothermal vents · Marine biodiversity · Mid-Atlantic Ridge · Taxonomy

Abbreviations

a	Ratio "body length/maximum body diameter"
b	Ratio "body length/length of pharynx"
c	Ratio "body length/length of tail"
c′	Ratio "length of tail/body diameter at anus"
c.b.d.	Corresponding body diameter
CV	Coefficient of variation, in %
L	Total body length
n	Number of specimens measured
SD	Standard deviation
V	Ratio "distance from anterior end to vulva/body length, in %"

Introduction

Hydrothermal vents scattered along the axis of the Mid-Atlantic Ridge constitute quite remarkable biotopes differing sharply from adjacent deep-sea environment in physical, chemical and biological conditions (Van Dover 2000). These sites are formed primarily by emissions of high-temperature (up to 400 °C) fluids enriched by reduced chemicals, mainly sulphides. Emanating hot fluids shape conical sulphide edifices, black and white smokers up to several metres in height. Besides locally high temperature, the hydrothermal sites are

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featured by strong fluctuations of temperature, pH, sulphide and oxygen concentrations, and often the absence of soft sediments. Macrobenthic communities dominated by alvinocaridid shrimp aggregations and mussel beds are arranged around vents in circular zones according to the temperature decreasing to periphery. Biomass of the macrobenthos in hydrothermal sites exceeds in three to four orders the poor biomass of the adjacent deep-sea floor. The quantitative abundance of benthic life depends on chemosynthetic primary production created by free-living and symbiotic chemoautotrophic bacteria that oxidize sulphides and methane to win energy for fixation carbon dioxide and producing organic substances. High biomass in hydrothermal sites is associated with often strong endemism and generally low diversity of benthic organisms compared to other deep-sea environments (Galkin 2006; Sarrazin et al. 2015; Turnipseed et al. 2003). Finally, the hydrothermal vents are dynamic and ephemeral ecosystems; they exist under variable conditions and may have limited term of life (Cuvelier et al. 2011; Gebruk et al. 2010).

Besides charismatic mega- and macrofauna, the deep-sea hydrothermal sites are populated by meiofauna invisible for human eyes and cameras. However, the information on the microscopic metazoans remains scant. Dinet et al. (1988) recorded on meiofauna of the East Pacific Rise and Explorer Ridge hydrothermal vents: the meiofauna consisted primarily of nematodes, various copepods, ostracods and macrofaunal juveniles. The authors stated that as a whole, species diversity and abundance of the hydrothermal meiofaunal assemblages are low in comparison with normal abyssal occurrences. Vanreusel et al. (1997) studied meiofauna in hydrothermal sediments in the North Fiji Basin, south-eastern Pacific. Nematodes prevailed (up to 1500 individuals per 150 cm^3 of active sediment), while other meiofaunal taxa were scarce: up to 16 harpacticoid copepods, 7 turbellarians, 5 bivalves, 3 polychaetes, 2 oligochaetes, 1 kinorhynch and 1 amphipod per 150 cm^3 sediment. Although nematodes always occurred in high abundance, their distribution was patchy. Similar ratios were revealed also on mussel *Bathymodiolus thermophilus* beds by Copley et al. (2007) on East Pacific Rise; however, prevalence of copepods over nematodes was observed in the youngest mussel beds. Goroslavskaya (2010) studied smaller organisms (unidentified nematodes and identified mostly up to genus- or family-level polychaetes, molluscs, pantopods and crustaceans) on some Mid-Atlantic Ridge hydrothermal sites and found that assemblages of smaller animals on mussel settlements are more diverse than those of shrimp colonies. Gollner et al. (2010) in their study of a hydrothermal site 9°50′N on the East Pacific Rise recorded low abundance of meiofauna ($\sim$100 ind. 10 cm^{-2}), which is in stark contrast to the macrofauna as well as low diversity of meiofauna, which increases with decreasing influence of vent fluid emissions. They also noted that many meiofauna genera and even some species from hydrothermal vents are well known from other ecosystems, which is contrary to what is known for most macrofauna.

There are a few studies conducted where hydrothermal nematode communities are analysed; the nematodes were identified to genus level, and for each genus, species were distinguished and got series numbers for comparison between samples. Vanreusel et al. (1997) examined nematode communities in hydrothermal sediments in the North Fiji Basin (SE Pacific) and found low species diversity both in number of species and in dominance in sharp contrast to the high diversity in the reference non-vent deep-sea sediments of the North Fiji Basin. Another important trait of the community, the nematodes in the hydrothermal sediments were twice as large as those in the reference sediments. Zekely et al. (2006c) found 15 species on mussel aggregations of *Bathymodiolus puteoserpentis* on a Mid-Atlantic Ridge vent (Snake Pit) and mentioned that the nematodes and harpacticoid copepods belong to generalist genera, which occur at a variety of habitats and are not restricted to hydrothermal vents or the deep sea. They also stated that the meiobenthos of those hydrothermal mussel beds constitutes a peculiar community different from those of other sulphidic habitats, including the thiobios of shallow-water sediments and the meiobenthos of deep-sea, cold-seep sediments. Other important conclusions of Zekely et al. (2006a) are dominance of primary consumers, mainly deposit feeders in trophic structure and absence of predatory meiofaunal species. Similar results were obtained for nematode communities from vents of the East Pacific Rise. Copley et al. (2007) presented a list of 17 nematode species from 14 genera and 11 families sampled on beds of the mussel *Bathymodiolus thermophilus* in two sites of the East Pacific Rise. It was also shown that there the nematode assemblages exhibited high dominance by a few species, the nematode species richness; species:genus ratios were low compared with other deep-sea habitats. Data on ecology and distribution of nematodes at deep-sea hydrothermal vents and other reduced milieus have been summarized by Vanreusel et al. (2010a). The authors came to several conclusions. First, in contrast to seeps, deep-water hydrothermal vents in general do not show high nematode densities or biomass (for example, nematode densities on bivalves were found 1–72 ind. 10 cm^{-2}, references therein). A possible reason is that hydrothermal vents provide living space for meiofauna and nematodes only on hard substrates with no or little sediment in crevices. Second, nematode diversity at deep hydrothermal vents is much lower than that in surrounding deep-sea sediments and even lower than at seeps. The authors considered that the reason of the low diversity and low evenness at vents might be that only a few species from the deep sea are adapted to such unfavourable environment as high concentration of reduced chemical compounds (hydrogen sulphide and hydrocarbonates) or low oxygen concentration. Third, there is no unique affinity with vents at genus level, suggesting a lower taxonomic level of endemicity for nematodes compared with mega- and macrofauna. Fourth, most nematodes from seeps and vents are classified as deposit feeders, based on their small buccal cavity and absence of teeth (see also Zekely et al. 2006c).

A few nematode species, usually prevailing in their communities, were described from various Pacific hydrothermal sites: *Dinetia nycterobia* from East Pacific Rise, *Cephalochaetosoma pacificum notium* from Lau-Fiji basin (both Draconematidae, Prochaetosomatinae; Decraemer and Gourbault 1997), *Desmodora alberti*, *Desmodorella balteata*, *D. spineacaudata* (East Pacific Rise, Guyamas), *Desmodora marci* (Lau Basin) (Desmodoridae; Verschelde et al. 1998), *Thalassomonhystera fisheri* (now transferred to the genus *Halomonhystera*—Tchesunov et al. 2015) and *Halomonhystera hickei* (both are Monhysteridae and both are in abundance associated with mussel *Bathymodiolus thermophilus* and tubeworm *Riftia pachyptila* at the East Pacific Rise—Zekely et al. 2006b), *Neochromadora* aff. *poecilosoma* (Chromadoridae) and *Linhomoeus caudipapillosus* (Linhomoeidae), both from the East Pacific Rise (Gollner et al. 2013).

The only nematode species identified on Mid-Atlantic Ridge hydrothermal sites is *Thalassomonhystera vandoverae* Zekely et al. (2006b) (Monhysteridae; now transferred to the genus *Halomonhystera*—Tchesunov et al. 2015) discovered by Zekely et al. (2006b) on Snake Pit. This species makes up 75–88 % to the total mussel bed-associated nematode community. Ramirez-Llodra et al. (2004) cited six nematode species identified up to genus level for Snake Pit vent; none of them coincides with genera of present research.

The aim of the present research is taxonomic identification of nematode species of six hydrothermal sites of the North Mid-Atlantic Ridge, comparison species assemblages between different sites, comparison nematode species composition with those of other taxa in order to reveal common and peculiar features of the nematofauna and biology of nematodes in hydrothermal biotopes.

Materials and methods

Material was collected in the course of 47th (2002), 49th (2003) and 50th (2005) cruises of Russian research vessel AKADEMIK MSTISLAV KELDYSH (Fig. 1). The samples represented mostly druses of mussels, pieces of rock taken by mechanical arm and net or silt sucked out from cracks between rocks by slurp gun were gathered during the dives of man-operated submersibles MIR. Only the Lost City site is an exception; no samples were taken there from mussels. List of samples is given in Table 1. Washout of the mussels and rocks was bolted through a sieve with 100 µm mesh size and fixed by buffered 4 % formol on filtered sea water on board. The samples were sorted under a binocular microscope.

Extracted nematodes were placed in vials with Seinhorst solution (70 parts distilled water, 29 parts 95 % ethanol and 1 part glycerine) and gradually proceeded to pure glycerine by slow evaporation of alcohol and water in thermostat at 40 °C. The specimens were then mounted into permanent glycerine slides with glass beads as spacers (beewax–paraffin is too soft matter to prevent slow squashing of nematode bodies) and sealed with melted mixture beewax–paraffin. The nematodes were for the considerable part crumpled or fragmented during sorting; hence, it was necessary to pick out intact specimens for description. Observations, measuring, drawing and taking pictures were done with microscope Leica DM 5000. Specimens for scanning electron microscopy were processed with a critical point dryer, coated with a mixture of platinum and palladium and studied with the scanning microscope Hitachi S-405 (Tokyo, Japan) at 15 kV voltage. Holotypes and part of paratype specimens of new species are deposited as permanent glycerine slides in the Senckenberg Natural History Museum (Frankfurt am Main, Germany). Part of the paratypes are kept in Nematological collection of the Center of Parasitology of the AN Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia.

Taxonomic part

Order ENOPLIDA Filipjev 1929
Family ONCHOLAIMIDAE Filipjev 1916
Oncholaimus Dujardin 1845
Oncholaimus scanicus (Allgén 1935)

Allgén 1935: 38–39, Fig. 13a–c (*Viscosia scanica*). Wieser 1953a: 124 (*Oncholaimus scanicus*).

Figures 2, 3, 4, 5, 6, 7, 8, Tables 2, 3, 4.

Material and localities

13 Males and 7 females from Lucky Strike; 27 males and 29 females from Menez Gwen; and 13 males and 8 females from Lost City (see Table 1).

Description

General

Large nematodes with long cylindrical filiform body. Cuticle looks smooth in optical microscope, but SEM

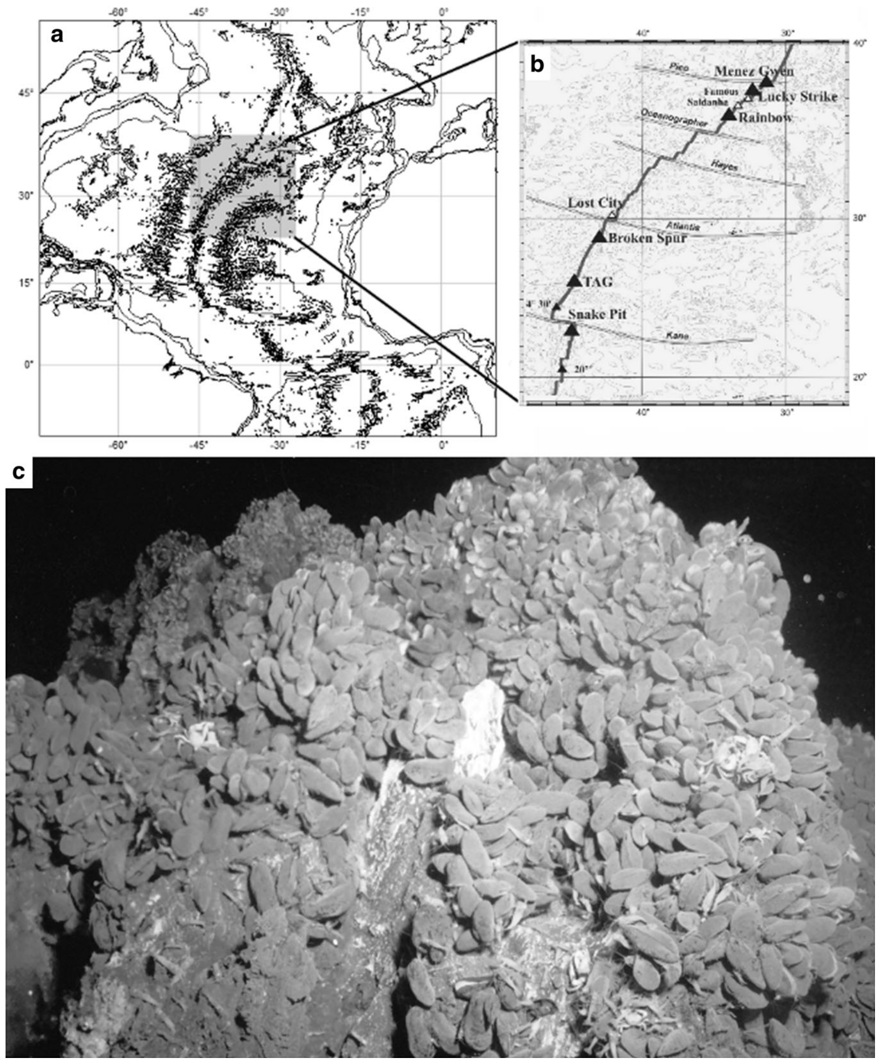


Fig. 1 Localities and habitat of hydrothermal species. **a** Mid-Atlantic Ridge in North Atlantic Ocean; **b** hydrothermal vents (*black triangles*) along the Mid-Atlantic Ridge; **c** aggregation of mussels *Bathymodiolus azoricus*, habitat of most nematode species here described, Lucky Strike (by courtesy of A. Sagalevitch, V. Nishcheta and S. Galkin)

reveals a very fine transversal striation (Fig. 8c), about five striae in 1 µm.

Mouth opening wide, surrounded with six rounded triangular lips. Six inner labial sensilla as papillae at the base of each lip. Six outer labial setae and four cephalic setae joined in common circle posterior to the inner labial papillae. All the anterior setae rather short and the cephalic setae equal to a little bit smaller than the outer labial setae (73–100 % of outer labial setae length in both males and females), slightly narrowed to the tips. Amphideal fovea as a crescent-shaped or cup-shaped thin-walled pocket with wide anterior aperture and posterior sclerotized short cylindrical amphideal duct; the fovea slightly larger in males than in females. Amphideal aperture as a transversal semilunar slit at the level of the midstoma. In males, amphideal aperture 19 µm (32 % of corresponding body diameter) wide; in females, 17 µm (27 %), respectively. Short somatic setae (6–11 µm long) distributed irregularly along the body, more numerous anterior to the nerve ring and sparsely on the postneural body. There orthometanemes present along the lateral fields.

Buccal cavity voluminous, cylindroid gymnostoma with sclerotized walls (rhabdions) thickening posteriad steppedly. Buccal cavity armed with three pointed onchs, the left lateroventral onch the largest while the dorsal and right lateroventral onchs smaller and about equal to one another. All three onchs with subapical outlets of the pharyngeal glands (Fig. 8b), all the outlets look ventrally. Pharynx cylindroid, evenly muscular along its length.

Ventral excretory/secretory pore as a tiny transversal slit (Figs. 6e, 8c) situated well posterior to the buccal cavity. Ventral gland cell body situated posterior to the cardia, usually ventrally and to the right of the intestine.

Tail short, its basal part conoid, distal part cylindroid; the tip may be slightly swollen. Caudal glands long, their cell bodies located well anterior to the anus. Caudal gland open in one terminal outlet pore (Figs. 6c, f, 8h).

Table 1 Localities (arranged from north to south) and sampling data

Hydrothermal site	Station-sample number and date of sampling	Geographical position	Depth (m)	Sample
Menez Gwen	4593, 01.08.2003	37°51′N and 31°31′W	840–865	Mussels *Bathymodiolus azoricus* and sediment
Menez Gwen	4595, 02–03.08.2003	37°51′N and 31°31′W	840–865	Stone with mussels *Bathymodiolus azoricus*
Rainbow	4399, 19.07.2002	36°13′N and 33°54′W	2260–2350	Mussels *Bathymodiolus azoricus*
Rainbow	4402, 20.07.2002	36°13′N and 33°54′W	2260–2350	Mussels *Bathymodiolus azoricus*
Rainbow	4812, 04.09.2002	36°14′N and 33°54′W	2307	Mussels *Bathymodiolus azoricus*
Rainbow	4819, 04.09.2002	36°14′N and 33°54′W	2318	Mussels *Bathymodiolus azoricus*
Lucky Strike	4376-1, 09.07.2002	37°17′N and 32°16′W	1635–1710	Eiffel Tower, mussels *Bathymodiolus azoricus*
Lucky Strike	4376-2, 09.07.2002	37°17′N and 32°16′W	1635–1710	Bacterial mat on rock
Lucky Strike	4377-2, 09.07.2002	37°17′N and 32°16′W	1635–1710	Mussels *Bathymodiolus azoricus*
Lucky Strike	4377-3, 09.07.2002	37°17′N and 32°16′W	1635–1710	Mussels *Bathymodiolus azoricus*
Lucky Strike	4379-1, 10.07.2002	37°17′N and 32°16′W	1635–1710	Mussels *Bathymodiolus azoricus*
Lucky Strike	4380-1, 10.07.2002	37°17′N and 32°16′W	1635–1710	Sintra, mussels *Bathymodiolus azoricus*
Lucky Strike	4380-2, 10.07.2002	37°17′N and 32°16′W	1635–1710	Sintra, mussels *Bathymodiolus azoricus*
Lucky Strike	4384-3, 11.07.2002	37°17′N and 32°16′W	1635–1710	Eiffel Tower, mussels *Bathymodiolus azoricus*
Lucky Strike	4384-4, 11.07.2002	37°17′N and 32°16′W	1635–1710	Eiffel Tower, mussels *Bathymodiolus azoricus*
Lucky Strike	4384-5, 11.07.2002	37°17′N and 32°16′W	1635–1710	Eiffel Tower, bacterial mat and mussels *Bathymodiolus azoricus*
Lost City	4368, 04.07.2002	30°07′N and 42°07′W	700–800	Bacterial mat, silt
Lost City	4371, 05.07.2002	30°07′N and 42°07′W	700–800	Bacterial mat, silt
Lost City	4607, 09.08.2003	30°07′N and 42°07′W	700–800	Active zone
Lost City	4800, 27–28.08.2005	30°07′N and 42°07′W	736	Slope of the chimney
Lost City	4803, 28.08.2005	30°07′N and 42°07′W	737	Upper slope of the chimney
Lost City	4805, 28–29.08.2005	30°07′N and 42°07′W	700–800	Washout from a coral
Lost City	29.08.2005	30°07′N and 42°07′W	849	Carbonate sediment below the chimney
Broken Spur	4797, 25–26.08.2005	29°10′N and 43°10′W	3059	Silt at the base of the Spire chimney
Snake Pit	4330, 21.06.2002	23°22′N and 44°57′W	3420–3480	Druse of mussels *Bathymodiolus puteoserpentis*

Males

Diorchic, anterior testis outstretched, posterior testis reflected. Both anterior and posterior testes located on the same side of the intestine, in 89 % males to the right and in 11 % to the left of the intestine. A long blind sac extended parallel to the anterior testis and reaches almost the testis tip (Figs. 2a, ant.b.s., 6a, d). The blind sac constitutes a bundle of coarsely granulated mass with hardly discernible faltering internal lumen. Bursal musculature represents a long series of about 95–104 preanal and 17–25 postanal dorsoventral muscle bundles.

Spicules short, strong, nearly straight, sword-shaped, proximally cephalated, distally pointed (Fig. 6b). Gubernaculum not developed. Cloacal opening flanked by a fringe of cuticular hair-like projections (Fig. 8e, f). A preanal midventral supplementary organ seen laterally as one fleshy papilla is actually a group of two or three pairs of short sensory papillae located very close to one another (Figs. 4b, 8e, f). An arcuate row of about six to eight subventral setae 14–15 μm long situated at either lateral side of the cloacal opening. The pericloacal arcuate row continued anteriorly and posteriorly as straight subventral rows; precloacal-to-caudal row of subdorsal setae present as well.

Females

Monodelphic, prodelphic. An only anterior ovary antidromously reflected and situated to the right side of intestine in 82 % females and to the left side of intestine in 18 % females. Uterus may contain up to 15 fertilized eggs. Eggs measuring 148–602 × 87–156 μm, depending greatly upon how many eggs packaged in the uterus and upon the female size. Demanian system corresponding to the *Oncholaimus* type as formulated by Rachor (1969). A long ductus uterinus extended from the uterus rearward (Fig. 7e, f) and terminally swollen into a bunch of convex cells, i.e. uvetta (Fig. 7g). The latter contacts laterally with the main tube. There left and right copulatory pores present as

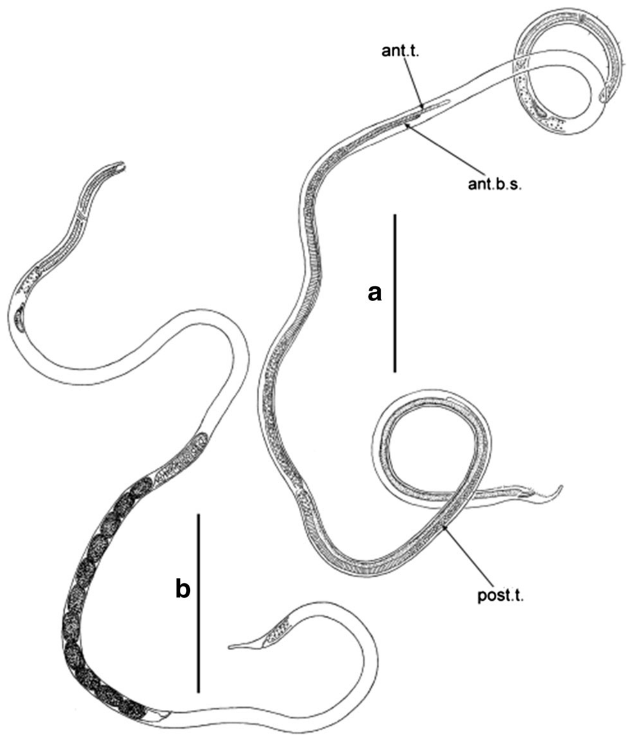


Fig. 2 *Oncholaimus scanicus*, entire. **a** male (Lost City, st. 4890); **b** female (Lucky Strike, st. 4376-1). *ant.b.s.* anterior blind sack, *ant.t.* anterior testis, *post.t.* posterior testis. *Scale bars* 1000 µm

transversal slits anteriorly to the anus (Figs. 7a, 8g). A short but strong duct (main duct) extended from each pore ahead. Posterior part of the main duct often filled with some cells (spermatozoa). The duct continues anterior to the uvetta as ductus entericus. Anterior termination of the ductus entericus (osmosium) difficult to observe.

Gut content

About half of male and female specimens have empty intestine, and other half specimens have some content in the gut. The latter may present a granular material condensed in a sausage or a few pinches of uncertain nature (Fig. 6h, i). The sausage of granular material may be as long as one-tenth of the midgut.

Diagnosis

Oncholaimus

Body large, filiform, 6274–12,379 µm long in males and 7149–13,826 µm in females, index *a* 83.7–118 in males and 58.9–120 in females. Outer labial setae 8.3–12.9 µm in males and 9.9–13 µm in females. Width of amphideal fovea 8.4–21 µm (21–36 % of corresponding body diameter) in males and 11–21 µm (19–26 % of corresponding body diameter) in females. Stoma 40.4–63.4 µm long and 28–42 µm wide in males, 43–68 µm long and 28–43 µm wide in females. Ventral pore situated at a distance 132–220 µm (males) and 139–228 µm (females) from cephalic apex. Tail conicocylindrical, index c' 2.36–4.24 in males and 2.71–4.4 in females. Spicules 81–128 µm long. No gubernaculum. In males, preanal midventral complex of papillae present, postanal midventral papillae absent. In females, preanal body region not narrowed abruptly.

