

***Desmotersia levinae*, a new genus and new species of free-living nematode from bathyal oxygen minimum zone sediments off Callao, Peru, with discussion on the classification of the genus *Richtersia* (Chromadorida: Selachinematidae)**

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Abstract

Desmotersia levinae gen. n., sp. n. is proposed, based on material found in bathyal oxygen minimum zone sediments off the coast of Peru. *Desmotersia* closely resembles *Richtersia* in the animals' general appearance and in spiny ornamentation of the body cuticle, but clearly differs in stoma structure and by the presence of a dorsal tooth. The systematic positions of the two genera are discussed, since *Desmotersia* apparently forms a link between Selachinematidae and Desmodoridae. *Desmotersia levinae* is characterized by a variety of spiny ornamentations anteriorly formed by bipartite spines arranged into a fin-like picket fence, by a head with an asymmetrical cephalic capsule, presence of two closely spaced ventral longitudinal rows of copulatory thorns, and by 2–4 ventral thorns in mid-tail positions on the male. The interaction between the new species and its habitat is discussed.

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Keywords: New genus; Classification; *Richtersia*; Oxygen minimum zone; SE Pacific Ocean

Introduction

Currently, there is an increasing interest in the study of benthic animals inhabiting reducing environments such as hydrothermal vents, methane seeps, and oxygen minimum zones (OMZs). The latter are midwater regions of the ocean, usually associated with highly productive upwelling regions, where dissolved oxygen concentrations fall below 0.5 ml l^{-1} (Kamykowski and

Zentara 1990). About 361,000 km² of the eastern Pacific Ocean seafloor are covered by OMZs (Helly and Levin 2004). Where OMZs intercept the sea bottom strong gradients of oxygen concentrations and organic matter occur, with these two factors mostly in an inverse relationship, and usually including build-up of toxic sulfide (Levin and Gage 1998). These gradients influence the biogeochemical properties of sediments as well as the faunal distribution; the permanent hypoxia represents a major oceanographic boundary for many species and a challenge in terms of adaptations required to live in such otherwise inhospitable habitats. Previous studies on the meiofauna of a bathyal OMZ area (305 m deep) off

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Callao, Peru, reported high abundances of nematodes (Neira et al. 2001b), among which a new species of the genus *Glochinema* (Epsilonematidae) was discovered (Neira et al. 2001a).

In the present paper, a new genus and new species of nematode are described. The corresponding discussion pertains to (A) the classification of *Desmotersia* gen. n. and *Richtersia* Steiner, 1916; (B) the use of cuticular structures in the buccal cavity for analyses of deep-level relationships; (C) the occurrence of the new species in a harsh environment; and (D) animal–sediment interactions.

Material and methods

Study area

The study area off the coast of Peru is one of the most productive regions of the world oceans (over $1 \text{ kg C m}^{-2} \text{ yr}^{-1}$), which is influenced by the Humboldt Current System (HCS) (Arntz et al. 1991, 2006). Its high productivity results, in part, from persistent wind-driven coastal upwelling that occurs off central Peru ($12\text{--}13^\circ\text{S}$). In this region the HCS exhibits a thin but intense midwater oxygen minimum layer, which is a major source of upwelled water. This layer is generally associated with the equatorial subsurface water mass (Morales et al. 1996); the most hypoxic portion intercepts the seafloor at bathyal depths.

Methodology

The samples were collected during the Panorama Leg 3a expedition aboard the R/V Melville (31 December 1997 to 3 January 1998) from a 305 m deep site (Station A; $12^\circ 22.70'\text{S}$, $77^\circ 29.07'\text{W}$), using a multiple corer. Sampling took place during the portion of the 1997–1998 El Niño with the greatest surface temperature anomaly off Callao (Sánchez et al. 2000). Further details of the cruise, environmental properties and meiofauna distribution have been reported by Neira et al. (2001b).

Sediment subcores (10 cm^2) were sliced vertically at 0–1, 1–2, 2–3, 3–5, and 5–10 cm, and treated and preserved as in Neira et al. (2001b). Metazoan meiofauna (here: organisms passing a $500 \mu\text{m}$ and retained on a $40 \mu\text{m}$ mesh sieve) were separated by the suspension–decantation method (Wieser 1960). Nematodes were sorted under a stereo dissecting microscope, and mounted in anhydrous glycerin–paraffin.

Measurements were made from digital pictures taken with a Victor SAN VISION video camera attached to a Carl Zeiss microscope and the software “Jiseki” (Japan) for image capture. For measuring specimens, the software NIH-Image 1.63 for Macintosh

(US National Institutes of Health; <http://mac.softpedia.com/get/Graphics/NIH-Image.shtml>) was used. Microscopic examination and drawing were performed using a Reichert Polyvar interference contrast microscope equipped with a camera lucida. Scanning electron microscope examination was performed on specimens dehydrated with ethanol, critical point dried (Samdri-790, Tousimis Research Corporation), and coated with Gold/Palladium. Specimens were examined with a Hitachi S2700 SEM.

Taxonomic section

Order Chromadorida Chitwood, 1933

Superfamily Chromadoroidea Filipjev, 1917

Family Selachinematidae Cobb, 1915

Desmotersia gen. n.

Etymology

The name combines elements from the genus names *Desmodorella* and *Richtersia*; it is feminine in gender for the purposes of nomenclature.

Type species

Desmotersia levinae sp. n.

Diagnosis

Selachinematidae. Body cuticle annulated and with longitudinal rows of spine-like ornamentations; lateral differentiation present. Head set off from body by thick sclerotized capsule, asymmetrical in lateral view, bilaterally symmetrical along dorso-ventral axis in frontal view. Lip region thin-walled, consisting of 12 lobes around mouth opening; each lobe with an inner cuticular tube, lining the cheilostome. Six inner labial setae on thin-walled lip region. Six outer labial setae and four cephalic setae arranged in a single crown at anterior border of head capsule; cephalic setae shorter than outer labial setae. Amphid with pore-like opening and associated oblique slit near anterior border of head capsule; amphideal fovea a single, ventrally whirled loop fitting in anterior wall of capsule as a flap-like structure in male; fovea more flattened and with partial loop loop in female and juvenile. Gland cells with yellowish granular appearance visible beneath cuticle of head capsule. Stoma s.l. with wide, cylindrical cheilostome, gymnostome with wall strengthened by tubular support (referred to as “prism” by Soetaert and Vincx 1987), and subdivided pharyngostome surrounded by pharyngeal tissue and a dorsal tooth inserted at level of subdivision. Pharynx largely cylindrical with slight posterior widening. Male reproductive system monorchic; anterior testis outstretched. Copulatory apparatus with long spicules

without differentiated capitulum but with a thin velum, slightly unequal in size; gubernaculum with apophyses. Female reproductive system didelphic–amphidelphic; ovaries reflexed and with variable position relative to intestine; vagina bipartite, vulva at mid-body or shortly posterior to that.

Relationships

Desmotersia gen. n. most closely resembles *Richtersia* in the animals' general appearance, yellow-brownish body, annulated body cuticle with longitudinal rows of spines, thin-walled lip region with 12 cuticular tubules and arrangement of anterior sensilla in two circles, spiral amphideal fovea, complex structure of stoma s.l., and in the reproductive systems being monorchic in the male, didelphic–amphidelphic in the female. *Desmotersia* differs from *Richtersia* mainly in pharyngostome structure, by the presence of a dorsal tooth, and in the amphideal fovea being positioned on a thin-walled lip region but largely covered by the anterior border of the cephalic capsule, into which it opens by a pore with small associated slit.

To a lesser extent, the new genus resembles taxa of the family Desmodoridae, particularly the genus *Desmodorella* Cobb, 1933. *Desmotersia* gen. n. shows similar body form, colour, presence of spiny ornamentation (though with spines far more pronounced and longer than in *Desmodorella*), presence of lateral ridge-like cuticle differentiation, an armed stoma, largely cylindrical pharynx slightly widened posteriorly, and reproductive systems monorchic in the male, didelphic–amphidelphic in the female. *Desmotersia* gen. n. differs from *Desmodorella* mainly in head structure, structure and cuticular reinforcements of the stoma s.l., absence of ventro-sublateral teeth, and in size and arrangement of the anterior sensilla (all setiform, rather than labial papilliform as in *Desmodorella*).

