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Epsilonematidae (Nematoda) from a cold-water coral environment in the Porcupine Seabight, with a discussion on the status of the genus *Metaglochinema* Gourbault & Decraemer, 1986

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Abstract

Thirteen species of nematodes from the family Epsilonematidae Steiner, 1927 were found to be associated with a cold-water coral reef in the Porcupine Seabight. Among them, four species were already known from various locations such as Chile and Papua New Guinea. Three new species are described here: *Glochinema trispinatum* sp. n. is recognized by three dorsal thorns in the pharyngeal region. This species was also recovered from the Antarctic shelf. *Epsilonema multispiralum* sp. n. is characterised by a multispiral amphid consisting of 3.25 coils. *Bathyepsilonema lopheliae* sp. n. is characterised by its body length, the position and relative width of the amphids and the nature of the cuticular ornamentation. Within the subfamily Glochinematinae Lorenzen, 1974, the number and arrangement of ambulatory setae is considered not to be of diagnostic importance. The former species *Metaglochinema strigosum* Gourbault & Decraemer, 1993 is therefore classified under the genus *Glochinema* Lorenzen, 1974. The original genus diagnosis of *Metaglochinema*, now a monotypic genus, is adjusted. The geographic distribution of epsilonematid nematodes is briefly discussed.

Abbreviations: L – total body length; N – number of cuticular rings, smooth tail tip not included; cs – length of the cephalic setae; dcs – distance from the anterior edge to the cephalic setae; Hdw – maximal width of the head capsule; Hdl – length of the head capsule; Amphw – amphidial width; Amph% – (Amphw / Hdw)*100; Ph – pharyngeal length, measured from the anterior end of the head capsule to the posterior border of the pharyngeal bulb, cardia not included; Asl – length of the anteriormost ambulatory seta of the outer subventral row; sup – length of the supporting setae; mvAsl – length of the middle medioventral or subventral ambulatory seta on the posterior body enlargement; mlvAsl – length of the middle lateroventral ambulatory seta on the second body enlargement; tail – tail length; tmr – length of the non-annulated tail tip; mbd ph – body diameter at the level of the pharyngeal bulb; mbd – maximal diameter of the posterior body region; (mbd) – minimal body diameter; mbd/(mbd) – proportion of the minimal body diameter to the maximal body diameter; ABD – anal body diameter; spic – length of the spicule, measured along the central axis of the structure; gub – length of the gubernaculum, measured along the central axis of the structure; V% – position of the vulva as a percentage of the total body length, measured from the anterior end; a – de Man a-ratio, i.e. L / mbd; b – de Man b-ratio, i.e. L / ph; c – de Man c-ratio, i.e. L / tail

Introduction

Epsilonematidae are marine nematodes with a characteristic ε-shaped body. The family is composed of 3 subfamilies: *Epsilonematinae* Steiner, 1927, *Glochinematinae* Lorenzen, 1974 and the monospe-

cific *Ketratonematinae* Gourbault & Decraemer, 1986. They occur frequently in the marine interstitial fauna but until recently, epsilonematid nematodes were unknown from deep sea habitats (Decraemer et al., 2001). In 2001, a new species *Glochinema bathyperuvensis* Neira et al., 2001 was found in oxygen-limited bathyal sediments from the Peru margin (Neira et al., 2001). Another species of the same genus (*G. kentrosaurides* Gad, 2002) was found recently on the plateau of the Great Meteor Seamount at 455 m depth (Gad, 2002). Epsilonematidae are known to have a looper-caterpillarlike locomotion (Lorenzen, 1973). This infers a preference for habitats providing fixed anchor points, such as coarse sands, carbonate sands and biogenic structures. Although coral fragments can be regarded as ideal substrates for epifaunal nematodes such as Epsilonematidae and Draconematidae, the meiofauna associated with cold-water corals has never been studied before. Degradation processes in coral reefs provide fragments of different sizes and shapes, resulting in a very high habitat complexity, especially when mixed with the sediment.

Nine new and four known species of Epsilonematidae were found to be associated with the cold-water coral *Lophelia pertusa* (Linnaeus, 1758). Three new species are described here, completed with SEM photos.

Materials and methods

Material was obtained with a NIOZ box corer (ø 32 cm) during the 9–19th June 2000 sampling campaign on the RV Belgica. The examined boxcore was collected on the 17th of June 2000, from the top of a coral mound in the Belgica Mounds region (Porcupine Seabight, coordinates: 51° 24′ 48,2″ N and 11° 45′ 55,4″ W). The boxcore penetrated about 15 – 20 cm into the sediment. The surface of the sediment was totally covered with several pieces of dead sponges (*Aphrocallistes bocagei* Schultze, 1886) and dead corals (*Lophelia pertusa* (Linnaeus, 1758)). The larger sponge and coral fragments were collected separately and fixed with 4% formaldehyde. Three bulk sediment cores of 10 cm^2 were taken.

A first stage juvenile of *Bathyepsilonema lopheliae* sp. n. was found in samples obtained from the same location during a may 2001 sampling campaign on the RV Belgica.

The *Lophelia* and sponge material was rinsed over a 1 mm and a 32 μm sieve. Meiofauna extraction from the sediment was done by density gradient centrifugation, using Ludox (density 1.18) as a flotation medium (Heip et al., 1985; Vincx, 1996). Nematodes were picked out individually and mounted on slides for detailled morphological observation with a Leica DMLB light microscope.

An image analysis apparatus (consisting of a Leitz Dialux 20 microscope, a Sanyo CCD videocamera and the Quantimet 500 software) was used to perform the measurements of several type specimens.

Scanning electron microscopic pictures were taken from formalin fixed specimens. After an ultrason treatment (to remove detritus attached to the body) the specimens were transferred in OsO_4, dehydrated, dried (*critical point drying*) and coated with gold particles.

Type material is stored in the collection of Ghent University, Museum voor Dierkunde (UGent), the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussel (KBIN) and the Natural History Museum in London (NHM).

Descriptions

* Remark regarding the descriptions: terminology concerning cuticular appendages was adapted from Verschelde & Vincx (1994).

Family **Epsilonematidae Steiner, 1927**
Subfamily **Glochinematinae Lorenzen, 1974**
Genus ***Glochinema Lorenzen***, 1974
Glochinema trispinatum **sp. n.** (Figs 1–4)

Type specimens.
Holotype male on slide RIT 676. Paratype males, females and juveniles on slide numbers RIT 677–681, 683, 688 (KBIN), MDNC 4021–4025, 4032, 4035 (UGent), other paratypes 2003.329–2003.334, 2003.336, 2003.337 and 2003.340–343 are stored at NHM.
Type locality. Porcupine Seabight, Belgica mounds, at a depth of 1005 m. Coordinates: 51° 24′ 48,2″ N and 11° 45′ 55,4″ W. Other representatives were found in the Belgica mound region at 51° 25′ 7,74″ N and 11° 46′ 9,32″ W, and in Antarctica (see second remark).
Date of collection. 17th of June 2000.
Type habitat. Deep sea environment, on the top of a coral mound. Associated with cold-water coral reef degradation zones. Epifaunal on sponge and coral fragments, as well as in the sediment.
Relative abundance. This species comprises 3.43% of

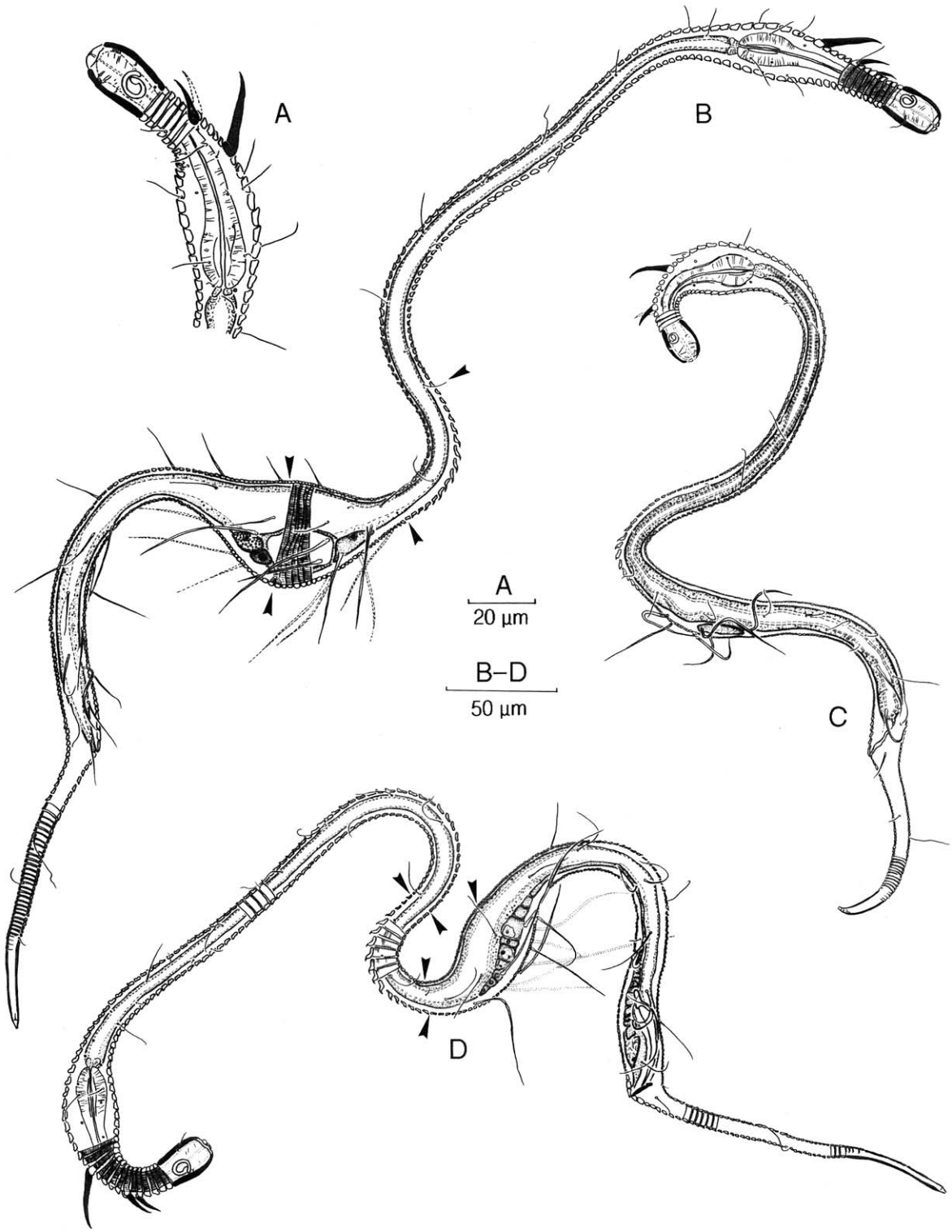

Figure 1. Glochinema trispinatum sp. n. (A) paratype ♂, head and pharynx. Cephalic and subcephalic setae only represented by their insertion sites; (B) paratype ♀, habitus. The mid body is slightly turned, which makes the vulva unclear; (C) juvenile IV, habitus; (D) holotype ♂, habitus. One cephalic seta only represented by its insertion site. Inversion sites are indicated with arrows.