Morphological identification

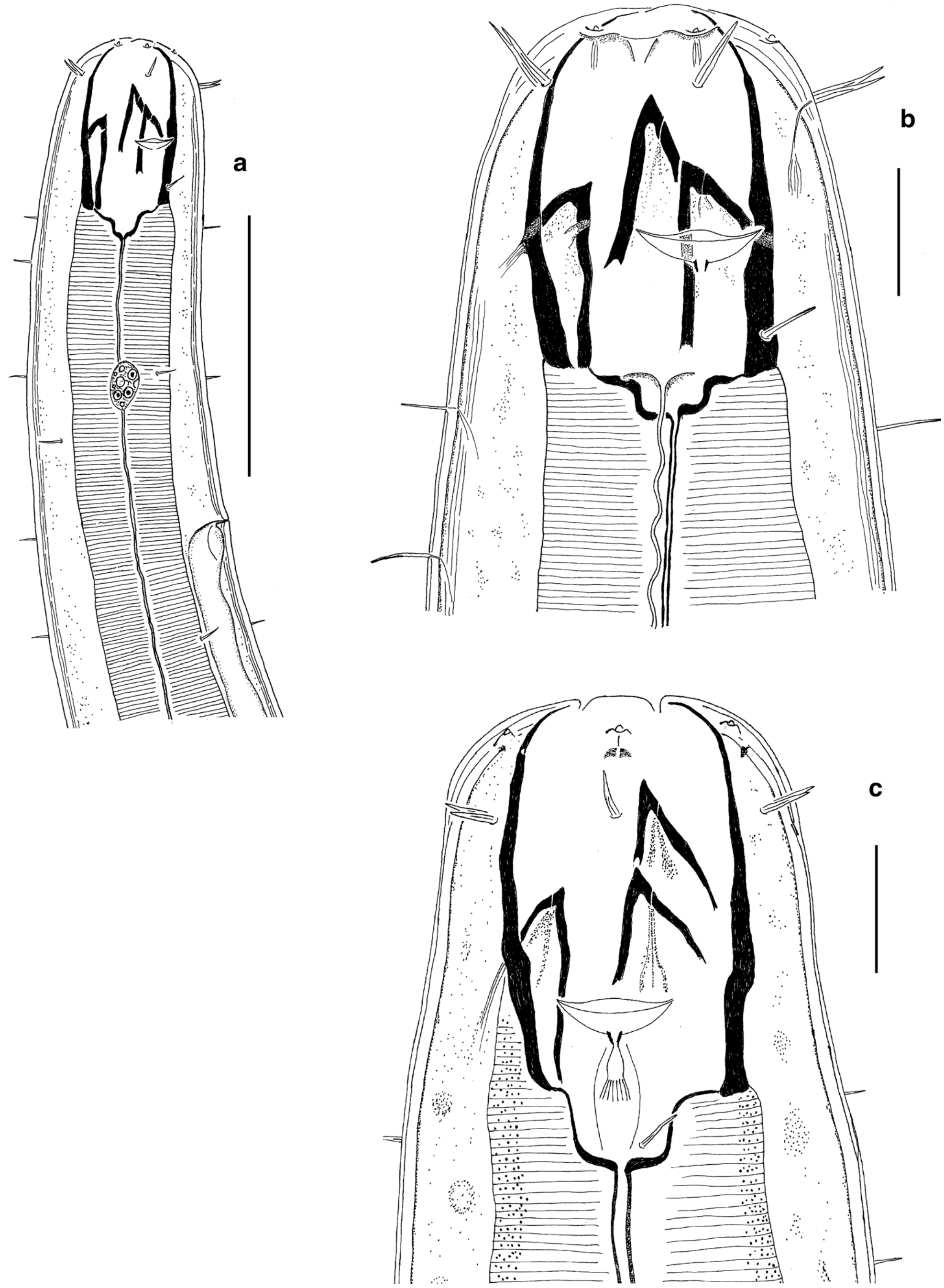
The large genus *Oncholaimus* contains over 100 species, according to NeMys database (Deprez et al. 2005) According to my analysis and count, only 80 species can be considered as valid, whereas other species suffer from incomplete or imperfect descriptions. The species can be easily clustered in two groups based on having or lacking of prominent midventral postanal papilla in males; the hydrothermal species belongs to the group of species lacking the postanal papilla. Most *Oncholaimus* species (58) are featured by modest body size, 2–4 mm in length. Twenty species are distinguished by larger body size and at the same time by the absence of postanal midventral papilla. The hydrothermal species clearly differs from 15 species of the latter group by evident differences in such characters as indices «*a*», «*c*», «c'», stoma length and width, position of secretory/excretory pore and length of spicules. Remaining group includes five closely related species differing in finer details from one another: *O. onchouris* Ditlevsen 1928 (Greenland, Godthaab, tide level), *O. problematicus* Coles 1977 (Cape Province of South Africa, depths 7–87 m, sand to shell gravel), *O. ramosus* Smolanko and Belogurov 1987[1] (Sea of Japan, silty sand, depth 1 m), *O. scanicus* (Allgén 1935) (Öresund, depth 11.5–28 m, clay) and *O. septentrionalis* Filipjev 1927 (Barents Sea, depth 70 m, clay silt).

The hydrothermal species differs from:

1. *O. onchouris*—in males, by indices «*a*» (84–118 vs. 71), «*c*» (45.4–68.7 vs. 30.6), larger distance from cephalic apex to ventral pore (132–220 vs. 70–80 µm, calculated), tail shape (in *O. onchouris* male, the distal digitiform part bent dorsally at an obtuse angle);
2. *O. problematicus*—by the more posterior position of the ventral pore from anterior end (132–220 µm or three stoma lengths vs. 110–150 µm or two stoma lengths); in males, by straight versus distinctly distally curved spicules (see Coles 1977, Fig. 10d) and

[1] Original name is *Oncholaimium ramosum* (Smolanko and Belogurov 1987). The name *Oncholaimium* Cobb 1930 is now considered as a junior synonym of *Oncholaimus* Dujardin 1845 (Rachor 1969: 137).

Fig. 3 *Oncholaimus scanicus*, anterior structures. **a** Male, anterior body (Lost City, st. 4803); **b** male, cephalic end (Lost City, st. 4803); **c** female, cephalic end (Lost City, st. 4890). *Scale bars* **a** 100 μm; **b**, **c** 20 μm



possibly by the presence of preanal midventral papilla (the latter is not mentioned in the original diagnosis of *O. problematicus*); in females, posterior body not swollen in area of preanal copulatory pores;

3. *O. ramosum*—in males, by stoma length (40.4–63.4 vs. 27–30.6 μm) and spicule length (81–198 vs. 66.9–77.6 μm); in females, by indices «*b*» and «*c*′» (8.41–12.4 and 2.71–4.4 vs. 14.8–17.5 and 5.3, respectively) and principally by only two versus numerous, up to 17 copulatory pores;
4. *O. scanicus*—by shorter anterior setae (8.3–13 μm vs. 15 μm); in males, by the presence of preanal midventral papilla (not mentioned in *O. scanicus* by Allgén 1935) and by the absence of two postanal lateral rows of six short conical elevations («2 laterale Längsreihen von 6 kurzen, konischen Erhebungen»); all other dimensions coincide in both species;
5. *O. septentrionalis* (an only female known)—by relatively slimmer body and, respectively greater index «*a*» (58.9–120 vs. 43.5), relatively longer tail (index

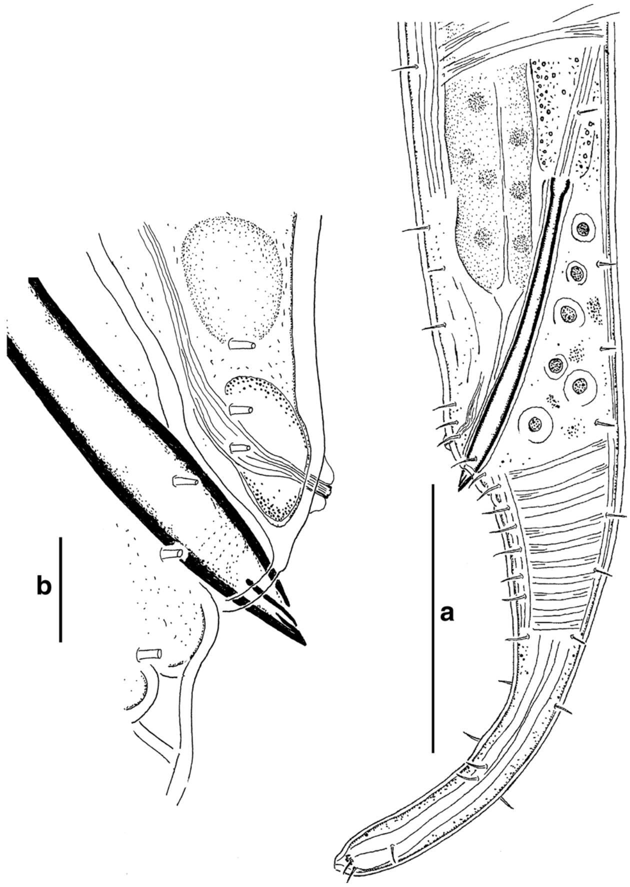


Fig. 4 *Oncholaimus scanicus*, male posterior structures. **a** Male, posterior end (Lost City, st. 4890); **b** spicules tip and preanal supplementary organ (Lost City, st. 4890). *Scale bars* **a** 100 µm; **b** 10 µm

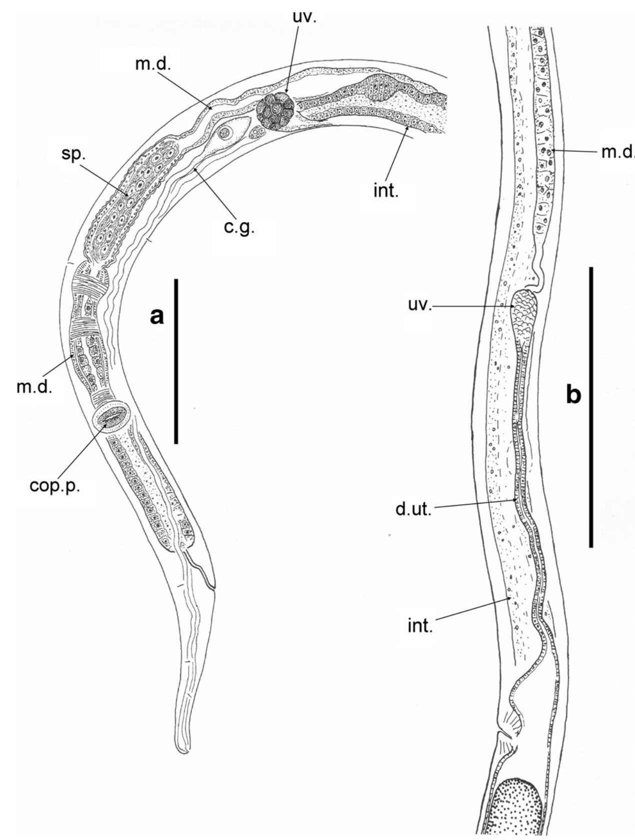


Fig. 5 *Oncholaimus scanicus*, female demanian system. **a** Posterior body (Lucky Strike, st. 4376-1); **b** postvulvar part of body (Lost City, st. 4800). *c.g.* caudal gland, *cop.p.* copulatory pore, *d.ut.* ductus uterinus, *int.* intestine, *m.d.* main duct, *sp.* sperm, *uv.* uvette *Scale bars* **a** 200 µm; **b** 100 µm

«c'» 2.71–4.4 vs. 2.4), bigger distance to the ventral pore (139–228 vs. 125 µm).

Comparison with published descriptions of those five *Oncholaimus* species shows that the hydrothermal species is most related to *O. scanicus* (Allgén 1935). *O. scanicus* has been described by Allgén (1935) on the base of three males, one female and eight juveniles (one male and one female of them are measured) from Öresund (Norway) and was never recorded again, as far as I know. Fortunately, some collection specimens are kept safe and available for study. Dr. Oleksandr Holovachov has kindly examined the specimens after my request and found that («2 laterale Längsreihen von 6 kurzen, konischen Erhebungen») present actually pericloacal setae common in all *Oncholaimus* species including the hydrothermal species. The absence (or presence) of a precloacal papilla could not be confirmed since the extant male type specimen lies not strictly laterally in the slide. In summary, I identify the hydrothermal species as *Oncholaimus scanicus* (Allgén 1935) despite the sharp disparity of habitats.

Notes on morphology of reproductive organs

Females *Oncholaimus scanicus* possess a kind of demanian system typical for *Oncholaimus* defined by Rachor (1969) and then Belogurov and Belogurova (1977). The demanian system named in honour of its discoverer, famous nematologist Johannes G. de Man is a peculiar set of canals, junctions and pores unique for some genera of Oncholaimidae and different in degree of development, from simple (primitive) to more complex (advanced) depending on genera/species; the main feature is the connection between the reproductive system and digestive system (intestine). Structures of the demanian system were studied and analysed thoroughly by Cobb (1930) and Rachor (1969). Coomans et al. (1988) clarified function and meaning of the demanian system by the example of *Oncholaimus oxyuris*. All parts of the demanian system except terminal ducts and copulatory pores are shaped already in virgin females prior to copulation. Maertens and Coomans (1979) and Coomans et al. (1988) observed a peculiar traumatic way of insemination when the male

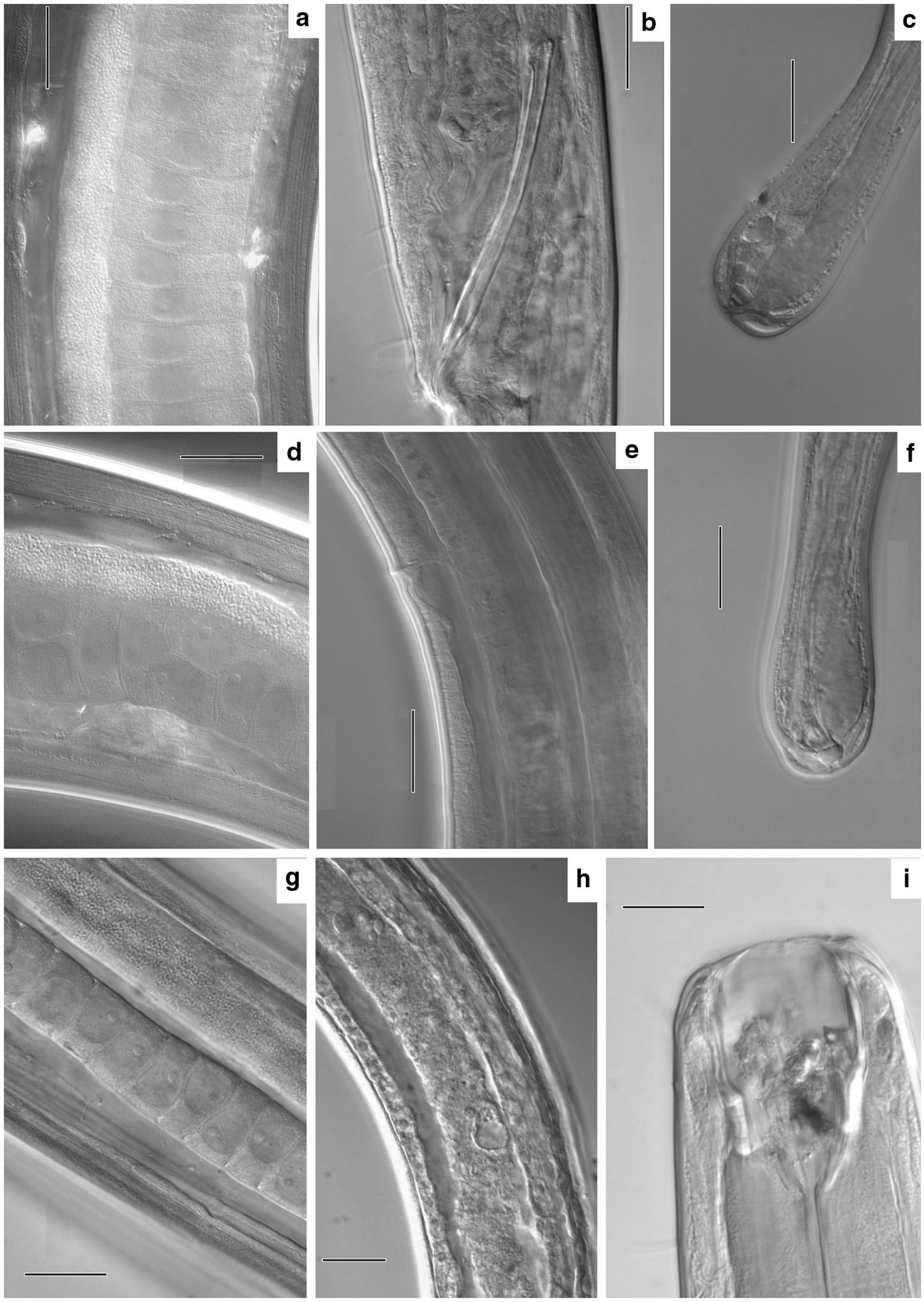


Fig. 6 *Oncholaimus scanicus*, details. **a**, **d** Male anterior testis and anterior blind sack (granular band beside a row of spermatocytes) (Lost City, st. 4800); **b** male spicule and joint of vas deferens with rectum forming cloaca (Menez Gwen, st. 4593); **c**, **f** tail tip and spinneret, female (Menez Gwen, st. 4595); **e** ventral pore and ampulla of secretory/excretory gland, female (Menez Gwen, st. 4595); **g** male posterior testis and vas deferens (Lost City, st. 4890); **h** gut content, female (Lucky Strike, st. 4384); **i** buccal cavity with food lump, female (Menez Gwen, st. 4593). *Scale bars* 20 µm

punctures cuticle of the female hindbody acting by his spicules and secretion. The male releases secret and then sperm through the wound (copulatory pore). The sperm injected into the female reach the main duct of the demanian system moving within the interstitial channel (i.e. terminal duct) shaped by secretion. The spermatozoa are driven forward in the main duct, stored temporarily in the region at uvette, enter through the uvette to the ductus uterinus and finally reach the uterus for fertilization. According to Coomans et al. (1988), the superfluous sperm

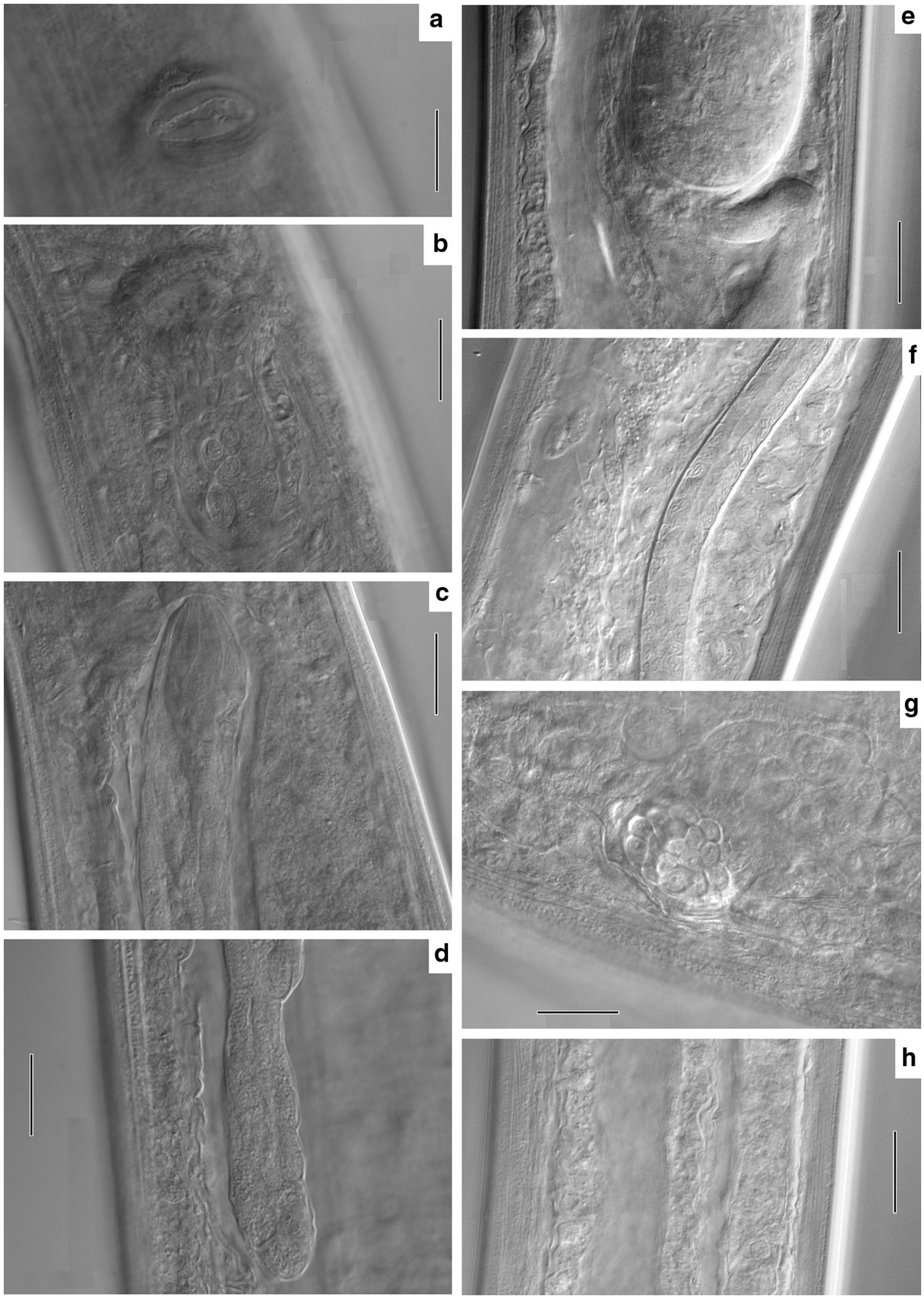


Fig. 7 *Oncholaimus scanicus*, details of female demanian system. **a** Copulatory pore (Menez Gwen, st. 4595); **b–d** rudiment of main duct growing from copulatory pore anteriad (Menez Gwen, st. 4595); **e** joint of uterus with ductus uterinus (Lost City, st. 4800); **f** ductus uterinus (Lost City, st. 4800); **g** uvette (Menez Gwen, st. 4595); **h** intestine and main duct (Lost City, st. 4800). *Scale bars* 20 μm

are moved further to the ductus entericus and evacuated to the intestine through the osmosium, terminal contact of the duct with the midgut wall. Coomans et al. (1988) supposed the sperm injected serves additional functions besides properly fertilization, namely increase in the female's body pressure facilitating egg laying, and supplementary nutrition allowing the female to increase her metabolism.

However, some aspects in reproductive system of *Oncholaimus* need further clarification. First, terminal ducts (interstitial channels of Coomans et al. 1988) in *O. scani-*

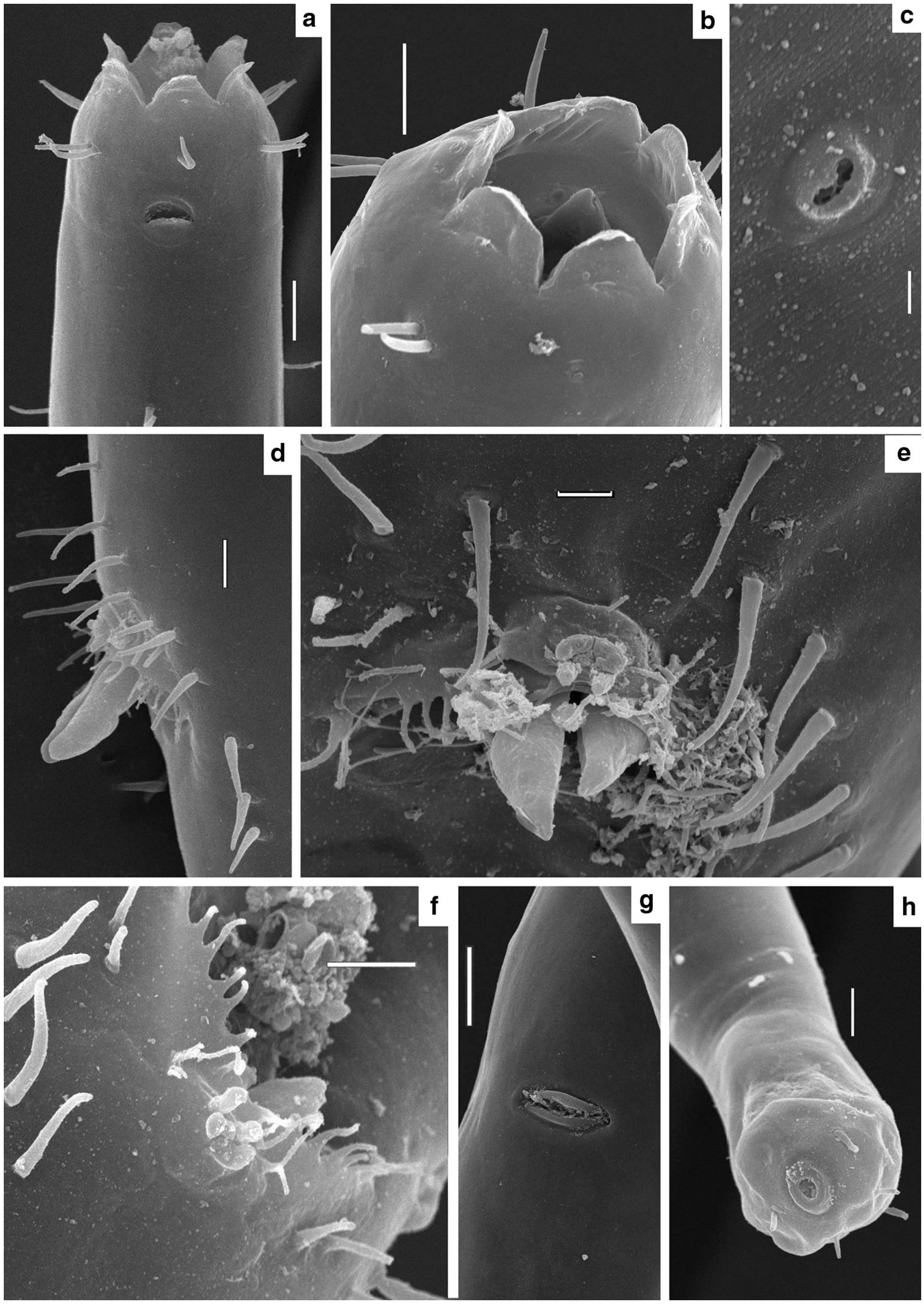


Fig. 8 *Oncholaimus scanicus*, surface structures. **a** Cephalic end laterally; **b** mouth opening with left subventral onch visible; **c** ventral pore; **d–f** precloacal setae, fringe of cuticular projections, spicule's tips, precloacal complex of papilla; **g** copulatory pore on female's posterior body; **h** tail tip with terminal pore. *Scale bars* **a** 10 µm; **b** 10 µm; **c** 1 µm; **d** 5 µm; **e** 3 µm; **f** 5 µm; **g** 20 µm; **h** 5 µm

cus seem to be well-shaped tubular organs with complicated (seemingly cellular) walls rather than purely sperm tract in secretion. In a recently inseminated female, the sprout of terminal duct growing from the copulatory pore forward to the main duct (Fig. 7b–d) looks as having compound wall. Coomans et al. (1988) observed that in *O. oxyuris* the epidermal tissue of lateral and dorsal regions becomes very prominent and shows glandular activity around the interstitial channels. Second point is stable number and position of copulatory pores in *O. scanicus*. Copulatory pores are always paired and bilateral in all females inspected and located always in preanal body

Table 2 Morphometrics of *Oncholaimus scanicus* from the site Menez Gwen

Character	Males					Females				
	n	Min–max	Mean	SD	CV	*n*	Min–max	Mean	SD	CV
L	27	6945–11,390	9544	1023	10.7	29	7690–11,230	9270	905	9.77
a	24	69.5–113	90	10.9	12.2	24	58.9–97.6	70.3	8.83	12.6
b	27	7.89–13.6	10.6	1.08	10.2	29	8.65–12.1	10.1	0.9	8.93
c	27	45.4–68.7	55.7	6.82	12.2	27	38.5–53.5	46.6	4.13	8.86
c′	26	2.64–4.24	3.27	0.34	10.4	25	3.0–0–4.25	3.39	0.32	9.44
V %	–	–	–	–	–	29	65.1–77.5	69.1	2.45	3.55
Body diameter at level of cephalic setae	26	43–53	47.5	2.09	4.4	29	43–55	48.4	2.36	4.88
Body diameter at level of nerve ring	22	68–99	82.1	6.98	8.51	30	73–107	85.5	8.26	9.67
Body diameter at level of cardia	21	77–128	100	14.9	14.9	26	91–144	107	14.4	13.5
Midbody diameter	24	80–151	106	16.9	15.8	25	99–176	134	21.8	16.3
Anal body diameter	26	45–60	52.8	3.57	6.76	26	45–68	59.5	5.23	8.79
Length of outer labial setae	10	9.2–12.9	10.9	1.15	10.5	9	10.4–13			
Width of amphideal fovea	5	10.7–12.7	11.8	0.79	6.68	5	11–13.8	12.0	1.09	9.07
Width of amphideal fovea as percentage of c.b.d., %	4	21.8–27.0	24.0	2.19	9.11	5	21.7–26.4	23.3	1.85	7.95
Total stoma length measured along ventral rhabdion	12	45–53	49.4	2.09	4.23	18	44.5–52	48.7	2.07	4.25
Maximal stoma width	12	28–33	30.7	1.91	6.22	18	28–37.3	31.6	3.13	9.92
Length of dorsal onch from tip to posterior end of rhabdion	8	27–30.5	28.6	1.39	4.85	11	25.3–31	28.1	1.96	6.99
Length of left subventral onch from tip to posterior end of rhabdion	8	32–39.6	36.3	2.82	7.76	11	32.9–37.9	35.4	1.69	4.78
Length of right subventral onch from tip to posterior end of rhabdion	8	24.6–34.5	29.6	3.08	10.4	11	21.9–33	27	3.02	11.2
Distance from cephalic apex to ventral pore	24	135–211	174	20.6	11.9	24	139–226	183	21.6	118
Spicule's length along arch	24	81–102	91.5	5.06	5.53	–	–	–	–	–

Measures in µm except for ratios

area. An open question is whether one female is inseminated obligatorily by two males or one male makes two copulatory pores, one on each lateral side of the body.

