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Research article

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Revision of Desmodorinae and Spiriniinae (Nematoda: Desmodoridae) with redescription of eight known species

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Abstract. The taxonomy of the family Desmodoridae (Nematoda: Desmodorida) is partially revised based on morphology. The diagnoses of the Desmodoridae and the subfamilies Desmodorinae and Spiriniinae are emended to accommodate re-analyzed morphological features. Eight known species are redescribed and the implication of the new findings for the taxonomy of the group is discussed. *Amphispira* and *Metadesmodora* are confirmed as *genera inquirendae*. *Alaimonema* and *Sigmophoranema*, and their corresponding type species, are proposed as *inquirendae* due to poor descriptions of the type material. The other three species of *Sigmophoranema* are transferred to the genus *Onyx* because they bear the diagnostic features of this group: spear-like dorsal tooth and s-shape precloacal supplements. *Echinodesmodora*, *Paradesmodora* and *Stygodesmodora* are transferred to the Spiriniinae based on the absence of a head capsule and on the amphidial fovea being surrounded by cuticle striation. *Paradesmodora toreutes* is transferred to the genus *Acanthopharyngoides* as *A. toreutes* comb. nov. The genus *Onepunema* does not fit in the family Desmodoridae because of diorchic males; thus, it is regarded as taxon *incertae sedis*. Lists of valid genera for the two subfamilies are provided. A dichotomic key for the identification of the 14 genera within the Spiriniinae is provided.

Keywords. Taxonomy, systematic, revision, morphology, Cuba.

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Introduction

The family Desmodoridae Filipjev, 1922 includes a diverse and heterogeneous group of free-living, mostly marine, nematodes (Decraemer & Smol 2006). Desmodorid nematodes are very abundant in

habitats such as tropical coral reefs (Tietjen 1991), sandy beaches (Verschelde & Vincx 1996) and seagrass beds (Ndaro & Ólafsson 1999), but also occur in deep-sea (Verschelde *et al.* 1998; Fonseca Cavalcanti *et al.* 2009) and freshwater habitats (Decraemer & Smol 2006). The species within the family probably are an important component of the functional diversity of benthic food webs due to their varied morphology and symbiotic relationships with bacteria (Ott 1996). They constitute the most abundant group in the marine sediments from a tropical coral reef in Punta Francés, Cuba, Caribbean Sea (Armenteros *et al.* 2012) and deserve a more thorough taxonomic study.

The family Desmodoridae belongs to the superfamily Desmodoroidea Filipjev, 1922, together with the families Draconematidae Filipjev, 1918 and Epsilonematidae Steiner, 1927. It is composed of six subfamilies, 35 genera and 318 species (Hodda 2011); but these figures may vary according to the source (e.g., 320 valid marine species in the World Register of Marine Species, accessed February 2014). The six subfamilies currently recognized (Decraemer & Smol 2006) are: Desmodorinae Micoletzky, 1924, Molgolaiminae (Jensen, 1978), Prodesmodorinae Lorenzen, 1981, Pseudonchinae Gerlach & Riemann, 1973, Spiriniinae Gerlach & Murphy, 1965 and Stilbonematinae Chitwood, 1936.

Several recent taxonomic studies dealt with taxa of the Desmodoridae (e.g., Blome & Riemann 1994; Verschelde *et al.* 1998, 2006). Five faunistic studies (Gerlach 1950, 1963; Wieser 1954; Wieser & Hopper 1967; Boucher 1975) described several species of desmodorids and proposed dichotomic keys to species. Further revisions (and/or identification keys) for specific genera within the family have been published, e.g., for *Chromadoropsis* Filipjev, 1918 (Furstenberg & Vincx 1988), *Chromaspirina* Filipjev, 1918 (Maria *et al.* 2009), *Croconema* Cobb, 1920 (Verschelde *et al.* 2006), *Desmodora* de Man, 1889 (Verschelde *et al.* 1998), *Laxus* Cobb, 1894 (Ott *et al.* 1995), *Metachromadora* Filipjev, 1918 (Maria *et al.* 2014), *Onyx* Cobb, 1891 (Dinh Tu *et al.* 2011), *Perspiria* (Wieser & Hopper, 1967) (Vincx & Goubault 1989), *Pseudonchus* Cobb, 1920 (Warwick 1969) and *Spirinia* Gerlach, 1963 (Coles 1987). Recently, the subfamily Stilbonematinae has also been revised (Tchesunov 2013; Armenteros *et al.* 2014). In the recently published Handbook of Zoology, Tchesunov (2014) provided an overview of the order Desmodorida.

The family Desmodoridae lacks any synapomorphy. It may be distinguished from the Draconematidae and Epsilonematidae by elimination taking into account the synapomorphies of these families: the distinctive body shape with swollen pharyngeal region and the presence of specialized somatic setae (Lorenzen 1994). Molecular evidence, based upon small subunit of ribosomal DNA (SSU rDNA), indicated that the family Desmodoridae is highly polyphyletic (van Megen *et al.* 2009). Even more, the systematics of the family is poorly understood, because (1) morphological characters are conflictive to unravel the relationships among taxa (Kampfer *et al.* 1998) and (2) phylogenetic analyses (Armenteros *et al.* in press) suggested the non-monophyletic nature of the subfamilies Desmodorinae and Spiriniinae and stressed the necessity to collect more data of previously non-sequenced genera and species. Additionally, the taxonomy of the Desmodoridae suffers from morphologically poorly defined taxa (e.g., *Laxonema* Cobb, 1933; *Metadesmodora* Schuurmans Stekhoven, 1942), lack of identification keys to some speciose genera (e.g., *Desmodora* de Man, 1889) and the absence of updated species lists.

A possibly effective approach to deal with this taxonomic problem is to carry out revisions of taxa in order to clarify, organize and compile taxonomic information (Wheeler 2004). We hereby used the morphological species concept based on the discontinuous variation of morphological features. Our approach is based on the differential fitness species concept (Hausdorf 2011), which allows the recognition of differences based on phenotypic clusters.

We identified 14 species belonging to three subfamilies of the Desmodoridae collected from the Punta Francés coral reef (Cuba). A first study dealt with six new and known species of the Stilbonematinae

(Armenteros *et al.* 2014). The available new material from Cuba allows a more detailed study of the morphology of known eight species belonging to the subfamilies Desmodorinae and Spiriniinae. The aim of the present contribution is a taxonomic revision of the subfamilies Desmodorinae and Spiriniinae. We provide: (1) emended diagnoses of the family and subfamilies, (2) comparative descriptions of the morphology of the species, with emphasis on the new findings arisen from our observations with interference light microscope (LM) and scanning electronic microscope (SEM), (3) an outline of the proposed taxonomic changes, (4) lists of valid genera for both subfamilies and (5) a dichotomic key to genus level for the Spiriniinae.

Material and methods

Collection and processing of samples

Nematodes were collected in the SW region of Cuban Archipelago, Punta Francés Reef (21°36'29.68'N, 83°10'34.40'W) during two sampling campaigns in July 2009 and July 2010. The collection site had conditions typical of coral reefs: salinity of 35.5, temperature of 28 °C, dissolved oxygen of 6–7 mg L⁻¹ and average depth of 2 m. Sediment samples were collected manually with plastic cores (syringes 2.6 cm diameter) from sand flats with scarce vegetation and seagrass meadows of *Thalassia testudinum* Banks ex König.

In the field, samples were sieved over a 45 µm mesh and preserved in 96 % ethanol until processing in the laboratory. Nematodes were extracted from the samples, left for 36 hours in a mixture of ethanol and glycerin within an incubator at 35 °C and afterwards mounted on glass slides following the procedure proposed by Vincx (1996).

Identification and morphological description

Measurements and drawings of specimens were done using a light microscope (LM) Leica DM2500 with interference contrast and drawing tube attachment. LM images were taken with a Color View digital camera coupled to a microscope Olympus BX41 with interference contrast and using the software Olympus cell^D. High magnification images were taken with a scanning electronic microscope (SEM) FEI Quanta 200, specimens used for SEM could not be included in LM observations.

The species identification was based on the taxonomic literature and on the database NeMys that recently migrated to the World Register of Marine Species (<http://www.marinespecies.org>). The invaluable checklist by Gerlach & Riemann (1973) has been used to double check for nomenclature and authorship issues.

For each species, we measured ten specimens per gender (i.e., male, female) and ten juveniles. Twelve morphometric variables were measured or calculated (Tables 1 and 2). We recorded other morphological characters that are valuable for species differentiation within the Desmodoridae such as cuticle striation, head capsule, relative position of cephalic sensilla, additional subcephalic setae, somatic setal pattern, shape and position of the amphidial fovea, buccal armature, pharynx structure, pre- and post-cloacal supplements and tail shape. This study includes only known species and therefore we offer a condensed description of the species, highlighting only those features that are new (e.g., body measures) or important for the taxonomy of the species.

The type material was revised, based on LM photographs of the type specimens of *Paradesmodora sinuosa* Ott, 1972 and *P. toreutes* Wieser & Hopper, 1967. Microscopic pictures were taken by the curators of the collections at the Smithsonian National Museum of Natural History (Washington, D.C.) and Canadian National Collection of Nematodes, respectively, since type material is no longer sent by mail to avoid loss or damage of type specimens.

List of abbreviations

af	=	amphidial fovea
bcc	=	border of head capsule
blr	=	border of lip region
cl	=	cloacal opening
cs	=	cephalic setae
ils	=	inner labial sensilla
ols	=	outer labial sensilla
ps	=	precloacal supplement
scs	=	subcephalic setae
sp	=	spinneret
ss	=	somatic setae (in Fig. 3 lss = large somatic setae, sss = short somatic setae)
str	=	cuticle striation
tb	=	tail bent (curvature)
tp	=	tail punctations
va	=	vulva

Results

The results have been structured in the following order: hierarchy and diagnosis of the family, diagnoses and species descriptions for subfamilies Desmodorinae and Spiriniinae, taxa proposed as inquirendae, taxa with new classification, list of valid genera for both treated subfamilies, and identification key to genera within Spiriniinae.

Phylum Nematoda Cobb, 1932
Class Chromadorea Inglis, 1983
Subclass Chromadoria Adamson, 1987
Order Desmodorida de Coninck, 1965
Suborder Desmodorina de Coninck, 1965
Superfamily Desmodoroidea Filipjev, 1922

Family **Desmodoridae** Filipjev, 1922

Type genus

Desmodora de Man, 1889 (syn. *Mastodex* Steiner, 1921: 25).

Diagnosis (emended from Decraemer & Smol 2006)

Amphidial fovea spiral, variable (mostly in Stilbonematinae). Pharynx with muscular posterior bulb except in Stilbonematinae with a tripartite pharynx with marked anterior procorpus, narrower isthmus and posterior bulb. Tail conical (rarely conical-cylindrical, only in *Perspiria* and *Spirodesma* Cavalcanti *et al.*, 2009). Gubernaculum mostly with apophysis dorsally oriented (rarely with dorso-caudal orientation, only in *Adelphos* Ott, 1997, *Catanema* Cobb, 1920, *Parabotrachus* Tchesunov, Ingels & Popova, 2012 and *Robbea* Gerlach, 1956).

There are three changes hereby proposed to the diagnosis by Decraemer and Smol (2006). First, the variable shape of the amphidial fovea (i.e., one to two turns) also at subfamily level, e.g., the mostly cryptospiral amphidial fovea in Desmodorinae and Spiriniinae can be a spiral of 1–2 turns in Stilbonematinae (*Eubotrachus* Greeff, 1869, *Laxus*) or a shepherd's crook (*Leptonemella* Cobb, 1920) or reduced to the aperture of the *canalis amphidialis* (*Stilbonema* Cobb, 1920). Second, the exception of conical-cylindrical tail to include the genera *Perspiria* and *Spirodesma*. Third, the correction of

apophysis orientation, which is mostly dorsally oriented except in four genera of Stilbonematinae (*Adelphos*, *Catanema*, *Parabotrachus* and *Robbea*). The scarcity of diagnostic features and the number of exceptions reflexes the morphological diversity of this family.

Subfamily **Desmodorinae** Micoletzky, 1924

Type genus

Desmodora de Man, 1889 (syn. *Mastodex* Steiner, 1921: 25).

Diagnosis [emended from Decraemer & Smol (2006) and Verschelde *et al.* (2006)]

Head capsule conspicuous, characterized by the thickened cuticle and mostly with an external demarcation between labial and cephalic regions, except in *Sibayinema* Swart & Heyns, 1991 (Verschelde *et al.* 2006). Amphidial fovea not surrounded by cuticle striations (but the posterior border of the fovea may contact the first annuli). Buccal cavity always with distinct teeth. Cuticle usually coarsely striated.

The diagnosis proposed by Verschelde *et al.* (2006) was expanded to include other features (e.g., demarcation between labial and cephalic region, buccal cavity) and we extended the presence of body coarse annuli as diagnostic feature for the subfamily. The modifications to the diagnosis by Decraemer and Smol (2006) were mainly the addition of the external demarcation as diagnostic feature and the deletion of the pharyngeal bulb that is a diagnostic feature to family level.

Genus *Acanthopharynx* Marion, 1870

Acanthopharynx denticulatus Wieser, 1954

Figs 1A–D, 2, Table 1

Acanthopharynx denticulatus Wieser, 1954: 36.

Material examined

10 ♂♂, 10 ♀♀ and 10 juveniles, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

Description

Cuticle strongly striated in the anterior part (annuli width ~ 1 µm) becoming finer at mid-body. Head capsule well developed. Six inner and six outer labial setae, both sets papilliform. Four cephalic setiform sensilla 4–8 µm long. Two circles of 10–12 subcephalic setae, 6–8 µm long and very close to each other. One pair of sublateral setae 4–6 µm long at level of amphidial fovea. Amphidial fovea cryptospiral located in the head capsule and not surrounded by cuticle striations. Eight longitudinal rows of short somatic setae (< 5 µm) running along the anterior body region, continuing as six longitudinal rows at mid-body and four rows on the tail. Buccal cavity with 12 cheilorhabdia, one large dorsal tooth and two smaller ventrosublateral teeth, a transverse row of 7–10 minute denticles at level of tip dorsal tooth. Pharynx meandering with posterior widened bulb marked by several plasmatic interruptions, internal lining well sclerotized. Cardia not conspicuous. Secretory-excretory system not observable. End portion of tail smooth, showing a characteristic ventral bend; spinneret well developed.

Male monorchic, the anterior testis to the right of the intestine. Spicules strongly bent, with capitulum, gubernaculum a straight rod oriented dorsally. Preloacal ventromedian supplements (13–16) visible as small pits located on a cuticular ridge.