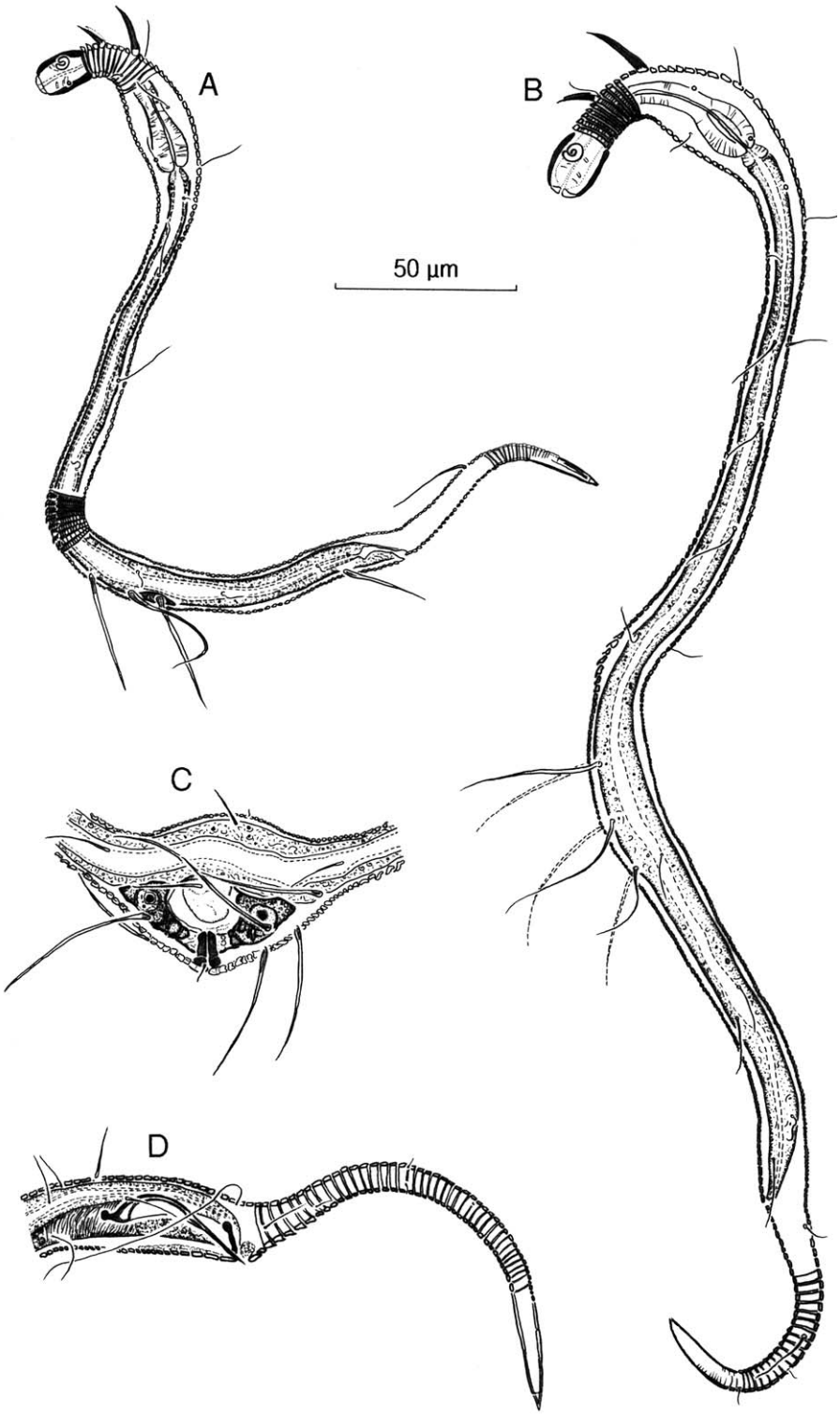

Figure 2. Glochinema trispinatum sp. n. (A) juvenile II, habitus; (B) juvenile III, habitus. One supporting seta not present in this specimen; (C) paratype ♀, detail of reproductive system; (D) paratype ♂, spicular apparatus and tail in surface view.

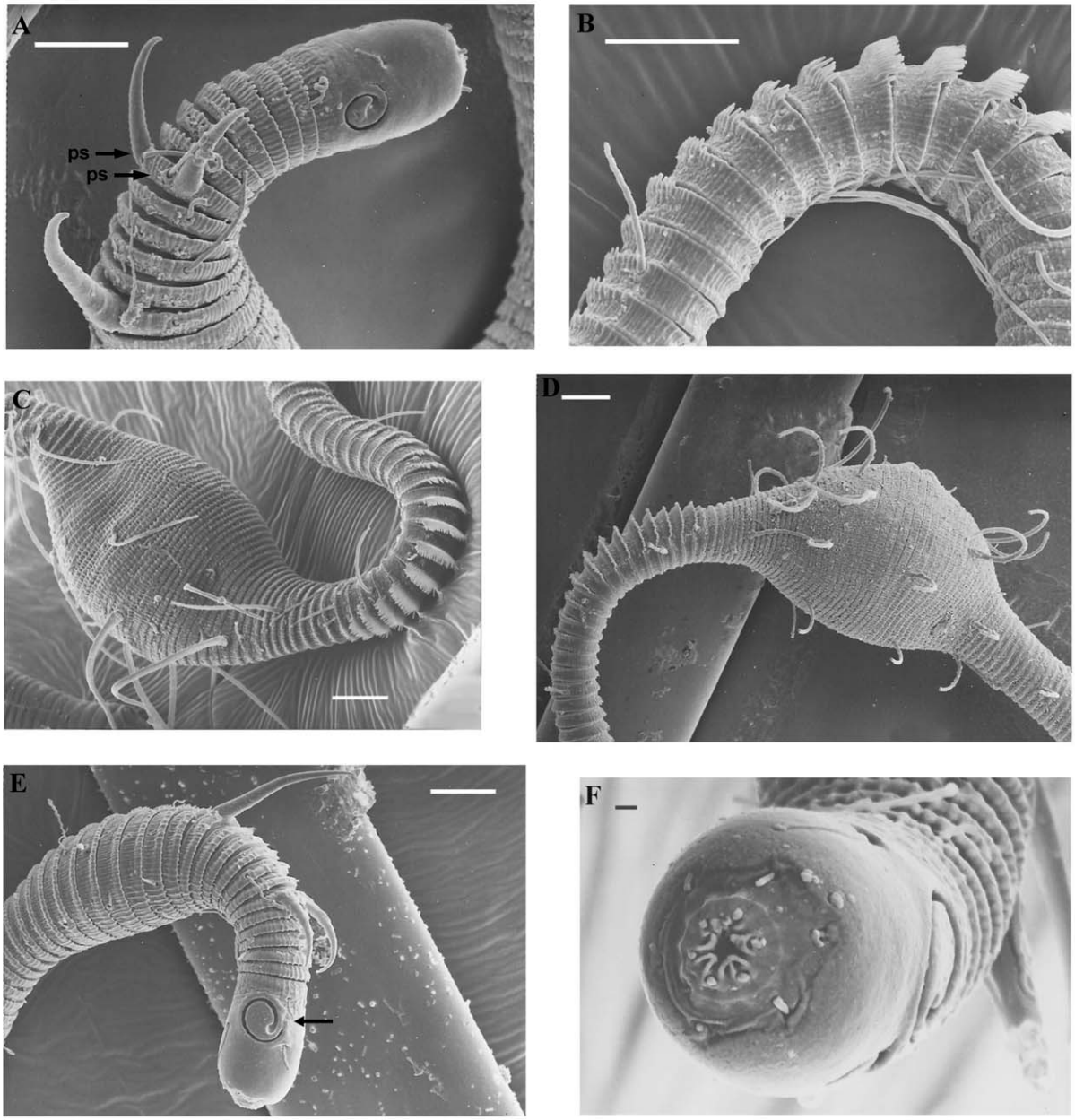

Figure 3. Glochinema trispinatum sp. n. (A) ♀, head capsule and anterior part of pharyngeal region: lateral-dorsal view; (B) ♂, comb-like cuticular appendages: lateral view; (C) ♂, ventral curvature and posterior body enlargement: lateral-ventral view; (D) ♀, ventral curvature and posterior body enlargement: lateral view; (E) ♂, head capsule and pharyngeal region: lateral view; (F) ♂, labial region: en face view. Scale bars: A,B,C,D and E: 10 μm; F: 1 μm.

the total nematode community at the type locality.

Etymology. The name refers to the number of pharyngeal thorns present in this new species. *Tri* comes from the Latin *tres, tria* (three); *spinatum* comes from the Latin noun *spina, spinae* (thorn).

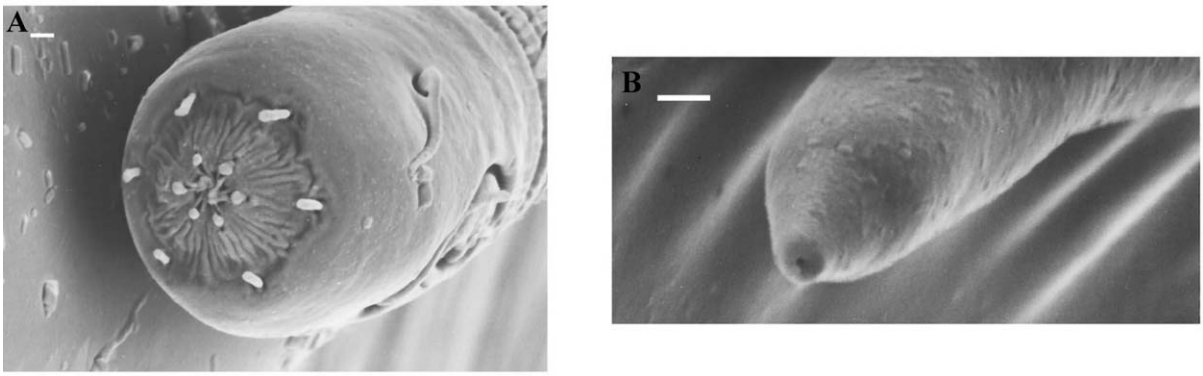

Figure 4. Glochinema trispinatum sp. n. (A) ♀, head capsule: en face view. The labial region is more retracted here than in Figure 3F; (B) ♀, non-annulated tail tip with terminal pore. Scale bars: 1 μm.

Table 1. Measurements of specimens of *Glochinema trispinatum* sp. n. All absolute values are in μm. The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript

	Holotype male	Paratype males ($n = 5$)	Paratype females ($n = 5$)	Juvenile stage II ($n = 8$)	Juvenile stage III ($n = 7$)	Juvenile stage IV ($n = 7$)
L	830	735–790 (760)	750–830 (775)	335–425 (380) [17]	430–560 (505) [21]	475–755 (625) [19]
N	266	245–271 (261)	241–257 (249)	197–213 (205) [5]	237–258 (247) [5]	254–262 (258) [5]
dcs	12.3	11.6–15.3 (13.3)	11.2–14.3 (12.6)			
Hdw	15.5	14.9–15.7 (15.5)	14.9–16.5 (15.6)	10.3–12.6 (11.1)	11.3–16.1 (14.0) [6]	13.7–17.3 (14.8)
Hdl	23.2	23–28.5 (25.0)	20.8–24.9 (22.9)	13.9–17.0 (15.8)	16.3–20.5 (18.2) [6]	19.9–22.5 (21.6)
Amphw	7.6	6.9–8.1 (7.5)	6.6–7.6 (7.3)	3.4–4.5 (4.0)	4.6–5.9 (5.1) [6]	5.0–6.4 (5.9)
Amph%	48.9	46.4–51.8 (48.3)	42.1–50.7 (46.5)	25.3–41.0 (34.6)	31.5–40.6 (36.4) [6]	27.1–44.4 (38.6)
ph	98.0	92.6–97.4 (94.8)	93.1–100.3 (97.1)	58.5–72.2 (64.4)	67.8–89.8 (77.6)	77.9–99.6 (85.7)
mvAsl	38.8	42.3–46.8 (44.2)	35.4–50.7 (42.3)			32.2–40.3 (37.6)
mlvAsl	74.7	44.6–65.6 (56.3)	39.2–68.8 (55.7)	34.3–42.3 (39.9)	42.0–47.9 (44.3)	31.7–55.7 (47.8)
tail	160.6	126.8–137.7 (131.9)	127.7–161.1 (136.7)	65.2–81.0 (71.7)	84.1–104.3 (93.8)	95.6–126.3 (113.1)
tmr	50.5	32.3–37.4 (34.8)	34.7–40.1 (37.2)		19.1–28.6 (24.9) [4]	27.2–33.9 (30.6) [2]
mbd ph	25.6	23.0–24.2 (23.8)	23.4–24.4 (24.1)	15.6–19.7 (18.2)	19.4–24.0 (22.0)	23.2–27.4 (25.2)
mbd	33.6	34.7–42.0 (38.6)	41.6–49.8 (46.8)	10.4–14.8 (13.2)	15.5–19.3 (17.3)	20.8–30.6 (26.7)
(mbd)	12.4	10.1–12.6 (11.4)	10.8–12.4 (11.5)	7.3–9.2 (8.3)	7.9–10.9 (9.8)	10.1–12.7 (11.4)
mbd/(mbd)	2.7	3.0–3.9 (3.4)	3.7–4.6 (4.1)	1.4–1.8 (1.6)	1.6–2.0 (1.8)	2.1–2.8 (2.4)
ABD	16.4	16.4–18.3 (17.2)	13.4–14.6 (13.9)	8.1–10.5 (9.7)	9.8–13.4 (11.9)	13.4–17.9 (15.1)
spic	54.8	42.9–53.8 (46.9)				
gub	9.8	7.3–7.9 (7.6)				
V%			55.9–58.7 (57.3)			
a	24.7	17.6–22.1 (19.8)	18.2–21.0 (19.5)	26.3–32.7 (29.0)	27.4–32.9 (29.8)	22.1–30.2 (25.9)
b	8.4	7.7–8.3 (8.0)	8.9–9.9 (9.4)	5.4–6.7 (5.9)	6.1–7.2 (6.6)	6.9–9.8 (8.1)
c	5.2	5.6–5.8 (5.8)	5.8–7.0 (6.7)	5.0–5.8 (5.3)	5.3–5.8 (5.5)	5.7–6.6 (6.1)

Measurements: Table 1

Males

The body is elongated, slender and clearly epsilon-shaped, with a very long anterior body region (Fig. 1D). There are pronounced enlargements at the level of the pharynx and in the posterior body region, at the level of the testis. At this last level the body reaches its maximal body diameter. The head and the first part of the pharyngeal region are curved ventrally, behind them the first dorsal curvature is situated. Along this curvature, the body is straight and slender. The first dorsal curvature is followed immediately by

the ventral curvature. Behind this conspicious 'S' the second body enlargement is situated, followed by the second dorsal curvature. There is a very thin and long tail clearly oriented dorsally.