The most striking structure observed in males of *Oncholaimus scanicus* but here not yet properly described and understood is anterior blind caecum. This is a very long bundle originated from the site of bifurcation of two testes and extended ahead parallel to the anterior outstretched male gonad (Fig. 6a). The testis and caecum lie clasped tightly, without any spaces between them. Anterior tip of the blind caecum almost reaches the tip of the anterior testis. The caecum represents a coarse granular mass with a hardly discernible tight axial canal; the blind caecum looks like a secretory organ. This structure is mentioned surprisingly rarely in publications on so common and well-known genus *Oncholaimus*. Cobb (1930, 1932) discovered and drew this caecum under the name "accessory gland" in species of *Adoncholaimus*, *Metoncholaimus* and *Oncholaimus*; he considered this structure as homologous of a part of female demanian system. Rachor (1969) found the blind caecum in species of the same genera and *Meyersia* and studied cross sections; he described the caecum built of columnar glandular epithelium resembling glandular part of vas deferens. Anterior blind caecum was also mentioned by Heyns and Coomans (1977), and Coomans and Heyns (1983) for two inland-water *Oncholaimus* species in Africa. Function of the anterior blind caecum remains unascertained, but probably it serves as an intense glandular organ whose secretion corroding the female cuticle during copulation and then building terminal ducts to the main tube.

Intersite variability

Oncholaimus scanicus was sampled in three sites, Menez Gwen, Lucky Strike and Lost City (Tables 3, 4, 5). Notably, this species is not found in the Rainbow site located in between Lucky Strike and Lost City. Populations of these three sites somewhat differ from one another. To evaluate differences, several most indicative characters were chosen for comparative morphological analysis. The number of measured specimens is the highest for Menez Gwen and much less for other two sites.

Table 3 Morphometrics of *Oncholaimus scanicus* from the site Lucky Strike

Character	Males					Females				
	n	Min–max	Mean	SD	CV	*n*	Min–max	Mean	SD	CV
L	13	6275–9820	7935	1112	14.0	7	7150–9875	8715	1049	12.0
a	9	83.7–118	97.8	11.6	12.0	7	80.2–97.4	86.5	8.16	9.43
b	9	9.23–11.1	10.2	0.58	5.70	7	10.1–11.3	10.7	0.47	4.39
c	9	40.5–59.5	47.7	6.44	13.5	7	39.5–54.2	45.7	5.96	13.1
c′	9	2.78–3.69	3.34	0.26	7.78	4	3.12–4.40	3.75		
V %	–	–	–	–	–	7	66.5–68.7	67.7	0.89	1.31
Body diameter at level of cephalic setae	8	38–43	41	1,85	4.51	3	40.0–44.0	41.7		
Body diameter at level of nerve ring	9	63–73	68	3.16	4.65	3	63.0–72.0	68.0		
Body diameter at level of cardia	7	63–78	72.4	5.62	7.76	3	72.0–99.3	81.4		
Midbody diameter	9	72–87	77.9	4.81	6.10	4	89.0–112	97.8		
Anal body diameter	9	45–52	47.9	2.37	4.95	4	47.0–55.0	52.1		
Length of outer labial setae	7	8.30–12.8	10.5	1.35	12.9	3	9.90–10.8			
Width of amphideal fovea	5	8.40–11.0	10.1	1.06	10.5	2	11.0–11.4			
Width of amphideal fovea as percentage of c.b.d., %	5	20.8–25	23.4	1.66		1	26,1			
Total stoma length measured along ventral rhabdion	8	40.4–46.5	43.9	2.14	4.88	3	43.0–48.0	45.1		
Maximal stoma width	8	28–32	29.8	1.28	4.29	3	28.9–32.0	30.5		
Length of dorsal onch from tip to posterior end of rhabdion	6	21–26	23.5	1.94	8.26	3	25.5–27.5	26.3		
Length of left subventral onch from tip to posterior end of rhabdion	7	30–37	32.4	2.23	6.77	3	32.0–35.0	33.9		
Length of right subventral onch from tip to posterior end of rhabdion	5	24.5–28	26	1.27	4.88	3	26.4–29.0	27.8		
Distance from cephalic apex to ventral pore	8	132–192	166	20.0	11.9	3	169–227	189		
Spicule's length along arch	9	83–89	86.1	2.62	4.88	–	–	–	–	–

Measures in µm except for ratios

Hypothesis formulated as "no differences between populations" was tested using classical discriminant analysis. For calculation, PAST package was employed. The missing data were supported by column average substitution. That is critical because of the type with unequal data sets and with a number of missing values. The output of program is a scatter plot of specimens along the first two canonical axes produces maximal and second to maximal separation between all groups. The axes are linear combinations of the variables as in PCA, and eigenvalues indicate amount variation explained by these axes. For further details of algorithms, see Hammer et al. (2001). These scatter plots are present in Fig. 9a, b for males and females separately.

Discriminant analysis confirms no differences between specimens from Menez Gwen and Lucky Strike. The data points are overlapping, while specimens of both sexes of the remote Lost City are separated well enough. That is supported by confusion matrix with no misclassification cases for males and one misclassification for females from there (Table 5). There are no clear separation and high number of failure between other two groups.

Males from Lost City separated well from other two populations by stoma length and spicules length. All individual characters for Menez Gwen and Lucky Strike are overlapping.

In discriminant analysis (Fig. 9), the first axes are responsible for segregation males from Lost City. It represents mostly the input of body length, length of spicules and stoma length. For females, the most important variables are body length, index *a* and index *V*. Taken separately these variables are shown in Fig. 9c, d for males and Fig. 9f–h for females. For each example, the 25–75 per cent quartiles are drawn using a box. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with short horizontal lines («whiskers»).

So, it is confirmed that no differences occur between populations from Menez Gwen and Lucky Strike, and specimens from Lost City differ significantly from other two sites. These results correspond well with the distance

Table 4 Morphometrics of *Oncholaimus scanicus* from the site Lost City, summarized 2002, 2003, 2005

Character	Males					Females				
	n	Min–max	Mean	SD	CV	*n*	Min–max	Mean	SD	CV
L	13	8715–12,380	10,455	1313	12.6	8	8990–13,825	11,245	1501	13.3
a	11	92.5–117	104	8.27	7.92	5	87.3–120	102	13.8	13.6
b	13	7.88–10.9	9.44	0.91	9.64	8	8.41–12.4	9.69	1.25	12.9
c	13	46.8–66.7	57.3	6.15	10.7	6	40.5–64.1	52	9.70	18.7
c′	10	2.36–3.31	2.85	0.35	12.3	5	2.71–3.75	3.20	0.49	15.3
V %	–	–	–	–	–	8	75.5–81.3	79.5	1.80	2.26
Body diameter at level of cephalic setae	11	48–57	52.2	2.57	4.92	4	49.0–56.0	51.7	2.99	5.78
Body diameter at level of nerve ring	11	83.4–95.5	86.9	3.62	4.17	4	87.0–89.0	87.8	0.96	1.09
Body diameter at level of cardia	10	85–105	92.7	5.79	6.24	5	83.0–96.9	91.4	5.42	5.93
Midbody diameter	11	88.6–118	101	8.76	8.65	5	101–124	109	9.08	8.33
Anal body diameter	10	56.7–70	64	3.74	5.85	5	60.0–69.0	63.6	3.78	5.95
Length of outer labial setae	7	8.8–12.6	11	1.51	13.7	2	9.00–12.4			
Width of amphideal fovea	9	17–21	19.1	1.39	7.27	3	19.2–21.0			
Width of amphideal fovea as percentage of c.b.d., %	9	27.5–35.6	30.7	2.57	8.36	3	31.6–35.6			
Total stoma length measured along ventral rhabdion	11	54.5–63.4	59.7	3.2	5.36	4	63.3–68.0			
Maximal stoma width	11	37.8–42	40	1.31	3.28	4	39.0–43.0			
Length of dorsal onch from tip to posterior end of rhabdion	11	25.5–36.9	32.3	3.42	10.6	4	30.0–41.0			
Length of left subventral onch from tip to posterior end of rhabdion	11	43.1–54.8	48.1	3.47	7.22	4	49.4–55.0			
Length of right subventral onch from tip to posterior end of rhabdion	10	25.5–38	33.2	3.62	10.9	4	33.8–39.0			
Distance from cephalic apex to ventral pore	10	145–220	180	27.3	15.2	6	149–228	193	33.0	17.1
Spicule's length along arch	12	106–128	118	6.69	5.65	–	–	–	–	–

Measures in µm except for ratios

between sites. Menez Gwen and Lucky Strike are situated in some 40 miles from each other, while Lost City lies more than 400 miles off. Apart the differences in environmental condition, the distance itself might be the most important factor for morphological differences between populations. Furthermore, nematode habitats are also different in Menez Gwen and Lucky Strike on the one hand and Lost City on the other hand: in first and second sites, the nematodes were sampled from aggregations of mussels *Bathymodiolus azoricus*, while from the third site from silt and bacterial mat on rocks (those mussels were not indicated as a dominant microbenthic species in Lost City—e.g. Kelley et al. 2007). Further genetic studies could elucidate significance of these morphometric differences of populations from different sites.

Order CHROMADORIDA Chitwood 1933
Family CYATHOLAIMIDAE Filipjev 1918
Paracanthonchus Micoletzky 1924
***Paracanthonchus olgae* sp. n.**

Table 5 Confusion matrix for males and females *Oncholaimus scanicus* from three sites

	Menez Gwen	Lucky Strike	Lost City	Total
Males				
Menez Gwen	25	3	0	28
Lucky Strike	3	10	0	13
Lost City	0	0	**13**	13
Total	28	13	13	54
Females				
Menez Gwen	28	2	1	31
Lucky Strike	2	5	0	7
Lost City	0	0	**8**	8
Total	30	7	9	46

Numbers of points in each given group (rows) are assigned to the different groups (columns) by the classifier. Ideally, each point should be assigned to fits respective given group, giving a diagonal confusion matrix. Off-diagonal counts indicate the degree of failure of classification

Bold figures mean complete correspondence

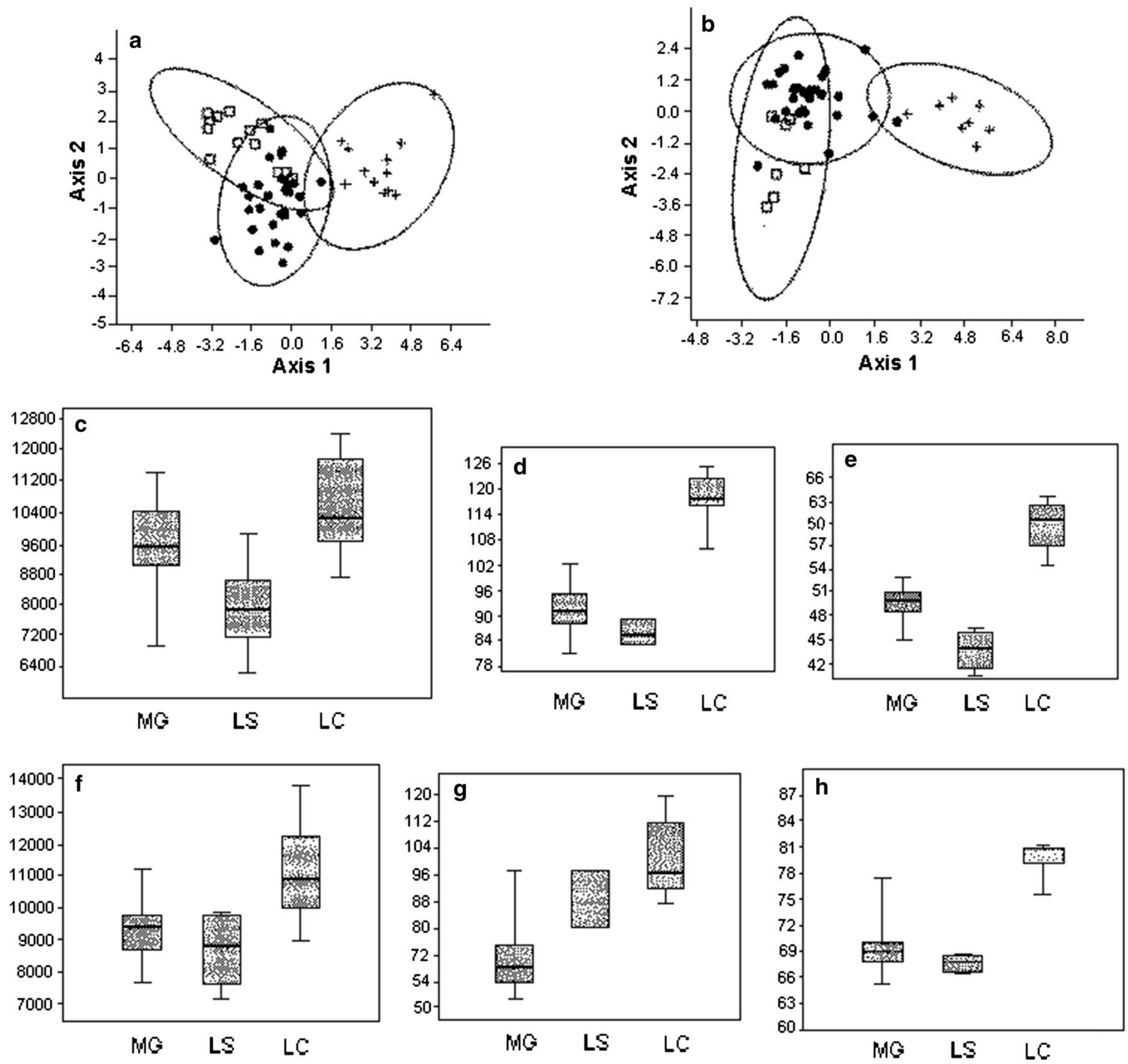


Fig. 9 Results of discriminant analysis (PAST v.3) for males (**a**) and females (**b**). Specimens from Menez Gwen are marked by dots, from Lucky Strike by open squares and from Lost City by crosses. 95 % Confidential ellipses are shown for each group; **c**–**e** "box and whiskers" plots for males in sites Menez Gwen (MG), Lucky Strike (LS) and Lost City (LC), **c** body length, **d** length of spicules, **e** length of buccal cavity; **f**–**h** the "box and whiskers" plots for females, **f** body length, **g** length of spicules, **h** length of buccal cavity

Figures 10, 11, 12, 13, 14, 15, Tables 6, 7: morphometrics.

Material

Holotype male (Rainbow, st. 4402), 20 paratype males (Rainbow, st. 4819) and 18 paratype females (Rainbow, st. 4819). The types are deposited in nematode collection of Senckenberg Institute (Frankfurt am Main, Germany) under the inventory numbers SMF 17028 (holotype) and SMF 17029–17033 (slides with paratypes).

Type locality

Northern Mid-Atlantic Ridge, Rainbow hydrothermal site (36°13′N and 33°54′W), depths 2260–2350 m. Washout from a druse of mussels *Bathymodiolus azoricus*. 47th cruise of RV «Academician Mstislav Keldysh», dive 27/30 of the submersible Mir-1, 2 July 2002.

Etymology

The species is named in honour of the scientist Olga Kamenskaya (P.P. Shirshov Institute of Oceanology,

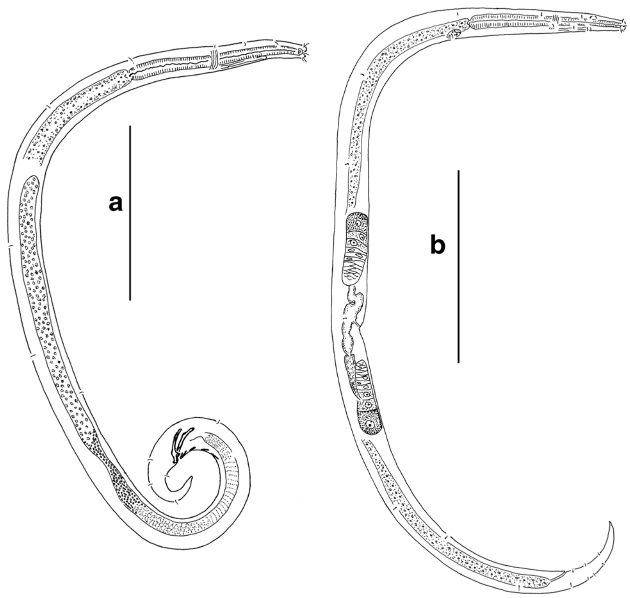


Fig. 10 *Paracanthonchus olgae* sp. n., entire. **a** Holotype male (Rainbow, st. 4402); **b** paratype female (Rainbow, st. 4819). *Scale bars* 200 μm

Moscow) who transferred me the collected nematodes for identification.

Description

General

Body elongate fusiform or elongate spindle-shaped. External striation of the cuticle clearly discernible at only concave areas of the body, e.g. on ventral side of the tail. Cuticle finely punctuated, without any trace of lateral differentiation. In the cervical region, the large punctuations intermitted with barely visible tiny dots; they arranged in regular close transversal rows. In the intestinal region, equally small punctuations arranged tight with unclear transversal rows. The punctuations again large and not arranged in rows on the lateral sides of the tail. Small crater-like pores arranged in two longitudinal rows, laterodorsal and lateroventral. Thus, the holotype male on the right body side with 74 pores in the laterodorsal row (16 pores in the pharyngeal region +49 pores in the midgut region +8 pores in the tail region) and 87 pores in the lateroventral row (15 + 63 + 8, respectively). The pores associated with subcuticular epidermal glands (Fig. 15c). Setae or setae-like structure (or filament secretions?) arising from some pores. A few true short (3–4 μm) somatic setae also present in the same rows.

Six inner labial setae short (1.7–3.0 μm in males, 1.2–2.5 μm in females) and smooth. Six outer labial setae long (7.7–9.0 μm in males, 6.3–9.0 μm in females) and slightly two-partite, at that proximal part about two-thirds and distal part one-third of total seta length. Four cephalic setae also slightly two-partite and 5.5–8.5 μm in males, 6.7–10.0 in females.

Amphideal fovea situated relatively close to the labial region, large, rounded in the external outline, ventrally coiled in a spiral of five turns. In males, amphideal fovea 8.0–11.0 μm (31–42.5 % c.b.d.) wide, distance from the cephalic apex to the fovea 6.0–9.9 μm; the same in females 6.0–7.0 μm (30–35 % c.b.d.), 8.0–9.5 μm, respectively.

Buccal cavity irregularly conoid or cyathiform, 15–25 μm long and 7.7–8.5 μm wide in males, 18.5–24 μm long and 4.5–10 μm wide in females. Cheilostoma 3.7–8.1 μm long in males and 5.2–7.6 μm long in females, strengthened by twelve distinct rugae (cheilorhabdia). Pharyngostoma irregularly conoid or cyathiform, armed with a large pointed dorsal tooth and two equal ventrosublateral pairs (left and right) of much smaller equal acute teeth. In each ventrosublateral pair, the teeth situated close one after another. The dorsal tooth is turned back in some fixed specimens in slides—this obviously indicates a moving of the tooth at an instant of food uptake (Fig. 15b). Pharynx cylindroid and evenly muscular throughout its length.

Small, slightly elongate ventral gland cell body with a nucleus and granulated cytoplasm situated ventrally to the cardia (Fig. 15d). Neck of the gland extended anterior becoming clearly discernible anteriorly to the nerve ring. The neck terminated in an oval ampule and short distinct canal with external ventral pore behind the buccal cavity. Distance from anterior end to the ventral pore 40–60 μm in males and 45–50 μm in females. There two oval vacuolized pseudocoelomocytes to the right and to the left of the ventral gland cell body (Fig. 15d).

Males

A single anterior outstretched testis situated to the right of the intestine in all males. Spicules weakly sclerotized, distally pointed, proximally slightly narrowed. Gubernaculum paired, consists of two large spoon-shaped parts a little shorter than spicules; wide truncated and arcuated distal ends of the parts armed with median conical spike and numerous tiny spinelets (Fig. 15a); the median spike may be not clearly discernible in lateral position of the body. Five midventral precloacal supplementary organs equal in shape and size, 10–12 μm long; two posteriormost supplements close together, whereas three anterior ones separated at greater equal distances from one another. Each supplement consists of a slanting slightly cuticular tube and a pit edged with a sclerotized rim. The tube disposed at a very acute angle to the body wall. The tube slightly widened posteriorly and protruded a little outward through the pit. However, the supplementary organs are hardly

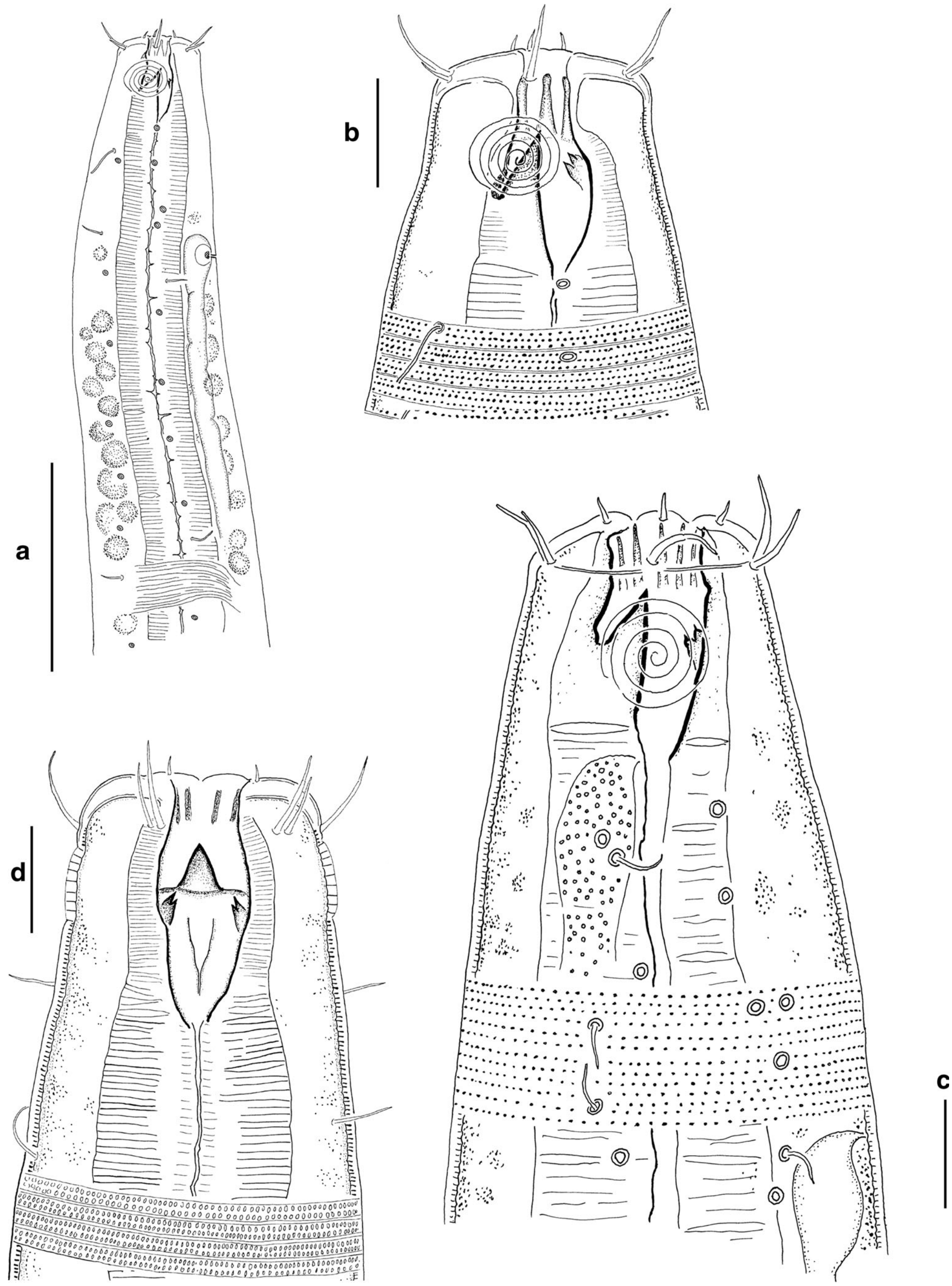


Fig. 11 *Paracanthonchus olgae* sp. n. anterior ends. **a** Holotype male (Rainbow, st. 4402), anterior body; **b** holotype male (Rainbow, st. 4402), cephalic end; **c** paratype female (Rainbow, st. 4819), cephalic end; **d** female (Lucky Strike, st. 4346), midventral view of cephalic end. *Scale bars* **a** 50 μm; **b–d** 10 μm

visible in some specimens. Five supplements more or less distinct in nine males out of 17 males; only two posteriormost precloacal supplements close to one another other discernible in six males, three solitary anteriormost and no two precloacal visible in one male, and no supplements at all in one male.

