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Taxonomic Revision

A review of the genera *Croconema* Cobb, 1920 and *Pseudochromadora* Daday, 1899 (Nematoda, Desmodoroidea): new species from the Coasts of Kenya and Australia

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Abstract

This article is a review of the subfamily Desmodorinae (Nematoda, Desmodoroidea) and two related genera within this subfamily, *Croconema* Cobb, 1920 and *Pseudochromadora* Daday, 1899 with keys to genus or species level, genus diagnoses and lists of valid species. An emended diagnosis of, and discussion on, *Sibayinema* Swart & Heyns, 1991, is presented. Three new species are described: *Croconema floriani* sp.n. from the coast of Kenya, *Pseudochromadora galeata* sp.n. and *P. securis* sp.n. from the coast of Australia.

Introduction

In 1988 Nicholas et al. published an article on field and laboratory studies concerning *Pseudochromadora cazca* Gerlach, 1956 from mangroves at the coasts of New South Wales, Australia. Closer study of the specimens has revealed that these specimens do not represent *P. cazca* but are in fact two different new species. We found that these two species are not the only members of the genus *Pseudochromadora* found in Australia, as we found yet another species namely *P. quadripapillata* Daday, 1899 in similar samples taken at the Museum Beach, Darwin, Northern Territory. Cohabiting with the two new species of *Pseudochromadora*, other desmodorid nematodes such as *Papillonema danieli* Verschelde & Vincx 1995 and *Onyx* spec. were found, as well as members of the genera *Microlaimus* and *Gomphionema*. For further details on the fauna associated with the two new *Pseudochromadora* species and their habitat we refer to Nicholas et al. (1991). The Kenyan species, *Croconema floriani* sp.n., forms the last of a long list of newly described species from the superfamily Desmodoroidea (Nematoda) found in sediments of tropical mangroves at the Kenyan coast. (Verschelde & Vincx, 1992, 1993a, b, 1994, 1995, 1996; Muthumbi et al., 1995 and Verschelde et al., 1995). It was found together with members of the following genera: *Akantopharynx, Anoplostoma, Arctarjania, Catanema, Cephalanticoma, Chromadorella, Chromaspirina, Cytolaimium, Daptonema, Desmoscolex, Dorylaimopsis, Echinodesmodora, Eubostrichus, Eurystomina, Gammanema, Gomphionema, Halochoanolaimus, Hypodontholaimus, Linhomoeus, Marylymnia, Metadesmolaimus, Metalinhomoeus, Microlaimus, Neochromadora, Onyx, Papillonema, Paracanthonchus, Paracomesoma, Parodonthophora, Polygastrophora, Psammonema, Pseudochromadora, Ptycholaimellus, Setosabatieria, Steineria, Stylotheristus, Syringolaimus, Theristus, Viscosia, Zalonema.*

Materials and methods

Sample collection and treatment

The Kenyan benthic sample was taken (by D. Verschelde) in a medium grain-sized sandy sediment (median 347 μm) at the mouth of the Gazi Creek in the Gazi Bay, Kenya, using a core-tube of 3.5 cm diameter which was pushed into the sediment down to 20 cm depth. Samples were fixed with a hot (70 °C) 4% formalin-seawater solution.

The sample is decantated over a 38 μm mesh-sized sieve. In the lab, nematode specimens were picked out by hand (fine needle). Nematodes are transferred to pure glycerine by the method of Seinhorst (1959), and mounted on Cobb-slides (Cobb, 1917).

For methods of collection and treatment of the Australian samples we refer to Nicholas et al. (1988).

Specimen analysis

Drawings were made with the aid of a *camera lucida* on a Leitz Dialux 20EB microscope.

Scanning Electron Microscope pictures were taken with a JEOL JSM 840 of formalin fixed animals, which were dehydrated, critical point dried, and coated with 20–25 nm of gold (Verschelde et al., 1998)

Sediment analyses were carried out with the COULTER^R LS Particle Analysis.

Type specimens are deposited in the collection of the Koninklijk Belgisch Instistuut voor Natuurwetenschappen (KBIN) of Brussels (Belgium), the Zoology Museum of the University of Ghent (UGMD; Belgium), and the CSIRO of Canberra (Australia).

Terminology

In keys and descriptions a lot of descriptive terms concerning parts of internal organs and cuticular appendages are used. For definitions of these terms we refer to Maggenti (1981; for terms concerning pharynx and reproductive system), Verschelde & Vincx (1994, cuticular appendages; 1996, head region); Verschelde et al. (1995, head region and setae; 1998, amphids – *fovea – apertura*).

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.

Taxonomy and descriptions

Desmodorinae Filipjev, 1922

Diagnosis: Head capsule mostly present; if not, body annuli are distinct (and coarse).