The cuticle is built up of 245–271 broad cuticular annules, counted dorsally. This number includes the partial annules present on the tail. Scanning electron micrographs indicate the presence of a zone with longitudinal rods (just as found on body annules) at the posterior edge of the head capsule (Fig. 3A). With a light microscope this 'first annule' cannot even be distinguished, so we do not consider this structure a separate annule.

The anteriormost annules are directed anteriorly. There are three inversions of orientation (►) along the body, so that in the posterior body region the annules are directed posteriorly. The location of these inversion sites is highly variable: the first inversion occurs somewhere between the annules 72 and 88 on the ventral side and between annules 76 and 92 on the dorsal side; the second inversion between annules 89 and 105 ventrally and between annules 84 and 104 dorsally; the third inversion occurs somewhere between annules 116 and 128 ventrally and between annules 116 and 137 dorsally. It was found that there is a certain correlation between the position of these inversion sites and the total number of body annules (indeed when the number of annules is higher, inversion sites occur further down the body, i.e. on annules of higher number. This can also be seen in the relative position of the inversion sites and the combs [see below]). Only a limited degree of overlap was observed between the annules, especially in the pharyngeal region and at the level of the ventral curvature. Body annules are narrowest posterior to the ventral curvature, especially at the level of the second enlargement. Very broad annules are found in the pharyngeal region, and around the cloacal opening. All annules are ornamented with longitudinal ridges, which are actually local elevations of the cuticle. Such elevations are most pronounced on the anterior edge of the annule, sometimes forming small protruding spines. This is obvious on the anterior annules (Fig. 3A) and in the cloacal region, but especially at the level of the ventral curvature (on annules 88–103 in the holotype male) were the (elongated and bent) spines group on the ventral side to form comb-like structures (Fig. 3B–D). These combs tend to occur immediately behind the first ventral inversion site.

The most conspicious cuticular appendages however are the three thorns in the cervical-pharyngeal region (Fig. 3A, E). Each thorn is associated with a seta (**ps** in Fig. 3A) at its insertion site. In most cases there are two small subdorsal thorns located on the same annule and a larger, mediodorsal thorn situated posteriorly to these two thorns. In 24 males, 29 females and 43 juveniles this normal pattern with three thorns was observed. Only one male, two females, one third stage juvenile and four fourth stage juveniles differed from this pattern as they had a higher (four to six) or lower (two) number of thorns. When the annules are given a number (starting behind the head, not counting the 'first annule' attached to the head as argued above), it is possible to formulate a certain 'configuration'. For example, when the two smaller thorns are situated on the seventh annule and the larger thorn is situated on the twelfth annule, the configuration would be 7 7 12. For every specimen this

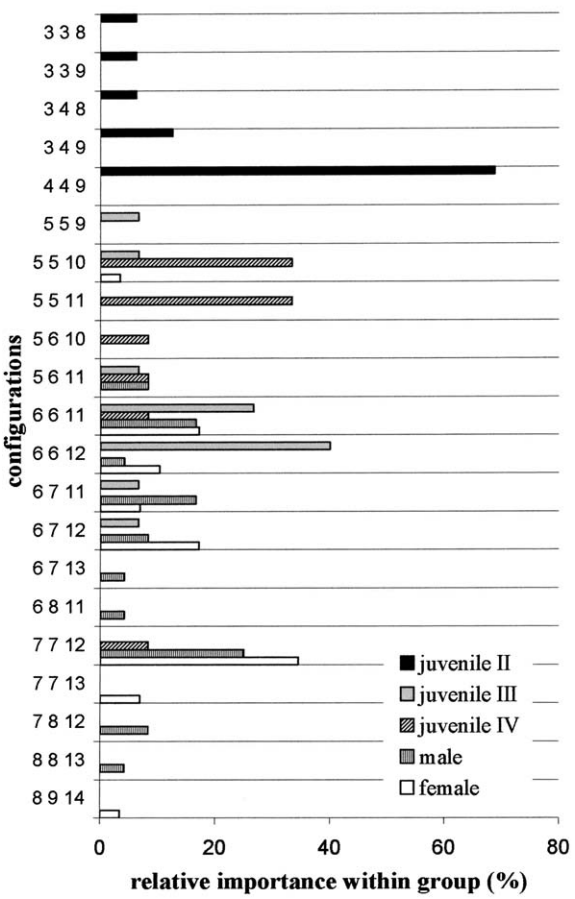

Figure 5. Distribution of pharyngeal thorns in *Glochinema trispinatum* sp. n. The length of the bars indicate the relative importance of each configuration within a group (i.e. juv II, juv III, juv IV, male and female) in percentage.

kind of configuration was formulated. The results are depicted in a graph (Fig. 5). Variability in the position of pharyngeal thorns will be further discussed below.

In the pharyngeal region, the somatic setae are arranged in nine rows: one mediodorsal row, two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. Immediately behind the head capsule there is also a mediolateral pore present, on the left side. A study of the precise distribution of the somatic setae in this region revealed that somatic setae keep their relative position (in relation to the location of the pharyngeal thorns) even when pharyngeal thorns occur on different annules.

Between the pharyngeal region and the dorsal curvature a very large number of setae is present, arranged on four rows: two laterodorsal-subdorsal rows and two lateroventral-subventral ones. A single subventral seta was also found in this region. Between the dorsal curvature and the second body enlargement, setae are arranged on two subventral rows and two subdorsal rows, although also one lateroventral and one laterodorsal seta occurs on each side.

There are two mediolateral rows of somatic setae present on the posterior body enlargement. They appear to be part of a series of setae including similar setae in front of the enlargement and behind it. In the same region there are also subdorsal, laterodorsal and lateroventral setae present.

The pattern that is present in the region behind the second body enlargement is similar to that in females, but in males it is subject to a greater amount of variability. Therefore it will be discussed only in females.

The ambulatory setae (Fig. 3C, D) are all of the same type: very long, robust, slightly curved and pointed at their distal end. They are arranged on four or five rows. There are two lateroventral rows each consisting of three to four ambulatory setae and two subventral rows each consisting of two to three ambulatory setae. Sometimes there are one or two single medioventral setae.

In the region behind the enlargement there are several long and robust supporting setae, but again their distribution has shown to be variable. In females there was a more consistent pattern which will be discussed below.

The head capsule is barrel-shaped: more or less cylindrical but slightly swollen anteriorly. Around the mouth opening there are six triangular lips (Fig. 3F). The papilliform internal labial sensilla are inserted at the base of each of these lips (Figs 3F and 4A). There are six short but setiform external labial sensilla, situated on the same radius as the internal ones. There is a great distance between the lip region and the four cephalic setae. The latter are inserted at the anterior border of the amphids: two of them are inserted subdorsally, the other two subventrally. There are two subdorsal subcephalic setae (**scs**) located at the base of the head (Fig. 3E). The amphidial fovea is an open spiral, oval in outline: ventrally wound, slightly more than one turn. Amphids are large: in males they take up half of the head width. The buccal cavity is narrow and long, teeth are absent. The pharynx is slender, swollen in the anterior part of the head (muscles attaching the pharynx to the head capsule can be clearly observed here) and at its posterior end, forming an elongated bulbus (Fig. 1A). The cardia is triangular and small.

The male reproductive system is monorchic; the testis is outstretched, located ventrally to and on the left of the intestine. It extends as far as the second enlargement. The vas deferens is narrow. The spicules are very slender and arcuate (Fig. 2D). The capitulum bears a knob-like appendix, directed to the anterior end. Because of this, the capitulum resembles the head of a human femur. The velum is obscure. The gubernaculum is short, but has a knob-like enlargement at its distal end. A thin cuticular flap covers the cloacal opening.

The tail is very long and slender (Fig. 1D). The number of annules on the tail varies from 39 to 50. This number includes the five to nine partial annules situated on the dorsal side of the tail tip. The tail tip is also remarkably long.

Females

They resemble the males in most respects. The second body enlargement is well developed in gravid females (Figs 1B and 2C). The number of annules is comparable to that in males: 241-257 counted subdorsally. The first ventral inversion (►) occurs somewhere between annules 73 and 81, the second one between annules 87 and 97, the third ventral inversion is positioned around the vulva (between annules 114 and 127). Dorsally only one inversion site was found, somewhere between the annules 116 and 129. Cuticular ornamentation is similar as in males. The number and position of pharyngeal thorns is also comparable to that in males (see below). In the pharyngeal region and between the pharyngeal region and the second enlargement, the arrangement of somatic setae is similar as in males.

On the second body enlargement two mediolateral rows of somatic setae are present. They form a continuous series together with mediolateral setae in front of the enlargement and behind it. In the same region there are also subdorsal and laterodorsal setae present, as well as four smaller setae near the vulva (two on each side).

Between the second body enlargement and the cloaca, several long mediodorsal and (sometimes) medioventral somatic setae are present. The series of mediolateral setae mentioned above splits into four rows: two laterodorsal rows of long somatic setae and two lateroventral rows of six to seven long and stronger built supporting setae. These supporting setae are shorter and not as strongly built as the ambulatory setae on the second body enlargement. In most cases they are straight.

The mediolateral setae at the level of the second body enlargement are not considered to be ambulatory, because they are not markedly longer or stronger built than the other somatic setae. The ambulatory setae are arranged in three or five rows: there are two lateroventral rows of three very long, robust and slightly curved ambulatory setae, a row of four long and unpaired medioventral setae, or three unpaired setae and a pair of subventral setae.

The reproductive system is didelphic and amphidelphic, with antidromously reflexed ovaries. It is positioned ventrally to the intestine (Fig. 2C). The uterus is often well-developed, the ovaries however are always short. The vulva is surrounded by a smooth region in the cuticula, the vagina is heavily cuticularised and consists of one piece.

There are 5 – 11 incomplete annules on the tail tip. Caudal glands are inconspicuous but scanning electron micrographs have shown that they end in a single pore (Fig. 4B).

Juveniles

First stage juveniles: not found

Second stage juveniles (Fig. 2A): seventeen specimens were found. There is only an obvious thickening of the body in the pharyngeal region, the second body enlargement is nearly absent. There are 197 – 213 body annules, which is clearly less than in adults. The tail consists of 35 – 47 annules and the non-annulated tail tip. The amphids are similar to those in adults, although they are more circular and narrower. There are no subcephalic setae.

In the pharyngeal region, somatic setae are arranged on five rows: one mediodorsal row, two subdorsal rows and two subventral rows. In the posterior body region (in this case the whole region behind the ventral curve is meant) there are two dorso-sublateral rows of somatic setae. Two subventral rows of three long ambulatory setae are present and there is only one pair of supporting setae, situated anterior to the anus.

Third stage juveniles (Fig. 2B): twenty-one specimens were found. Except for the absence of a clear second body enlargement, the body resembles that of adults. The number of annules (237–258) is higher than in juvenile stage II, but it is still lower than in adults. The tail consists of 30 – 36 annules and the tail tip. This number includes the four to eight partial annules. Amphids are not so narrow wound as in second stage juveniles, but they are still relatively circular in contour. There are no subcephalic setae present.