Tail conical, with terminal conical spinneret 5–9 μm long.

Females

In nearly all females, the body narrowed ventrally just posterior to the vulva. Ovaries paired and antidromously reflexed. Anterior ovary situated either to the right of the intestine and posterior ovary to the left of the intestine (nine females) or anterior ovary to the left and posterior ovary to the left of the intestine (one female).

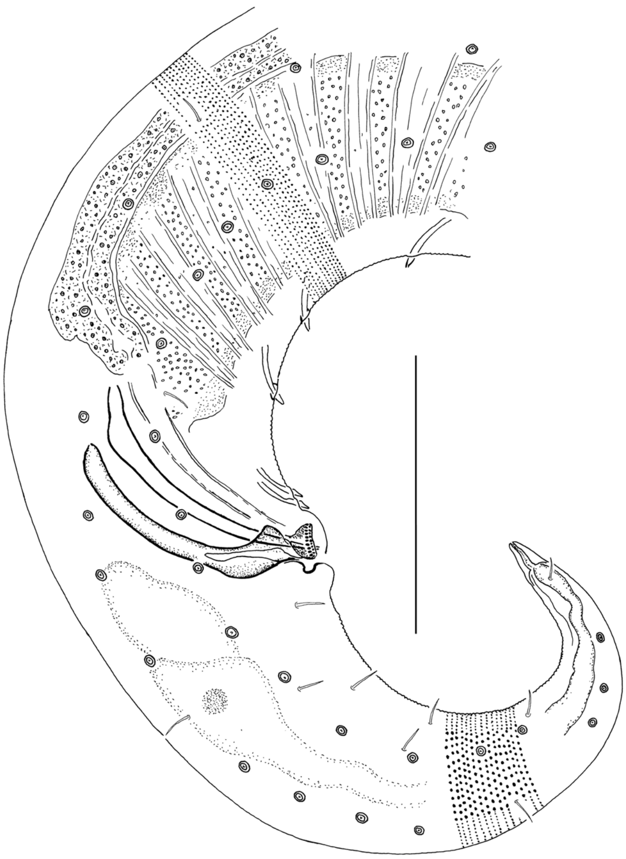


Fig. 12 *Paracanthonchus olgae* sp. n., posterior body of the holotype male (Rainbow, st. 4402). *Scale bar* 50 µm

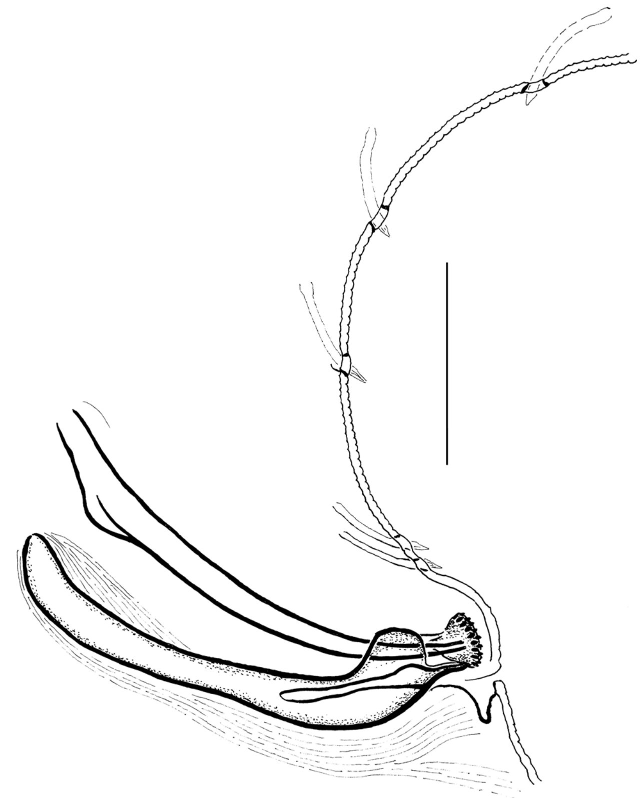


Fig. 13 *Paracanthonchus olgae* sp. n., copulatory apparatus and supplementary organs of the holotype male (Rainbow, st. 4402). *Scale bar* 20 µm

Gut content

Midgut is filled in about 62–63 % males and females. Composition of the gut content varies considerably. Spheric to oval bodies 5–9 µm in size, with granular content occur in the gut lumen commonly (Fig. 15h). They are often accompanied with pinches of granular fibrous particles, yellowish drops, strings of granular paste with addition of some bigger particles (Fig. 15f, g). One female even contains a nematode juvenile swallowed in the gut (Fig. 15i).

Diagnosis

Paracanthonchus

Body length 1299–1799 µm in males, 1325–1852 µm in females. Amphideal fovea spirally coiled in about five turns. Buccal cavity armed with one large acute dorsal tooth and two pairs of minute ventrosublateral teeth. Monorchic, testis outstretched. Five equal weakly cuticularized midventral supplementary tubules, two posteriormost tubules situated close together and just close to the cloacal opening; the supplements may vary in number and distinctness. Gubernaculum paired, proximal part elongate spoon-like, distal part expanded and bears submedian spike and numerous tiny denticles. Female body with a distinct ventral narrowing just posterior to vulva. Oviparous.

Variability of supplementary organs

Population of the Rainbow hydrothermal site shows a remarkable individual variability in number and even shape of the midventral preanal supplementary organs. An only male has five well-developed and very distinct tubular supplementary organs, two posteriormost of them are close together and situated just anterior to the cloacal opening and three other are separated by nearly equal distances (pattern 1 + 1 + 1 + 2). This specimen is denoted as holotype (Fig. 13). Seven other males possess also five supplements arranged in the same pattern 1 + 1 + 1 + 2, but the supplements look weak or very weak and less distinct; in two males, the pattern may be even 1 + 1 + 1 + 1 since it is almost impossible to discern, whether the posteriormost preanal supplement is single or paired. Six males have only two posteriormost supplements

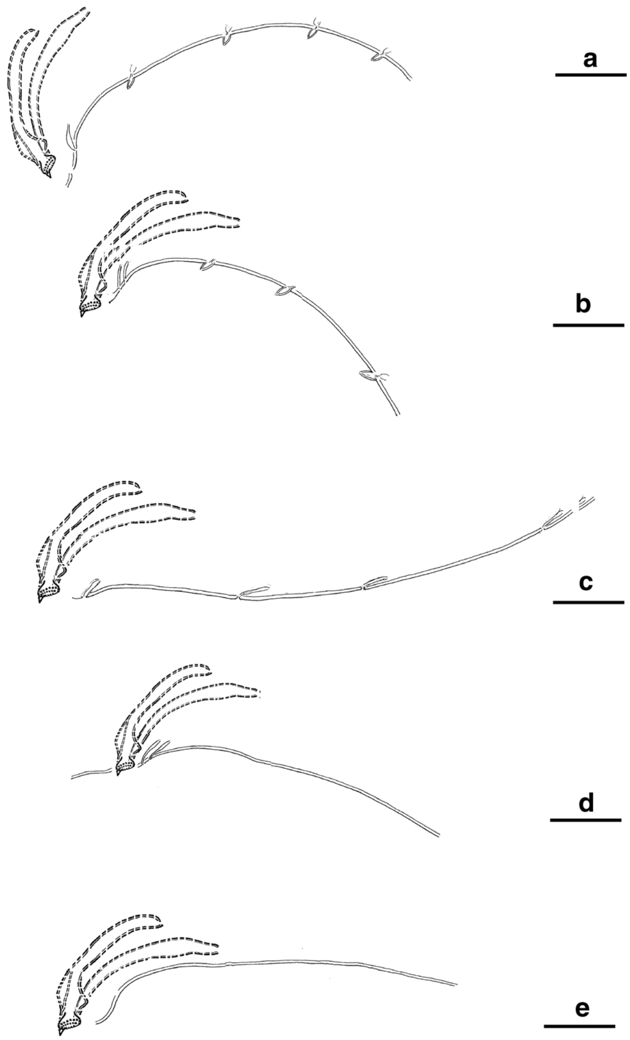


Fig. 14 *Paracanthonchus olgae* sp. n., variation of supplements (Rainbow, st. 4819) in male paratypes. *Scale bars* 20 µm

close together (pattern 0 + 0 + 0 + 2). One male has three supplements 1 + 1 + 1 + 0, and these supplements are conical papilloid projections, not tubes. In two males with pattern 1 + 1 + 1 + 2 or 1 + 1 + 1 + 1, the supplements present weak tubes combined with conical projections. At last, in four males no supplements at all were found (Fig. 14).

I assume the supplement pattern 1 + 1 + 1 + 2 as a basic one, and other variations as deviations. Comparison with other species is also conducted taking into consideration the 1 + 1 + 1 + 2 pattern. However, variability of the supplement row lowers reliability of this character in species identification.

Comparison

Paracanthonchus is a very large genus. According to the newest review of Miljutina and Miljutin (2015), the genus includes 63 valid species names except for those which have been considered formerly by somebody as *species inquirendae* or junior synonyms. The list permits to be further shortened during a future revision by excluding some more species having doubtful generic identity because of, for example, other type of precloacal supplements or whose descriptions lack males and other important details.

The new species belong to a set of species grouping around *Paracanthonchus caecus* (Bastian 1865) and sharing a buccal cavity armed with a large pointed dorsal tooth and two pairs of minute subventral teeth, gubernaculum distally (ventrally) expanded and armed with numerous tiny denticles, and four to six nearly equal tubular preanal supplements with two posteriormost ones often close to one another. Vincx et al. (1982) performed a very detailed study of *Paracanthoncus* species related to *P. caecus* and defined characters for discrimination close species. The most evident and reliable character for species discrimination is dentition of the distal gubernaculum. Seven species share a similar gubernaculum with numerous minute denticles on the expanded distal part: *P. austrospectabilis* (Wieser 1954), *P. heterodontus* (Schulz 1932), *P. kamui* Kito 1981, *P. latens* Gourbault 1985, *P. margaretae* Inglis 1970, *P. sabulicolus* Bouwman 1981, *P. serratus* Wieser 1959.[2] The hydrothermal species differs from all of them by, respectively: from *P. austrospectabilis*—inner labial setae 1.7–3.3 versus 4.5 µm, outer labial setae 7.7–9 versus 17 µm, number of preanal tubular supplements five versus six; from *P. heterodontus*—inner labial setae 1.7–3.3 versus 4 µm, outer labial setae 7.7–9 versus 11 µm, width of the amphideal fovea 8–11 versus 13 µm, monorchic versus diorchic male reproductive system, and oviparity versus ovoviviparity; from *P. kamui*—outer labial setae 7.7–9 versus 13 µm, monorchic versus diorchic reproductive system, five equal versus six unequal tubular supplements; from *P. latens*—body length in males 1299–1779 versus 1840–2458 µm, five equal versus four unequal tubular supplements; from *P. margaretae*—five equal versus six unequal tubular supplements; from *P.sabulicolus*—five versus four tubular supplements and c′ 2.4–3.4 versus 4.4; from *P. serratus*—body length in males 1299–1779 versus 2690 µm, five versus six tubular supplements.

Order CHROMADORIDA Chitwood 1933
Family CHROMADORIDAE Filipjev 1927
Prochromadora Filipjev 1922
Prochromadora helenae sp. n.

Figures 16, 17, 18c, e, g, h, Table 8: morphometrics

[2] Lorenzen (1972a) considered *Paracanthonchus serratus* as a junior synonym of *P. macrodon* (Ditlevsen 1918).

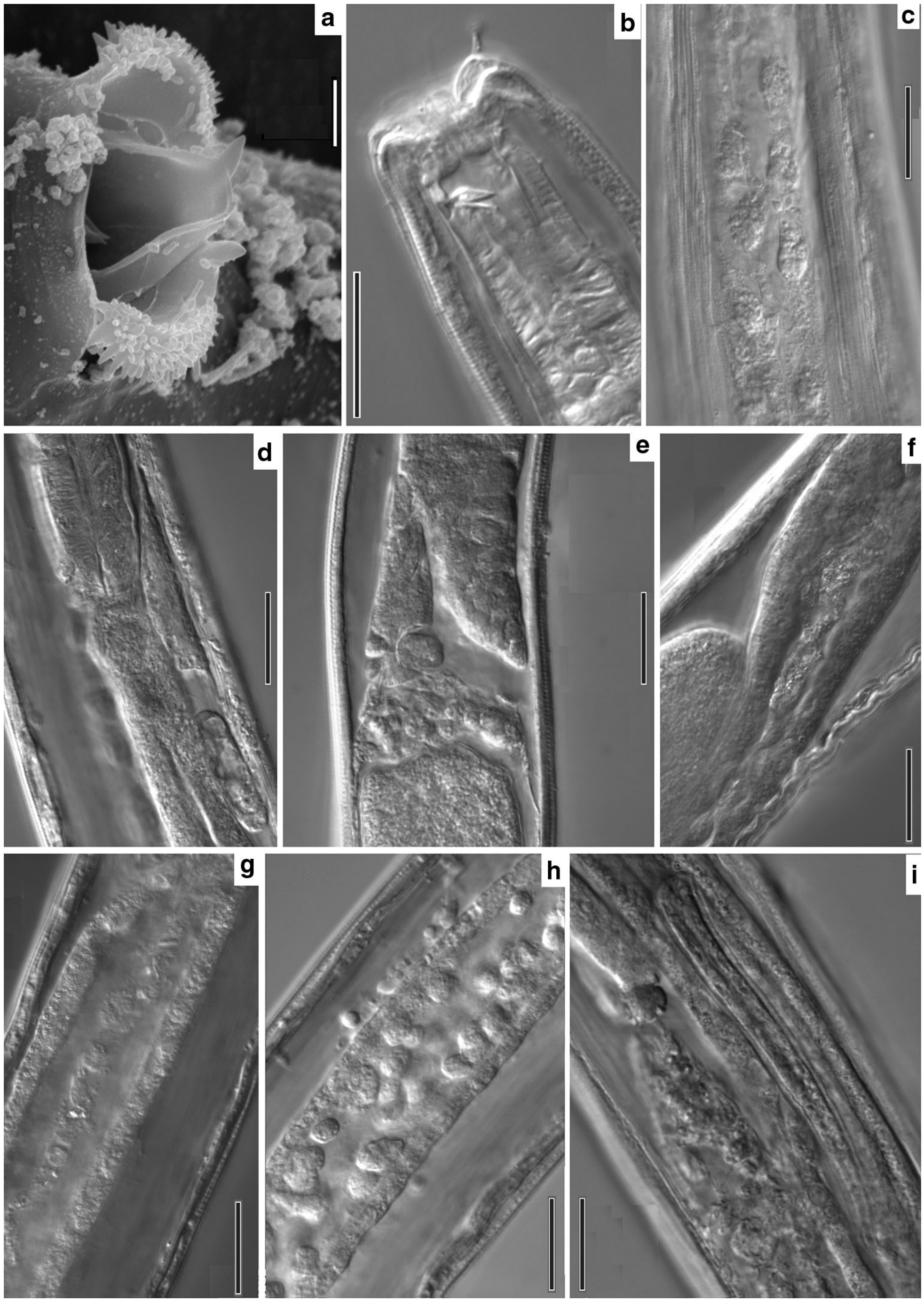


Fig. 15 *Paracanthonchus olgae* sp. n., details. **a** Male cloacal opening with distal parts of the gubernaculum protruded (SEM); **b** buccal cavity with the dorsal tooth turned back; **c** lateral epidermal glands; **d** area of posterior pharynx—anterior midgut, ventral gland cell body and a pseudocoelomocyte; **e** part of the female reproductive system, germinal zone of the ovary, oviduct, sphincter, part of the uterus with spermatozoa and ovum; **f** part of a maturing oocyte and midgut with content as light-refracting grains; **g** midgut content as a mass of irregular light-refracting particles; **h** midgut content as spherical bodies with heterogeneous content; **i** midgut with part of prey nematode body swallowed. *Scale bars* **a** 3 µm; **b-i** 20 µm

Material

35 type specimens including one male holotype, twenty male paratypes and fourteen females. The types are deposited in nematode collection of Senckenberg Institute (Frankfurt am Main, Germany) under the inventory numbers SMF 17034 (holotype), SMF 17035–17039 (slides with paratypes).

Table 6 Morphometrics of *Paracanthonchus olgae* sp. n. from the site Rainbow

Character	Males						Females				
	Holotype	*n*	Min–max	Mean	SD	CV	*n*	Min–max	Mean	SD	CV
L	1595	21	1300–1780	1575	145	9.22	12	1445–1850	1600	142	8.89
a	29.0	21	24.6–37.9	32.2	3.76	11.7	8	26.7–33.3	29.0	2.50	8.61
b	5.66	21	5.01–6.78	5.82	0.40	6.87	10	5.43–6.72	6.01	0.42	6.99
c	12.5	20	10.5–13.6	12.0	0.78	6.51	10	10.7–13.4	11.9	0.72	6.06
c′	2.44	20	2.44–3.40	3.11	0.23	7.70	8	3.20–4.71	4.14	0.51	12.3
V %	–	–	–	–	–	–	12	50.4–61.9	53.9	3.02	5.60
Body diameter at level of cephalic setae	21	21	19.0–25.0	22.4	1.68	7.51	8	21.5–26.0	23.0	1.57	6.84
Body diameter at level of nerve ring	43	21	35.6–49.0	40.8	3.04	7.44	8	39.0–47.0	41.9	2.69	6.42
Body diameter at level of cardia	50	21	37.0–55.0	47.6	4.72	9.91	8	42.5–58.0	48.7	5.67	11.6
Midbody diameter	55	21	38.0–62.0	50.2	6.30	12.5	8	50.0–65.0	57.3	4.98	8.69
Anal body diameter	47	21	36.5–47.0	42.1	3.11	5.52	8	32.0–36.0	33.8	1.58	4.68
Spicule's length along arch	58.5	21	44.5–64.0	57.3	4.33	7.55	–	–	–	–	–
Gubernaculum's length	50	21	42.0–69.0	54.7	6.19	11.3	–	–	–	–	–

Measures in μm except for ratios

Table 7 Morphometrics of *Paracanthonchus olgae* sp. n. from the site Lucky Strike

Character	Males					Females				
	n	Min–max	Mean	SD	CV	*n*	Min–max	Mean	SD	CV
L	8	1335–1830	1595	144	9.04	12	1500–2065	1805	164	9.07
a	8	28.4–42.5	35.0	4.99	14.2	10	24.6–34.4	29.3	2.77	9.44
b	8	5.18–6.48	5.80	0.53	9.14	12	5.43–6.94	5.98	0.40	6.69
c	8	10.9–14.7	12.8	1.08	8.44	12	9.81–13.3	11.9	1.18	9.91
c′	8	2.75–3.25	3.09	0.18	5.83	12	3.4–4.8	4.12	0.37	8.98
V %	–	–	–	–	–	12	51.7–54.7	53.0	0.97	1.83
Body diameter at level of cephalic setae	8	21–25	23.2	1.13	4.87	10	21–26	23.0	1.61	7.02
Body diameter at level of nerve ring	8	32–43	38.3	3.45	9.01	10	38–47	41.8	3.46	8.28
Body diameter at level of cardia	8	40–50	45	3.74	8.31	10	42–55	49.9	4.68	9.38
Midbody diameter	8	42–54	47	4.21	8.96	10	55–75	62.6	6.79	10.8
Anal body diameter	8	35–46	40.3	3.81	9.47	9	32.5–40	36.2	2.45	6.76
Spicule's length along arch	7	52–60	58.0	2.76	4.76	–	–	–	–	–
Gubernaculum's length	7	43–53	48	3.74	7.79	–	–	–	–	–

Measures in μm except for ratios

Locality

Mid-Atlantic Ridge, hydrothermal site Lucky Strike, st. 4379-1 (37°17′N, 32°16′W), depths 1635–1710 m. Washout from druses of mussels *Bathymodiolus azoricus* taken in the vicinity of the white smoker Eiffel Tower. 47th voyage of the RV «Academician Mstislav Keldysh», dive 22/315 submersible apparatus «Mir-1», 22 July 2002.

Etymology

The species name is given in honour of Dr. Elena I. Rybakova (maiden name Goroslavskaya) who provided the material.

Description

Body spindle-shaped, ventrally curved. Cuticle striated and with longitudinally very mild homogeneous punctuations.

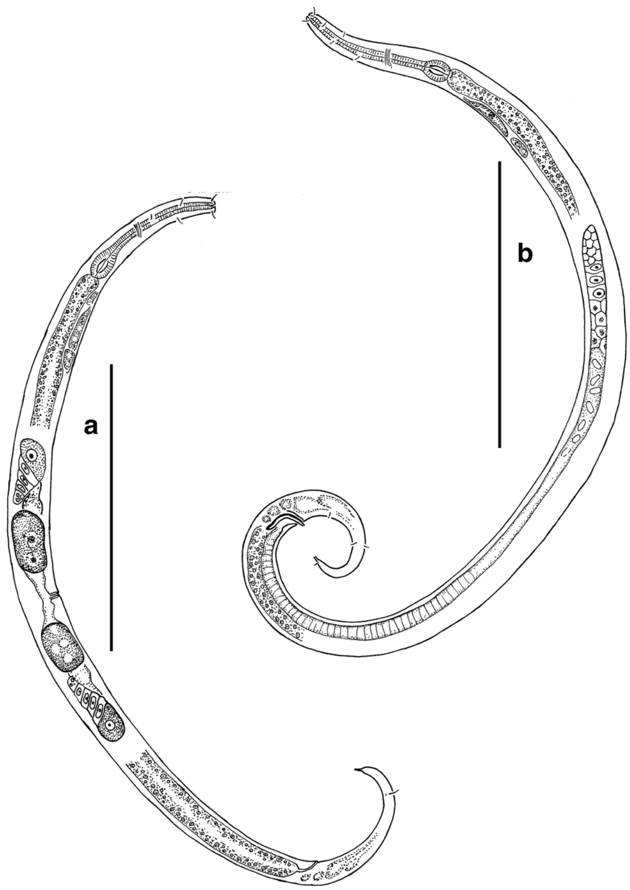


Fig. 16 *Prochromadora helenae* sp. n., entire. **a** Male paratype; **b** female paratype. *Scale bars* 200 µm

In the midbody, the striae ornamented with punctuations as equal short longitudinal rods; the rods are not very light-refractive and appear to languish medially. The punctuations more definite to both body ends; the rods seem to be equally definite pronounced around the body. The punctuations begin from anteriorly as smaller unclear dots at the level of cephalic setae and amphideal fovea.

Labial region not set off. Six inner labial papillae close to the small round mouth opening and six outer labial papillae just anterior to the cephalic setae visible only in SEM (Fig. 18e). Four moderately long cephalic setae (in males, 3.7–6 µm; in females, 4.3–5.9 µm long). Amphideal fovea poorly visible, small, transversally oval in the outline, hardly discernible spiral in 1.5 turns. Somatic setae 3.1–3.5 µm, shorter than cephalic setae. There a few sublateral somatic setae in the pharyngeal and tail region and very scarce shorter setae along the intestinal region.

Cheilostoma with crown of weak rugae (cheilorhabdia). In most specimens, there one dorsal distinct tooth and no opposite teeth in the pharyngostoma. In nearly half specimens, armament of the pharyngostoma obscure; ventrosublateral teeth may be discernible in some specimens even more distinct than the dorsal tooth. Pharynx muscular throughout its length, almost not widened anteriorly, largely evenly cylindrical but ends as a clear terminal bulb with thickened internal cuticular lining. Cardia small. Midgut contains scattered vesicles or homogeneous drops.