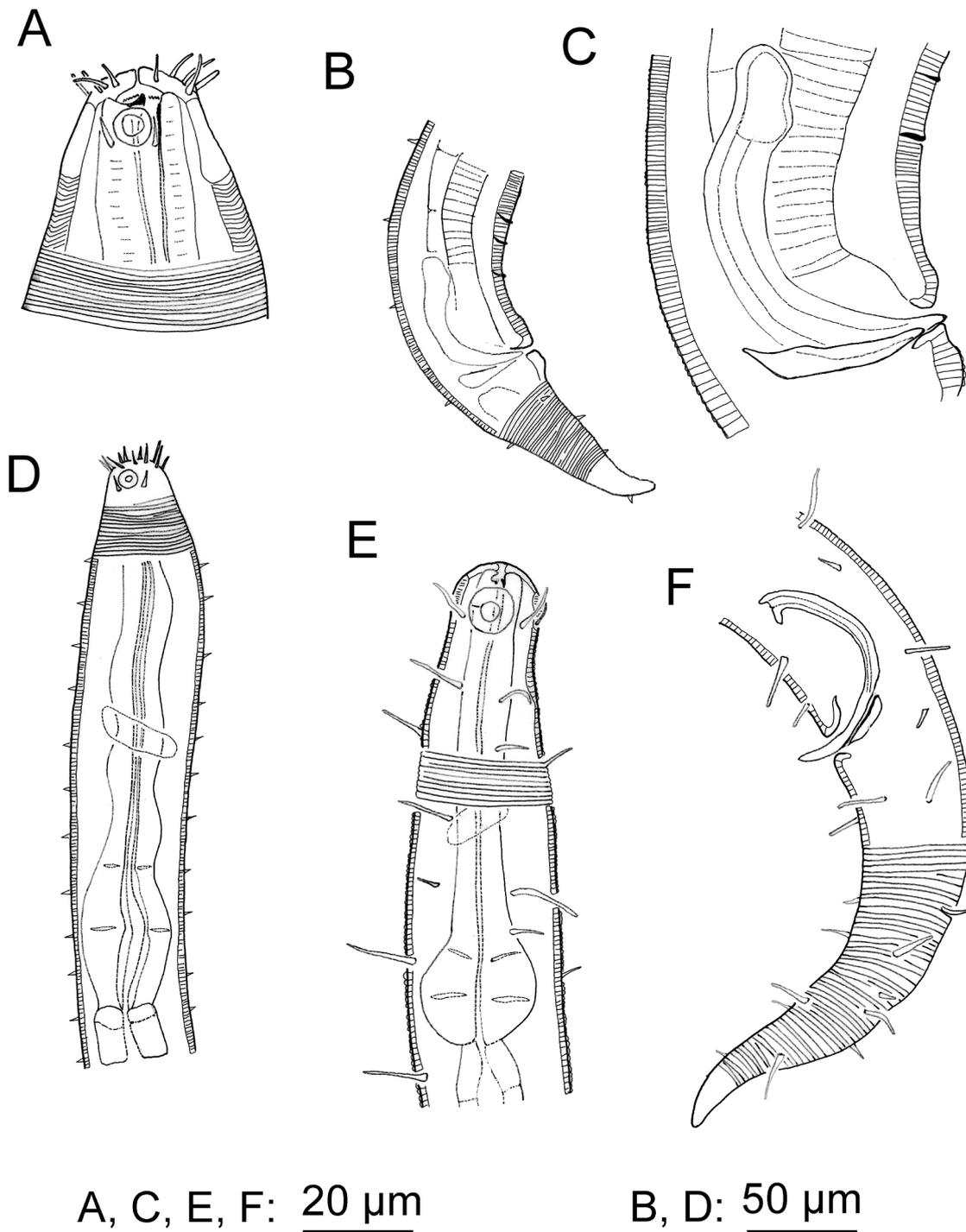


Fig. 1. A–D. *Acanthopharynx denticulatus* Wieser, 1954, ♂. A. Head region. B. Tail region. C. Copulatory apparatus. D. Neck region. E–F. *Bolbonema brevicolle* Cobb, 1920, ♂. E. Neck region. F. Posterior region with tail end in surface view.

Female didelphic, ovaries antidromously reflexed, anterior genital branch to the right of the intestine, posterior genital branch to the left.

Juveniles are similar to adults except for the development of the reproductive system.

Remarks

At present, the genus *Acanthopharynx* Marion, 1870 includes 11 valid species. A dichotomous key to eight of the species was published by Wieser (1954). At least two species, *A. brachycapitata* Allgén,

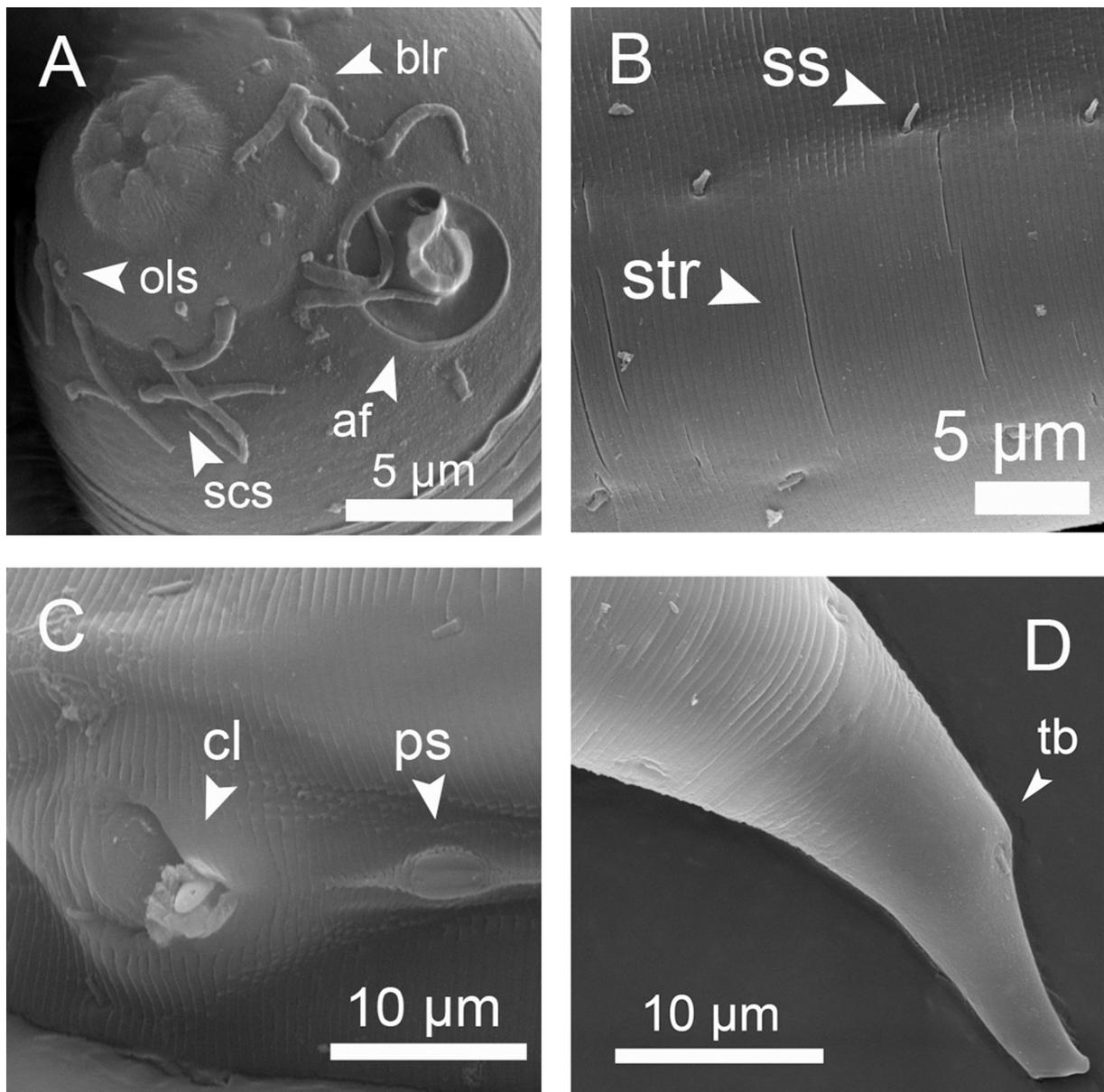


Fig. 2. *Acanthopharynx denticulatus* Wieser, 1954, SEM microphotographs of ♂. **A.** Head oblique *en face* view. **B.** Cuticle striation at mid-body. **C.** Cloacal region, from a different ♂ specimen than A, B and D. **D.** Tail tip, showing ventral bent.

1947 (Allgén 1947: 148) and *A. similis* Allgén, 1932, have to be regarded as *species inquirendae* due to their poor description. The differences among the *Acanthopharynx* species are subtle and consequently their identification is quite difficult. The features with diagnostic values are the relative size and shape of amphidial fovea, number of subcephalic setae, presence/absence of denticles, de Man ratio a, number of precloacal supplements and length of spicules and gubernaculum. For instance, *A. denticulatus* differs from *A. rigida* Schuurmans Stekhoven, 1950 only in the presence of a row of tiny denticles that are not easy to observe. The specimens of *A. denticulatus* described in this work fit the original description by Wieser (1954) apart from a larger body length of type specimens (male: 2170–2780 µm, female: 2600 µm) vs ours (male: 1234–1745 µm, female: 1299–1796 µm). However, we regard these differences as intraspecific variation among populations.

Genus *Bolbonema* Cobb, 1920

Bolbonema brevicolle Cobb, 1920

Figs 1E–F, 3, Table 1

Bolbonema brevicolle Cobb, 1920: 264.

Desmodora (Bolbonema) brevicolle – Gerlach 1963: 90.

Material examined

6 ♂♂, 7 ♀♀ and 1 juvenile, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

Description

Cuticle annulated in the anterior region (annuli 0.6–0.8 µm width) becoming finely striated at mid-body (0.2–0.3 µm). Head capsule well developed, surface appearing with a fingerprint pattern by LM, SEM microphotographs suggest some depressions in the surface. Six inner and six outer labial sensilla papilliform. Four cephalic sensilla (10–13 µm long) at the base of the head capsule, four subcephalic setae (6–8 µm long) next to the cephalic ones. Amphidial fovea cryptospiral, relatively large, posterior border is in contact with cuticle striations. Eight longitudinal rows of somatic setae running from cervical region to level of anus; long setae (18–22 µm long) alternate with two shorter setae (~ 4 µm long). Buccal cavity small, with one small dorsal tooth and two ventrosublateral denticles, not always visible. Pharynx muscular with well-developed posterior bulb and plasmatic interruptions. Cardia and excretory-secretory system not observable. Tail region with only four longitudinal rows of setae.

Male monorchic; anterior testis to the right of the intestine. Spicule capitulum with a characteristic ventral process. No precloacal supplements.

Female didelphic, ovaries antidromously reflexed and both genital branches to the right of the intestine. Vulva a simple transversal slit-like aperture.

Juveniles are similar to adults except for the development of the reproductive system.

Remarks

Our specimens largely agree with the original description of this species by Cobb (1920) and redescriptions by Gerlach (1963) and Pastor de Ward (1988). The single clear difference in our specimens is the presence of four subcephalic setae in subdorsal and subventral positions slightly smaller than the four cephalic sensilla and inserted closely to the latter (Fig. 3B). These setae were clearly visible with SEM and could have been overlooked by mentioned authors in LM; actually, we could not see them clearly in

all specimens. The body length shows some variation for the different populations with a considerably smaller female (737 μm) described by Gerlach (1963), and larger specimens described by Pastor de Ward (1988) (range: 1550–1950 μm). The range of body length of our specimens is more in agreement with the type specimens (males: 1051–1372 μm , females: 942–1387 μm) and it is closer to the holotype described by Cobb (1920) (female: \sim 1300 μm). The cuticle heterogeneity in annulation is quite marked in *B. brevicolle* with the anterior annuli being rings three-fold wider than the striation in the posterior region; however, this feature has not been mentioned in previous descriptions.

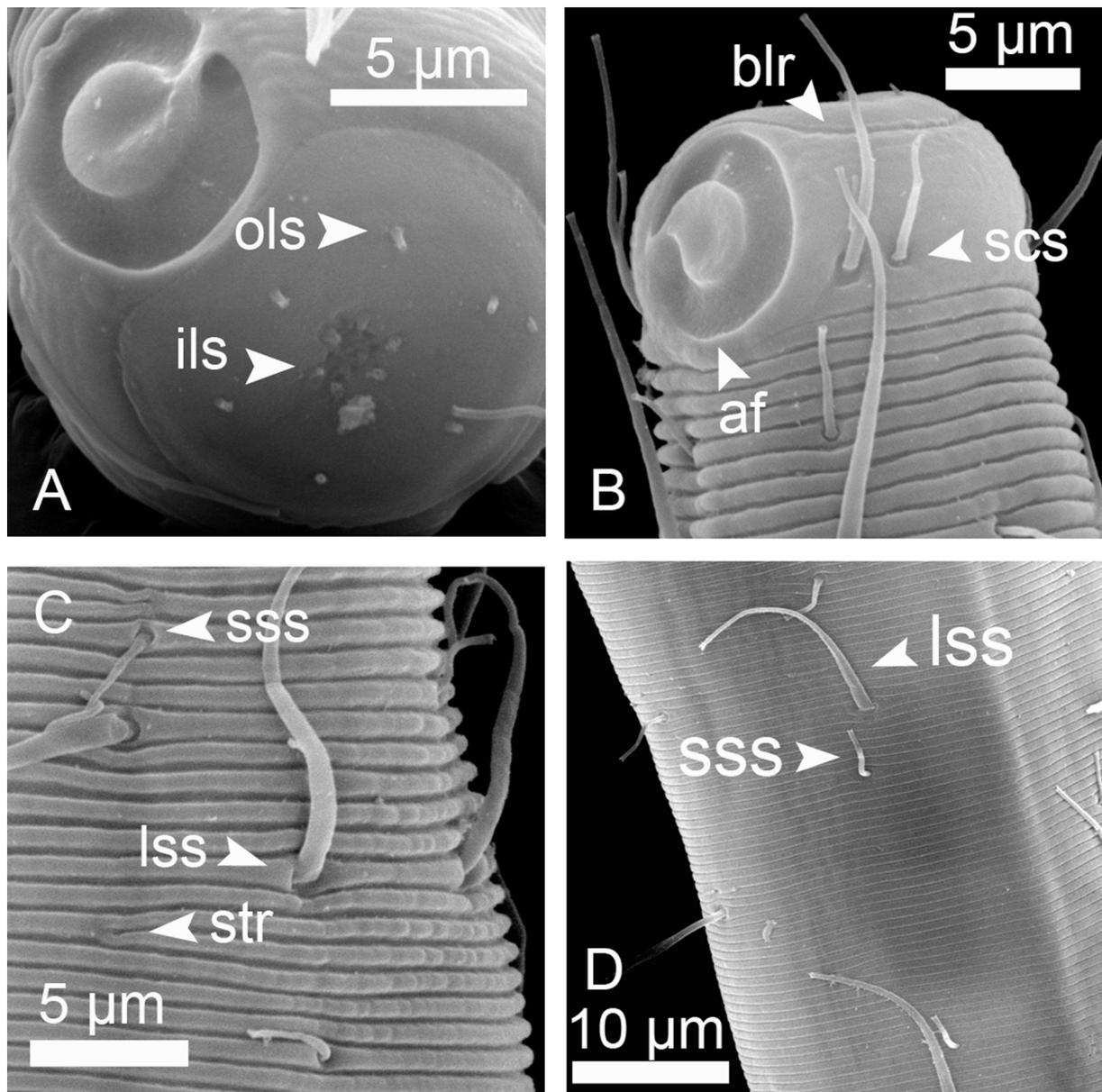


Fig. 3. *Bolbonema brevicolle* Cobb, 1920, SEM microphotographs of ♂ (A) and ♀ (B, C & D). A. Head in oblique *en face* view. B. Head in oblique lateral view. C. Cuticle striation at anterior region. D. Cuticle striation at mid-body region.

