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Psammonema gen.n. and *Pseudochromadora* DADAY, 1889 (Nematoda, Desmodoridae) from sandy sediments of Gazi, Kenya

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Abstract

Three new species (*Psammonema ovisetosum* gen. et sp.n., *Pseudochromadora coomansi* sp.n. and *Pseudochromadora buccobulbosa* sp.n.; including all juvenile stages) belonging to a known and to a new genus of the family Desmodoridae (Nematoda, Desmodoroidea) were found in sandy sediments of the intertidal zone in front of the estuarine mangroves of Gazi, Kenya. *Psammonema* gen.n. differs from *Pseudochromadora* DADAY, 1889 in shape and number of somatic setae in pharyngeal region, in position and shape of lateral alae, and in the anterior position of the amphids on the head capsule. Comments are given on the ecto-symbiotic organisms, feeding habits of the species and on the ontogenetic transformations of some morphological characters.
Key words: Marine Nematodes, Desmodoridae, systematics.

Résumé

Trois espèces (*Psammonema ovisetosum* gen. et sp.n., *Pseudochromadora coomansi* sp.n. et *Pseudochromadora buccobulbosa* sp.n.) d'un genre connu et d'un genre nouveau de la famille Desmodoridae ont été trouvées dans les sables de Gazi, Kenya. *Psammonema* gen.n. diffère de *Pseudochromadora* DADAY, 1889 par la forme et le nombre de sois somatiques dans la région pharyngienne, par la position et en forme des ailes latérales, et par la position antérieure des amphides sur la capsule cephalique. La présence d'ectosymbiotes et leurs importance comme source nutritionelle, ainsi que les transformations ontogénétiques de certain charactères morphologiques sont commentariées.
Mots-clefs: Nématodes marins, Desmodoridae, systématique.

Introduction

In July and August of 1989, samples were taken in an estuarine mangrove system of the Gazi Creek (about 50 km south of Mombasa, Kenya). In these sediments, total meiofauna densities vary between 1976 and 6707 individuals 10 cm^{-2} of which 53.5% to 95.1% are nematodes (VANHOVE, S. *et al.*, 1992). Many of those nematodes are representatives of the Desmodoroidea, a group which often flourishes in the intertidal, coarse (coral) sandy sediments of tropical beaches.

Psammonema ovisetosum gen. et sp.n. and *Pseudochromadora coomansi* sp.n. were found in the vicinity of *Sonneratia alba* trees, dwelling together with many other nematode species of 85 different genera. *Pseudochromadora buccobulbosa* sp.n. was found between *Bruguiera gymnorrhiza* and *Sonneratia alba* trees, together with other nematode species of 34 different genera.

Material and Methods

Benthic samples were taken (by D. VERSCHELDE) using a core of 3.5 cm diameter which is pushed into the sediment down to 20 cm depth. Samples were fixed with a hot (70°C) 4% formalin-seawater solution. Nematodes were transferred to pure glycerine by the method of SEINHORST (1959).
Drawing were made with the aid of a camera lucida on a LEITZ DIALUX 20EB microscope.
Scanning Electron Microscope pictures were taken from formalin fixed animals, transferred in OsO_4, dehydrated, dried, and coated with 20-25 nm of gold (type of SEM: JEOL JSM 840).
Type specimens are deposited in the collection of the Koninklijk Belgisch Instistuut voor Natuurwetenschappen (KBIN) of Brussels (Belgium), of the Muséum national d'Histoire Naturelle (MNHN) of Paris (France), of the British Museum of Natural History (BMNH) of London (Great Britain), and of the Zoology Institute (ZIRUG) and Marine Biology Section (MBRUG) of the University of Gent (Belgium).

Abbreviations

a: body length divided by maximum body diameter; a(ar): body length divided by body diameter measured anterior to the region of the reproductive system; 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; 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.

Descriptions

Familia DESMODORIDAE FILIPJEV, 1922

Genus **Psammonema** gen.n.

TYPE SPECIES

Psammonema ovisetosum gen. et sp.n.

