# REVISION OF DESMODORA WITH DESCRIPTIONS OF NEW DESMODORIDS (NEMATODA) FROM HYDROTHERMAL VENTS OF THE PACIFIC

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In this article four species of Desmodoridae, *Desmodora alberti* sp. nov., *Desmodora marci* sp. nov., *Desmodorella balteata* sp. nov. and *Desmodorella spineacaudata* sp. nov. (Nematoda: Desmodoridae), are described from hydrothermal vents of the Pacific. The genus *Desmodora* is revised and lists of valid species are provided; four subgenera are reinstated as genera; *Xenodesmodora* is regarded as genus inquirendum. Definitions of some morphological structures are given.

#### INTRODUCTION

Free living marine nematodes belonging to the family Desmodoridae have been mentioned in most of the assemblages studied from deep sea sediments, but always in few numbers, their relative abundance reaching a maximum of 1% of the total bulk (Soetaert & Heip, 1995). From a manganese nodule area of the eastern South Pacific, however, seven genera were recorded, corresponding to 4.7% of the infauna (Bussau, 1993). Sampling sites where nematodes species composition are known, have been listed recently (Soetaert & Heip, 1995; Soetaert et al., 1995).

The report of 'very large numbers of nematodes belonging to the closely related families Epsilonematidae and Draconematidae' in hydrothermal vents of the East Pacific (Dinet et al., 1988), was thus quite surprising. Now, the advanced study of this material indicates clearly that all the draconematids recorded belong to one species of a new genus to be described in the near future (Decraemer & Gourbault, in press). But, contrary to the report of Dinet et al. (1988), no epsilonematids were found; the numerous specimens recorded appeared to correspond to three new species of Desmodoridae. They are described below, together with a fourth desmodorid species collected from the Basin of Lau-Fidji in south-western Pacific.

Describing these species, again required the question of the status of the genus *Desmodora* de Man, 1889 (*sensu* Lorenzen, 1981) and its members, and with it the urge for a revision.

#### MATERIALS AND METHODS

The specimens of both new species of *Desmodorella*, and of *Desmodora alberti* sp. nov. were found in the sediment samples from hydrothermal sites of the Guyamas Basin in the East Pacific Rise (1981–1982, with the submersible 'Alvin', Woods Hole Oceanographic Institution, USA). Site and methodology are described in Dinet et al. (1988). The specimens of *Desmodora marci* sp. nov. were sorted out together with draconematid specimens in the Laboratoire Arago (Banyuls-Sur-Mer, France) after the BIOLAU cruise in south-western Pacific back-arc basins, the North Fiji and Lau Basins (Mai, 1989; French submersible 'Nautile'; see Desbruyères et al., 1994).

Specimens were fixed with warm formalin (4%), transferred over an alcohol-glycerine solution to glycerine by an adapted method of Seinhorst (1959; modified by De Grisse, 1965), and mounted on Cobb slides (Cobb, 1917).

Drawings were made with the aid of a camera lucida on a Leitz Diaplan microscope.

Scanning electron microscope (JEOL JSM 840) preparation starts from glycerine mounted specimens which are hydrated dropwise with distilled H<sub>2</sub>O (over a period of 4 h); the specimens are washed in an ultrasonic bath; dehydration in alcohol is done stepwise, first in a 25% absolute ethanol—water solution (12 h), followed by a bath of pure absolute ethanol (also 12 h); the specimens are then dried with the standard critical-point-method (with a CPD 020, Balzern Union), mounted on stubs and coated with 20–25 nm of gold (SCD 040, Balzers Union). Between hydration and dehydration, the specimens are not transferred to OsO<sub>4</sub>: this step in preparation is futile as the fatty acids are already washed out from the specimens by the alcohol-based transfer to glycerine.

Type specimens are deposited in the nematode collections of the Muséum National d'Histoire Naturelle, Paris (MNHN, France) and the Zoology Institute (ZIRUG) and the Marine Biology Section (MBRUG) of the University of Gent (Belgium).

#### Abbreviations used in tables

a, body length divided by maximum body diameter; abd, anal body diameter; amph%, diameter of the amphid as a percentage of the corresponding head diameter; aw, amphidial width; b, body length divided by pharyngeal length; bdcs, body diameter at level of the cephalic setae; bdnr, body diameter at level of nerve ring; c, body length divided by tail length; cardia, length of the cardia; cs, length of cephalic setae; da, distance from anterior to anus; dcs, distance from anterior edge to cephalic setae; dnr, distance from anterior edge to nerve ring; dv, distance from anterior to vulva; gub, length of gubernaculum measured along the arc; hw, head width; L, body length; mbd, maximum body diameter; mbdph, maximum body diameter at level of the pharynx; ph, pharyngeal length; spic, length of spicules measured along the arc; t, tail length; tmr, length of non-annulated tail end; V, position of vulva as a percentage of the total body length from anterior.

#### REVISION OF DESMODORA DE MAN, 1889

#### Family DESMODORIDAE Filipjev, 1922

According to the taxonomy of Lorenzen (1981; adapted and translated to English in 1994) the genus *Desmodora* de Man, 1889 comprises six subgenera: *Bolbonema*, *Croconema*, *Desmodora*, *Pseudochromadora*, *Xenodesmodora*, and *Zalonema*; Lorenzen (1976) regards *Desmodorella* as a synonym of *Desmodora*. Allowing such a great pool of subgenera and hence sometimes very different species in one large genus has lead to a situation where the members of *Desmodora* show a large variety of characters, rendering the genus an image of disorder and unidentifiable. In recent years, already *Croconema* Cobb, 1920 (in Gourbault & Vincx, 1990), *Pseudochromadora* Daday, 1899 (in Gourbault & Vincx, 1996) Muthumbi et al., 1995) and *Zalonema* Cobb, 1922 (in Verschelde & Vincx, 1996) have been treated or were re-established as separate genera.

Based on the presence of separate combinations of characters, the species can be grouped in separate entities and hence the subgenera are re-established to genus level with emended diagnoses.

For Bolbonema, Croconema, and Pseudochromadora, only a short summary of main characters is given together with a list of species without further comment as the elaborate emended diagnoses together with the descriptions of newly found species will be published in a next article. An elaborate genus diagnosis of Zalonema Cobb, 1920 has already been published in previous work (Verschelde & Vincx, 1996). Xenodesmodora is regarded to be a genus inquirendum.

Lists of species are based on the Bremerhaven checklist of Gerlach & Riemann (1973), updated, altered and adapted to the revised standards. The declension of every species name was grammatically checked and has been altered where necessary.

Bolbonema Cobb, 1920

Synonym

Desmodora (Bolbonema) (Cobb, 1920) Gerlach, 1963.

Diagnosis

Desmodorinae. Globular head capsule; cephalic setae located posterior to the fovea amphidialis<sup>1</sup>; long and shorter somatic setae (the name is partially derived from the Greek word *nema* meaning thread; its gender is neutral).

In descriptions of most members of the Desmodoroidea 'amphid' is used for what in fact is the fovea amphidialis, a part of the actual amphid (Coomans, 1978). In some members however, (e.g. genus *Dracognomus* Allen & Noffsinger, 1978) the fovea amphidialis is sunk within the cuticle of the head capsule and the organ opens only to the outside through a small pore which is called the apertura amphidialis (Coomans, 1978). Here in the two new species of *Desmodora* and in *Desmodorella balteata* sp. nov., it is observed that what is visible superficially of the 'amphids' is much narrower to slit-like compared to the true size of the fovea amphidialis (Figure 1A, 4C–E; compare also Figure 6A with 9A); so in these species we find a long, narrow or slit-like cryptospiral to multispiral apertura amphidialis.

Type species

Bolbonema brevicolle Cobb, 1920.

List of valid species

Bolbonema brevicolle Cobb, 1920 (syn. Desmodora (B.) brevicollis (Cobb, 1920) Gerlach, 1963); B. longisetosum (Jensen, 1985) comb. nov. (syn. Chromaspirina longisetosa Jensen, 1985).

#### Croconema Cobb, 1920

Synonym

Aculeonchus Kreis, 1928; Desmodora (Croconema) (Cobb, 1920) Allgén, 1959.

Diagnosis

Desmodorinae. Thick body cuticle; coarse annuli; long head capsule; fovea amphidialis located anteriorly on the head capsule; many subcephalic setae arranged in three (or more) circles.

Type species

Croconema cinctum Cobb, 1920.

List of valid species

Croconema boucheri Ott, 1976 (syn. Croconema aff. longiseta in Boucher, 1973; Desmodora (Croconema) boucheri Ott, 1976). Croconema cinctum Cobb, 1920 (syn. Desmodora (C.) cincta (Cobb, 1920) Gerlach, 1963). Croconema longiseta Schuurmans Stekhoven, 1950 (syn. Desmodora (Xenodesmodora) longiseta (Stekhoven, 1950) Gerlach, 1963 syn. nov.); Croconema mammillatum Steiner & Hoeppli, 1926 (syn. Desmodora (C.) mammillata (Steiner & Hoeppli, 1926) Gerlach, 1963). C. mawsonae Inglis, 1968 (syn. Desmodora (C.) mawsoni (Inglis, 1968) Gerlach & Riemann, 1973. Gerlach & Riemann (1973) changed the species name from mawsonae to mawsoni (lapsus linguae?) this, however, is not correct. Croconema mediterraneum Wieser, 1954 (syn. Desmodora (C.) mediterranea (Wieser, 1954) Gerlach, 1963). Croconema otti Gourbault & Vincx, 1990. Croconema ovigerum Ott, 1976. Croconema sphaericum (Kreis, 1928) Luc & De Coninck, 1959 (syn. Aculeonchus sphaericus Kreis, 1928; Desmodora (C.) sphaerica (Kreis, 1928) Kreis in Wieser, 1954a);. Croconema stateni (Allgén, 1928) Wieser, 1954 (syn. Desmodora stateni Allgén, 1928; Desmodora armata Ditlevsen, 1930; Desmodora reducta Allgén, 1953; Desmodora stateniaberrans Allgén, 1953; Desmodora parasitifera Allgén, 1949 (nom. nud., in Gerlach, 1963)). Croconema torquens (Gerlach, 1963) comb. nov. (syn. Desmodora torquens Gerlach, 1963; Desmodora (Xenodesmodora) torquens (Gerlach, 1963) Gerlach, 1964 syn. nov.).

The species *C. stateni* needs special attention. Gerlach (1963) discussed that the original specimens of Allgén (1928) are different to specimens found and described as *C. stateni* (Allgén, 1928) by Wieser (1954b) are not the same species. In the same article, Gerlach synonymized *Desmodora armata*, *D. reducta*, *D. parasitifera*, and *D. stateniaberrans* with the

original *D. stateni* of Allgén. However, as the original species was described only from a female, there is no real basis to reject or accept differences between the original specimens and those of Wieser. Furthermore, the description of the male of *D. armata* by Ditlevsen (1930) agrees with the descriptions of the specimens of *C. stateni* of Wieser and of Pastor de Ward (1988). As Gerlach accepted the species of Ditlevsen as a synonym of Allgén's species, we conclude that all these species and specimens represent and are synonyms with *Croconema stateni* (Allgén, 1928) Wieser, 1954.

In the same article, Gerlach proposes *C. cinctum* Cobb, 1920 and *C. stateni* (of Allgén) as possible synonyms; we do not agree with this notion as Cobb (1920) described his species having a tail of which the non-annulated tail end is half of the total tail length; this is clearly not the case in *C. stateni*.