Table 1. Mean (range) of morphological measures for five nematode species of the subfamily Desmodorinae from the Punta Francés coral reef, Cuba. N = number of specimens, J = juvenile. For each variable the first row corresponds to males, the second to females and the third to juveniles. Abbreviations: a.b.d. = anal body diameter; Amp. Fovea c.b.d. = relation of amphidial fovea diameter to corresponding body diameter; de Man ratios are the relation of body length to body diameter (a), to pharynx length (b) and to tail length (c) respectively; c' = relation of tail length to anal body diameter, V % = distance (relative to body length) of vulva to anterior end.

Species/Variable	<i>Acanthopharynx denticulatus</i>	<i>Bolbonema brevicolle</i>	<i>Croconema cinctum</i>	<i>Desmodora pontica</i>	<i>Zalonema ditlevseni</i>
N	10 ♂♂, 10 ♀♀, 10 J	6 ♂♂, 7 ♀♀, 1 J	10 ♂♂, 9 ♀♀, 10 J	10 ♂♂, 10 ♀♀, 11 J	10 ♂♂, 10 ♀♀, 10 J
Body length (µm)	1533 (1234–1745) 1487 (1299–1796) 1084 (847–1387)	1157 (1051–1372) 1143 (942–1387) 869	2016 (1528–2475) 2237 (1270–2781) 972 (518–2095)	1320 (1037–1555) 1288 (1029–1431) 1016 (613–1438)	1201 (847–2022) 1088 (898–1380) 807 (402–1329)
de Man ratio a	28 (24–43) 27 (21–37) 27 (21–39)	33 (30–39) 30 (24–37) 32	34 (23–64) 30 (23–60) 23 (16–36)	31 (25–36) 24 (18–28) 26 (18–32)	22 (17–28) 26 (20–32) 20 (16–26)
de Man ratio b	6 (5–7) 6 (5–6) 6 (5–7)	14 (12–16) 14 (13–16) 13	12 (9–19) 12 (9–20) 8 (5–13)	9 (8–10) 10 (7–17) 9 (5–10)	8 (7–10) 8 (7–10) 7 (5–9)
de Man ratio c	19 (16–21) 18 (16–21) 14 (11–16)	13 (12–14) 14 (13–15) 12	19 (13–27) 25 (18–37) 11 (7–20)	16 (13–19) 15 (13–18) 14 (9–21)	14 (10–21) 11 (5–14) 10 (6–16)
Amp. fovea c.b.d. (%)	31 (25–34) 31 (27–34) 30 (24–35)	53 (48–57) 50 (44–60) 42	16 (15–17) 20 (14–35) 21 (16–26)	33 (26–43) 31 (26–35) 31 (26–38)	30 (23–36) 35 (27–40) 32 (28–40)
Pharynx length (µm)	262 (220–284) 253 (214–286) 189 (153–240)	88 (74–95) 81 (73–88) 69	175 (106–213) 187 (130–219) 124 (89–186)	143 (111–158) 144 (116–176) 116 (88–151)	150 (127–200) 137 (116–160) 118 (74–158)
Maximum body ø (µm)	53 (38–66) 56 (42–71) 42 (31–60)	35 (32–39) 40 (27–48) 27	64 (31–78) 85 (44–103) 40 (30–62)	43 (39–53) 55 (44–80) 40 (32–71)	55 (45–86) 43 (37–48) 41 (22–64)
Tail length (µm)	83 (78–86) 83 (77–90) 79 (67–87)	93 (87–97) 84 (71–93) 70	107 (75–123) 91 (70–110) 86 (60–106)	81 (71–90) 83 (70–93) 75 (64–93)	84 (76–110) 97 (85–109) 80 (61–94)
Tail length c'	2.0 (1.6–2.2) 2.9 (2.6–3.1) 3.1 (2.3–3.8)	3.9 (3.3–4.1) 4.4 (4.0–4.8) 4.1	2.3 (2.0–2.8) 2.3 (1.7–2.8) 3.3 (1.9–4.3)	2.3 (2.0–2.8) 3.0 (1.8–3.9) 3.0 (2.2–3.8)	2.5 (1.7–3.1) 4.1 (3.5–4.6) 3.2 (2.2–4.6)
V %	53 (49–59)	49 (46–53)	58 (48–60)	63 (51–74)	48 (46–51)
Spiculum length (µm)	71 (64–81)	42 (39–48)	83 (47–113)	61 (50–69)	51 (41–84)
Gubernaculum length (µm)	30(25–34)	13 (11–15)	23 (16–29)	26 (18–32)	21 (14–27)

Genus *Croconema* Cobb, 1920

Croconema cinctum Cobb, 1920

Figs 4, 5, Table 1

Croconema cinctum Cobb, 1920: 332.

Desmodora (Croconema) cincta – Gerlach, 1963: 87.

Material examined

10 ♂♂, 9 ♀♀ and 10 juveniles, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

Description

Cuticle coarsely striated (annuli ~ 2 µm width). Head capsule well-developed and relatively extended longitudinally. Inner labial sensilla papilliform. Outer labial sensilla setiform papillae and minute (1–2 µm

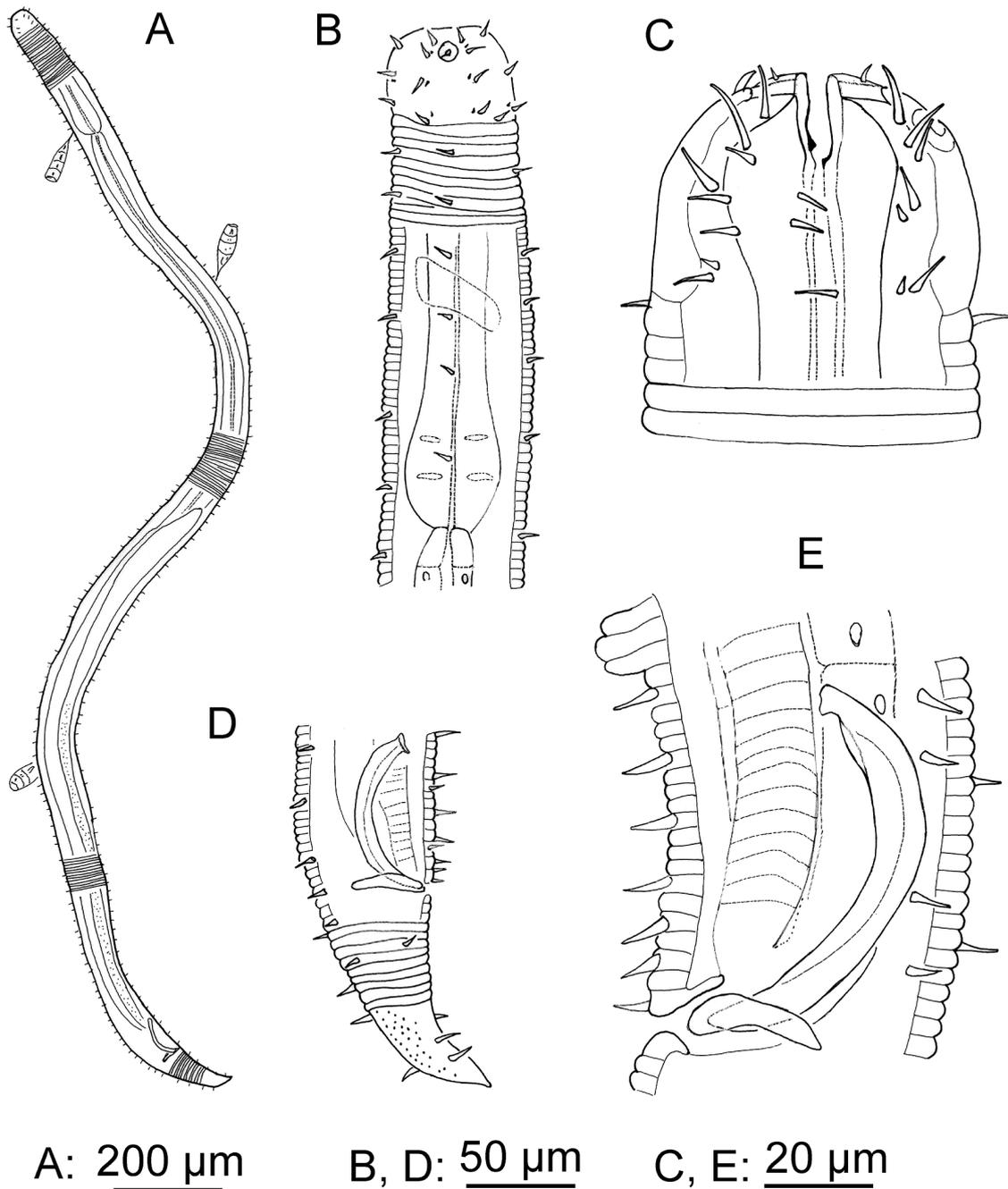


Fig. 4. *Croconema cinctum* Cobb, 1920, ♂ specimen 1 (A, B & D) and specimen 2 (C & E). A. Habitus. B. Neck region. C. Head. D. Tail region. E. Copulatory apparatus.

long). Four cephalic setiform sensilla (5–10 μm long); three circlets of eight subcephalic setae (5–10 μm long) on the head capsule: the first circle very close to cephalic sensilla, the second circle posterior to the amphidial fovea and the third circle close to the posterior border of the capsule. Amphidial fovea cryptospiral, relatively small and located ahead in the capsule. Eight longitudinal rows of short somatic setae (4–5 μm long) running along body length, at the posterior region continuing as six rows. Buccal cavity narrow, elongate, with one dorsal tooth and two minute ventrosublateral teeth. Pharynx muscular with posterior bulb. Cardia extended. Secretory-excretory system not observable. Tail non-striated in the last third, conspicuously punctuated and with few scattered subterminal setae (2–3 μm long).

Male monorchic, anterior testis to the right of the intestine. Spicule curved, slightly cephalated, gubernaculum a narrow cuticularized rod. Two ventromedian precloacal supplements formed by the

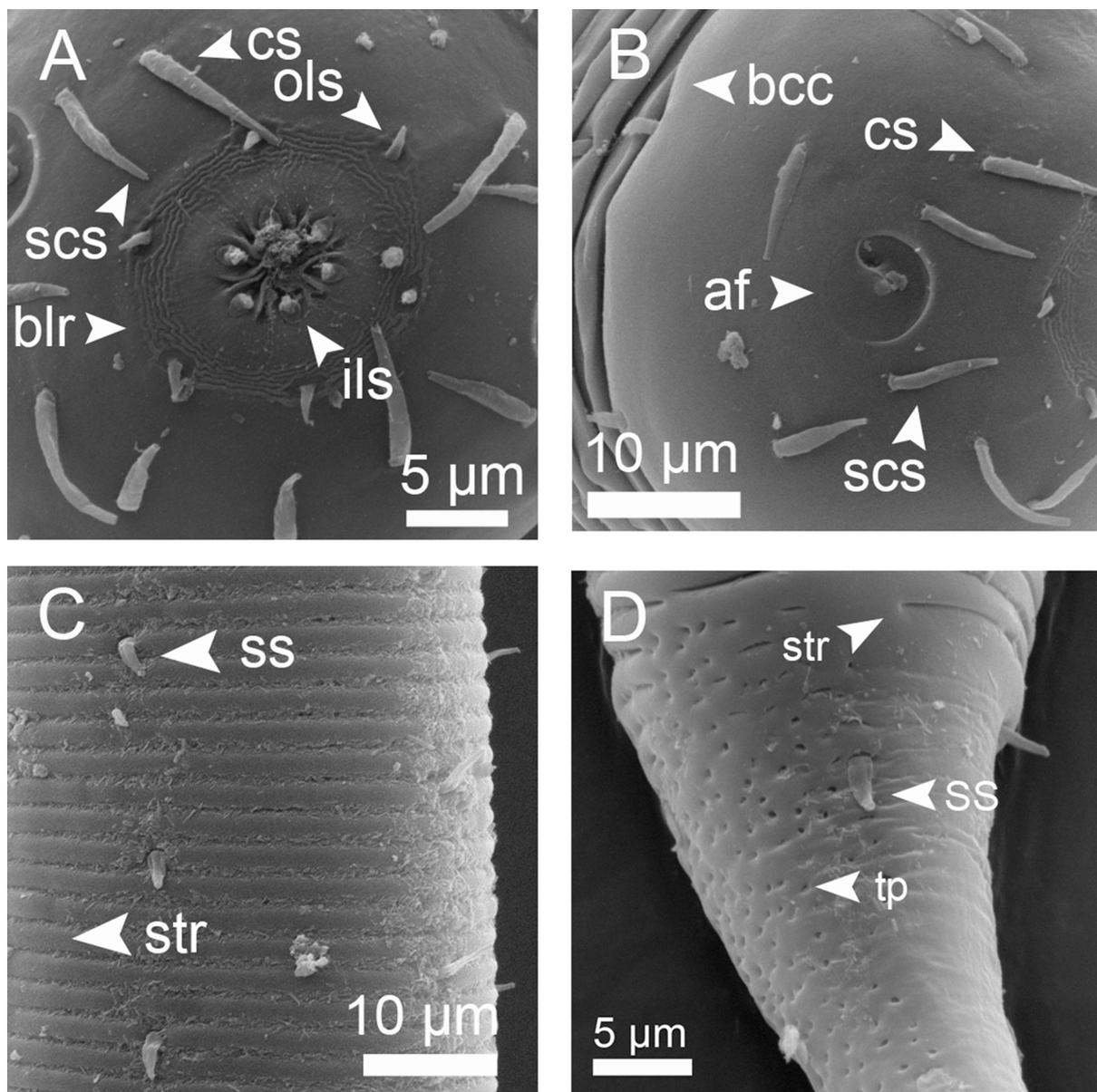


Fig. 5. *Croconema cinctum* Cobb, 1920, SEM microphotographs of ♂ specimen 1 (A, B & D) and specimen 2 (C). **A.** Labial region, *en face* view. **B.** Head capsule, lateral view. **C.** Cuticle striation at mid-body region. **D.** Part of tail tip.

enlargement/protrusion of three consecutive annuli (mid one larger than others) (only one supplement is depicted in Fig. 4E).