Desmotersia levinae sp. n.

Etymology

The species name is dedicated to Professor Lisa Levin of the Scripps Institution of Oceanography, who led the Panorama Leg 3a cruise, in recognition of her contributions to the knowledge of OMZs worldwide.

Type material

Holotype: Male (slide RIT717); continental slope off Callao, Peru (12°22.70'S, 77°29.07'W), 305 m depth, 1st January 1998.

Paratypes: One male (slide RIT717), one male (RIT719), two males (NTO 18, NTO 19), allotype female (RIT718), eight females (all on slide RIT719), one juvenile (RIT719); collecting data as for holotype.

The holotype and 12 paratypes (RIT717, RIT718, RIT719) have been deposited at the Royal Belgian Institute of Natural Sciences (KBIN), Brussels, two paratypes (NTO18, NTO19) at the Scripps Institution of Oceanography (SIO) Benthic Invertebrates Collection.

Habitat and environment

Marine, bathyal, microxic (bottom water O₂ concentration 0.013 ml l⁻¹); organic carbon-rich muddy sediment. Mainly in subsurface sediments (61% of specimens found at 1–3 cm depth). Relative dominance within total nematodes at 0–1 cm depth: 10% (Fig. 1).

Sediment (1–3 cm depth): soupy, organic carbon-rich (>17% organic carbon), 81% water content, 95% porosity. Sediment redox potential 176 mV, C:N ratio 9.3, percent biopolymeric organic carbon 20.4% (as sum of carbohydrate, lipid, and protein carbon), chloroplastic pigment equivalents 88 µg g⁻¹. Top 5 cm bioturbated; laminations present beyond 5 cm depth. Bottom water salinity 34.7 psu, temperature 10.2 °C.

Diagnosis

Desmotersia levinae sp. n. is characterized by the animals' appearance: a large yellow-brownish body, annulated body cuticle with longitudinal rows of a variety of spiny ornamentations. Ornamentation in neck region formed by densely arranged, bipartite spines resembling a fin-like picket fence; posteriorly spines uniform; ridge-like lateral differentiation of body cuticle flanked by a longitudinal row of spines. Head with cephalic capsule, asymmetrical in lateral view due to shorter dorsal side, bilaterally symmetrical along dorso-ventral axis in frontal view; labial region with thin

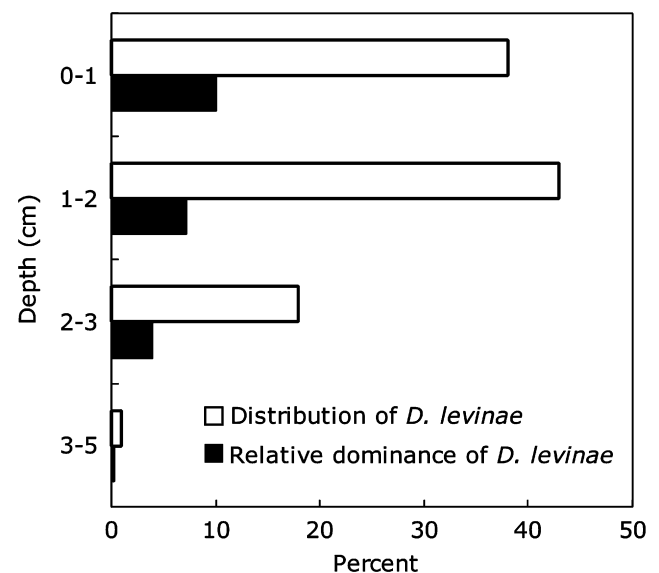


Fig. 1. Vertical distribution of *Desmotersia levinae* gen. n., sp. n., and relative dominance among total nematodes.

cuticle, forming 12 lobes (lobes subdivided by insertion of inner labial setae). Anterior sensilla, all setiform, arranged in two crowns: outer labial setae and shorter cephalic setae inserted at same level as amphideal fovea, i.e. near border of cephalic capsule. Amphideal fovea a more or less flattened ventral loop with pore-like outlet and associated slit anteriorly on head capsule. Buccal cavity s.l. wide cylindrical anteriorly to funnel-shaped posteriorly; pharyngostome subdivided and with a dorsal tooth. Males with long, thin spicules of slightly different lengths; gubernaculum with apophyses. Strong copulatory thorns, more or less arranged in two close longitudinal ventral rows of 9–13 thorns from about 300 μm anterior to cloacal opening and along anterior parts of retracted spicules; 2–4 thorns present ventrally at about mid-tail. Sexual dimorphism observed in cephalic capsule (more thickly sclerotized and with more pronounced asymmetry in female and juvenile), in cuticular ornamentation (more diverse in male), and in structure of amphideal fovea (complete ventral loop in male; partial loop in female and juvenile).

Description

(Figs. 2–10; for morphometric data, see Table 1)

Male. Body long, largely cylindrical, rather stout with largest width at mid-body, slightly tapered anteriorly to a truncated end, more strongly tapered in tail region; habitus sometimes S-shaped or looped upon fixation. Body cuticle annulated, except at extremities (head capsule and tail cone); annules 2.5 μm wide anteriorly, 3.5 μm in posterior body region. Body annules densely covered with diverse spine-like ornamentations varying from single hair-like to stout thorn-like or complex bipartite spines. Anterior half of neck region with complex spine-like ornamentation of 8–17 μm long bipartite spines, densely arranged in about 30 longitudinal rows (holotype) together resembling a fin-like picket fence (Figs. 2B and 4A); spines smallest just posterior to head, of maximum length at distance from head border of $1.5 \times$ head length, differences due to tube-like proximal portions of spines varying between 3 and 7.5 μm in length. Bipartite spines composed of broader proximal tube and hair-like, posteriorly bent distal part (Figs. 6B and 10B). At level of weak pharyngeal bulb, number of longitudinal rows of spines increasing subdorsally and subventrally to a total of about 40; proximal parts of bipartite spines becoming finer and continuing as unipartite spines (Fig. 2a). Lateral differentiation of cuticle (Figs. 8A and C) beginning 185 μm posterior to pharyngeal base (holotype) as a single longitudinal row of short thorn-like structures flanked by a narrow region devoid of spines (Fig. 2b); total number of longitudinal rows decreasing to about 20 rows of 12–15 μm long, posteriorly oriented filiform spines. Near level of tip of germinal zone of

testis (820 μm from anterior end in holotype) spines clustered in groups of 3–6 (Fig. 2c); in lateral field spines long and hair-like. Posteriorly, ventral/subventral spines becoming thorny. From about level of anterior vas deferens, ventral and subventral longitudinal rows of spines lacking. Strong copulatory thorns, more or less arranged in two close longitudinal rows of 9 and 10 thorns, respectively, in holotype, 10 and 13 in a paratype (Figs. 2C and 9F), appearing about 300 μm anterior to cloacal opening and extending along anterior parts of retracted spicules.

Somatic setae (14–18 μm) inserted between spine-like cuticular ornamentation, arranged in eight longitudinal rows in neck region, six rows at mid-body, and four longitudinal rows on tail. Somatic setae finer in neck region than posteriorly. In region of copulatory thorns and spicules, subventral somatic setae becoming more robust and more numerous; preloacally setae becoming shorter. Subdorsal setae without such differentiation.

Tail annulated and long, ending in a smooth cone about 30% of total tail length. Ventrally to subventrally rows of spines absent, dorsally longitudinal rows of spines extend to level of mid-tail. Robust preloacal subventral somatic setae extending on tail as six stout and long setae anteriorly, three fine short setae posteriorly. Ventrally and at about mid-tail, four copulatory thorns (of which the two middle ones form a pair) present in holotype (Fig. 2C); 2–3 thorns in paratypes. Three caudal glands extending anteriorly beyond cloacal opening and ending posteriorly in a spinneret.