#### Incertae sedis

Desmodora (Croconema) punctata Jensen, 1985 is not accepted as a member of the genus Croconema, but as the descriptions and drawings are not exclusive enough to grant an opinion onto the true position of this species, it is regarded as an incertae sedis till the type material can be studied.

#### Species inquirendae

The following species are considered as species inquirendae because of incomplete or inadequate descriptions: *C. acrospiculum* (Allgén, 1951) Wieser, 1954; sp. inq. in Wieser, 1954b (syn. *Desmodora acrospiculum* Allgén, 1951). *Croconema pararotundicapitata* (Allgén, 1959) Gerlach, 1963; sp. inq. in Gerlach, 1963 (syn. *Desmodora pararotundicapitata* Allgén, 1959). *Croconema rotundicapitata* (Allgén, 1959) Gerlach, 1963; sp. inq. in Gerlach, 1963 (syn. *Desmodora rotundicapitata* Allgén, 1959).

#### Desmodora de Man, 1889

# Synonym

Mastodex Steiner, 1921.

# Emended diagnosis

Desmodorinae. Cylindrical body with well-developed head capsule and short conical to long conico-cylindrical tail. Fine, short somatic setae arranged in six or eight longitudinal rows. Distinct body annuli slender (i.e. short) to coarse. No special ornamentation or appendages.

Distinct head capsule consisting of a short or long lip region, followed by a large main part with distinctly thicker inner layer of the cuticle, on which the fovea amphidialis and, if present, the subcephalic setae are located; cephalic setae are located either in the lip region or on the main part of the head capsule. A fine sutura can be visible between lip region and main part of the head capsule; the head capsule can either be smooth or partly to entirely ornamented with small vacuoles (inner cuticle). Four cephalic setae located in front of or at the level of the anterior edge of the

fovea amphidialis; subcephalic setae absent or present, when present few in number and mainly located posterior to the fovea amphidialis; few additional setae<sup>2</sup> can be present when subcephalic setae are absent. Distinct fovea amphidialis cryptospiral to multispiral, seldom loop-shaped, of which the apertura amphidialis is equally sized with or smaller than the fovea amphidialis.

Buccal cavity with large dorsal tooth and two (seldom one) subventral teeth. Cylindrical pharynx with muscular endbulb.

Male reproductive system monorchic; short spicules arched, capitulum present, velum present but often obscure. Pore-like precloacal supplements can be present. Female reproductive system didelphic, amphidelphic with reflected ovaries (*dora* meaning 'skin'; Greek, noun, feminine).

## Differential diagnosis

Desmodora is related to and resembles the following genera: Croconema Cobb, 1920; Desmodorella Cobb, 1933; Pseudochromadora Daday, 1899; Pseudodesmodora Boucher, 1975; and Zalonema Cobb, 1922. Desmodora can be distinguished from Croconema by the combination of the following characters: finer body annuli without ornamentation (annuli longer (more coarse), often ornamented with inconspicuous ridges in Croconema); fine somatic setae vs short, broad and distinct somatic setae; head capsule without or with few subcephalic setae vs many subcephalic setae arranged in three circles; slender conical tail vs broad tail in Croconema. Desmodora can be distinguished from Desmodorella by the absence of longitudinal rows of spines on the body cuticle, which presence is typical for Desmodorella. Desmodora can be distinguished from Pseudochromadora by the absence of lateral alae. Desmodora can be distinguished from Zalonema by the combination of the following characters: more coarse annuli (finer and more numerous in Zalonema); shape of the head capsule (rounded-triangular in Zalonema); multispiral fovea amphidialis less than two turns (slender fovea amphidialis two turns or more in Zalonema); pharynx (slender with pyriform endbulb in Zalonema); and shape of male spicules (no velum in Zalonema). Desmodora can be distinguished from Pseudodesmodora by the absence of an amphidial plate.

# Type species

Desmodora communis (Bütschli, 1874) de Man, 1889 (syn. Spilophora communis Bütschli, 1874 (erratum in Gerlach & Riemann (1973): 'Spiliphera')).

<sup>&</sup>lt;sup>2</sup>Additional setae (see also Verschelde & Vincx, 1994, 1995) is a term used for small and slender setae which are located on a head capsule, but are not true subcephalic setae and so are not regarded as a genus characteristic (which is normally the case for subcephalic setae). Additional setae are much weaker and more slender in shape than subcephalic setae; they often differ in numbers, position and even presence according to the specimen within a single species. They also often appear asymmetrically. It is because of the 'non-constant features' that they are regarded to be different than subcephalic setae and not to be representable as a genus character.

List of valid species

Desmodora alberti sp. nov. Desmodora brachypharynx Allgén, 1947 (syn. D. (Pseudochromadora) brachypharynx (Allgén, 1947) Gerlach, 1963). Desmodora californica Allgén, 1947. Desmodora communis (Bütschli, 1874) de Man, 1889 (syn. Spilophora communis Bütschli, 1874; Desmodora serpentulus de Man, 1889; Desmodora serpentulus subsp. suecica Allgén, 1929; Desmodora gracilis Kreis, 1928; Desmodora leucocephala Schulz, 1932; Desmodora problematica Allgén, 1929). Desmodora conica Vitiello, 1971. Desmodora coniseta Schuurmans Stekhoven, 1950 (syn. D. (Pseudochromadora) coniseta (Schuurmans Stekhoven, 1950) Gerlach, 1963). Desmodora cuddlesae Inglis, 1963. Desmodora deconincki Inglis, 1968 (syn. D. (Pseudochromadora) deconincki (Inglis, 1968) Gerlach & Riemann, 1973). Desmodora dimorpha Hopper, 1961 (syn. Chromaspirina dimorpha (Hopper, 1961) Gerlach, 1963.). Desmodora gerlachi Vitiello, 1971 (syn. D. conocephala sensu Gerlach, 1963; D. cf. tenuicauda sensu Gerlach, 1958). Desmodora granulata Vincx & Gourbault, 1989. Desmodora inflexa Wieser, 1954 (syn. Chromaspirina inflexa (Wieser, 1954) Gerlach, 1963). Desmodora marci sp. nov. Desmodora masira Warwick, 1973. Desmodora microchaeta Allgén, 1929 (syn. D. (Pseudochromadora) microchaeta (Allgén, 1929) Gerlach, 1963. Desmodora macramphis Stekhoven, 1950 (in Gerlach, 1963; drawing of male head capsule doubtful: no head capsule?)). Desmodora minuta Wieser, 1954. Desmodora nani Murphi, 1965. Desmodora nini (Inglis, 1963) comb. nov. (syn. Desmodora (Xenodesmodora) nini (Inglis, 1963) Wieser & Hopper, 1967; Bla nini Inglis, 1963). Desmodora pilosa Ditlevsen, 1926 (syn. D. (Desmodora) gorbunovi Filipjev, 1946; D. (Desmodora) gorbunovi perforata Filipjev, 1946). Desmodora pontica Filipjev, 1922 (syn. Desmodora (Pseudochromadora) pontica (Filipjev, 1922) Gerlach, 1963). Desmodora poseidoni Steiner, 1916. Desmodora scaldensis de Man, 1889 (syn. Spilophora communis sensu Bütschli, 1874 figure 27C, not figure 27A,B,D in the opinion of Bresslau & Stekhoven 1940 (all in Gerlach & Riemann (1973)); D. paramicrochaeta Allgén, 1947). Desmodora septentrionalis Kreis, 1963. Desmodora varioannulata (Kreis, 1928) comb. nov. (syn. Desmodora (Xenodesmodora) varioannulata (Kreis, 1928) Gerlach, 1963; Heterodesmodora varioannulata Kreis, 1928). Desmodora wieseri Inglis, 1968 comb. nov., reinstated name (syn. Desmodora (Xenodesmodora) wolfgangi (Inglis, 1968) Gerlach & Riemann, 1973 pro Desmodora (Xenodesmodora) wieseri (Inglis, 1968) secondary homonym to Desmodora wieseri Gerlach, 1963 (was the nom. nov. pro Desmodora perforata Wieser, 1954, which is here transferred to Desmodorella); Xenodesmodora wieseri Inglis, 1968).

Gerlach (1963) transferred *D. inflexa*, *D. dimorpha*, and *D. rabosa* to the genus *Chromaspirina* Filipjev, 1918, but we agree with Wieser & Hopper (1967) who reinstated these species to their original status.

#### Incertae sedis

The following species is accepted as valid, but as it has 'conflicting' characters, we cannot assign it to a specific genus and we need to regard it as an incertae sedis: Desmodora campbelli Allgén, 1932. Synonym Desmodora (Pseudochromadora) campbelli (Allgén, 1932) Gerlach, 1963 syn. nov. Synonym Desmodora paracampbelli Allgén, 1959; Desmodora (Pseudochromadora) campbelli striaticapitata Allgén, 1959; Desmodora (Pseudochromadora) campbelli reductoides (Allgén, 1959) Gerlach, 1963.

After a preliminary study of Allgén's type material from Campbell Island (provided by the Swedish Museum of Natural History), of specimens from Cavendish Point (found and provided by Dr C. Pastor de Ward; Pastor de Ward, 1988), and of some specimens from Antarctica (D.V., unpublished data), it is clear that for the time being this species cannot be placed in any of the revised genera until further comparative study is done. The species shows slender lateral alae (character for Pseudochromadora) but has distinct subcephalic setae (character for Desmodora). But to make the puzzle even greater, we found that specimens recovered from Antarctica show only faint setae on the head capsule, resembling more additional setae than subcephalic setae.

#### Species with new destination

Desmodora abyssorum, D. curvispiculum, D. filispiculum, D. hirsuta, D. papillistoma, D. sanguinea, D. schulzi, D. sinuata and D. wieseri (=D. perforata) are transferred to the genus Desmodorella.

Desmodora maldivensis is transferred to Zalonema.

Desmodora fröyensis Allgén, 1946 was transferred by Gerlach (1963) to the genus Leptonemella.

## Species inquirendae

The following species are either badly described or known only from one female and/or juvenile(s), and are as such hard to recognize; therefore these species are regarded as species inquirendae.

Desmodora angusticollis Daday, 1901; inc. sed. in Steiner, 1916 (see Gerlach & Riemann, 1973); to Chromadoridae in Gerlach, 1963. Desmodora aucklandiae Ditlevsen, 1921. Desmodora australis Allgén, 1959; sp. inq. in Gerlach, 1963. Desmodora brachycapitata Allgén, 1947 (synonym of Acanthopharynx brachycapitata (Allgén, 1947)). Desmodora cephalophora Allgén, 1947; sp. inq. in Gerlach, 1963. Desmodora conocephala Steiner, 1918 not sensu Gerlach, 1963; sp. inq. in Vitiello, 1970. Desmodora crassa Allgén, 1951; sp. inq. in Gerlach, 1963. Desmodora dubia Allgén, 1947; sp. inq. in Gerlach, 1963. Desmodora deveslita Wieser, 1960; sp. inq. in Gerlach, 1963 (nomen nudum). Desmodora elegans Allgén, 1959; sp. inq. in Gerlach, 1963. Desmodora eucraspedota Schulz, 1932; sp. inq. in Stekhoven, 1935 (see Gerlach & Riemann, 1973). Desmodora extensa Wieser, 1954. Desmodora falklandiae Allgén, 1959; sp. inq. in Gerlach, 1963. Desmodora greenpatchi Allgén, 1953; sp. inq. in Gerlach, 1963. Desmodora intermedia Allgén, 1940; sp. inq. in Gerlach, 1963. Desmodora irregularis Filipjev, 1946. Desmodora kerguelensis (Steiner, 1921) Gerlach, 1963; sp. inq. in Gerlach, 1963 (syn. Mastodex kerguelensis Steiner, 1921). Desmodora leptura Allgén, 1959; sp. Inq. In Gerlach, 1963. Desmodora longicaudata Allgén, 1959. Desmodora merostomacha Steiner, 1921 (syn. of Acanthopharynx merostomacha (Steiner, 1921)). Desmodora michaelseni Steiner, 1918. Desmodora microchaetoides Allgén, 1933; sp. inq. in Gerlach, 1963. Desmodora notomicrochaeta Allgén, 1959; in Gerlach, 1963. Desmodora nudicapitata Cobb, 1920; sp. inq. in Gerlach, 1963. Desmodora odhneri Allgén, 1959; sp. inq. in Gerlach, 1963. Desmodora papillata Daday, 1901; inc. sed. in Steiner, 1916 (see Gerlach & Riemann, 1973); to Chromadoridae in Gerlach, 1963. Desmodora parabullata Allgén, 1929 (synonym of Leptonemella parabullata (Allgén, 1929)). Desmodora parintermedia Allgén, 1947; in Gerlach, 1963. Desmodora polychaeta Allgén, 1929.