Just as in second stage juveniles, somatic setae in the pharyngeal region are arranged on one mediodorsal row, two subdorsal rows and two subventral rows. Similar as in adults, a series of (in this case laterodorsal instead of mediolateral) somatic setae is present around the second body enlargement. There are two subventral rows of three long ambulatory setae. In the posterior body region there are two laterodorsal rows of somatic setae, and two lateroventral rows of three supporting setae.

Fourth stage juveniles (Fig. 1C): nineteen specimens were found. A second body enlargement is present here, although not as well-developed as in adults. The number of body annules (254–262) is only slightly lower than in adults. The tail consists of 44 – 47 annules and the tail tip. This number includes the five to nine partial annules. Subcephalic setae are absent.

The arrangement of somatic setae in the pharyngeal region is comparable to that in adults, although the number of setae is smaller. At the level of the enlargement, somatic setae are arranged on one mediodorsal row and two mediolateral rows. As in adults, the mediolateral setae form a series together with similar setae in front of and behind the enlargement. There are two lateroventral rows of three ambulatory setae and three long and unpaired medioventral ambulatory setae. Behind the enlargement, the series of long somatic setae splits into four rows just like in the adults. There are two laterodorsal rows of somatic setae, and two lateroventral rows of three to five supporting setae. In addition, a few small laterodorsal and lateroventral somatic setae are present in the posterior body region.

Diagnosis

Glochinema trispinatum sp. n. is characterised by its large size (length in males 770 μm on average, in females 775 μm on average), the large number of annules (in males between 245 and 271, in females between 241 and 257), the slender body with a very long tail oriented dorsally and 2+1 thorns in the pharyngeal region. Comb-like cuticular appendages are present on the ventral curvature. In males, ambulatory setae are arranged in two lateroventral rows of three to four setae, two subventral rows of two to three setae and sometimes one or two medioventral setae. In females, there are three to five rows of ambulatory setae: two rows of three lateroventral setae and next to this four medioventral setae, or only three medioventral setae and two subventral setae (one on each side). In the region behind the enlargement there are two lateroventral rows of six to seven supporting setae. The head capsule is barrel-shaped, the amphid is an oval spiral consisting of one loop; there are two subdorsal subcephalic setae. The males are characterised by their long and slender spicules (48.22 μm on average) with a capitulum bearing a knob-like appendix.

Differential diagnosis, with a discussion on the systematic position within the subfamily Glochinematinae Lorenzen, 1974

According to Gourbault & Decraemer (1986), the genus *Metaglochinema* Gourbault & Decraemer, 1986 differs from *Glochinema* Lorenzen, 1974 in the number of rows of ambulatory setae, the presence of two types of ambulatory setae instead of only one type, and in the number of subcephalic setae. In *Metaglochinema*, the ambulatory setae are arranged on five rows: the setae on the ventral row and those on the two subventral rows are bent and pointed at their distal end, but those on the two 'dorsosublateral' rows are short, fine and tubular. In *Glochinema*, the ambulatory setae are all bent and pointed at their distal end. They are arranged in four subventral rows. In *Metaglochinema* there are only two subcephalic setae, in *Glochinema* four to seven.

The diagnosis of both genera had to be adjusted because of difficulties to distinguish medioventral setae from subventral setae (Gourbault & Decraemer, 1993). This influences the interpretation of row numbers and therefore the distinction between the 2 genera.

In overall appearance, *Glochinema trispinatum* sp. n. is closest to *Metaglochinema strigosum* Gourbault & Decraemer, 1993. The two species can be distinguished by the presence of three pharyngeal thorns in *G. trispinatum* sp. n., the shape of its tail and the structure of the spicules. As in species of the genus *Metaglochinema*, this new species has two rows of long laterodorsal ('dorsosublateral') setae. However, these setae are not short and tubular here. Moreover, we do not consider these setae in *G. trispinatum* sp. n. and in *M. strigosum* to be ambulatory, because there are no clear differences with somatic setae. Laterodorsal setae similar to these can be found in *G. bathyperuvensis* Neira et al., 2001, in *G. kentrosaurides* Gad, 2002 (where they are indicated as extremely long, sensory setae), in *G. agile* Lorenzen, 1974 and in *G. chilense* Lorenzen, 1974. Only in *M. globicephalum* Gourbault & Decraemer, 1986 these setae appear to be clearly tubular.

In *G. trispinatum* sp. n., there are three to five rows of ambulatory setae (depending on the sex). It is obvious that the correct interpretation of setae arrangement is crucial here to find out to which genus this new species belongs. One can also observe that in *G. kentrosaurides* Gad, 2002 the number of rows of ambulatory setae is identical to that in *G. trispinatum* sp. n., a species very close to *M. strigosum*. In short, it appears to us that the arrangement of ambulatory setae is not a good feature to distinguish the two genera in the subfamily Glochinematinae. As argued by Gad (2002) there is also an overlap in the number of subcephalic (or additional cephalic) setae, a feature of great diagnostic importance in Epsilonematidae. In *G. kentrosaurides* there are two subcephalic setae in the males, a number until now only found within *Metaglochinema.* In *G. bathyperuvensis* there are even no subcephalic setae present.

We conclude that *M. strigosum* shows more similarities with species of *Glochinema* than with *M. globicephalum.* The features used to argue its systematic position within *Metaglochinema* have little diagnostic value. Therefore, this species is transferred to the genus *Glochinema*. The genus *Metaglochinema* is maintained for *M. globicephalum*, a species well defined by the presence of strongly built, tubular, dorsosublateral ambulatory setae. The original genus diagnosis by Gourbault & Decraemer (1986) is adjusted:

Metaglochinema Gourbault & Decraemer, 1986 is morphologically similar to *Glochinema* Lorenzen, 1974. However, it can be distinguished from this genus by the presence of strongly built, tubular, dorsosublateral ambulatory setae in addition to the medioventral and subventral rows of ambulatory setae already present in *Glochinema.*

At present, the genus *Glochinema* is thus comprised of seven species:

1. *Glochinema agile* Lorenzen, 1974
2. *Glochinema chilense* Lorenzen, 1974
3. *Glochinema phaleratum* Gourbault & Decraemer, 1993
4. *Glochinema strigosum* (Gourbault & Decraemer, 1993)
5. *Glochinema bathyperuvensis* Neira et al., 2001
6. *Glochinema kentrosaurides* Gad, 2002
7. *Glochinema trispinatum* sp. n.

Remarks

1. *Pharyngeal thorns* (Fig. 5)

Observation of 25 males, 31 females, 16 second stage juveniles, 16 third stage juveniles and 16 fourth stage juveniles showed that the position of the pharyngeal thorns is highly variable. On the graph (Fig. 5) it can be seen that in males as well as in females the most common configuration is 7 7 12, while in juveniles (when considered as one group) it is 4 4 9. Generally, in juveniles the pharyngeal thorns tend to occur more frequently on annules that are situated more anteriorly than in adults. There seems to be a clear backward shift in the position of the pharyngeal thorns during ontogeny, probably due to the formation of new annules anteriorly. However, this trend is not clear when the different juvenile stages are compared. In juvenile II specimens the most common configuration is 4 4 9, in juvenile III it is 6 6 11 and 6 6 12 (this is still consistent with the hypothesis), but in juvenile IV it is 5 5 11. At present, this can not be explained.

2. *Antarctica specimens*

Some material obtained from the Antarctic shelf in 1996 and 1998 also contained several specimens of *Glochinema trispinatum* sp. n. The samples were taken near Kapp Norvegia at depths of 182 m and 805 m. In this case, the substrate consisted of sponge spicules (forming spicule mats) and bryozoan debris. The microhabitat is roughly comparable to that in the Porcupine Seabight, especially to the underlying sediment consisting of a mixture of sponge fragments (and spicules), small coral fragments and sediment.

The animals found in Antarctica are morphologically similar to those in the North Atlantic: they also have three pharyngeal thorns and the arrangement of ambulatory and supporting setae, as well as the shape of the head capsule and spicules is identical. There are however certain morphometrical differences: the Antarctica specimens are longer and more slender than those from the type location. The amphids are also relatively larger, and the number of annules is slightly higher. One male was measured: L: 1213.3 μm; spic: 48.9 μm; N: 284; Amph%: 56.6; mbd/(mbd): 3.8; de Man a: 27.0; de Man b: 9.2; de Man c: 5.5.

Family **Epsilonematidae Steiner, 1927**
Subfamily **Epsilonematinae Steiner, 1927**
Genus ***Epsilonema* Steiner, 1927**
***Epsilonema multispiralum* sp. n.** (Figs 6 and 7)

Type specimens.
Holotype male on slide RIT 681. Paratype males, females and juveniles on slide numbers RIT 681–684, 688 (KBIN), MDNC 4026–4030, 4034 (UGent), other paratypes 2003.335, 2003.338, 2003.339, 2003.344 and 2003.345 are stored at NHM.
Type locality. Porcupine Seabight, Belgica mounds, at a depth of 1005 m. Coordinates: 51° 24′ 48,2″ N; 11° 45′ 55,4″ W. *Remark:* other representatives were found in the Belgica mound region at 51° 25′ 7,74″ N and 11° 46′ 9,32″ W.
Date of collection. 17th of June 2000.
Type habitat. Deep sea environment, on the top of a coral mound. Associated with cold-water coral reef degradation zones. Epifaunal on sponge and coral fragments. These nematodes showed a clear preference for coral fragments as a substrate.
Relative abundance. This species comprises 2.96% of the total nematode community at the type locality.
Etymology. The name refers to the shape of the amphids, consisting of 3.25 coils. From the Latin adverb *multus, a, um* (much) and the Latin adjectif *spiralis* (coiled).

Measurements: Table 2

Males

These are small nematodes with a distinct ϵ-shaped body. The body is enlarged at the level of the pharynx and at the level of the testis, but the first enlargement is often less conspicious (Figs 6A and 7C). The ventral curvature is usually sharp.

There are 136–149 body annules. Ventrally, the inversion of orientation (►) occurs between annules 45 and 46 (or 47 and 48), dorsally between annules 62 and 63 (or 65 and 66). The first annules behind the head capsule and those at the level of the second body enlargement are narrow. In the pharyngeal region and around the cloacal opening the annules are broadest. Only a limited degree of overlap was observed. Each

