



A new species of *Glochinema* (Epsilonematidae: Nematoda) from the oxygen minimum zone off Baja California, NE Pacific and phylogenetic relationships at species level within the family

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Abstract: *Glochinema spinithorni* sp. nov. is described from muddy, bathyal sediments of the oxygen minimum zone (OMZ) of the north eastern Pacific Ocean off Baja California. It is characterized by a rather large body length (over 1 mm), a large number of body rings (242-282), sexual dimorphism in the number and position of pharyngeal thorns near the head region, cuticular ornamentation with numerous hairy spines and two sets of stronger spines ventrally in the anterior body half, mid-sized spiral amphids, and by the number and arrangement of ambulatory setae and long spicules (over 100 μ m). The finding of a second OMZ *Glochinema* species with similar morphological characteristics supports the presumption that OMZs function as isolated habitats promoting endemism at low taxonomic levels. Results of phylogenetic analyses at the species level restricted to the Glochinematinae and Keratonematinae suggest that both OMZ species form a monophyletic group. An attempt was made to recognize phylogenetic relationships at species level within the family. The phylogenetic analyses were based upon a data matrix of 96 ingroup taxa and 25 characters. The results support the monophyly of the genera *Leptepsilonema*, *Metepsilonema*, *Perepsilonema* and *Polkepsilonema* (with or without *Pternepsilonema*).

Résumé : Une nouvelle espèce du genre *Glochinema* (Epsilonematidae : Nematoda) de la zone de minimum en oxygène au large de la Basse Californie, Pacifique NE et relations phylogénétiques au niveau spécifique au sein de la famille. Une nouvelle espèce, *Glochinema spinithorni* sp. nov., provenant de sédiments bathyaux envasés de la zone de minimum en oxygène (OMZ) au large de la Basse Californie, est décrite. La nouvelle espèce est caractérisée par son corps long (> 1 mm), le grand nombre d'anneaux corporels (242-282), un dimorphisme sexuel dans le nombre et la position des cornes pharyngiennes près de la tête, l'ornementation cuticulaire avec de nombreuses épines fines et deux groupes de fortes épines ventrales dans la région antérieure du corps, les amphides spiralées de taille moyenne, le nombre et l'arrangement des soies ambulatoires et de longs spicules (> 100 μ m). La découverte au niveau de l'OMZ d'une seconde espèce de *Glochinema* avec des caractéristiques morphologiques similaires soutient l'hypothèse que les OMZ fonctionnent comme des habitats isolés favorables à l'endémisme à un faible niveau taxonomique. Les résultats d'analyses phylogénétiques au niveau de l'espèce pour les Glochinematinae et Keratonematinae suggèrent que les deux espèces trouvées dans l'OMZ forment un groupe monophylétique. Une tentative est faite d'analyser la relation phylogénétique au niveau de l'espèce dans la famille. Les analyses phylogénétiques ont été basées sur un matrice de données de 96 taxons et 25 caractères. Les résultats font

apparaitre la structure monophylétique des genres *Leptepsilonema*, *Metepsilonema*, *Perepsilonpsilonema* et *Polkepsilonema* (avec ou sans *Pterepsilonema*).

Keywords: *Glochinema spinithorni* sp. nov., Nematoda, Epsilonematidae, Phylogeny, Oxygen minimum zone, Deep sea, Eastern Pacific Ocean, Baja California margin

Introduction

Representatives of the family Epsilonematidae Steiner, 1927 are frequently found worldwide in marine supralittoral or intertidal sandy sheltered beaches but until recently they were unknown from deep-sea habitats (Neira et al., 2001a). In early 1998, a new species, *Glochinema bathyperuvensis* Neira, Gad, Arroyo & Decraemer, 2001 was found in muddy bathyal (305 m depth) sediments of the oxygen minimum zone off Callao, Peru (Neira et al., 2001a). More recently two other bathyal species of *Glochinema* were described: *G. kentrosaurides* Gad, 2002, from the plateau of the Great Meteor Seamount (455 m depth), and *G. trispinatum* Raes, Vanreusel & Decraemer, 2003, from the top of a coral mound in the Porcupine Seabight (1005 m depth), both well-oxygenated environments. Currently there is an increasing interest in benthic communities inhabiting oxygen minimum zones ($O_2 < 0.5 \text{ ml l}^{-1}$) (e.g. Levin et al., 1991; Neira et al., 2001b,c; Levin et al., 2002). Where OMZs intercept the continental margin, strong gradients are formed in organic-matter input and bottom-water oxygen availability (Levin et al., 1991). These gradients influence the biogeochemical properties of sediments (Cowie et al., 1999) and faunal distributions and diversities (Wishner et al., 1990; Tyson & Pearson, 1991). Recent estimates indicate that over 10^6 km^2 of the world seafloor are covered by OMZs, of which, approximately 33% ($361,000 \text{ km}^2$) occurs in the eastern Pacific Ocean (Helly & Levin, 2004). These areas of permanent hypoxia represent a major oceanographic boundary for many species and a challenge in terms of adaptations required to live in such otherwise inhospitable habitats. In the present paper, a new species of the genus *Glochinema* is described from bathyal muddy sediments of the OMZ off Baja California, Northeastern Pacific Ocean.

Gourbault & Decraemer (1996) reviewed the family Epsilonematidae and made an attempt to recognize phylogenetic relationships within the family. The results of these analyses were based upon a data matrix of 13 taxa at generic level in the ingroup and 16 characters and suggested the monophyly of the family. They also suggested that *Glochinema*, *Metaglochinema* and *Keratonema* form a monophyletic group in relation to the other genera. However, the relationships among the genera remained unclear. It was suggested that a better way to analyse the

phylogenetic relationships at the generic level would be to start at the species level (Gourbault & Decraemer, 1996).

With this contribution we try to explore this recommendation.

Material and Methods

Sediment samples were collected with a multicorer during the cruise of *R/V New Horizon* (NH-01) off Baja California, Mexico in November/December 2001 from a 398-m site (Station 13, $23^\circ 33.61' \text{N}$; $111^\circ 35.01' \text{W}$), off Cabo San Lucas and from a 455-m site (Sta. 32, $21^\circ 10.22' \text{N}$; $105^\circ 53.47' \text{W}$) off San Blas. Subsamples were taken with a Perspex tube (0-5 cm depth, 20 cm^2 , formerly taken for macrofauna) or with a syringe corer (0-1, 1-2, 2-3 cm depth, 60 cm^3 each) and fixed with 8% buffered formalin. The sediment of each sample was examined for meiofauna after filtering through a $40 \mu\text{m}$ -mesh. Specimens were sorted under a stereo dissecting microscope. They were kept in 70% ethanol and further mounted in glycerin-paraffin preparations. Microscopic examination was performed using a Carl Zeiss (Axioscop) interference contrast microscope and a Reichert Polyvar equipped with camera lucida. For SEM examination, specimens were dehydrated with ethanol, critical-point dried (Samdri-790, Tousimis Research Corporation), and subsequently coated with Gold/Palladium. Observations and photographs of specimens were made with a FEI Quanta 600 and a Hitachi S2700 SEM. The slides with type material are deposited in the nematode collection of the Royal Belgian Institute of Natural Sciences (KBIN), Brussels.

To analyse the phylogenetic relationships within the Epsilonematidae, a data matrix was used consisting of 96 ingroup taxa at species level and 25 characters. The phylogenetic reconstruction was based on a Wagner parsimony program (Hennig 86, version 1.5 – Farris, 1989), with heuristic search (mh*, bb*) and with the number of trees and consensus tree retained by the program.

The polarity of the characters was determined on the basis of outgroup-analyses, ontogenetic criteria and the complexity of characters. A hypothetical ancestor with all the plesiomorphic characters was chosen because no appropriate existing outgroup could be selected, though the combination of the characters of the outgroup largely agrees

with the family Desmodoridae Filipjev, 1922. The plesiomorphic character states were coded 0 and the apomorphic states were scored 1 or more and characters considered ordered or unordered.

Results

Family EPSILONEMATIDAE Steiner, 1927
Subfamily Glochinematinae Lorenzen, 1974
Genus *Glochinema* Lorenzen, 1974

Glochinema spinithorni sp. nov.
Morphometric data: Table 1

Type material

3 males, 4 females, all from same locality. Holotype male (slide RIT 694), two paratype males (slides RIT 694, 695), four paratype females (slides RIT 694, 695).

Type locality

Continental slope (398 m depth) off Cabo San Lucas, Baja California, Mexico (23°33.61N; 111°35.01W), Nov. 26, 2001.

Habitat

Marine, bathyal, microoxic ($O_2 < 0.1$ ml l⁻¹), muddy sediments containing some foraminiferal sand, uppermost sediment layer.

Environmental data

Station 13: bottom water temperature 8.5°C, salinity 34.2, $O_2 < 0.05$ ml l⁻¹, methane 2 nM, silicate 53 µM, TCO₂ 2.38 µM.

Station 32: bottom water temperature 8.0°C, salinity 34.2, O_2 undetectable, methane 80 nM, silicate 60 µM, TCO₂ 2.20 µM. Sediments laminated, with bacterial mats on the surface.

Ethymology

The specific name refers to the dense hairy- spiny body ornamentation and cuticular thorns.

Description

Male. Body large, more or less epsilon-shaped (Figs. 1A, 5A, C). Anterior body region, except for the widening at the level of the posterior pharyngeal region, slender and very elongated, extending to about mid-body, i.e. to just posterior the ventral bend; some specimens showing a pronounced ventral bending of the anterior neck region. Minimum

body diameter lying just posterior of the head region, i.e. between annuli 3 to 4 (Figs. 1A, 5E). Posterior half of the body strongly enlarged at the level of the testis, tapering at first slightly from the dorsal bend on, to more pronounced in the tail region; tail region with a slight dorsal bend (Figs. 1B, 5C).