Head set off from body by thick sclerotized capsule; asymmetrical in lateral view (Fig. 10D), bilaterally symmetrical along dorso-ventral axis in frontal view (Fig. 10C). Head capsule in lateral view extending further backwards laterally, slightly shorter ventrally, shortest on dorsal side. Lip region with thinner cuticle, appearing as a labial collar with 12 lobes, each lobe with an inner cuticular tubular support. Thin-walled labial collar often partially retracted in fixed specimens, sutura with capsule weak. Anterior sensilla apparently arranged in two circles: six inner labial setae (7.5 μm long) inserted on thin-walled lip region between labial lobes; six external labial setae (7 μm) and four cephalic setae (5 μm) inserted at level of amphidial fovea, i.e. near anterior border of cephalic capsule. Eight short sub-cephalic setae scattered irregularly on head capsule. Amphidial fovea (11 μm wide) a slightly flattened spiral with single ventral loop, positioned almost frontally and partially covered by head capsule; impression on inner side of anterior border of head capsule visible as a 8 μm wide flap (Fig. 6D). Amphid with pore-like opening and fine oblique slit, near anterior border of head capsule (Fig. 4A). Gland cells with yellow-brownish granular appearance visible beneath cuticle of head capsule.

Stoma s.l. 31–34 μm long, with wide (8 μm) cylindrical cheilostome with cuticular tubes (5.2 μm) of labial lobes,

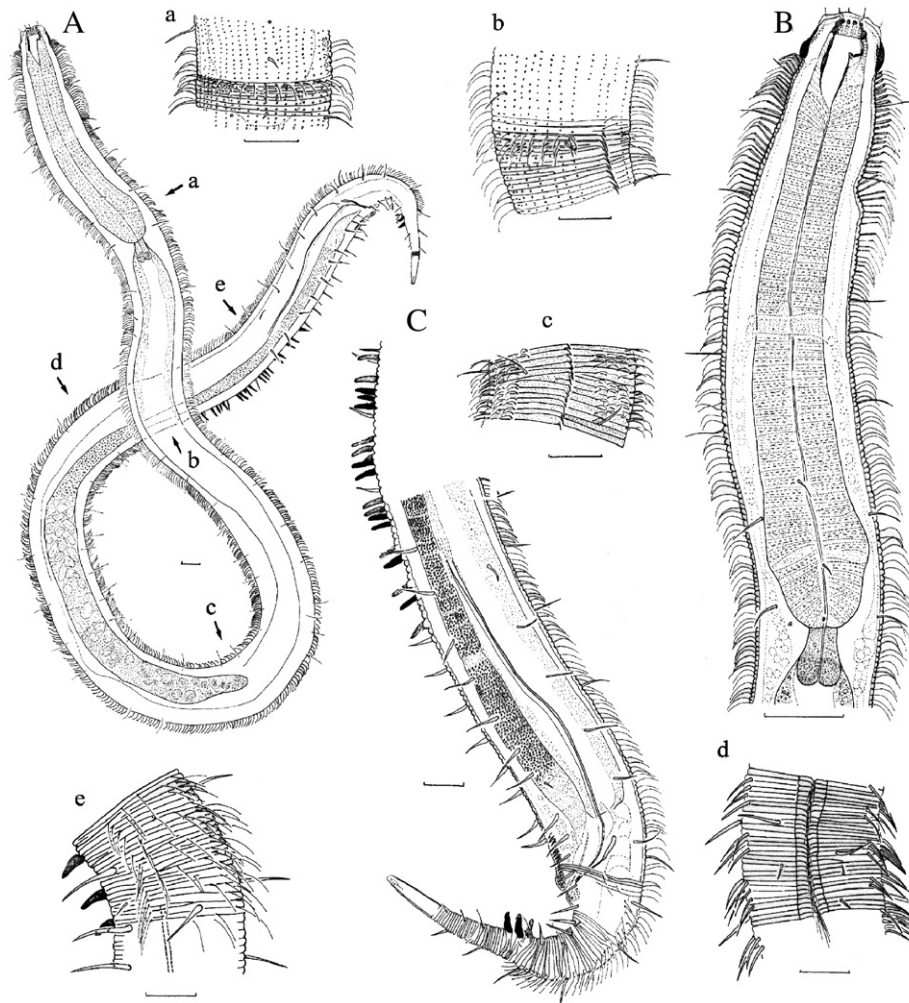


Fig. 2. *Desmotersia levinae* gen. n., sp. n.; male holotype: (A) Whole body; arrows indicate locations of cuticular areas shown in surface view in detail figures a–e. (B) Neck region. (C) Posterior body region, showing copulatory apparatus, copulatory thorns, and tail in surface view. Scale bars = 20 μ m.

gymnostome with wall strengthened by rigid bars 4 μ m in length (see prism system in *Richtersia*) and with subdivided pharyngostome surrounded by pharyngeal tissue (anterior cylindrical part 10 μ m long; posterior part funnel-shaped, 15 μ m long); dorsal tooth inserted at transition between both portions (Figs. 4B and 5K). Pharynx long, largely cylindrical but gradually widened posteriorly to a short, weak, bulb-like structure. Nerve ring at mid-pharynx, rather obscure. Cardia rather long (21 μ m; Fig. 9D). Intestinal cells with larger granules anteriorly, finer ones posteriorly; intestinal lumen lined with a microvillar wall visible as a long band in optical section. Cloacal region may be enlarged.

Reproductive system monorchic; outstretched testis not reaching into pharyngeal region and lying partially ventral to intestine. Vesicula seminalis with large rounded sperm cells; vas deferens with dense, fine granulations (Fig. 2A). Spicules long and thin, distally needle-like and ventrally curved, without differentiated

capitulum but with thin velum (Fig. 2C). Spicules slightly unequal in size (left spicule 178 μ m long, right spicule 183 μ m in holotype; 199 and 188 μ m, respectively, in a paratype). Gubernaculum 36 μ m long in holotype, composed of a single trough-shaped corpus parallel to spicule and extended with two apophyses (15 μ m).

Female. Body enlarged towards mid-body region of reproductive system; often S-shaped upon fixation. Less variation in cuticular ornamentation compared to male; body covered with evenly distributed spiny ornamentation. Anterior region with comparable bipartite spiny ornamentation, picket fence-like, arranged as in male; with 30–36 longitudinal rows of bipartite spines in anterior neck region; about 80 longitudinal rows more posteriorly. Bipartite spines with basal part longest (9.5 μ m, i.e. half of spine) at short distance from posterior border of head capsule; at base of pharynx bipartite spines with 3 μ m short base and 7.5 μ m long,