Genera inquirenda:

Amphispira Cobb, 1920 (one badly described female) and *Metadesmodora* Stekhoven, 1942 (one juvenile) are no longer accepted as valid genera as they were erected based on only one doubtful specimen and the other possible members were transferred to other genera. If one, on the other hand, wants to maintain *Metadesmodora*, it should be added to the key as follows:

2(1) –Anterior edge of amphids located on lip region, not within first body annuli .... *Paradesmodora*
–Circular *fovea amphidialis* located on a basal plate ..... *Metadesmodora*
–Amphids entirely surrounded by body annuli 3

Key to genera of the Desmodorinae

1 – No head capsule, annuli present from posterior to lip region onwards; amphids

located partially or entirely within the first few body annuli 2
– Head capsule present; amphids located on the head capsule 4

2(1) – Anterior edge of amphids located on lip region, not within the first body annuli ..... *Paradesmodora*
– Amphids entirely surrounded by body annuli 3

3(2) – Unispiral amphids located on an amphidial plate ..... *Stygodesmodora*
– Uni- or multispiral amphids, no amphidial plate ..... *Echinodesmodora*

4(1) – Cephalic setae in front of or at the level of the anterior edge of the amphids 5
– Cephalic setae posterior to or at the level of the posterior edge of the amphids ..... *Bolbonema*

5(4) – Pharynx with long *postcorpus* (prolonged terminal bulb), lumen with thick cuticle 6
– Pharynx with rounded or only slightly prolonged terminal bulb 7

6(5) – Head capsule smooth ..... *Acanthopharynx*
– Head capsule formed out of a number of cuticular plates (*suturae* between plates visible with light-microscope) ..... *Acanthopharyngoides*

7(5) – Lateral alae present along the body 8
– Lateral alae absent 9

8(7) – Anterior edge of amphids located anterior on the main part of the head capsule; buccal cavity with denticles ; lateral alae starting behind head capsule, in the pharyngeal region ..... *Psammonema*
– Amphids located centrally or more posterior on the main part of the head capsule; buccal cavity without denticles; lateral alae starting at or posterior to level of the cardia ..... *Pseudochromadora*
– Amphids located centrally on main part of head capsule; body cuticle of adults ornamented with eight rows of clustered brush-like spines or ornaments ..... *Sibayinema*

9(7) – A large number of subcephalic setae arranged in three (or more) circles on the head capsule; amphids anterior on the thickly cuticularized head capsule; coarse body annuli, non-annulated tail-end perforated; short but broad somatic setae ..... *Croconema*
– No or few subcephalic setae; if many subcephalic setae are present, then the non-annulated tail-end is not perforated, body annuli are not so coarse, somatic setae are fine and amphids are located more centrally on the head capsule 10

10(9) – Triangular or rounded-triangular head capsule; multispiral amphids of two turns or more; finer body annuli throughout; slender pharynx with pyriform (i.e. onion-shaped) terminal bulb ..... *Zalonema*
– Blunt or rounded head capsule; coarse (broad) body annuli, at least in the pharyngeal region if not throughout, large muscular pharynx 11

11(10) – Amphids located on an amphidial plate ..... *Pseudodesmodora*
– No amphidial plate 12

12(11) – Body ornamented with longitudinal rows of ridges or spines ..... *Desmodorella*
– No longitudinal rows of ridge or spines ..... *Desmodora*

Remark: A similar key, yet independent of this one, to the genera of the Desmodorinae has been constructed by Decraemer & Smol, and will be published in Eyualem et al. (in press).

Verschelde et al. (1998) re-established all subgenera of the genus *Desmodora* de Man, 1889 as separate valid genera. They argued their revision with combinations of partially new characters, which previously were not always recognised by other authors. Based on these sets of combined characters they were able to give emended diagnoses for each of the re-established genera. Of *Bolbonema* Cobb, 1920, *Croconema* Cobb, 1920 and *Pseudochromadora* Daday, 1899 they only gave short diagnoses in view of more elaborate emended diagnoses which were to be published in a next article. Here we now give the emended diagnoses of *Sibayinema*, *Croconema* and *Pseudochromadora*, again based on sets of combined characters.

Sibayinema *Swart & Heyns, 1991: Syn.:* Desmodora *(*Sibayinema*) Swart & Heyns, 1991*

Emended diagnosis: Desmodorinae. Cylindrical body with short, distinct head capsule and slender cylindrico-conical tail. Distinct, coarse

body annuli. Lateral *alae* present, but in adults hidden by lateral rows of clustered, short hair-like spines (Verschelde & Vincx, 1994) forming rows of bristles or brush-like ornaments. SEM-pictures narrowly reveal that the annuli split in two at the level of the lateral *alae* (it cannot be seen if these interdigitate as seen in most species of *Pseudochromadora*). In total there are eight rows of bristles or brush-like ornaments (formed by clustered short hair-like spines). Short somatic setae arranged in eight longitudinal rows along the body.

Two regions can be recognized on the head capsule, without suture between the two areas: slender rounded labial region, followed by the main part of the head capsule which has an extra-thick inner layer of the cuticle. Four cephalic setae located on the labial region at the anterior rim of the main part of the head capsule. Loop-shaped (males) to unispiral *fovea amphidialis* (at least in females in case of sexual dimorphism) located centrally on the main (posterior) region of the head capsule. No subcephalic setae.

Cylindrical pharynx with bipartite, strongly sclerotized terminal bulb.

Arched spicules; *gubernaculum* without *capitulum*.

Non-annulated tail tip perforated.