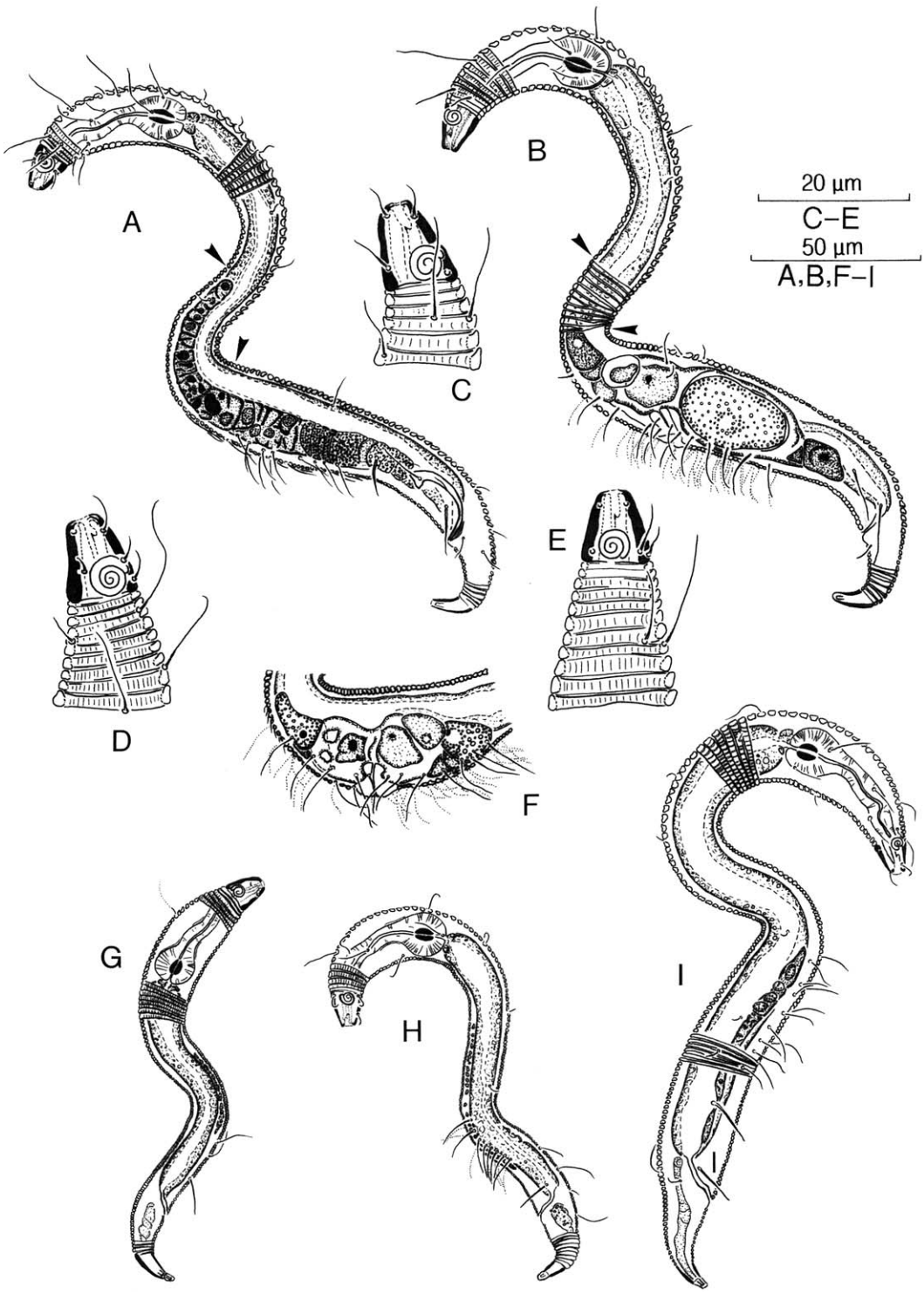

Figure 6. Epsilonema multispiralum sp. n. (A) holotype ♂, habitus; (B) paratype ♀, habitus; (C) paratype ♀, surface view of head capsule; (D) paratype ♂, surface view of head capsule; (E) juvenile IV, surface view of head capsule; (F) paratype ♀, detail of reproductive system; (G) juvenile II, habitus; (H) juvenile III, habitus; (I) juvenile IV, habitus. Inversion sites are indicated with arrows.

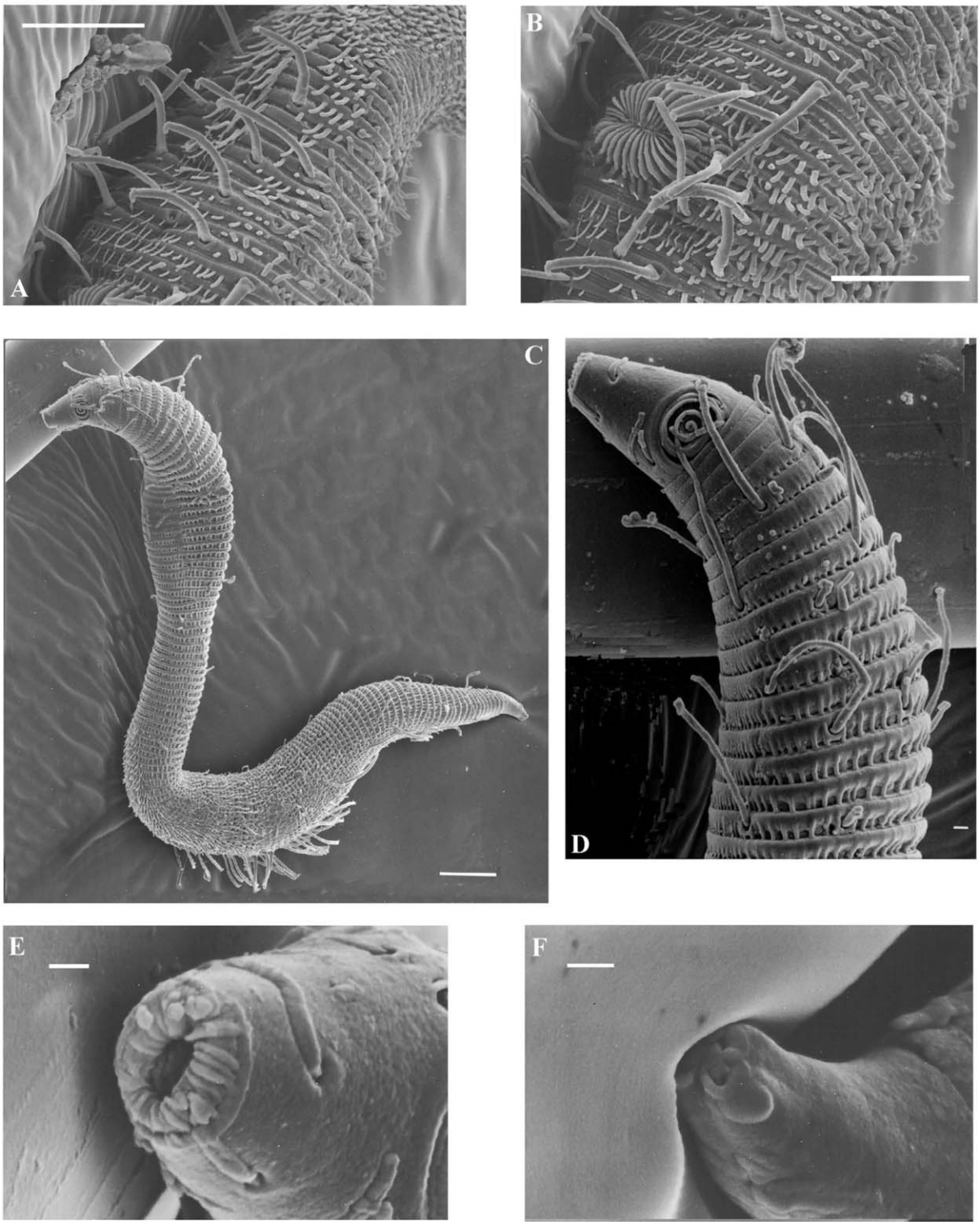

Figure 7. *Epsilonema multispiralum* sp. n. (A) ♀, cuticle in front of the vulva, with ambulatory setae: lateral-ventral view; (B) ♀, cuticle around the vulva: lateral-ventral view; (C) ♂, habitus; (D) ♂, head capsule and pharyngeal region: lateral view; (E) ♂, labial region: en face view; (F) ♂, tail tip. Scale bars: A,B,C: 10 μm; D,E & F: 1 μm.

Table 2. Measurements of specimens of *Epsilonema multispiralum* sp. n. All absolute values are in μm. When different from the total number, the number of specimens that was measured is indicated between brackets in superscript

	Holotype male	Paratype males ($n = 5$)	Paratype females ($n = 5$)	Juvenile stage II ($n = 1$)	Juvenile stage III ($n = 4$)	Juvenile stage IV ($n = 12$)
L	305	285–310 (300)	275–315 (295)	150	180–215 (200)	210–275 (245)
N	149	136–144 (139)	138–145 (141)	161	146–154 (150)	141–166 (153)
cs	4.0		4.1–5.8 (5.0) [(2)]			3.6–5.7 (4.5) [(6)]
dcs	2.1	3.0 [(1)]	1.7–2.1 (1.9) [(2)]	3.3	3.3 [(1)]	3.2–4.9 (3.9) [(8)]
Hdw	9.8	9.3–10.6 (9.9)	9.4–11.3 (10.1)	8.7	7.9–9.1 (8.4)	8.0–9.7 (9.3)
Amphw	6.0	6.0–6.8 (6.4)	5.1–6.2 (5.5)	4.1	3.5–4.4 (3.9)	3.9–5.2 (4.5)
Amph%	61.8	59.7–70.3 (65.4)	50.4–58.7 (54.5)	47.0	41.8–55.7 (46.2)	40.7–55.4 (48.1)
ph	57.5	59.0–68.2 (63.4)	56.4–62.8 (60.0)	42.1	48.4–55.2 (51.7)	49.0–62.2 (56.0)
Asl	12.2	11.4–13.9 (12.7)	10.9–13.6 (12.5)	10.3	11.5–13.6 (12.7)	9.5–17.9 (12.5)
sup	15.4	14.6–21.1 (17.2)	13.5–20.4 (16.0)	14.2	12.2–16.2 (14.2)	10.5–15.9 (14.2) [(11)]
tail	35.3	35.0–38.2 (36.6)	31.7–36.4 (33.7)	25.1	24.3–30.3 (26.9)	28.5–38.3 (30.3)
tmr	12.6	8.2–12.4 (10.4)	11.1–12.0 (11.6)	5.7	7.8–10.3 (8.5)	7.7–9.9 (8.7)
mbd ph	19.0	18.2–20.5 (19.0)	18.5–20.9 (20.0)	16.2	16.1–18.2 (17.2)	18.0–22.0 (20.3)
mbd	25.0	20.8–23.1 (21.9)	29.0–32.3 (30.5)	11.9	12.0–15.8 (14.2)	15.7–21.6 (18.9)
(mbd)	14.1	13.2–14.9 (14.0)	14.7–15.9 (15.3)	10.9	10.7–13.5 (12.5)	13.4–17.4 (15.6)
mbd/(mbd)	1.8	1.5–1.7 (1.6)	1.9–2.1 (2.0)	1.1	1.1–1.2 (1.1)	1.1–1.3 (1.2)
ABD	14.4	13.9–16.3 (14.8)	11.2–13.5 (12.7)	10.3	10.4–12.5 (11.4)	10.3–16.2 (13.5)
spic	35.1	33.0–41.3 (37.3)				
gub	14.5					
V%			40.1–65.3 (55.1)			
a	12.2	13.1–14.3 (13.6)	9.0–10.9 (9.7)	12.8	13.2–14.8 (14.0)	11.8–14.5 (13.0)
b	5.3	4.5–5.1 (4.7)	4.7–5.1 (4.9)	3.6	3.3–4.1 (3.9)	3.7–4.8 (4.4)
c	8.7	7.4–8.7 (8.2)	7.8–10.0 (8.8)	6.0	7.0–7.6 (7.4)	6.9–8.4 (8.4)

annule is ornamented with vacuoles: these are actually indentations of the body cuticle, separated by cuticular ridges. A row of vacuoles occupies more than half the annule length, the other half of the annule is smooth. On the first annules vacuoles are less obvious. Vacuoles are more pronounced dorsally than ventrally, especially in the posterior body region. In the region posterior to the ventral curvature and on the tail, the ventral side of the body is covered with hair-like spines protruding from the posterior edge of the annules. Medioventrally these structures are much finer than lateroventrally, where they are relatively short and thick (Fig. 7A, B). The same type of spines is found also on the lateral and dorsal side of the second enlargement (Fig. 7C). There are seven rows of somatic setae in the pharyngeal region: only one mediodorsal seta, two subdorsal rows, two mediolateral rows and two subventral rows. A few more somatic setae occur scattered in this region.

In the region of the ambulatory setae, somatic setae are arranged on two subdorsal, almost mediodorsal rows. In the region of the supporting setae there are a few mediodorsal, subdorsal and medioventral setae.

The ambulatory setae are quite short and clearly bent in a posterior direction. Their distal end is knicked. They are positioned in four subventral rows: the inner rows each consist of 10 –11 setae, the outer rows of 10 –12 setae.

Between the ambulatory setae and the cloacal opening two ventrosublateral, longitudinal rows of three straight and robust supporting setae were found.

The head capsule is triangular, truncated anteriorly (Figs 6D and 7D). Because in fixed specimens the lipregion is usually retracted, the internal and external sensilla are inconspicious, even on SEM micrographs. The lip region consists of several radial, cuticular ridges (Fig. 7E). There are four cephalic setae, 4 μm in length (holotype male). There are six subcephalic setae, situated at the level of the amphid: one subventral, one ventrolateral and one subdorsal (nearly mediodorsal) pair (Fig. 7D). The amphids are whirled ventrally, multispiral with 3.25 coils. They are lo-

cated near the base of the head capsule, clearly shifted dorsally. In males they take up 64.75% of the head width on average. The buccal cavity is relatively narrow (however in some cases the buccal cavity can become wider due to fixation) and bears a large dorsal tooth (Fig. 6D). The pharynx is short but has a strong muscular posterior bulb with strongly cuticularised valves. The cardia is small.

The tail consists of fifteen to seventeen annules and the tail tip. No partial annules were observed. The tail is short and the overall shape is conical. The caudal glands are not obvious, but an SEM micrograph shows that they end in three separate pores (Fig. 7F).

There is one outstretched testis extending into the ventral curve (anterior to the ambulatory setae), positioned ventrally of the intestine. The spicules are slightly curved and slender, velum obscure, with a triangular capitulum pointing ventrally (Fig. 6A). The gubernaculum is 4 μm long (in the holotype male), lying adjacent to the spicules. Copulatory thorns were not observed.