Thick body cuticle with distinct transverse striae (the area between two transverse striae is here referred to as a ring or annule), 275 annules in holotype (range 251-273 in paratypes); annules anteriorly orientated in the anterior part of body, changing in orientation in the holotype: dorsally between rings 115-116 (at level of rings 108-113, paratype) (Fig. 3A), and ventrally between rings 102-103 (at level of rings 88-104, paratype) (Fig. 3B); overlap of the annules by the hyaline outer layer of the cuticle minor. Anteriormost annules devoid of hairy spines (Figs. 1D, 3C). From ring nine on (holotype), hairy spines appear first only ventrally, gradually extending over the entire ring at the level of ring eighteen and becoming longer posteriorly. Ventrally to sub-ventrally, hairy spines intermingled with two sets of strong spines in the anterior intestinal region i.e. between annules 46-51 (Fig. 5E) and between 66-77, and laterally at the level of the pronounced ventral bend where the strong spines may reach up to 20 µm in length (Fig. 1A). In the region of the retracted spicules, the hairy spines are restricted to the laterodorsal part of the body with a field of somewhat stronger spines subdorsally at the level of the cloacal opening; in the tail region a few stronger spines are present dorsally (Figs. 1A,B, 3E).

Close to the head region, a series of four pairs of pharyngeal thorns (although not always inserted on the same ring on left and right side of the body) range from sublateral anteriorly to subdorsal posteriorly. Thorns inserted in the holotype on rings 5, 8, 11, 17 left body side, rings 5, 7, 11, 16 on body right side and, followed by a single mid-dorsal thorn on ring 21 (holotype) (Figs. 1A, E, 3C), rings 20 to 22 (paratypes) (Figs. 1D, 3C, 5B, E). Pharyngeal thorns becoming longer and stronger posteriorly with anteriormost pair 23-24 µm long, posteriormost pair, 34-38 µm long and mid-dorsal thorn 38-45 µm long (Figs. 1D, 3C).

Somatic setae in neck region arranged in 8 longitudinal rows and on 6 rows in narrow region and posterior body region. Ambulatory setae arranged in 4 longitudinal rows: two inner subventral rows with 8 long, and two outer subventral rows with 12 slender, elongated ambulatory setae; ambulatory setae fine with open tip. The outer rows of ambulatory setae are followed by a longitudinal row of slightly modified somatic setae (more numerous, slightly thicker and posteriorly orientated than the dorso-submedian row of somatic setae) extending into the post cloacal tail region; preanally about 20 setae. These hardly differentiated somatic setae cannot be considered as "stiltborsten" or supporting setae though inserted in the same position.

Table 1. Measurements of *Glochinema spinithorni* sp. nov. from bathyal sediments off Baja California (Dimensions in μm).
Tableau 1. Données biométriques de *Glochinema spinithorni* sp. nov. des sédiments bathyaux (Dimensions en μm).

Measurements	Holotype (male)	Allotype (female)	Males (range) (n = 7)	Females (range) (n = 9)
Total body length	1230	1270	1200 - 1310	895 - 1360
Number of annules	275	262	251 - 275	242 - 282
Maximum body diameter: mbd	46	124	46 - 96	98 - 124
Minimum body diameter: (mbd)	17	17	16.5 - 25	16 - 25
mbd/(mbd)	2.7	7.3	2.7 - 5.5	4.3 - 7.3
Tail length	110	142	110 - 145	130 - 150
Length of non-annulated tail	52	66	49 - 60	56.6 - 69
% non-annulated tail of total tail length	47.3	46.5	40.7 - 49.1	39.3 - 50.8
Head diameter	22	26	21 - 29.5	24.6 - 28
Head length (capsule)	23.5	28	23.5 - 24 *	28 - 31 **
Diameter of amphideal fovea	6	6.5	6 - 7.5	7.4 - 9.8
Distance amphideal fovea from anterior	15	21	15 - 20	14.7 - 23
Pharynx length	160	192	156 - 185	148 - 209
Length pharyngeal bulb	50	58	50 - 71 *	58 - 72 **
Body diameter at pharynx basis	35	38	30 - 40	35 - 41.8
Body diameter at anus level	27	28	27 - 35	26 - 35
Spicule length by chord	71	-	59 - 83.5	-
Spicule length along arc	92	-	82 - 120	-
Gubernaculum	23.5	-	19 - 27	-
Length anterior to vulva	-	793	-	555 - 885
Position of vulva from anterior end (%)	-	62.4	-	61.1 - 65.1
Length of dorsal pharyngeal thorn	43	49	38 - 52.5	45 - 57
Diameter at basis of dorsal pharyngeal thorn	7.5	8.5	7.4 - 10	8.5 - 12.3
Coefficients of de Man:				
a: Body length/max. body width	26.7	10.2	13 - 26.7	8.5 - 13.5
a': Body length/min. body width	72.4	74.7	49.6 - 76.7	48.8 - 79.4
b: Body length/Pharynx length	7.7	6.6	6.7 - 8.1	4.7 - 8.3
c: Body length/Tail length	11.2	8.9	8.3 - 11.5	6.6 - 9.9
Thorns length:				
pharyngeal thorn 1	24	17.5	23 - 24 *	8 - 22 **
pharyngeal thorn 2	26.5	19.5	26 - 29 *	8.5 - 25.5 **
pharyngeal thorn 3	33.5	25	20 - 33.5 *	17 - 28.5 **
pharyngeal thorn 4	38	26	34 - 38 *	20 - 32 **
pharyngeal thorn 5 (single dorsal)	43	20	38-52.5	20 - 36.5 **
Pharyngeal thorn 6	-	28.5	-	26 - 41 **
Pharyngeal thorn 7	-	32.5	-	32.5 - 50 **
Pharyngeal thorn 8	-	37	-	37 - 42 **
Pharyngeal thorn 9	-	47	-	45 - 47 **
Pharyngeal thorn 10 (single dorsal)	-	49	-	45 - 57

* n = 3 ; ** n = 4

Lips not protruding from helmet; 6 inner labial papillae (Fig. 3F). Anterior crown of 6 outer labial setae located near the anterior border of helmet (Fig. 3F); 4 cephalic setae arranged at mid-length of the helmet; a pair of short subdorsal subcephalic setae may be present near the posterior head border (Figs. 1D, 3D); in some specimens cepha-

lic setae are accompanied by a pore. Amphids spiral, ventral wound, with about a single turn (Figs. 1D, 3D, 5B), medium-sized and located in posterior head region and slightly shifted dorsally. Head on both sides showing an indentation anterior to the amphideal fovea (Fig. 3D).

Cheilostom short, provided with rhabdia; pharyngostom

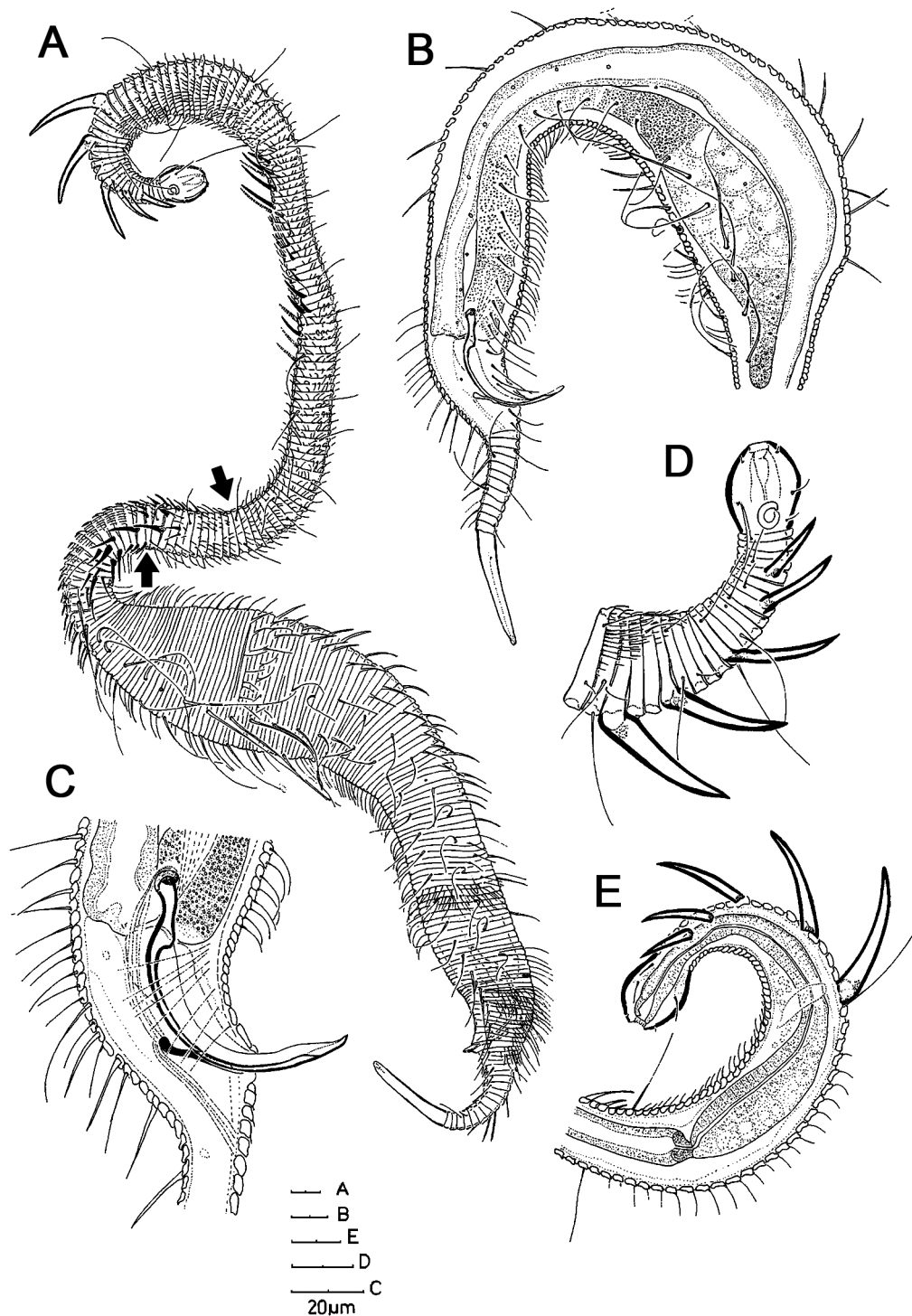


Figure 1. *Glochinema spinithorni* sp. nov. **A.** Habitus, holotype male. Inversion sites indicated by arrows. **B.** Mid- and posterior body region showing tail dorsal bent, intestine and reproductive system with large sperm cells; paratype male. **C.** Copulatory apparatus, paratype male. **D.** Head and neck region in surface view, showing pharyngeal thorns and anterior annules dorsally devoid of hairy spines, paratype male. **E.** Anterior body region, holotype.