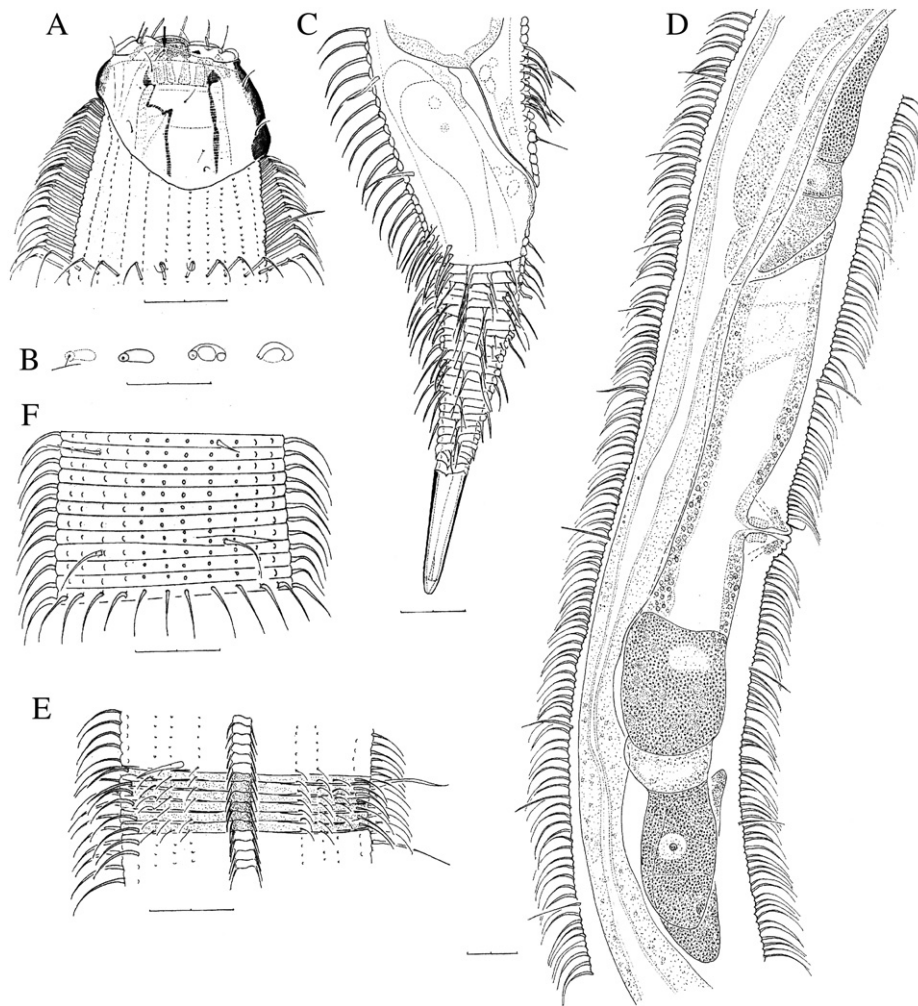


Fig. 3. *Desmotersia levinae* gen. n., sp. n.; female paratype: (A) Anterior body region in surface view; one complete row of spines shown, others marked as insertion points only. (B) Amphid in four successively more internal aspects, from surface pore (far left) to sausage-shaped fovea at deepest level (far right). (C) Tail region; posterior part in surface view. (D) Female reproductive system. (E) Lateral differentiation of juvenile cuticle just anterior to anterior genital branch. (F) Detail of cuticle just posterior to neck region; one complete row of spines shown. Scale bars = 20 µm.

hairy distal portion. Just anterior to anterior genital branch, lateral differentiation of body cuticle appearing as ridge-like structure flanked by long row of short spines (Fig. 3E); bipartite spine-like ornamentation (Figs. 8E and F) replaced by stout uniform spines 14 µm in length. Arrangement of spines not grouped in bundles as in male. Tail shorter, more densely ornamented with regular straight spines, longest dorsal ones 16 µm long, ventrally 10 µm (Fig. 3C). Postanal region may be swollen; beneath cuticle dark granules present. Somatic setae about 20 µm, far apart (18–45 µm) and arranged in six longitudinal rows.

Head capsule sclerotized more thickly than in male, in lateral view appearing more asymmetrical due to dorsal side being short, i.e. half as long as ventral side (Fig. 3A). Amphideal fovea smaller, consisting of only

half a turn, at surface of head capsule with pore-like opening and posterior slit (Fig. 7C).

Reproductive system didelphic–amphidelphic. Ovaries reflexed towards the same or to opposite sides of body, both lying on same or opposite sides of intestine or one branch ventral to intestine (Fig. 3D). Vulva with protruding lips devoid of spines, situated at mid-body or a little more posterior. Vagina bipartite with short pars distalis vaginae and longer pars proximalis vaginae surrounded by strong sphincter muscles (Fig. 3D); vagina surrounded by vaginal glands with dark yellow to brownish granules.

Juvenile. Only one specimen was observed, probably belonging to a third developmental stage based on body length and length of genital system. Body more or less

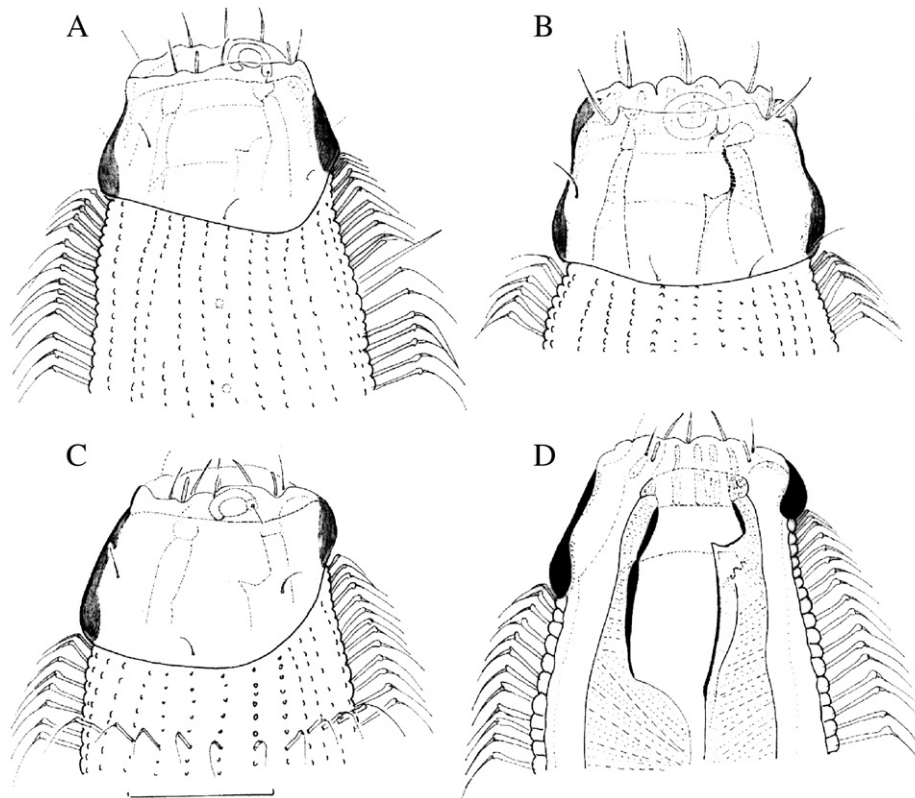


Fig. 4. *Desmotersia levinae* gen. n., sp. n.; head region: (A) Male holotype, surface view. (B) Male paratype, surface view. (C) Juvenile, surface view. (D) Buccal cavity. Scale bar = 20 μm.

cylindrical; cuticular ornamentation comparable to female but with lower number of longitudinal rows of spines and without lateral ridge-like differentiation of body cuticle. Head and arrangement of anterior sensilla and amphid as in female; three subcephalic setae on either side of cephalic capsule. Stoma 38 μm long, structured as in adult; replacement tooth visible. Genital primordium 67 μm long.

Discussion

Morphology of stomatal and labial regions

(Figs. 5A–M, a–h)

The morphology of the stomatal and labial regions in *Desmotersia* gen. n. shows similarity with that described for *Richtersia* species by Soetaert and Vincx (1987). These authors recognized two extreme types of buccal morphology within *Richtersia* (Figs. 5I, i and J, j), with 12 tubular structures partially lining the cheilostome or not and followed posteriorly by another set of 12 bar-like structures indicated as “prisms”. Soetaert and Vincx (1987) described the prisms as part of the anterior half of the stoma s.str.; the posterior part of the latter being surrounded by pharyngeal tissue. When the lips are

retracted, the bar-like constructions referred to as “Balkenwerk” by Kreis (1929) probably represent the prism system in the anterior part of the stoma s.str. However, Soetaert and Vincx (1987) did not clearly define what they considered as the stoma s.str.; apparently, they also included the stoma part surrounded by pharyngeal tissue.

In the present contribution, we define the stoma s.str. as the cheilostome, the stoma s.l. as composed of cheilostome and pharyngostome. The part of the stoma inwards of the cheilostome and not lined by pharyngeal tissue is indicated as the gymnostome (De Ley et al. 1995).