Female didelphic, ovaries antidromously reflexed, anterior genital branch to the left, posterior to the right, vulva a transversal slit.

Juveniles. Juveniles are similar to adults except for the development of the reproductive system.

Remarks

Verschelde *et al.* (2006) proposed a dichotomous key and a table with diagnostic features for the genus *Croconema*. Cuban specimens are quite similar to the holotype described by Cobb (1920) and to those described from the Maldives (Gerlach 1963) and the Red Sea (Gerlach 1964). We noted in some specimens the presence of additional smaller setae at the base of the subcephalic setae (Fig. 4B–C), but we could not reveal more evidence to allow identification with another *Croconema* species.

Genus *Desmodora* de Man, 1889

Desmodora pontica Filipjev, 1922
Figs 6A–B, 7, Table 1

Desmodora pontica Filipjev, 1922: 119.

Desmodora (Pseudochromadora) pontica – Gerlach 1963: 84.

Material examined

10 ♂♂, 10 ♀♀ and 11 juveniles, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

Description

Cuticle coarsely striated (annuli ~ 2 µm width) in the anterior region but finer at mid-body region (annuli ~ 1 µm width). Strong head capsule with labial region clearly marked by a suture. Inner labial setae papilliform. Outer labial sensilla relatively long (2–3 µm long). Four cephalic setae (4–8 µm long); one circle of four subcephalic setae (4–8 µm long) posterior to the amphidial fovea. Amphidial fovea cryptospiral. Eight longitudinal rows of short somatic setae (2–4 µm long) running along the entire body length, continuing as four rows on the tail region. Buccal cavity narrow, elongate, with one dorsal tooth and two minute ventrosublateral teeth at the same level. Pharynx muscular with posterior bulb and plasmatic interruptions, internal lining well sclerotized. Cardia extended. Secretory-excretory system not observable. Posterior half of tail conspicuously punctuated and without striation.

Male monorchic, anterior testis to the left of the intestine. Spicule strongly curved and cephalated. Gubernaculum a narrow rod. No supplements.

Female didelphic, ovaries antidromously reflexed, both genital branches to the right of the intestine. Vulva a transversal slit.

Juveniles are similar to adults, except for the development of the reproductive system.

Remarks

Suctorians (Ciliophora) are common commensals on *D. pontica*. The genus *Desmodora* de Man, 1889 is speciose, with a complicated taxonomy. It has included several subgenera later raised to genus level

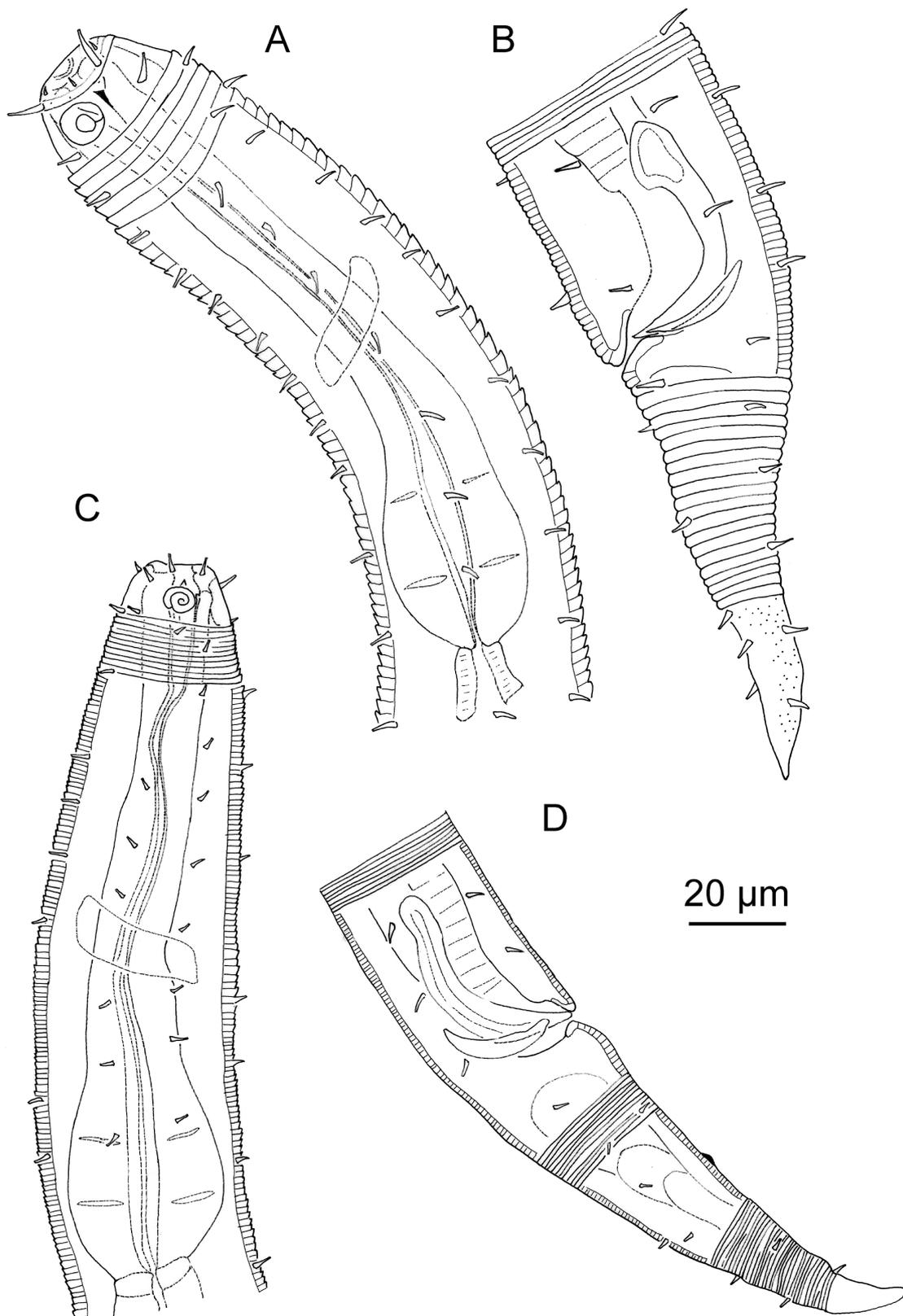


Fig. 6. A–B. *Desmodora pontica* Filipjev, 1922, ♂. A. Anterior region. B. Tail region, partim in surface view and copulatory apparatus. C–D. *Zalonema ditlevseni* (Micoletzky, 1922), ♂. C. Anterior region. D. Tail region and copulatory apparatus.

by Verschelde *et al.* (1998) (e.g., *Croconema*, *Pseudochromadora* and *Zalonema*) and a plethora of bad descriptions and doubtful species. The most comprehensive study about *Desmodora* has been made by Verschelde *et al.* (1998) and an outdated dichotomous key was provided by Wieser (1954). Our specimens resemble the descriptions of *D. pontica* by Schuurmans Stekhoven (1950) and Gerlach (1952). The female specimen depicted and described by Boucher (1975) as *D. pontica* differs in two important features: outer labial sensilla are considerable longer (i.e., as long as the cephalic setae) and the posterior border of the head capsule reaches the first cuticle annuli. Based on our material, males seem to have amphidial fovea well in the central part of the head capsule (i.e., no contact with the striation) and juveniles and females tend to have amphidial fovea posterior on the capsule (i.e., touching the first annuli).

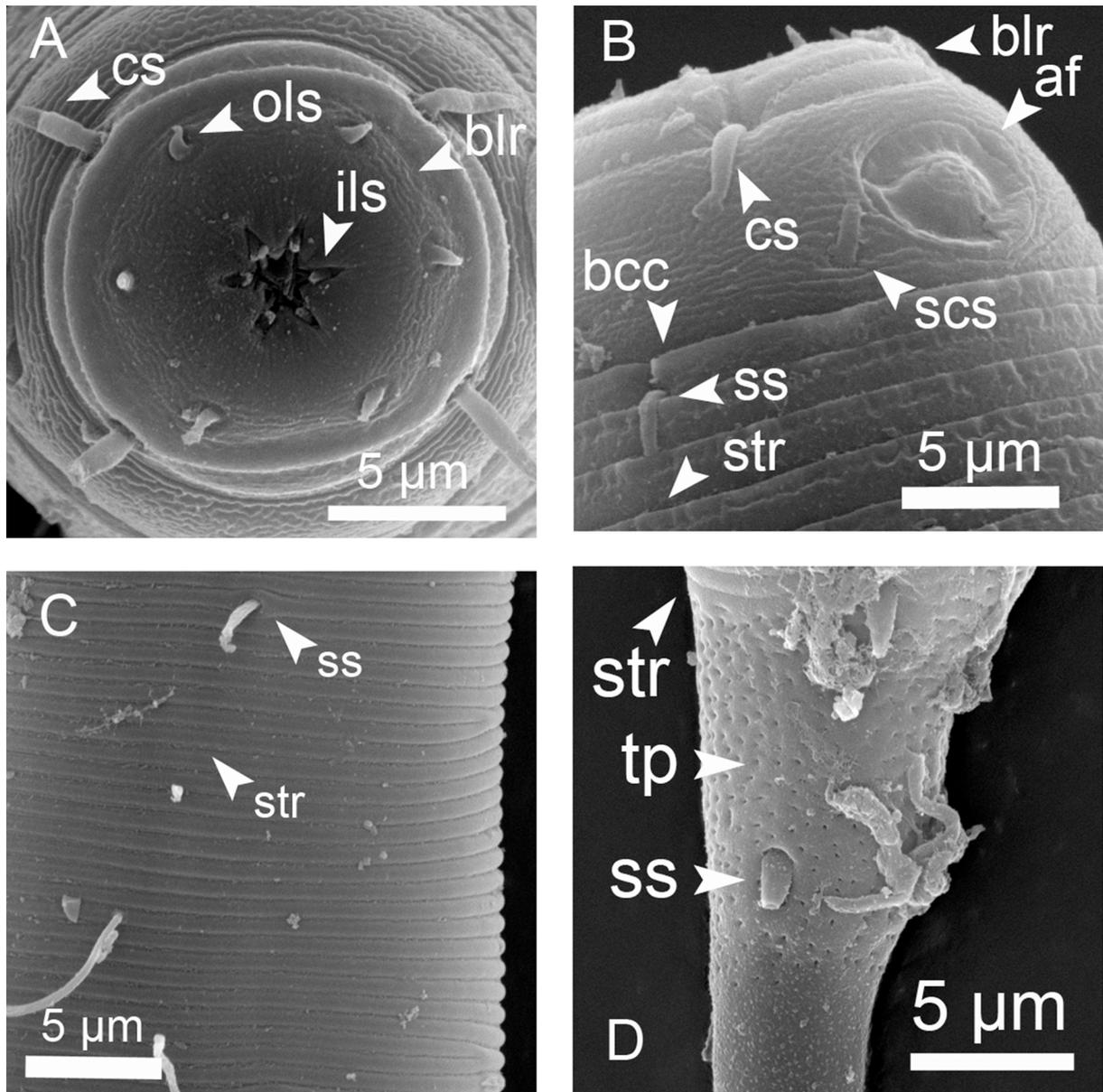


Fig. 7. *Desmodora pontica* Filipjev, 1922, SEM microphotographs of ♂ specimen 1 (A & C) and specimen 2 (B & D). **A.** *En face* view. **B.** Head, oblique lateral view **C.** Cuticle striation at mid-body region. **D.** Part of tail tip.

Genus *Zalonema* Cobb, 1920

Zalonema ditlevseni (Micoletzky, 1922)

Figs 6C–D, 8, Table 1

Heterodesmodora ditlevseni Micoletzky, 1922: 89.

Desmodora ocellata Wieser, 1954: 172.

Desmodora (Zalonema) ditlevseni – Gerlach 1963: 92.

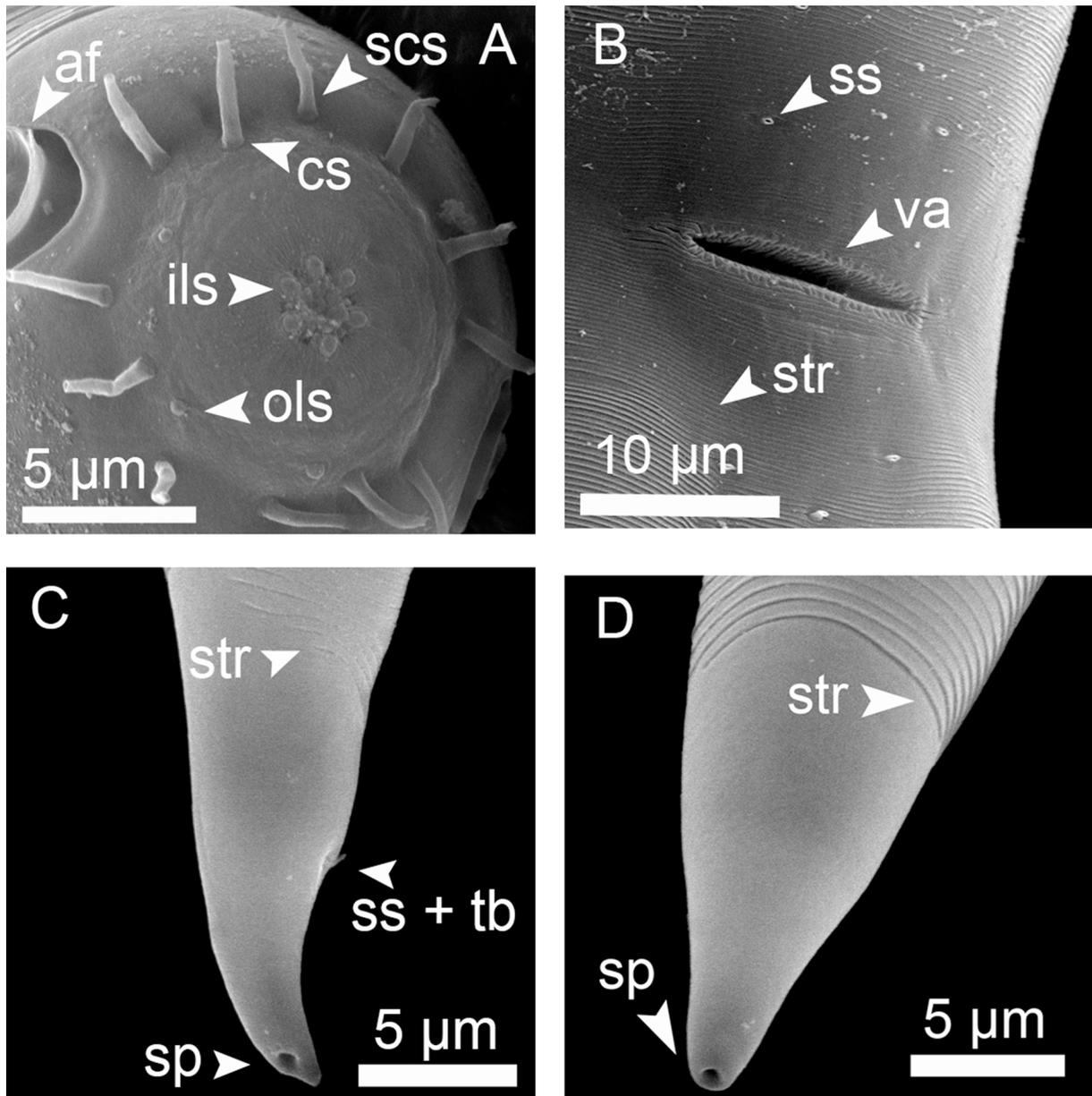


Fig. 8. *Zalonema ditlevseni* (Micoletzky, 1922), SEM microphotographs of ♂ (C) and ♀ (A, B & D). **A.** Head in oblique *en face* view. **B.** Vulva region. **C.** Tail tip of ♂, subterminal opening of caudal glands. **D.** Tail tip of ♀.