Desmodora rabosa Gerlach, 1956. Desmodora roscoffiensis Luc & De Coninck, 1959. Desmodora similis Allgén, 1932 (synonym of Acanthopharynx similis (Allgén, 1932)). Desmodora tenuicauda Allgén, 1932 (not Desmodora cf. tenuicauda sensu Gerlach, 1958). Desmodora tenuidentata Kreis, 1963.

#### Desmodorella Cobb, 1933

Synonym

Desmodora (Desmodorella) (Cobb, 1933) Wieser, 1954.

#### Emended diagnosis

Desmodorinae. Cylindrical body with distinct head capsule and conical tail. Slender body annuli ornamented with regularly ordered longitudinal rows of ridges or spines. Somatic setae arranged in four, six or eight longitudinal rows.

Conical to long conical head capsule, lip region separated from it by a sutura or not; main part of the head capsule thickly cuticularized, smooth or ornamented with numerous vacuoles. Four cephalic setae located at the level of the anterior part of the fovea amphidialis. Large multispiral fovea amphidialis of at least 1·25 turns but mostly of more than two turns, located anteriorly on the head capsule. Subcephalic setae can be absent but are mostly present (up to 16 setae); in case of absence, few additional setae can be present. Buccal cavity with large dorsal and one or two (sub)ventral teeth.

Males either have slender, slightly arched spicules without or with only a tiny capitulum (rounded spicule tip), or have very long, filliform spicules without capitulum; no velum. Gubernaculum can have lateral pieces (crurae).

# Differential diagnosis

Desmodorella Cobb, 1933 resembles Desmodora de Man, 1889 but can easily be distinguished from it by the presence of ordered longitudinal rows of ridges or spines along the body.

#### Discussion

Lorenzen (1976) synonymized *Desmodorella* with the subgenus *Desmodora* after rejecting the differences in amphidial shape noted by Gerlach (1963) as a differential character. Indeed, there is too little difference in amphidial shape for it to be used as a single differential character to split up the two subgenera concerned. However, *Desmodorella* is recognized and lifted from its subgenus level to be reinstated as a genus, based on the following character(s): the constant character of the presence of regularly ordered longitudinal rows of ridges or spines (present in all 12 species and not once in *Desmodora*); this character is aided by the shape of the male spicules (no or only tiny capitulum, no velum) and the slight difference in amphidial shape.

# Type species

Desmodorella cephalata Cobb, 1933 = Desmodorella tenuispiculum (Allgén, 1928) Gerlach, 1963.

List of valid species

Desmodorella abyssorum (Allgén, 1929) Gerlach, 1963 (syn. Desmodora abyssorum Allgén, 1929). Desmodorella balteata sp. nov. Desmodorella curvispiculum (Jensen, 1985) comb. nov. (syn. Desmodora (Desmodora) curvispiculum Jensen, 1985). Desmodorella filispiculum (Lorenzen, 1976) comb. nov. (syn. Desmodora (Desmodora) filispiculum Lorenzen, 1976). Desmodorella hirsuta (Chitwood, 1936) comb. nov. (syn. Desmodora hirsuta (Chitwood, 1936) Gerlach, 1963; Heterodesmodora hirsuta Chitwood, 1936). Desmodorella papillostoma (Murphy, 1962) comb. nov. (syn. Desmodora papillostoma Murphy, 1962). Desmodorella perforata (Wieser, 1954) comb. nov.; reinstated name (syn. Desmodora (Desmodora) wieseri Gerlach, 1963 (erat nomen novum pro Desmodora perforata Wieser, 1954, homonym to D. (Desmodora) gorbunovi perforata Filipjev, 1946); Desmodora perforata Wieser, 1954). Desmodorella sanguinea (Southern, 1914) comb. nov. (syn. Desmodora sanguinea Southern, 1914). Desmodorella schulzi (Gerlach, 1950) comb. nov. (syn. Desmodora schulzi Gerlach, 1950). Desmodorella sinuata (Lorenzen, 1976) comb. nov. (syn. Desmodora (Desmodora) sinuata Lorenzen, 1976). Desmodorella spineacaudata sp. nov. Desmodorella tenuispiculum (Allgén, 1928) (syn. Desmodora tenuispiculum Allgén, 1928; Desmodora (Desmodorella) tenuispiculum (Allgén, 1928) Gerlach, 1963; Desmodorella cephalata Cobb, 1933; Desmodora (Desmodora) cephalia Gerlach & Riemann, 1973 pro Desmodora (Desmodorella) cephalata (Cobb, 1933), secondary homonym to Desmodora (Pseudochromadora) cephalata (Cobb, 1920).

## Species inquirendae

Desmodorella bullata (Steiner, 1916); sp. inq. in Gerlach, 1963. Desmodorella nybelini (Allgén, 1954); sp. inq. in Gerlach, 1963.

# Pseudochromadora Daday, 1899

Synonym

Desmodora (Pseudochromadora) (Daday, 1899) Gerlach, 1963; Micromicron Cobb, 1920; Bradylaimoides Timm, 1961.

# Diagnosis

Desmodorinae. Unispiral fovea amphidialis (at least in females) located centrally on the head capsule; no subcephalic setae; strong somatic setae; distinct lateral alae.

# Type species

Pseudochromadora quadripapillata Daday, 1899.

# List of valid species

Pseudochromadora buccobulbosa Verschelde & Vincx, 1995. Pseudochromadora cazca Gerlach, 1956 (syn. Desmodora cazca Gerlach, 1956; Desmodora (Pseudochromadora) cazca (Gerlach, 1956) Gerlach, 1963; Metachromadora (Bradylaimoides) benepapillata Timm, 1961). Pseudochromadora coomansi Verschelde & Vincx, 1995. Pseudochromadora incubans Gourbault & Vincx, 1990; Pseudochromadora interdigitata Muthumbi et al., 1995. Pseudochromadora quadripapillata Daday, 1899 (syn. Desmodora (Pseudochromadora)

quadripapillata (Daday, 1899) Gerlach, 1963; Desmodora (Pseudochromadora) cephalata (Cobb, 1920) Gerlach, 1963; Micromicron cephalatum Cobb, 1920; Desmodora (Pseudochromadora) luticola (Timm, 1952) Andrassy, 1959 (syn. in Gerlach, 1963); Micromicron luticola Timm, 1952).

#### Species with new destination

Desmodora (Pseudochromadora) bipapillata Gerlach, 1967 and Desmodora (Pseudochromadora) bulbosa Jensen, 1985 are transferred to the genus Pseudodesmodora as Pseudodesmodora bipapillata (Gerlach, 1967) comb. nov. and Pseudodesmodora bulbosa (Jensen, 1985) comb. nov.

Desmodora campbelli Allgén, 1932 is regarded as an incertae sedis (see above) and is taken out of *Pseudochromadora*.

Six other species were already transferred to the genus *Desmodora* in Muthumbi et al. (1995).

## Zalonema Cobb, 1920

#### Synonym

Desmodora (Zalonema) (Cobb, 1920) Gerlach, 1963; Heterodesmodora Micoletzky, 1924.

## Diagnosis

Desmodorinae. Fine body annuli; rounded triangular head capsule; subcephalic setae present; multispiral fovea amphidialis (two turns or more). Slender cylindrical pharynx with pyriform endbulb.

# Type species

Zalonema nudum Cobb, 1920 = Zalonema megalosoma (Steiner, 1918) Gerlach, 1963.

# List of valid species

Zalonema ditlevseni (Micoletzky, 1922) Gerlach, 1963 (syn. Desmodora ditlevseni Micoletzky, 1922; Heteradesmodora ditlevseni (Micoletzky, 1922) Micoletzky, 1924; Desmodora (Z.) ditlevseni (Micoletzky, 1922) Gerlach, 1963; Desmodora ocellata Wieser, 1954); Zalonema megalosoma (Steiner, 1918) Gerlach, 1963 (syn. Desmodora megalosoma Steiner, 1918; Desmodora (Zalonema) megalosoma (Steiner, 1918) Gerlach, 1963; Zalonema nudum Cobb, 1920; Desmodora (Zalonema) nuda (Cobb, 1920)). Zalonema maldivensis (Gerlach, 1963) comb. nov. (syn. Desmodora (Desmodora) maldivensis Gerlach, 1963), this species is accepted as a member of the genus Zalonema because of the presence of eight subcephalic setae anterior to the fovea amphidialis, the character of the amphidial shape is disregarded because there is some doubt towards its true shape. Thus, the character of the position of the subcephalic setae is regarded as more important than the shape of the fovea amphidialis. Zalonema myrianae Verschelde & Vincx, 1996.

## Species inquirenda

Zalonema propingua (Allgén, 1951) Gerlach, 1963 (syn. Desmodora propingua Allgén, 1951; Desmodora (Z.) propingua (Allgén, 1951) Gerlach, 1963).

Genus inquirendum Desmodora (Xenodesmodora) (Wieser, 1951) Gerlach, 1963

Synonym

Xenodesmodora Wieser, 1951.

Discussion

When Wieser (1951) erected the taxon (at a genus level) he gave the following diagnosis: 'The genus *Xenodesmodora* is characterized by the sausage-shaped, single spiral fovea amphidialis; small cylindrical buccal cavity with two very small, hollow teeth (dorsal and ventral); inner head capsule; and the perforated tail.'

Indeed the type species was described with small teeth, but all other members added to this taxon since its erection, have a large prominent dorsal tooth. Also do these more recent species lack the 'inner head capsule', mentioned in the type species and genus diagnosis. Therefore, these species are transferred elsewhere. Furthermore, are the type species and genus only known from one single female so that this species and genus are regarded as species inquirenda and (sub)genus inquirendum.

Type and only species

Desmodora (Xenodesmodora) porifera (Wieser, 1951) Gerlach, 1963 sp. inq. (syn. Xenodesmodora porifera Wieser, 1951 sp. inq.).

The species (i.e. Desmodora (Xenodesmodora) nini (Inglis, 1963) Wieser & Hopper, 1967; Desmodora (Xenodesmodora) varioannulata (Kreis, 1928) Gerlach, 1963; Desmodora (Xenodesmodora) wolfgangi (Inglis, 1968) Gerlach & Riemann, 1973) are transferred to the genus Desmodora. Both Desmodora (Xenodesmodora) longiseta (Stekhoven, 1950) Gerlach, 1963 and Desmodora (Xenodesmodora) torquens (Gerlach, 1963) Gerlach, 1964 are placed in the genus Croconema.

