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Research article

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New *Spirinia* and *Stygododesmodora* species (Nematoda, Spiriniinae) from the Southwest Pacific, and a revision of the related genera *Spirinia*, *Chromaspirina* and *Perspiria*

Daniel LEDUC^{1,3} & Dominick VERSCHELDE^{2,4}

¹ National Institute of Water and Atmospheric Research, Private Bag 14-901, Wellington, New Zealand. Corresponding author: Daniel.Leduc@niwa.co.nz

² Ghent University - Zoology Museum, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium

³ urn.lsid:zoobank.org:author:9393949F-3426-4EE2-8BDE-DEFFACE3D9BC

⁴ urn.lsid:zoobank.org:author:80C09028-E083-4DF0-B514-9C92A12ED78E

Abstract. Two new species of the family Desmodoridae are described from the upper continental slope of New Zealand, Southwest Pacific, and the genera *Spirinia*, *Chromaspirina* and *Perspiria* are revised. *Spirinia verecunda* sp. nov. is characterised by a short, stout body, cuticle covered in minute, hair-like structures, unispiral amphideal aperture and cryptospiral amphideal fovea, buccal cavity with small dorsal tooth and minute subventral teeth, eight oblong glands surrounding anterior portion of pharynx, large sperm cells, spicules with weak capitulum, and the absence of precloacal supplements. *Stygododesmodora confusa* sp. nov. is characterised by a relatively short body, spiral amphids with 1.2–1.4 turns, cephalic setae situated at or slightly posterior to mid-level of amphid, and males with four precloacal supplements consisting of short setae on wide bases. Like other species of the genus, *S. confusa* sp. nov. is characterised by an annulated head region, but in some specimens the cuticle annulations are restricted to the dorsal and ventral sides of the head. *S. confusa* sp. nov. shows similarities with species of other desmodorid genera (i.e., *Echinodesmodora*, *Bolbonema*), but can be differentiated from them by the presence of an annulated head region and amphideal plates. The genera *Spirinia*, *Chromaspirina* and *Perspiria* have very similar morphologies and differ mainly in the size and structure of the buccal cavity (*Spirinia* vs *Chromaspirina*) or the shape of the tail and placement of the amphids relative to the cuticle annulations (*Spirinia* vs *Perspiria*); their diagnoses are clarified and some nomenclatural changes are proposed to eliminate overlap in the definitions of these genera.

Keywords. Desmodoridae, deep-sea, meiofauna, Chatham Rise, southern Hikurangi Margin

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Introduction

Spirinia Gerlach, 1963 is a relatively common genus and twelve valid species have been described to date (Silva *et al.* 2009). *Spirinia* is very similar to *Chromaspirina* Filipjev, 1918 in the shape and structure of

the head region, amphids, pharynx, and male copulatory apparatus. The main distinction between the two genera is the shape of the buccal cavity: *Spirinia* is characterised by a narrow and lightly cuticularised buccal cavity with no or a small dorsal tooth and no or minute subventral teeth, whereas *Chromaspirina* is characterised by a more heavily cuticularised, medium to large buccal cavity with a large dorsal tooth and smaller subventral teeth. A third genus, *Perspiria* Wieser & Hopper, 1967, is also similar to *Spirinia* and differs from the latter in having a conico-cylindrical to filiform tail and by the amphids not completely surrounded by body annulations. Species of these three genera show considerable overlap in the above-mentioned morphological characteristics, however, and the boundaries between them have become somewhat blurred. Here, we describe *S. verecunda* sp. nov. from the Chatham Rise crest (350 m water depth) on the continental margin of New Zealand, and we propose several nomenclatural changes to species of *Spirinia* and *Chromaspirina* to allow a more consistent distinction between the genera based on buccal morphology. Several nomenclatural changes are also suggested for the genus *Perspiria* to reflect differences in tail shape and body annulations of the head region between the latter genus and *Spirinia*.

Stygodesmodora Blome, 1982 is a relatively uncommon genus comprising only two species: *S. bacillicauda* (Gerlach, 1963) and *S. epixantha* Blome, 1982. These species were described from shallow sandy sediments in the Indian Ocean and North Sea, respectively. Here a third species, *S. confusa* sp. nov., is described from the continental margin of New Zealand (350 and 686 m water depth); it is the first species of the genus to be described from the deep sea.

Material and Methods

Samples for species descriptions were obtained from the Chatham Rise and southern Hikurangi margin, Southwest Pacific. The Chatham Rise is a submarine ridge that extends eastwards from the South Island of New Zealand, over water depths ranging from *ca.* 250 to 3000 m. The highly productive Subtropical Front (STF) is geographically constrained near the southern flank of the rise at around 44° S (Murphy *et al.* 2001). The southern Hikurangi margin lies on the south-eastern extremity of the North Island of New Zealand and is situated north of the Chatham Rise. Samples were collected at two sites: one situated near the head of a canyon on the southern Hikurangi margin during National Institute of Water and Atmospheric Research (NIWA) cruise TAN1004 (station 92, 686 m water depth, 41.8921° S, 174.6347° E), and one at an open slope site located near the central Chatham Rise crest during NIWA cruise TAN1103 (station 69, 350 m water depth; 43.331° S, 178.288° E).

Sediment samples were collected using an Ocean Instruments MC-800A multicorer (MUC; core internal diameter = 9.52 cm). Each sample consisted of one subcore of internal diameter 26 mm taken to a depth of 5 cm. Samples were fixed in 10% formalin and stained with Rose Bengal. Samples were subsequently rinsed on a 1 mm sieve to remove large particles and on a 45 µm sieve to retain nematodes. Nematodes were extracted from the remaining sediments by Ludox flotation and transferred to pure glycerol (Somerfield & Warwick 1996). Species descriptions were made from glycerol mounts using differential interference contrast microscopy, and drawings were made with the aid of a camera lucida. Specimens for scanning electron microscopy (SEM) were transferred to a 2% glutaraldehyde solution with sodium cacodylate buffer overnight, then transferred to a 4% osmium tetroxide solution for 2 hours. They were then gradually transferred to pure ethanol using a graded ethanol series, critical point dried, and mounted onto stubs before being coated with gold using a sputter coater. Observations were made using a Hitachi TM3000 tabletop SEM at high vacuum mode.

All measurements are in µm, and all curved structures are measured along the arc. Type specimens are held in the NIWA Invertebrate Collection, Wellington, New Zealand. Abbreviations in the text are as follows:

- a = body length/maximum body diameter
abd = anal body diameter
b = body length/oesophagus length
c = body length/tail length
cbd = corresponding body diameter
%V = vulva distance from anterior end of body \times 100/total body length.

Results

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 (synonym: *Mastodex* Steiner, 1921).

Emended diagnosis (modified from Lorenzen 1981 and Decraemer & Smol 2006)

Member of Desmodoroidea. Cuticle with coarse annulations, at least in anterior body region, or striated. Specialised somatic setae, such as adhesion tubes (Draconematidae) or ambulatory setae (Epsilonematidae) not present. Amphideal fovea usually spiral, unispiral, cryptospiral, or cryptocircular, and sometimes loop- or pore-shaped. Buccal cavity with small to large dorsal tooth and smaller or indistinct subventral teeth. Pharynx usually with round muscular posterior bulb, with or without cuticularised lumen; sometimes bulb is pyriform, elongated, or indistinct. Gubernaculum without dorsal apophyses. Males usually monorchic, except in *Onepunema* Leduc & Verschelde, 2013 (diorchic). Vulva usually posterior to middle of body. Tail conical.

Remarks

Armenteros *et al.* (2014) recently argued that the genus *Onepunema* Leduc & Verschelde, 2013 is more closely related to the Microlaimidae than to the Desmodoridae because of the presence of two testes (a feature common in the former but not found in the latter). The Microlaimidae, however, are characterised by the presence of outstretched ovaries, while *Onepunema* possesses reflexed ovaries, a characteristic of the Desmodoridae. This trait, in combination with the presence of a cephalic capsule in *Onepunema* (an important characteristic for the classification of supraspecific taxa within the Desmodorida and never found within the Microlaimoidea) suggests closer affinities with the Desmodoridae (and Desmodorinae in particular) than with the Microlaimidae. Armenteros *et al.* (2014: 26) incorrectly stated that "... the presence of reflexed ovaries [...] suggest a relationship with *Bolbolaimus* Cobb, 1920, *Calomicrolaimus* Lorenzen, 1976 and *Microlaimus* de Man, 1880". Reflexed ovaries are not found in any of these genera; perhaps *Bolbolaimus* was confused with *Bolbonema* Cobb, 1920 (see comments under *Chromaspirina longisetosa* Jensen, 1985 below), which belongs to the Desmodoridae due to the presence of reflexed ovaries and a globular cephalic capsule.

Subfamily **Spiriniinae** Chitwood, 1936

Type genus

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

Diagnosis (from Decraemer & Smol 2006)

Member of Desmodoridae. Body cuticle with fine annulations. Head not demarcated as a cephalic capsule. Amphideal fovea usually a simple spiral. Buccal cavity small or large, with a distinct or a minute dorsal tooth; two small ventrosublateral teeth may be present or absent.

Differential diagnosis

This subfamily is similar to the Desmodorinae but can be differentiated from the latter by the absence of a head capsule.