Ventral gland cell body situated ventrally of the intestine just posterior to the cardia, but neither neck nor ventral pore can be discernible. A small oval pseudocoelomocyte situated just posterior to the ventral gland cell body.

Female gonads antidromously reflexed, paired, and in all fourteen females the anterior ovary situated to the right and posterior ovary to the left of the intestine.

Male with a single, outstretched anterior testis located in all but one males to the right of the intestine. No midventral supplementary organs except a very short midventral seta about 1.5 µm long close anterior to the cloacal opening. Spicules short, archly bent, with rounded distal tips and slightly widened asymmetrical proximal knobs. Gubernaculum as paired bars parallel to the spicules but twice shorter.

Tail elongate conical, with a few subdorsal and subventral setae and terminal caudal tube.

Gut content

Nothing but some spherical vacuoles with homogeneous content occur in the midgut lumen (Fig. 18c).

Diagnosis

Prochromadora

Body length 626–1012 µm in males and 779–1066 µm in females; index *a* 24.8–35 in males and 23.7–29.8 in females; index c' 5.05–6.89 in males and 5.61–8.72 in females. Cuticle homogeneously punctuated; punctuations as short longitudinal rods; no lateral differentiation of the cuticle. Cephalic setae in males 3.7–6 µm; in females, 4.3–5.9 µm long. Amphideal fovea small, transversally oval in outline, situated at the level or just posterior to the cephalic setae. Buccal armament consisted of one dorsal tooth and two ventrosublateral teeth, more or less distinct. Pharynx terminated posteriorly with a round to oval bulb with lens-like thickened inner cuticle. Tail elongate conical. Spicules short, arcuate. Gubernaculum as paired bars parallel to the spicules. Short midventral seta just anterior to the cloaca present. No midventral precloacal supplementary organs.

Differential diagnosis

The new species differs from all known *Prochromadora* species except *P. asupplementata* Hopper 1961 in lacking of any male precloacal midventral supplementary organs.

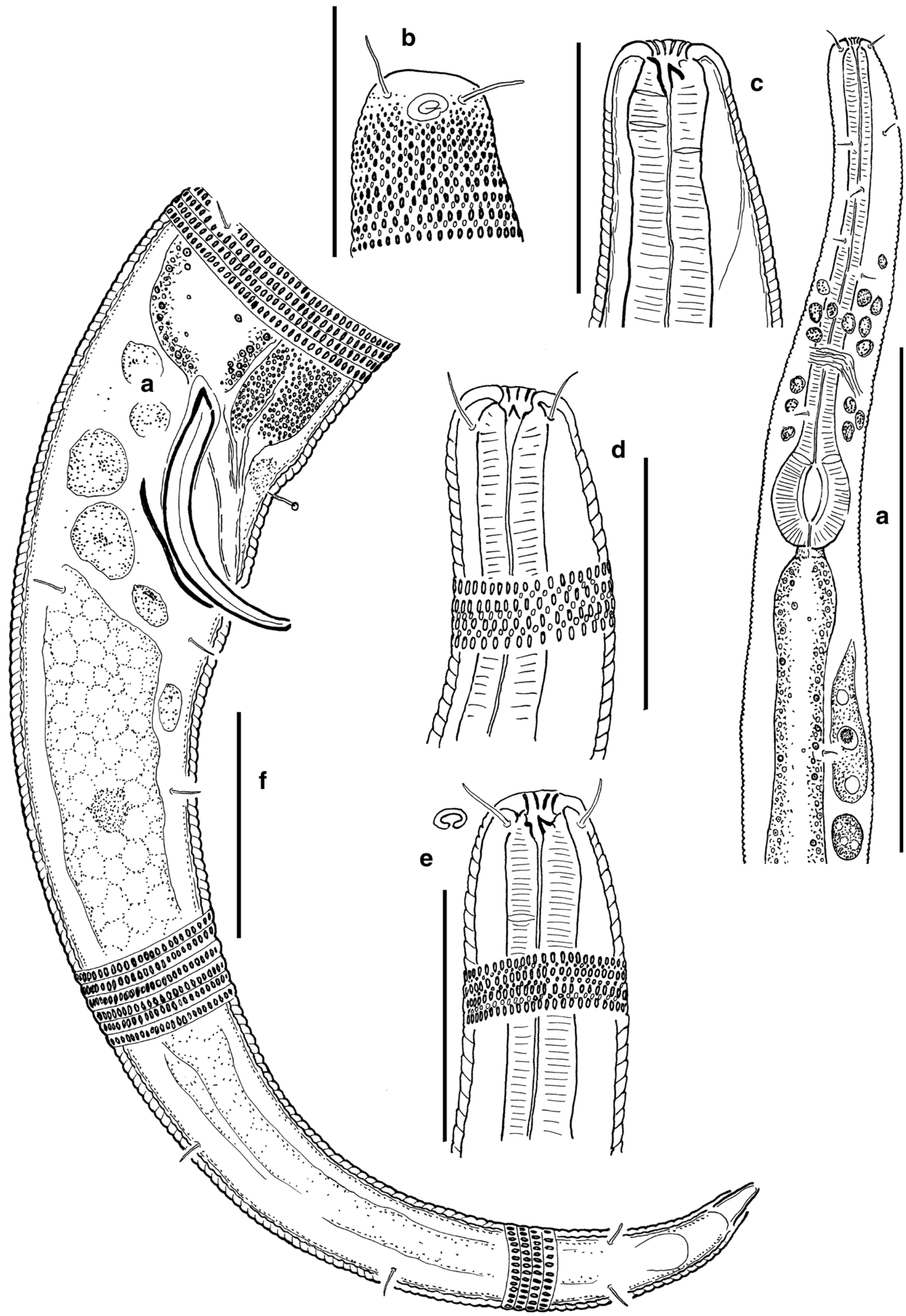


Fig. 17 *Prochromadora helenae* sp. n., details. **a** Anterior body, male paratype; **b** cephalic end, surface view, holotype; **c** cephalic end, optical section, holotype; **d**, **e** cephalic ends of two female paratypes (amphideal fovea depicted separately beside the female **e**); **f** posterior body of the male holotype. *Scale bars* **a** 100 μm; **b**–**f** 50 μm

Males of *P. helenae* sp. n. differ from *P. asupplementata*, the only known *Prochromadora* species without supplements (Hopper 1961), with index "*a*" (25–35 vs. 23.3), narrower terminal pharyngeal bulb (15–18 vs. 24 μm, shorter spicules (24–33 vs. 38.5 μm) and gubernaculum (9–15 vs. 16 μm).

Order DESMODORIDA De Coninck 1965
Family DESMODORIDAE Filipjev 1922
Desmodora de Man 1889
Desmodora marci Verschelde, Gourbault et Vincx 1998

Figures 18a, b, d, f, 19, 20, Table 9: morphometrics

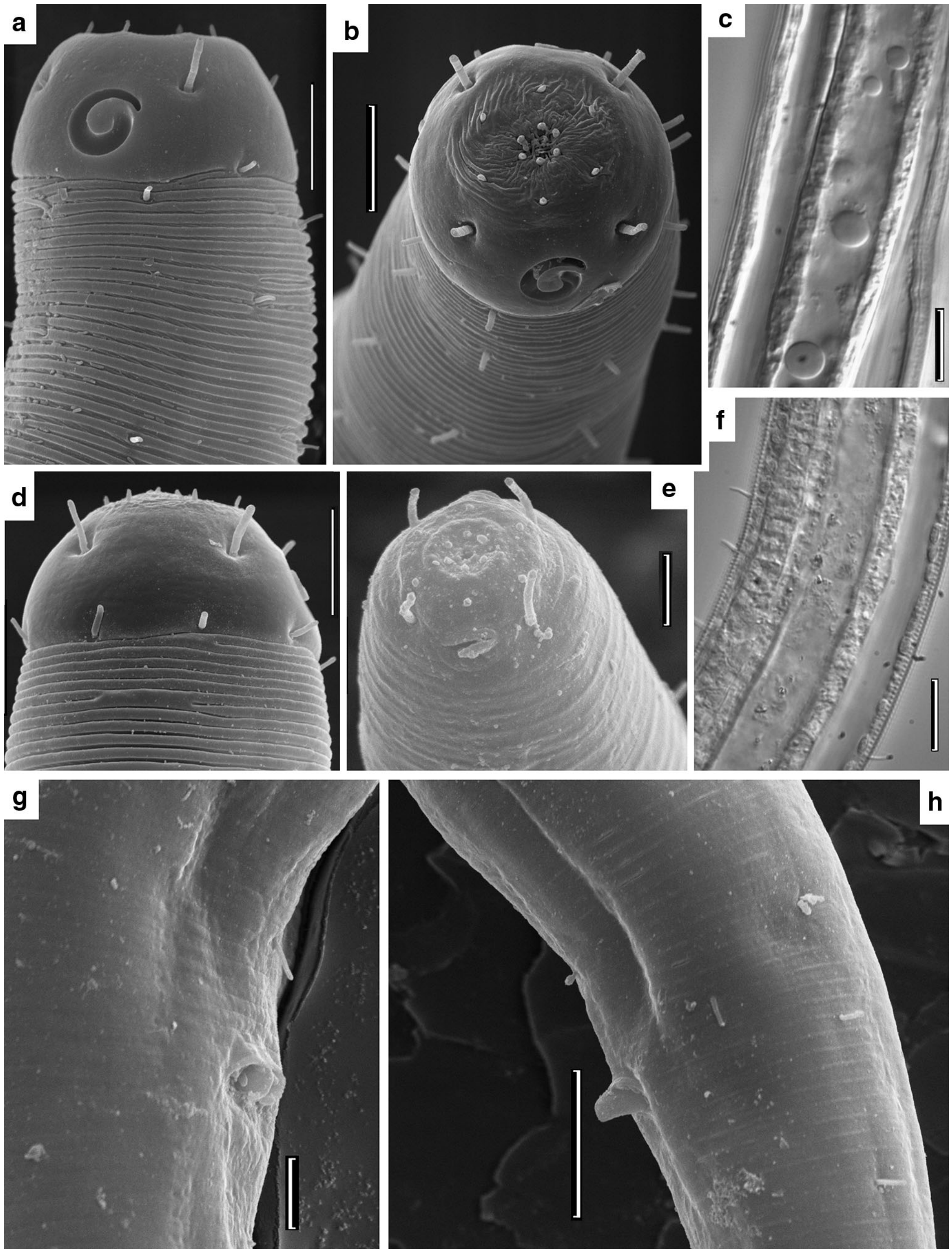


Fig. 18 *Desmodora marci* and *Prochromadora helenae* sp. n., details. **a** *D. marc*i, head, lateral view; **b** *D. marci*, apical view; **c** *P. helenae*, gut content; **d** *D. marci*, head, median view; **e** *P. helenae*, subapical view, **f** *D. marci*, gut content; **g, h** *P. helenae*, precloacal seta and cloacal opening. *Scale bars* **a–d** 10 µm; **e**, **g**, **h** 3 µm, **f** 20 µm

Material

16 Males and 13 females.

Locality

Lucky Strike (37°17′N, 32°16′W), depth 1682 m. Washout from a piece of the sulphide tube overgrown with mussels *Bathymodiolus azoricus*; the piece taken off the white smoker Eiffel Tower. 47th voyage of the RV «Academician Mstislav Keldysh», dive 23/329 submersible apparatus «Mir-2», 11 July 2002.

Description

Body elongate spindle-shaped to nearly cylindrical apart from tail. Body yellowish to brownish, with epidermal inclusions pigmented more densely. Body cuticle fine but

Table 8 Morphometrics of *Prochromadora helenae*, Lucky Strike

Character	Males						Females				
	Holotype	*n*	min–max	mean	SD	CV	*n*	min–max	mean	SD	CV
L	806	20	626–1010	821	83.1	10.1	14	779–1060	858	74.0	8.63
a	26	20	24.8–35.0	28.7	2.76	9.61	14	23.7–29.8	26.8	1.81	6.75
b	7.53	20	5.91–8.04	7.21	0.55	7.63	14	6.59–8.59	7.40	0.56	7.57
c	7.20	20	6.02–7.62	6.90	0.44	6.38	14	5.85–6.92	6.42	0.37	5.76
c'	5.44	19	5.05–6.89	6.02	0.43	7.14	14	5.61–8.72	7.38	0.86	11.7
V %	–	–	–	–	–	–	14	43.2–47.5	44.7	1.16	2.59
Body diameter at level of cephalic setae	9.3	20	8.2–11.2	9.6	0.87	9.05	14	8.7–12.4	9.95	0.97	9.75
Body diameter at level of nerve ring	18.8	20	18.0–22.8	20.3	1.14	5.63	14	17.3–22.7	19.7	1.42	7.19
Body diameter at level of cardia	23.1	20	20.7–24.4	22.3	1.09	4.89	14	22.1–25.0	23.2	0.98	4.23
Midbody diameter	31.0	20	17.9–32.5	28.9	3.63	12.6	14	27.5–35.7	31.9	2.14	6.71
Anal body diameter	20.6	19	17.2–22.0	19.6	1.28	6.52	14	16.2–22.0	18.3	1.69	9.24
Length of cephalic setae	5.6	14	3.7–6.0	5.1	0.75	14.6	7	4.3–5.9	4.84	0.53	11.0
Midpharynx width	8.3	17	5.5–8.3	6.9	0.78	11.3	12	5.1–8.0	6.7	0.87	12.9
Length of terminal pharyngeal bulb	20.9	20	19.0–24.1	21.7	1.64	7.55	14	18.9–26.0	22.7	2.06	9.07
Width of terminal pharyngeal bulb	15.9	20	14.8–17.8	16.0	0.82	5.12	14	14.5–17.9	16.5	0.96	5.82
Spicule's length along arch	33.0	19	24.0–33.0	27.0	2.37	8.77	–	–	–	–	–
Gubernaculum's length	15.2	6	9.4–15.2	13.0	2.07	15.9	–	–	–	–	–

Measures in μm except for ratios

distinctly annulated, about eight annules in 10 μm in cervical region, up to 20 notably narrower annules in 10 μm in the midgut region, up to 13 again wider annules on the tail. The annules can be fused and split here and there. The body cuticle not marked by any longitudinal structures or lateral differentiation. The body here and there may be pubescent with epizoic (?)phycomycetes.

Cephalic cuticle non-annulated and modified into an about hemispherical and slightly convex cephalic capsule. Cuticle of the cephalic capsule rather thin apically and gradually thickens posterior becoming thicker than the body cuticle. Cephalic cuticle lacks any traces of annulation. There are few minute pores with thin canals on the cephalic capsule.

Cuticle around the mouth opening wrinkled in irregular folds. Anterior sensilla presented by six inner labial and six outer labial short peg-like papillae, and four slender cylindrical cephalic setae at the level of the anterior margin of the amphideal fovea. There is an irregular circle of about eight of smaller somatic (cervical setae) at the base of the cephalic capsule or just posterior to it. Somatic setae, like cephalic setae, slender, cylindrical, truncated apically. The somatic setae rather short (about 4 μm), fairly numerous and arranged in irregular longitudinal rows.

Amphideal fovea of moderate size, larger in males than in females, spirally coiled in 1.5 turns in males and in about 1.1 turns in females, situated laterally in the middle of the cephalic capsule.

Somatic cuticle not thickened around the mouth opening. Cheilostoma tight, with hardly discernible longitudinal folding. Pharyngostoma narrow and provided with a small slightly sclerotized triangular tooth. Pharynx evenly muscular throughout its length and terminated with a rounded bulb. Inner cuticular lining in the bulb not thickened and not differs from that of the pharynx. Cardia not surrounded by intestine, trapezoidal, with meandering inner cuticular lining.

No ventral gland found. Some ovoid pseudocoelomocytes at the level of the anterior midgut present.

Ovaries paired, antidromously reflected, situated either both to the left or right side of the intestine, or anterior and posterior ovaries to the different sides of the intestine. No sperm visible in female organs.

An only anterior male gonad outstretched, situated either to the left or right side of the intestine. Spermatozoa (or spermatids?) rather large (about 27–30 × 18–22 μm), oval, with homogeneous core and slightly radially striated cortex. Spicules short, flat, arcuate, often poorly discernible. Gubernaculum as paired short bars parallel to distal parts of the spicules. No true supplementary organs besides short midventral setae as a continuation of a midventral row of somatic setae.

Tail elongate conical, with terminal cone devoid of cuticular annulation.

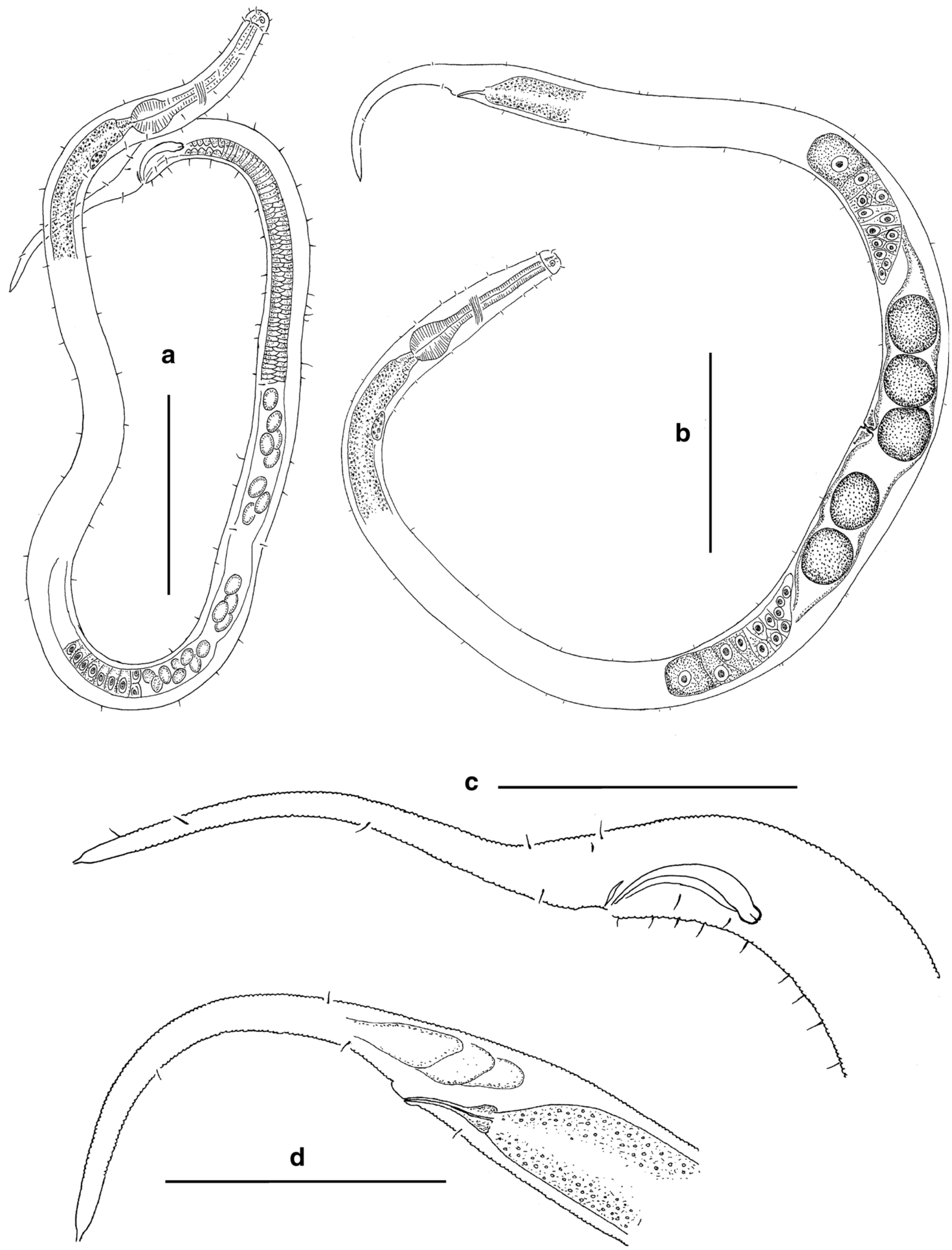


Fig. 19 *Desmodora marci* (Lucky Strike, st. 4384), entire and tails. **a** Male, entire; **b** female, entire; **c** male tail; **d** female tail. *Scale bars* **a**, **b** 200 μm; **c**, **d** 100 μm

Gut content

About 33 % males 80 % females have some sparse midgut content as pinches of granular fibrous material (Fig. 18f).

Discussion

The specimens from Lucky Strike morphologically is very similar to the original description of Verschelde et al. (1998) except for mention on ventrosublateral teeth in buccal cavity which poorly discernible in most specimens. All the measurements and ratios coincide or largely overlap.

Desmodora marci was initially collected in sites of the hydrothermal vents in the Lau Basin in the South-West Pacific with aid of a French submersible «Nautile». Type specimens were sampled in the Hine Hina site (22°32′S 176°43′W) at depth about 1700 m. This is a cold site; the temperature there is under 20 °C. The nematodes were washed out from the «coffin» with mussel and Solenidae (Verschelde et al. 1998). Sapir et al. (2014) found *D. marci* on carbonate rocks and sulphide-oxidizing bacterial mats at

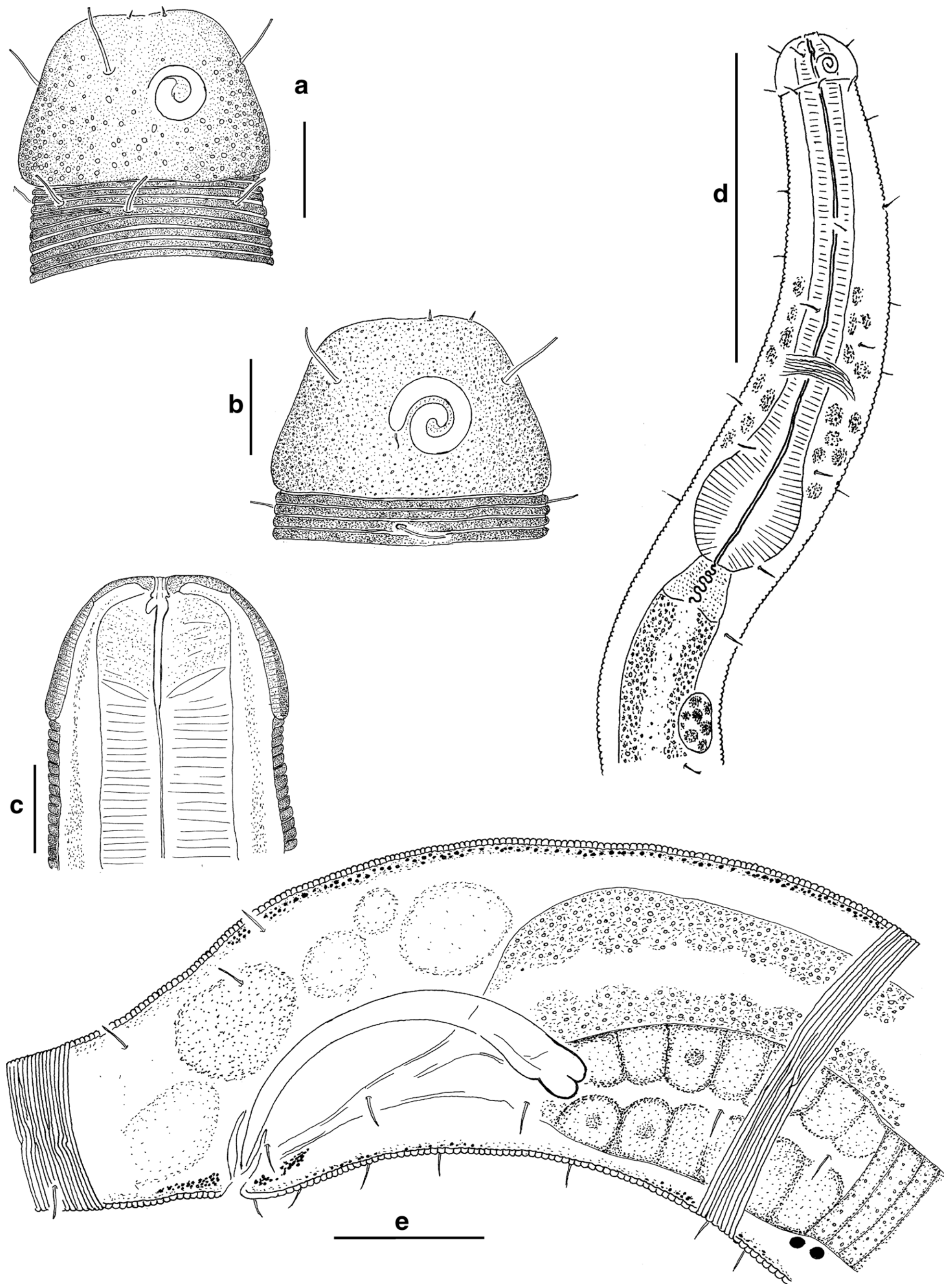


Fig. 20 *Desmodora marci* (Lucky Strike, st. 4384), details. **a** Male head, surface view; **b** female head, surface view; **c** female head, optical section; **d** male, anterior body; **e** male, cloacal region. *Scale bars* **a**–**c** 10 µm; **d** 100 µm; **e** 20 µm

Hydrate Ridge methane seeps, off the coast of Oregon (North-East Pacific) at 587–810 water depth. This nematode species is there infected by a fungus-related parasitic microsporidium *Nematocenator marisprofundi* Sapir et al. 2014 which causes lysis of body wall muscle cells. In connection with high presence of spores in reproductive system and their absence in intestine, the authors suggested a sexual transmission of the parasite, in contrast to the faecal-oral transmission of most microsporidia (Sapir et al. 2014).

Family Draconematidae Filipjev 1918
Prochaetosoma Micoletzky 1922
Prochaetosoma ventriverruca sp. n.