#### **DESCRIPTIONS**

Family DESMODORIDAE Filipjev, 1992 Genus *Desmodora* de Man, 1889

Desmodora alberti sp. nov. (Figures 1–3; Tables 1 & 2)

Type specimens

Holotype males: slide BN 296 (MNHN); allotype female: slide BN 299 (MNHN); other paratypes:  $18 \, 33$ ,  $21 \, 99$ ,  $8 \, JJ$ , slides BN 296, BN 298, BN 299, BN 302–304, BN 306 (MNHN), slides 3937–3941 (ZIRUG) and slides 10285–10287 (MBRUG).

Type locality

Hydrothermal vents of the East Pacific Rise, Guyamas, 27°N-111°24′W; depth 2000 m; heterogeneous sediment covered with bacteria.

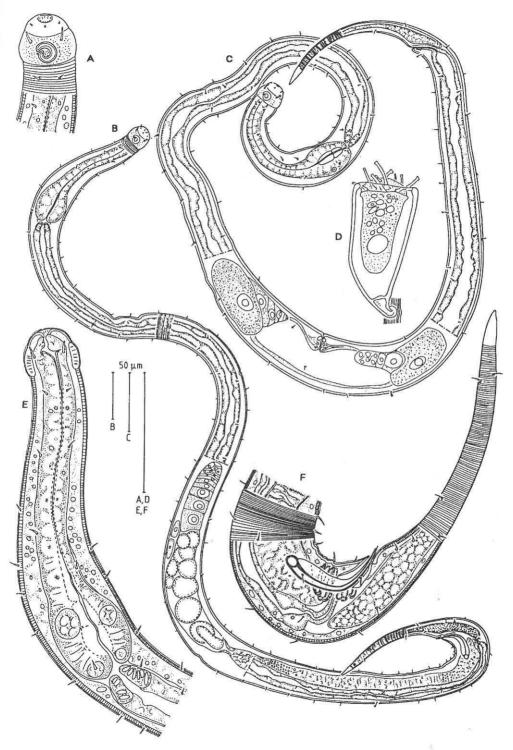


Figure 1. Desmodora alberti sp. nov. (A) Holotype male  $(\mathfrak{J}_1)$ , head capsule; (B)  $\mathfrak{J}_1$ , habitus; (C) allotype female  $(\mathfrak{P}_1)$ , habitus; (D) Suctoria specimen attached to a paratype male; (E)  $\mathfrak{J}_1$ , pharyngeal region; (F)  $\mathfrak{J}_1$ ; tail and copulatory apparatus.

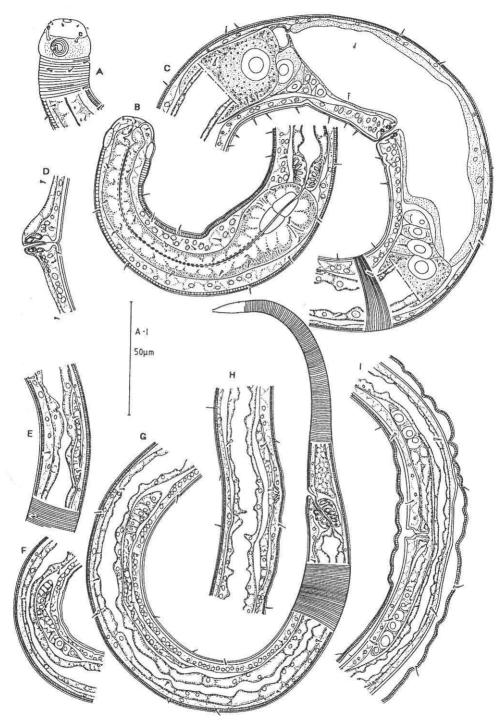


Figure 2. Desmodora alberti sp. nov. (A) Allotype female  $(\mathcal{Q}_1)$ , head capsule; (B)  $\mathcal{Q}_1$ , pharyngeal region; (C) paratype  $\mathcal{Q}_2$ , reproductive system; (D)  $\mathcal{Q}_1$ , vulva; (E)  $J_{III}$ , genital primordium; (F) late  $J_{III}$  or early  $J_{III}$ , genital primordium; (G)  $J_{III}\mathcal{Q}$ , genital primordium; (H) late  $J_{III}\mathcal{Q}$  or early  $J_{IV}\mathcal{Q}$ , genital primordium; (I)  $J_{IV}\mathcal{Q}$ , reproductive system and body cuticle fully developed.

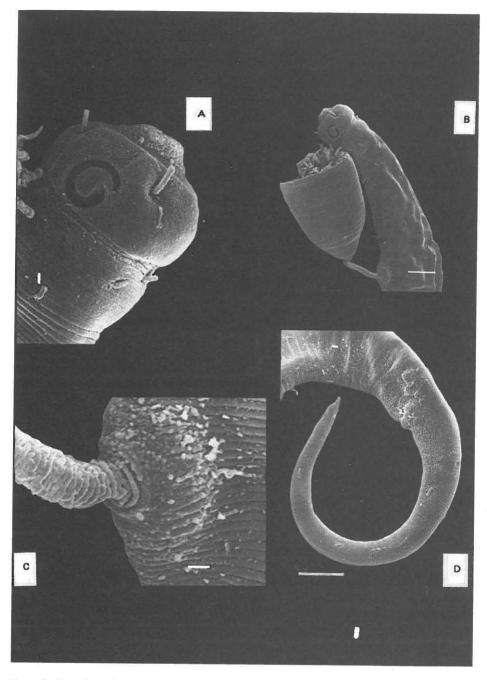


Figure 3. Desmodora alberti sp. nov., paratype female ( $\mathcal{Q}_3$ ). (A) Head capsule; (B) pharyngeal region with attached Suctoria specimen; (C) detail of implanting of Suctoria specimen into cuticle; (D) tail. Scale bars: A,C, 1  $\mu$ m; B,D, 10  $\mu$ m.

Table 1. Measurements (µm) and ratios of Desmodora alberti sp. nov.

	Holotype ರೆ		Paratyp	pe	Allotype $\varphi$		Paratyp \$\text{P}\$	e
		Min.	N=7 Max.	Mean $\pm SD$		Min.	N=7 Max.	Mean ±SD
*	1011	EE.C	1070	054 1 104	1146	054	1006	071   040
L	1211	756	1078	$954 \pm 104$	1146	854	1096	$971 \pm 84.3$
cs	6	4	7	$5 \pm 0.98$	6	3	6	$5 \pm 1.15$
dcs	11	6	8	$7 \pm 0.69$	9	4	9	$7 \pm 2.36$
amph%	41	35	41	$38 \pm 2.08$	34	33	38	$35 \pm 1.8$
aw	9	7	9	8 ±0.69	7	7	9	$8 \pm 0.69$
hw	23	18	23	$20 \pm 1.77$	22	21	22	$22 \pm 0.49$
dnr	87	4.00			92	69	73	$71 \pm 2.83$
ph	149	103	145	$117 \pm 13.3$	152	107	163	$125 \pm 18.7$
mbd ph	37	26	32	$28 \pm 2.06$	35	27	37	$33 \pm 3.95$
mbd	43	27	39	$32 \pm 4.04$	46	34	47	$39 \pm 5.26$
bdnr	29				27	25	31	$28 \pm 4.24$
bdcs	20	18	20	$19 \pm 0.82$	20	16	21	$19 \pm 1.8$
spic	51	32	50	$40 \pm 5.97$				
gub	12	13	17	$14 \pm 1.5$				
dv					640	445	656	$540 \pm 64.3$
V					56	52	60	$56 \pm 2.39$
da	1072	661	967	$846 \pm 97.6$	1018	730	953	$845 \pm 78.3$
abd	20	17	24	$19 \pm 2.41$	17	15	17	$16 \pm 0.76$
t	120	96	118	$107 \pm 8.04$	127	116	134	$124 \pm 5.82$
tmr	14	12	18	$15 \pm 2.23$	17	12	17	$15 \pm 1.73$
a	28-2	26.9	35.6	$29.6 \pm 3.03$	24.9	19.9	27.9	$25.1 \pm 2.86$
b	8.1	7.3	8.8	$8.2 \pm 0.6$	7.5	6.7	8.7	$7.8 \pm 0.72$
c	10.1	7.88	9.54	$8.93 \pm 0.61$	9	6.8	8-6	$7.8 \pm 0.63$

# Etymology

Named in honour of Philippe Albert (Banyuls-Sur-Mer) who sorted the nematodes for us.

#### Measurements

See Tables 1 & 2.

#### Description

*Males*. Cylindrical body with rounded head capsule and long, slender conical tail (Figure 1B). Thin body annuli slightly broader in pharyngeal region (ten annuli measure 9  $\mu$ m) than along the rest of the body (ten annuli measure 6  $\mu$ m); body cuticle distinctly multi-layered. Short somatic setae arranged in six longitudinal rows; some setae with secreted gluten. In some specimens large epizoic Suctoria (25×82  $\mu$ m) are attached to the body: the base of the suctorian specimens 'roots' into the cuticle (Figures 1D, 3C).

Head capsule consists of two parts: a slender lip region 'separated' with a seam from the thickly cuticularized, rounded main part of the head capsule which is ornamented with numerous small vacuoles (head capsule resembling that of *Pseudochromadora* spp.). Cryptospiral (1·1–1·2 turns) fovea amphidialis located

Table 2. Measurements (µm) and	d ratios of juveniles	of Desmodora alberti sp. nov.
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	J4 N=1	J3/4 N=1	M	J3 N=3	M	J2/3 N=1	J2 N=1
			Min.	Max.	Mean		
L	843	745	757	889	836	744	606
cardia	4	6	7	9	8	4	7
CS	4 3 8	4	4	5	4	4	2
dcs	8	4	6	11	8	6	7
amph%	30	34	36	41	39	39	30
aw	6	5	6	8	7	7	5
hw	20	18	19	20	19	18	16
dnr				61			
ph	105	94	99	103	101	93	92
mbd ph	24	25	23	26	25	22	21
mbd	26	26	22	26	24	21	21
bdnr				20			
bdcs	18	15	17	18	17	16	15
da	728	644	638	753	714	650	517
abd	15	15	15	17	16	14	14
t	117	99	112	126	117	98	92
tmr	14	12	14	14	14	12	11
a	32	29	32	40	35	35	29
b	8	7.9	7.6	8.7	8.3	8	6.6
c	7.2	7.5	6.8	7-7	7.2	7.6	6.6

centrally on the main part of the head capsule; broad fovea and slimmer apertura amphidialis (Figure 1A). Four cephalic setae located at the level of the anterior edge of the fovea amphidialis. Subcephalic setae absent.

Buccal cavity with large dorsal tooth, ventral teeth not observed. Cylindrical pharynx with distinct endbulb; in the holotype male gland cells are visible in the terminal bulb (Figure 1E); cuticular lumen with bipartite cuticular valves in endbulb (not distinct in holotype). Nerve ring not observed. Nuclei in epidermal cells distinct.

Monorchic reproductive system located ventrally to and at the left (testis tip) of the intestine. Large, globular sperm cells. Short, arched spicules with small capitulum and broad velum; simple, short gubernaculum (Figure 1F). No special cuticular appendages related to the male reproductive system.

Long, slender conical tail. Caudal glands extending as far as the mid of the spicules.