Material examined

10 ♂♂, 10 ♀♀ and 10 juveniles, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

Description

Cuticle coarsely striated in anterior body region (annuli ~ 0.6–0.8 µm width) but narrower at mid-body (annuli ~ 0.5 µm). Head capsule well-developed. Inner and outer labial sensilla setiform papillae. Four cephalic sensilla (4–6 µm long) and eight subcephalic setae (4–6 µm long) almost at the same level on the head capsule. Amphidial fovea spiral with 2.0–2.5 turns. Eight longitudinal rows of short somatic setae (~ 1–3 µm long), reduced to six rows at mid body and four rows in the posterior region. Buccal cavity with 12 cheilorhabdia, a strong dorsal tooth and two smaller ventrosublateral teeth. Pharynx muscular with posterior bulb and plasmatic interruptions, internal lining conspicuous and well-sclerotized. Cardia relatively small. Secretory-excretory system not observable. Tail conical, showing sexual dimorphism i.e., markedly bent in males and with two short subterminal setae in the tip, while more regularly conical and without subterminal setae in female.

Male monorchic, anterior testis to the right of the intestine. Spicules wide, curved, weakly cephalated. Gubernaculum a narrow rod. One or two small post-cloacal supplements in form of pits.

Female didelphic, ovaries antidromously reflexed, both genital branches to the left of intestine. Vulva a narrow transversal aperture.

Juveniles are similar to adults, except for the development of the reproductive system.

Remarks

There exist only a few detailed descriptions of *Z. ditlevseni* despite the high number of junior synonymies for this species. The body size of the single male specimen described by Gerlach (1964) lies within the range of the Cuban specimens (males: 1590 µm vs 847–2022 µm); however, the single female specimen described by Schuurmans Stekhoven (1950) is slightly outside the higher range for the Cuban specimens (female: 1420 µm vs 898–1380). The relatively wide range of morphological variation in the body length of the species possibly masks a complex of cryptic species.

Subfamily **Spiriniinae** Gerlach & Murphy, 1965

Type genus

Spirinia Gerlach, 1963 (syn. *Spira* Bastian, 1865: 159).

Diagnosis [emended from Decraemer & Smol (2006)]

Body cuticle finely striated (except the genera *Echinodesmodora* Blome, 1982, *Spirodesma* and *Stygodesmodora* Blome, 1982). Head capsule absent (i.e., cuticle not strongly thickened) and without demarcation between labial and cephalic regions. Amphidial fovea spiral located lateral and anterior on the body, its posterior border partially or completely surrounded by cuticle striations. Buccal cavity rather small, from minute to medium-sized with dorsal tooth, two smaller ventrosublateral teeth maybe present or absent.

The main modification to the diagnosis in Decraemer & Smol (2006) is the inclusion of coarse cuticle as exception in order to accommodate the transferred genera *Echinodesmodora*, *Spirodesma* and *Stygodesmodora*. We also acknowledge the absence of a head capsule.

Genus *Chromaspirina* Filipjev, 1918

Chromaspirina inaurita Wieser & Hopper, 1967
Figs 9A–B, 10, Table 2

Chromaspirina inaurita Wieser & Hopper, 1967: 273.

Material examined

3 ♂♂, 5 ♀♀ and 8 juveniles, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

Description

Cuticle faintly and homogeneously striated (annuli 0.8–1 µm width). Inner labial setae papilliform. Six outer labial sensilla short setiform (~ 1–3 µm long), more or less at the same level of the four cephalic sensilla (~ 8–10 µm long) and two additional setae, one ventral and one dorsal. Amphidial fovea cryptospiral located far forward in the head, only the posterior border contacts the first cuticle annuli. Eight longitudinal rows of somatic setae running along the whole body, the most anterior longer (6–8 µm) than the others (~ 1–3 µm). Buccal cavity with three small teeth, one dorsal and two ventrosublateral. Pharynx muscular with posterior bulb. Cardia extended longitudinally. Secretory-excretory system not observable. Tail conical, final portion without striation and surface smooth.

Male monorchic, anterior testis to the left of the intestine, no precloacal supplements, three postcloacal supplements like papillae (sometimes a fourth posterior smaller one). Spicules curved and slightly cephalated. Gubernaculum a simple rod with proximal end slightly widened.

Female didelphic, ovaries antidromously reflexed, both genital branches to the left of the intestine. Vulva a transversal slit.

Juveniles are similar to adults, except for the development of the reproductive system.

Remarks

Maria *et al.* (2009) made a revision of *Chromaspirina* Filipjev, 1918 and provided an illustrated key to the species. The morphology of the measured specimens closely resembles the type species described by Wieser & Hopper (1967) from Florida. However, two important differences occurred: (1) Florida specimens were smaller than the ones from Cuba (1180–1350 µm vs 2110–2592 µm) and (2) there was no evidence of sexual dimorphism in the shape and size of the amphidial fovea. The adaptation of the species to local environments seems to be the most plausible explanation for this phenotypic plasticity, but existence of a complex of cryptic species is also possible.

Genus *Paradesmodora* Schuurmans Stekhoven, 1942

Paradesmodora immersa Wieser, 1954
Fig. 9C–D, Table 2

Paradesmodora immersa Wieser, 1954: 39.

Material examined

2 ♂♂ and 4 juveniles, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

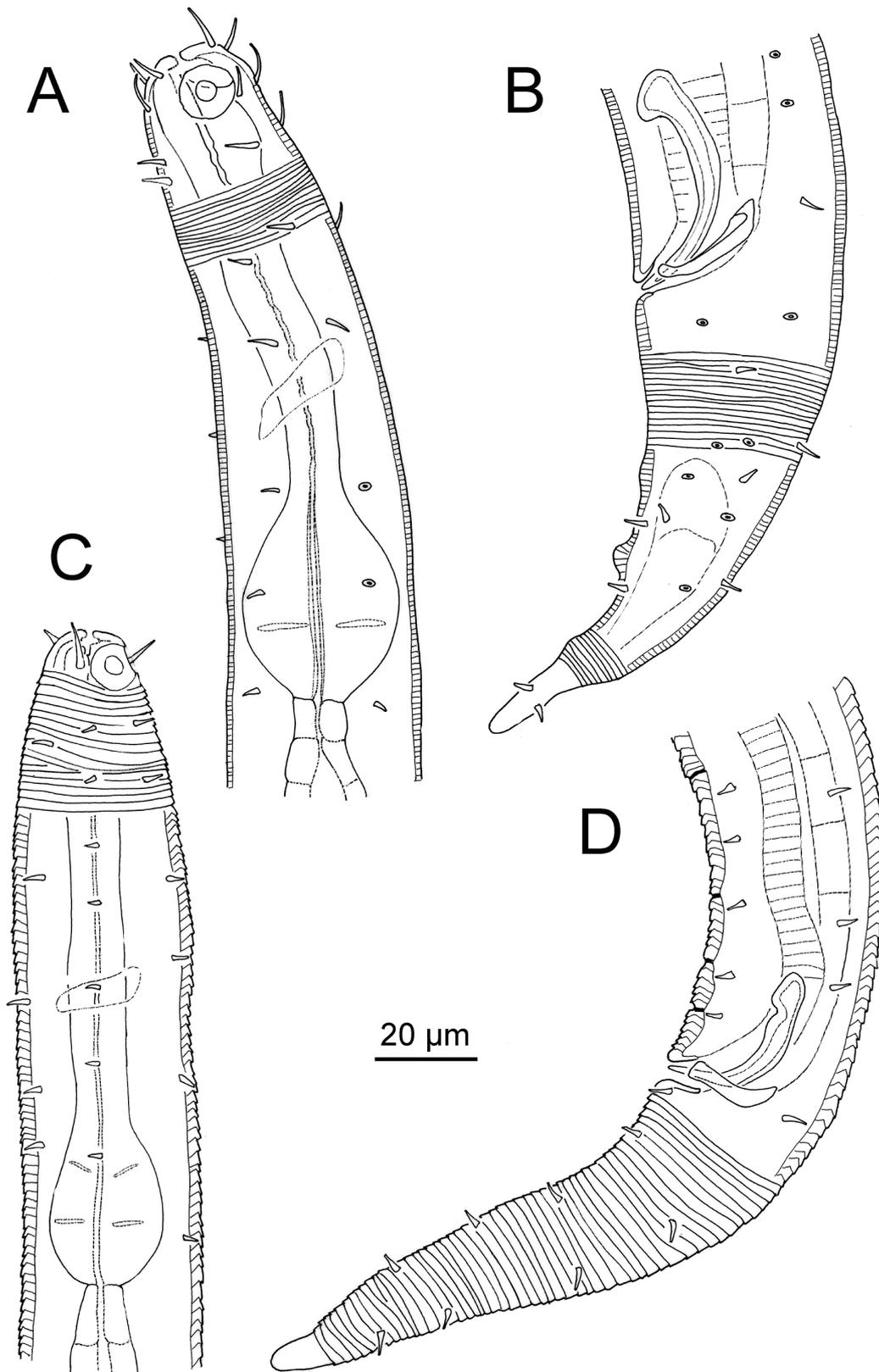


Fig. 9. A–B. *Chromaspirina inaurita* Wieser & Hopper, 1967, ♂. A. Anterior region. B. Tail region and copulatory apparatus. C–D. *Paradesmodora immersa* Wieser, 1954, ♂. C. Anterior region. D. Tail region and copulatory apparatus.

Description

Cuticle coarsely striated (annuli ~ 1 µm width). Inner and outer labial sensilla not observable. Four cephalic sensilla setiform (~ 4 µm long) at anterior level of amphidial fovea, no subcephalic setae. Amphidial fovea cryptospiral located far forward on the head. Six longitudinal rows of short somatic setae (~1–3 µm long) running along anterior and mid body region; they become in four rows on the posterior region. Buccal cavity medium-sized, one dorsal tooth, two ventrosublateral smaller teeth. Pharynx muscular with posterior bulb and plasmatic interruptions. Cardia extended. Secretory-excretory system not observable. Tail conical, last portion without striation, short setae present, spinneret present.

Male monorchic, anterior testis to the left of intestine. Spicules curved and slightly cephalated. Gubernaculum a narrow rod. Precloacal supplements (12–16) like small marks in the ventral cuticle.

Juveniles are similar to adults, except for the development of the reproductive system.

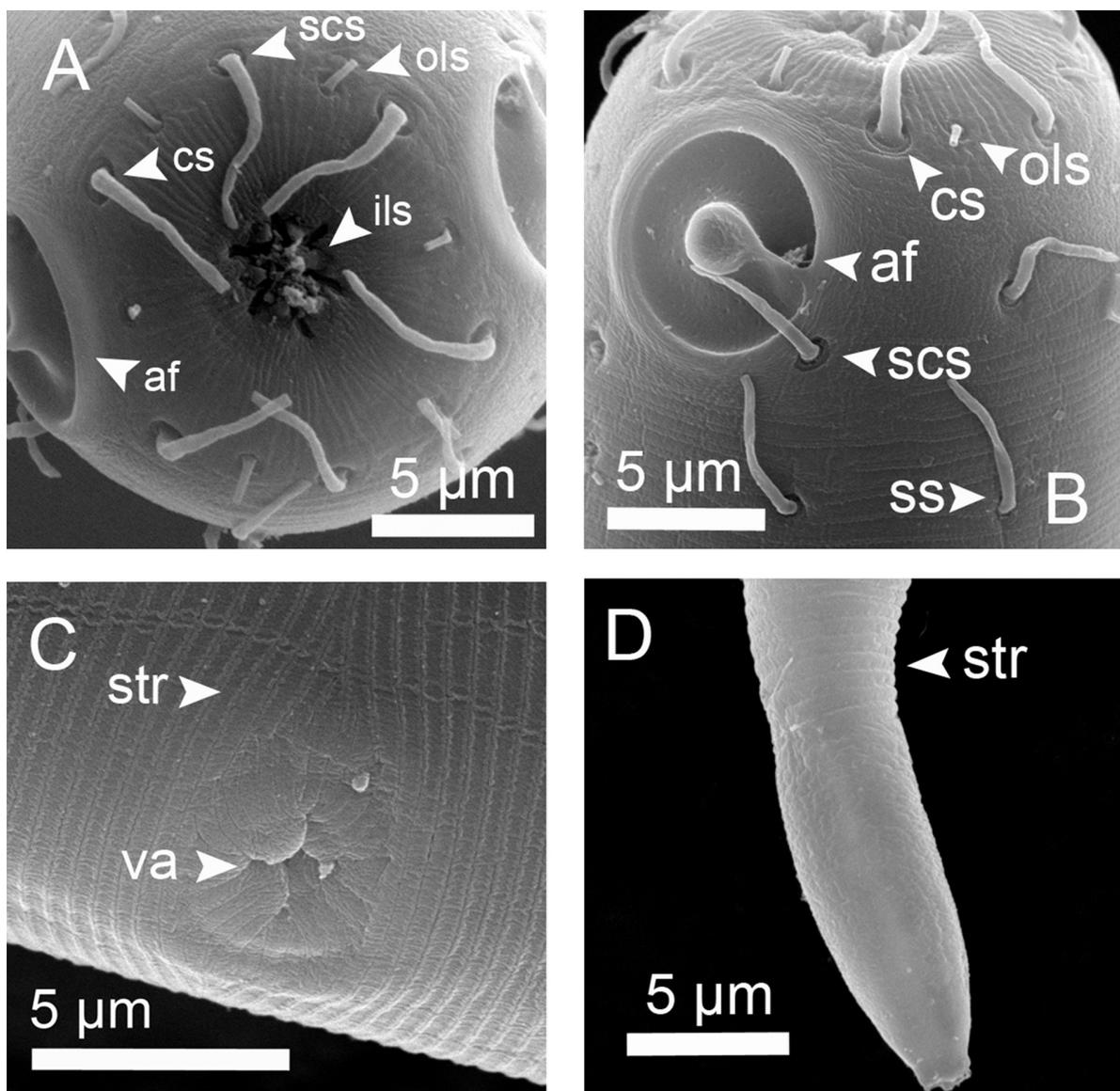


Fig. 10. *Chromaspirina inaurita* Wieser & Hopper, 1967, SEM microphotographs of ♀. **A.** Labial region, en face view. **B.** Head, oblique lateral view. **C.** Vulva region. **D.** Tail tip.