Figures 21, 22, 23, 24, Table 10: morphometrics

Material

28 Type specimens including one holotype male, twelve paratype males and eight female paratypes. The types are

Table 9 Morphometrics of *Desmodora marci*, Lucky Strike

Character	Males					Females				
	n	Min–max	Mean	SD	CV	*n*	Min–max	Mean	SD	CV
L	16	1825–2525	2135	158	7.42	13	1855–2360	2070	146	7.06
a	16	30.3–41.5	35.7	3.27	9.16	13	21.6–45.3	30.3	6.30	20.8
b	16	9.05–11.6	10.7	0.68	6.37	13	8.54–12.1	10.3	0.91	8.84
c	16	9.8–13.5	11.6	1.01	8.68	13	9.89–12.5	11.0	0.87	7.88
c'	14	4.90–6.78	5.80	0.60	10.3	13	5.81–7.50	6.63	0.57	8.60
V %	–	–	–	–	–	13	46.6–57.4	53.6	2.59	4.83
Body diameter at level of cephalic setae	15	20.0–28.0	23.3	2.18	9.36	13	20.9–24.0	22.4	1.04	4.64
Body diameter at level of nerve ring	11	36.0–50.0	41.9	3.76	8.97	11	38.0–54.0	45.5	4.73	10.4
Body diameter at level of cardia	14	34.3–50.4	46.4	2.42	5.21	13	40.0–52.7	46.6	3.19	6.85
Midbody diameter	16	44.0–71.2	60.5	7.68	12.8	13	41.0–91.0	71.0	14.7	20.7
Anal body diameter	14	28.0–36.0	31.7	2.51	7.91	13	25.0–36.0	29.7	3.09	10.4
Cephalic capsule length	14	16.0–21.0	18.1	1.40	7.74	13	15.0–21.0	17.2	1.83	10.6
Length of cephalic setae	16	5.0–7.1	6.4	0.76	11.9	13	4.3–7.0	5.84	0.84	14.4
Width of amphideal fovea	13	7.0–9.6	8.2	0.86	10.5	12	7.00–9.00	7.98	0.75	9.40
Width of amphideal fovea as percentage of c.b.d., %	12	25.9–34.6	29.8	3.26	10.9	11	25.0–34.6	29.7	3.17	16.7
Distance from cephalic apex to anterior rim of amphideal fovea	11	6.0–10.0	8.11	1.31	16.2	12	5.0–12.3	8.64	2.45	28.4
Length of terminal pharyngeal bulb	15	38.0–54.1	47.3	4.01	8.48	13	43.8–56.0	49.1	3.76	7.66
Width of terminal pharyngeal bulb	15	34.0–45.0	38.4	2.77	7.21	13	34.8–38.2	36.6	1.25	3.42
Length of cardia	15	10.0–19.7	13.6	3.00	22.1	13	9.2–22.0	14.8	3.62	24.5
Spicule's length along arch	14	58.5–72.0	65.0	4.14	6.37	–	–	–	–	–
Gubernaculum's length	15	17.0–25.0	21.4	2.51	11.7	9	21.1–24.2	22.4	0.99	4.42

Measures in μm except for ratios

deposited in nematode collection of Senckenberg Institute (Frankfurt am Main, Germany) under the inventory numbers SMF 17040 (holotype), SMF 17041–17043 (slides with paratypes).

Locality

Mid-Atlantic Ridge, hydrothermal site Lucky Strike, 37°17′N, 32°16′W), depth 1682 m. Washout from a piece of the sulphide tube overgrown with mussels *Bathymodiolus azoricus*; the piece taken off the white smoker Eiffel Tower. 47th voyage of the RV «Academician Mstislav Keldysh», st. 4384, dive 23/329 submersible apparatus «Mir-2», 11 July 2002.

Etymology

The species name is derived from Latin words *venter* (=belly) and *verruca* (=wart) and refers to the midventral cuticular projection in males.

Description

Body short and stout, roughly conical anteriorly, prominently bulging in the region of the nerve ring and postneural pharynx, notably narrowed from the level of cardia to the anterior gonad, then evenly swollen posteriad to anus. Body of all specimens sharply bent ventrally in the narrowed postpharyngeal region. Tail rather short, conical.

Head (rostral) cuticle smooth or seemingly slightly rough. Body cuticle distinctly annulated from the posterior margin of the amphideal fovea posteriad. The anteriormost annulations (six–ten annules) fine, dense and not quite regular; then, the annules becoming broader and pronounced at the level of cephalic adhesive tubes (CATs); annulations in the middle (intestinal) body region more fine but very distinct, annules of the posterior body to the tail again broad and distinct. The annules may be dorsally split and ventrally fused here and there. The annules are not ornamented with spines or other sculpture. Tail tip as a terminal cone with non-annulated rough cuticle.

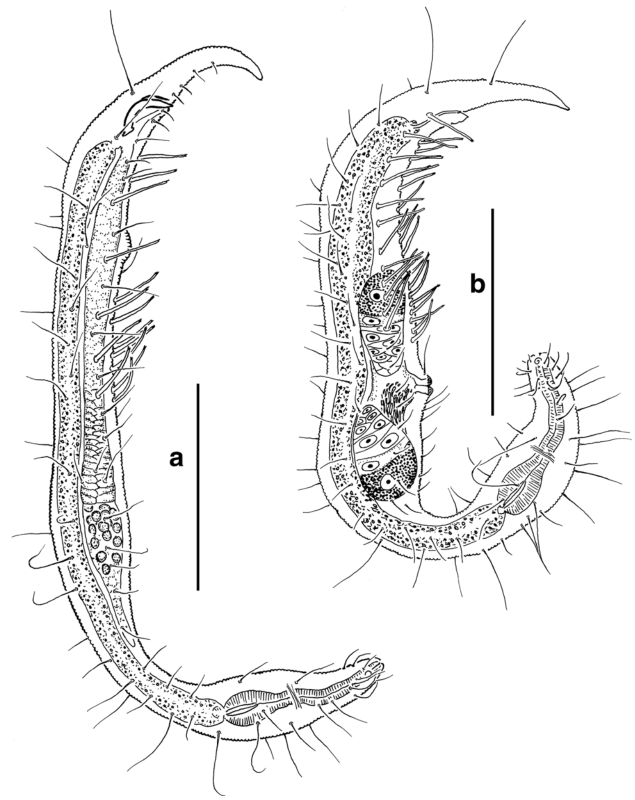


Fig. 21 *Prochaetosoma ventriverruca* sp. n., entire. **a** Paratype male; **b** female paratype. *Scale bars* 100 μm

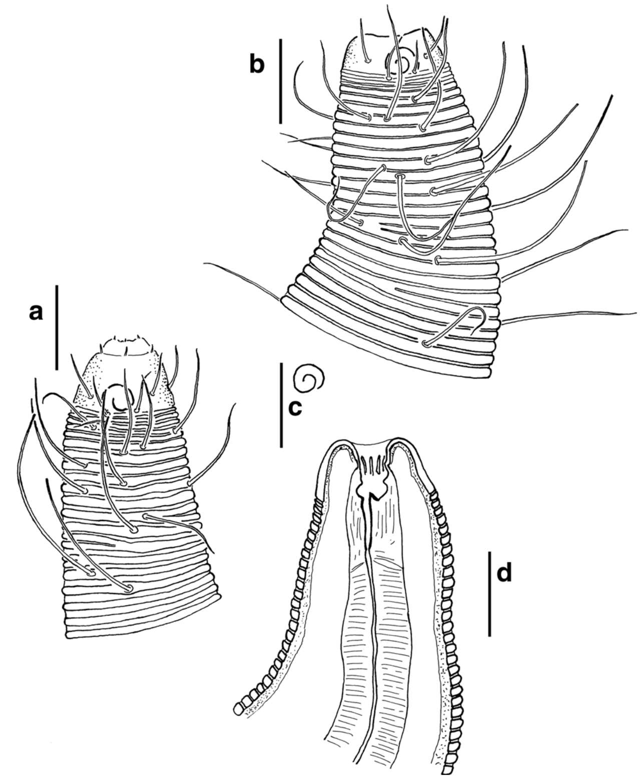


Fig. 22 *Prochaetosoma ventriverruca* sp. n., anterior ends. **a** Holotype male; **b** paratype female, surface view; **c** Amphideal fovea of the same female; **d** optical section of the same female. *Scale bars* 10 μm

Labial region withdrawn in most specimens. Four rather short cephalic setae (4.7–6.3 μm in male, 5.1–6.7 μm in females) at the level of the amphideal fovea. Amphideal fovea as a round contoured spiral, ventrally coiled in about 1.5–2 turns in males and >1 turn in females. Width of the amphideal fovea 3.1–4.4 μm in males and 3.5–4.2 μm in males.

Somatic setae directly inserted on body cuticle; insertion site visible as a « cuticular pore » . Four rows of somatic setae extended throughout the body on each lateral body side.

Male, left body side. Subventral row: 12 normal sensory setae from the head to the subventral adhesive tubes, continued by 11 subventral adhesive tubes (SvATs) decreasing in length tailwards 25–18 μm long, the posteriormost of them situated anterior to the cloaca. Lateroventral row: 15 setae of variable length from the amphideal fovea to the lateroventral adhesive tubes (SlATs), the longest two of them 28–31 μm, further posteriad setae much shorter, 9–11 μm; six SlATs decreasing in length from 28 to 22 μm tailwards; the SlATs alternate with normal sensory setae 27–8 μm long, then 9 short sensory setae 7–8 μm long to almost tail tip. Laterodorsal row: 36 singular setae in all arranged in a slightly irregular line; anteriormost normal seta 11 μm, then four cephalic adhesive tubes (CATs) bowed anteriad 12.5–14.5–18–18.5 μm; then, 28 setae of variable length—the longest are seta 40 μm at the level of the pharyngeal bulb, seta 30 μm at the level of the testis tip, 32 μm at the level of the midventral preanal wart. Subdorsal row: approximately 23–24 setae, the anteriormost subcephalic normal seta, then three CATs 13.5–16–22 μm long; most setae are rather short (8–12 μm in the middle body region), but some setae are much longer— the longest seta 33 μm at the nerve ring.

Female, left body side. Subventral row: 13 singular setae 11–13.3 μm long from the head to the vulva level, at that seven last setae just posterior to the postpharyngeal body narrowing more thick, the thickest and longest (19 μm) are prevulvar and postvulvar setae; the row is continued by 19 subventral adhesive tubes (SvATs) 18–26 μm long, the posteriormost of them situated anterior to the anus. Lateroventral row: two subsequent pairs of subcephalic setae 11–12 μm long, then 18 singular setae whose length drops backward gradually from the anteriormost setae (31 μm) to the shorter setae on the postpharyngeal body narrowing (11–12 μm); the row is continued by 12 lateroventral adhesive tubes (SlATs) 24–30 μm long, the posteriormost of them situated anterior to the anus.

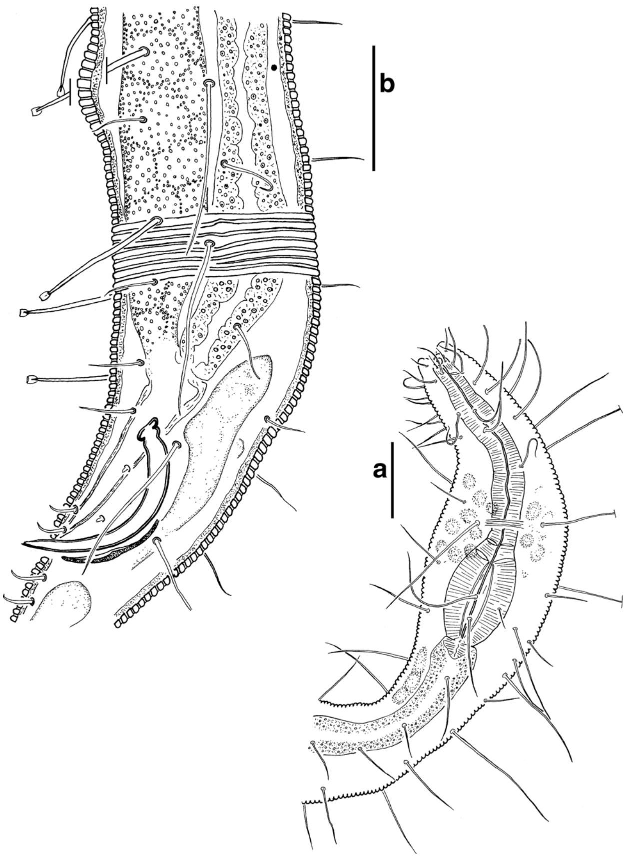


Fig. 23 *Prochaetosoma ventriverruca* sp. n., details. **a** Anterior body of paratype female; **b** paratype male, copulatory apparatus and pericloacal region. *Scale bars* 20 µm

Laterodorsal row: 36 singular setae in all arranged in a slightly irregular line; anteriormost seta is the shortest (4 µm) anterior fourth and fifth setae are modified as cephalic adhesive tubes (CATs) bowed anteriad; then, shorter setae up to 16–19 µm alternate with longer ones (eighth seta 35 µm long, tenth 37 µm, 14th 40 µm, the last 36th 50 µm). Subdorsal row: approximately 28 setae, the anteriormost three of them are CATs 13–16–20 µm long; most setae are rather short (12–14 µm in the middle body region), but some setae are much longer—eighth seta 40 µm, posteriormost seta on the tail 29 µm long.

Cephalic adhesive tubes long and delicate, hardly distinguished from sensory somatic setae, archly bent anteriad, their tips slightly modified. There are two sets of CATs on each body side, one subdorsal and one laterodorsal. Each set consists of three CATs gradually increasing in length posteriad.

Body or posterior adhesive tubes (PATs) arranged in two rows on each body side, lateroventral and subventral ones. Lateroventral row is shorter and consists of lesser numbers of PATs than the subventral one (e.g. 12 vs. 19). PATs are thick, strong and almost straight; their tip is modified into a small pellucid goblet-like structure.

Cheilostoma with unclear inner structure. Pharyngostoma with slightly sclerotized walls; its anterior compartment short and widened; a small but distinct triangular dorsal tooth 1–1.5 µm juts out into this chamber. Posterior part of the pharyngostoma narrow. Buccal cavity wholly 11–13 µm long and 2.3–2.5 µm wide in both males and females.

Pharynx short, with distinct radial muscular striation. Anterior half of the pharynx very slightly widened (12 µm), then the pharynx slightly narrowed (9 µm) in the region of the nerve ring, and posteriorly with a clear oval muscular bulb 27 µm long and 20 µm wide (figures of a female). Inner cuticular lining is distinct but thin in the prebulbar pharynx and forms slight lens-like thickening in the bulb. Cardia short, hemispherical. Midgut with wavy internal lumen. Rectum relatively long. Large anal flap covers the anal opening.

Ventral gland is not found as such, but there is an elongate cell posterior to the cardia ventrally of the midgut.

Short ovaries paired and antidromously reflected. Vulva slightly protruded as a small truncate cone. Condensed mass of tiny spermatozoa may be visible in uterus and vagina lumen. Position of the gonads in relation to the intestine varies greatly: anterior ovary to the right and posterior ovary to the left observed in two females; anterior to the left, posterior to the right in five females; both anterior and posterior to the left in two females; both anterior and posterior to the right in three females.

A single anterior outstretched male gonad situated altogether ventrally of the intestine occasionally shifted a little to right or to the left. Spermatozoa usually condensed in a vermiculated mass. Spicules short, arcuate, proximally cephalated and distally pointed. Gubernaculum as an elongate trough without an apophysis. There is a midventral cuticular swelling without evident sensory and glandular structures, situated at a rather variable distance anterior to the cloaca.

Tail elongate-conical, with terminal spinneret. Terminal cuticular cone indistinctly separated from the annulated cuticle.

Gut content

About 10 % males and 43 % female have a sparse midgut content as a few loose pinches of granular material.

Diagnosis

Prochaetosoma. Body length 400–600 µm, index *a* 8–16. Amphideal fovea spirally coiled in 1–2 turns, rounded. 5–6

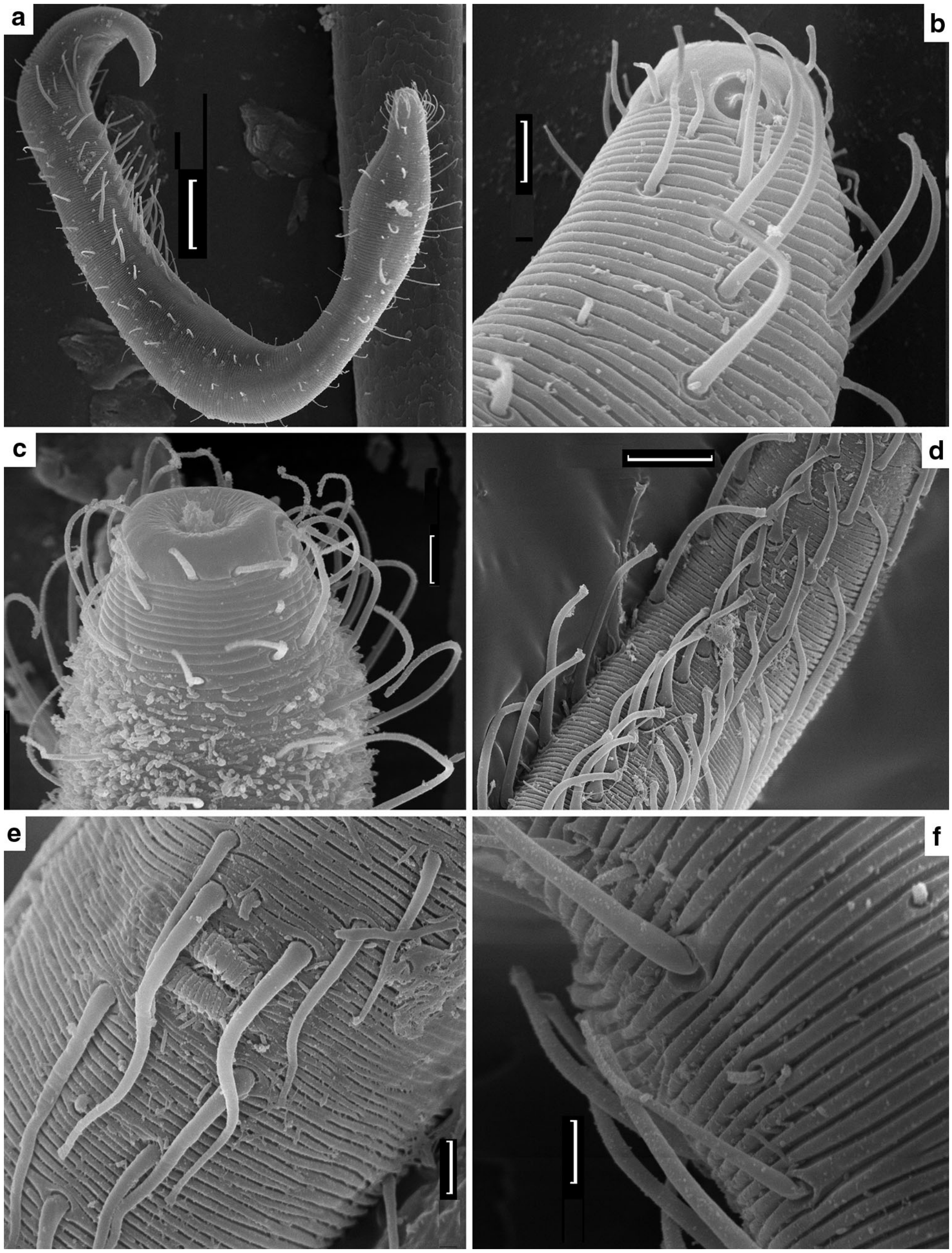


Fig. 24 *Prochaetosoma ventriverruca* sp. n., SEM pictures. **a** Male, entire; **b** head laterally; **c** head ventrally; **d** adhesive tubes of the midbody; **e** vulva with two prevulvar setae; **f** male midventral preanal wart laterally. *Scale bars* **a** 30 µm; **b**, **c**, **e**, **f** 3 µm; **d** 10 µm

CATs, 11–14 SlATs, 14–19 SvATs on either body side; the posteriormost AT situated anterior to the anus. Spicules 33–39 µm along the arc. Midventral preanal wart (cuticular swelling) present in males.

Differential diagnosis

The family Draconematidae and the genus *Prochaetosoma* were reviewed by Decraemer et al. (1997), and then, Rho et al. (2010) summarized eleven valid *Prochaetosoma* species and provided a table and a key for their identification.

Prochaetosoma ventriverruca sp. n. differs certainly from all seven *Prochaetosoma* species with known males in having a peculiar midventral preanal wart (cuticular swelling). Of three species with unknown males, *P. primitivum* (Steiner 1916) has been described on the base of the only J4 stage and hence can unlikely be compared

Table 10 Morphometrics of *Prochaetosoma ventriverruca*, Lucky Strike

Character	Holotype male	Paratype males					Paratype females				
		n	Min–max	Mean	SD	CV	*n*	Min–max	Mean	SD	CV
L	506	13	439–513	475	28.8	6.07	18	407–594	475	37.4	7.87
a	14.0	11	11.7–16.2	13.7	1.16	8.50	16	8.12–12.4	10.1	1.21	11.9
b	5.42	11	4.94–5.83	5.35	0.28	5.23	18	4.71–5.60	5.22	0.26	4.98
c	8.60	11	7.42–8.64	8.16	0.43	5.27	18	6.90–8.53	7.82	0.44	5.63
c′	3.27	10	2.92–3.53	3.21	0.22	6.85	16	3.47–4.81	4.09	0.35	8.56
V %	–	–	–	–	–	–	18	45.5–52.4	49.3	1.92	3.90
Body diameter at level of cephalic setae	11.4	11	11–13	11.9	0.66	5.54	17	11.2–13.8	12.1	0.63	5.19
Body diameter at level of amphideal fovea	11.4	11	11.1–13	11.9	0.62	5.19	17	11.2–13.8	12.1	0.63	5.19
Body diameter at level of nerve ring	30.7	11	30.7–35.2	32.7	1.32	4.03	17	30.2–37.0	33.5	1.71	5.11
Body diameter at level of anterior swelling	33.2	7	32.5–36.3	33.7	1.27	3.77	13	31.3–37.3	34.6	1.56	4.51
Body diameter at level of cardia	25.4	11	23.9–28.5	26.6	1.42	5.35	13	22.3–33.0	28.3	2.55	9.00
Body diameter at level of anterior narrowing	19.7	11	19.7–22.5	20.8	0.92	4.43	17	20.7–28.8	22.5	1.90	8.44
Midbody diameter	36.2	11	30.0–41.4	35.5	3.19	8.98	16	40.7–58.4	47.5	5.76	12.1
Anal body diameter	18.0	10	16.6–19.3	18.1	0.98	5.4	16	13.3–18.2	15.1	1.39	9.20
Number of left posterior adhesion tubes in sublateral row	5	11	5–6	5.18	0.40	7.72	11	11–14	12.6	0.93	7.41
Number of left posterior adhesion tubes in subventral row	10	11	9–13	10.9	1.04	9.53	11	14–19	17.1	1.76	10.3
Number of right posterior adhesion tubes in sublateral row	6	6	4–6	5.00	0.63	12.6	13	11–14	12.4	0.77	6.22
Number of right posterior adhesion tubes in subventral row	13	6	9–13	10.8	1.37	12.8	13	14–18	16.2	1.46	9.04
Spicule's length along arch	37.0	11	33–38.7	36.2	1.99	5.50	–	–	–	–	–
Gubernaculum's length	15.8	11	13.4–19.8	16.1	2.09	12.9	–	–	–	–	–
Length of midventral precloacal wart	10.4	10	9.1–13.5	11.7	1.52	13.0	–	–	–	–	–
Distance from midventral precloacal wart to cloaca	41.3	10	37.6–66.7	45.9	9.78	21.3	–	–	–	–	–

Measures in µm except for ratios

with adult characters of other species. *Prochaetosoma primitivum* (Steiner 1916) is considered as *species inquirenda*. Of two remaining species with unknown males, *P. ventriverruca* sp. n. differs from *P. arcticum* (Kreis 1963) by shorter body (407–594 vs. 687–1002 µm) and greater number of SvATs (14–19 vs. 12) and from *P. lugubre* (Gerlach 1957) by shorter body (407–594 vs. 700 µm) and greater number of SvATs (14–19 vs. 4–5).

Order PLECTIDA Malakhov 1982
Family LEPTOLAIMIDAE Örley 1880
Leptolaimus de Man 1876
Leptolaimus hydrothermalis sp. n.

Figures 25 and 26, Table 11: morphometrics

Material

Males: one holotype male, one paratype male and five paratype females. The types are deposited in nematode collection of Senckenberg Institute (Frankfurt am Main, Germany) under the inventory numbers SMF 17044 (holotype), SMF 17045–17046 (slides with paratypes).

Locality

Mid-Atlantic Ridge, hydrothermal site Lucky Strike, 37°17′N–32°16′W, 1680 m deep, suspension washed off mussels *Bathymodiolus azoricus*. 11 July 2002.