Females. Largely similar to males. Ten body annuli in the pharyngeal region measure 8–12  $\mu$ m; 5–7  $\mu$ m further along the body. An epizoic Suctorial specimen found on a female measures 87  $\mu$ m in length and 24  $\mu$ m in diameter (Figure 3B).

Bipartite cuticular valves in endbulb of pharynx distinct (Figure 2B).

Reproductive system didelphic, amphidelphic with ventrally reflected ovaries (Figure 2C) located both to the left or to the right of the intestine according to the specimen. Vulva a broad, transverse slit. Vagina vera short, vagina uterina with sphincter muscle (Figure 2D). An egg found in the uterus of one female measures 19 by 27  $\mu$ m.

Slender tail (Figure 3D).

Juveniles. First stage juveniles not found.

Body shape, annuli, head capsule with ornamentation, position of cephalic setae, position and shape of fovea amphidialis, pharynx and intestine of all three stages found are similar to adults.

Large cryptospiral fovea amphidialis (1.2 turns) with broad fovea and narrower apertura. No real differences concerning external morphology (e.g. cuticular appendages), except for measurements, is noted between the different juvenile stages.

Few somatic setae in second stage juveniles, slightly more in third and fourth. Long, slender tail.

Genital primordium in second stage juveniles consists out of a short, slender string of cells (Figure 2E).

In late second or young third stage juveniles the genital primordium is a broader strand of cells (Figure 2F), in such cases it is extremely difficult to decide on the stage (second or third) as there are no further differences in characters between them.

In third stage juveniles, the male gential primordium consists of a slender testis of which the future vans deferens is still some distance from the rectum (Figure 2G). In late third or young fourth stage juveniles the female genital primordium shows a small group of two times three vaginal cells, located ventrally to the mid of the primordium of uterus and ovaries (Figure 2H); here also it is difficult to decide on the juvenile stages, as further differences are not available and measurements overlap.

In fourth stages juveniles, the female reproductive system is characterized by a strand of cells in which the ovaries are recognizable at both distal ends; two groups of three cells align the position of the future vagina, the future duct is visible. In late forth stage juveniles the vulva and vagina are completely developed (Figure 2I).

# Diagnosis

Desmodora alberti sp. nov. is characterized by a combination of the following characters: slender body and annuli; rounded head capsule (reminiscent of that of Pseudochromadora spp.); absence of subcephalic setae; large cryptospiral fovea amphidialis with narrow apetura and board fovea; and the bipartite cuticular valves in the terminal bulb of the pharynx. Males are characterized by their large globular sperm cells and short bent spicules.

# Differential diagnosis

Desmodora alberti sp. nov. resembles *D. minuta* Wieser, 1954, *D. granulata* Vinx & Gourbault, 1989 and *D. marci* sp. nov. *Desmodora alberti* sp. nov. can be distinguished from *D. minuta* by the size of the fovea amphidialis (only half as long as the length of the main part of the head capsule in *D. minuta*) and by the size and shape of the male spicules and capitulum (length of spicules only 22–26 µm, but with larger capitulum in *D. minuta*). *Desmodora alberti* sp. nov. can be distinguished from *D. granulata* by the shape of the head capsule (straighter in *D. granulata*), the size and shape of the dorsal tooth (smaller but more distinct in *D. granulata*), by the shape of the tail (broader in *D. granulata*), and by the shape of the capitulum of the male spicules (connected to the velum with an anterior 'hook' in *D. granulata*). *Desmodora alberti* sp. nov. can easily be distinguished from *D. marci* sp. nov. by its body size (the latter is almost twice as long), and by the shape of the male spicules (complex capitulum in *D. marci* sp. nov.).

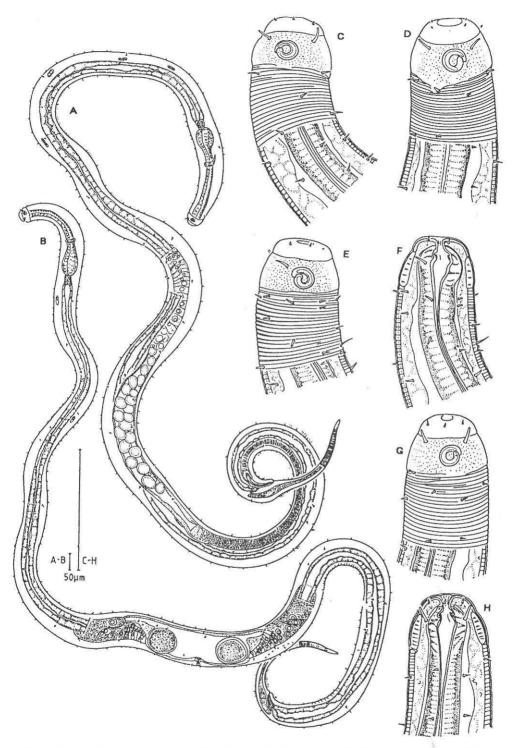


Figure 4. *Desmodora marci* sp. nov. (A) Holotype male  $(\beta_1)$ , habitus; (B) allotype female  $(\beta_1)$ : habitus; (C) paratype male  $(\beta_2)$ , head capsule; (D)  $\beta_3$ , head capsule; (E)  $\beta_1$ , head capsule; (F)  $\beta_1$ , buccal cavity; (G)  $\beta_2$ , head capsule; (H)  $\beta_2$ , buccal cavity.

Desmodora alberti sp. nov. bears a remarkable resemblance (in general body shape and shape of the head capsule) to the species of *Bolbonema* but can be easily excluded from this genus by the anterior position of the cephalic setae and the absence of long somatic setae.

Desmodora marci sp. nov. (Figures 4 & 5; Table 3)

Type specimens

Holotype male: slide BN 300 (MNHN); allotype female BN 301 (MNHN); other paratypes: 4 33, 27 99, slides BN 300–301 (MNHN) and slides 3934–3935 (ZIRUG).

Type locality

Hydrothermal vents in the Lau Basin. Hine Hina site: 22°32′S 176°43′W; maximum depth 1707 m. Cold site, under 20°C; material collected in the water from the 'coffin' with mussels and Solenidae.

Etymology

This species has been named after Marc Vander Bruggen (Puyenhof Wachtebeke, Gent, Belgium).

Measurements

See Table 3.

#### Description

*Males*. Long cylindrical body with strong head capsule and slender conico-cylindrical tail (Figure 4A). Distinct body annuli broader in pharyngeal region (ten annuli measure  $16 \mu m$ ) than along the rest of the body (ten annuli measure  $6 \mu m$ ). Filamentous epigrowing organisms can be found attached to the cuticle along the body and tail (Figure 5A). Short somatic setae in six longitudinal rows; some of the setae secreting gluten.

Head capsule consists of two parts separated by a sutura: a distinct rounded lip region, and a second, thickly cuticularized, main part of the head capsule which is ornamented with numerous small vacuoles (Figure 4C,D); the main part makes out half to two thirds of the entire length of the head capsule. Lip setae located on the first part, cephalic setae on the second part of the head capsule. Four, distinctly hollow, cephalic setae located at a level just in front of the anterior edge of the fovea amphidialis; cryptospiral (multispiral with 1·2 turns) fovea amphidialis located in the centre of the main part of the head capsule; broad fovea and slimmer apertura amphidialis (Figure 4C,D); the apertura does not reach as far around as the fovea, varying between 0·7 to maximum 0·9 turns depending on the specimen. No subcephalic setae; zero to three additional setae can be present at the posterior edge of the head capsule.

Dorsal tooth and one (or two?) ventral tooth located anteriorly in the buccal cavity, hard to distinguish in most specimens. Cylindrical pharynx with muscular terminal bulb; lumen cuticle quite thick, but the presence of valves in terminal bulb is obscure

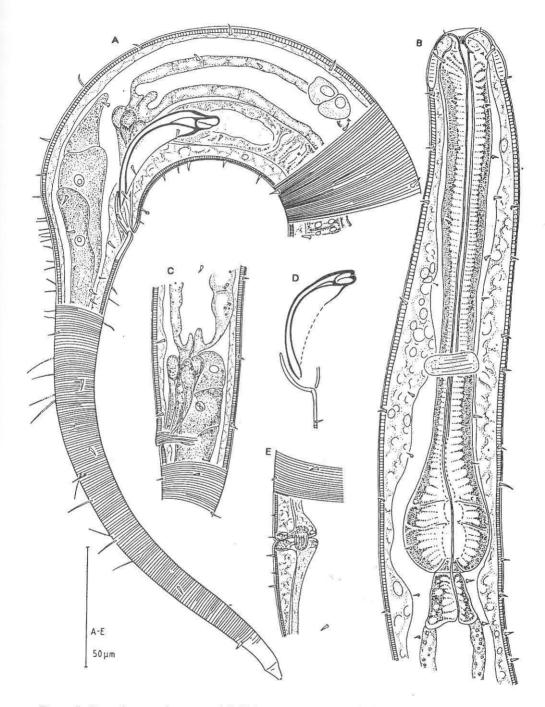


Figure 5. Desmodora marci sp. nov. (A) Holotype  $\mathcal{J}_1$ , posterior body region; (B) Paratype  $\mathcal{J}_3$ , pharyngeal region; (C)  $\mathcal{J}_2$ , anal region; (D)  $\mathcal{J}_2$ , spicule; (E)  $\mathcal{L}_1$ , vagina.

Table 3. Measurements	$(\mu m)$	and	ratios	of	Desmodora	marci	sp.	nov.
그리고 한 경기가 하면 하는 그것이라고 하면 하는 것이 되었다면 하는 것이 없는데 하는데 하는데 하는데 하는데 나를 하는데	1 55 1 5 5 6			-1				

	Holotype		Paratyp	pe	Allotype		Paratyp	e
	O		N=4		+		N=7	
		Min.	Max.	Mean $\pm SD$		Min.	Max.	Mean $\pm SD$
L	2728	2261	2761	2542 ±223	2535	2111	2507	2356 ±151
Cardia	13	17	21	$19 \pm 1.7$	18	13	19	$17 \pm 2.26$
cs	6	6	7	$7 \pm 0.58$	7	6	8	$7 \pm 0.82$
dcs	6	9	12	$10 \pm 1.41$	11	7	13	$11 \pm 2.08$
amph%	26	29	34	$31 \pm 2.21$	30	28	34	$31 \pm 1.99$
aw	9	9	11	$10 \pm 1.15$	9	9	11	$10 \pm 0.9$
hw	35	31	33	$32 \pm 1$	29	30	33	$32 \pm 0.95$
dnr	127	116	138	$126 \pm 9.81$	128	114	133	$127 \pm 6.18$
ph	215	192	227	$209 \pm 15.4$	215	192	215	$209 \pm 8.08$
mbdph	56	46	51	$49 \pm 2.06$	49	45	55	$51 \pm 3.59$
mbd	73	52	70	$59 \pm 7.8$	80	72	81	$77 \pm 4.19$
bdnr	48	43	48	$46 \pm 2.22$	47	44	54	$47 \pm 3.46$
bdcs	27	27	30	$28 \pm 1.5$	27	27	30	$28 \pm 1.21$
spic	70	63	72	$66 \pm 4.24$				
gub	19	18	23	20 ± 2·22				
dv					1296	1127	1352	$1247 \pm 82.2$
V					51	50	55	$53 \pm 1.88$
da	2511	2033	2556	$2331 \pm 241$	2268	1878	2282	$2121 \pm 150$
abd	36	32	36	$34 \pm 1.71$	32	25	34	$29.4 \pm 3.15$
t	220	206	237	$216 \pm 14.4$	241	219	255	$232 \pm 12.5$
tmr	25	20	24	$22 \pm 2.06$	21	19	26	$22 \pm 2.69$
a	37.4	38.2	48.4	$43.5 \pm 4.21$	31.7	26.7	34.8	$30.8 \pm 2.5$
b	12.7	11.8	12-4	$12.2 \pm 0.28$	11.8	10.4	12.1	$11.3 \pm 0.54$
c	12-4	10.4	13.4	$11.8 \pm 1.37$	10.5	9.3	11.4	$10.2 \pm 0.65$

(Figure 5B). Long cardia. Intestinal cells filled with many lipid droplets. Rectum surrounded by rectal cells (Figure 5A). Quite a few pseudocoelomocytes are present along the body.