Figure 1. *Glochinema spinithorni* sp. nov. **A.** Habitus, holotype mâle. Zones d'inversion indiquées par les flèches. **B.** Région moyenne et postérieure du corps montrant la courbure caudale, le système intestinal et le système reproducteur avec de grandes cellules spermatiques, paratype mâle. **C.** Appareil copulateur, paratype mâle. **D.** Tête et région antérieure montrant les épines pharyngiales et les anneaux antérieurs dépourvus dorsalement d'épines poilues, paratype mâle. **E.** Région antérieure du corps, holotype.

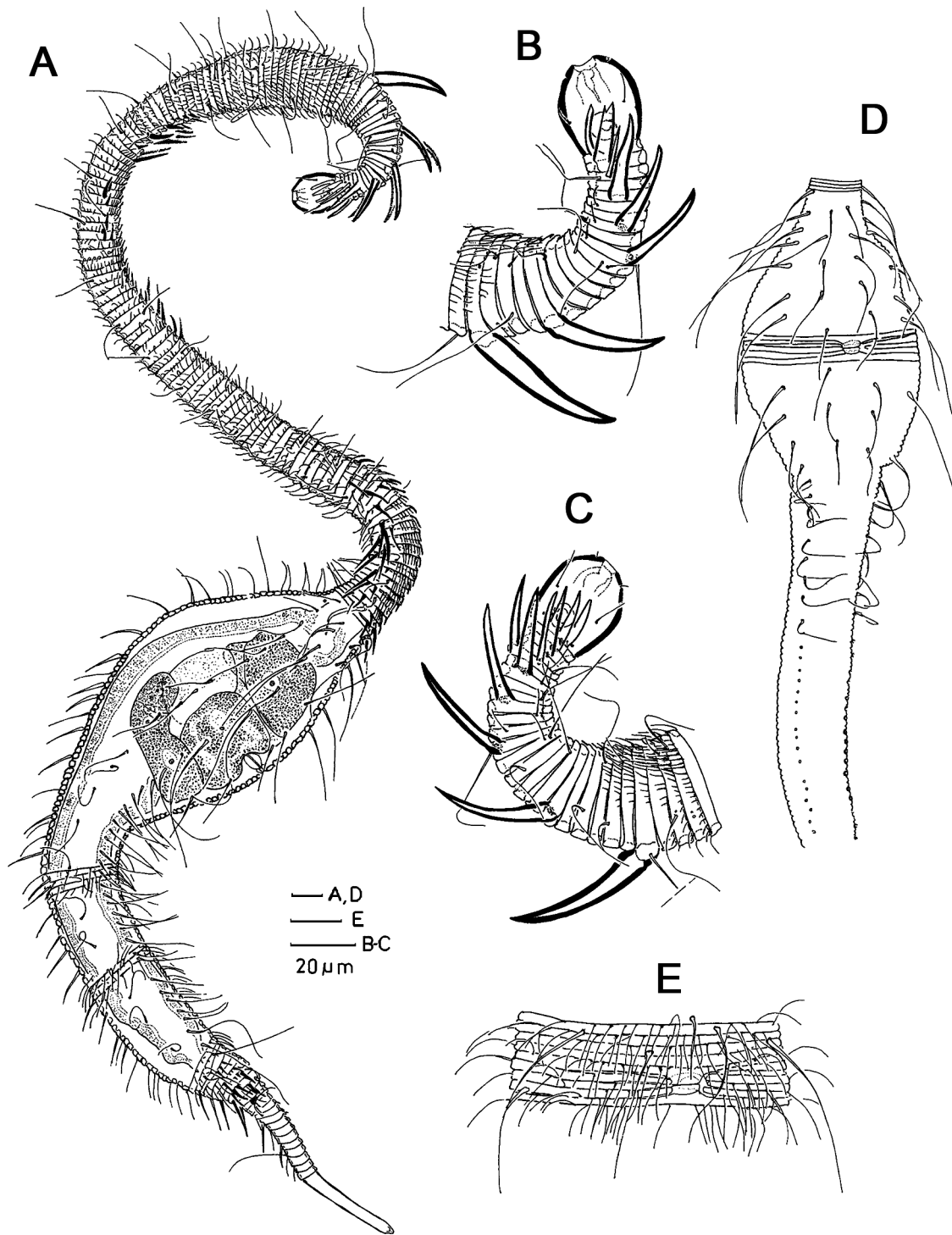


Figure 2. *Glochinema spinithorni* sp. nov. **A.** Habitus, allotype female showing anterior body region and tail in surface view. **B.** Head and neck region showing distribution of pharyngeal thorns and modified protrusions, paratype female. **C.** Allotype female showing neck region with different distribution, number and shape of pharyngeal thorns. **D.** Ventral view of mid-body region with ambulatory setae in 4 rows. **E.** Ventral view of vulva, surface view.

Figure 2. *Glochinema spinithorni* sp. nov. **A.** Habitus, allotype femelle montrant la surface des parties antérieure et caudale. **B.** Tête et région antérieure montrant la distribution des épines pharyngiales et des protubérances, paratype femelle. **C.** Allotype femelle montrant une distribution différente dans la région antérieure du nombre et de la forme des épines pharyngiales. **D.** Vue ventrale de la région médiane portant des soies locomotrices en 4 rangées. **E.** Vue ventrale de surface de la vulve.

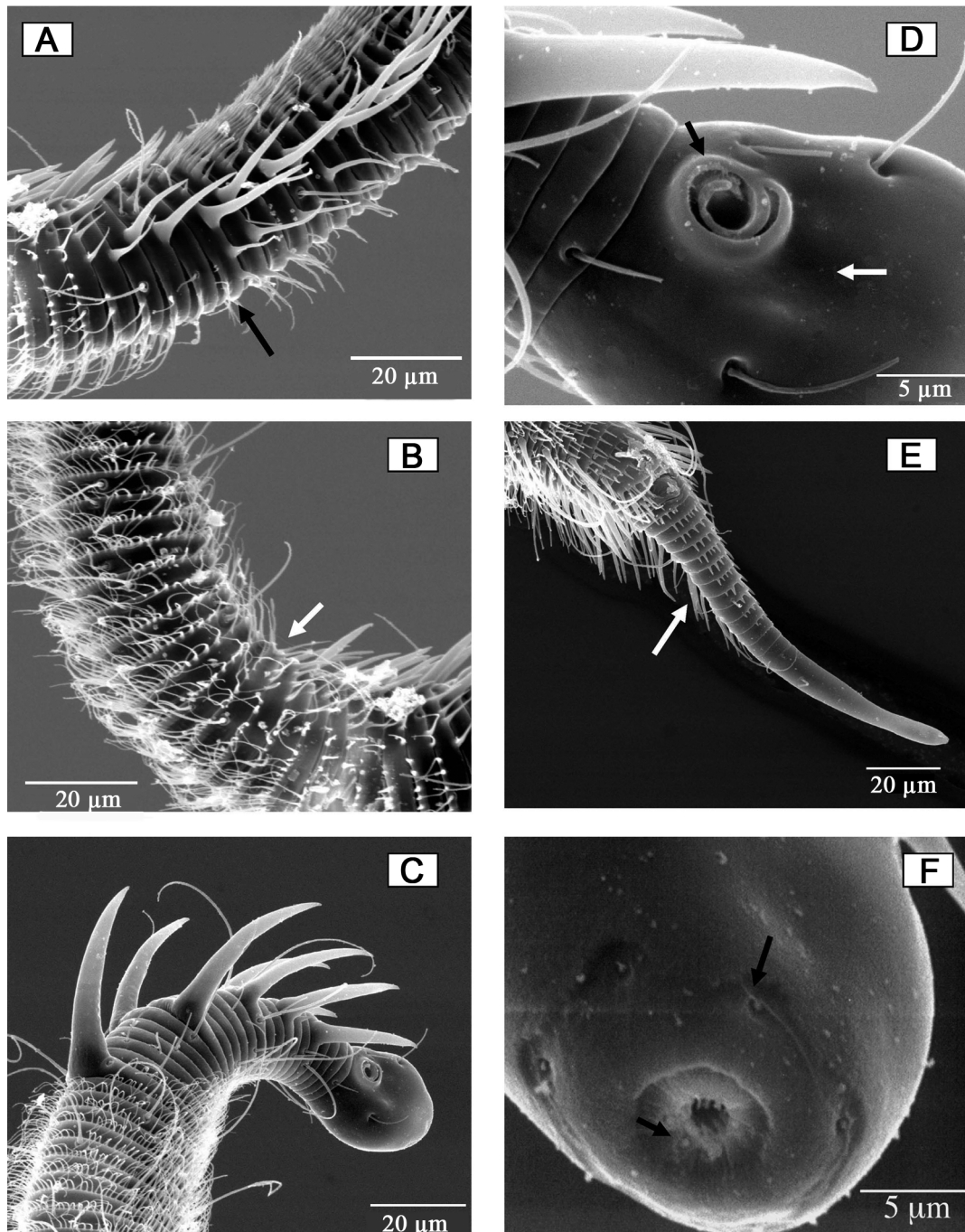


Figure 3. *Glochinema spinithorni* sp. nov. SEM micrographs. **A.** Spines and hairy ornamentation of a paratype male showing dorsal inversion (arrow). **B.** Same individual showing ventral inversion at level of the ventral bent (arrow). **C.** Lateral view of the anterior region of male showing arrangement of pharyngeal thorns, somatic setae, and dorsal hairy spines-free annules. **D.** Detail of head showing spiral amphid (black arrow) and lateral indentation (white arrow). Cephalic setae are visible as well as one subcephalic seta dorsally of the amphid. **E.** Tail showing smooth conico-cylindrical end ring, paratype male. Arrow indicates dorsal spines. **F.** Buccal stoma. Arrows indicate inner labial papillae and outer labial setae (broken), paratype male.