Remarks

The tribe Spirinacea was originally established by Chitwood (1936), before being raised to subfamily, family and superfamily rank by De Coninck (1965). According to the Principle of Coordination (ICZN, 1999, Article 36), “a name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group; (...). The name has the same authorship and date at every rank.” The appropriate authorship for Spiriniinae should therefore be attributed to Chitwood (1936), and not Gerlach & Murphy (1965), as is often done (e.g., Armenteros *et al.* 2014).

Valid genera (Cavalcanti *et al.* 2009; Armenteros *et al.* 2014)

Alaimonema Cobb, 1920
Chromaspirina Filipjev, 1918
Metachromadora Filipjev, 1918
Onyx Cobb, 1891
Papillonema Verschelde *et al.*, 1995
Paradesmodora Schuurmans Stekhoven, 1950
Parallelocoilas Boucher, 1975
Perspiria Wieser & Hopper, 1967
Polysigma Cobb, 1920
Pseudometachromadora Timm, 1952
Sigmophoranema Hope & Murphy, 1972
Spirinia Gerlach, 1963
Spirodesma Cavalcanti *et al.*, 2009
Stygodesmodora Blome, 1982

We provide emended diagnoses and updated lists of valid species for *Chromaspirina*, *Spirinia*, and *Perspiria* below to clarify the distinctions between them. These lists are based on the original and any subsequent descriptions; as many of the original descriptions (especially early ones) lack type material, we often had to rely on short descriptions and/or illustrations.

Genus *Chromaspirina* Filipjev, 1918

Type species

Chromaspirina pontica Filipjev, 1918.

Emended diagnosis (modified from Maria *et al.* 2009 and Muthumbi *et al.* 1995)

Robust body with rounded or rectangular head region and short conical tail; fine body annulations. Annulated or non-annulated head region; body annulations envelop the amphideal fovea partly, entirely, or only begin at posterior edge of amphids. Amphideal fovea uni-, crypto- or multispiral, or loop-shaped. Cephalic setae at anterior edge or further posteriorly alongside amphids. Distinct buccal cavity,

conspicuously cuticularised; large dorsal tooth and smaller subventral teeth; ventral field of denticles may be present. Pharynx with round or oval posterior bulb, sometimes weakly developed, and without cuticularised lumen. Precloacal supplements may be present.

Valid species

C. chabaudi Boucher, 1975. Main diagnostic characters: "... a medium-sized dorsal tooth and two small subventral teeth. Anterior portion with twelve chelohabdia." Drawings show a distinct cuticularised dorsal tooth and subventral teeth (Boucher 1975: fig. 2).

C. crinita Gerlach, 1952. Main diagnostic character: "The dorsal tooth is massive and extraordinarily strong."

C. cylindricollis (Cobb, 1920). Main diagnostic characters: Only an 'onchium' is mentioned, without further comment, but a distinct cuticularised dorsal tooth is visible on the drawing (Cobb 1920: 325).

C. dubia Inglis, 1968. Drawing shows a very large dorsal tooth (Inglis 1968: fig. 53).

C. gerlachi Blome, 1982. Drawing shows a distinctly cuticularised dorsal tooth and subventral teeth (Blome 1982: fig. 20).

C. indica Gerlach, 1963. Drawing shows a very large dorsal tooth and thickly cuticularised subventral teeth (Gerlach 1963: fig. 1).

C. inglisi Warwick, 1970. Main diagnostic character: "... a prominent heavily cuticularized dorsal tooth..."; also clear in drawing (Warwick 1970: fig. 12).

C. lunatica Gerlach, 1965. Main diagnostic character: "...a strong dorsal tooth ..."; also clear in drawing (Gerlach 1965: fig. 13).

C. madagascarensis Gerlach, 1953. Main diagnostic characters: "...a rather large dorsal tooth ..."; drawing shows a large and thick dorsal tooth and subventral teeth (Gerlach 1953: fig. 4).

C. modesta Bussau, 1993. Drawing shows a large, heavily cuticularised dorsal tooth and subventral teeth (Bussau 1993: figs 55–57).

C. multipapillata Jayasree & Warwick, 1977. Main diagnostic characters: "Buccal cavity bearing a dorsal tooth and two small subventral teeth"; drawing unclear. It is difficult to draw a firm conclusion from the description and hence this species is left in this genus.

C. parapontica Luc & De Coninck, 1959. Main diagnostic characters: "Large dorsal tooth..."; drawing shows a large dagger-like dorsal tooth (Luc & De Coninck 1959: fig. 35).

C. pellita Gerlach, 1954 (synonym: *C. renaudae* Boucher, 1975). Drawing shows a very large dorsal tooth and conspicuous subventral teeth (Gerlach 1954: fig. 4).

C. pontica Filipjev, 1918. Main diagnostic character: "Three teeth...: one large dorsal ..., and two small subventrals."

C. thieryi De Coninck, 1943. Main diagnostic character: "...with strong dorsal tooth..."; also clear in drawing (De Coninck 1943: fig. 5).

C. vanreuselae Vershelde & Vincx, 1996. Main diagnostic characters: "...with huge dorsal tooth and smaller single ventral tooth"; also clear in drawing (Vershelde & Vincx 1996: fig. 1).

Species inquirendae

C. amabilis (De Man, 1922). Considered *species inquirenda* by Jensen (1978).

C. cobbi Chitwood, 1938. Considered *species inquirenda* by Jensen (1978).

C. robusta Wieser, 1954. Considered *species inquirenda* by Wieser & Hopper (1967).

Remarks

Chromaspirina cylindricollis (Cobb, 1920) (synonym: *Mesodorus cylindricollis* Cobb, 1920). This species was in our opinion rightly transferred to *Chromaspirina* as it was described with an annulated head region. Maria *et al.* (2009), however, mistakenly showed a drawing of the head capsule of *Pseudochromadora quadripapillata* Daday, 1899 (synonym: *Micromicron cephalatum* Cobb, 1920), in their key to *Chromaspirina* species, instead of the non-annulated head region of *C. cylindricollis* (Maria *et al.* 2009: fig. 26).

Chromaspirina denticulata (Gerlach, 1953). This species was originally described as *Bolbolaimus denticulatus*. Luc & De Coninck (1959) later synonymized *Bolbolaimus* with *Chromaspirina*. However, Jensen (1978) rightly re-established the genus and re-instated *Bolbolaimus denticulatus* Gerlach, 1953 as a valid combination. However, he gave the wrong species authority in his identification key (Cobb, 1920 instead of Gerlach, 1953). Maria *et al.* (2009) included *C. denticula* (Gerlach, 1953) (*erratum?*) in their list of invalid *Chromaspirina* species. In conclusion, we recognize the re-establishment of *Bolbolaimus denticulatus* Gerlach, 1953 as a valid combination (as suggested by Jensen 1978) with the synonyms *Chromaspirina denticulata* (Gerlach, 1953), *Bolbolaimus denticulatus* Cobb, 1920 syn. nov., and *Chromaspirina denticula* (Gerlach, 1953) syn. nov.

Chromaspirina dimorpha (Hopper, 1961) and *C. inflexa* (Wieser, 1954) were rightly transferred back to *Desmodora* by Wieser & Hopper (1967).

Chromaspirina longisetosa Jensen, 1985. This species was transferred to *Bolbolaimus* (*erratum?*) by Muthumbi *et al.* (1995), but later transferred to *Bolbonema* by Vershelde *et al.* (1998). Because this species clearly has a head capsule and cephalic setae located posterior to the amphids, we confirm that it belongs to *Bolbonema*. Thus, we propose the combination *Bolbonema longisetosum* (Jensen, 1985) with the synonyms *Chromaspirina longisetosa* Jensen, 1985 and *Bolbolaimus longisetosus* (Jensen, 1985).

Chromaspirina lunatica Gerlach, 1965 (synonym: *C. lunata* Gerlach, 1965 syn. nov.). Gerlach (1965) described *C. lunatica*, but the species is incorrectly labelled as *C. lunata* in a figure caption (p. 132).

Chromaspirina pellucida (Cobb, 1920) and *C. punctata* (Cobb, 1920) were rightly transferred back to *Bolbolaimus* by Jensen (1978).

Chromaspirina rabosa (Gerlach, 1956). This species was originally described as *Desmodora rabosa* and later transferred to *Chromaspirina* by the same author (Gerlach 1963). Muthumbi *et al.* (1995) argued that the species should be left in the genus *Desmodora* because it has "... a well-developed head capsule with the amphids situated outside the rings." We note, however, that the cephalic setae are situated posterior to the amphids, and this species is therefore transferred to the genus *Bolbonema*. Thus, we propose the combination *Bolbonema rabosum* (Gerlach, 1956) comb. nov. with the synonyms *Desmodora rabosa* Gerlach, 1956 and *Chromaspirina rabosa* (Gerlach, 1956).

Chromaspirina spinulosa (Wieser, 1959). This species was transferred to *Metadesmodora* by Gerlach (1963) and then to *Echinodesmodora* by Blome (1982). Thus, we propose the combination *Echinodesmodora spinulosa* (Wieser, 1959) with the synonyms *Chromaspirina spinulosa* (Wieser, 1959) and *Metadesmodora spinulosa* (Wieser, 1959).

Genus *Perspiria* Wieser & Hopper, 1967

Type species

Perspiria hamata Wieser & Hopper, 1967.

Emended diagnosis (modified from Vincx & Gourbault 1989)

As for *Spirinia* (see below), but amphids almost never completely surrounded by body annulations (seldom more than half of amphids surrounded by body annulations), amphids are entirely surrounded by annuli in some rare cases; tail conico-cylindrical to filiform. Preloacal supplements usually present.