Emended differential diagnosis: *Sibayinema* resembles *Desmodorella* Cobb, 1933, *Psammonema* Verschelde & Vincx, 1995, and most of all *Pseudochromadora* Daday, 1899; it slightly resembles *Croconema* Cobb, 1920. It can be distinguished from *Croconema*, *Psammonema*, and *Pseudochromadora*, by the presence of (eight) longitudinal rows of brush-like ornaments along the body (absent in *Croconema*, *Psammonema*, and *Pseudochromadora*), and from *Desmodorella* by the loop-shaped to unispiral *fovea amphidialis* and presence of lateral alae along the body (multispiral amphids and no lateral alae in *Desmodorella*).

Discussion: Concerning the unispiral *fovea amphidialis*: Swart & Heyns (1991) speak of a 'circular amphid aperture', but this is incorrect as the amphid has a central spot, making it an unispiral fovea and not a circular fovea, which doesn't have a central spot.

The combination of the following characters is unique within the subfamily Desmodorinae: the absence of subcephalic setae on the head capsule, the central position of the unispiral (at least in females) *fovea amphidialis* on the main part of the head capsule, the presence of lateral *alae* along the body, together with the presence of eight longitudinal rows of brush-shaped ornaments or bristles. The first three characters are, in fact, identical to *Pseudochromadora*, but the longitudinal rows of bristles are not! As the presence of longitudinal rows of spines has been accepted as a distinguishing generic character for *Desmodorella* (Verschelde et al., 1998), it is evident to accept the longitudinal rows of bristles as a differentiating and unique character for *Sibayinema*, and thus distinguishing it from *Pseudochromadora*. As Verschelde et al. (1998) re-established all other subgenera of *Desmodora* as separate genera, it is also evident to render *Sibayinema* the generic status.

Type species: Sibayinema natalensis Swart & Heyns, 1991: Syn.: *Desmodora (Sibayinema) natalensis* Swart & Heyns, 1991.

Habitat: fresh-water.

Croconema *Cobb, 1920*

Emended diagnosis: Desmodorinae. Cylindrical body with blunt head capsule and short conical tail. Thick cuticle; broad body annuli often ornamented with ridges or spines. Short, broad somatic setae arranged in six to eight longitudinal rows; setae can be distinctly hollow with a short narrow tip.

Long (high) head capsule with thick cuticle; lip region often separated from the rest of the head capsule by a *sutura*; six inner and six outer labial setae; four cephalic setae located just in front of the amphids; amphids with multispiral (1.2–1.5 turns) *fovea amphidialis* located anterior on the head capsule, sexual dimorphism can occur; numerous subcephalic setae arranged in three (or more) circles on the head capsule.

Buccal cavity with prominent dorsal tooth and one or two small (sub)ventral teeth, denticles can be present. Cylindrical pharynx with slightly prolonged terminal bulb.

Male reproductive system monorchic, slender arched spicules with capitulum (velum?) and

complex gubernaculum. Often there are copulatory thorns and non-annulated tail-end can show ornaments such as thorns, indentations or ventro-lateral alae. In males of all known species the ventro-lateral rows of somatic setae, from the level of the copulatory thorns to the tail, are arranged closely together in a fashion similar to that seen from the supporting setae of Epsilonematidae (see Verschelde & Vincx, 1994); these setae are thought to give support during copulation.

Position of the vulva in females quite posterior (V around 60% or more). Brood protection can occur (Ott, 1976; Verschelde & Vincx, 1995).

Inner cuticle of non-annulated tail end perforated.

Differential Diagnoses: *Croconema* Cobb, 1920 resembles *Pseudochromadora* Daday, 1899 and *Psammonema* Verschelde & Vincx, 1995 but can be distinguished from them by the following combination of characters: the presence of subcephalic setae arranged in three or more circles on the head capsule and the absence of lateral alae in *Croconema*, compared to the absence of subcephalic setae and the presence of lateral *alae* in *Pseudochromadora* and *Psammonema* (the latter has additional setae, Verschelde & Vincx, 1994, 1995).

Discussion: The combination of the following characters is unique for the genus within the subfamily Desmodorinae: the anteriorly placed *fovea amphidialis* on the long head capsule, the many subcephalic setae arranged in three or more circles on the head capsule, the absence of lateral *alae* along the body and the coarse annuli with thick body cuticle.

Type species: *C. cinctum* Cobb, 1920

Representatives of the genus *Croconema* are mostly found in medium to coarse sandy sediments, but have also been found in some muddy sediments and even in black mud. They are found in intertidal, littoral, eulittoral and sublittoral areas of tropical to temperate seas. In the species list we added the localities of every species.

Including *Croconema floriani* sp.n., there are now twelve valid species in the genus *Croconema* (see Verschelde et al., 1998): *C. boucheri* Ott, 1976 (Banyuls-sur-mer, France, Mediterranean Sea); *C. cinctum* Cobb, 1920 (Jamaica; Addu-Atoll, Maldives; Red Sea; Salvador, Bahia, Brazil); *C. floriani* sp.n. (Gazi, Kenya); *C. longiseta* Schuurmans Stekhoven, 1950 (black mud of Villefranche); *C. mammillatum* Steiner & Hoeppli, 1926 (Japan); *C. mawsonae* Inglis, 1968 (St. Vincent's Bay, New Caledonia); *C. mediterraneum* Wieser, 1954 (Menorca, Mediterranean Sea); *C. otti* Gourbault & Vincx, 1990 (Guadeloupe); *C. ovigerum* Ott, 1976 (Rovinj, Yugoslavia); *C. sphaericum* (Kreis, 1928) Luc & De Coninck, 1959 (Roscoff, Mediterranean Sea); *C. stateni* Allgen, 1928 (State-Islands, Chile;