Figure 3. *Glochinema spinithorni* sp. nov. Photographies au MEB. **A.** Épines et soies chez un paratype mâle montrant l'inversion dorsale (flèches). **B.** Même individu, inversion ventrale au niveau de la courbure ventrale (flèche). **C.** Vue latérale de la région antérieure montrant la disposition des épines pharyngiales, des soies et des anneaux sans épine, mâle. **D.** Détail de la tête montrant l'amphide spiralée (flèche noire) et l'indentation latérale (flèche blanche). Les soies céphaliques sont visibles ainsi qu'une soie subcéphalique dorsale. **E.** Partie caudale, extrémité annelée lisse, paratype mâle. La flèche indique les épines dorsales. **F.** Ouverture buccale. Les flèches indiquent les papilles labiales internes et les soies labiales externes (cassées), paratype mâle.

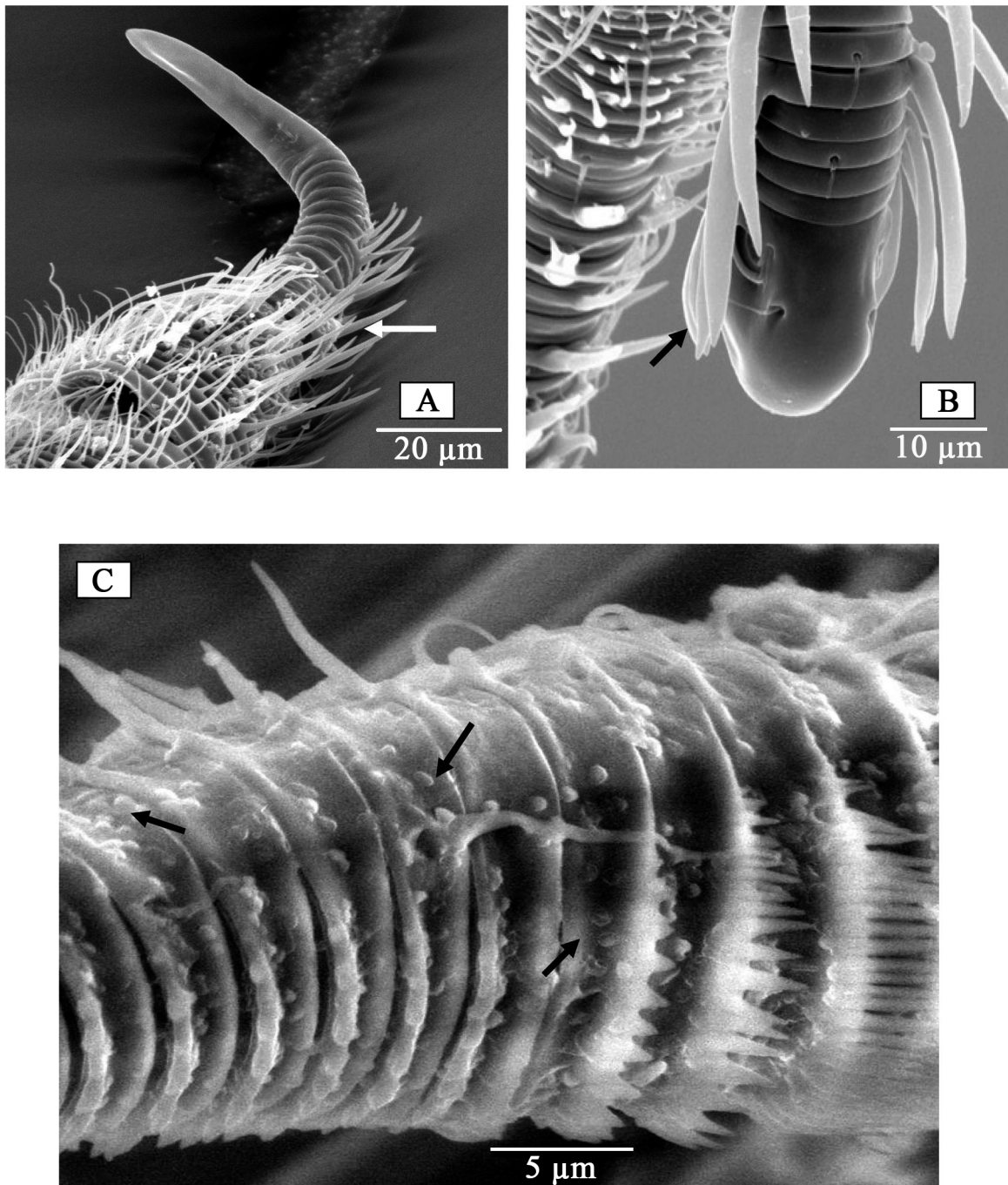


Figure 4. *Glochinema spinithorni* sp. nov. SEM micrographs. **A.** Paratype female showing cloaca opening, latero-dorsal spines, and cylindrical end ring. **B.** Paratype female. Latero-dorsal view of head-neck region showing the anteriormost blade-like protrusions (flattened thorns) and lateral indentation. **C.** Paratype male. Detail of elongated anterior body region showing prokaryotic ectobionts distributed on the annular and inter-annular cuticle.

Figure 4. *Glochinema spinithorni* sp. nov. Photographies au MEB. **A.** Paratype femelle, ouverture du cloaque, épines latéro-dorsales et extrémité annulée cylindrique. **B.** Paratype femelle. Vue latéro-dorsale de la région antérieure montrant les protubérances en lames les plus antérieures (épines aplaties) et l'indentation latérale. **C.** Paratype mâle. Détail de la partie antérieure allongée du corps, ectobiontes prokaryotes sur et entre les parties annulées de la cuticule.

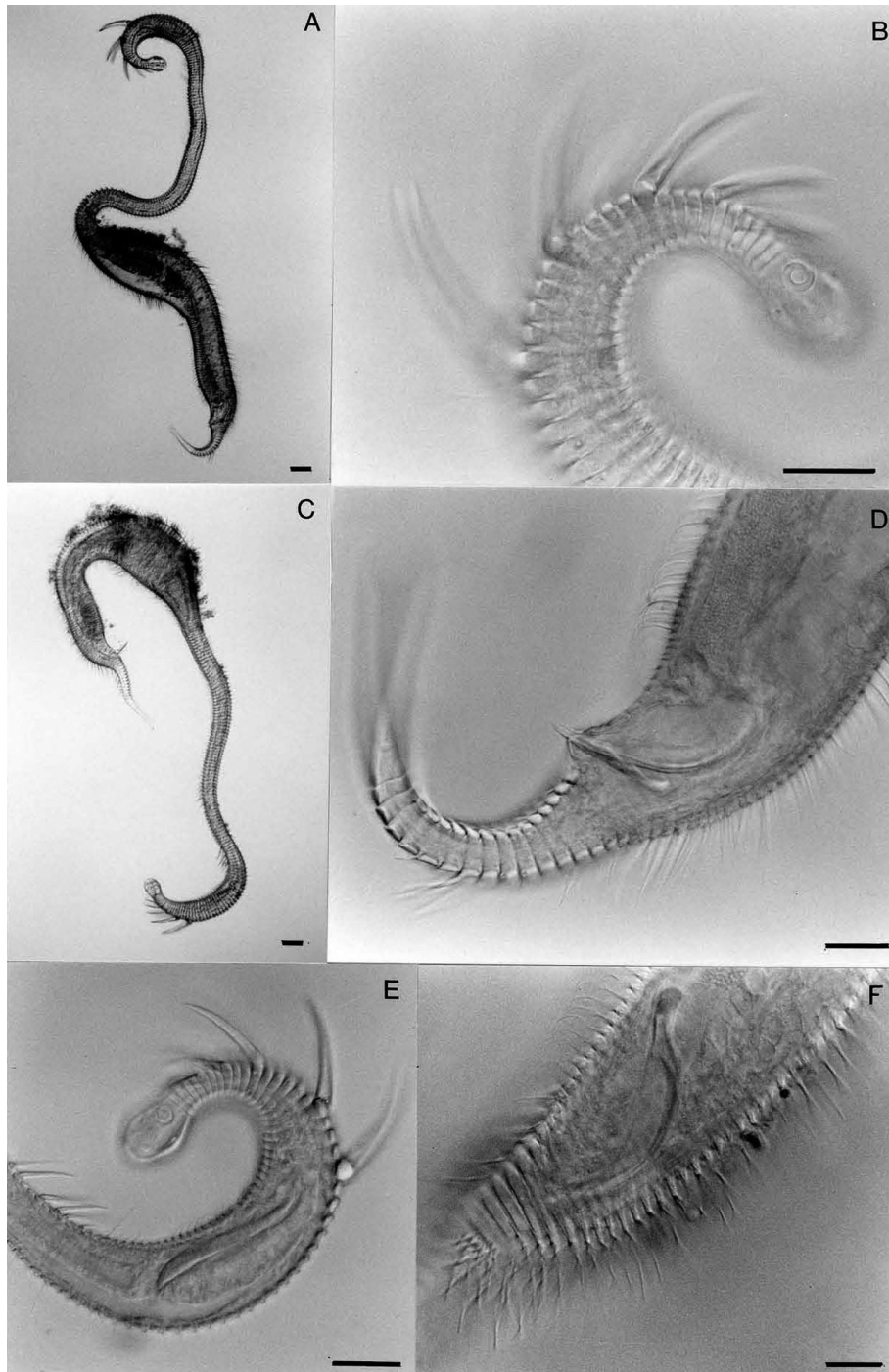


Figure 5. *Glochinema spinithorni* sp. nov. Males. **A, C.** Total view of male holotype and male paratype, respectively. **B.** Anterior body region and head with amphideal fovea, holotype. **D.** Copulatory apparatus and tail region, holotype. **E.** Anterior body region with focus on pharyngeal thorns, holotype. **F.** Cloacal region showing head of spiculum. Scale bar is 20 μ m.

Figure 5. *Glochinema spinithorni* sp. nov. Mâles. **A, C.** Vues globales respectives d'un holotype et d'un paratype male. **B.** Région antérieure et tête, holotype. **D.** Appareil copulateur et région caudale, holotype. **E.** Partie antérieure garnies d'épines pharyngiennes, holotype. **F.** Région cloacale, extrémité de spicule. Echelle : 20 μ m.