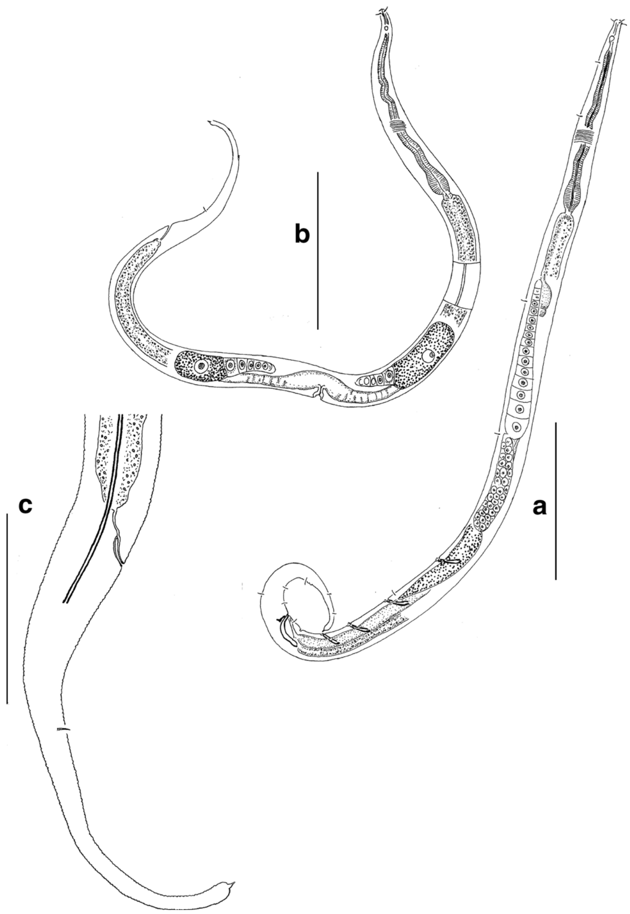


Fig. 25 *Leptolaimus hydrothermalis* sp. n., entire and female's tail. **a** Holotype male, entire; **b** paratype female, entire; **c** paratype female tail. *Scale bars* **a**, **b** 100 μm, **c** 50 μm

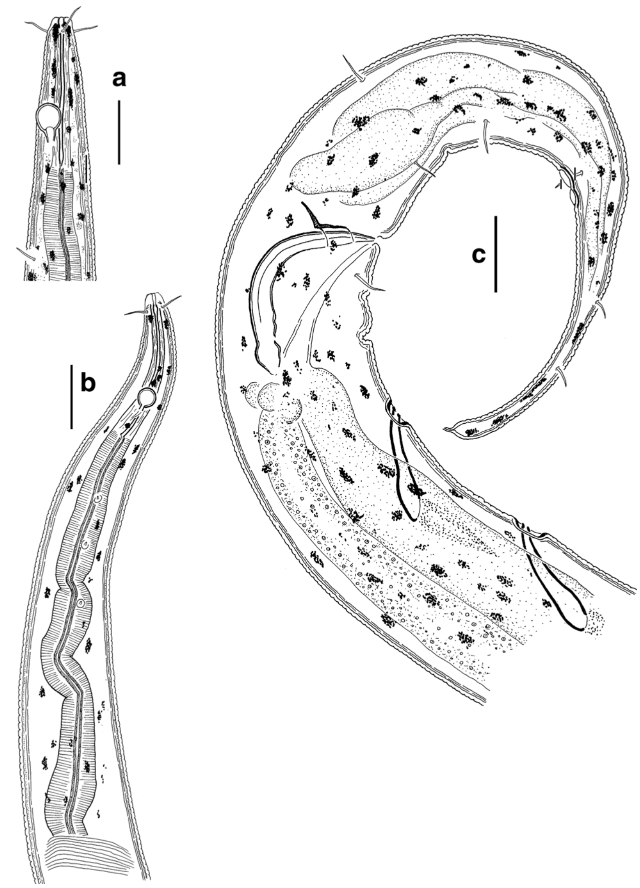


Fig. 26 *Leptolaimus hydrothermalis* sp. n., details. **a** Holotype male, cephalic end; **b** paratype female, anterior region; **c** holotype male, posterior body. *Scale bars* 10 μm

Etymology

The species name is derived from « *hydrothermal* » , a peculiar biotope created in sites of ejection of thermal waters in the sea.

Description

Body slender, elongate spindle-shaped. Cuticle very fine annulated, the annulation not clearly discernible in some body parts. A narrow and sharp lateral crest extends from the level of the nerve ring along the body to the preanal region in males and to the anterior third of the tail in females. There are accumulations of dark pigment granules scattered beneath cuticle in the epidermis, not only within the lateral fields, but in the entire body circumference.

Anterior end attenuated. Neither inner, nor outer labial sensilla observable. Four relatively long cephalic setae present. Amphideal fovea situated at a distance from the cephalic apex, with an oval sclerotized rim, pear-shaped because of anterior sclerotized part of amphideal duct. Amphideal fovea in females a little smaller than in males. On the left side, two lateral somatic setae, anterior postamphideal one 2 μm long and posterior preneural one 3.5 μm long. Scarce setae visible throughout the body.

Narrow tubular stoma extends posterior behind the amphideal fovea. The tubular stoma enveloped by a narrow pharyngeal cuff. Stoma walls weakly differentiated from internal cuticular lining of the pharynx. Pharynx muscular throughout its entire length, slender, 6 μm wide at the level of the nerve ring. Posterior region of the pharynx inflated a bit, thus forming a slight pear-shaped widening (10 μm wide) with scarcely modified internal cuticle. Cardia not surrounded by intestinal tissue, small, 2.5 μm long.

Ventral pore not seen. Ventral gland cell body, however, present posterior to the cardia, to the right of the intestine. The cell body continues anteriorly into a gland neck. A small pseudocoelomocyte nestled up close to the gland cell body posteriorly.

Female gonads antidromously reflected; anterior ovary situated to the right, posterior to the left of the intestine.

Table 11 Morphometrics of the type specimens *Leptolaimus hydrothermalis* sp. n

Character	Males		Paratype females				
	Holotype	Paratype male	1	2	3	4	5
L	610	561	627	629	755	573	641
a	30.5	31.2	27.3	26.8	31.5	27.3	31.3
b	4.66	4.56	4.66	4.54	4.86	4.97	4.76
c	6.29	8.11	6.37	6.20	6.92	5.74	6.31
V %	–	–	51.5	51.8	55.2	49.6	50.2
c'	5.00	5.15	7.17	7.07	6.56	7.38	7.39
Body diameter at level of cephalic setae	4.0	4.0	4.0	4.5	5.0	3.5	4.5
Body diameter at level of amphideal fovea	8.0	7.5	7.5	8.0	8.0	6.0	6.5
Body diameter at level of nerve ring	16.5	14.5	17.0	14.0	17.0	15.0	14.5
Body diameter at level of cardia	18.0	15.5	19.0	19.0	19.0	16.0	17.0
Midbody diameter	20.0	18.0	23.0	23.5	24.0	21.0	20.5
Anal body diameter	17.0	17.0	14.5	14.0	15.0	12.5	12.5
Length of cephalic setae	3.0	3.0	2.5	2.5	3.0	2.5	2.5
Width of amphideal fovea	3.5	3.0	2.5	2.5	2.5	2.5	2.5
Width of amphideal fovea as percentage of c.b.d., %	44	40	33	31	31	42	38
Distance from cephalic apex to anterior rim of amphideal fovea	12.5	13.0	14.0	16.0	16.5	15.0	13.5
Stoma length	22.0	21.0	22.5	22.0	26.0	22.0	20.0
Length of posteriormost precloacal supplementary tube	14.0	14.0	–	–	–	–	–
Distance from I (anteriormost) to II supplementary tube	44.0	44.0	–	–	–	–	–
Distance from II to III supplementary tube	31.0	28.0	–	–	–	–	–
Distance from III to IV (posteriormost) supplementary tube	23.0	24.0	–	–	–	–	–
Spicule's length along arch	29.1	27.2	–	–	–	–	–
Length of apophysis of the gubernaculum	3.5	5.0	–	–	–	–	–

Measures in µm except for ratios

Male gonads paired; anterior testis outstretched, situated ventrally and to the right of the intestine; posterior testis looks different, reflexed and situated to the left of the intestine. Vas deferens to the left of the intestine and supplementary tubes. Four posterior midventral tubular supplementary organs. Proximal (anterior or inner) end of the supplements widened asymmetrically funnel-shaped; distal (posterior or outer) end emerges out in a small pit (alveolus) with sclerotized margin (posterior margin thicker). Spicules short, arcuate, proximally cephalate and distally pointed. Gubernaculum with a pair of short and weak dorsal apophyses.

Tail consists of anterior conical and posterior slender cylindrical portions gradually transforming to one another. Terminal spinneret tube present. There a midventral structure as two close consecutive alveolar pits in the middle of the tail. Posterior paired setae: one preanal subventral, one postanal subdorsal, three consecutive postanal lateroventral setae (these and previous 3.5–4 µm long) on the conical tail portion, two consecutive dorsolateral setae 2.5–3 µm long on the cylindrical tail portion.

Diagnosis

Leptolaimus

Body length 561–610 µm in males and 573–755 µm in females; *a* 30.5–31.2 in males and 26.8–31.5 in females; c' 5–5.15 in males and 6.56–7.39 in females. Lateral cuticular crest along the body present. Cephalic setae 2.5–3 µm. Amphideal fovea in males 3–3.5 µm (40–44 % c.b.d.), distance from anterior end 12.5–13 µm; the same in females, respectively, 2.5 µm (31–42 % c.b.d.), 13.5–16.5 µm. Alveolar precloacal supplements absent; four tubular precloacal supplements present. Spicules 29.1–27.2 µm long (arc). Gubernaculum with dorsal apophyses 3–5 µm long. A midventral postcloacal organ consisting of two close consecutive alveolar pits (alveole-like structure) present.

Discussion

Recently, Holovachov and Boström (2013) have revised the genus *Leptolaimus*. They listed 58 valid species and eight *species inquirendae*; five species were transferred to other genera. Thirteen species of *Leptolaimus* possess anterior alveolar and posterior tubular midventral supplementary organs, 41 species—only tubular organs, three species—only alveolar organs and one species—no supplementary organs at all. Alekseev and Rassadnikova (1977) treated the groupings as subgenera *Leptolaimus* s.str., *Tubulaimus*, *Alvaeolaimus* and *Boveelaimus*, respectively, but the designations were not approved by Holovachov and Boström (2013).

Leptolaimus hydrothermalis sp. n. differs sharply from all *Leptolaimus* species except *L. papilliger* de Man 1876 by the presence of a midventral postcloacal alveole-like structure on the tail. *L. hydrothermalis* can be separated from *L. papilliger* by cephalic setae 3 µm long *versus* immeasurable small cephalic papillae and lack of precloacal alveolar supplementary organs. Other species of the "*Leptolaimus* subgenus" related to *L. hydrothermalis* are *L. cupulatus* Lorenzen 1972b, *L. danicus* Jensen 1978 and *L. mixtus* Lorenzen 1972b; *L. hydrothermalis* differs from them by the presence of the postcloacal alveole-like organ and lack of precloacal alveolar supplementary organs. Among the species of "*Tubulaimus* subgenus", *L. hydrothermalis* is close to *L. antarcticus* (Cobb 1914), *L. cangionensis* (Gagarin and Thanh 2007), *L. elegans* Schuurmans Stekhoven and De Coninck 1933 (redescription of Holovachov and Boström 2013), *L. puccinellae* Gerlach 1959 (redescription of Lorenzen 1969) and *L. venustus* Lorenzen 1972b in many dimensions. Besides the presence of alveole-like structure, *L. hydrothermalis* differs from *L. antarcticus* by smaller cephalic setae (3 vs. 4–5 µm), higher number of precloacal tubular supplements (four vs. three), tail shape in males (c' 5–5.15 vs. 3.2–4.8); from *L. cangionensis* by bigger cephalic setae (3 vs. 1.5–2 µm), distance between two anteriormost supplements not so greater than distances between second and third, and third and fourth supplements, bigger spicules along the arc (27.2–29.1 vs. 16–18 µm); from *L. elegans* by bigger cephalic setae (3 vs. 1.5–2 µm) and lesser number of tubular supplements (four vs. five); from *L. puccinellae* by higher number of tubular supplements (four vs. three) and tail shape in males (c' 5–5.15 vs. 7–9.5); from *L. venustus* by longer cephalic setae (3 vs. 1.5–2 µm) and longer spicules (27.2–29.1 vs. 18–22 µm).

Order MONHYSTERIDA Filipjev 1929
Family MONHYSTERIDAE De Man 1876
Genus *Halomonhystera* Andrássy 2006
Halomonhystera vandoverae (Zekely et al. 2006a, b, c)

Zekely et al. 2006b: 27–31, Figs. 1, 2A–O, 3A–K, Table 1 (*Thalassomonhystera vandoverae*). Tchesunov et al. 2015: 63.

Figures 27, 28, 29, Table 12: morphometrics

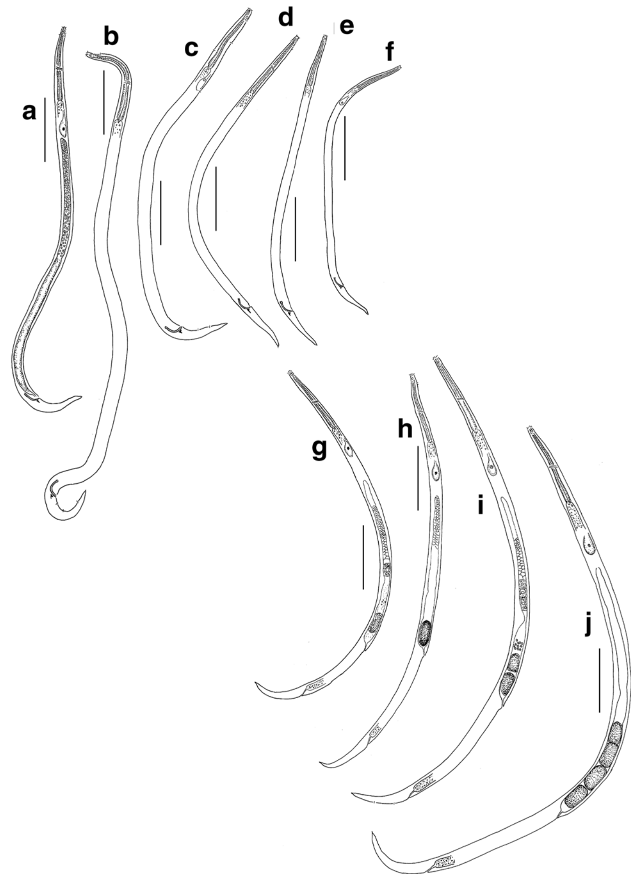


Fig. 27 *Halomonhystera vandoverae* Zekely et al. 2006a, b, c, variation in habitus. **a–f** Males; **g–j** females. *Scale bars* 100 µm

Material

Thirteen males and eleven females.

Locality

Mid-Atlantic Ridge, hydrothermal site Snake Pit (23°22′ N, 44°57′ W, 3420–3480 m depth), washout from a mussel druse *Bathymodiolus puteoserpentis*. 21.06.2002.

Description

Very small nematodes. Body spindle-shaped, slender. Among fixed specimens, males mostly curved ventrally and females curved dorsally. Cuticle thin, smooth. Multitudinous small light-refracted grains scattered in the body, apparently within the hypodermis; the grains well discernible even at lower magnification.

Anterior end and labial region not set off. Inner labial sensilla not seen. Ten very short anterior setae (1.5–2 µm in both sexes); probably, four cephalic setae a bit longer than six outer labial setae.

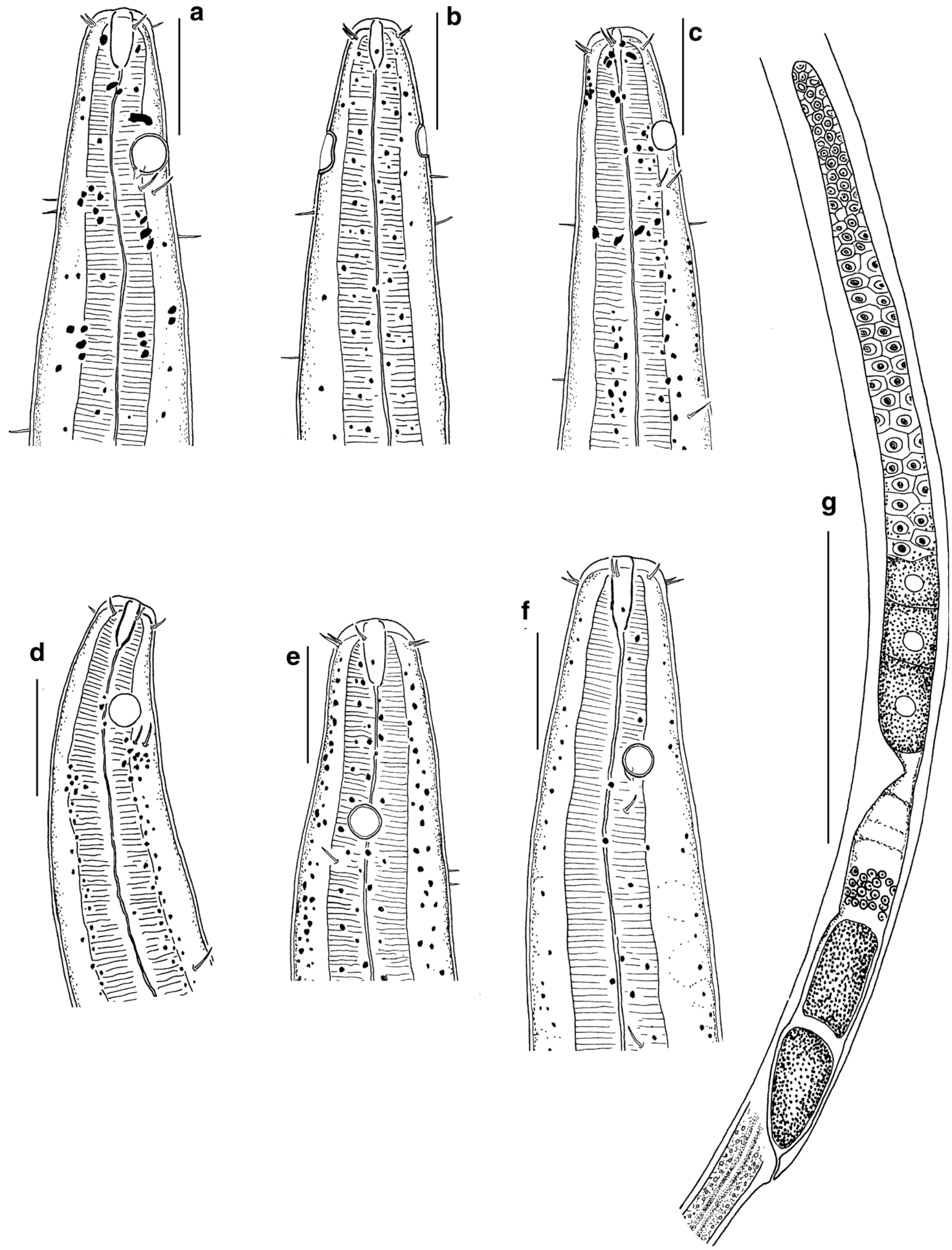


Fig. 28 *Halomonhystera vandoverae* Zekely et al. 2006a, b, c, details. **a–d** Cephalic ends of males; **e–f** cephalic ends of females; **g** female reproductive system. *Scale bars* **a–f** 10 µm; **g** 100 µm

Amphideal fovea circular, with distinct cuticular rim, situated posterior to the stoma level. Amphideal fovea in females is a bit smaller than in males, with a thinner and less distinct cuticular rim. Width of the fovea in males 3–3.5 µm (30–37.5 % c.b.d.), in females 2.5–3 µm (24–29 % c.b.d.).

One or two lateral setae just posterior to the amphideal fovea, one lateroventral seta at half distance to the nerve ring, another one lateroventral seta at the nerve ring, one postneural lateral seta and few dispersed somatic setae along the rest of the body. Postamphideal and cervical setae may be a bit longer than the anterior setae.

Buccal cavity small, cylindro-conoid, with weakly sclerotized rhabdions. Pharynx cylindroids, relatively wide, evenly muscular throughout its length. Neither pharyngeal glands nor marginal tubes visible.

Renette cell body posterior to the cardia, to the right of the intestine; neck, terminal ampulla and pore not seen.

Male gonad to the right of the intestine. Spicules slender, arcuate, distally pointed, proximally with weakly developed knobs. Gubernaculum with short, paired caudal apophyses. No preanal papillae.

Female gonad to the right of the intestine. Female gonopore at a considerable distance anterior to the anus, on

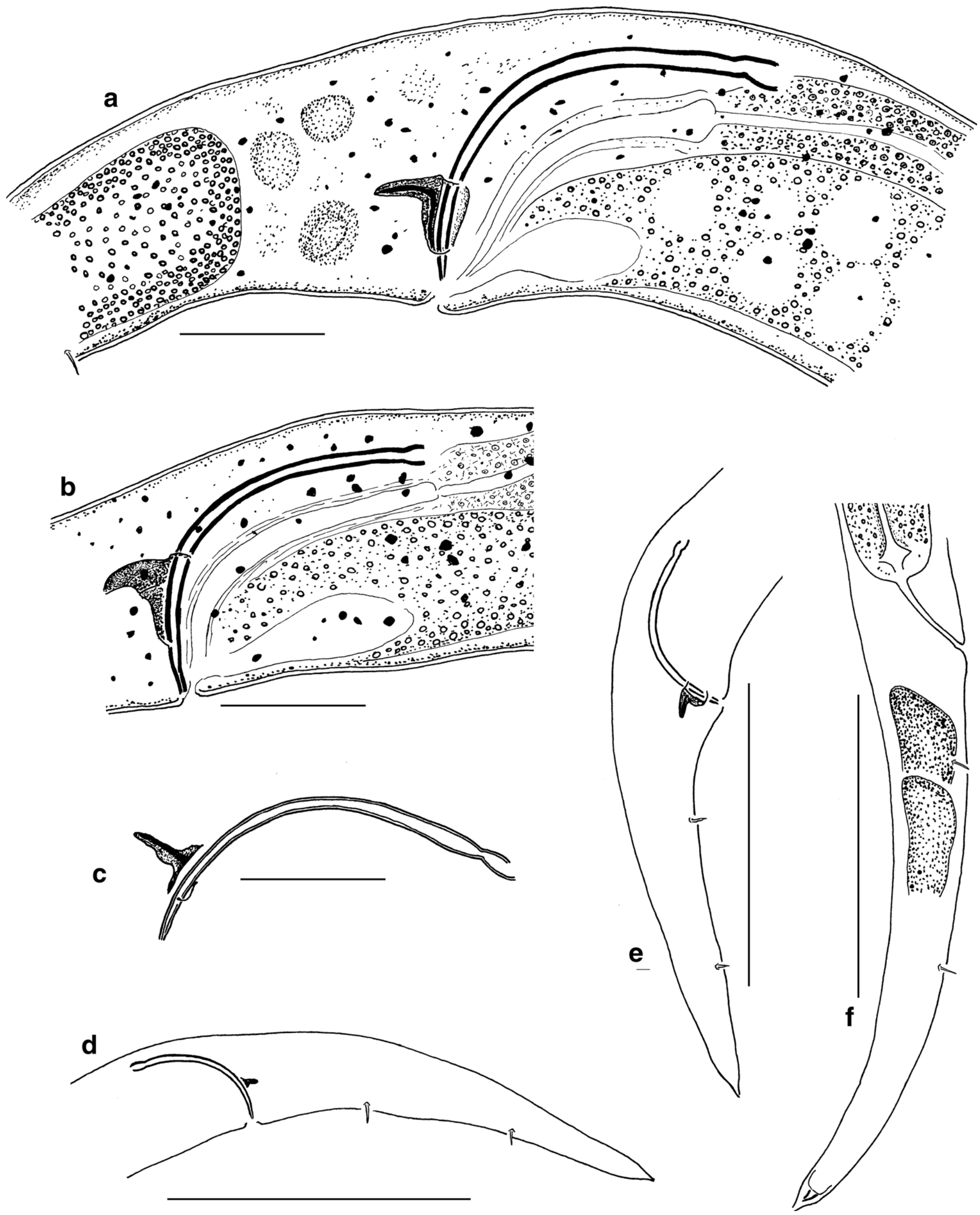


Fig. 29 *Halomonhystera vandoverae* Zekely et al. 2006a, b, c, variation in tail and copulatory apparatus. **a**–**c** Male copulatory apparatus; **d**, **e** male tails; **f** female tail. *Scale bars* **a**–**c** 10 μm, **d**–**f** 50 μm

the bottom of the vulvar depression. Postvulvar body notably narrowed. Vulva non-sclerotized. Uterus may contain one to four fertilized eggs about 16 × 38 to 19 × 42 in size. Tine spherical spermatozoa in between fertilized eggs and immature oocytes.

Tail conical, terminated with a conical spinneret. There are about two pairs of lateroventral setae 5.5–3 μm and two subterminal setae 1–2 μm long. In females, the tail is mostly dorsally bent.

Gut content

In the majority of specimens, the midgut is empty throughout its length or contains vague fibrosity; in few specimens, the midgut of a single female contains diffuse granularity and a few larger bodies (?cells) 3–4 μm in size. However, buccal cavity of all specimens is filled with swallowed medium-sized particles.

Remarks

Our specimens correspond well to the original diagnosis of Zekely et al. (2006b). Our description supplements the original diagnosis with indication on numerous subcuticular inclusions, presence of lateral subamphidial setae in both sexes, two pairs of lateroventral setae on the male tail. Tchesunov et al. (2015) transferred the species to the genus

Table 12 Morphometrics of *Halomonhystera vandoverae*, Snake Pit, st. 4330

Character	Males					Females				
	n	Min–max	Mean	S.D.	C.V.	*n*	Min–max	Mean	S.D.	C.V.
L	13	472–882	647	111	17.2	11	685–1010	790	110	13.9
a	13	31.1–40.5	36.0	2.99	8.31	11	31.4–38	34.6	2.53	7.32
b	13	4.56–6.74	5.85	0.72	12.3	11	4.75–7.71	6.38	0.81	12.7
c	13	4.50–10.4	8.68	0.82	9.45	11	8.15–10.2	9.16	0.72	7.87
c′	13	3.78–5.35	4.57	0.51	11.2	11	5.69–7.00	6.32	0.41	6.43
V %	–	–	–	–	–	11	65.0–71.4	68.1	2.13	3.13
Body diameter at level of cephalic setae	12	4.50–6.50	5.30	0.58	11.0	10	5.00–7.00	6.10	0.57	9.31
Body diameter at level of amphideal fovea	12	8.00–9.50	9.58	0.70	7.32	11	10.0–12.0	11.0	0.65	5.94
Body diameter at level of nerve ring	13	13.5–18.0	15.2	1.26	8.35	11	15.0–19.5	17.0	1.21	7.12
Body diameter at level of cardia	13	14.0–20.5	16.2	1.71	10.6	11	16.5–21.0	18.5	1.29	7.01
Midbody diameter	13	14.5–23.5	18.2	2.55	14.0	11	20.0–26.0	22.8	1.92	8.41
Anal body diameter	13	15.0–19.5	16.9	1.60	9.45	11	13.5–18.5	15.5	1.59	10.3
Distance from cephalic apex to anterior rim of amphideal fovea	12	9.00–12.0	10.9	1.11	10.2	9	11.5–14.5	13.1	1.01	7.77
Distance from cephalic apex to postamphideal setae	9	14.0–22.0	17.9	2.94	16.4	7	17.0–21.0	19.0	1.63	8.59
Spicule's length along arch	13	24.2–32.0	28.7	2.30	7.99	–	–	–	–	–

Measures in µm except for ratios

Halomonhystera in frame of a taxonomic review of the genus *Halomonhystera* Andrássy 2006.