Table 1. Species characters for the genus *Croconema*

	Copulatory thorns	Precloacal thorns	Sexual dimorph amphids	Tail end normal	Tail end with (sub)ventral thorns	Tail end with subventral alae	Denticles
C. boucheri	–	–	–	+	–	–	–
C. cinctum	+	+	–	?	?	–	–
C. floriani sp.n.	+	–	+ (shape)	–	–	+	–
C. longiseta	–	–	–	+	–	–	–
C. mammillatum	~+	–	–	–	+	–	+
C. mawsonae	–	–	–	+	–	–	+
C. mediterraneum	+	–	–	–	+	–	–
C. otti	–	–	+ (size)	~+	–	–	–
C. ovigerum	+	–	+ (size)	–	+	–	+
C. sphaericum	+	–	–	–	~+	–	–
C. stateni	+	+	+ (size)	–	+	–	+ (dentated ring)
C. torquens	+	+	+(shape)	–	+	–	–

Santa Cruz, Argentina); *C. torquens* (Gerlach, 1963) Gerlach, 1964 (Red Sea).

For construction of the key, a number of mainly male characters were considered (see Table 1).

1 – Amphids similar in both sexes (no sexual dimorphism) 2
– Amphids sexual dimorph either in size or in shape or both 8
$2_{(1)}$ – Copulatory thorns present 3
– Copulatory thorns absent 6
$3_{(2)}$ – Precloacal thorns present ..... *Croconema cinctum*
– Precloacal thorns absent 4
$4_{(3)}$ – Buccal cavity with denticles ..... *C. mammillatum*
– Buccal cavity without denticles 5
$5_{(4)}$ – Two copulatory thorns ..... *C. mediterraneum*
– About nine copulatory thorns ..... *C. sphaericum*
$6_{(2)}$ – Buccal cavity with denticles ..... *C. mawsonae*
– Buccal cavity without denticles 7
$7_{(6)}$ – Somatic setae in six longitudinal rows ..... *C. longiseta*
– Somatic setae in eight longitudinal rows ..... *C. boucheri*
$8_{(1)}$ – Amphids sexual dimorph only in size 9
– Amphids sexual dimorph in size and shape 11
$9_{(8)}$ – Copulatory thorns present 10
– Copulatory thorns absent ..... *C. otti*
$10_{(9)}$ – Precloacal thorns present ..... *C. stateni*
– Precloacal thorns absent ..... *C. ovigerum*
$11_{(8)}$ – Copulatory and precloacal thorns present ..... *C. torquens*
– Only copulatory thorns (no precloacal thorns) ..... *C. floriani.*

Croconema floriani sp.n.: Figures 1 and 2; Table 2

Type specimens: Holotype male: slide UGMD 102993 – specimen no. 2; allotype: slide UGMD 102994 – specimen 2; paratype male: slide UGMD 102994 – specimen 1 (Ghent University Zoology Museum).

Type locality: Kenya, Gazi (09/08/1989). Coarse sand sample taken at the mouth of the Gazi Creek, in the pits of the 'pits and bumps' area.

Etymology: This species has been named in honour of Florian Verschelde.

Measurements: see Table 2.

Description:

Males: Desmodorinae. Cylindrical body with well developed, large head capsule and short conical tail. Thick, multi-layered cuticle with numerous, broad annuli (ten annuli measure 38 μm in the pharyngeal region, 36 μm in the rest of the body) and distinct interannual spaces (1–2 μm). Transparent epicuticle of the first two body annuli overlaps the head capsule (Fig. 1a, b). Annuli ornamented with fine ridges (Fig. 1a, e; similar to those seen in members of the Epsilonematidae, see Verschelde & Vincx, 1994) and thorn-like spines, which are present both at the anterior as well as at the posterior edge of the annuli (Fig. 1g). Thick, broad and hollow somatic setae located in eight longitudinal rows in the pharyngeal region, in seven (single ventral row) along the rest of the body, and in four rows on the tail. The setae have a special structure (best observed in the anterior half of the body; Fig. 1a, b, d): the broad setae abruptly narrow down distally to a slender nipple-shaped tip. Somatic setae of the ventro-lateral rows, located between the region of the copulatory thorns and the mid tail region, are oriented similar to supporting setae in epsilonematids (see Verschelde & Vincx, 1994), here probably rendering support during copulation (Figs. 1g, 2b). In the same area numerous small thorns are visible. Strands of brownish hypodermal glands follow the course of the somatic setae (Figs. 1d, 2a).