Valid species

P. elongata (Castro *et al.*, 2006) comb. nov. (synonym: *Spirinia elongata* Castro *et al.*, 2006). Main diagnostic characters: "...one very small subventral tooth and two small dorsal teeth." The drawings show amphids completely surrounded by body annulations, but the authors describe a conico-cylindrical tail with annuli which are more evident in the tail region compared to those along the rest of the body; thus, we transfer this species to *Perspiria* (Castro *et al.* 2006: figs 3c, 4).

P. flagellata Vitiello, 1971. Main diagnostic characters: "Amphid situated anterior to cuticle striations or partially surrounded by them"; very long and slender, almost filiform tail (Vitiello 1971: fig. 29).

P. hamata Wieser & Hopper, 1967. Drawing shows amphids only partially located within the body annuli; long and slender, almost filiform tail (Wieser & Hopper 1967: fig. 18).

P. lara (Silva *et al.*, 2009) comb. nov. (synonym: *Spirinia lara* Silva *et al.*, 2009). Main diagnostic characters: "Buccal cavity with one dorsal tooth and two minute ventrosublateral teeth" and "Cuticle with transverse striae..., less obvious in head region than in tail." Drawing shows amphid with annulations to mid-level of amphid only, and tail is described as conico-cylindrical. This species is therefore transferred to *Perspiria* (Silva *et al.* 2009: figs 2–3).

P. megamphida Vincx & Gourbault, 1989. Drawing shows substantial portion of the amphids is located on the non-annulated lip region; conico-cylindrical tail with more prominent annuli (Vincx & Gourbault 1989: fig. 1).

P. mokii Coles, 1987. Main diagnostic character: "...cuticle appears smooth...", hence amphids are not surrounded by annuli; long and slender filiform tail (Coles 1987: fig. 5).

P. papillata Vincx & Gourbault, 1989. Drawing shows anterior half of amphids on non-annulated lip region and posterior half located within the annulated head region; long, conico-cylindrical tail (Vincx & Gourbault 1989: fig. 2).

P. septentrionalis (Cobb, 1914) comb. nov. (synonyms: *Spirinia septentrionalis* (Cobb, 1914) and *Spira septentrionalis* Cobb, 1914). Main diagnostic characters: "From the anus the tail tapers for two-thirds of its length, then becomes cylindroid to the swollen terminus..." Drawings by Wieser (1954: fig. 126) clearly show the amphids in the head region with only their posterior half within the body annulations,

leaving the anterior half on the non-annulated head region. The tail is conico-cylindrical. Thus, this species is transferred to the genus *Perspiria*.

P. striaticaudata (Timm, 1962). Tail long (11–17 abd) and slender with distinct annuli; thus it is transferred to *Perspiria*. Synonym: *Spirina striaticaudata* Timm, 1962.

Species inquirenda

Perspiria sabulicola (Filipjev, 1918/1921) comb. nov. (synonym: *Spirina sabulicola* Filipjev, 1918/1921). This species was described with a ‘long tail (length 4 × width)’ and hence should be transferred to the genus *Perspiria*. However, as the species was described based on only one female, it is regarded as a *species inquirenda*.

Genus *Spirinia* Gerlach, 1963

Type species

Spira parasitifera Bastian, 1865.

Emended diagnosis

Robust body with rounded or conical head region and conical tail, fine body annulations. Annulated head region; body annulations normally completely surround the amphideal fovea, with few exceptions. Spiral amphideal fovea. Buccal cavity narrow, lightly cuticularised; no or small/inconspicuous dorsal tooth, no or minute subventral teeth. Pharynx with small pyriform, oval, or rounded posterior bulb without cuticularised lumen. Precloacal supplements usually absent. Short conical tail.

Valid species

Spirinia gerlachi (Luc & De Coninck, 1959). Main diagnostic characters: “Annulations beginning halfway down the lateral organ... long attenuated conical tail”; also clear in drawings (Luc & De Coninck 1959: fig. 25). Despite the presence of an amphid only partially surrounded by cuticle annulations, this species is left within *Spirinia* because of the shape of the tail (conical), which is the primary trait for differentiating between *Spirinia* and *Perspiria*.

Spirinia gnaigeri Ott, 1977. Amphids almost entirely located within the body annulations in one male, but only the posterior half of another male’s amphid is surrounded by body annulations (compare figs 42 and 43 in Ott 1977); however, as the species has a conical tail, it belongs within *Spirinia*.

S. guanabarensis (Maria *et al.*, 2009) comb. nov. (synonym: *Chromaspirina guanabarensis* Maria *et al.*, 2009). Main diagnostic characters: “Buccal cavity large with an acute dorsal tooth and two smaller ventrosublateral teeth.” However, later in the text it is stated that: “*Chromaspirina guanabarensis* sp. nov. belongs to the group of species characterized by a poorly developed dorsal tooth.” Drawings also show a small buccal cavity with a small dorsal tooth and minute subventral teeth (Maria *et al.* 2009: fig. 1). Tail is conical. This species is therefore transferred to *Spirinia*.

S. hopperi Coles, 1987. Main diagnostic characters: “Cuticle without striations... small dorsal tooth is present in the narrow mouth cavity.” Drawings show a conical tail (Coles 1987: fig. 3).

S. inaurita (Wieser & Hopper, 1967) comb. nov. (synonym: *Chromaspirina inaurita* Wieser & Hopper, 1967). Main diagnostic characters: “Buccal cavity with three small teeth (these teeth are smaller than in most other species of *Chromaspirina* and stress the proximity of the genus to *Spirinia*).”; the drawings are inconclusive, but the description clearly describes small teeth. This species is therefore transferred to *Spirinia*.

S. laevioides Gerlach, 1963. The drawing shows a small buccal cavity, a small dorsal tooth, and amphids located within the annulated head region (Gerlach 1963: fig. 2).

S. laevis (Bastian, 1865) (synonym: *S. pilosa* Allgén, 1935). The drawing shows small teeth, amphids located entirely within the annulated head region, and a short conical tail (Bastian 1865: fig. 204).

S. okemwai (Muthumbi *et al.*, 1995) comb. nov. (synonym: *Chromaspirina okemwai* Muthumbi *et al.*, 1995). We studied the type material, which shows that this species has a cylindrical pharynx with only a slightly swollen terminal bulb, whose shape cannot be described. The teeth are difficult to distinguish and hence cannot be called ‘large’ or ‘distinct’; therefore, we transfer this species to the genus *Spirinia*.

S. parasitifera (Bastian, 1865). Some descriptions of this species show the amphids being only partially surrounded by annulations (Gerlach 1963; Vincx & Gourbault 1989), and others describe specimens with amphids entirely surrounded by annulations (Coles 1987; Vincx & Gourbault 1989); furthermore, additional descriptions and drawings depict either a conical tail (Gerlach 1963: fig. 1; Coles 1987: fig. 3) or a prolonged conical to long conical tail (Wieser & Hopper 1967: fig. 17). Hence, until further examination and comparison of these different specimens can be done, we leave this species within *Spirinia*.

S. parma (Ott, 1972) comb. nov. (synonym: *Chromaspirina parma* Ott, 1972). Main diagnostic characters: “... stoma conical, with a small acute dorsal tooth and two minute ventral teeth...”; this species is therefore transferred to the genus *Spirinia*.

S. schneideri (Villot, 1875). Luc & Deconinck (1959) describe this species with a smooth cuticle, and Coles (1987) describes it “without cuticular striations”. The SEM micrograph by Coles (1987: fig. 9a), however, shows striations surrounding the amphids. The tail is short and conical.

S. sophia Silva *et al.*, 2009. Main diagnostic characters: “Buccal cavity with one dorsal tooth and two minute, ventrosublateral teeth”; clear in drawings, which also show the amphid completely surrounded by cuticle annulations (Silva *et al.* 2009: fig. 6). Tail conical.

Species inquirendae

Spirinia granulata (Allgén, 1929) comb. nov. (synonym: *Spirina granulata* Allgén, 1929). This species was described based on two juveniles only, with very poor drawings and inadequate descriptions. Hence, we have to regard this species as *species inquirenda*.

S. paucispira (Schuurmans Stekhoven, 1950) comb. nov. (synonym: *Chromaspirina paucispira* Schuurmans Stekhoven, 1950). This species was considered *species inquirenda* by Wieser & Hopper (1967) and Muthumbi *et al.* (1995), because the original description was based on a single female specimen. It was stated that the buccal cavity of this species has an “indication of a dorsal tooth”. Based on this character, which is sufficient to distinguish between *Spirinia* and *Chromaspirina*, this species is transferred to the genus *Spirinia* (but remains *species inquirenda* due to the incomplete nature of the original description).

S. similis (Cobb, 1898) (synonym: *Spira similis* Cobb, 1898). Considered invalid by Coles (1987) due to lack of illustrations.

S. tenuicauda (Allgén, 1959) (synonym: *Spirina tenuicauda* Allgén, 1959). This species has to be regarded as a *species inquirenda*, as the only description Allgén made was to write “differing from *Sp. parasitifera*,” and his drawings are inadequate.

Spirinia verecunda sp. nov.

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Figs 1–3; Table 1

Diagnosis

Spirinia verecunda sp. nov. is characterised by a short, stout body, cuticle covered in minute hair-like structures, unispiral amphideal aperture and cryptospiral amphideal fovea, buccal cavity with a small dorsal tooth and minute subventral teeth, eight elongated glands surrounding the anterior portion of the pharynx, large sperm cells, spicules with weak capitulum, and absence of preloacal supplements.