Like *Richtersia*, *Desmotersia* gen. n. has a lobed, thin-walled labial region with 12 cuticular tubes, but tubes completely internally, apparently strengthening the cheilostome. In *Desmotersia*, the second set of reinforcements or prisms of *Richtersia* are considered as belonging to the gymnostome. The pharyngostome, i.e. the anteriormost part of the pharynx, is subdivided, as is clearly indicated by the sclerotizations of the lumen wall. The pharyngostome consists of a shorter, cylindrical anterior part and a longer, funnel-shaped posterior part; at the transition between both portions a well developed dorsal tooth inserts. The pharyngostome in *Richtersia* is unipartite and unarmed. Currently,

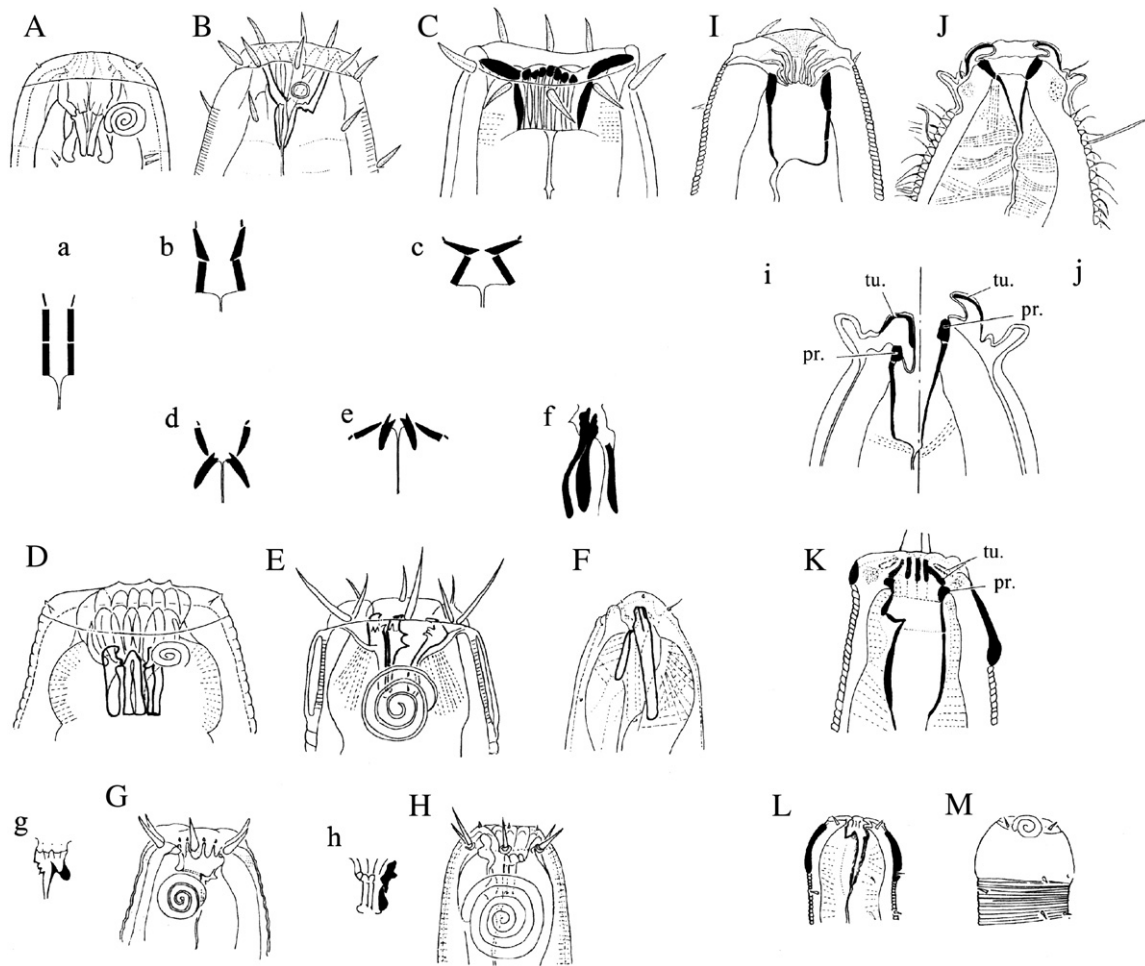


Fig. 5. Cuticular structures in the buccal cavity in *Desmotersia levinae* gen. n., sp. n. (K), other Selachinematidae (A–J, a–j), and Desmodoridae (L, M). (a–h) Schematics after Gerlach (1964); a shows hypothetical primitive form: (A) *Halichoanolaimus dolichurus* (after Gerlach 1964). (B, b, C, c) *Latronema deconincki*, male (modified from Boucher 1976). (D, d) *Synonchium obtusum*, male (after Gerlach 1953). (E, e) *Synonchiella hopperi*, male (after Ott 1972). (F, f) *Cheironchus paravorae*, male (after Castillo-Fernandez and Decraemer 1993). (G, g) *Paracyatholaimus* sp. (H, h) *Choniolaimus panicus* (after Gerlach 1956). (I) *Richtersia coomansi*, female (after Soetaert and Vincx 1987). (J) *Richtersia bathyalis*, male (after Soetaert and Vincx 1987). (K) *Desmotersia levinae*. (L, M) *Desmodorella spinicaudata*, male; M shows head in surface view (after Verschelde et al. 1998).

Richtersia is classified within the Selachinematidae (see also below).

Gerlach (1964) revised the taxa in Selachinematidae (which at that time was divided in two groups, the Choniolaiminae and Selachinematinae), based on analyses of the buccal cavity and cuticular structures, and compared them with Cyatholaimidae (Figs. 5G, g). In Choniolaiminae and Selachinematinae, the buccal cavity consists of a reduced cheilostome or vestibulum, has no dorsal tooth, and the posterior part of the buccal cavity has developed into a “new” part with longitudinal cuticular bars, comparable to the bars in the anterior part (Figs. 5A, a, H, and h). Where the two sets of cuticular bars meet, tooth-like structures appear that are different from teeth in the Cyatholaiminae sensu Gerlach (1964). Moreover, the anterior part of the stoma can open so that the anterior set of bars is oblique

to horizontal in position (Figs. 5B, b versus Figs. 5C, c). In the Choniolaiminae, tooth-like structures have developed at the posterior edge of the cuticular bars of the anterior stoma portion (Figs. 5B, b, C, and c), whereas in the Selachinematinae tooth-like structures have developed from the anterior part of the cuticular bars of the posterior stoma portion (Figs. 5D, d, E, and e), in their extreme form as dented jaws (Figs. 5F and f).

Boucher (1975) described an additional species, *Richtersia kreisi*, with six lips surrounding a crown of cheilorhabdia composed of 12 bars, which Soetaert and Vincx (1987) interpreted as similar to the cuticular tubes in their paper. Boucher (1976), dealing with a new species of *Latronema*, discussed the close resemblance of the latter genus to *Richtersia* (see below). He described the buccal cavity in *Latronema* as composed of two chambers, both reinforced with bars and at the junction