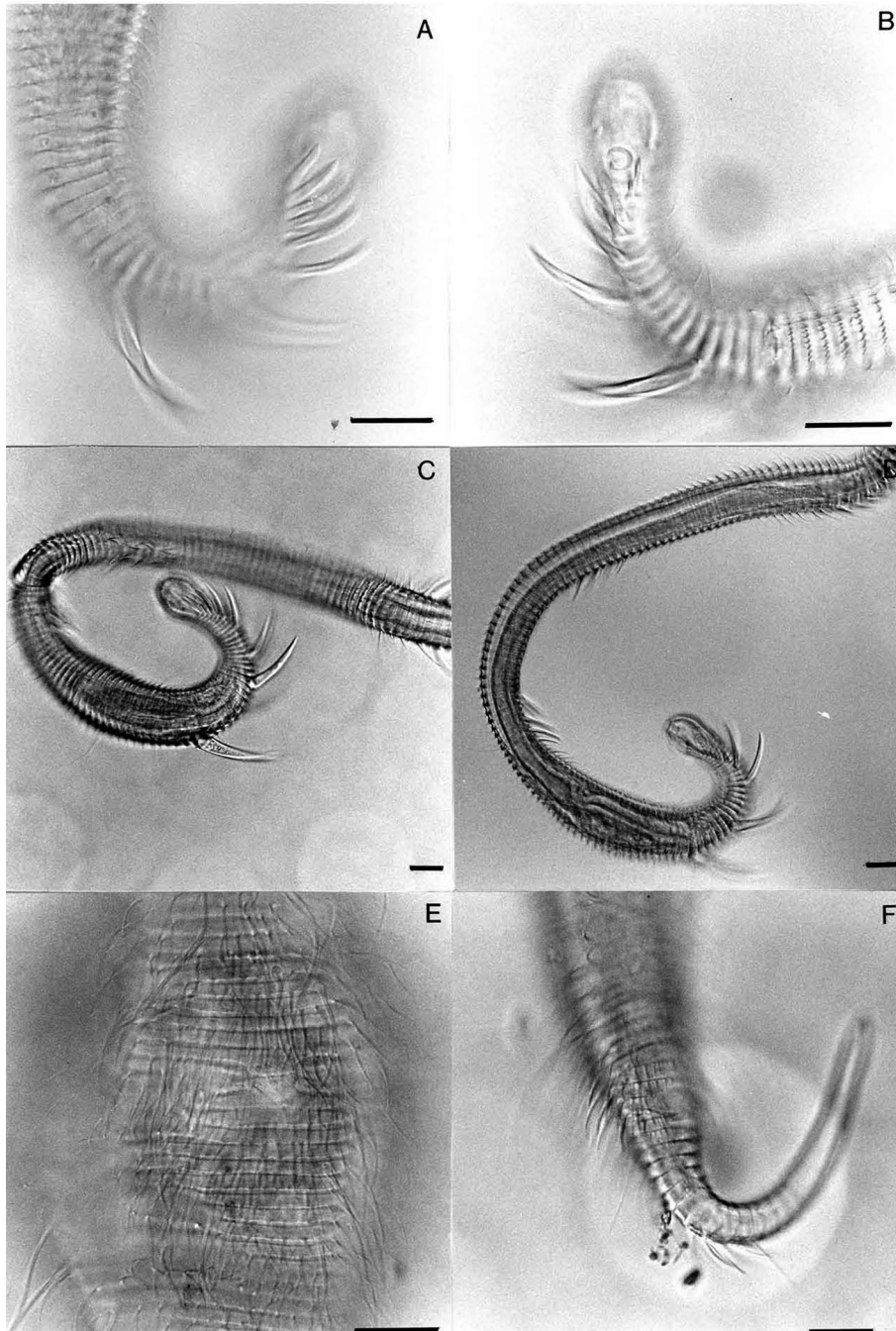


Figure 6. *Glochinema spinithorni* sp. nov. Females. **A.** Pharyngeal thorns. **B.** Head region with amphideal fovea, and pharyngeal thorns. **C.** Anterior body half, surface view. **D.** Anterior body half showing strong ventral body spines. **E.** Vulva region in ventral view. **F.** Tail region. Scale bar is 20 μ m.

Figure 6. *Glochinema spinithorni* sp. nov. Femelles. **A.** Épines pharyngiennes. **B.** Région céphalique, fossette amphidéale et épines pharyngiennes. **C.** Moitié antérieure du corps, vue superficielle. **D.** Moitié antérieure du corps montrant les fortes épines ventrales. **E.** Zone de la vulve en vue ventrale. **F.** Région caudale. Echelle : 20 μ m.

wide and 11-12 μm long, with small dorsal tooth (Fig. 1E). Pharynx largely cylindrical, gradually enlarged posteriorly to an elongated bulb (Fig. 5E). Intestine lying largely dorsal of the reproductive system. Reproductive system typically monorchic; vas deferens finely granular. Spicules paired, sickle-like with elongated capitulum within knob-like thickened cap around anterior tip for adherence of spicule protractor and retractor muscles (Figs. 1C, 5F); spicule blade ventrally with distinct velum, distally becoming narrower. Gubernaculum corpus partially enveloping spicules and dorsally clearly sclerotized (Figs. 1C, 5D).

Tail with 19 annules in the holotype (15-19 in paratypes); smooth conico-cylindrical end ring provided with three short setae; caudal glands extending anteriorly beyond cloacal opening.

Female. Very similar to male in habitus and cuticular ornamentation except for ventral and subventral hairy spines (Fig. 6D) continuing in the anal region and the presence of stronger spines latero-dorsal in anal region (Figs. 2A, 4A).

Different from male are the number, position and shape of pharyngeal thorns close to the head region (Figs. 1A, B, 6A). In the female, the pharyngeal thorns show large individual variation, ranging in number from 14 to 21, shifting in position from subventral anteriorly to mid-dorsal posteriorly (rarely irregular) and showing a transition in shape in some specimens from blade-like anterior protrusions (flattened thorns) (Figs. 2B,C, 4B) to typical thorns; they may also vary in size. The posterior most thorn is single, mid-dorsal, inserted between rings 19-27 and largest pharyngeal thorn (Figs. 6B, C). The other pharyngeal thorns are more or less paired as in the male, usually increasing in length posteriorly. There may be a difference of one or two thorns between the left and right body side.

Inversion in direction of body annules ventrally at the level of rings 89-99 and dorsally of rings 102 and 118 (Fig. 6C). Amphideal fovea and lateral indentation (Figs. 4B, 6B) are as in the male. Ambulatory setae arranged as in the male: 2 inner subventral ones with 7 to 8 ambulatory setae, 3 being posterior to the vulva and 2 outer ventrolateral rows with 9 to 10 ambulatory setae, followed by about 22 slightly differentiated somatic setae, comparable in position with supporting setae but not strong and straight.

Reproductive system didelphic-amphidelphic with reflexed ovaries e.g. anterior branch to the left and posterior to the right of the uterus (Fig. 2A). Vulva situated mid-ventrally at 61-65% of total body length from anterior end (Figs. 2D, 6E). Vagina with short *pars distalis vaginae* (4.5 μm) lined with body cuticle and longer non-cuticularized *pars proximalis vaginae* (10 μm) (Fig. 2A). In ventral view vulva visible as a transverse slit (11.5 μm wide), lying opposite three body annuli and devoid of spines (Figs. 2D, E, 6E). Anterior part of tail slightly narrower than in male

(Figs. 2A, 6F).

Juveniles. Not found.

Diagnosis

Glochinema spinithorni sp. nov. is characterized by a rather large body length (> 1 mm), large number of body rings (242-282); the sexual dimorphism in the number and position of pharyngeal thorns near the head region; mid-sized spiral amphids of about one to one and a half turns and located in posterior head region, slightly shifted dorsally; long spicules (> 100 μm); no supporting setae but instead on each side a longitudinal row of numerous long, slightly modified somatic setae, and cuticular ornamentation with numerous hairy spines and two sets of stronger spines in the anterior half of a narrow intestinal region and one set at the level of the ventral bend of the body in both sexes and, in the female also in the anal region.

Relationships within the family Epsilonematidae

Morphology and character evaluation, explanation of polarity. The characters used by Gourbault & Decraemer (1996) have been adapted and new characters added.

Strong cuticular thorns (Table 2, features 5-7) present ventrally or dorsally in the post-pharyngeal region in some species of *Glochinema* Lorenzen, 1974, *Epsilonema* Steiner, 1927, *Metepsilonema* Steiner, 1927, *Akantepsilonema* Gourbault & Decraemer, 1991, *Pternepsilonema* Verschelde & Vincx, 1993, *Polkepsilonema* Verschelde & Vincx, 1993 but absent in the other genera and in the out-group (Desmodoridae). They are considered apomorphic as well as the blade-like protrusions.

Supporting setae (Table 2, features 13-14) are modified ventrolateral somatic setae situated in two longitudinal rows, restricted to the Epsilonematinae. In contradiction to Lorenzen (1973, p. 447), some *Epsilonema* species do possess ambulatory setae and supporting setae (supporting setae are more pronounced in length, thickness and are straight). Therefore this feature is included in assessing the relationships at the species level. The absence of the supporting setae is considered plesiomorphic; the most strongly differentiated type is more advanced.