Type material

Holotype

NEW ZEALAND: ♂, NIWA 88379, 20 Feb. 2011, NIWA cruise TAN1103, station 69, central Chatham Rise, 43.331° S, 178.288° E, 350 m.

Paratypes

NEW ZEALAND: 2 ♀♀, NIWA 88380, same data as holotype.

Etymology

The species name is derived from the Latin word *verecundus* (bashful, shy, coy), in reference to the anterior part of the head region deeply folded inwards.

Description

Male

Body stout, cylindrical, pale orange colour, tapering slightly towards both ends. Annulated cuticle, no lateral differentiation; annulations 0.6–0.8 µm apart; cuticle slightly thicker in pharyngeal region than elsewhere (2.2–2.5 vs 1.6–2.0 µm). Cuticle covered with dense layer of minute hair-like structures from posterior to amphid to near tail tip (barely visible under light microscope; Fig. 3A–B); larger, 1 × 5 µm bacteria-like structures with narrow base also attached in pharyngeal region (Fig. 1D). A single protist, 74 µm long and 18 µm wide attached subdorsally near cloaca (Fig. 3E). Short somatic setae arranged in eight longitudinal rows along entire body length.

Blunt, slightly rounded annulated head region with annulations completely surrounding amphid (Fig. 1A–B). Four cephalic setae near anterior edge of amphid; inner and outer labial sensillae not observed because labial region is folded inwards from level of cephalic setae. Cryptospiral amphideal fovea with slightly cuticularised outline and unispiral amphideal aperture (Fig. 3A–B).

Buccal cavity with slightly cuticularised dorsal tooth and minute subventral teeth. Eight elongated glands, 12–17 µm in length, distributed around anterior portion of pharynx just posterior to buccal cavity (Figs 1C–D, 3C). Pharynx muscular, oval-shaped posterior pharyngeal bulb, lumen not cuticularised. Nerve ring at 40–50% of pharynx length. Secretory-excretory system not observed. Cardia 10–12 µm long.

Reproductive system monorchic, with relatively large, outstretched testis situated to the left of intestine. Mature sperm large, globular to elongated in shape, up to 16 µm in length. Short, arcuate spicules with weak capitulum and tapering distally; velum present (Fig. 1G). Gubernaculum with cuneus broadest in middle portion and tapering proximally and distally; poorly developed lateral crurae (Fig. 1H). Preloacal supplements not observed. Tail conical, with two pairs of short subventral setae and one pair of subdorsal setae; three caudal glands restricted to tail region and spinneret present.

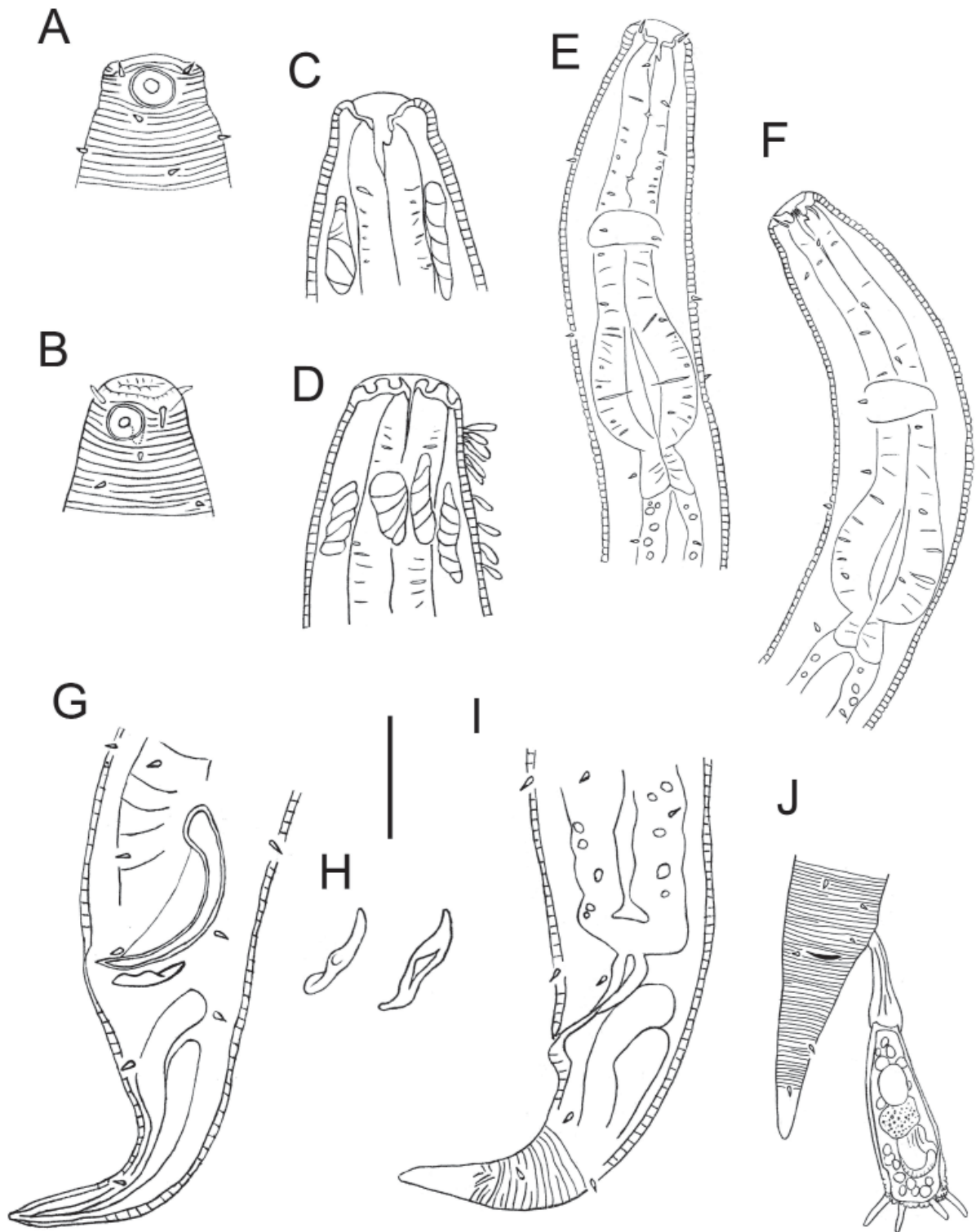


Fig. 1. *Spirinia verecunda* sp. nov. **A.** Surface view of male head. **B–C.** Male head, showing buccal cavity. **D.** Female head, showing bacteria attached to cuticle. **E.** Anterior body region of male. **F.** Anterior body region of female. **G.** Posterior body region of male. **H.** Gubernaculum, with details of crurae (left) and cuneus (right). **I.** Posterior body region of female. **J.** Posterior body region of female, showing attached protist. Scale bar: A–D, I = 20 μ m, E–F = 30 μ m, G = 16 μ m, H = 12 μ m, J = 35 μ m.

Female

Similar to male, but with wider body. One specimen bears a single protist (suctorian) on tail. Reproductive system didelphic, amphidelphic with reflected ovaries situated either both on the right or both on the left of intestine. Vulva located slightly post median. Cuticular pars distalis vaginae and pars proximalis vaginae surrounded by constrictor muscle.