Monorchic reproductive system outstretched, located partially to the left and partially to the right of the intestine (Figure 4A). Spermatogonia in testis tip with large nucleolus in their nuclei; globular sperm cells. Short, arched spicules with complex capitulum and broad but indistinct velum; the shape of the spicule tip and capitulum can vary according to the angle by which they are observed (compare Figure 5A&D).

Three caudal gland cells; the most distal one extending as far as the mid of the retracted spicules. The slender tail narrows down quickly posterior to the cloaca from a conical to a cylindrical shape. Valve in spinneret visible.

Females. General body shape largely similar to males.

Reproductive system didelphic, amphidelphic with reflected ovaries (Figure 4B). Both ovary tips are reflected towards the ventral body wall. Entire reproductive system is located to the left or to the right of the intestine. Vulva is a broad transverse slit. Cuticular alignment of both vagina vera and vagina uterina distinct; vagina uterina with sphincter muscle (Figure 5E). In the uterus of some females up to four eggs were counted.

Juveniles. Not found.

#### Diagnosis

Desmodora marci sp. nov. is characterized by the combination of the following characters: long slender body, shape of head capsule and fovea amphidialis (shorter apertura than fovea amphidialis). Males are characterized by their spicules with complex capitulum. Females are characterized by the position of the vulva (V=50–55%).

## Differential diagnosis

Desmodora marci sp. nov. slightly resembles D. granulata Vincx & Gourbault, 1989, and D. minuta Wieser, 1954, and closely resembles D. masira Warwick, 1973, in general shape and characters. This new species can easily be distinguished from either D. granulata or D. minuta by the differences in body length (1040–1270  $\mu$ m and 800–925  $\mu$ m respectively), and in shape and size of spicules (simple capitulum, 44–46  $\mu$ m, 22–26  $\mu$ m respectively). D. marà sp. nov. can be distinguished from D. masira by the difference in amphidial shape (a two turn, multispiral forva amphidialis in D. masira), tail shape (conical in D. masira), spicules in males (finer in D. masira), and position of the vulva in females (V=39–42% in D. masira).

Genus Desmodorella Cobb, 1933 Desmodorella balteata sp. nov. (Figures 6–9; Tables 4 & 5)

## Type specimens

Holotype male: slide BN 298 (MNHN); allotype female: slide BN 299 (MNHN); other paratypes:  $14\ 33$ ,  $10\ 99$ ,  $14\ JJ$ , slides 296–299, BN 303–306 (MNHN), slides 3936–3941 (ZIRUG) and slides 10285–10287 (MBRUG).

# Type locality

Hydrothermal vents in the East Pacific Rise, Guyamas, 27°N-111°24′W; depth 2000 m; heterogeneous sediment covered with bacteria.

# Etymology

From the Latin word *balteum*, -i, girdle; *balteatus*; -a, -um, with girdle; referring to the cuticular rings constricting the body in some specimens.

#### Measurements

See Tables 4 & 5.

## Description

*Males*. Cylindrical body with well developed head capsule and short conical tail (Figure 6C). Distinct annuli slightly broader in pharyngeal region (ten annuli measuring 14  $\mu$ m), slender posterior to it (ten annuli measuring 10  $\mu$ m), where they are ornamented with longitudinal rows of fine, often indistinct (light microscope) ridges or short spines (Figures 6C,E & 9C). The spines of the two lateral pairs of longitudinal rows are conspicuously more developed, giving at first view the false impression of

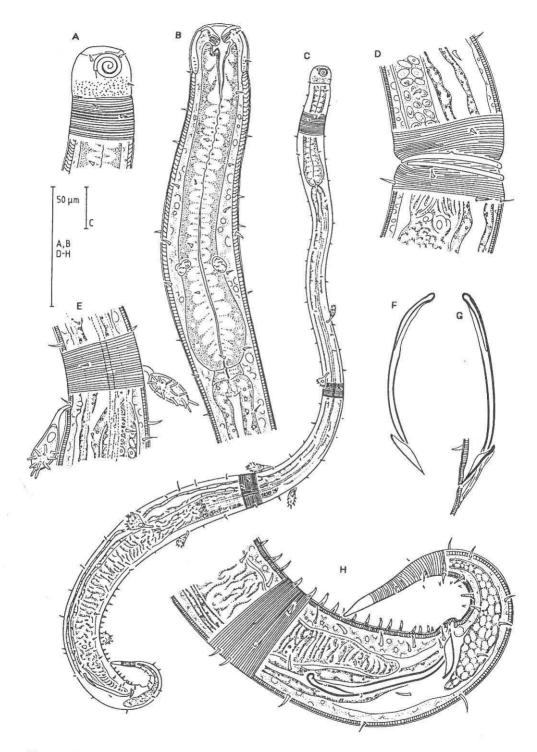


Figure 6. Desmodorella balteata sp. nov. (A) Holotype male  $(\mathcal{J}_1)$ ; head capsule; (B)  $\mathcal{J}_1$ , pharyngeal region; (C)  $\mathcal{J}_1$ , habitus; (D) paratype male  $(\mathcal{J}_2)$ , cuticular rings arround body; (E)  $\mathcal{J}_1$ , body annuli with spines, attached Suctoria specimens; (F)  $\mathcal{J}_3$ , spicule; (G)  $\mathcal{J}_4$ , spicule; (H)  $\mathcal{J}_1$ , tail region.

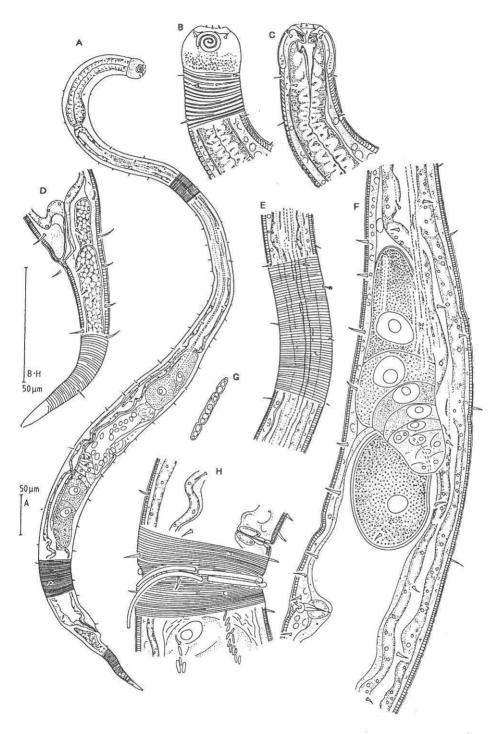


Figure 7. Desmodorella balteata sp. nov. (A) Allotype female  $(\mathcal{Q}_1)$ , habitus; (B)  $\mathcal{Q}_1$ , headcapsule; (C)  $\mathcal{Q}_1$ , head region with detail of buccal cavity; (D) paratype female  $(\mathcal{Q}_2)$ , tail; (E)  $\mathcal{Q}_1$ , body annuli with rows of spines; (F)  $\mathcal{Q}_2$ , reproductive system; (G) Detail of Beggiatoa (?) specimen, found in intestine of  $\mathcal{Q}_1$ ; (H)  $\mathcal{Q}_3$ , cuticular rings on body.

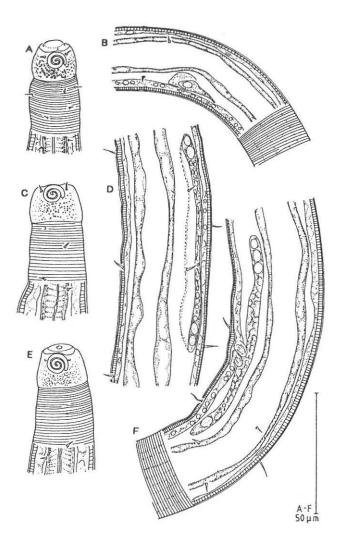


Figure 8. Desmodorella balteata sp. nov. (A) J<sub>II</sub>, head capsule; (B) J<sub>II</sub>, genital primordium; (C) J<sub>III</sub>, head capsule; (D) J<sub>III</sub>, genital primordium; (E) J<sub>IV</sub>, head capsule; (F) J<sub>IV</sub>, genital primordium.

the presence of lateral alae (they demarcate 'false lateral alae'; Figure 9B,C) extending from posterior to the pharynx as far as the beginning of the last third of the body. Some specimens carry a number of small, laterally flattened epizoic Suctoria attached to their body cuticle  $(16\times7\times33~\mu\text{m};$  Figure 6C,E). The body of a few specimens is constricted posteriorly by two big cuticular 'rings' which did not originate from the animal itself and which are reminiscent to the trapping-rings of nematophage fungi (but they show no cellular structure; Figure 6D). Short somatic setae arranged in six longitudinal rows. Precloacally the setae of the single ventral row, and those of, be it less pronounced, the two latero-ventral rows are strongly developed (Figure 6H); the ventral precloacal setae resemble those found in males of most species of the genus *Pseudochromadora* Daday, 1899.

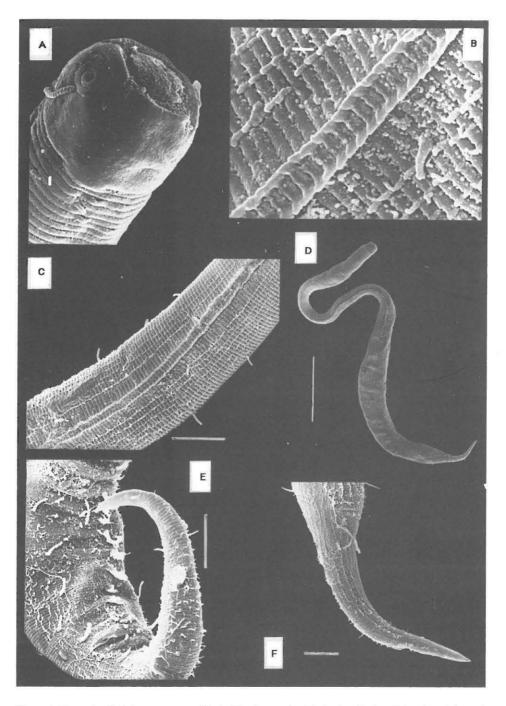


Figure 9. Desmodorella balteata sp. nov. (A)  $\circlearrowleft_5$ , Head capsule; (B)  $\circlearrowleft_5$ , detail of well developed lateral spines; (C)  $\circlearrowleft_5$ , view on longitudinal rows of spines; (D)  $\circlearrowleft_4$ , habitus; (E)  $\circlearrowleft_5$ , tail region; (F)  $\circlearrowleft_4$ , tail. Scale bars: A,B, 1  $\mu$ m; C,E&F, 10  $\mu$ m; D, 100  $\mu$ m.