Two-part head capsule: the short labial region is separated from the rest of the large head capsule by a *sutura*. Six distinct inner labial setae located at the rim of the buccal cavity, six smaller outer labial setae located half-way between inner labial setae and the *sutura*, the four cephalic setae and first circle of eight subcephalic setae are located at the sutura between lip region and main region of the head capsule (Fig. 2d); further posterior on the main region are three more circles of subcephalic setae located posterior to the amphids carrying four (to six), eight, and six (to four) subcephalic setae respectively; this adds up to a total of 24–26 subcephalic setae distributed over four circles. Large crypto-spiral to closed loop-shaped *fovea amphidialis* (smaller in female: sexual dimorphism), located at the anterior margin of the main part of the head

Table 2. Measurements (in μm) and ratios of *Croconema floriani* sp.n

	Hol.♂	Par.♂ $n=1$	All.♀
L	1728	1956	2022
cs	11	8	8
dcs	10	8	7
amph%	34	41	27
aw	13	16	9
hw	38	38	36
dnr	133	137	
ph	265	267	279
mbd ph	79	81	85
mbd	79	78	121
bdnr	70	73	
bdcs	28	29	30
spic	82	91	
gub	35	37	
dv			1500
V			74
da	1583	1845	1900
abd	67	71	49
t	137	133	122
tmr	47	39	70
a	21.9	25.1	16.7
b	6.5	7.3	7.3
c	12.6	14.7	16.6

capsule just posterior to the *sutura*. In the paratype male the *corpus gelatum* (Coomans, 1978; Verschelde & Vincx, 1992) bulges out from the *fovea amphidialis* (Fig. 1b).

Large stoma with big dorsal tooth and two tiny subventral teeth, denticles not observed (Fig. 1d). Muscular pharynx with slender *procorpus* and slightly prolonged, tripartite terminal bulb; thickened cuticular lumen wall (Figs. 1c, 2a). Intestinal cells filled with lipid droplets.

Reproductive system monorchic, located ventrally to the intestine. Testis with globular sperm cells. Slender spicules arcuate, with small *capitulum*; it is very hard to be sure whether a fine velum is present or not (marked by the dotted line in Fig. 1g and h; it could also be a muscle). Complex *gubernaculum* with broad median part (*cuneus*) and straight lateral *crurae* (Fig. 1h). A group of many copulatory thorns is located anterior to the cloaca (Figs. 1g, 2b; on a small ventral bump).

Short tail with perforated non-annulated tail tip; non-annulated tail tip carrying 14 somatic setae of which three pairs are located latero-ventrally beside the latero-ventral pair of 'tail *alae*' (Fig. 1e, f). Caudal glands extending as far as the spicules; large valve in spinneret distinct.

Female: Body (Fig. 2c), cuticle, shape and pattern of somatic setae, shape and ornamentation of the annuli (Fig. 2g), buccal cavity (Fig. 2e), and pharynx similar to males.

Head capsule, lip sensillae, cephalic and subcephalic setae arranged as in males. Distinct *sutura* between lip region and main region of the head capsule. Small multi-spiral (1.25 turns) amphids (sexual dimorphism; Fig. 2d). Epicuticle of the first two annuli overlaps the head capsule.

Reproductive system didelphic, amphidelphic with reflected ovaries, small vulva located posteriorly along the body (V=74%), *vagina vera* cuticular, *vagina uterina* with sphincter muscle. Reproductive system located ventrally to the intestine.

Somatic setae on tail mainly arranged in four longitudinal rows. Perforated non-annulated tail end longer than in males; short somatic setae. Valve in spinneret visible (Fig. 2f).

Juveniles: not found.

Diagnosis: Desmodorinae. *Croconema floriani* sp.n. is characterized by the combination of the following characters: straight head capsule with distinct *sutura* between lip region and main region, sexual dimorphism in shape of the amphids, short (i.e. compared to those of other species of the genus) and broad setae with slender nipple-shaped distal tips, annuli with thorn-like spines both at anterior and posterior edge of each annule. Males are characterized by their large number of copulatory thorns and latero-ventral *alae* on the non-annulated tail tip.

Differential diagnosis: *Croconema floriani* sp.n. resembles *C. mammillatum* Steiner & Hoeppli, 1926; *C. ovigerum* Ott, 1976; *C. otti* Gourbault & Vincx, 1990 and *C. stateni* Allgen, 1928 but can be distinguished easily from all of them by the combination of the following characters: none of the above species show the spiny ornamentations of the annuli, the short, broad setae with nipple-shaped distal tip, and none of their males show a