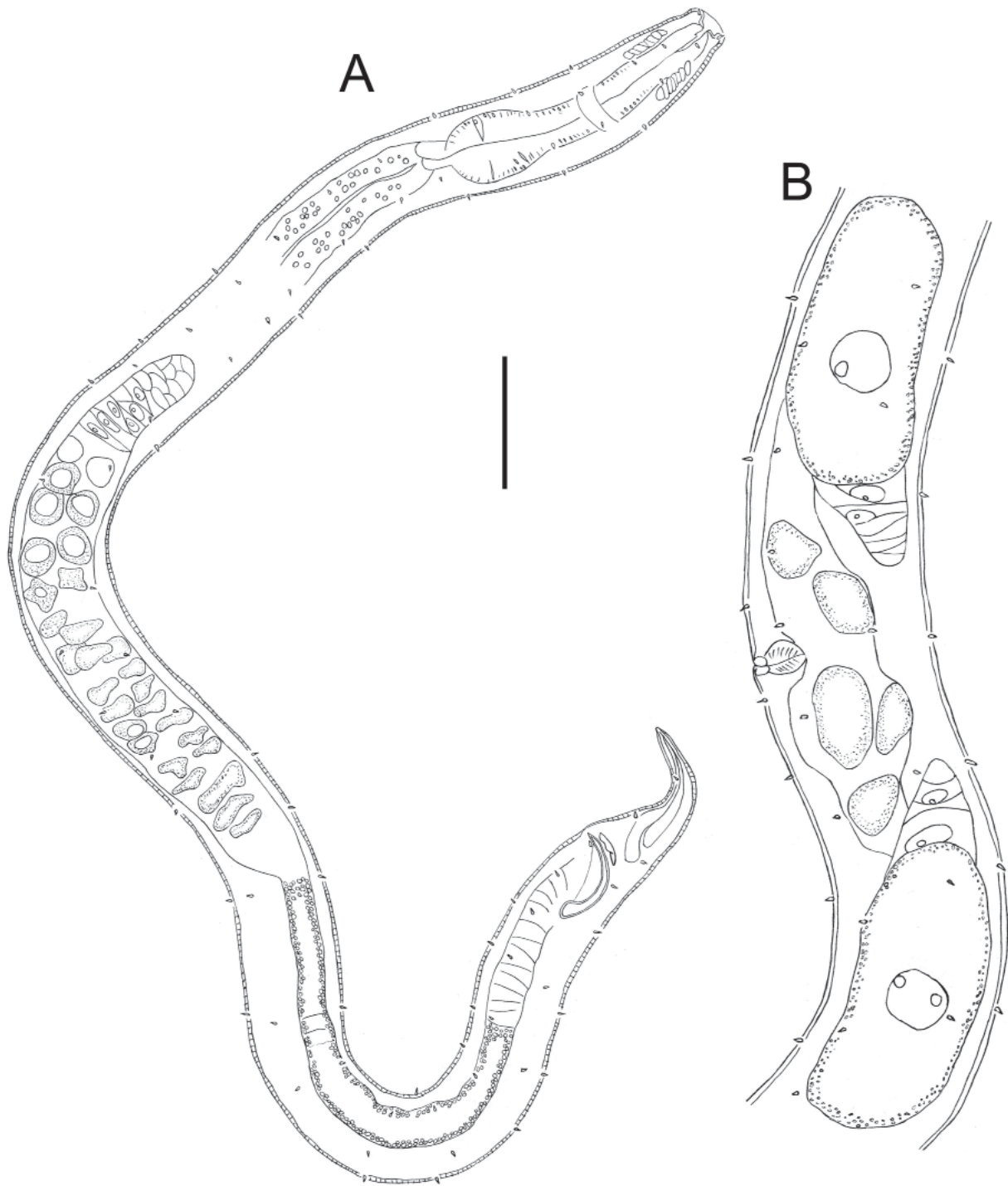


Fig. 2. *Spirinia verecunda* sp. nov. **A.** Entire male. **B.** Female reproductive system. Scale bar: A = 50 μ m, B = 30 μ m.

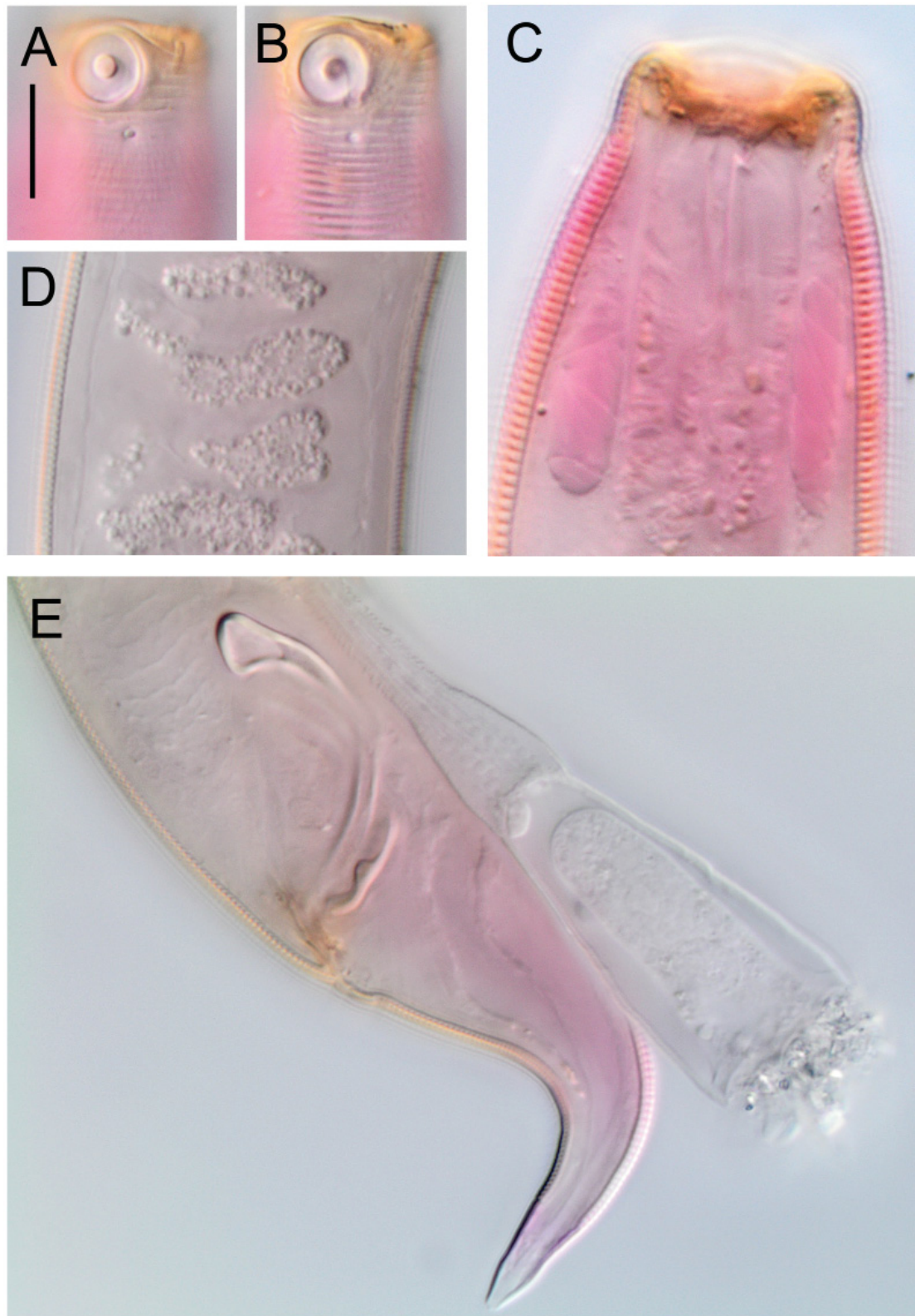


Fig. 3. *Spirinia verecunda* sp. nov., light micrographs. **A.** Male head, showing amphideal aperture and cuticular hair-like structures. **B.** Male head, showing amphideal fovea. **C.** Male anterior body region showing buccal cavity and elongated glands. **D.** Mature sperm cells. **E.** Posterior body region of male, showing copulatory apparatus and attached protist. Scale bar: A–B, D–E = 10 μ m, C = 8 μ m.

Table 1. Morphometrics (μm) of *Spirinia verecunda* sp. nov. and *Stygodesmodora confusa* sp. nov. — a, body length/maximum body diameter; abd, anal body diameter; b, body length/pharynx length; c, body length/tail length; cbd, corresponding body diameter; V, vulva distance from anterior end of body; %V, V/total body length.

	<i>Spirinia verecunda</i> sp. nov.		<i>Stygodesmodora confusa</i> sp. nov.		
	♂ Holotype	♀♀ Paratypes	♂♂ Holotype	♂♂ Paratype	♀♀ Paratypes
n	-	2	-	1	5
L	757	667, 675	1241	795	778–1029
a	22	17	35	28	22–34
b	8	6, 7	11	8	8–10
c	15	13	13	14	12–15
Head diameter	17	17, 18	18	14	14–16
Length of cephalic setae	2	2	7–8	6–9	5–9
Amphid height	6	6, 7	11	6	5–6
Amphid width	6	6, 7	11	6	6–7
Amphid width/cbd (%)	35	33, 41	61	43	40–47
Amphid from anterior end	2	3	4	5	3–7
Nerve ring from ant. end	49	45, 53	68	59	57–62
Nerve ring cbd	32	32, 33	29	25	24–25
Pharynx length	100	100, 107	109	95	92–105
Pharyngeal bulb diameter	26	27	22	20	20–22
Pharyngeal bulb cbd	31	33, 34	29	25	25–28
Max. body diameter	35	39, 40	35	42	30–37
Spicule length	38	-	39	42	-
Gubernaculum length	13	-	10	12	-
Anal body diameter	24	21, 22	28	21	17–20
Tail length	49	51, 52	93	57	62–85
Tail length/abd	2.0	2.4	3.3	2.7	3.5–4.5
V	-	347, 361	-	-	428–558
%V	-	51, 54	-	-	53–55
Vulval body diameter	-	39, 40	-	-	30–37

Remarks

Spirinia verecunda sp. nov. shows similarities with several *Spirinia* and *Chromaspirina* species, i.e., *Spirinia guanabarensis* comb. nov., *S. inaurita* comb. nov., *S. okemwai* comb. nov., *S. parma* comb. nov., *Chromaspirina chabaudi*, and *C. multipapillata*. Of these, *S. verecunda* sp. nov. resembles *S. okemwai* comb. nov. the most in cuticle ornamentation (annulated head region, cuticle with minute hair-like structures), size and shape of the amphids, presence of large sperm cells, and absence of precloacal supplements. *S. verecunda* sp. nov. differs from the latter in having shorter body length (667–757 vs 966–1425 μm), lower values of a (17–22 vs 22–27), shorter cephalic setae (2 vs 3–6 μm), shorter spicules (38 vs 41–50), and shorter gubernaculum (13 vs 19–25). *S. verecunda* sp. nov. also differs from *S. okemwai* comb. nov. in the presence of elongated glands in the anterior region of the pharynx (absent in *S. okemwai* comb. nov.) and the structure of the gubernaculum (hook absent vs dorsally directed proximal hook). *S. verecunda* sp. nov. can most readily be distinguished from *S. inaurita* comb. nov. and *S. parma* comb. nov. by the size of the amphids (in males: 35% cbd in *S. verecunda* sp. nov. vs >

60% cbd in *S. inaurita* comb. nov. and *S. parma* comb. nov.), from *Chromaspirina chabaudi* by the structure of the gubernaculum (not surrounding spicules in *S. verecunda* sp. nov. vs surrounding spicules distally in *C. chabaudi*), from *C. multipapillata* by the absence of precloacal supplements (present in *C. multipapillata*), and from *S. guanabarensis* comb. nov. by its small body size (< 800 µm in *S. verecunda* sp. nov. vs >1800 µm in *S. guanabarensis* comb. nov.) and low values of *a* (17–22 vs 30–48).