	Holotype ਹੰ		Paratyp ਹੋਰ N=7	pe	Allotype ♀		Paratyp çç N=7	pe
		Min.	Max.	Mean $\pm SD$		Min.	Max.	Mean $\pm SD$
L	1045	872	1011	955 ±55-5	1078	867	1078	987 ±80·7
cs	3	2	4	$3 \pm 0.82$	3	2	4	$3 \pm 0.9$
dcs	4	3	7	$5 \pm 1.21$	5	3	6	$4 \pm 1.41$
amph%	50	46	50	$48 \pm 1.4$	45	44	52	$47 \pm 3.18$
aw	11	9	11	$10 \pm 0.98$	11	10	12	$11 \pm 0.76$
hw	23	20	23	$22 \pm 1.15$	24	22	25	$23 \pm 1.07$
cardia	8	7	11	$8 \pm 1.4$	3	6	9	$7 \pm 1.51$
ph	145	115	148	$134 \pm 12.9$	147	136	156	$148 \pm 6.83$
mbd ph	33	29	33	$31 \pm 1.86$	34	34	37	$35 \pm 1.21$
mbd	51	36	48	$43 \pm 4.11$	53	48	64	$58 \pm 5.62$
bdcs	21	18	21	$20 \pm 1.11$	21	18	22	$20 \pm 1.6$
spic	70	65	85	$73 \pm 6.7$				
gub	17	15	19	$17 \pm 1.63$				
dv					706	578	800	$670 \pm 76$
V					66	66	74	$68 \pm 2.79$
da	956	783	911	855 ±52.8	978	777	978	$889 \pm 77.3$
abd	27	23	27	$25 \pm 1.73$	25	19	24	$23 \pm 1.98$
t	101	83	115	$97 \pm 10.2$	90	88	103	$96 \pm 5.53$
tmr	14	10	17	$14 \pm 2.04$	15	11	17	$14 \pm 2.27$
a	20.5	18.5	26.3	$22.3 \pm 2.78$	20.3	15.7	18.1	$16.9 \pm 0.83$
b	7.2	6.7	7.6	$7.2 \pm 0.32$	7.3	5.9	7.4	$6.7 \pm 0.56$
c	10.3	8.7	10.6	$9.9 \pm 0.68$	12	9.23	12.3	$10.3 \pm 1.02$

Table 4. Measurements (µm) and ratios of Desmodorella balteata sp. nov.

Long, well developed head capsule with separate, retractable lip region. Large multispiral fovea amphidialis (2.6 turns), with broad fovea but slit-like apertura amphidialis (apertura not drawn in figure, but distinctly visible on SEM pictures; compare Figure 6A with 9A); fovea amphidialis located anterior on the head capsule sided by the four cephalic setae (Figure 6A). Posterior to the fovea amphidialis, the head capsule is ornamented with numerous, small vacuoles. No subcephalic setae; zero to four additional setae located posteriorly on the head capsule.

Buccal cavity with cheilorhabdia in cheilostome; large dorsal and smaller ventral tooth in pharyngostome (Figure 6B). Cylindrical pharynx with thin lumen cuticle and slightly enlarged endbulb. Position of nerve ring obscure. Large cardia; intestinal cells with only few lipid droplets.

Reproductive system monorchic; testis straight, located ventrally to the intestine. Well developed, slightly arched spicules with tiny, rounded capitulum and no velum. Short gubernaculum with wide lateral crurae (Figure 6F–H).

Caudal glands extending as far as gubernaculum or mid of the retracted spicules. Short conical tail.

Females. Largely similar to males.

Nuclei and lipid droplets in intestinal cells distinct. Rectum thickly cuticularized (Figure 7D). In the intestine of the allotype female part of a filamentous bacteria was observed; this bacteria resembles the filamentous bacteria of the genus *Beggiatoa* 

		J4 N=7		J3 N=1		J2 N=3		J1+2 N=3	J1 N=1
	Min.	Max.	Mean		Min.	Max.	Mean		
L	778	881	819	800	454	625	564	578	402
cardia	5	8	7	8	5	6	6	5	5
CS	5 2 3	8	7	8 3 3	2	4	3		
dcs	3	6	4	3	2	3	3		3
amph%	35	53	45	52	41	47	43	38	43
aw	6	10	8	9	7	8	8	7	6
hw	17	19	18	17	17	19	18	17	14
dnr					58				
ph	107	121	113	112	87	97	93	85	77
mbd ph	26	31	29	26	21	26	24	22	19
mbd 1	33	38	36	36	19	26	23	25	17
bdnr					24				
bdcs	16	18	17	17	16	16	16	14	13
da	689	775	724	706	384	532	480	494	330
abd	18	2S	20	20	16	17	17	17	12
t	84	109	94	88	70	92	84	87	70
tmr	12	21	15	12	13	14	13	12	13
a	21	24	23	22	24	25	24	23	24
b	6.7	7.6	7.3	7.1	5.2	6.5	6	6.8	5.2
С	7.9	10	8.8	9.1	6.5	6.9	6.7	6.6	5.7

Table 5. Measurements (µm) and ratios of juveniles of Desmodorella balteata sp. nov.

which were observed and found in 'large mats' on the sediments of the hydrothermal vents where the samples were taken (Dinet et al., 1988; Figure 7A,G). Cuticular rings, constricting the body, were found in a few females (Figure 7H).

Reproductive system didelphic, amphidelphic with reflected ovaries (Figure 7A,F). Vulva a transverse slit; vagina vera with thick cuticle, vagina uterina with strong, spherical sphincter muscle. Scaled eggs present in the uterus of a few females (egg width 34  $\mu$ m, egg length 49  $\mu$ m; Figure 7F).

Short conical tail (Figure 9F).

Juveniles. Largely similar to adults. Juveniles have a relatively longer conical tril, which is increasingly more distinct in earlier stages; this can also be seen by the increasing c-value during ontogeny towards adults.

Fourth stage juveniles have distinct lateral rows of spines present ('false lateral alae'); aside to the regular rows of indistinct spines which are even less pronounced than in adults.

Head capsule completely ornamented with larger vacuoles in some specimens, only posterior to the fovea amphidialis in others (Figure 8E).

Young female reproductive system with straight ovaries, vagina or vaginal cells present (Figure 8F). Young male reproductive primordium consist of a straight testis; vas deferens reaches the rectum; spicule primordium present but obscure.

In third stage juveniles the two pairs of distinct lateral rows of spines present. Entire head capsule ornamented with vacuoles (vacuoles larger than in fourth stage, smaller than in second stage juveniles; Figure 8C).

Female genital primordium consist out of a slender straight cord of cells; no vaginal cells (Figure 8D).

In second stage juveniles somatic setae present. The two pairs of lateral rows of spines either slightly more distinct than the other rows, or all longitudinal rows equally developed and visible. Head capsule ornamented with larger vacuoles (Figure 8A).

Genital primordium consist out of a small to more elongated group of cells (Figure 8B).

In first stage juvenile very few somatic setae present. Body annuli of pharyngeal region slender, no distinction from those along the rest of the body. Longitudinal rows of ridges or spines hardly visible but regularly aligned; no 'false lateral alae'.

Entire head capsule ornamented with large vacuoles; large multispiral fovea amphidialis of which the apertura equals the fovea.

# Diagnosis

Desmodorella balteata sp. nov. is characterized by the combination of the following characters: the presence of two pairs of lateral rows with more distinct spines, among the other rows of spines; long head capsule with large multispiral fovea amphidialis with broad fovea and slit-like (multispiral) apertura; absence of subcephalic setae and varying number (0–4) of additional setae. Males are characterized by the presence of a ventral row of strongly built precloacal setae.

# Differential diagnosis

Desmodorella balteata sp. nov. is closely related to D. tenuispiculum Allgén, 1928 but can easily be distinguished from it by its smaller (aw=9–11  $\mu$ m) and more anterior located fovea amphidialis, covering only the anterior half of the head capsule (aw=13  $\mu$ m, fovea amphidialis covering almost entire length of head capsule in D. tenuispiculum); absence of subcephalic setae (eight distinct subcephalic setae in D. tenuispiculum), males differ in the presence of strong ventral precloacal setae (normal somatic setae in D. tenuispiculum).

Desmodorella spineacaudata sp. nov. (Figures 10-12; Tables 6 & 7)

# Type specimens

Holotype male: slide BN 297 (MNHN); allotype female: slide BN 298 (MNHN); other paratypes: 10 33, 8 99, 11 JJ, slides BN 296–297, 302–303 (MNHN), slides 3937–3941 (ZIRUG) and slides 10285–10287 (MBRUG).

# Type locality

Hydrothermal vents in the East Pacific Rise, Guyamas, 27°N-111°24'W; depth 2000 m; heterogeneous sediment covered with bacteria.

# Etymology

The name spineacaudata refers to the presence of ventral thorns on the male tail.

## Measurements

See Tables 6 & 7.

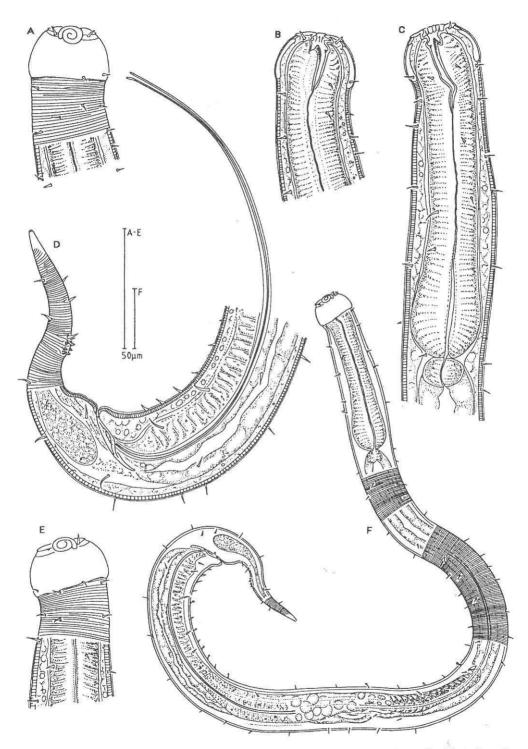


Figure 10. Desmodorella spineacaudata sp. nov. (A) Paratype male  $(\mathcal{J}_2)$  head capsule; (B)  $\mathcal{J}_2$ , buccal cavity; (C) Holotype male  $(\mathcal{J}_1)$ , pharyngeal region; (D)  $\mathcal{J}_1$ , tail region and spicules; (E)  $\mathcal{J}_1$ , head capsule; (F)  $\mathcal{J}_1$ , habitus.