Geographical distribution and ecology

The species has been described from the same hydrothermal site on the Mid-Atlantic Ridge, i.e. Snake Pit, 3492 m depth, aggregations of mussels *Bathymodiolus puteoserpentis* growing on bare basalt where *H. vandoverae* made up 75–88 % of the total nematode fauna (Zekely et al. 2006b). In our sample, the portion of *H. vandoverae* is even higher, 91 % of all specimens in the nematode community.

Ecological part

Meiofauna or meiobenthos are usually treated as metazoans and protists passing through a sieve with 1 mm mesh size and retained on a 63 µm or smaller mesh-sized sieve (Giere 2009). Therefore, the nematode samples are not representative enough for presentation species ratio and may present only fraction of bigger species of the nematode community because of partial loss of smaller species and juveniles of bigger species through the sieve of 100 µm mesh size used for this material. Another circumstance impeding a proper quantitative characterization and comparison of communities from different sites is unequal samples of specimens (Table 13). Nevertheless, it is possible to do some general remarks in conclusion.

Species composition and specimen numbers in all the hydrothermal sites studied are summarized in Table 13. A total of 1384 specimens from six sites are presented by 26 morphospecies belonging to 24 genera, 19 families and six orders. Only seven of 26 morphospecies could be described and identified here because of either insufficient material (lack of adult stages) or/and poor condition of specimens in glycerine slides. However, the list gives a general presentation on diversity and taxonomic structure of nematode assemblages in Mid-Atlantic hydrothermal sites.

Various sites differ from one another significantly in species numbers and ratios. The collection from Lucky Strike hydrothermal site is the most abundant in terms of both specimen (700) and species (16) numbers. The Lost City collection is presented by fewer number of specimens (172) but comparable number of species (14). On the other hand, the northernmost site Menez Gwen and southernmost Snake Pit are characterized low diversity with high dominance of one species, the large-bodied *Oncholaimus scanicus* in Menez Gwen (98.5 % of specimens) and small-bodied *Halomonhystera vandoverae* in Snake Pit (91.3 % of specimens).

Table 13 Specimens and species per hydrothermal site

Species	Hydrothermal site						
	Menez Gwen	Rainbow	Lucky Strike	Lost City	Broken Spur	Snake Pit	Total
Enoplus sp.				19			19
Anticomidae g.sp.		3		1	2		6
Leptosomatides sp.				2			2
Metacylicolaimus sp.				1			1
Syringolaimus sp.			4	1		2	7
Oncholaimus scanicus (Allgén 1935)	260		129	96			485
Enchelidiidae g.sp.				7			7
Prochromadora helenae sp. n.			74	1	1		76
Parapinnanema sp.	2						2
Actinonema sp.				1			1
Paracanthonchus olgae sp. n.		105	137	1	4		247
Halichoanolaimus sp.			1				1
Desmodora marci (Verschelde et al. 1998)		6	68	18		1	93
Prochaetosoma ventriverruca sp.n.		24	229	6			259
Epsilonematidae g.sp.			1				1
Microlaimus sp.			11				11
Leptolaimus hydrothermalis sp. n.			9				9
Leptolaimus sp.						3	3
Camacolaimus sp.	1						1
Paralinhomoeus sp.				17		3	20
Halomonhystera vandoverae (Zekely et al. 2006a, b, c)						94	94
*Halomonhyster*a sp.			22				22
Thalassomonhystera sp.			9				9
Theristus sp.			1				1
Daptonema.sp.	1		3	1			5
Benthimermitidae g.sp.			2				2
Total	264	138	700	172	7	103	1384

Discussion

Body size and feeding types

In the most studies of deep-sea meiofauna, a decrease in average body size of nematodes from shelf to slope and further downwards is revealed (e.g. Soltwedel et al. 1996; Udalov et al. 2005); this is connected usually with decrease in organic nutrients available. Nematodes of Mid-Atlantic hydrothermal sites are rather large: the long-bodied *Oncholaimus scanicus*, *Paralinhomoeus* sp. and *Enoplus* sp. (body length 7–14 mm) predominate or are common in some stations, and the medium-sized *Paracanthonchus olgae*, *Desmodora marci* (body length 1.3–1.8 and 1.8–2.5 mm, respectively) are also often prevail in the communities (Table 13). Evidently, large or medium body size of dominant species is connected with specific eutrophic conditions of these deep-sea hydrothermals.

Most nematode species from the hydrothermal sites have well-developed buccal cavity with armature. According to the general adopted trophic classification (Wieser 1953b; Heip et al. 1985), they belong to omnivores/predators with large stoma and large onchs (type 2B, *Oncholaimus scanicus*, *Enoplus* sp., Enchelidiidae g. sp.), epistrate feeders with scraping tooth in stoma (type 2A, *Paracanthonchus olgae*, *Prochromadora helenae* and other species of Chromadoridae, *Desmodora marci*, *Prochaetosoma ventriverruca*, *Microlaimus* sp.), and non-selective deposit feeders, actually bacteria feeders (type 1B, *Daptonema* sp., Anticomidae g. sp., *Halomonhystera vandoverae*, *Thalassomonhystera* sp., *Leptolaimus* spp.). Noteworthily, selective feeders (actually bacteria feeders, type 1A, stoma absent as such or tight, narrow tubular) are absent in the community; admittedly however, *Leptolaimus* spp. with their tight tubular stoma may be classified also as selective feeder.[3] The heightened portion of 2A and 2B feeding type species ingesting coarse and large particles differs hydrothermal nematode assemblages from background slope and abyssal communities with predominance of tiny species belonging to feeding type 1A or with very tight or lacking stoma or less to 1B, both ingesting minute particles (i.e. bacteria). About half of specimens of *O. scanicus*, *P. olgae*, *D. marci* and less than half of specimens *P. ventriverruca* have some granular or fibrous content in the intestine lumen, evidently swollen as a food. There are no true predatory species in the hydrothermal assemblages, but finding of an ingested nematode in the intestine of *P. olgae* indicates that this species may be a facultative predator. *P. helenae* specimens have some spherical vesicles and no solid particles that agree with the way of feeding of chromadorids by piercing and sucking out content of hard-shelled cells (e.g. Moens and Vincx 1997). Midgut of *H. vandoverae* specimens is usually empty, but buccal cavity is always filled with medium-sized particles (see paragraph «Gut content» in species descriptions). Significant portion of specimens with filled intestine indicates on intensive feeding of most hydrothermal species.

Species composition

The numbers of nematode species in the hydrothermal sites studied (Table 13) are very low for the most marine habitats, also for the deep sea. For comparison, 147 morphospecies were isolated from 1340 nematode individuals sampled in abyssal sediment of Angola Basin, south-east Atlantic, at depths about 5500 m (Tchesunov 2010). Evidently, the low diversity is connected with characteristic property of the milieu: there are bare rocks overgrown by mussels around vents. Habitats of nematodes there are small amounts of silt accumulated in crevices between rocks and between shells. Structurally, this milieu relates to that of shallow-water epiphytic nematodes dwelling in detritus caught in the algae rhizoids and kelp holdfasts (Heip et al. 1985; Danovaro and Fraschetti 2002) featured by lower diversity in comparison with adjacent sediments.

Only seven species are identified to species level, four of them are described here as new for science and three species were recorded previously from elsewhere. Two species were already known in deep-sea reduced environments, *Desmodora marci* Verschelde et al. 1998 in remote hydrothermal vents of Lau Basin (South-West Pacific) (Verschelde et al. 1998) and Hydrate Ridge methane seeps (North-East Pacific) (Sapir et al. 2014), and *Halomonhystera vandoverae* (Zekely et al. 2006a, b, c) from the same Mid-Atlantic Ridge hydrothermal vent Snake Pit (Zekely et al. 2006b). The third species *Oncholaimus scanicus* (Allgén 1935) was known hitherto from only type locality, non-hydrothermal upper sublittoral site in Öresund (Norway Sea) (Allgén 1935). Other species including new ones belong to genera common in littoral and sublittoral habitats of North Atlantic seas. As mentioned in differential diagnoses, all the four new species here described are also related to known shallow-water species and not to deep-sea species. Close relation of many deep-sea nematode species to shallow-water species was also confirmed with molecular-genetic methods (Bik et al. 2010; Van Campenhout et al. 2014). Genus composition of the North Mid-Atlantic Ridge hydrothermal nematode assemblages is disparate to those of slope and abyssal sediments of comparable depths where such genera as *Acantholaimus*, *Halalaimus*, *Thalassomonhystera*, *Desmoscolex* usually predominate (see, e.g. Vanreusel et al. 2010b). Summarizing, the hydrothermal vent nematode communities of the North Mid-Atlantic Ridge look like rather poor shallow-water communities that also fits to conclusions of Zekely et al. (2006c), Gollner et al. (2010, 2013) and Vanreusel et al. (1997, 2010a, b).

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References

Alekseev VM, Rassadnikova IV (1977) A new species and taxonomic analysis of the genus *Leptolaimus* (Nematoda, Araeolaimida). Zoologicheskii Zhurnal 56:1766–1774 (in Russian, English summary)

Allgén C (1935) Die freilebende Nematoden des Öresunds. Capita Zoologica 6(3):1–192

Andrássy I (2006) *Halomonhystera*, a new genus distinct from *Geomonhystera* Andrássy, 1981 (Nematoda: Monhysterida). Meiofauna Marina 15:11–24

Bastian HC (1865) Monograph on the Anguillulidae, or free Nematoids, marine, land, and freshwater; with descriptions of 100 new species. Trans Linn Soc Lond 25:73–184

Belogurov OI, Belogurova LS (1977) Systematics and evolution of Oncholaiminae (Nematoda). I. Significance of the demanian system. Russ J Marine Biol 3:36–47 (in Russian, English summary)

[3] Bouwman et al. (1984) have shown that a closely related species *Leptolaimus papilliger* consumed bacteria selectively.

Bik HM, Thomas WK, Lunt DH, Lambshead PJ (2010) Low endemism, continued deep-shallow interchanges, and evidence for cosmopolitan distributions in free-living nematodes (order Enoplida). BMC Evol Biol 10:389. http://www.biomedcentral.com/1471-2148/10/389
Bouwman LA (1981) A survey of nematodes from the Ems Estuary. Part I: systematics. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 108:335–385
Bouwman LA, Romeyn K, Admiraal W (1984) On the ecology of meiofauna in an organically polluted estuarine mudflat. Estuar Coast Shelf Sci 19:633–653
Cobb NA (1914) Antarctic marine free-living nematodes of the Shakleton Expedition. Contrib Sci Nematol (Baltimore) 1:1–33
Cobb NA (1930) The demanian vessels in nemas of the genus *Oncholaimus*; with notes on four new *Oncholaimus*. J WashAcad Sci 20:225–241
Cobb NA (1932) *Metoncholaimus pristiurus*, a nema suitable for laboratory courses in Zoology. J Wash Acad Sci 22:344–354
Coles JW (1977) Freeliving marine nematodes from Southern Africa. Bulletin of the British Museum (Natural History). Zoology 31(1):3–49
Coomans A, Heyns J (1983) *Oncholaimus sahariensis* sp.n. (Nematoda) from the Algerian Sahara. Hydrobiologia 107:193–201
Coomans A, Verschuren D, Vanderhaeghen R (1988) The demanian system, traumatic insemination and reproductive strategy in *Oncholaimus oxyuris* Ditlevsen (Nematoda, Oncholaimina). Zool Scr 17(1):15–23
Copley JTP, Flint HC, Ferrero TJ, Van Dover CL (2007) Diversity of meiofauna and free-living nematodes in hydrothermal vent mussel beds on the northern and southern East Pacific Rise. J Marine Biol Assoc UK 87:1141–1152
Cuvelier D, Sarrazin J, Colaço A, Copley JT, Glover AG, Tyler PA, Santos RS, Desbruyères D (2011) Community dynamics over 14 years at the Eiffel Tower hydrothermal edifice on the Mid-Atlantic Ridge. Limnol Oceanogr 56(5):1624–1640
Danovaro R, Fraschetti S (2002) Meiofaunal vertical zonation on hard-bottoms: comparison with soft-bottom meiofauna. Mar Ecol Prog Ser 230:159–169
De Man JG (1876) Onderzoekingen over vrij in de aarde levende Nematoden. Tijdschriftder Nederlandsche dierkundige Vereeniging 2:78–196
Decraemer W, Gourbault N (1997) Deep-sea nematodes (Nemata, Prochaetosomatinae): new taxa from hydrothermal vents and a polymetallic nodule formation of the Pacific (East Rise; North Fiji and Lau Basins; Clarion-Clipperton fracture zone). Zool Scr 26(1):1–12
Decraemer W, Gourbault N, Backeljau T (1997) Marine nematodes of the family Draconematidae (Nemata): a synthesis with phylogenetic relationships. Hydrobiologia 357:185–202
Deprez T, Steyaert M, Vanaverbeke J, Spreybroeck J (2005) NeMys database. www.nemys.ugent.be. Accessed March 2014
Dinet A, Grassle F, Tunnicliffe V (1988) Premières observations sur la méofaune des sites hydrothermaux de la dorsale Est-Pacifique (Guaymas, 21°N) et de l'Explorer Ridge. Proceedings of the hydrothermalism, biology and ecology symposium, Paris, 4–7 November 1985. Oceanol Acta 85:7–14
Ditlevsen H (1918) Marine freeliving nematodes from Danish waters. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening I Kjobenhavn 70:147–214
Ditlevsen H (1928) Free-living marine nematodes from Greenland waters. Meddelelser om Grønland 23:199–250
Filipjev I (1927) Les Nématodes libres des mers septentrionales appurtenant a la famille des Enoplidae. Archiv für Naturgeschichte 91 A(6):1–216
Gagarin VG, Thanh NguyenVu (2007) Two new species of the genus *Halaphanolaimus* de Man, 1876 (Nematoda: Leptolaimidae) from Cangio mangrove forest, Vietnam. Tap chí SINH HOC 29(3):7–14
Galkin SV (2006) Spatial structure of hydrothermal communities on the Mid-Atlantic Ridge. In: Vinogradov ME, Vereshchaka AL (eds) Ecosystems of the Atlantic hydrothermal vents. Nauka, Moscow, pp 163–202 **(in Russian)**
Gebruk A, Fabri MC, Briand P, Desbryères D (2010) Community dynamics over a decadal scale at Logatchev, 14 degrees 45′N, Mid-Atlantic Ridge. Cahiers de Biologie Marine 51(4):383–388
Gerlach SA (1957) Die Nematodenfauna des Sandstrandes an der Küste von Mittelbrasilien (Brasilianische Meeres-Nematoden IV). Mitteilungen aus dem Zoologischen Museum in Berlin 33(2):411–459
Gerlach SA (1959) Neue Meeres-Nematoden aus dem Supralitoral der deutschen Küsten. Internationale Revue der gesamten Hydrobiologie und Hydrographie 44:463–467
Giere O (2009) Meiobenthology, 2nd edn. Springer, Berlin
Gollner S, Riemer B, Martínez Arbizu P, Le Bris N, Bright M (2010) Diversity of meiofauna from the 9°50′N East Pacific Rise across a gradient of hydrothermal fluid emissions. PLoS ONE 5(8):e12321. doi:10.1371/journal.pone.0012321
Gollner S, Miljutina M, Bright M (2013) Nematode succession at deep-sea hydrothermal vents after a recent volcanic eruption with the description of two dominant species. Org Diversity Evol 13:349–371
Goroslavskaya E (2010) Benthic fauna associated with mussel beds and shrimp swarms at hydrothermal vents on the Mid-Atlantic Ridge. Cah Biol Mar 51:393–400
Gourbault N (1985) Nématodes abyssaux (Campagne Walda du navire ocèanographique Jean-Charcot). 1. Espèces nouvelles de Cyatholaimidae. Cah Biol Mar 21:61–71
Hammer Ø, Harper DAT, Ryan PD (2001) PAST: palaeontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9
Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanography and marine biology. Ann Rev Lond 23:399–489
Heyns J, Coomans A (1977) Freshwater nematodes from South Africa. 2. *Oncholaimus deconincki* n. sp. Revue de Zoologie Africaine 91:906–912
Holovachov O, Boström S (2013) Swedish Plectida (Nematoda). Part 4. The genus *Leptolaimus* de Man, 1876. Zootaxa 3739(1):1–99
Hopper BE (1961) Marine nematodes from the coast line of the Gulf of Mexico. Can J Zool 39:183–199
Inglis WG (1970) Cyatholaimidae (Nematoda) from the coast of Western Australia. Rec South Aust Mus 16(5):1–13
Jensen P (1978) Four Nematoda Araeolaimida from the Öresund, Denmark, with remarks on the oesophageal structures in *Aegialoalaimus*. Cah Biol Mar 19:221–231
Kelley DS, Früh-Green KarsonJA, Ludwig KA (2007) The Lost City hydrothermal field revisited. Oceanography 20(4):90–99
Kito K (1981) Studies on the free-living marine nematodes from Hokkaido, IV. J Fac Sci Hokkaido Univ (Sapporo) Ser VI 22(3):250–278
Kreis H (1963) Marine nematoda. Zool Icel 2(14):1–68
Lorenzen S (1969) Freilebende Meeresnematoden aus dem Schlickwatt und den Salzwiesen der Nordseeküste. Veröffentlichungen des Instituts für Meeresforschungen in Bremerhaven 9:195–238
Lorenzen S (1972a) Die Nematodenfauna im Verklappungsgebiet für Industrieabwässer nordwestlich von Helgoland: III. Cyatholaimidae mit einer Revision von *Pomponema* Cobb, 1917. Veröffentlichungen des Instituts für Meeresforschungen in Bremerhaven 13:285–306
Lorenzen S (1972b) *Leptolaimus*-Arten (Freilebende Nematoden) aus der Nord- und Ostsee. Kileler Meeresforsch 28:92–97

Maertens D, Coomans A (1979) The function of the demanian system and an atypical copulatory behavior in *Oncholaimus oxyuris*. Annales de la Société royale zoologique de Belgique 108:83–87

Miljutina MA, Miljutin DM (2015) A revision of the genus *Paracanthonchus* (Cyatholaimidae, Nematoda) with a tabular key to species and a description of *P. mamubiae* sp. n. from the deep North-Western Pacific. Deep Sea Res II 111:104–118

Moens T, Vincx M (1997) Observations on the feeding ecology of estuarine nematodes. J Marine Biol Assoc UK 77:211–227

Rachor E (1969) Das de Mansche Organ der Oncholaimidae, eine genito-intestinale Verbindung bei Nematoden. Z Morphol Okol Tiere 66:87–166

Ramirez-Llodra E, Blanco M, Arcas A (2004) ChEssBase: an online information system on biodiversity and biogeography of deep-sea chemosynthetic ecosystems. Version 1. World Wide Web electronic publication. www.soc.soton.ac.uk/chess/db_home.php

Rho HS, Min WG, Decraemer W, Kim DS (2010) *Prochaetosoma dokdoense* sp. nov (Nematoda: Draconematidae) from Dokdo, Korea: First record of the genus *Prochaetosoma* from a shallow subtidal zone in the northwest Pacific Ocean. Marine Biol Res 6:172–188

Sapir A, Dillman AR, Connon SA, Grupe BM, Ingels J, Mundo-Ocampo M, Levin LA, Baldwin JG, Orphan VJ, Sternberg PW (2014) Microsporidia-nematode associations in methane seeps reveal basal fungal parasitism in the deep sea. Front Microbiol 5(43):1–12. doi:10.3389/fmicb.2014.00043

Sarrazin J, Legendre P, De Busserolles F, Fabri M-C, Guilini K, Ivanenko V, Morineaux M, Vanreusel A, Sarradin P-M (2015) Biodiversity patterns, environmental drivers and indicator species on a high-temperature hydrothermal edifice, Mid-Atlantic ridge. Deep Sea Research part II: topical studies in oceanography, IN PRESS. Open access version. http://archimer.ifremer.fr/doc/00266/37713/

Schulz E (1932) Beiträge zur Kenntnis mariner Nematoden aus der Kieler Bucht. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 62:331–430

Schuurmans Stekhoven JH, De Coninck LA (1933) Diagnoses of new Belgian marine nematodes. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 9:1–13

Smolanko OI, Belogurov OI (1987) *Oncholaimium ramosum* sp. n. and some remarks on the stoma structure in the Oncholaimidae (Nematoda). Zoologicheskii Zhurnal 66(4):490–498 (in Russian, English summary)

Soltwedel T, Pfannkuche O, Thiel H (1996) The size structure of deep-sea meiobenthos in the north-eastern Atlantic: nematode size spectra in relation to environmental variables. J Marine Biol Assoc UK 76(2):327–344

Steiner G (1916) Freilebende Nematoden aus der Barentssee. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 39:511–676

Tchesunov AV (2010) Peculiarities of deep-sea nematode fauna by the example of Angola Basin. 14th International Meiofauna conference, 11–16 July 2010 FourtIMCo, Ghent, Belgium. Abstract Book, p 75

Tchesunov AV, Portnova DA, van Campenhout J (2015) Description of two free-living nematode species of *Halomonhystera disjuncta* complex (Nematoda: Monhysterida) from two peculiar habitats in the sea. Helgol Mar Res 69:57–85. doi:10.1007/s10152-014-0416-1

Turnipseed M, Knick KE, Lipcius RN, Dreyer J, Van Dover CL (2003) Diversity in mussel beds at deep-sea hydrothermal vents and cold seeps. Ecol Lett 6:518–523

Udalov AA, Mokievsky VO, Azovsky AI (2005) Depth-related pattern in nematode size: does the depth itself really mean? Prog Oceanogr 67(1–2):1–23

Van Campenhout J, Derycke S, Tchesunov A, Portnova D, Vanreusel A (2014) The *Halomonhystera disjuncta* population is homogeneous across the Håkon Mosby mud volcano (Barents Sea) but is genetically differentiated from its shallow-water relatives. J Zool Syst Evol Res 52(3):203–216. doi:10.1111/jzs.12054

Van Dover CL (2000) The ecology of deep hydrothermal vents. Princeton University Press, Princeton, New Jersey

Vanreusel A, Van den Bossche I, Thiermann F (1997) Free-living marine nematodes from hydrothermal sediments: similarities with communities from reduced habitats. Mar Ecol Prog Ser 157:207–219

Vanreusel A, De Groote A, Gollner S, Bright M (2010a) Ecology and biogeography of free-living nematodes associated with chemosynthetic environments in the deep sea: a review. PLoS ONE 5(8):e12449. doi:10.1371/journal.pone.0012449

Vanreusel A, Fonseca G, Danovaro R, da Silva MC, Esteves AM, Ferrero T, Gad G, Galtsova V, Gambi C, da Fonsêca Genevois V, Ingels J, Ingole B, Lampadariou N, Merckx B, Miljutin D, Miljutina M, Muthumbi A, Netto S, Portnova D, Radziejewska T, Raes M, Tchesunov A, Vanaverbeke J, Van Gaever S, Venekey V, Nara Bezerra T, Flint H, Copley J, Pape E, Zeppilli D, Martinez Arbizu P, Galeron J (2010b) The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity. Mar Ecol 31:6–20

Verschelde D, Gourbault N, Vincx M (1998) Revision of *Desmodora* with description of new desmodorids (Nematoda) from hydrothermal vents of the Pacific. J Marine Biol Assoc UK 78:75–112

Vincx M, Sharma J, Smol N (1982) On the identity and nomenclature of *Paracanthonchus caecus* (Bastian, 1865), with a redefinition of the genus *Paracanthonchus*. Zool Scr 11(4):243–263

Wieser W (1953a) Free-living marine nematodes. I. Enoploidea. Acta Univ lund (N. F. 2) 49(6):1–155

Wieser W (1953b) Beziehungen zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden, marinen Nematoden. Arkiv für Zool 2:439–484

Wieser W (1954) Free-living marine nematodes. II. Chromadoroidea. Acta Univ lund (N. F. 2), 50(16):1–148

Wieser W (1959) Free-living nematodes and other small invertebrates of Puget Sound beaches. University of Washington Press, Seattle

Zekely J, Gollner S, Van Dover CL, Govenar B, Le Bris N, Nemeschkal HL, Bright M (2006a) Nematode communities associated with tubeworm and mussel aggregations on the East Pacific Rise. Cahiers Biol Marine 47:477–482

Zekely J, Sørensen M, Bright M (2006b) Three new nematode species (Monhysteridae) from deep-sea hydrothermal vents. Meiofauna Marina 15:25–42

Zekely J, Van Dover CL, Nemeschkal HL, Bright M (2006c) Hydrothermal vent meiobenthos associated with mytilid mussel aggregations from the Mid-Atlantic Ridge and East Pacific Rise. Deep Sea Res I 53:1363–1378