Genus *Stygodesmodora* Blome, 1982

Type species

Stygodesmodora epixantha Blome, 1982.

Emended diagnosis (modified from Blome 1982)

Cuticle with coarse annulations; numerous long somatic setae may be present; annulated head region (sometimes intraspecific variation, with the head of some specimens only partially annulated in dorsal and ventral regions). Amphid unispiral or spiral located on amphideal plate; small to medium sized buccal cavity with dorsal tooth and (usually) smaller subventral teeth. Pharynx with rounded or pyriform posterior bulb, without cuticularised lumen. Pre-cloacal supplements present or absent; spicules short, arcuate, and with well-developed capitulum; gubernaculum present.

Valid species

S. bacillicauda (Gerlach, 1963)

S. epixantha Blome, 1982

Species inquirenda

S. rotundicephala (Cobb, 1920)

Stygodesmodora confusa sp. nov.

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Figs 4–7; Table 1

Diagnosis

Stygodesmodora confusa sp. nov. is characterised by a relatively short body (778–1241 µm), spiral amphids with 1.0–1.25 turns, cephalic setae situated at or slightly posterior to mid-level of amphid, and males with four precloacal supplements consisting of short setae on wide bases.

Type specimens

Holotype

NEW ZEALAND: ♂, NIWA 88377, 24 Apr. 2010, NIWA cruise TAN1004, station 92, canyon axis on southern Hikurangi Margin, 41.8921° S, 174.6347° E, 686 m.

Paratypes

NEW ZEALAND: 1 ♂, 2 ♀♀, NIWA 88378, 20 Feb. 2011, NIWA cruise TAN1103, station 69, central Chatham Rise, 43.331° S, 178.288° E, 350 m; 3 ♀♀ (same data as other paratypes) were measured to provide morphometric data and then processed for scanning electron microscopy.

Etymology

The species name is derived from the Latin adjective *confusus*, meaning confused, perplexed or obscure (feminine form used, as *-dora* is feminine), and refers to the close affinities of this species with other desmodorid genera (see Remarks), which resulted in initial confusion in the placement of this species.

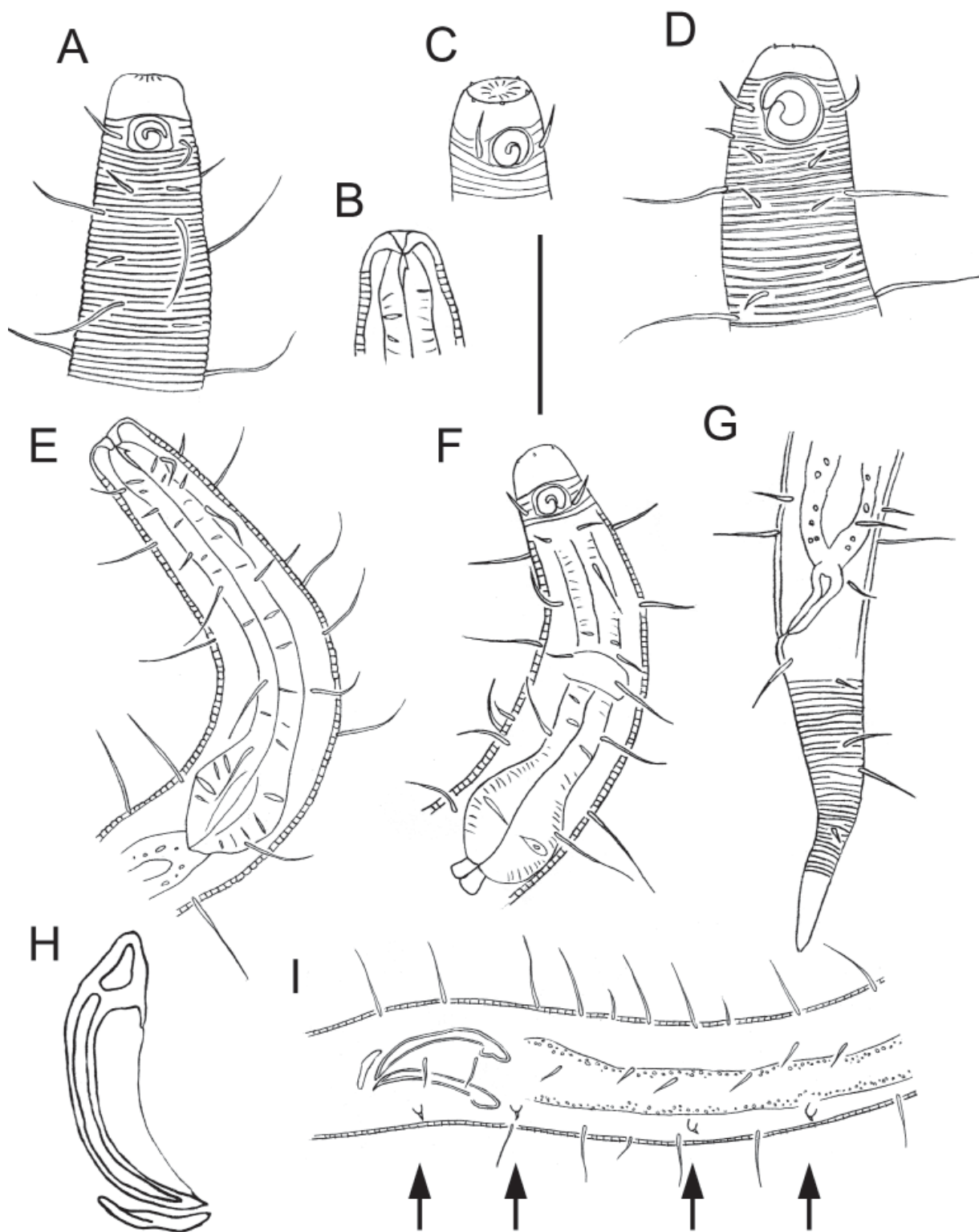


Fig. 4. *Stygodesmodora confusa* sp. nov. **A.** Anterior body region of female. **B.** Male head (holotype). **C.** Male head (paratype). **D.** Male head (holotype). **E–F.** Anterior body region of female. **G.** Female posterior body region. **H.** Right spicule and gubernaculum. **I.** Male copulatory apparatus. Arrows show position of pre-cloacal supplements. Scale bar: A–D = 30 μm , E–G = 36 μm , H = 20 μm , I = 40 μm .

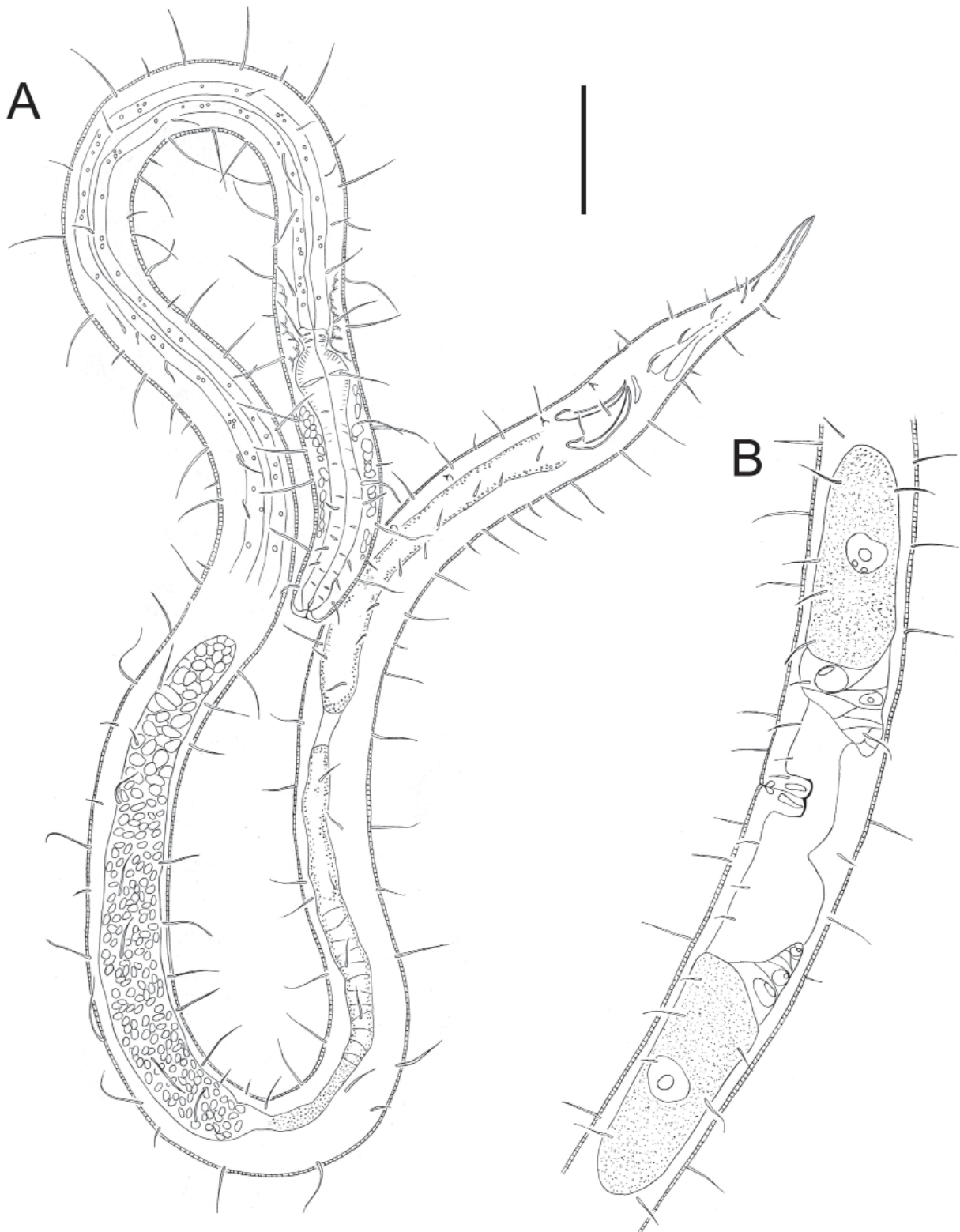


Fig. 5. *Stygodesmodora confusa* sp. nov. **A.** Entire male. **B.** Female reproductive system. Scale bar: A = 50 μ m, B = 36 μ m.