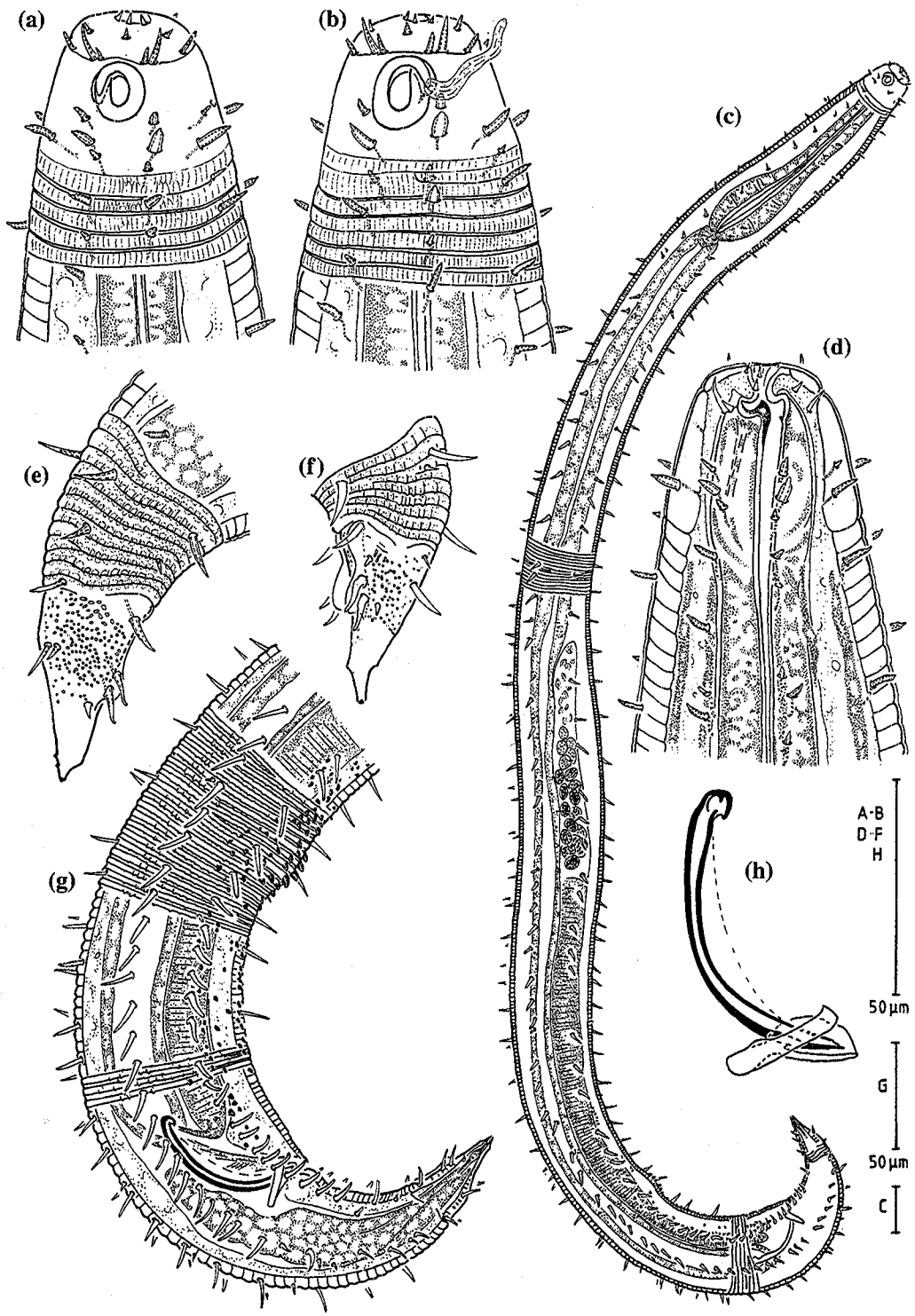

Figure 1. Croconema floriani sp.n. (a) Holotype male (M_1), head capsule. (b) Paratype male (M_2), head capsule. (c) M_1, habitus. (d) M_1, buccal cavity. (e) M_1, part of tail. (f) M_2, part of tail. (g) M_1, posterior body region. (h) M_1, spicule and gubernaculum.