Females

The females resemble the males in most respects (Fig. 6B, C). However, the second enlargement of the body is more pronounced than in the males, especially in gravid females. The number of annules is also comparable (138–145). The tail consists of thirteen annules (including the tail tip). Ventrally, the inversion (►) occurs between the annules 46–47, 47–48 or 48–49. Dorsally the inversion is not clear, probably it is between annules 58–60 or 62–63. Cuticular ornamentation is similar as in males.

The position of the somatic setae in the pharyngeal and posterior body region, as well as the position and number of subcephalic setae, is comparable to that in males.

There are four rows of ambulatory setae: two outer rows of 10 –12 setae and two inner rows of 10 –11 setae.

The number and location of supporting setae is identical to that in males.

The reproductive system is situated on the ventral side of the intestine: it is didelphic and amphidelphic (Fig. 6F). The vulva is surrounded externally by a large number of radial cuticular ridges (Fig. 7B). In some cases, the vulva is bulged out markedly. At the level of the vulva, thread-like spines are finer than on the rest of the body.

Juveniles

First stage juveniles: not found

Second stage juvenile (Fig. 6G): only a single, moulting specimen was found. Moulting was inferred from the presence of a double distal part of the tail tip. Second stage juveniles are clearly smaller than adults. The body is not as slender as in adults, where the body region between the first dorsal curvature and the ventral curvature is clearly more elongated. There is no posterior enlargement. There are 161 body annules: this is far more than in the adults. Annules are also narrower compared to those in adults. In the pharyngeal region each annule is ornamented with a single row consisting of a large number of small vacuoles. In the posterior body region the annules are even thinner than in the pharyngeal region (as a result, vacuoles can no longer be distinguished). The ratio amphids-head width is slightly lower than in adults. The amphids consist of 2.25 turns. There are no subcephalic setae.

In the pharyngeal region only a single long subdorsal seta (on the left) and a very short medioventral seta were found. Ambulatory setae were difficult to observe; probably there are four setae on a single row. The most posterior seta is straight and in this respect it resembles a supporting seta. In the posterior region, no somatic setae were found.

Third stage juveniles (Fig. 6H): four specimens were found. Compared to second stage juveniles their overall body shape is more similar to that of adults, however they are smaller and the posterior body enlargement is still absent. The number of annules varies from 146 to 154, which is still more than in adults. The tail consists of seventeen to eighteen annules plus the tail tip. Cuticular ornamentation is similar to that in second stage juveniles, however vacuoles tend to be larger and fewer in number. Only three subcephalic setae were observed: a medium-sized mediodorsal one and two short subventral setae (one on each side).

In the pharyngeal region there are mediodorsal, laterodorsal and subventral somatic setae. There are two rows of eight bent ambulatory setae (the last one is slightly shifted more dorsally), followed by one pair of robust ventrosublateral supporting setae. On each side, a long subdorsal seta is situated immediately behind the most posterior ambulatory setae. Next to this, several short setae are found in the posterior body region.

Fourth stage juveniles (Fig. 6E, I): twelve specimens were examined, most of them older individuals. They resemble adults in most respects, however they are slightly smaller and have still got a larger number of annules (between 141 and 166). The tail consists of

17 annules and the tail tip. There are five subcephalic setae: one pair of subventral setae (however in most cases only one seta was actually observed), one pair of ventrolateral setae and a single long mediodorsal seta.

In the pharyngeal region somatic setae are arranged in five rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows. Sometimes there is a single short mediolateral seta situated immediately behind the head capsule. The bent ambulatory setae are arranged in four subventral rows: the outer rows consist of nine setae, the inner rows of six setae. In the posterior body region, there are two pairs of long and straight supporting setae and several subdorsal setae.

Diagnosis

Epsilonema multispiralum sp. n. is a small nematode (length of males 300 μm on average, females 295 μm on average), characterised by the combination of the following characters: the cuticle consists of a large number of narrow annules (in males between 136 and 149, in females between 138 and 145), the cuticular ornamentation is made up of a single row of large vacuoles. It has large, dorsally shifted amphids consisting of 3.25 whirls. Males are characterised by slightly curved and slender spicules with a triangular capitulum and no clear velum. Copulatory thorns are absent.

Differential diagnosis

The amphids of *Epsilonema multispiralum* sp. n. resemble those of *E. meunierorum* Decraemer & Gourbault, 1987 in size and the number of coils. However, there are markedly fewer body annules in the latter species (in males on average: 139 in *E. multispiralum* sp. n. vs 88 in *E. meunierorum* Decraemer & Gourbault, 1987). The new species is clearly smaller (males of *E. multispiralum* sp. n. have an average body length of 299.4 μm, those of *E. meunierorum* Decraemer & Gourbault, 1987 have an average body length of 385 μm) and it bears no precloacal copulatory thorns. Next to this, the cuticle of *E. meunierorum* Decraemer & Gourbault, 1987 has only an obscure vacuolar ornamentation where in this new species large vacuoles occur. All other species of this genus have amphids of different size and shape.

Family **Epsilonematidae Steiner, 1927**
Subfamily **Epsilonematinae Steiner, 1927**
Genus ***Bathyepsilonema* Steiner, 1931**
Bathyepsilonema lopheliae **sp. n.** (Figs 8–11)

Type specimens.
Holotype male on slide RIT 685. Paratype males, females and juveniles on slide numbers RIT 687–688 (KBIN), MDNC 4022, 4031–4036 (UGent), other paratype 2003.346 is stored at NHM.
Type locality. Porcupine Seabight, Belgica mounds, at a depth of 1005 m. Coordinates: 51° 24′ 48,2″ N; 11° 45′ 55,4″ W. *Remark:* other representatives were found in the Belgica mound region at 51° 25′7,74″ N and 11° 46′ 9,32″ W.
Date of collection. 17th of June 2000.
Type habitat. Deep sea environment, on the top of a coral mound. Associated with cold-water coral reef degradation zones. Epifaunal, preferably on sponge fragments.
Relative abundance. This species comprises 0.57% of the total nematode community.
Etymology. The name refers to the unique substrate on which it lives: the deep-water coral *Lophelia pertusa* (Linnaeus, 1758).

Measurements: Table 3

Males

The body is relatively stout and clearly epsilon-shaped, with conspicuous enlargements in the pharyngeal region and at the level of the second dorsal curvature (Figs 8A and 10A). The first dorsal curvature and the ventral curvature are most pronounced: as a result the anterior body region often lies adjacent to the mid-body region. The posterior body region is hardly bent at all. There is a short tail ending in a conical tail tip (Fig. 10F).

The cuticle is built up of 89 – 93 broad cuticular annules, clearly overlapping in the pharyngeal and posterior body region. Ventrally (in the holotype male), the inversion of orientation (►) occurs between annules 31 and 32, dorsally between the 44th and 45th annule. The annules are ornamented with vacuoles (Fig. 8E, F), except on the first two annules (Fig. 10C). Along the tail the pattern of vacuoles fades away, resulting in a more irregular pattern of cuticular ripples.

The somatic setae in the pharyngeal region are long and arranged on six rows: two subdorsal rows, two laterodorsal rows also and two subventral rows.

On the posterior body region, behind the ambulatory setae, the somatic setae are positioned in four to five rows: two subdorsal rows, two subventral rows and sometimes a few very long mediodorsal setae.

The ambulatory setae are all located on the ventral curvature, restricted to a small region extending

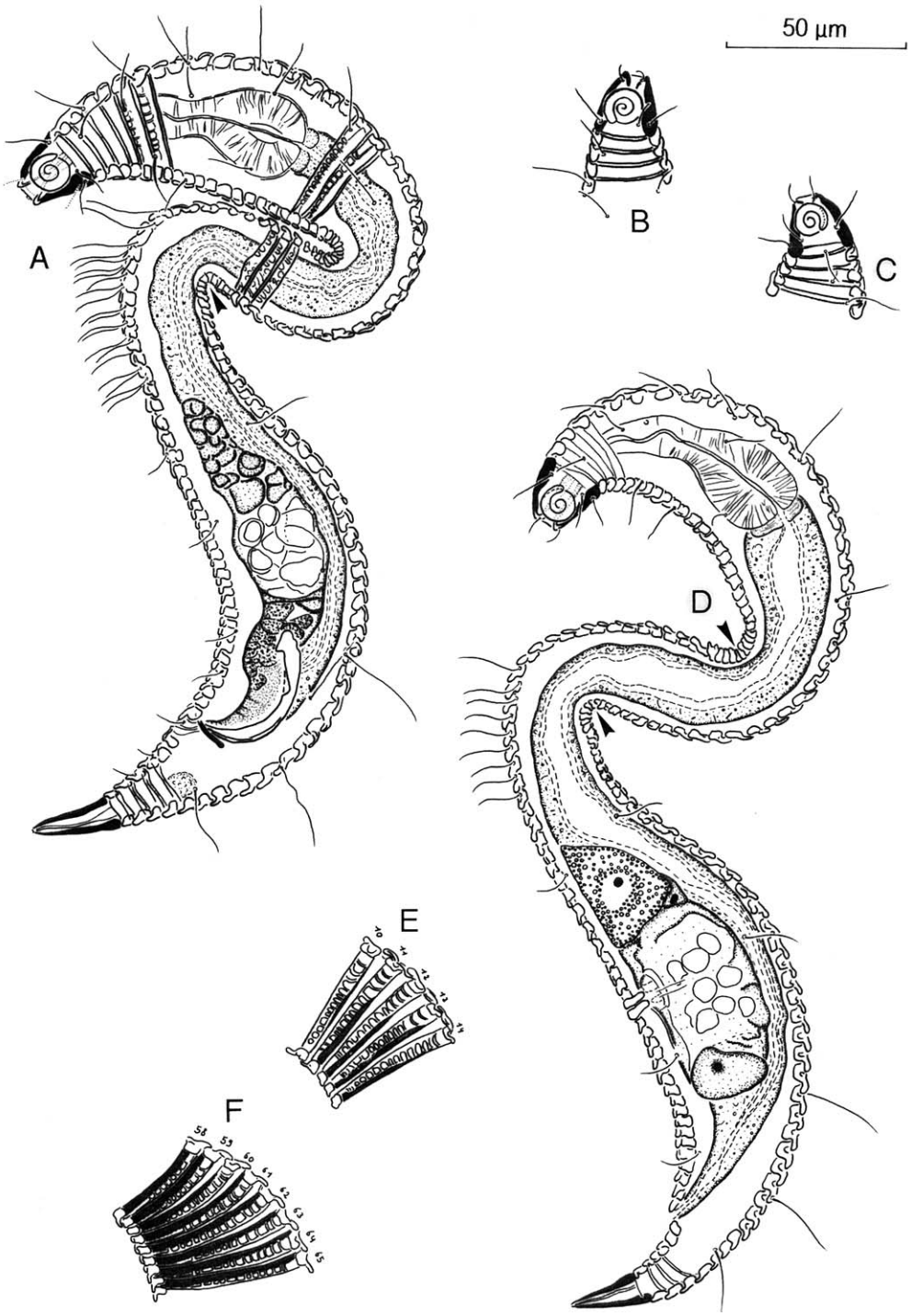

Figure 8. Bathyepsilonema lopheliae sp. n. (A) holotype ♂, habitus; (B) paratype ♂, surface view of head capsule; (C) paratype ♀, surface view of head capsule; (D) paratype ♀, habitus; (E) paratype ♂, detail of cuticular ornamentation in pharyngeal region; (F) paratype ♂, detail of cuticular ornamentation in posterior body region. Inversion sites are indicated with arrows.