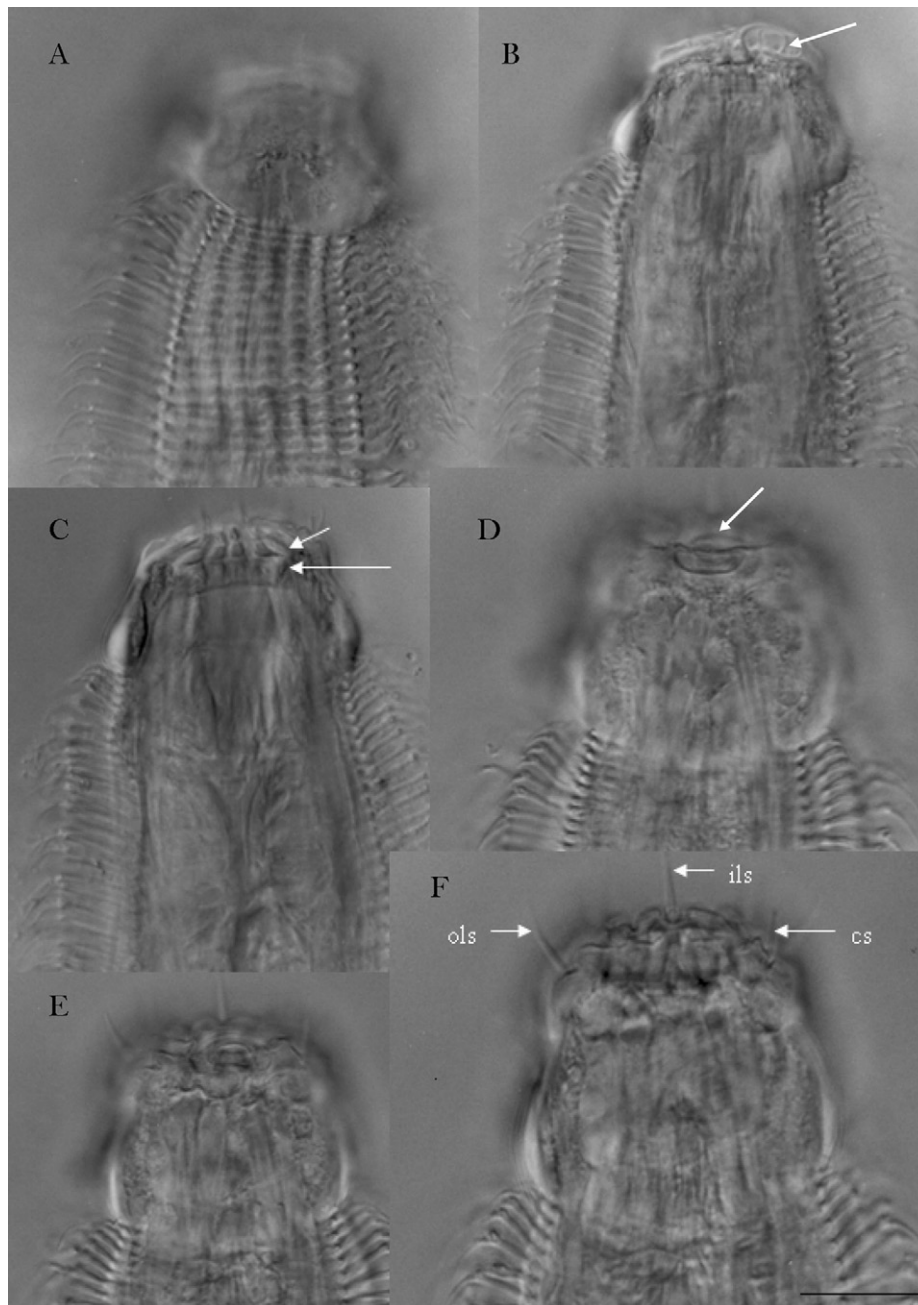


Fig. 6. Male head: (A) Holotype, surface view. (B) Holotype, focused at level of amphideal fovea (arrow). (C) Holotype, buccal cavity showing tubules (anterior arrow) and “prism” (posterior arrow). (D) Paratype, focused on flap-like impression of fovea in inner wall of capsule (arrow). (E) Paratype, focused on fovea. (F) Paratype; cs = cephalic setae, ils = inner labial setae, ols = outer labial setae. Scale bar = 20 μ m.

with 21 spine-like structures; the anterior chamber was described as “prostomial” (? = cheilostome).

Imprecise terminology of the stoma parts and lack of ultrastructural studies concerning the cellular layers surrounding the different parts of the stoma hamper inferences on homology of those parts. In [Gerlach \(1964\)](#), the two sets of bar-like reinforcements appear to be considered as part of the pharyngostome; thus, the latter is subdivided, with tooth-like structures (where

present) at the transition, a condition similar to that in *Desmotersia*. In contrast, [Boucher \(1976\)](#) described the first set of bars as prostomial by position in *Latronema*.

Classification of *Desmotersia* gen. n.

[Lorenzen \(1981, 1994\)](#) provided the first phylogenetic classification system of free-living nematodes based on

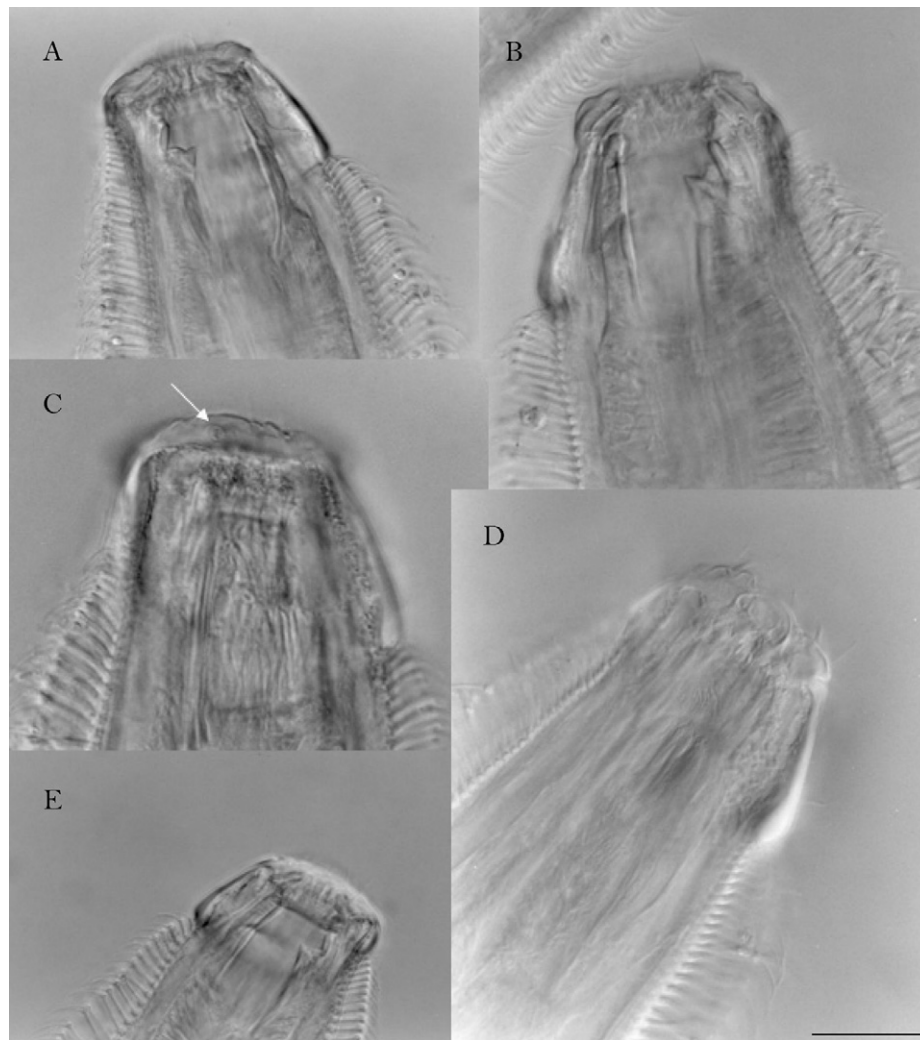


Fig. 7. Head region: (A, B) Female paratypes, showing respective stoma with dorsal tooth. (C) Female paratype in surface view, showing pore at level of fovea (arrow). (D) Female paratype at level inwards of amphid pore, showing receptor and fovea. (E) Juvenile, stoma with dorsal tooth. Scale bar = 20 μ m.

the cladistic principles, with which [Hennig \(1950, 1966\)](#) had sought to establish holophyly of taxa based upon the possession of shared derived characters.

According to [Lorenzen \(1981, 1994\)](#), the family Selachinematidae is characterized by the holapomorphy of a spacious buccal cavity without teeth or only with teeth referred to as jaws, the latter not being homologous with teeth in Chromadorida ([Gerlach 1964](#)). The holapomorphy for the superfamily Chromadoroidea, to which the Selachinematidae belong, consists of a transversely striated body cuticle covered with dots or with adornments developed from dots.

No holapomorphy has been found for the family Desmodoridae, but the superfamily Desmodoroidea is characterized by (1) the holapomorphy of a single anterior testis, a feature unique within the Chromadorina (sensu [Lorenzen 1981, 1994](#)), plus (2) a

yellowish–brownish body in glycerine preparations which in formalin-fixed specimens cannot be stained with cotton blue, (3) the buccal cavity with a distinct dorsal tooth while small “subventral” teeth may be present or absent, and (4) the variable position of the gonads relative to the intestine.