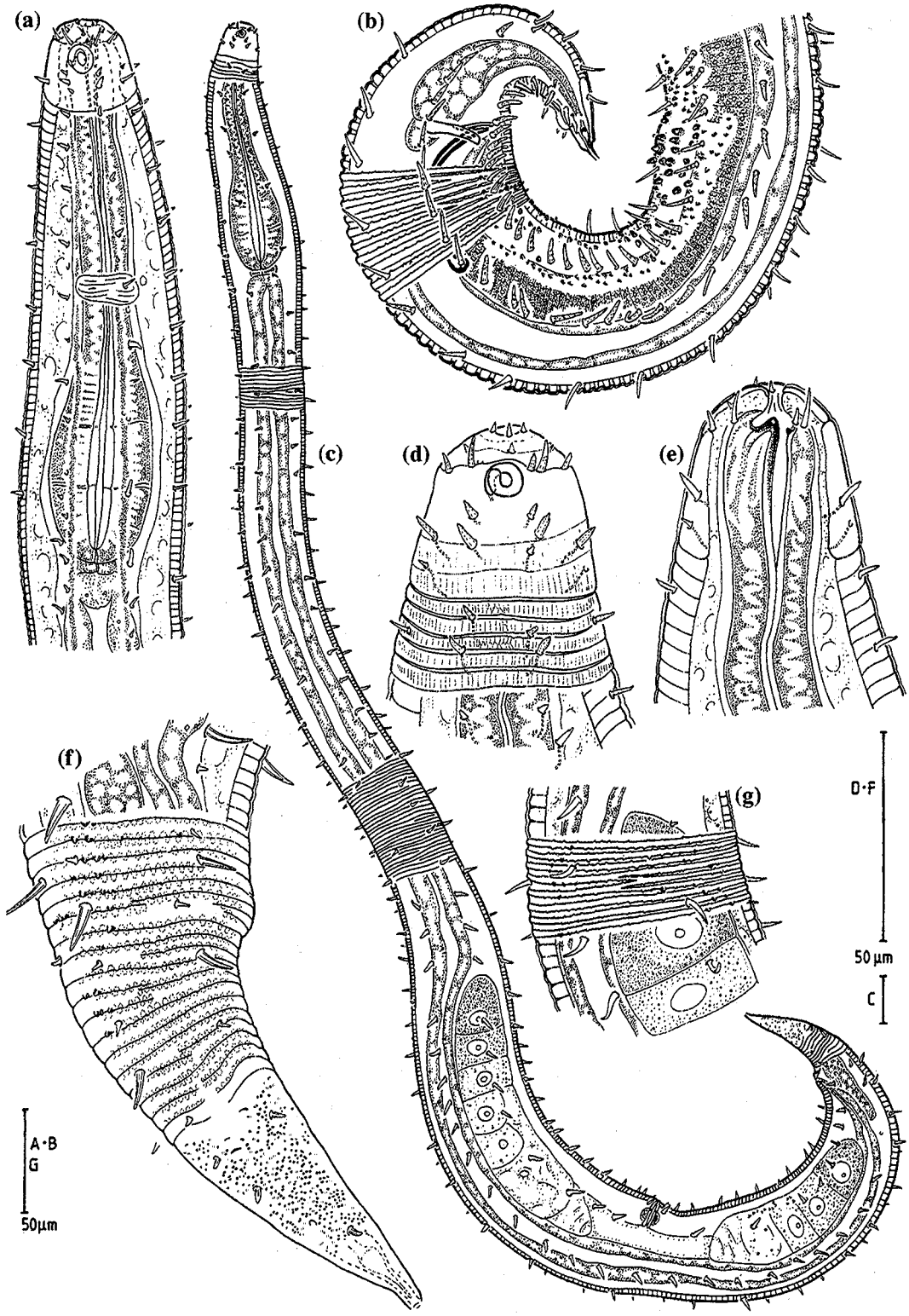

Figure 2. Croconema floriani sp.n. (a) M_1, pharyngeal region. (b) M_2, posterior body region. (c) Allotype female (F_1), habitus. (d) F_1, head capsule. (e) F_1, buccal cavity. (f) F_1, tail. (g) F_1, annuli.

large group of small copulatory thorns and latero-ventral *alae* on the non-annulated tail end as is found in *C. floriani* sp.n.

Discussion: The posterior position of the vulva is similar to what one would see in females of brood protecting species (*cfr.* Gourbault & Vincx, 1990; Verschelde & Vincx, 1995), but as only one female was found, there is no hard evidence yet to state that brood protection occurs in this species.

Pseudochromadora *Daday, 1899*

Emended diagnosis: Desmodorinae. Short cylindrical body with short head capsule and short conical tail. Body annuli with distinct interannual spaces. Lateral *alae* extending from posterior to the pharynx as far as the tail; in most species (one exception) the annuli split up and interdigitate at the level of the lateral alae. Short somatic setae arranged in six longitudinal rows.

Two (or three) part head capsule: slender rounded labial region, followed by the main part of the head capsule which has an extra-thick inner layer of the cuticle; a *sutura* can be present between the two (three) regions of the head capsule. Four cephalic setae located either on the labial region or on the anterior rim of the main part of the head capsule. Unispiral amphids (at least in females in case of sexual dimorphism) located centrally on the main (posterior) region of the head capsule. No subcephalic setae; additional setae (Verschelde et al., 1998) may be present.

Short cylindrical pharynx with bipartite terminal bulb.

Males of most species (one exception) have copulatory thorns and postcloacal thorns. Arched spicules; *gubernaculum* with *capitulum*.

Differential diagnosis: *Pseudochromadora* resembles *Croconema* Cobb, 1920 and *Psammonema* Verschelde & Vincx, 1995. It can be distinguished from *Croconema* by the presence of lateral *alae* along the body (absent in *Croconema*), and from *Psammonema* by the central position of the *fovea amphidialis* on the head capsule (anterior position in *Psammonema*) and the position of origin of the lateral *alae* (posterior to the level of the pharyngeal terminal bulb in *Pseudochromadora*, anterior to the level of the terminal bulb in *Psammonema*).

Discussion: The combination of the following characters is unique within the subfamily Desmodorinae: the absence of subcephalic setae on the head capsule, the central position of the unispiral (at least in females) *fovea amphidialis* on the main part of the head capsule and the presence of lateral *alae* along the body which start posterior to the pharynx.

Type species: *P. quadripapillata* Daday, 1899.

Representatives of the genus *Pseudochromadora* are found in medium to coarse grain-sized sandy sediments, as well as in mud and muddy sediments. They are found in estuarine, mangrove, intertidal and littoral areas of tropical to cold seas; it is a cosmopolitan genus. Sporadically they can even be found in brackish or fresh water. In the species list we added the localities of every species.

Including the present two new species, the genus now has eight valid species (Verschelde et al., 1998): *Pseudochromadora buccobulbosa* Verschelde & Vincx, 1995 (Gazi, Kenya); *P. cazca* Gerlach, 1956 (Porto Novo, Sao Sebstiao, Brazil); *P. coomansi* Verschelde & Vincx, 1995 (Gazi, Kenya); *P. incubans* Gourbault & Vincx, 1990 (Guadeloupe); *P. interdigitatum* Muthumbi et al., 1995 (Gazi, Kenya); *P. galeata* sp.n. (New South Wales, Queensland, Australia); *P. quadripapillata* Daday, 1899 (Berlinharbor, Seleo Island, German New Guinea, New Guinea; Punta Arena, Pacific coast of Costa Rica; Cananeia, Brazil; Chesapeake Bay, Maryland, USA; Annapolis, USA; Mangla, Nil Kamal; Bay of Bengal; Nova Scotia, Canada; Solomon Islands; Darwin, Australia); *P. securis* sp.n. (New South Wales, Queensland, Australia).