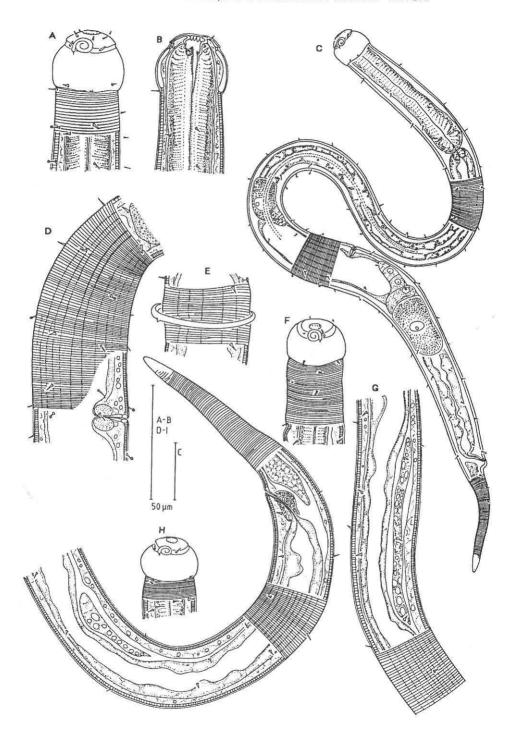


Figure 11. Desmodorella spineacaudata sp. nov. (A) Allotype female  $(\mathbb{P}_1)$ , head capsule; (B)  $\mathbb{P}_1$ , buccal cavity; (C)  $\mathbb{P}_1$ , habitus; (D)  $\mathbb{P}_1$ , body annuli and rows of spines, vulva; (E) paratype female  $(\mathbb{P}_2)$ ; cuticular ring on body; (F)  $J_{\mathbb{I}\mathbb{I}\mathbb{I}\mathbb{P}}$ , head capsule; (G)  $J_{\mathbb{I}\mathbb{I}\mathbb{I}\mathbb{P}}$ , genital primordium.

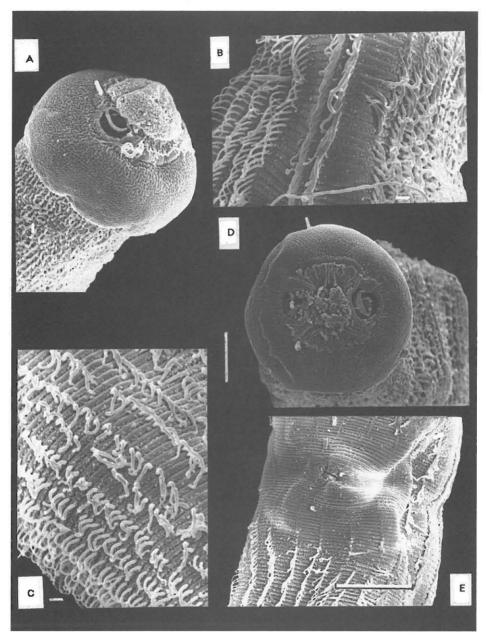


Figure 12. *Desmodorella spineacaudata* sp. nov. (A)  $\circlearrowleft_3$ , head capsule; (B)  $\circlearrowleft_3$ , detail of distinct lateral spines; (C)  $\circlearrowleft_3$ , detail of longitudinal rows of spines; (D)  $\circlearrowleft_3$ , head capsule; (E)  $\circlearrowleft_3$ , vulva. Scale bars: A–C, 1  $\mu$ m; D,E, 10  $\mu$ m.

# Description

Males. Body cylindrical with rounded head capsule and short conical tail (Figure 10F). Body cuticle ornamented with numerous (indistinct) spines, aligned densely on the annuli of the pharyngeal region (Figure 12A), aligned in regular longitudinal rows of

Table 6. Measurements (µm) and ratios of Desmodorella spineacaudata sp. nov.

	Holotype ೆ		Paratyp	be	Allotype ♀		Paratyp \$\text{P}\$	pe
			N=7				N=7	
		Min.	Max.	Mean ±SD		Min.	Max.	Mean ±SD
L	865	746	956	867 ±84·6	888	767	861	807 ±31·7
CS	4	2	5	$3 \pm 0.98$	3	3	4	$3 \pm 0.49$
dcs	2	2	5	$4 \pm 1.11$	6	2	6	$3 \pm 1.62$
amph%	45	27	43	$37 \pm 5.37$	43	33	54	$42 \pm 6.95$
aw	10	6	9	$7 \pm 1.25$	9	6	8	$7 \pm 0.75$
hw	22	17	22	$20 \pm 1.86$	21	14	20	$18 \pm 2.15$
mhw	32	27	32	$\frac{-}{29} + 1.86$	32	28	31	29 + 1.21
ph	138	111	145	$127 \pm 14$	146	108	119	$114 \pm 4.14$
mbd ph	35	25	34	$30 \pm 3.35$	34	28	31	$29 \pm 0.95$
mbd	38	30	39	$37 \pm 3.24$	43	29	42	$37 \pm 4.5$
cardia	9	6	11	8 + 1.72	10	7	12	$9 \pm 1.83$
bdcs	21	17	22	$19 \pm 1.95$	23	14	20	$18 \pm 2.31$
spic	232	142	232	$180 \pm 31.8$				
gub	30	16	32	$24 \pm 5.31$				
ďv					576	478	521	$500 \pm 18.3$
V					65	60	64	$62 \pm 1.3$
da	771	667	861	$772 \pm 76.1$	789	678	767	$718 \pm 30.4$
abd	28	21	27	$25 \pm 2.08$	23	17	20	$19 \pm 1.35$
t	93	75	100	$91 \pm 8.3$	100	81	89	$87 \pm 2.87$
tmr	9	9	11	$10 \pm 0.79$	15	11	15	$12 \pm 1.51$
a	22.8	19.6	25.6	$23.6 \pm 1.89$	20.7	19.7	26-4	$22.3 \pm 2.69$
b	6.3	6.2	8	$6.9 \pm 0.59$	6.1	6.7	7.4	$7.1 \pm 0.21$
C	9.3	8.7	10.7	$9.6 \pm 0.63$	8-9	8.8	10.1	$9.3 \pm 0.45$

spines along the rest of the body (Figures 10F & 12B,C); along the mid-third of the body, two lateral pairs of these longitudinal rows show much more distinct spines, giving at first glance the false impression of the presence of lateral alae. Few somatic setae arranged in six longitudinal rows. Approximately the last twelve ventral setae in front of the cloaca are located much closer to each other and are strongly built (Figure 10D,F). Slender, distinct body annuli in pharyngeal region slightly broader (ten annuli measuring 12–13  $\mu$ m) along the rest of the body (ten annuli measuring 6–11  $\mu$ m). In two specimens a large epizoic Suctoria specimen (33×73  $\mu$ m) was found attached to the body cuticle.

Smooth head capsule (no ornamentation of the inner layers of the cuticle; on SEM pictures, however, superficially the epicuticle is slightly wrinkled; Figure 12A) consists of three regions: the very short lip region is helmet-shaped and fits on the also short second part of the head capsule; this second region forms the transition between lip region and the large rounded third part of the head capsule. The four cephalic setae and the mid level of the fovea amphidialis are located on the short second part (Figures 10A,E & 12A). Multispiral fovea amphidialis (two turns) with deep fovea, located very anteriorly and spread over all three parts of the head capsule: anterior edge of fovea amphidialis located on the lip region, posterior edge of fovea amphidialis located anterior on the main part of the head capsule (Figures 10A,E & 12A). Six (or eight, obscure) subcephalic setae located at the posterior edge of the head capsule; sometimes part of them are shifted to the interannual space between head capsule and first body annule.

Table 7. Measurements (μm) and ratios of	juveniles of Desmodorella spineacaudata sp.
	100.

	J4 N=1		J3 N=7		J2 N=1
		Min.	Max.	Mean	
L	678	616	728	671	583
cardia	8	3	4	3	7
CS	3	3	4	3	7 3 3
dcs	2	1	6	3	3
amph%	52	29	44	39	39
aw	7	5	7	6	6
hw	13	13	17	16	17
mhw	26	25	26	26	25
ph	106	92	110	98	84
mbd ph	29	25	27	26	23
mbd 1	30	26	29	27	24
bdcs	13	13	17	16	17
da	594	533	622	581	495
abd	20	18	25	20	17
t	78	81	91	86	81
tmr	10	10	15	12	11
a	23	21	27	25	24
b	6.4	6.4	7.4	6.9	6.9
c	8.7	7.4	9	7.9	7.2

Buccal cavity with large dorsal tooth (3  $\mu$ m) and two smaller subventral teeth; strong muscular, broad cylindrical pharynx with slightly enlarged terminal bulb; fine lumen cuticle (Figure 10B,C). Intestinal cells with many lipid droplets. Nerve ring not observed.

Monorchic reproductive system straight; broad testis; spherical sperm cells. Very long filiform spicules without capitulum; velum not observed (Figure 10D). Gubernaculum with short lateral crurae.

Short conical tail with a group of postcloacal thorns arranged latero-ventrally in four 'longitudinal' rows of three to four thorns (such postcloacal thorns are also often seen in males of *Pseudochromadora* spp.).

Females. Largely similar to males (Figures 11A-D & 12D).

In one female a cuticular ring, similar to those found on the specimens of *Desmodorella balteata* sp. nov., was seen surrounding the body (Figure 11E).

Reproductive system didelphic, amphidelphic with reflected ovaries, located alternately at the right or at the left of the intestine according to the specimen. Ovary tips reflected towards the ventral or dorsal side of the body. Small vulva (Figure 12E); short vagina vera, vagina uterina with sphincter muscle. Nuclei of large oocytes with many nucleoli.

Juveniles. First stage juveniles not discovered.

In all three stages found, general body shape, annuli, shape of head capsule, fovea amphidialis, buccal cavity, pharynx, and intestine are very similar to the adults. There are no subcephalic setae on the head capsule. The spines in the longitudinal rows are all equally distinct.

In the second stage juveniles the longitudinal rows of spines are aligned more densely than in the successive stages. Genital primordium consists of a short cord (group) of cells.

In third stage juveniles (Figure 11F–I) the female genital primordium can be recognized as a strand of cells with both anterior and posterior distal tips swollen; no vaginal cells observed (Figure 11F,G). The male genital primordium consists of a slender string (bundle) of cells with swollen anterior tip (testis tip) and fine posterior end; the posterior end of the future vas deferens is still located some distance away from the rectum; a little spicular primordium surrounds the rectum (Figure 11I).

In fourth stage juveniles (young female, ready to moult) the vagina and vulva are present, but the ovaries are still outstretched.

#### Diagnosis

Desmodorella spineacaudata sp. nov. is characterized by the following characters: presence of distinct lateral rows of spines among the less distinct longitudinal rows of spines, the smooth three-part rounded head capsule, the extreme anterior position of the fovea amphidialis, the position of the subcephalic setae at the posterior edge of the head capsule. Males are characterized by the long filiform spicules but especially by the group of postcloacal thorns on the tail.

# Differential diagnosis

Desmodorella spineacaudata sp. nov. resembles D. filispiculum Lorenzen, 1976, D. sanguinea Southern, 1914, and D. sinuata Lorenzen, 1976.

Desmodorella spineacaudata sp. nov. can be distinguished from D. filispiculum by the position of the fovea amphidialis on the head capsule (posterior edge of fovea amphidialis reaching as far as the centre of the main part of the head capsule in D. filispiculum), the number and position of the subcephalic setae (eight to ten and more spread to anterior on the head capsule in D. filispiculum). Desmodorella spineacaudata sp. nov. can be distinguished from D. sanguinea by the position of the fovea amphidialis (entirely on the main part of the head capsule), and absence of the distinct lateral rows of spines in D. sanguinea. Desmodorella spineacaudata sp. nov. can be distinguished from D. sinuata by the presence of vacuolar ornamentation of the head capsule and body annuli in D. sinuata.

Next to these characters, *D. spineacaudata* sp. nov. can very easily be distinguished of all three related species by the presence of the group of postcloacal thorns in males (absent in all other species).

#### Discussion

The presence of the male postcloacal thorns and in some degree, the presence of the firm ventral precloacal setae (such setae are also present in *Desmodorella balteata* sp. nov.) refer to a possible phylogenetic link with the closely related genus *Pseudochromadora* Daday, 1899.

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