Classification of *Richtersia* and validity of the monogeneric Richtersiidae [Kreis, 1929](#)

The position of *Richtersia* and the family Richtersiidae has been subject to much discussion. [Filipjev \(1934\)](#) regarded Richtersiidae as closely related to Cyatholaiminae (Chromadorida) based on the structure of the pharynx, spiral amphids, and dotted cuticle. [Chitwood and Chitwood \(1950\)](#), [De Coninck \(1965\)](#),

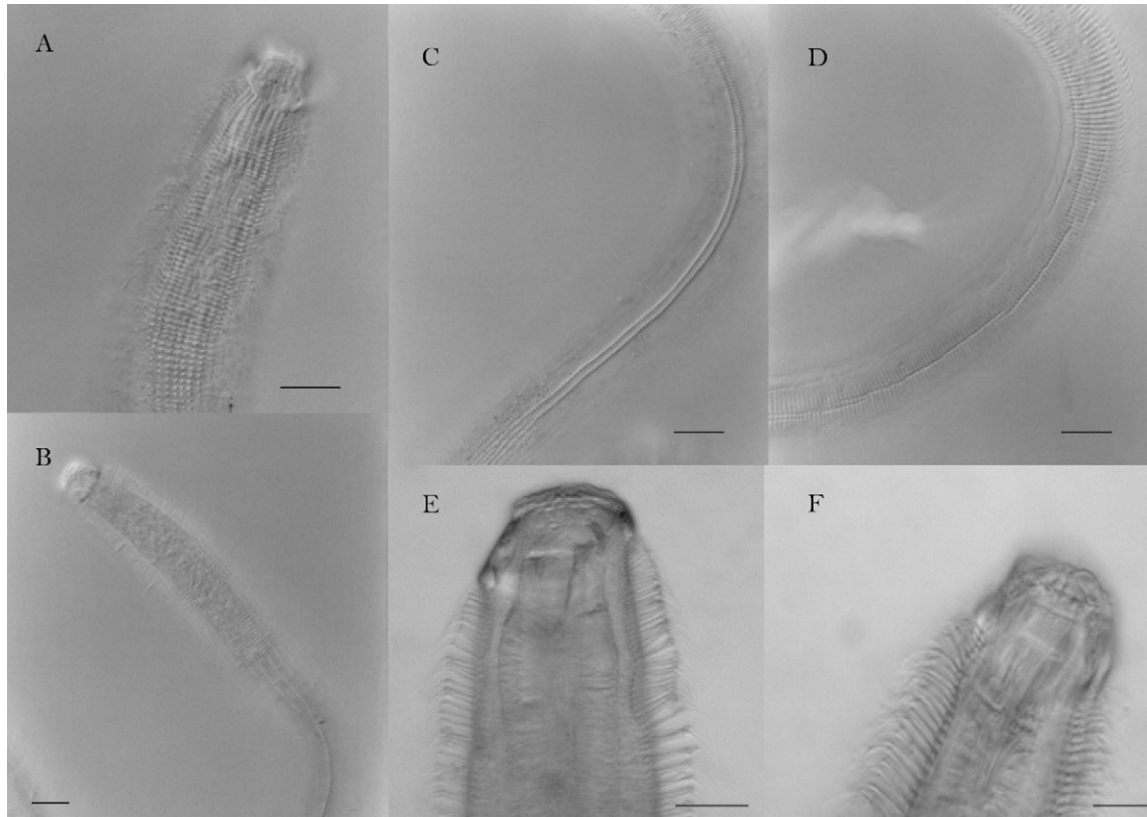


Fig. 8. Cuticle ornamentation: (A) Male holotype, neck region. (B) Male paratype, transition between neck and intestinal regions. (C) Female paratype, differentiation of lateral cuticle anterior to vagina. (D) Female paratype, lateral view of posterior body region. (E, F) Allotype and another female paratype, details of bipartite spiny ornamentation just posterior to head capsule. Scale bars = 20 µm.

and Gerlach and Riemann (1973) placed Richtersiidae in the Desmodorida Filipjev, 1922. De Coninck (1965) classified Richtersiidae together with Monoposthiidae in the superfamily Monoposthiioidea (suborder Desmodorina), the latter being characterized by an annulated cuticle with longitudinal rows of spiny ornamentation and by the lack of a cephalic capsule. Lorenzen (1981, 1994) considered Richtersiidae as rather aberrant in Desmodorida in view of the large, toothless buccal cavity and the setiform inner labial sensilla (in contrast to the usual small buccal cavity mostly armed with a dorsal tooth, two small ventrosublateral teeth, and the papilliform inner labial sensilla).

According to Boucher (1976), *Latronema* (Selachinematidae, Chromadorina) closely resembles *Richtersia* (Desmodorina) mainly in general appearance and cuticular ornamentation. The differences concerning the buccal cavity and arrangement of anterior sensilla were not considered as contradictory to a close relationship between the two genera. Despite this argument, Lorenzen (1981) followed Boucher (1976) and synonymized Richtersiidae with Selachinematidae (Chromadorida), a classification that was followed until now.

Although there has been a drastic increase in molecular data for marine metazoa, only De Ley et al.

(2005) have published on *Richtersia*. A neighbor-joining tree based upon the D2D3 expansion segment clustered *Richtersia* with *Metachromadora* (Spiriniinae, Desmodoridae), and both taxa appeared to be more closely related to the Chromadoridae than to Selachinematidae (e.g. *Choanolaimus*). However, no bootstrap support was given, and the authors remarked that deeper relationships were not necessarily resolved, the D2D3 locus being too short and too divergent for that purpose. An improved molecular phylogeny with emphasis on marine taxa (Holterman et al. 2006) placed Selachinematidae outside of Chromadorida, but could not determine the exact position of the former. In that study, as in Meldal et al. (2007), the Desmodorida did not result as a monophyletic group, since the superfamily Microlaimoidea did not cluster with Desmodoroidea, but was placed at the base of the class Chromadorea. In a recent revision of the genus *Richtersia*, Pastor de Ward and Lo Russo (2007) assumed that *Latronema* and *Richtersia* are two intermediate genera, from which the Desmodoroidea lineage has evolved.

Based upon the holapomorphy for the Selachinematidae of a spacious buccal cavity without teeth (Lorenzen 1981, 1994), *Desmotersia* gen. n. does not fit within this

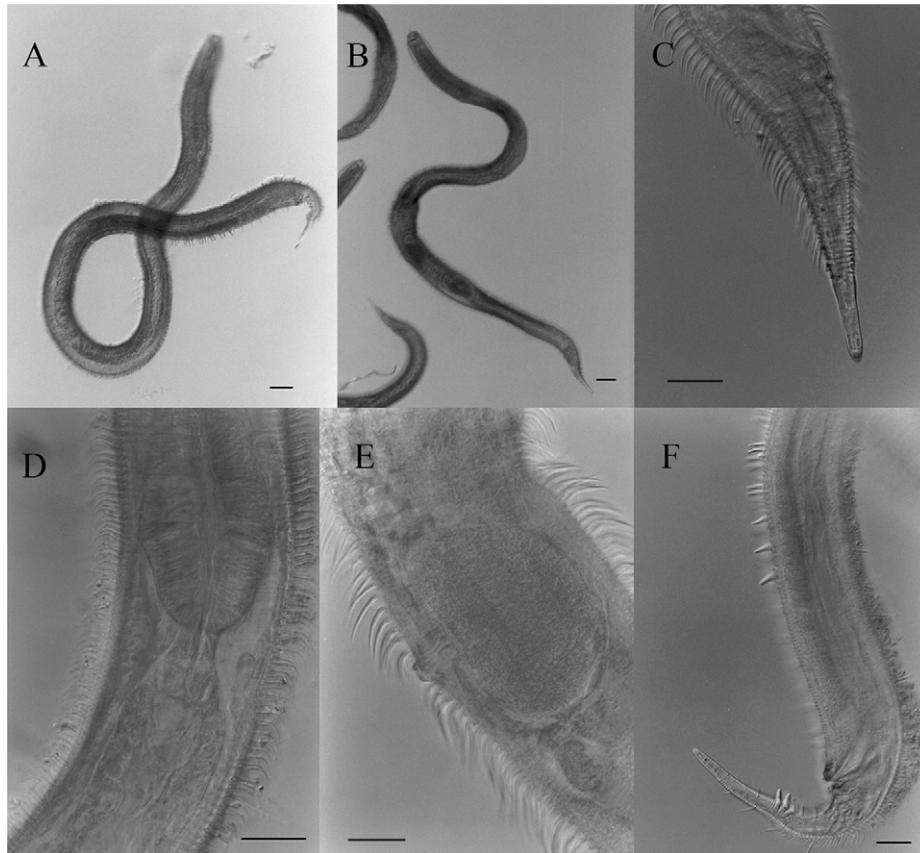


Fig. 9. (A) Male holotype, habitus. (B) Female paratype, habitus. (C) Female paratype, tail region. (D) Male holotype, cardia region. (E) Female paratype, vagina region with egg. (F) Male paratype, posterior body region showing copulatory thorns and gubernaculum. Scale bars: A, B = 50 μ m, C–F = 20 μ m.

family. On the other hand, no morphological holapomorphy for the Desmodoroidea has been found. Moreover, *Desmotersia* does show a single anterior testis, yellow-brownish body colour, and variable position of the gonads relative to the intestine, i.e. three of the four features characteristic of the Desmodoroidea (see above).