Here a key to the species of the genus *Pseudochromadora* is presented:

1. – Body annuli split up and interdigitate at the level of the lateral alae; males with copulatory thorns 2
   – Body annuli do not split up at the level of the lateral alae; males without copulatory thorns, but with cup-shaped pre-cloacal supplements ..... *Pseudochromadora quadripapillata* Daday, 1899
2(1) – Hat-shaped labial region distinct from on the main part of the head capsule 3
   – Rounded labial region 4

3(2) – Buccal cavity with complex dorsal tooth oriented towards a ventral plate, ventral tooth with opposite dorsal plate posterior to this (Figs. 7c, 8c); males with large unispiral amphids ..... *P. securis* sp.n.
– Buccal cavity with large dorsal tooth oriented opposite to the small subventral teeth (Fig. 3b); males with (open) loop-shaped *apertura amphidialis* ..... *P. galeata* sp.n.

4(2) – Amphids shifted towards a dorso-lateral position on the head capsule; fertilized females with protruded anterior lip of the vulva .....*P. incubans* Gourbault & Vincx, 1990
– Amphids located laterally (centrally) on the main part of the head capsule 5

5(4) – Buccal cavity with a dorsal plug followed by the dorsal tooth in the pharyngostome; muscles of pharyngostome swollen, forming a buccal bulb; males with closed loop-shaped amphids (sexual dimorphism).....
.....*P. buccobulbosa* Verschelde & Vincx, 1995
– Buccal cavity without dorsal plug anterior to the dorsal tooth; no sexual dimorphism in amphidial shape..... 6

6(5) – Cephalic setae located on the labial region of the head capsule..... 7
– Cephalic setae located at the transition (*sutura*) between the labial and main region of the head capsule .....
.....*P. coomansi* Verschelde & Vincx, 1995

7(6) – Copulatory thorns clustered; spicules with rounded *capitulum* .... *P. cazca* Gerlach, 1956
– Copulatory thorns more dispersed longitudinally; spicules with funnel-shaped capitulum .....
.....*P. interdigitatum* Muthumbi et al., 1995

Pseudochromadora galeata sp.n.: (Figs 3, 4, 5, 6, Table 3 and 4).

Type specimens: Holotype male: slide ANIC NEM COLLN 662 specimen 2504 (CSIRO). Paratypes: allotype female: slide ANIC NEM COLLN 664 specimen 2521; other paratypes: 7 males, 7 females, 14 JJ: slides ANIC NEM COLLN 661 (specimens 2501–2502), 662 (specimens 2503, 2505–2507), 663 (specimens 2509, 2510, 2512, 2514–2516, 2519; CSIRO); slides UGMD 102995–102999 (Ghent University Zoology Museum).

Type locality: Waterfall Creek on the Clyde River estuary at Batemans Bay in S.E. New South Wales, Australia.

The species is widely spread over the *Avicennia* mud-flats (Nicholas et al., 1988).

Other localities: Hunter River estuary (New South Wales) and Pine River estuary (Queensland).

Etymology: The species name is derived from the Latin word *galea, -ae* = foot-soldier's helmet; *galeatus, -a, -um* = with helmet; referring to the cap-shaped lip region of the species. The genus name *Pseudochromadora* (from Greek *-dora* meaning skin) is feminine, hence *galeata*.

Measurements: see Table 3 & 4.

Description:

Males: Short cylindrical body with blunt head and slender conical tail (Figs. 3a, 5a). Body annuli ornamented with long slit-like vacuole, at the level of the lateral *alae* the annuli split up into two (seldom three) and interdigitate; distinct inter-annual spaces. Annuli with small spines (Verschelde & Vincx, 1994) on their posterior edge mainly dorsally, more distinct in the posterior half of the body (Fig. 5d). Lateral *alae* start just behind the posterior edge of *cardia* extending to the level of the postcloacal thorns on the tail (Fig. 3a,g). Epizoic *Suctoria* specimens can be found attached to the cuticle (Fig. 3k), measuring up to 54μm in length and 28μm in width.

Somatic setae arranged in six longitudinal rows, of which the setae of the ventral row are connected with gland cells.

Two part head capsule: lip region 'sits' as a flattened hat on the main (second) region of the head capsule where a *sutura* marks the anterior margin of the extra-thick inner layer of the cuticle (Figs. 3c–f, 5b). Six tiny inner and six large outer labial setae located on the cap-shaped lip region (Fig. 5b); four cephalic setae located just posterior to the edge of the lip region. Main (second) part of the head capsule ornamented with numerous tiny vacuoles; no additional setae. Amphids: large open loop-shaped *apertura amphidialis*, closed loop-shaped to cryptospiral *fovea amphidialis* (sexual dimorphism; Fig. 3c–f).

Buccal cavity with small cheilorhabdia in cheilostome, large dorsal tooth in pharyngostome,