Description

Male

Relatively short cylindrical body, pale golden colour, tapering slightly towards both ends. Cuticle 0.9–1.4 μm thick, with coarse annuli, approximately 1 μm apart, no lateral differentiation. Ventral ala absent. Somatic setae of different sizes (4–19 μm long; Fig. 5A), set out in eight longitudinal rows in anterior one fifth of body length and in six longitudinal rows along rest of body except on tail, where they are irregularly arranged.

Annulated head region with annulations completely surrounding amphid (Figs 6A–C, 7C); in some specimens, there is a seemingly non-annulated head region, but some partial annulation of the dorsal

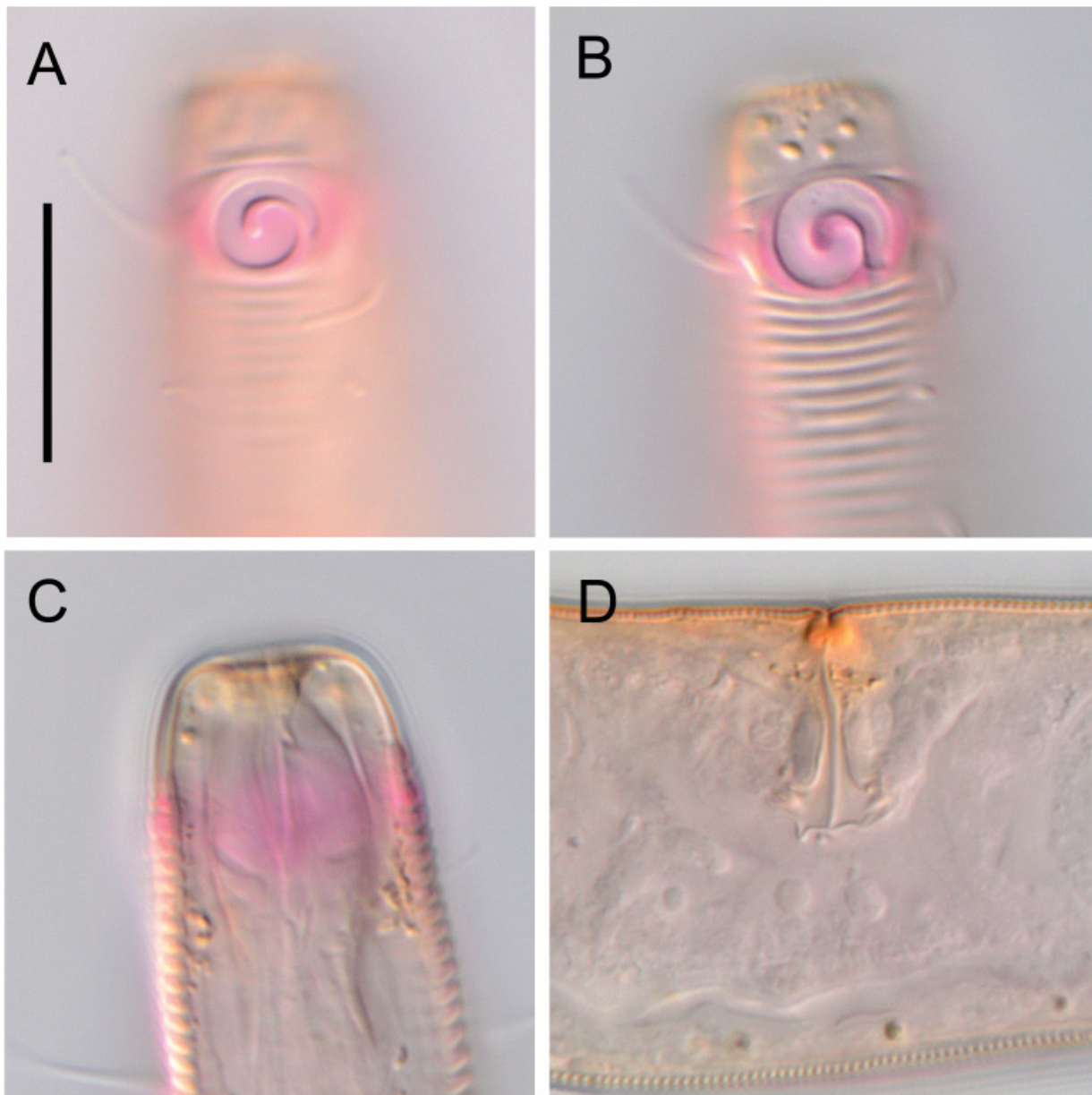


Fig. 6. *Stygodesmodora confusa* sp. nov., light micrographs of female. **A.** Head region showing amphideal aperture. **B.** Head region showing amphideal fovea. **C.** Head region showing buccal cavity. **D.** Vulva. Scale bar: A–C = 15 μm , D = 18 μm .

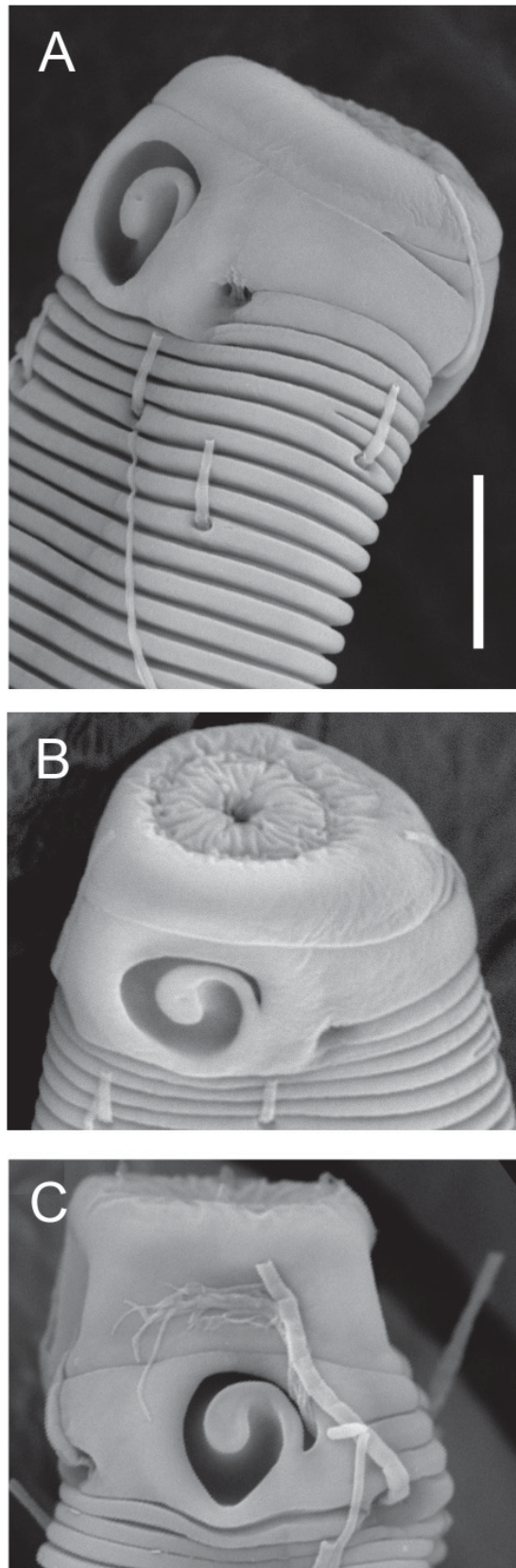


Fig. 7. *Stygodesmodora confusa* sp. nov. Scanning electron micrographs. Female head (three different specimens). Scale bar = 5 μ m.

and ventral sides of the head can be observed (Fig. 7A–B); both forms are considered annulated head regions, even though the degree of annulation differs between the two morphotypes. Labial region folded inwards in all specimens. Six papilliform outer labial sensillae and four cephalic setae, 44–57% cbd long, situated at or slightly posterior to mid-level of amphid. Spiral amphideal fovea, 1.2–1.4 turns, located on a cuticularised amphideal plate (Figs 6B, 7B), larger in holotype than in paratype (~0.6 vs 0.4 cbd, respectively; Fig. 4C–D); amphideal aperture with similar shape to amphideal fovea but tapering proximally (compare Fig. 6A and 6B).