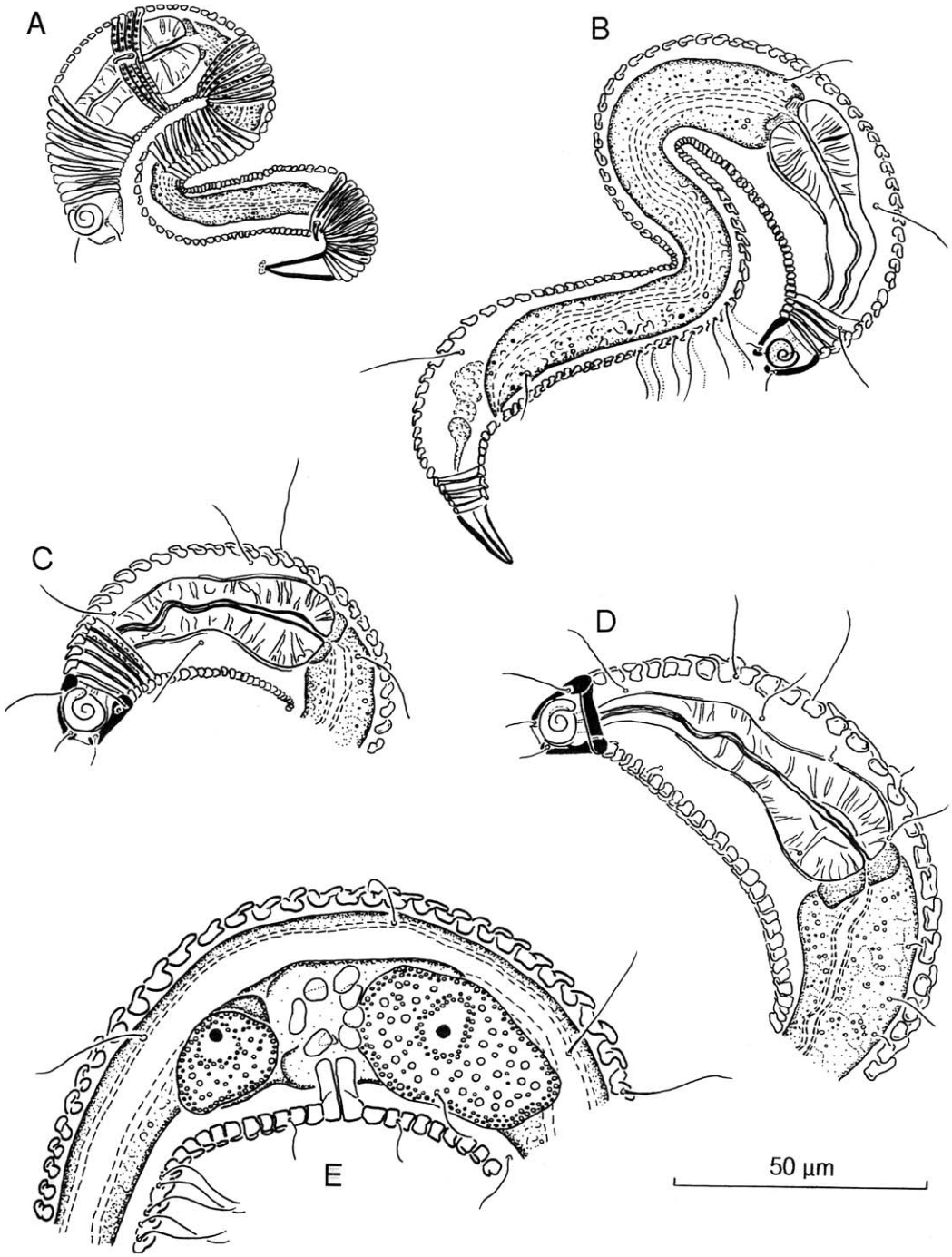

Figure 9. Bathyepsilonema lopheliae sp. n. (A) juvenile I, habitus and surface view of cuticle; (B) juvenile II, habitus; (C) juvenile III, head and pharyngeal region; (D) juvenile IV, head and pharyngeal region; (E) paratype ♀, detail of reproductive system.

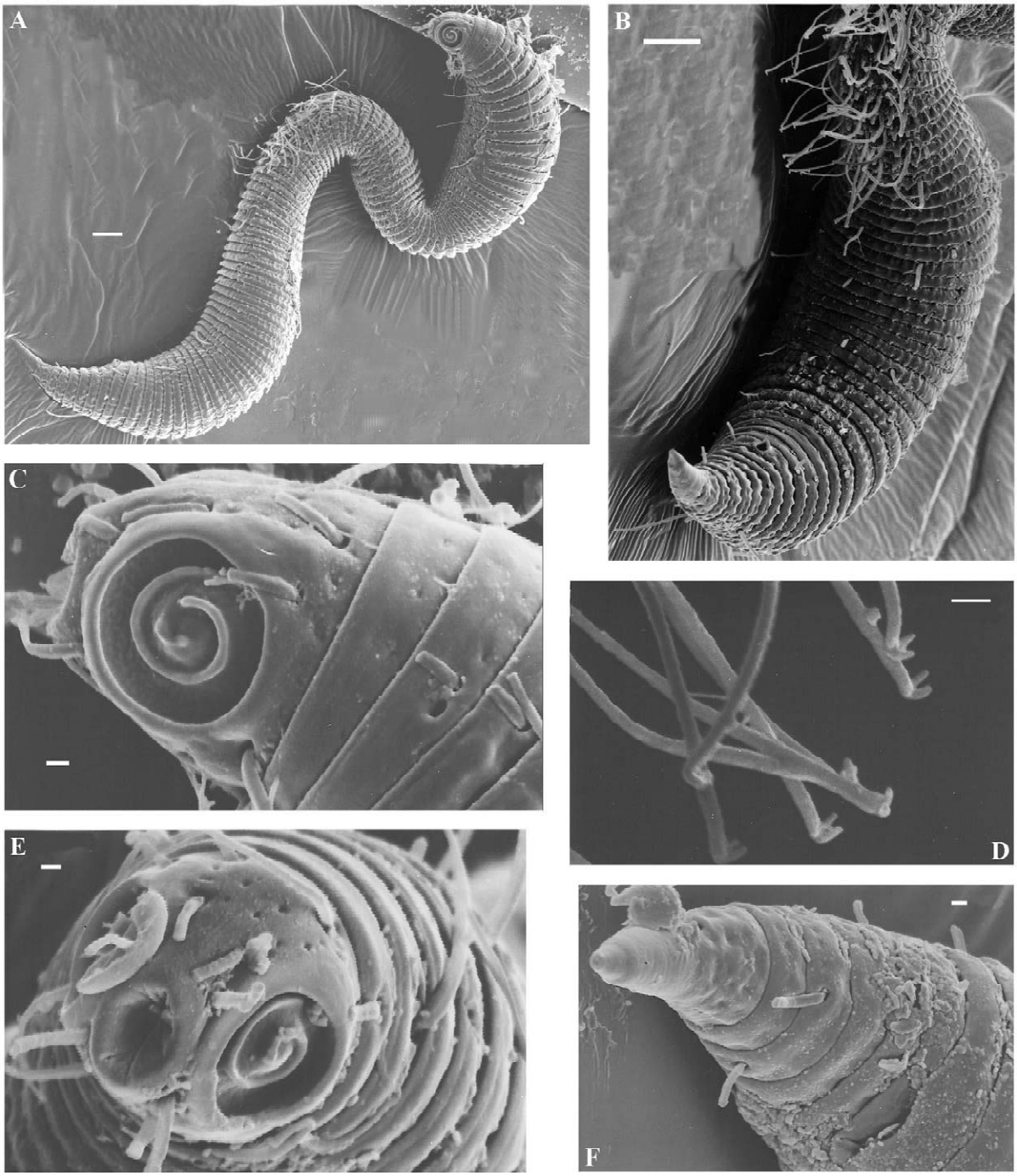

Figure 10. Bathyepsilonema lopheliae sp. n. (A) ♂, habitus; (B) ♂, posterior body region: lateral-ventral view; (C) ♂, head capsule: lateral view; (D) ♂, distal end of ambulatory setae; (E) ♀, head capsule: en face view; (F) ♀, anus and tail tip. Scale bars: A,B: 10 μm; C,D,E & F: 1 μm.

between the ventral curvature and the anterior tip of the testis. The setae are clearly arranged in six longitudinal rows. Each row consists of 12 –13 setae, although the exact number is difficult to determine. The proximal part of each seta lies adjacent to the body, oriented in a posterior direction. The distal end

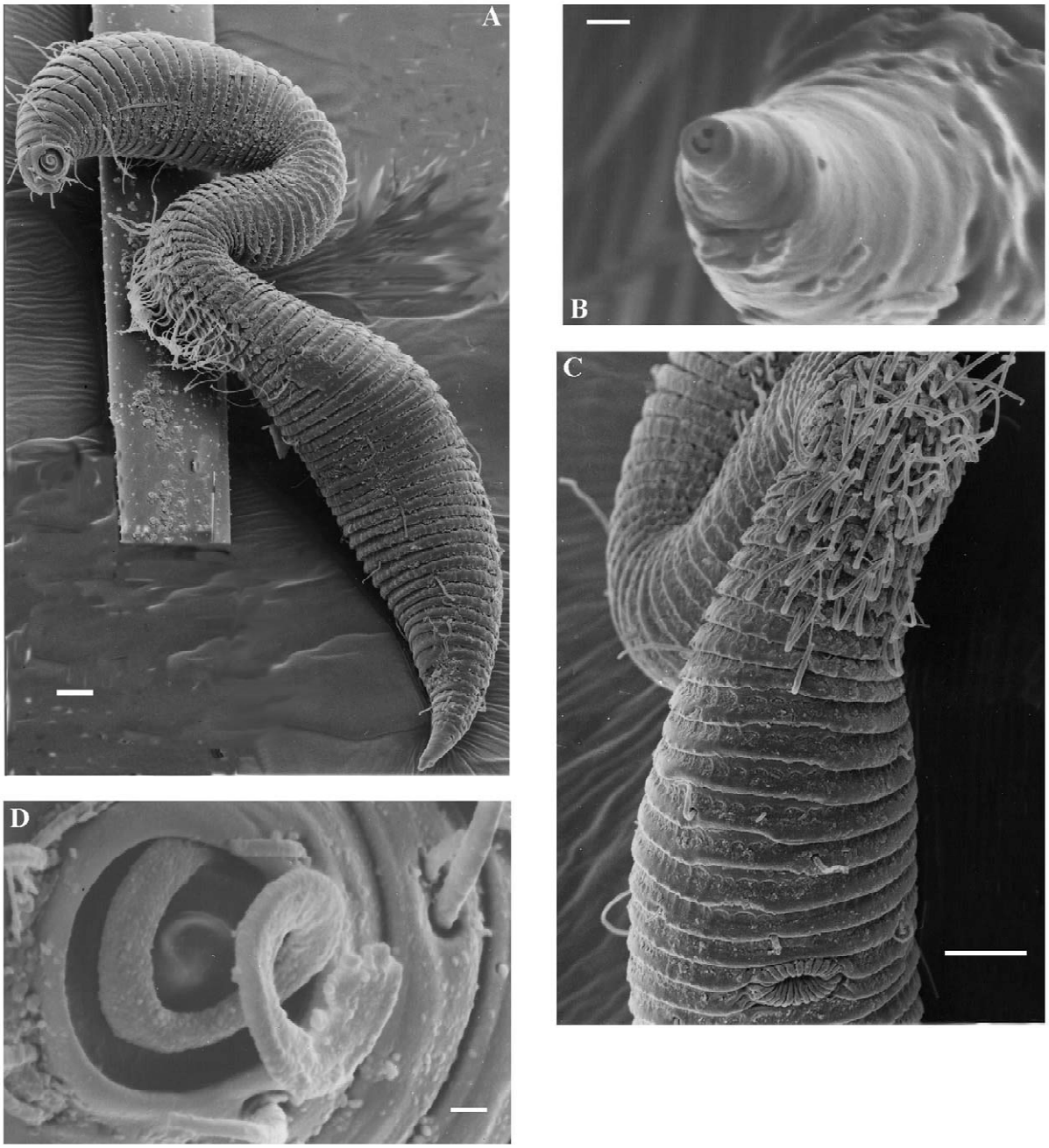

Figure 11. Bathyepsilonema lopheliae sp. n. (A) ♀, habitus; (B) ♂, tail tip with terminal pore and slit-like opening; (C) ♀, vulva and ambulatory setae: ventral view; (D) ♂, protruded corpus gelatum. Scale bars: A,C: 10 μm; B & D: 1 μm.

bears two small hooks forming a bifid appendix attached to the seta at a right angle (Fig. 10B, D). No supporting setae were observed.