Remarks

Measured specimens resemble the holotype of *P. immersa* described by Wieser (1954); unfortunately, there are no other records of this species. Specimens in Wieser (1954) were larger (male: 2200 μm ; female: 2410 μm) than ours (males: 1424–2081 μm , no females measured). The number of precloacal supplements reported by this author is 15 and this fits the range of specimens in our study (12–16).

Paradesmodora toreutes has been collected from a nearby region (Florida). It can be clearly differentiated from *P. immersa* by: (1) the cuticular differentiation of the head (plates surrounding the amphids vs no plates); (2) the proximal end of spicule with a notch in the capitulum vs rounded shape); (3) the number of precloacal supplements (10 vs 15); and (4) longer tail in males ($c' = 6$ vs $c' = 3$).

Genus *Spirinia* Gerlach, 1963

Spirinia parasitifera (Bastian, 1865)

Figs 11, 12, Table 2

Spira parasitifera Bastian, 1865: 159.

Spiliphera oxycephala Bütschli, 1874: 47.

Spirinia nidrosiensis Allgén, 1933: 60.

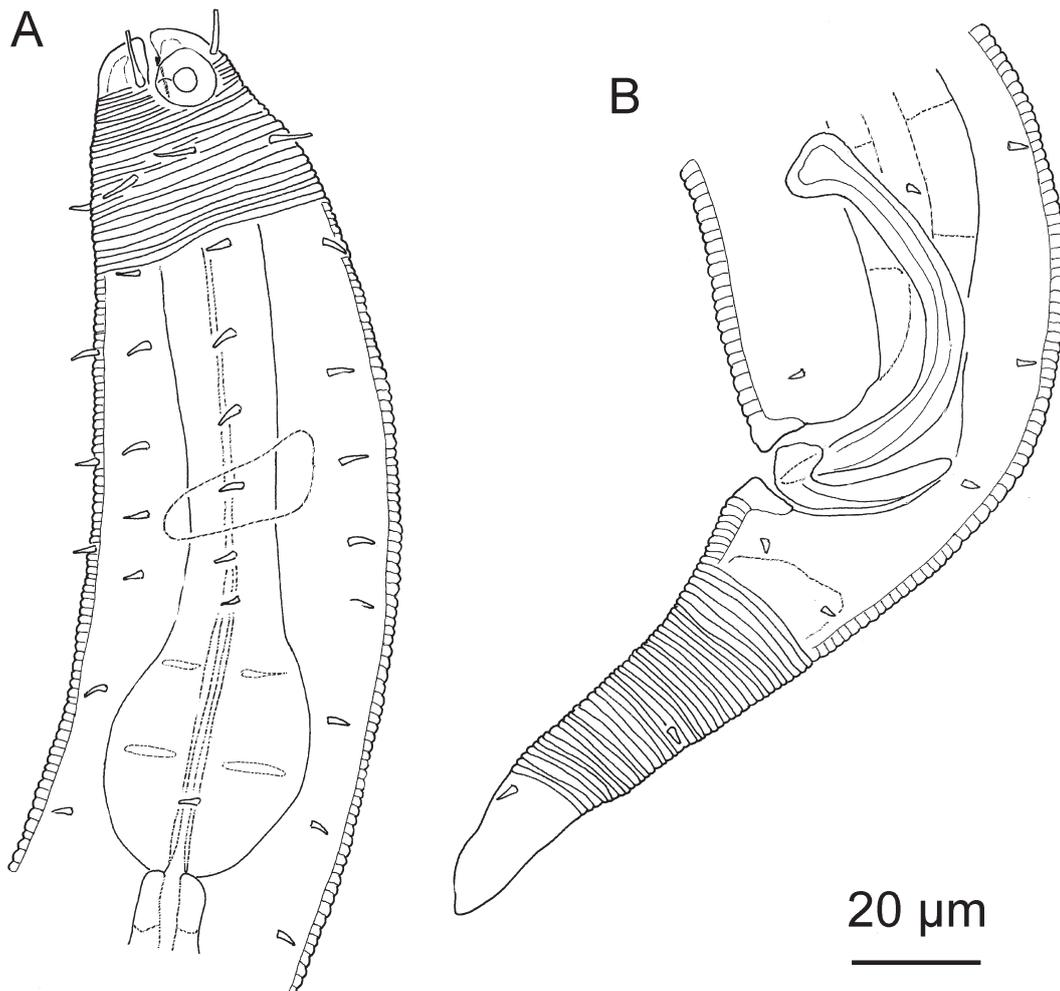


Fig. 11. *Spirinia parasitifera* (Bastian, 1865). **A.** Anterior region of a juvenile. **B.** Posterior region of ♂.

Table 2. Mean (range) of morphological measures for three nematode species of the subfamily Spiriniinae from the Punta Francés coral reef, Cuba. N = number of specimens, J = juvenile. For each variable the first row corresponds to males, the second to females and the third to juveniles. Abbreviations: a.b.d. = anal body diameter; Amp. Fovea c.b.d. = relation of amphidial fovea diameter to corresponding body diameter; de Man ratios are the relation of body length to body diameter (a), to pharynx length (b) and to tail length (c) respectively; c' = relation of tail length to anal body diameter, V % = distance (relative to body length) of vulva to anterior end.

Species/Variable	<i>Chromaspirina inaurita</i>	<i>Paradesmodora immersa</i>	<i>Spirinia parasitifera</i>
N	3 ♂♂, 5 ♀♀, 8 J	2 ♂♂, 4 J	2 ♂♂, 2 ♀♀, 3 J
Body length (µm)	2380 (2110–2592) 2393 (1825–2701) 1226 (694–1744)	1753 (1424–2081) – 914 (277–1635)	2712 (1854–3570) 3300 (2803–3796) 1151 (1007–1307)
de Man ratio a	59 (59–60) 53 (49–55) 39 (24–50)	47 (37–58) – 30 (13–61)	39 (29–49) 43 (41–45) 28 (27–30)
de Man ratio b	19 (17–20) 20 (18–22) 12 (8–16)	14 (11–18) – 9 (5–13)	21 (18–24) 23 (21–26) 9 (8–11)
de Man ratio c	23 (23–24) 30 (21–34) 17 (12–20)	24 (22–27) – 12 (5–22)	25 (21–29) 25 (22–28) 18 (17–19)
Amp. fovea c.b.d. (%)	38 (31–43) 36 (30–52) 29 (26–33)	54 (48–59) – 41 (38–47)	36 (33–38) 37 (36–38) 42 (35–48)
Pharynx length (µm)	124 (121–129) 120 (100–129) 99 (81–119)	124 (119–128) – 96 (53 – 130)	127 (102–151) 142 (136–148) 124 (122–125)
Maximum body ø (µm)	40 (36–43) 45 (33–45) 32 (20–43)	38 (36–39) – 30 (22–44)	69 (65–73) 77 (62–92) 41 (34–46)
Tail length (µm)	101 (92–109) 81 (69–89) 78 (60–96)	75 (52–97) – 71 (51–119)	106 (88–123) 133 (130–137) 63 (60–68)
Tail length c'	2.9 (2.7–3.0) 2.6 (2.2–3.6) 2.7 (2.1–3.0)	2.6 (1.9–3.3) – 3.4 (2.0–4.3)	2.2 (2.1–2.2) 2.7 (2.6–2.8) 2.2 (2.0–2.3)
V %	55 (48–67)	–	51
Spiculum length (µm)	51 (50–52)	45 (34–55)	81 (72–89)
Gubernaculum length (µm)	24 (22–27)	19 (18–20)	28 (25–31)

Material examined

2 ♂♂, 2 ♀♀ and 3 juveniles, deposited in the nematode collection at Centro de Investigaciones Marinas, Universidad de La Habana, CUBA.

Description

Cuticle finely striated in the anterior region (annuli ~ 1 µm width) but even narrower in the mid-body and tail region. Inner and outer labial sensilla papilliform (1–2 µm long), four cephalic setae (7–10 µm long) at level of amphidial fovea. Amphidial fovea cryptospiral located forward in the head (< 6 µm from apex). Eight longitudinal rows of somatic setae decreasing in length from the cervical region (7–10 µm long) to papillae at mid-body and tail region. Pharynx muscular with posterior bulb and internal lining sclerotized. Cardia inconspicuous. Secretory-excretory system not observable. Tail conical, last portion without striations.

Male monorchic; spicules strongly bent, with capitulum, gubernaculum a bent rod dorsally oriented; without precloacal supplements.

Female didelphic, amphidelphic with reflexed ovaries, vulva a transversal aperture.

Juveniles are similar to adults, except for the development of the reproductive system.

Remarks

S. parasitifera is a cosmopolitan species recorded from several habitats and biogeographical regions. Coles (1987) noted that the main differences among populations from widely divergent coasts (England, Canada and USA) were the shape of the proximal end of the spicules and the body size. He reported

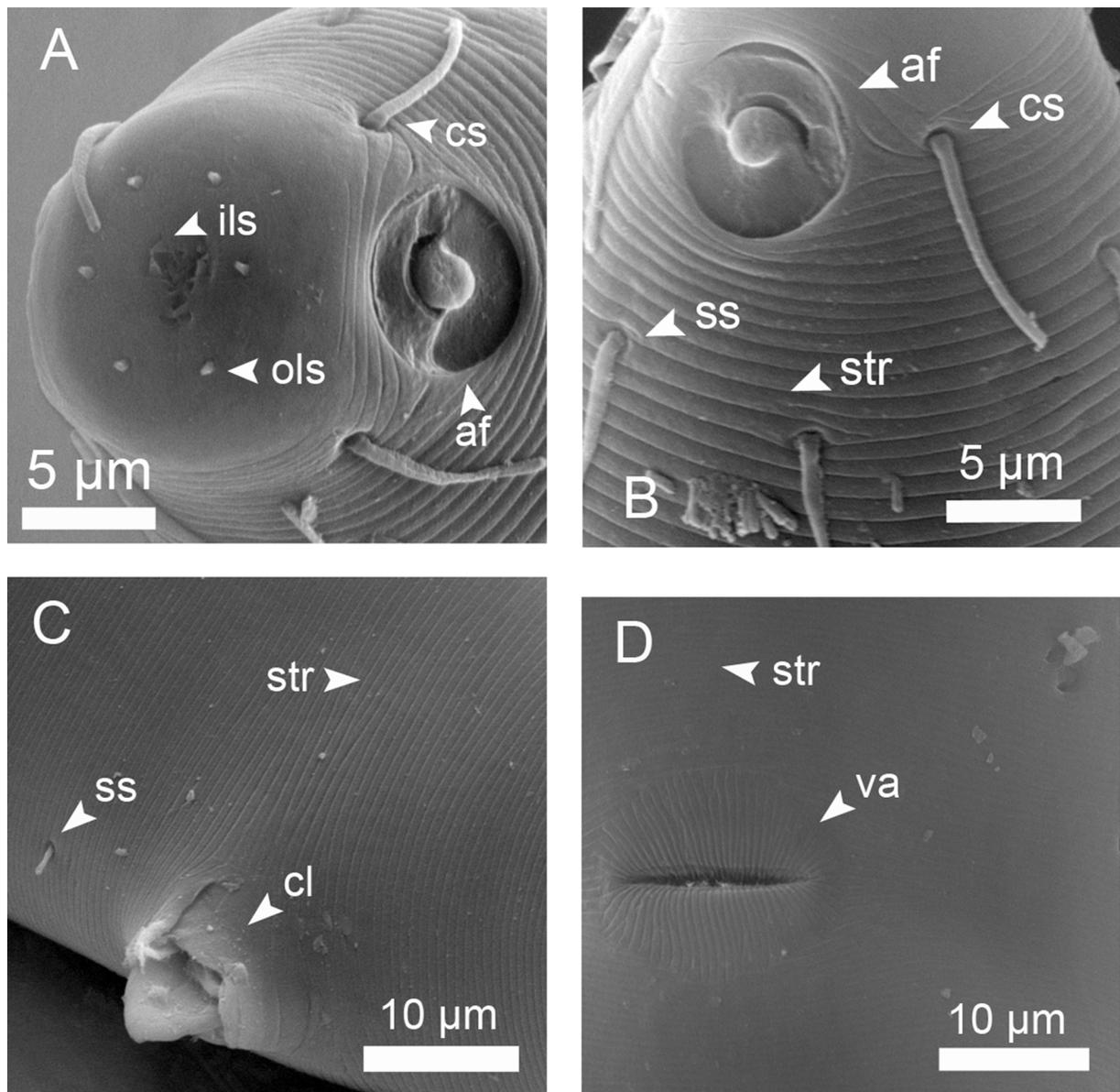


Fig. 12. *Spirinia parasitifera* (Bastian, 1865), SEM microphotographs of ♂ (A, B & C) and ♀ (D). **A.** Head in frontal view. **B.** Head in lateral view. **C.** Anal region with portion of protruding spicule. **D.** Vulva.

that specimens from warmer waters (Florida) had smaller body size (males: 1650–2150 µm; females: 1650–1910 µm) compared to specimens from temperate waters (males: 2000–3300 µm; females: 2020–3180 µm). However, our specimens from a tropical area (Caribbean Sea) had body size closer to those from colder waters (males: 1854–3570 µm; females: 2803–3796 µm). Therefore, a negative relationship between water temperature and body size is not plausible for this species. For some species we studied in this paper this negative relationship is supported (e.g., *Acanthopharynx denticulatus*, *Paradesmodora immersa*) but not for other (e.g., *Spirinia parasitifera*, *Chromaspirina inaurita*). The considerable geographic variation in the morphology of *S. parasitifera* suggests the existence of cryptic species within this nominal species.