Subcephalic setae (Table 2, features 15-17), as the cephalic setae, are derived from the somatic setae with bilateral symmetrical arrangement. Eight subcephalic setae are present at the posterior base of the head in *Akantepsilonema*, *Bathyepsilonema* Steiner, 1931, *Epsilonema*, *Triepsilonema* Decraemer, 1982, 4 or even 6 of them being anterior to the amphids in *Leptepsilonema* Clasing, 1983 and *Perepsilonema* Lorenzen, 1973, respectively. The genus *Polkepsilonema* and *Pternepsilonema* are characterized by 14 subcephalic setae or more, while spe-

Table 2. Polarity of taxonomic characters.**Tableau 2.** Polarité des caractères taxonomiques

-
- 1 General body shape
 - 0 cylindrical/almost cylindrical
 - 1 enlarged at level of pharynx
 - 2 Habitus
 - 0 about straight or ventrally curved
 - 1 S- or epsilon-shaped with elongated anterior region
 - 2 S- or epsilon-shaped
 - 3 S- or epsilon-shaped with posterior body region folded up
 - 3 Shape of head capsule
 - 0 rostrum globular with low lip region
 - 1 rostrum a truncate cone with high lip region (usually retracted in fixed specimens)
 - 4 Dorsal cuticular thorns in pharyngeal region
 - 0 absent
 - 1 present
 - 5 Strong dorsal thorns in post pharyngeal region
 - 0 absent
 - 1 present
 - 6 Blade-like protrusions in anterior pharyngeal region
 - 0 absent
 - 1 present
 - 7 Strong ventral thorns in post pharyngeal region
 - 0 absent
 - 1 present
 - 8 Tail ornamentation with subdorsal longitudinal rows of spines
 - 0 absent
 - 1 present
 - 9 Ambulatory setae
 - 0 absent
 - 1 present
 - 10 Shape of ambulatory setae
 - 0 one type, arranged in longitudinal rows
 - 1 two types, arranged in longitudinal rows
 - 2 one type, irregularly arranged, very strong and glandular
 - 11 Number of longitudinal rows of ambulatory setae
 - 0 less than six rows
 - 1 six or more rows
 - 12 Arrangement of ambulatory setae in relation to vulva
 - 0 most setae posterior to vulva apart from a few which may be anterior to vulva
 - 1 most setae anterior to vulva apart from a few which may be posterior to vulva
 - 2 all setae well anterior to vulva
 - 13 Supporting setae in male
 - 0 absent
 - 1 only as slightly differentiated somatic setae
 - 2 strong supporting setae
 - 14 Supporting setae in female
 - 0 absent
 - 1 only as slightly differentiated somatic setae
 - 2 strong supporting setae
 - 15 Subcephalic setae: number in male
 - 0 absent
 - 1 two

- 2 between two and six
 - 3 six, regular arrangement
 - 4 eight, regular arrangement
 - 5 more than eight
 - 16 Subcephalic setae: number in female
 - 0 absent
 - 1 two
 - 2 between two and six
 - 3 six, regular arrangement
 - 4 eight, regular arrangement
 - 5 more than eight
 - 17 Subcephalic setae: arrangement
 - 0 in a single transverse row
 - 1 in two transverse rows
 - 2 more than two rows or irregular
 - 18 Amphideal fovea in female
 - 0 spiral
 - 1 round, non-spiral
 - 2 pore-like
 - 19 Amphideal fovea in male
 - 0 spiral
 - 1 loop-shaped
 - 2 loop-shaped with a flap, with pore at centre of the amphid
 - 3 small arrow or groove
 - 4 inconspicuous, pore-like (?)
 - 20 Structure of ovaries
 - 0 antidromously reflexed
 - 1 outstretched
 - 21 Caudal glands
 - 0 with one outlet or with separate outlets but without cuticular differentiation at tail tip
 - 1 with three separate outlets with tubular cuticular differentiation at tail tip
 - 22 Cuticular "ring"
 - 0 smooth, massive
 - 1 smooth with central lumen
 - 2 with a single transverse row of small vacuoles
 - 3 with several small vacuoles or granulation
 - 4 with a single transverse row of large often rectangular vacuoles
 - 23 Cuticular ornamentation
 - 0 absent
 - 1 ring partially with longitudinal striae
 - 2 ring completely with longitudinal striae, ridges, protruding or not as minute spines
 - 3 garland-like ornamentation, typical for *Bathyepsilonema* species
 - 4 pearl-like ornamentation restricted to the anterior and posterior borders
 - 5 short spines
 - 24 Hairy cuticular spines (long)
 - 0 absent
 - 1 present but restricted to a certain region
 - 2 numerous all over the ring
 - 3 arranged in longitudinal rows
 - 25 Male copulatory thorns
 - 0 absent
 - 1 present as a single group of field
 - 2 present in two or more groups
-

cies of the genus *Metepsilonema* possess only 2 subcephalic setae. A small number of setae are considered as plesiomorphic based upon ontogenetic evidence; juvenile stages display fewer subcephalic setae than adults. An anterior position of these setae is considered as the derived state, e.g. anterior to the amphids (*Leptepsilonema*, *Polkepsilonema*) is considered apomorphic. Ontogenetic evidence could be found in the position of some setae still on the anteriormost body rings (e.g. stage III juveniles of *Epsilonema mangrovense* Clasing, 1984 and *Perepsilonema tubuligerum* Gourbault & Decraemer, 1988).

Cuticular vacuolization (Table 2, feature 22) is a feature largely used to differentiate species. Since the state of the feature varies along the body, we have taken the character at the mid-body level, although this is not always taxonomically the most relevant region. Absence of vacuoles or central lumen is considered plesiomorphic upon outgroup (Desmodoridae) comparison. The polarity within the series i.e. going within an annule from a single transverse row of small vacuoles or numerous minute vacuoles to a transverse row of large rectangular vacuoles as the most advanced stage is difficult to determine; here the commonality principle was followed as well as ontogenetic evidence.

Cuticular ornamentation of striae, ridges, short spines (Table 2, feature 23) is also a very diversified feature along the body. It is a feature which is probably more a phenetic character than a feature underlining evolution. Hence, we considered the less common and most complex state as the apomorphic state and absence of the feature as plesiomorphic.

Cuticular hairy spines (Table 2, feature 24) is a feature considered of importance especially in relation to possible adaptation to harsh environments such as the OMZ (see Neira et al., 2001a). Here, we followed the commonality principle.

Copulatory thorns in males (Table 2, feature 25). Their absence is considered plesiomorphic upon outgroup (Desmodoridae) comparison, the most complex feature is the most derived. Although their presence is of taxonomic importance, their phylogenetic significance is unclear.

Phylogenetic relationships among species

In a first attempt, all features and all taxa (species) were included. The characters were first treated unordered (Fig. 7), and then as ordered (Fig. 8). The results are respectively as follows:

More than 985 trees were found but the strict consensus tree was based on the first 985 trees retained (tree length as number of steps, $L = 166$; consistency index, $CI = 31$). In the consensus tree the genera *Perepsilonema* and *Leptepsilonema* behave as monophyletic groups. *Polkepsilonema* together with *Pternepsilonema* also for-

med a clade (Fig. 7).

More than 986 trees were found but the strict consensus tree was based on the first 986 trees retained ($L = 208$; $CI = 25$). In the strict consensus tree *Perepsilonema*, *Leptepsilonema*, *Polkepsilonema* and *Pternepsilonema* (only one taxon) behave as monophyletic groups (Fig. 8).

In a second attempt, we omitted three species: *Archepsilonema celidotum* Steiner, 1931, *Epsilonema cygnoides* (Metschnikoff, 1867) Gerlach & Riemann, 1973 and *E. multispiralum* Maes, Vanreusel & Decraemer, 2003 which grouped with the species of the genus *Metepsilonema*. The unusual position of these taxa might be explained for the first two species by lack of data on important features as e.g. on the subcephalic setae and for *E. multispiralum* by the supporting setae, being different from the other species of the genus but comparable with *Metepsilonema* species. In this second attempt with just 93 ingroup taxa included all features were retained. The characters were first treated unordered (Fig. 9), and then as ordered (Fig. 10). The results are respectively as follows:

More than 1022 trees were found but the strict consensus tree was based on the first 1022 trees retained ($L = 16$; $CI = 32$). In the consensus tree Epsilonematinae + Glochinematinae, and Epsilonematinae are monophyletic. Within the Glochinematinae, little information is revealed on the relationship between the species except for the two species described from the bathyal OMZ, which are joined together. Within the Epsilonematinae, the species of the genera *Leptepsilonema*, *Metepsilonema*, *Perepsilonema* and *Polkepsilonema* + *Pternepsilonema* behave as monophyletic clades (Fig. 9). No relationships were found for the other taxa (species and genera).

1022 trees retained ($L = 200$; $CI = 26$). In the consensus tree *Leptepsilonema*, *Metepsilonema*, *Perepsilonema*, *Polkepsilonema* and *Pternepsilonema* (single taxon) and also *Polkepsilonema* + *Pternepsilonema* behave as monophyletic clades (Fig. 10). All *Bathyepsilonema* species but one (*Bathyepsilonema lissum* Clasing, 1984 with aberrant cuticular ornamentation) group together. No relationships were observed among the species of *Epsilonema*, *Triepsilonema* (based on a single taxon), *Keratonema* Gourbault & Decraemer, 1986 (based on single taxon) and the Glochinematinae. The two bathyal species from OMZ do not group together (Fig. 10). The most obvious feature within the Glochinematinae, i.e. the presence of dorsal pharyngeal thorns which are absent in the other taxa, is of no importance for unraveling phylogenetic relationships.

A similar analysis restricted to the species of *Glochinema*, *Metaglochinema* (Glochinematinae) and *Keratonema* (Keratonematinae) was carried out. The characters were first treated unordered (Fig. 11), and secondly as ordered (Fig. 12). The results are respectively as follows:



Figure 7. Relationships among the 96 taxa of the Epsilonematidae with features treated non-additive.
 Figure 7. Relations entre les 96 taxons d'Epsilonematidae (caractères non ordonnés).