At this time the taxonomic position of *Richtersia* remains questionable, all the more so on account of the discovery of *Desmotersia* with its great similarity to *Richtersia* but also the contrasting possession of a dorsal tooth. Because of its great similarity with *Richtersia* and to avoid taxonomic inflation, *Desmotersia* gen. n. is not placed in a new family but instead is placed in Selachinematidae, in anticipation of information from future molecular analyses.

Animal–sediment interaction

Desmotersia levinae thrives preferentially in subsurface (1–3 cm deep) sediments rich in organic carbon (over 17%), in which the biopolymeric fraction (as the sum of proteins, carbohydrates and lipids) potentially

available to consumers amounts to 20%, mostly of phytoplanktonic origin (Neira et al. 2001b). Under these conditions, food does not appear to be a limiting factor for nematodes in such OMZ environments. Instead, hypoxia, occasionally anoxia, and high sulfide concentrations seem to be the factors controlling invertebrate distribution (Levin 2003). Concurrent work at our study site on protozoan meiofauna (Foraminifera; E. Pérez, pers. comm.) and macrofauna (Levin et al. 2002) shows that all the faunal groups examined (i.e. agglutinated and calcareous Foraminifera, metazoan meiofauna and macrofauna) exhibited the highest densities at this site, where bottom water dissolved oxygen concentrations were lowest but food availability was highest. In general, metazoan meiofauna are more tolerant to hypoxic conditions than macrofauna; within the meiofauna, nematodes are more tolerant than other taxa (Giere 1993; Gooday et al. 2000). At the study site, metazoan meiofauna (99.3% nematodes) and macrofauna (dominated to 85% by a non-feeding oligochaete that uses energy from sulfide-oxidizing, endosymbiotic bacteria; Giere and Krieger 2001) reached the highest densities (Neira et al. 2001b; Levin et al. 2002). Interestingly, both *D. levinae* and oligochaetes were found at subsurface

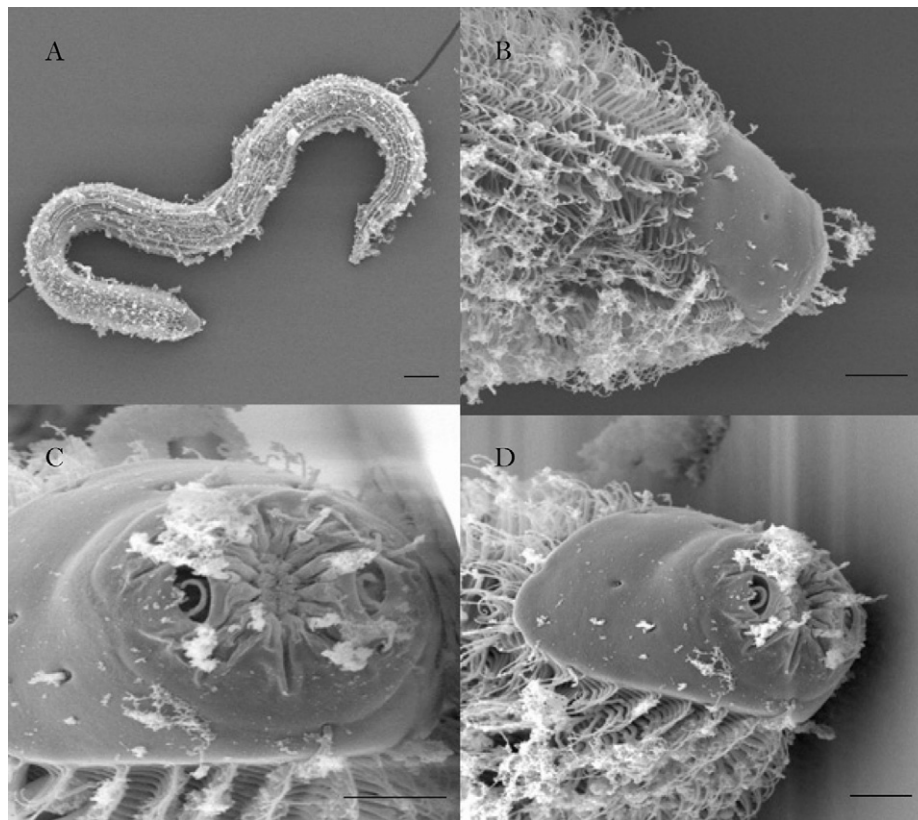


Fig. 10. Male, SEM images: (A) Whole body. (B) Anterior body region showing cephalic capsule and bifid spiny ornamentation. (C) Head in frontal view, dorsal side at bottom. (D) Head in lateral view, dorsal side at bottom. Scale bars: A = 50 μ m, B–D = 10 μ m.

Table 1. Morphometric data (all dimensions in μ m) for *Desmotersia levinae* gen. n., sp. n. from Peruvian OMZ bathyal sediments.

Character	Male		Female		Juvenile
	Holotype	Range ($n = 5$)	Allotype	Range ($n = 8$)	
Body length	1760	1529–2230	1985	1640–2035	1285
Greatest body width (other than at vulva)	61	61–77	84	69–124	57
Head width at base	35	35–52	44	41–44	35
Width at pharynx end	54	54–70	66	58–69	56
Body width at level of vulva	–	–	84	66–99	–
Body width at level of anus	46	46–52	39	37–43	40
Tail length	148	140–180	120	120–141	145
Pharynx length	268	240–317	318	227–324	232
Length anterior to anus	1638	1381–2038	1841	1486–1883	–
Length anterior to vulva	–	–	1157	941–1360	–
Position of vulva (% of body length)	–	–	58.2	58.2–66.8	–
Genital primordium	–	–	–	–	67
Coefficients of de Man:					
a: body length divided by greatest body width	28.9	22.8–29.3	23.6	16.2–27.8	22.9
b: body length divided by pharyngeal length	7.3	6.9–7.4	7.0	6.7–8.0	5.5
c: body length divided by tail length	11.9	10.9–12.5	16.5	12.7–16.5	8.9
c': tail length divided by body width at level of anus	3.2	2.9–3.5	3.1	3.0–3.5	3.6
Number of tail thorns	4	2–4	–	–	–

depths of 2–5 cm (Levin et al. 2002). In the hypoxic/sulfidic Santa Barbara Basin, symbiosis has been demonstrated to be a prevalent characteristic (Bernhard et al. 2000), but endosymbiotic bacteria have not been observed in *D. levinae*.

Benthic animals respond to hypoxic and sulfidic conditions with diverse physiological and morphological adaptations. Organisms with little motility may inhabit near-surface sediments to mitigate the effects of these stressors. The distribution of *D. levinae* in the sediment column (Fig. 1) suggests that members of this species are able, and prefer, to move in subsurface sediments to exploit the associated abundant food supply. This could be an advantage over potential competitors such as *Glochinema bathyperuensis*, an epsilonematid abundant in the top 1 cm (Neira et al. 2001a). Muddy and soupy sediments with high water and organic matter content are common in OMZs. Since nematodes are the dominant meiofaunal taxon there, this means that several species have become well adapted to these otherwise stressful conditions. Among them large, rather slender nematodes with dense spiny and setaceous body ornamentation, such as *D. levinae*, appear to be more common than in other habitats. Their appearance and dense ornamentation may contribute to better motility and balance, and enable the animals to avoid sinking deep in slurry sediments.

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