Another rare sympatric species, belonging to the genus *Spirinia*, has been recorded in our samples with only two specimens. The species was characterized by the small body size (male: 686 µm; female: 684 µm) and two kinds of somatic setae (long: 28–35 µm and short 5–8 µm). It is closer to *S. gnaigeri* Ott, 1977 (Ott 1977: 134); however, body size of type specimens in Ott (1972) is larger (males: 860–913 µm; females: 836–955 µm) and the length of both somatic setae shorter (long setae: 20–22 µm; short setae: 4–5 µm). However, more specimens should be examined in order to evaluate if this is really a new species of *Spirinia*.

Taxa inquirendae

The subfamilies Desmodorinae and Spiriniinae have 11 and 14 valid genera, respectively (after the change we propose below). Within the subfamilies, some species-rich genera have a reasonably good taxonomic account such as *Croconema* (12 species revised in Verschelde *et al.* 2006), *Desmodora* (27 species revised in Verschelde *et al.* 1998) and *Chromaspirina* (20 species revised in Maria *et al.* 2009). However, many unidentified species are present in collections of speciose genera, such as *Acanthopharynx*, *Croconema*, *Onyx* and *Perspiria* (Venekey *et al.* 2010). For other genera, only single species have been described (e.g., *Psammonema* Verschelde & Vincx, 1995; *Parallelocoilas* Boucher, 1975). In some old publications, the descriptions did not cover the needed diagnostic characters and for these genera, further taxonomic identification was not possible. On this basis we propose *Alaimonema* Cobb, 1920 and *Sigmophoranema* (Cobb, 1933) as *genera inquirendae*.

Alaimonema Cobb, 1920 was classified within Spiriniinae by Lorenzen (1994) based on the presence of posterior pharyngeal bulb, the single anterior testis and the structure of precloacal supplements; but for the first and third features no drawings were provided by Cobb (1920). The original description of the genus does not provide information on essential characters for a proper evaluation. Diagnostic features that are missed in the description are: (1) cuticle striation in respect to the amphidial fovea, (2) shape of the pharynx and spicules, (3) number, shape and position of the precloacal supplements and (4) tail shape. This monospecific genus would be part of the *Spirinia* or even the closely related *Perspiria*. Therefore, we classify *Alaimonema* as *genus inquirenda* and the species *A. multinctum* Cobb, 1920 as *species inquirenda*.

Sigmophoranema (Cobb, 1933) was proposed after Nathan A. Cobb's death by M. V. Cobb (1933) based on N.A. Cobb's manuscripts with the original name of *Sigmophora*. No drawings were presented neither of the genus nor of the type species *Sigmophora rufum* Cobb, 1933. Hope and Murphy (1972) proposed a new name (*Sigmophoranema*) since the original genus name was already occupied by a hymenopteran. We declare *Sigmophoranema* as *genus inquirenda* and *S. rufum* as *species inquirenda* based on the absence of any drawing of the type species and on the relatively poor descriptions of the described specimens. We transfer the species *S. brevispiculatum* Inglis, 1963 (Inglis 1963: 537), *S. litorale* Schulz, 1939 (Schulz 1939: 119) and *S. monstrosum* Gerlach, 1956 (Gerlach 1956: 431) to the genus *Onyx* Cobb, 1891 as *O. brevispiculatum* comb. nov., *O. litorale* comb. nov. and *O. monstrosum* comb. nov.,

respectively. The latter three species bear the two diagnostic features of the genus *Onyx*: large spear-like dorsal tooth and s-shaped precloacal supplements.

Other two already proposed *genera inquirendae* within Desmodoridae were *Amphispira* Cobb, 1920 and *Metadesmodora* Schuurmans Stekhoven, 1942. They were proposed by Verschelde *et al.* (2006) and we agree with them because their types species were poorly described from single female and juvenile specimens respectively.

Taxa with new classification

Paradesmodora Schuurmans Stekhoven, 1950 with type species *P. cephalata* Schuurmans Stekhoven, 1950 currently contains six more species: *P. campbelli* (Allgén, 1932); *P. immersa* Wieser, 1954; *P. punctata* Gerlach, 1963; *P. sinuosa* Ott, 1972; *P. supplementatis* Inglis, 1968 (Inglis 1968: 58); and *P. toreutes* Wieser & Hopper, 1967. The latter authors considered the type species *P. cephalata* as *species inquirenda* because it was described from a juvenile female only. This genus was formerly included in the Desmodorinae by Decraemer & Smol (2006) and by Verschelde *et al.* (2006). We transfer *Paradesmodora* to the Spiriniinae based on three diagnostic features: (1) absence or poorly developed head capsule (i.e., cuticle not thickened compared to body cuticle) without demarcation between labial and cephalic region; (2) fine to medium striation of the body cuticle; and (3) amphidial fovea partially surrounded by cuticle striations.

In *P. sinuosa* Ott, 1972, however, the head capsule is more or less delimited by the smooth cuticle; but, we do not consider that it is “well-developed” as stated by Ott (1972). The amphidial fovea, due to its posterior position, is partially surrounded by the anterior most body annules. Therefore, taking into account these two features, we still consider *P. sinuosa* to belong to the genus *Paradesmodora*.

Wieser & Hopper (1967) characterized their new species *P. toreutes* by the cuticular differentiations of the head that they describe as “head very much enlarged and forming plates which surround the anterior portions of the amphids”. The illustration of a male and LM microphotographs of the holotype show a protruding lip region, a subdivided smooth head capsule by an anterior suture, and the presence of an enlarged head capsule with cuticular plates. These features are different from the Spiriniinae. Therefore, we consider that *P. toreutes* Wieser & Hopper, 1967 fits neither in the genus *Paradesmodora* nor in the subfamily Spiriniinae. Thus, it is transferred, within the subfamily Desmodorinae, to the genus *Acanthopharyngoides* Chitwood, 1936 as *A. toreutes* comb. nov. *A. toreutes* comb. nov. fits within *Acanthopharyngoides* because of the unique combination of body size, shape of the spicule (hook-shaped), number of pre-cloacal supplements (10) and the posterior border of the fovea surrounded by cuticle annuli. This genus has by now seven species: *A. bidentatus* Jensen, 1985 (Jensen 1985: 256); *A. chitwoodi* Wieser, 1954; *A. duplex* Gerlach, 1963; *A. quintus* Riemann & Schrage, 1977 (Riemann & Schrage 1977): 49; *A. scleratus* Gerlach, 1963; *A. thyrrhenicus* Wieser, 1954 and *A. toreutes* (Wieser & Hopper, 1967) comb. nov.

Echinodesmodora Blome, 1982 is transferred from the subfamily Desmodorinae to the Spiriniinae because the diagnoses of both subfamilies changed. The characters that support the membership to the Spiriniinae are: (1) the absence of the head capsule; (2) no demarcation between labial and cephalic regions; (3) the amphidial fovea is surrounded by cuticle striations; and (4) the presence of one dorsal tooth and two ventrosublateral teeth. The coarse striation of the cuticle suggests resemblance with the Desmodorinae, but this character within this subfamily is variable (e.g., coarse striation in *Croconema*, fine striation in *Acanthopharyngoides*) and does not support membership of the Desmodorinae.

Stygodesmodora Blome, 1982 resembles *Echinodesmodora*, but is mainly differentiated by the amphidial fovea located on a basal plate and the absence of subcephalic setae present in *Echinodesmodora*.

Stygodesmodora also possesses diagnostic characters of the Spiriniinae such as absence of a head capsule, no demarcation between labial and cephalic regions, amphidial fovea surrounded by cuticle striation and one dorsal tooth and two smaller ventrosublateral teeth.

A new monospecific genus *Onepunema* Leduc & Verschelde, 2013 has recently been introduced and classified within the Desmodorinae, based mainly on the presence of a head capsule (Leduc & Verschelde 2013). The new genus is also characterized by two testes, a character that disagrees with the single holapomorphy (monorchic males) of the superfamily Desmodoroidea (Lorenzen 1994). The presence of diorchic males is characteristic for the superfamily Microlaimoidea Micoletzky, 1922. Within the Microlaimoidea, didelphic females and coarsely annulated body cuticle are typical features of the Microlaimidae Micoletzky, 1922. Further, the presence of reflexed ovaries, pores in the cuticle connected to epidermal gland cells and the absence of somatic setae suggest a relationship with *Bolbolaimus* Cobb, 1920, *Calomicrolaimus* Lorenzen, 1976 and *Microlaimus* de Man, 1880. The taxonomy of these three genera is not completely understood according to Platt & Warwick (1988) and Decraemer & Smol (2006). Further descriptions of new species and genus have been done (e.g., Muthumbi & Vincx 1999; Armenteros *et al.* 2010) but the relationships among the genera remain unclear. In conclusion, we refrain from including *Onepunema* within the family Desmodoridae and regard it as taxa *incertae sedis*.

List of valid genera of Desmodorinae (11)

Acanthopharyngoides Chitwood, 1936; *Acanthopharynx* Marion, 1870; *Bolbonema* Cobb, 1920; *Croconema* Cobb, 1920; *Desmodora* de Man, 1889; *Desmodorella* Cobb, 1933; *Psammonema* Verschelde & Vincx, 1995; *Pseudochromadora* Daday, 1899; *Pseudodesmodora* Boucher, 1975; *Sibayinema* Verschelde *et al.*, 2006; *Zalonema* Cobb, 1920.

The keys for genera of the Desmodorinae provided in Decraemer & Smol (2006) and Verschelde *et al.* (2006) are still useful since they start with the three genera we transferred and which can be easily omitted and they did not include the recent genus *Onepunema*.

List of valid genera of Spiriniinae (14)

Chromadoropsis Filipjev, 1918; *Chromaspirina* Filipjev, 1918; *Echinodesmodora* Blome, 1982; *Metachromadora* Filipjev, 1918; *Onyx* Cobb, 1891; *Papillonema* Verschelde, Muthumbi & Vincx, 1995; *Paradesmodora* Schuurmans Stekhoven, 1942; *Parallelocoilas* Boucher, 1975; *Perspiria* (Wieser & Hopper, 1967); *Polysigma* Cobb, 1920; *Pseudometachromadora* Timm, 1952; *Spirinia* Gerlach, 1963; *Spirodesma* Cavalcanti *et al.*, 2009; *Stygodesmodora* Blome, 1982.

Key to the genera of Spiriniinae

1. Cuticle coarsely striated..... 2
– Cuticle finely striated..... 4
2. Tail conical-cylindrical *Spirodesma* Cavalcanti *et al.*, 2009
– Tail conical..... 3
3. Amphidial fovea on a cuticular plate, somatic setae present and spines absent.....
..... *Stygodesmodora* Blome, 1982
– Amphidial fovea not on a cuticular plate, somatic setae and spines present.....
..... *Echinodesmodora* Blome, 1982
4. Buccal cavity spacious, parallel and sclerotized walls 5
– Buccal cavity approximately conical (of large or medium size) or minute..... 6

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5. Amphidial fovea multispiral, buccal armature with one dorsal tooth and no ventrosublateral teeth ..
 *Parallelocoilas* Boucher, 1975
 – Amphidial fovea cryptospiral, buccal armature with one dorsal tooth and two ventrosublateral
 teeth..... *Pseudometachromadora* Timm, 1952
6. Buccal cavity small-sized, one minute dorsal tooth 7
 – Buccal cavity from medium to larger size, dorsal tooth large 8
7. Tail conical and finely striated..... *Spirinia* Gerlach, 1963
 – Tail conical-cylindrical (including filiform) and coarsely striated
 *Perspiria* (Wieser & Hopper, 1967)
8. Single or multiple pharyngeal posterior bulb muscular enlarged and internal lining of the pharynx
 thickened..... 9
 – Single pharyngeal posterior bulb rounded and internal lining of the pharynx not thickened..... 12
9. Dorsal tooth large spear-like, preloacal supplements S-shaped..... *Onyx* Cobb, 1891
 – Dorsal tooth not spear-like, preloacal supplements not S-shaped 10
10. Pharynx posterior bulb barrel-shaped, buccal cavity large-sized, dorsal tooth prominent.....
 *Metachromadora* Filipjev, 1918
 – Pharynx posterior bulb other shaped, buccal cavity medium-sized 11
11. Pharynx posterior bulb divided in 2–4 bulbi, outer labial sensilla setiform, subcephalic setae present,
 preloacal supplements as cuticular plates *Chromadoropsis* Filipjev, 1918
 – Pharynx posterior bulb not divided in bulbi, outer labial sensilla papilliform, subcephalic setae
 absent, preloacal supplements as papillae..... *Papillonema* Verschelde *et al.*, 1995
12. Preloacal supplements S-shaped *Polysigma* Cobb, 1920
 – Preloacal supplements with other shape or absent..... 13
13. Subcephalic setae present *Chromaspirina* Filipjev, 1918
 – Subcephalic setae absent..... *Paradesmodora* Schuurmans Stekhoven, 1942

Discussion

The systematics of the family Desmodoridae has been addressed mainly from a morphological approach. However, a recent molecular analysis (Armenteros *et al.* in press) reports the monophyly of this family within the Nematoda. These authors suggest that Desmodorinae and Spiriniinae seem to be paraphyletic. The main limitation to address the systematics of these subfamilies are the poor representation of taxa in the phylogenetic studies. A future prospectus should include the sampling and DNA sequencing of more desmodorid genera in order to place them more firmly in a phylogenetic framework. It may result in the identification of clades that would be upgraded to the subfamily level. Until now, our proposal of the systematics for Desmodorinae and Spiriniinae is the most updated and complete for these groups. The proposed taxonomic changes lead to a more coherent grouping of the species and enhance the further assignation of sampled specimens into the groups.

The diversity of desmodorid species is high and distributed asymmetrically across the genera. There are speciose genera (e.g., *Desmodora*, *Metachromadora* and *Spirinia*), but other with only one or two species (e.g., *Papillonema*, *Parallelocoilas*). Coral reefs in particular seem to be very rich in desmodorid species and further research should discover new taxa in this family.