Buccal cavity small, with small dorsal tooth; subventral teeth not observed (Fig. 6C). Pharynx muscular, slightly swollen at anterior extremity, and with pyriform bulb at posterior extremity. Nerve ring at 60–62% of pharynx length. Secretory-excretory system not observed. Cardia short.

Reproductive system monorchic, with single anterior testis situated to the right of intestine, 53–63 μm long, outstretched and opposed. Mature sperm small, globular, $2\text{--}3 \times 3\text{--}5 \mu\text{m}$. Short, arcuate spicules tapering distally; well-developed capitulum and broad velum (Fig. 4H). Small, plate-shaped gubernaculum without crurae. Four pre-cloacal supplements consisting of short setae on broad bases (Fig. 4I), 23–45 μm apart, beginning 15 μm anterior to cloaca. Tail conical, with three small caudal glands and spinneret.

Female

Similar to males. Female reproductive system didelphic, amphidelphic with reflected ovaries situated either to the right or left of intestine, with anterior and posterior ovaries always situated on opposite sides. Vulva located slightly post median. Cuticular pars distalis vaginae and pars proximalis vaginae surrounded by constrictor muscle. Mature eggs $66\text{--}73 \times 25 \mu\text{m}$.

Remarks

Stygodesmodora confusa sp. nov. can most easily be differentiated from the other two species of the genus by the location of the cephalic setae at mid-level of amphids (vs anterior to amphids in *S. bacillicauda* and *S. epixantha*). *S. confusa* sp. nov. also differs from *S. bacillicauda* in the presence of pre-cloacal supplements (absent in *S. bacillicauda*) and the absence of lateral crurae on the gubernaculum (present in *S. bacillicauda*), and from *S. epixantha* by the presence of numerous long somatic setae (short somatic setae in *S. epixantha*).

Stygodesmodora confusa sp. nov. closely resembles species of other desmodorid genera, and distinguishing it from these other species requires careful examination of the head region. *S. confusa* sp. nov. resembles *Echinodesmodora moensi* Verschelde & Vincx, 1996 in the absence of a cephalic capsule, numerous long somatic setae, and cephalic setae at or slightly posterior to mid-level of amphids, but can be differentiated from the latter by the absence of pharyngeal lumen cuticularisation (present in *E. moensi*), amphid shape (≤ 1.25 turns vs 1.5–2.0 turns in *E. moensi*), presence of setose precloacal supplements (absent in *E. moensi*), and the absence of knotty protrusions on the tail (present in *E. moensi*). The most important distinction, however, is the presence of an amphideal plate in *S. confusa* sp. nov. This species is also superficially similar to species of *Bolbonema*, i.e., *B. brevicolle* (Cobb, 1920), *B. longisetosum* (Jensen, 1985) comb. nov., and *B. spiralis* Hourston & Warwick, 2010, in the presence of both short and long somatic setae, cephalic setae just posterior to mid-level of amphid, and in the structure of the copulatory apparatus. The amphideal plates in *S. confusa* sp. nov. give a swollen appearance to the head region laterally (see Fig. 7A), and in some specimens there is a gap in the body annulations in the head region (compare Fig. 7A and 7C), which may be wrongly interpreted as a non-annulated head region or even a head capsule. *S. confusa* sp. nov., however, is clearly defined by an annulated region, and not a head capsule, because (1) the swollen part of the head is mostly restricted

to the area surrounding the amphids (i.e., the amphideal plates), (2) the cuticle is the same thickness in head and body regions (see Fig. 6C), and (3) annulations are present dorsally and ventrally at least to mid-level of amphids, with one continuous annulation anterior to the amphid (see Figs 6B, 7A–C). The genus *Bolbonema*, however, is characterized by a globular head capsule (i.e., conspicuously thicker cuticle and absence of annulations; Verschelde & Vincx 1996; Verschelde *et al.* 1998).

Discussion

Muthumbi *et al.* (1995) provided an emended diagnosis for *Chromaspirina* and, more recently, Silva *et al.* (2009) provided an emended diagnosis for *Spirinia*. Maria *et al.* (2009) briefly discussed the relationship between *Chromaspirina* and *Spirinia*. They identified the size of the buccal cavity and dorsal tooth, and the shape of the posterior pharyngeal bulb as the main distinguishing features between the two genera and noted that several *Chromaspirina* species have a small dorsal tooth which “emphasises the close relationship of this genus with *Spirinia*...” and that “further investigation is needed into the relationships [of] *Spirinia* with *Chromaspirina*” (Maria *et al.* 2009: 28). In his review of *Spirinia*, Coles (1987) identified buccal morphology as the main distinguishing feature between the two genera.

We argue that the shape of posterior pharyngeal bulb and the presence or absence of preloacal supplements show too much overlap to be useful diagnostic features to distinguish *Spirinia* and *Chromaspirina*. For example, *S. okemwai* comb. nov. and *S. guanabarensis* comb. nov. lack preloacal supplements (a trait usually associated with *Spirinia*), but possess relatively weakly developed, oval-shaped posterior pharyngeal bulbs (a trait usually associated with *Chromaspirina*; see Maria *et al.* 2009). *S. sophia* Silva *et al.*, 2009 also appears to be intermediate between the two genera: it possesses preloacal supplements (absent in all other *Spirinia* species but present in some *Chromaspirina* species) and a round to oval-shaped posterior pharyngeal bulb (despite *Spirinia* being defined as having a round posterior pharyngeal bulb; see Silva *et al.* 2009). Differences in the morphology of the pharyngeal bulb and preloacal supplements are not reliable traits to distinguish between *Chromaspirina* and *Spirinia* because (1) differences in the shape of pharyngeal bulbs are often subtle (e.g., pyriform *vs* elongated or oval) and (2) preloacal supplements in these two genera are often difficult to distinguish and may have been omitted in some species descriptions. Buccal morphology provides the clearest and most consistent way to differentiate between *Spirinia* and *Chromaspirina* because it can easily be observed; morphological features of the head region are also the most important traits for differentiating between desmodorid genera.

Perspiria was originally described as a subgenus of *Spirinia* by Wieser & Hopper (1967). The only distinguishing feature of this subgenus given by the latter authors was “the more prominently striated and flagellate tail.” Coles (1987) also gave the same distinguishing features between the two subgenera. Vincx & Gourbault (1989) later raised *Perspiria* to generic status and included two key characteristics in their diagnosis of the genus: amphids only partially surrounded by cuticle annulations and a “prominently striated” and “filiform” tail, which we interpret as a coarsely annulated, conico-cylindrical tail from the drawings (see figs 1 and 2 in Vincx & Gourbault 1989). Some *Spirinia* species, however, have coarsely annulated (e.g., *S. verecunda* sp. nov.) or conico-cylindrical tails (e.g., *S. septentrionalis* (Cobb, 1914)), and others have amphids not completely surrounded by the body annulations (e.g., *S. lara* Silva *et al.*, 2009). Here, we propose to differentiate between *Spirinia* and *Perspiria* primarily based on tail shape (conical *vs* conico-cylindrical to filiform), as well as position of amphids relative to cuticle annulations (entirely *vs* partially surrounded), and have suggested nomenclatural changes to reflect these distinctions.

The monospecific genus *Spirodesma* was recently described by Cavalcanti *et al.* (2009) from continental slope sediments in the Southwest Atlantic. The authors argued that the genus is most similar to *Chromaspirina* based on the rounded shape of the head, annulated cuticle, spiral amphideal fovea, and

conical tail. We consider these arguments invalid because (1) an annulated cuticle is also a characteristic of some *Spirinia* (e.g., *Spirinia verecunda* sp. nov.) and *Perspiria* species (e.g., *P. papillata* Vincx & Gourbault, 1989), (2) the spiral amphideal fovea in *Spirodesma* is in fact very similar in shape to the cryptospiral amphideal fovea found in some *Spirinia* species (e.g., *S. verecunda* sp. nov.) and to the spiral amphideal fovea of *Perspiria papillata*, and (3) the tail of *Spirodesma* is conico-cylindrical (as stated in the original description), not conical. In addition, head shape is not a particularly informative trait for differentiating between genera. In our opinion, *Spirodesma* is most closely related to *Perspiria* because of the similar buccal cavity (narrow with small or minute teeth), the position of the amphids (only partially surrounded by cuticle annulations), and the shape of the tail (conico-cylindrical). The only difference between these genera appears to be the relative size of the teeth: *Perspiria* is characterised by a narrow, lightly cuticularised buccal cavity with no or a small/inconspicuous dorsal tooth and no or minute subventral teeth, while *Spirodesma* is characterised by a narrow, lightly cuticularised buccal cavity with three small, equal teeth. *Spirodesma* and *Perspiria* may therefore need to be synonymised in the future as more information becomes available on the former genus.

Stygodesmodora rotundicephala (Cobb, 1920) was originally described as *Amphispira rotundicephala* and was included in the World Register of Marine Species list of *Stygodesmodora* species at the time the present study was conducted (WoRMS Editorial Board 2014). The original description, which is based on a single juvenile specimen, clearly shows a head capsule, whereas no amphideal plate was described. Based on the drawing, the specimen/species could possibly belong in *Zalonema*, but, as the original species description of *Amphispira rotundicephala* was based only on one juvenile, we regard *A. rotundicephala* Cobb, 1920 to be a *species inquirenda*.

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