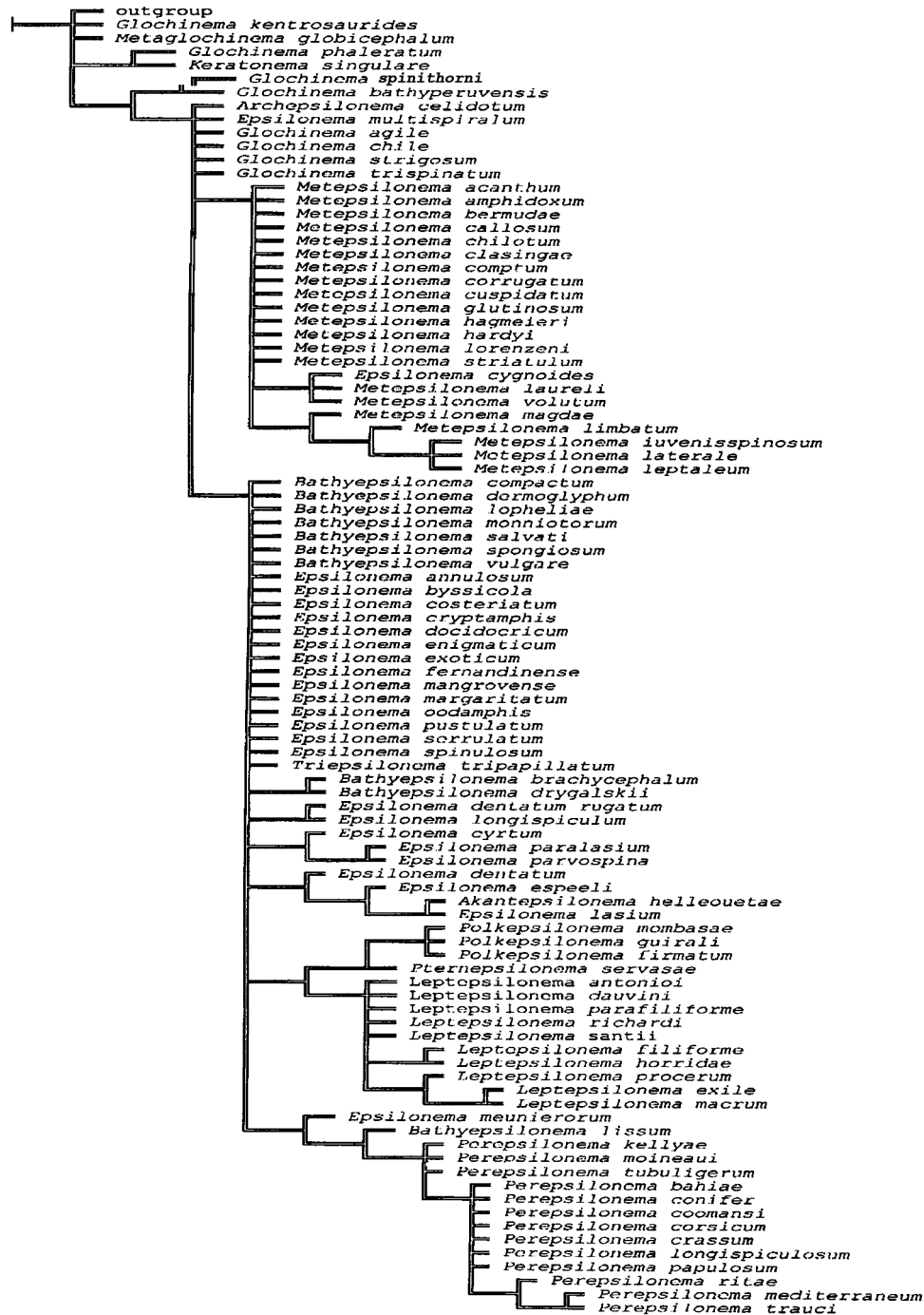


Figure 8. Relationships among the 96 taxa of the Epsilonematidae with features treated additive.

Figure 8. Relations entre les 96 taxons d'Epsilonematidae (caractères ordonnés).



Figure 9. Relationships among the 93 taxa of the Epsilonematidae with features non-additive.

Figure 9. Relations entre les 93 espèces d'Epsilonematidae gardées pour l'analyse (caractères non ordonnés).

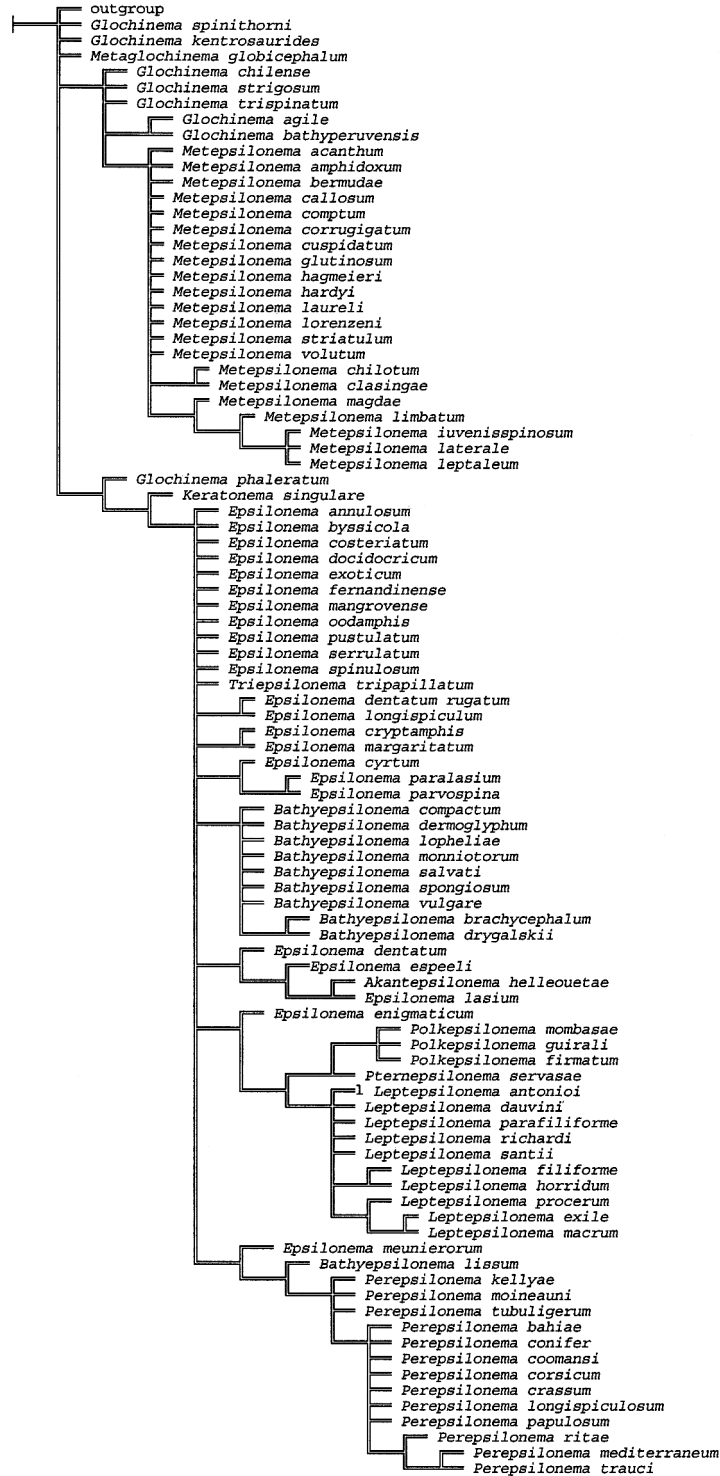


Figure 10. Relationships among 93 taxa of the Epsilonematidae with features additive.

Figure 10. Relations entre les 93 espèces d'Epsilonematidae gardées pour l'analyse (caractères ordonnés).

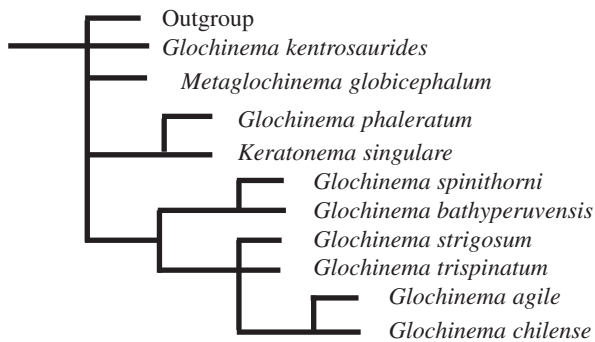


Figure 11. Phylogenetic relationships among the species of the Glochinematinae and Keratonematinae with features non-additive.

Figure 11. Relations phylogénétiques entre les espèces de Glochinematinae et de Keratonematinae (caractères non ordonnés).

Two trees were obtained ($L = 35$; $CI = 82$). In the strict consensus tree, Glochinematinae or *Glochinema* and *Metaglochinema* behave as monophyletic groups. Within the genus *Glochinema*, two monophyletic groups are observed respectively with three species (including a grouping of the two species from bathyal OMZ: *G. bathyperuvensis* Neira, Gad, Arroyo & Decraemer, 2001 and *G. spinithorni* sp. n. and four species including a joining of the two species from Chile, *G. agile* and *G. chilense* (Fig. 11).

Two trees were obtained ($L = 49$; $CI = 65$). In the strict consensus tree no information on the relationship between the genera was obtained. Within the genus *Glochinema*, the two species from the bathyal OMZ (*G. bathyperuvensis* and *G. spinithorni*) grouped together (Fig. 12).

Discussion

Morphological and phylogenetic relationships

Hitherto 7 species of *Glochinema* have been described, 4 from intertidal sandy shores (*G. agile* Lorenzen, 1974, *G. chilense* Lorenzen, 1974, *G. phaleratum* Gourbault & Decraemer, 1993, *G. strigosum* (Gourbault & Decraemer, 1993) Raes, Vanreusel & Decraemer, 2003, one from bathyal coarse sands of the Plateau of the Great Meteor Seamount (*G. kentrosaurides*), one associated with a cold-water coral reef in the Porcupine Seabight (*G. trispinatum*), and one from bathyal muds of the south eastern OMZ off Peru (*G. bathyperuvensis*). Also, from intertidal sandy sediments, the closely related genus *Metaglochinema* Gourbault & Decraemer, 1986 contributes one species (*M. globicephalum* Gourbault & Decraemer, 1993). The most relevant features of all species of *Glochinema* and

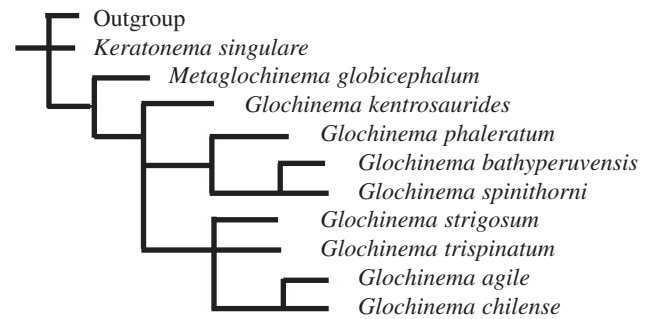


Figure 12. Phylogenetic relationships among the species of the Glochinematinae and Keratonematinae with features additive.