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References

- Allgén C. 1933. Freilebende Nematoden aus dem Trondhjemsfjord. *Capita Zoologica* 4 (2):1–162.
- Allgén C.A. 1947. West American marine nematodes (Papers from Dr. Th. Mortensen's Pacific Expedition 1914-1916, 75). *Videnskabelige Meddelelser Dansk Naturhistorisk Forening* 110: 65–219.
- Armenteros M., Rojas-Corzo A., Ruiz-Abierno A., Derycke S., Backeljau T., Decraemer W. In press. Systematics and DNA barcoding of free-living marine nematodes with emphasis on tropical desmodorids using nuclear SSU rDNA and mitochondrial COI sequences. *Nematology*. <http://dx.doi.org/10.1163/15685411-00002824>
- Armenteros M., Ruiz-Abierno A. & Decraemer W. 2014. Taxonomy of Stilbonematinae (Nematoda: Desmodoridae): description of two new and three known species and phylogenetic relationships within the family. *Zoological Journal of the Linnean Society* 171 (1): 1–21. <http://dx.doi.org/10.1111/zoj.12126>
- Armenteros M., Ruiz-Abierno A., Sosa Y. & Pérez-García J.A. 2012. Habitat heterogeneity effects on macro- and meiofauna (especially nematodes) in Punta Francés coral reef (SW Cuban Archipelago). *Revista de Investigaciones Marinas* 32 (1): 50-61.
- Armenteros M., Vincx M. & Decraemer W. 2010. *Guitartia tridentata* n. gen., n. sp. (Monhysterida: Xyalidae) and *Macrodontium gaspari* n. gen., n. sp. (Chromadorida: Microlaimidae), free-living marine nematodes from the Caribbean Sea. *Nematology* 12 (3): 417–427. <http://dx.doi.org/10.1163/138855409X12559479585007>
- Bastian H.C. 1865. Monograph of the Anguillulidae, or Free Nematoids, Marine, Land, and Freshwater; with Descriptions of 100 New Species. *Transactions of the Linnean Society of London* 25 (2): 73–184. <http://dx.doi.org/10.1111/j.1096-3642.1865.tb00179.x>
- Blome D. & Riemann F. 1994. Sandy Beach Meiofauna of Eastern Australia (Southern Queensland and New South Wales). III.* Revision of the Nematode Genus *Onyx* Cobb, 1891, with a Description of Three New Species (Nematoda: Desmodoridae). *Invertebrate Taxon* 8 (6): 1483–1492. <http://dx.doi.org/10.1071/IT9941483>
- Boucher G. 1975. Nématodes des sables fins infralittoraux de la Pierre Noire (Manche occidentale). I. Desmodoridae. *Bulletin du Muséum national d'Histoire naturelle, 3e série Zoologie* 285: 101–128.
- Bütschli D. 1874. Zur Kenntnis der freilebenden Nematoden, insbesondere der des Kieler Hafens. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 9 (3):237–292
- Cobb N.A. 1920. IX. One hundred new nemas. In: Cobb N.A. *Contributions to a Science of Nematology*: 217–234. Williams & Wilkins Co., Baltimore. <http://dx.doi.org/10.5962/bhl.title.20608>
- Cobb N.A. 1933. New Nemic Genera and Species, with Taxonomic Notes. *Journal of Parasitology* 20 (2): 81–94. <http://dx.doi.org/10.2307/3272166>

- Coles J.W. 1987. Observations on the marine nematode genus *Spirinia* Gerlach, 1963 (Desmodoridae: Spiriniinae) with descriptions of two new species. *Bulletin of the British Museum (Natural History). Zoology* 53 (2): 79–101.
- Decraemer W. & Smol N. 2006. Chapter 17. Orders Chromadorida, Desmodorida and Desmoscolecida. In: Abebe E., Traunspurger W. & Andr assy I. (eds) *Freshwater nematodes: Ecology and taxonomy*: 497–573. CABI Publishing, Wallingford. <http://dx.doi.org/10.1079/9780851990095.0497>
- Dinh Tu N., Smol N., Vanreusel A. & Vu Thanh N. 2011. Six new species of the genus *Onyx* Cobb, 1891 (Nematoda: Desmodoridae) from Coastal Areas in Vietnam. *Russian Journal of Nematology* 19 (1): 1–20.
- Filipjev I.N. 1922. Sur les N ematodes libres de la mer d'Azov. *Trudy Stavropol'skogo Sel'skokhozyaistvennago Instituta* 1 (7): 185–208.
- Fonseca Cavalcanti M., Silva M.C. & Fons eca-Genevois V. 2009. *Spirodesma magdae* nov. gen. nov. sp. (Nematoda: Desmodoridae) from the Brazilian deep sea (Campos Basin, Rio de Janeiro, Brazil). *Zootaxa* 2096: 109–118.
- Furstenberg J.P. & Vincx M. 1988. Three new *Chromadoropsis* species (Nematoda, Desmodoridae) from Southern Africa and the North Sea. *South African Journal of Zoology* 23: 215–223.
- Gerlach S.A. 1950.  ber einige Nematoden aus der Familie der Desmodoriden. *Zoologischer Anzeiger* 145: 178–198.
- Gerlach S.A. 1952. Nematodes aus dem K stengrundwasser. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse* 6: 315–372.
- Gerlach S.A. 1956. Neue nematoden aus dem kustengrundwasser des Golfes de Gascogne (Biskaya). *Vie et Milieu* 6: 426–434.
- Gerlach S.A. 1963. Freilebende Meeresnematoden von den Malediven II. *Kieler Meeresforschungen Sonderheft* 19: 67–113.
- Gerlach S.A. 1964. Freilebende Nematoden aus dem Roten Meer. *Kieler Meeresforschungen Sonderheft* 20 : 18–34.
- Gerlach S.A. & Riemann F. 1973. *The Bremerhaven checklist of aquatic nematodes. A catalogue of Nematoda Adenophorea excluding the Dorylaimida*. Kommissionsverlag Franz Leuwer, Bremen.
- Hausdorf B. 2011. Progress toward a general species concept. *Evolution* 65 (4): 923-931. <http://dx.doi.org/10.1111/j.1558-5646.2011.01231.x>
- Hodda M. 2011. Phylum Nematoda Cobb 1932. In: Zhang Z.-Q. (ed.) *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148: 63–95.
- Hope D. & Murphy D.G. 1972. *A Taxonomic Hierarchy and Checklist of the Genera and Higher Taxa of Marine Nematodes*. Smithsonian Contributions to Zoology 137, Smithsonian Institution Scholarly Press, Washington. <http://dx.doi.org/10.5479/si.00810282.137>
- Inglis W.G. 1963. New marine nematodes from off the coast of South Africa. *Bulletin of the British Museum (Natural History) Zoology* 10 (9): 529–552.
- Inglis W.G. 1968. Interstitial nematodes from St. Vincent's Bay, New Caledonia. In: *Exp dition Fran aise sur les r cifs coralliens de la Nouvelle Cal donie*. Volume 2: 29–74.  ditions de la Fondation Singer-Polignac, Paris.
- Jensen P. 1985. The nematode fauna in the sulphide-rich brine seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico. I. Chromadorida. *Zoologica Scripta* 14 (4): 247–263. <http://dx.doi.org/10.1111/j.1463-6409.1985.tb00195.x>

- Kampfer S., Sturmbauer C. & Ott J. 1998. Phylogenetic Analysis of rDNA Sequences from Adenophorean Nematodes and Implications for the Adenophorea-Secernentea Controversy. *Invertebrate Biology* 117 (1): 26–36. <http://dx.doi.org/10.2307/3226849>
- Leduc D. & Verschelde D. 2013. One new genus and two new free-living nematode species (Desmodorida, Desmodoridae) from the continental margin of New Zealand, Southwest Pacific Ocean. *Zootaxa* 3609 (3): 274–290. <http://dx.doi.org/10.11646/zootaxa.3609.3.2>
- Lorenzen S. 1994. *The phylogenetic Systematics of Freelifving Nematodes*. The Ray Society, London.
- Maria T.F., Morgado-Esteves A., Smol N., Vanreusel A. & Decraemer W. 2009. *Chromaspirina guanabarensis* sp. n. (Nematoda: Desmodoridae) and a new illustrated dichotomous key to *Chromaspirina* species. *Zootaxa* 2092: 21–36.
- Maria T.F., Smol N. & Esteves A.M. 2014. Two new species of *Metachromadora* (Nematoda: Desmodoridae) from Guanabara Bay, Rio de Janeiro, Brazil, and a revised dichotomous key to the genus. *Journal of the Marine Biological Association of the United Kingdom* 94 (1): 105–114. <http://dx.doi.org/10.1017/S0025315413001161>
- Micoletzky H. 1922. Die freilebenden Erd-Nematoden mit besonderer Berücksichtigung der Steiermark und der Bukowina, zugleich mit einer Revision sämtlicher, nicht mariner, freilebender Nematoden in Form von Genus-Beschreibungen und Bestimmungsschlüsseln. *Archiv für Naturgeschichte Berlin Abteilung A* 87 (8): 1–649.
- Muthumbi A.W. & Vincx M. 1999. Microlaimidae (Microlaimoidea: Nematoda) from the Indian Ocean: description of nine new and known species. *Hydrobiologia* 397: 39–58. <http://dx.doi.org/10.1023/A:1003686212934>
- Ndaro S.G.M. & Ólafsson E. 1999. Soft-bottom fauna with emphasis on nematode assemblage structure in a tropical intertidal lagoon in Zanzibar, eastern Africa: I. Spatial variability. *Hydrobiologia* 405: 133–148. <http://dx.doi.org/10.1023/A:1003874122971>
- Ott J.A. 1972. Twelve New Species of Nematodes from an Intertidal Sandflat in North Carolina. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 57 (3): 463–496. <http://dx.doi.org/10.1002/iroh.19720570307>
- Ott J.A. 1996. Sulphide ectosymbioses in shallow marine habitats. In: Uiblein F., Ott J.A. & Stachowitsch M. (eds) *Deep-sea and extreme shallow-waters habitats: affinities and adaptations*: 369–382. Biosystematics and Ecology Series 11, Austrian Academy of Science Press, Vienna.
- Ott J.A., Bauer-Nebelsick M. & Novotny V. 1995. The genus *Laxus* Cobb, 1894 (Stilbonematinae: Nematoda): description of two new species with ectosymbiotic chemoautotrophic bacteria. *Proceedings of the Biological Society of Washington* 108 (3): 508–527.
- Pastor De Ward C. 1988. Nematodos marinos de la ria Deseado (Desmodoroidea: Desmodoridae, Draconematidae), Santa Cruz, Argentina 7. *Physis Secciones A, B y C* 46: 61–72.
- Platt H.M. & Warwick R.M. 1988. *Free-living marine nematodes*. Part II. *British Chromadorids*. Synopses of British Fauna 38, The Linnean Society of London and The Estuarine and Brackish-water Sciences Association, Leiden.
- Riemann F. & Schrage M. 1977. Zwei neue Nematoda Desmodorida aus der Iberischen Tiefsee. *Meteor Forschungsergebnisse. Reihe D: Biologie* 25: 49–53.
- Schulz E. 1939. Beiträge zur Morphologie und Systematik freilebender mariner Nematoden, I. *Kieler Meeresforschungen Sonderheft* 3: 114–121.

- Schuermans Stekhoven J.H. 1950. *The freeliving marine nemas of the Mediterranean*. I. *The Bay of Villefranche*. Mémoires de l'Institut Royal des Sciences Naturelles de Belgique, deuxième série 37, Institut Royal des Sciences Naturelles de Belgique, Brussels.
- Steiner G. 1921. Beiträge zur Kenntnis mariner Nematoden. *Zoologische Jahrbücher* 44:1–68.
- Tchesunov A.V. 2013. Marine free-living nematodes of the subfamily Stilbonematinae (Nematoda, Desmodoridae): Taxonomic review with descriptions of a few species from the Nha Trang Bay, Central Vietnam. *Meiofauna Marina* 20: 71–94.
- Tchesunov A.V. 2014. 7.13 Order Desmodorida de Coninck, 1965. In: Schmidt-Rhaesa A (ed.) *Handbook of Zoology Online*: 399-434. De Gruyter, Berlin. Available from <http://www.degruyter.com/view/db/zoology> [accessed 13 May 2014]
- Tietjen J.H. 1991. Ecology of free-living nematodes from the continental shelf of the Central Great Barrier Reef Province. *Estuarine, Coastal and Shelf Science* 32 (5): 421–438. [http://dx.doi.org/10.1016/0272-7714\(91\)90032-7](http://dx.doi.org/10.1016/0272-7714(91)90032-7)
- van Megen H., van den Elsen S., Holterman M., Karssen G., Mooyman P., Bongers T., Holovachov O., Bakker J. & Helder J. 2009. A phylogenetic tree of nematodes based on about 1200 full-length small subunit ribosomal DNA sequences. *Nematology* 11 (6): 927–950. <http://dx.doi.org/10.1163/156854109X456862>
- Venekey V., Fonseca-Genevois V.G. & Santos P.J.P. 2010. Biodiversity of free-living marine nematodes on the coast of Brazil: a review. *Zootaxa* 2568: 39–66.
- Verschelde D., Gourbault N.E. & Vincx M. 1998. Revision of *Desmodora* with description of new Desmodorids (Nematoda) from hydrothermal vents of the Pacific. *Journal of the Marine Biological Association of the United Kingdom* 78 (1): 75–112. <http://dx.doi.org/10.1017/S0025315400039977>
- Verschelde D., Nicholas W. & Vincx M. 2006. A review of the genera *Croconema* Cobb, 1920 and *Pseudochromadora* Daday, 1899 (Nematoda, Desmodoroidea): new species from the Coasts of Kenya and Australia. *Hydrobiologia* 571 (1): 17–40. <http://dx.doi.org/10.1007/s10750-006-0194-0>
- Verschelde D. & Vincx M. 1995. *Psammonema* gen.n. and *Pseudochromadora* Daday, 1889 (Nematoda, Desmodoridae) from sandy sediments of Gazi, Kenya. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 65: 11–39.
- Verschelde D. & Vincx M. 1996. Four new species of the family Desmodoridae (Nematoda, Desmodoroidea) from Kenya. *Zoologica Scripta* 25 (1): 1–20. <http://dx.doi.org/10.1111/j.1463-6409.1996.tb00148.x>
- Vincx M. 1996. Meiofauna in marine and freshwater sediments. In: Hall G.S. (ed.) *Methods for the examination of organismal diversity in soils and sediments*: 187–195. CAB International, Wallingford.
- Vincx M. & Gourbault N.E. 1989. Desmodoridae from the Bay of Morlaix (Brittany) and the Southern Bight of the North Sea. *Cahiers de Biologie Marine* 30 (1): 103–114.
- Warwick R.M. 1969. Two new species of *Pseudonchus* Cobb (Nematoda, Choanolaimidae) from the British Coast. *Cahiers de Biologie Marine* 10 (4): 375–382.
- Wheeler Q. 2004. Taxonomic triage and the poverty of phylogeny. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359 (1444): 571–583. <http://dx.doi.org/10.1098/rstb.2003.1452>
- Wieser W. 1954. *Free-living marine nematodes II. Chromadoroidea*. Acta Universitatis Lundensis (N. F. 2) 50, C.W.K. Gleerup, Lund.
- Wieser W. & Hopper B. 1967. Marine Nematodes of the east coast of North America. I. Florida. *Bulletin of Museum of Comparative Zoology* 135: 239–344.

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