The head capsule is dome-shaped and heavily cuticularised (Figs 8B and 10C). The amphids are very large and surrounded by a cuticular rim, causing the head to flatten off laterally (Fig. 10E). In males, the amphids take up 61.8% of the total head width on average. They are circular in shape, spiral with two turns and in some cases the corpus gelatum is protruded (Fig. 11D). The internal and external labial sensilla are not obvious (even on SEM micrographs)

Table 3. Measurements of specimens of *Bathyepsilonema lopheliae* sp. n. All absolute values are in μm. The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript

	Holotype male	Paratype males ($n = 2$)	Paratype females ($n = 4$)	Juvenile stage I ($n = 1$)	Juvenile stage II ($n = 1$)	Juvenile stage III ($n = 1$)	Juvenile stage IV ($n = 4$)
L	420	415–420 (415)	414–440 (420)	165	220	230	310–360 (350)
N	91	89–93 (91)	91–94 (93)	100	94	87	87–92 (90)
cs	7.1	5.5–8.1 (6.8)	5.8–7.2 (6.7)	6.6	3.6	4.8	4.2–6.2 (5.2)
dcs	1.2	2.1–2.7 (2.4)	1.5–2.0 (1.8)	3.9	1.2	2.2	0.9–1.7 (1.2)
Hdw	16.4	15.9–17.2 (16.6)	16.6–16.9 (16.8)	10.9	11.4	12.6	14.6–15.6 (15.1)
Amphw	10.5	9.4–10.6 (10.0)	8.8–10.2 (9.5)	6.9	6.7	8.0	8.3–9.9 (8.9)
Amph%	64.2	54.7–66.3 (60.5)	53–61.5 (56.7)	62.9	58.8	63.5	55.1–65.2 (59.3)
ph	83.3	89.2–91.2 (90.2)	80.4–87.5 (84.0)	57.4	59.8	66.8	76.9–82.5 (80.3)
Asl	24.2	20.9–21.4 (21.1)	20.9–23.6 (22.4)		16.3	19.5	17.0–21.1 (18.5)
tail	59.9	50.7–50.7 (50.7)	42.0–44.5 (43.2)	28.4	39.7	39.0	39.9–46.8 (45.6)
tmr	27.8	24.4–26.9 (25.7)	19.4–23.0 (21.6)	15.3	12.7	16.3	18.1–21.5 (20.4)
mbd ph	40.0	34.7–34.7 (34.7)	37.0–38.0 (37.4)	21.2	27.5	25.2	32.1–36.8 (35.1)
mbd	41.5	35.8–37.2 (36.5)	45.1–46.5 (45.6)	12.8	20.3	19.0	26.1–34.5 (32.0)
(mbd)	24.8	22.3–24.6 (23.5)	22.3–24.0 (23.4)	11.8	15.5	15.6	20.7–23.7 (22.7)
mbd/(mbd)	1.7	1.5–1.6 (1.6)	1.9–2.0 (2.0)	1.1	1.3	1.2	1.3–1.5 (1.4)
ABD	22.0	21.3–23.1 (22.2)	19.9–20.7 (20.2)	13.5	17.9	16.8	18.2–23.5 (20.8)
spic	55.9	51.1–52.4 (51.8)					
gub	7.1	9.6 [(1)]					
V%			67.9–71.3 (69.8)				
a	10.1	11.2–11.7 (11.4)	9.0–9.5 (9.3)	13.0	11.0	12.0	10.4–11.9 (11.0)
b	5.1	4.6–4.7 (4.6)	4.8–5.4 (5.0)	2.9	3.7	3.4	3.9–4.7 (4.3)
c	7.0	8.2–8.3 (8.2)	9.4–10.1 (9.8)	5.8	5.6	5.8	7.3–7.9 (7.7)

because in most specimens the lip region is retracted. There are four cephalic setae, situated at the anterior end of the amphids. There are eight subcephalic setae (Fig. 10C): two short subdorsal setae can be found at the level of the amphidial fovea. The other subcephalic setae are situated at the posterior border of the head capsule: on each side there is one long subdorsal seta and one shorter lateroventral seta. There is also an unpaired, very short laterodorsal seta and a single short lateroventral seta. These two unpaired setae are both situated on the right side of the head capsule. It is very important to notice that the two subcephalic setae at the level of the amphid are only visible using SEM, not with a light microscope. The buccal cavity is not clear because the lip region is always retracted. Teeth were not observed though this can again be due to the retraction of the lip region. The pharynx shows two enlargements: there is a small swelling in the middle of the pharynx and a well-developed muscular end bulb. The pharynx lumen is strongly cuticularised. The cardia is flattened.

The tail is short and conical, bearing six (sometimes seven) annules without distinct vacuoles. The tail endring is quite irregularly shaped at its base, but becomes more smooth and cylindrical posteriorly. At its tip a small spinneret can be observed. The caudal glands end in one pore and a curved slitlike opening (situated dorsally of this pore) at the terminal end of the tail tip (Fig. 11B). A pair of strongly built setae is positioned just before the tail tip.

There is one broad, outstretched testis extending between the ventral and second dorsal curvature (Fig. 8A). The spicules are slender and they describe an angle of 90°. The capitulum is triangular, the proximal part of the calomus is clearly broader than the distal part. There is a fine but clear velum. The gubernaculum is small and slender. Small copulatory thorns were observed in front of the cloacal opening (Fig. 10B).

Females

The females are similar to the males in most respects (Fig. 8C, D), though the second enlargement is more pronounced (Fig. 11A). The cuticle consists of 91–94

annules. Inversion (►) occurs ventrally between annules 28 and 29, dorsally between annules 42 and 43. Cuticular ornamentation is similar as in males.

The arrangement of somatic setae in the pharyngeal region is comparable to that in males. At the level of the second enlargement, behind the ambulatory setae, the somatic setae are positioned on four to five rows: a row of very long mediodorsal setae, two subdorsal rows and two subventral rows.

The position of ambulatory setae is identical to that in males. In this case this also means that the ambulatory setae are all positioned in front of the vulva. No supporting setae were observed.

The shape of the head and amphid, as well as the number and position of subcephalic setae is similar as in males.

The reproductive system is didelphic and amphidelphic (Fig. 9E). The vulva is surrounded externally by a large number of radial, cuticular ridges (Fig. 11C). The vagina consists of two parts, the distal part is heavily cuticularised. The caudal glands seem to end in one pore only: the curved opening that was found in males is not observed here (Fig. 10F).

Juveniles

First stage juvenile (Fig. 9A): one individual was found in 2001 on the type location. This first stage juvenile is very small. Compared to adults, the anterior body region has a great relative length (de Man b is 2.9 compared to 4.8 in adult males on average). The relative proportion and the shape of the amphids is similar as in adults, although the amphids consist of one and a half turns only (instead of two). There are 100 cuticular annules, all of comparable size. Some annules are ornamented with a single transverse row of small vacuoles. Between the first dorsal curve and the ventral curve there seems to be a longitudinal, mediolateral ridge on both sides. No subcephalic setae were found.

There are two short but very thick laterodorsal somatic setae present at the level of the pharyngeal bulb (one on each side), and two thick and short mediolateral setae (one on each side) near the anus. There are no ambulatory setae present.

Second stage juvenile (Fig. 9B): only a single specimen was found. In overall appearance it resembles the adults, however it is clearly smaller. There are 94 body annules, a number comparable to that in adults. There are no subcephalic setae.

In the pharyngeal region there are subdorsal, mediolateral and lateroventral somatic setae present. In the posterior body region the somatic setae are located subdorsally, mediolaterally and subventrally.

The ambulatory setae are arranged in two subventral rows, each consisting of six setae.

Third stage juvenile (Fig. 9C): only a single specimen was found, in size comparable to the second stage juvenile. There are 87 body annules, which is slightly less than in adults and second stage juveniles. There is one long subdorsal subcephalic seta present at the right side of the head.

Compared to the distribution of somatic setae in the pharyngeal region in second stage juveniles, a mediodorsal row is added in third stage juveniles. In the posterior body region, the distribution of somatic setae is similar as in second stage juveniles, although there is a higher number of setae. The ambulatory setae are arranged in two rows, each consisting of 12 setae.

Fourth stage juveniles (Fig. 9D): one young (future female) and three older fourth stage juveniles (one future male, two future females) were found. They resemble the adults in most respects (e.g. the number of annules), however they are somewhat smaller. There are two subcephalic setae: a subventral and a subdorsal one.

In the pharyngeal region, somatic setae are arranged on subdorsal and subventral rows, sometimes a long mediodorsal seta is also present. In the posterior body region there are mediodorsal, subdorsal, lateroventral, subventral and medioventral rows of somatic setae. The ambulatory setae are arranged in four rows of approximately 10 setae.

Diagnosis

Bathyepsilonema lopheliae sp. n. is characterised by its body length (in males 417 μm on average, in females 423 μm on average), the number of body annules (in males between 89 and 93, in females between 91 and 94), a dome-shaped head with large amphids (in males 61.75% on average, in females 56.71% on average) positioned centrally or slightly shifted anteriorly on the head capsule. There are eight subcephalic setae, of which two setae are only visible using SEM. The cuticle is ornamented with large vacuoles.

Differential diagnosis

Bathyepsilonema lopheliae sp. n. is very closely related to *B. brachycephalum* Steiner, 1931. There are nevertheless some important differences: in this new species, the amphids are clearly larger (for males: 43.2–52.0% of the head width in *Bathyepsilonema brachycephalum* Steiner, 1931 vs 54.7–66.3% in *B.*

lopheliae sp.n) and they take up almost the entire head length. The new species also differs in the overall shape of the head capsule, its smaller body size (for males: 450–595 μm in *Bathyepsilonema brachycephalum* Steiner, 1931 vs 415–421 μm in *B. lopheliae* sp.n) and the number of body annules (for males: 95–99 in *Bathyepsilonema brachycephalum* Steiner, 1931 vs 89–93 in *B. lopheliae* sp.n). The cuticle shows no garland-like ornamentation delimiting faint vacuoles: there are large and clear vacuoles on one row at the level of both enlargements. In between these enlargements, the vacuoles are smaller and are not positioned in a single row.

Other Epsilonematidae associated with this cold-water coral environment

In total, 13 species of Epsilonematidae belonging to five genera were found to be associated with *Lophelia* and *Aphrocallistes* skeletons in the Porcupine Seabight (samples from 2000 and 2001). Several new species of this family, other than those described above, were found but will not be described here because of the lack of an adequate number of specimens to examine.

The genus *Glochinema* is represented only by the new species described above.

The genus *Epsilonema* is represented by seven species: *Epsilonema multispiralum* sp. n., four other new species but also two known species. *Epsilonema margaritatum* Decraemer & Gourbault, 1987 was already known to be cosmopolitic. Until now it was reported from intertidal and lagoon habitats in the Caribbean Sea (Decraemer & Gourbault, 1987) and Papua New Guinea, as well as from sublittoral habitats (the Channel and the Mediterranean Sea). In all cases, the substrate was coarse to medium sand (Decraemer et al., 2001). *Epsilonema cygnoides* (Metschnikoff, 1867) was already reported from Norway (Barents Sea) and Kiel Bay, but there the substrate consisted of algae (Decraemer et al., 2001).

The genus *Bathyepsilonema* is represented by three species: the new species *Bathyepsilonema lopheliae* sp. n., another new species and *B. spongiosum* Clasing, 1986. The last species is also known from intertidal coarse sand in Chile (Clasing, 1986).

A new species of the genus *Metepsilonema* Steiner, 1927 was found but will not be described here.

The monotypic genus *Triepsilonema* Decraemer, 1982 is also represented here. *Triepsilonema tripapillatum* Decraemer, 1982 has been described from a lagoon in Papua New Guinea (Decraemer, 1982). The substrate there was very coarse, consisting of fragments of the coralline alga *Halimeda*.

Discussion

Based on these findings, one can assume that cosmopolitism in epsilonematid nematodes occurs more frequently than formerly accepted. However, more material has to be examined to improve our view on the geographical distribution of Epsilonematidae. The use of specific dispersion routes between oceans is another aspect that needs attention. Transoceanic dispersal occurs frequently among free-living marine nematodes. Marine benthic communities from the Antarctic shelf possess characteristics reminiscent of deep-sea communities (Aronson & Blake, 2001). The same is probably true for marine epifaunal communities. This hypothesis is supported by the geographical distribution of some epsilonematid nematodes. *Glochinema trispinatum* sp. n. for example occurs in the North-Atlantic deep-sea as well as on the Antarctic shelf. *Bathyepsilonema lopheliae* sp. n. is very closely related to *B. brachycephalum* Steiner, 1931, a species found in the Ross and Weddell Sea in Antarctica. The extent of morphological similarities and morphometrical differences between the specimens from Antarctica and those from the Porcupine Seabight indicates a certain genetic divergence, however it lies within the range of one species. This aspect can nevertheless only be fully understood by conducting a molecular phylogenetic survey.

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