Figure 12. Relations phylogénétiques entre les espèces de Glochinematinae et de Keratonematinae (caractères ordonnés).

Metaglochinema are enumerated in Table 3.

Glochinema spinithorni sp. nov. resembles *G. bathyperuvensis* (the other OMZ species) in its large body size, posterior position of medium-sized amphideal fovea, spiny cuticular ornamentation, sickle-shaped spicules and number and arrangement in four longitudinal rows of the fine elongated ambulatory setae. The new species differs of *G. bathyperuvensis* by (1) the absence of a palisade of blade-like cuticular protrusions in the anterior neck region, (2) the presence of sexual dimorphism in the number, shape and position of pharyngeal thorns showing in some female specimens a transition from blade-like anterior protrusions to typical thorns, and in males, much longer spicules (mean value $115 \mu\text{m}$ vs $84 \mu\text{m}$, measured along the spicule). Lateral indentations of the head capsule present but not so conspicuous as in *G. bathyperuvensis*.

Since little is known about the evolution of the characters chosen, it seems more appropriate to treat them as unordered. Such analysis gives the “best” resolution and suggested that *Leptepsilonema*, *Metepsilonema*, *Perepsilonema*, *Polkepsilonema* + *Pternepsilonema* are monophyletic clades. Yet, these phylogenetic analyses do not resolve the relationships among the genera. The consistency index (CI) is rather low because of the use of a data set with too few characters (about 1/4th of the number of taxa). Hence, the morphological features used only partially resolve phylogenetic relationships among the taxa at the species and genus level and do not fulfill the recommendation by Gourbault & Decraemer (1996). The data set should be extended with additional new ultrastructural and molecular features.

Morphological adaptations in response to a “stressful” habitat

OMZs can greatly influence faunal community structure.

Table 3. Comparison of *Glochinema spinithorni* sp. nov. and the others *Glochinema* and *Metaglochinema* species (dimensions in μm).
Tableau 3. Comparaison de *Glochinema spinithorni* sp. nov. et des autres espèces de *Glochinema* (dimensions en μm).

Characters	<i>G. spinithorni</i> sp. nov.	<i>G. bathyperuvensis</i>	<i>G. trispinatum</i>	<i>G. kentrosaurides</i>	<i>G. chilense</i>	<i>G. agile</i>	<i>G. phaleratum</i>	<i>G. strigosum</i>	<i>M. globicephalum</i>
L male	1200-1310	1050-1215	735-825	500	520-560	395-445	760	355-365	424-450
L female	895-1360	1040-1335	750-830	450-480	490-575	375-445	770	350-395	424-437
N male	251-275	247-274	245-271	178	148-158	182-185	165	165-169	149-150
N female	242-282	255-268	241-257	150-168	140-144	170-189	174	168-177	148-151
spicule									
- by chord	59-83.5	50-75		18	21-23	23-24 μm	-	-	
- along arc	82-120	72.5-90	43-55	28	-		62-63	30-34	47
shape capitulum	elongated knob	enlarged knob	knob-like	enlarged knob	enlarged	enlarged	not enlarged	enlarged knob	enlarged knob
mbd/(mbd): male	2.7-5.5	4.7-6.3	2.7-3.9	2.7	2.2-2.9	1.8-2.3	1.5	2.3-2.8	3.2-3.0
mbd/(mbd): female	4.3-7.3	4.6-5.8	3.7-4.6	2.8-3.0	2.0-3.0	1.8-3.0	2.1	3.1-3.3	3.6-4.1
pharyngeal thorns	9 male; 14-18 female	>15	3	2	2	5	6-7	5-6	3-5
number cephalic setae	2	0**	2	2 male; 4 female	5	4*	7 male; 6 female	2	2
position cephalic setae	ant. of amphid; mid-head	ant. of amphid; mid-head	at base of head	ant. of amphid; anterior head	ant. of amphid; mid-head	ant. of amphid	ant. of amphid ,anterior head	ant. of amphid; mid-head	ant. of amphid; mid-head
amphidial fovea									
- sexual dimorphism	absent	absent	absent	absent	absent	present	absent	absent	present
- shape male	small round, posterior head	small, posterior head	large open spiral, 1 turn; posterior head	small round, posterior half head	large oval, covering head	large oval, post. Half head	large round, mid-head	medium round; mid-head	large spiral; mid-head
- shape female	small round, posterior head	small, posterior head	large open spiral, 1 turn; posterior head	small round, posterior half head	large oval, covering head	small round, mid-head	large round, mid-head	medium round; mid-head	small spiral, anterior head
male and female									
Body ornamentation (M, f)									
- small keels	absent	absent	present	absent	present	present	present	present	present
- big ventral spines	present	present	absent	absent	absent	absent	absent	absent	absent
- fine dorsal spines	present	absent	absent	present	absent	absent	absent	absent	absent
- blade protrusions in cervical region	absent male, present female	present	absent	absent	absent	absent	absent	absent	absent
Ambulatory setae (male;female)									
- total n° rows	4; 4	4; 4	5; 5	5; 5	4; 4	4; 4	3; 3	6; 6	5; 5
- total n° of amb. setae	20; 16-18	42; 31		28; 24	34; 34	34; 34	22; 20	26; 28	31; 28
- n° along external (vl) rows	12	9-12; 8	3-4	7; 5	8; 6	8; 6	6; 5	5; 6	8; 7
- n° along inner (sv) rows	8	8-9; 5-6	2-3	6; 4	9; 8	9; 8	5; 5	5; 4	5; 5
- n° along mid-ventral row	22	-;	0-2	2; 6	-;	-;	-;	3; 4	5; 4
- shape	straight	straight			knicked	knicked	straight		
- n° of types	single	single			single	single	single	2	2
mid-body enlargement	present	present		present	present	absent	absent	present	present

*Subcephalic seta difficult to see; may also be inserted on the anteriormost body rings. **Originally, the external labial seta were not observed and so the 4 subventral lateral seta of the external labial crown were interpreted as cephalic setae; no subcephalic setae are present but on each side of the head a pore may be present at the level of the amphid.

The benthic macrofaunal and meiofaunal communities within the OMZs tend to be dominated by polychaetes and nematodes, respectively (Cook et al., 2000; Neira et al., 2001b, c). Metazoan meiofauna both from the deep-sea and shallow waters, in general, appear to be more tolerant to hypoxic conditions than the macrofauna (Giere, 1993). Within the metazoan meiofauna, nematodes are more tolerant than other meiofaunal taxa (Giere, 1993) and, in some cases, they exhibit higher densities and even maximal abundances within the OMZs relative to outside them (Neira et al., 2001b, c). At our study sites, *G. spinithorni* was as abundant as the closely related species *G. bathyperuvensis* from the Peru OMZ (about 60 ind. 10 cm⁻²), whereas the macrofauna, was poorly represented, with only three polychaetes and one bivalve per core (0-5 cm, 20 cm²) at Sta. 13 and no macrofauna at Sta. 32 (L. Levin, unpublished).

In general, relatively few taxa have adapted to cope with the stressful conditions in the core of OMZs, which can include persistent hypoxia, usually high sulfide levels and other limiting physical constraints (e.g. reduction of habitat heterogeneity) (Levin & Gage, 1998). The bottom-water dissolved oxygen levels associated with the OMZ sites off Baja California where *G. spinithorni* sp. nov. was found were very low, < 0.05 ml l⁻¹ for Sta. 13 (398 m depth) and undetectable for Sta. 32 (455 m depth) at the time of sampling. The sediments at both sites were highly reduced, and at Sta. 32 were also laminated (indicative of unbioturbated sediment deposition, Gorsline et al., 1996) with bacterial mats on the surface (J. Bernhard, pers. comm.). Nematodes that flourish in the OMZ, reflect an adaptation to extreme low oxygen concentrations and high concentrations of sulfide, and potentially, indirectly due to the reduced effect of predators and competitors (Rogers, 2000; Neira et al. 2001b). Because *G. spinithorni* is closely related to *G. bathyperuvensis* both in life style and in the kind of environment where it lives, most of the adaptations suggested for *G. bathyperuvensis* (see Neira et al., 2001a) appear to be valid for *G. spinithorni*. These are (1) body exceptionally large (2) body highly ornamented: presence of dense hairy/spiny cuticular body ornamentation, (3) large number of modified somatic setae positioned similarly to supporting setae, (4) increased body surface area through dense setaceous and hairy ornamentation, and (5) a well muscularized pharynx to suction fluid sediment.

Bacterial symbionts found on or in some invertebrates, including nematodes in the nearly anoxic Santa Barbara Basin, have been considered to have a sulfide detoxification function (Bernhard et al. 2000). Indeed, Bernhard et al. (2000) reported the occurrence of ectosymbiotic bacteria harbored by the nematode *Desmodora masira* Warwick, 1983 (and other animals). They were seen as a barrier against toxic sulfide. Observations of *G. bathyperuvensis*

did not reveal the presence of ectosymbionts (Neira et al. 2001a). Scanning electron microscopy observations of some specimens of *G. spinithorni* sp. nov. revealed the presence of bacteria-like particles (Felbeck, pers. comm., M. Bright, pers. comm.) distributed on the annular and inter-annular cuticle (Fig. 4C). However, it is still uncertain whether these are actually ectosymbionts or environment contamination.

The OMZ promotes endemism

On long time scales, OMZs have served as biogeographic barriers, limiting cross slope movements of populations and have been recognized as key oceanographic boundaries for animals intolerant to hypoxia (White, 1987). It has been postulated that if OMZs comprise a broad, continuous habitat, OMZ taxa might be expected to have global distributions, whereas if OMZs function as isolated habitats, a high degree of endemism should develop (Levin, 2003). The finding of *G. spinithorni* sp. nov. in the OMZ off Baja California, in abundances similar to those of the closely related species *G. bathyperuvensis* from the Peru OMZ (about 60 ind. 10 cm⁻²), suggests that OMZs function as isolated habitat more than a continuous one. Strong gradients in oxygen over short distances and the creation of barriers that block gene flow or reduce migration, are mechanisms that influence the evolution of slope populations and species, isolating populations and promoting allopatric speciation (White, 1987). Both species are from basins, which provides a more powerful isolating mechanism (i.e. topographic).

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