ETYMOLOGY

From Greek: *psammos* = sand, *nema* = thread (neuter)

DIAGNOSIS

Cylindrical body with distinct head capsule and conical tail. Numerous fine body annuli, with a multi-layered cuticle. Fine lateral alae present, extending from the level of the first third of the pharynx to the anal region; they are formed by the local lateral raising of each annule, without interdigitations among these annuli. Slender, long somatic setae in eight longitudinal rows in the pharyngeal region, in six rows along the rest of the body. Females can have different kinds of somatic setae: in the last third of the body, setae are firm and thorn-shaped; when brood protection occurs, the ventro-lateral setae of the mid-third of the body are prolonged to help hold the eggs.
Thick head capsule with well set-off labial region: the labial region sits as a helmet on the rest (main part) of the head capsule. Six inner and six outer labial setae located in the labial region. Four cephalic setae located on the head capsule at the level of the anterior half of the amphids. No subcephalic setae; however, in some specimens (two to four) 'additional setae' (Ergängzungsborsten, LORENZEN (1973); soies additionnelles, DECRAEMER & GOURBAULT (1990); additional (subcephalic) setae, VERSCHELDE & VINCX (1994)) are present on the head capsule, located just at the posterior edge of the head capsule (or at the transition to the first body annule), these are not regarded to be real subcephalic setae because of their irregular presence and appearance. Sexual dimorphism in shape of the amphids: open loop-shaped in males, cryptospiral to closed loop-shaped in females. Amphids are located anteriorly on the head capsule (anterior edge of the amphid touches the anterior edge of the head capsule), when the amphids are open loop-shaped they can cover the whole length of the head capsule.
Buccal cavity with a crown of denticles, a large strong dorsal tooth and two small subventral teeth. Muscular pharynx with (tripartite) slightly prolonged terminal bulb; thin lumen cuticle, bulb without real cuticular valves.
Male reproductive system monorchic, arched spicules and conspicuous gubernaculum. Female reproductive system didelphic, amphidelphic with reflected ovaries; brood protection can occur.

Differential diagnosis
Psammonema gen.n. is closely related to *Pseudochromadora* DADAY, 1889 and *Croconema* COBB, 1920. *Psammonema* gen.n. differs from *Pseudochromadora* in position and shape of the lateral alae (in *Pseudochromadora* the beginning of the broader lateral alae is located posterior to the pharynx; also in most of its species, body annuli interdigitate at level of the lateral alae), in the anterior position of the amphids on the head capsule (compared to midway or posterior position in *Pseudochromadora*), in the presence of denticles in the buccal cavity (none in *Pseudochromadora*), in the fine cuticular pharyngeal lumen (thick lumen cuticle with conspicuous valves in the terminal bulb in *Pseudochromadora*), in the prolonged tripartite pharyngeal endbulb (bipartite with strong and conspicuous valves in *Pseudochromadora*) and in the different types of somatic setae in females (no discrimination into different setae in *Pseudochromadora*). *Psammonema* gen.n. differs from *Croconema* in the presence of lateral alae (absent in *Croconema*), and in absence (or few additional setae) of subcephalic setae (compared to many in *Croconema*).

Psammonema ovisetosum gen. et sp.n.
(Fig. 1, 2; Plate 1-3; Table 1, 2)

TYPE SPECIMENS

Seven males, thirteen females, fourteen juveniles.
Holotype male: slide RIT 466 (KBIN)
Paratypes: allotype female: slide RIT 467 (KBIN). Other paratypes: slides RIT 466-467 (KBIN; 1♂, 1♀, 1J), 1995.127-128 (BMNH; 1♂, 1♀), BN 268 (MNHN; 5J), 3821-3822 (ZIRUG; 1♂, 5♀♀), 10280-10281 (MBRUG; 1♂, 2♀♀).

TYPE LOCALITY

Kenya, Gazi (09/08/1989): core sample (upper few cm) taken of the coarse coral sands of the right front tip of the sandbank, in the pits of the 'pits and bumps area', in the mouth of the Gazi Creek river.

Table 1: Psammonema ovisetosum *gen. et sp.n. (measurements in* µm)

	Hol.♂	Par♂♂			All.♀	Par♀♀		
		n=6				n=7		
		min	max	avg		min	max	avg
L	910	967	1039	1003	1063	861	1106	986
cs	4	5	7	6	5	4	6	5
dcs	10	5	9	7	8	4	10	8
amph %	37	36	44	40	36	36	45	41
aw	9	10	12	11	10	9	11	10
mbdar					42	41	44	43
dnr	76	73	82	79	92	74	88	79
ph	158	156	163	159	182	154	178	163
mbd ph	39	42	44	43	46	43	48	45
mbd	38	41	45	43	84	64	90	81
bdnr	36	37	40	39	41	37	41	39
bdcs	23	22	26	24	26	20	27	24
spic	48	46	52	50				
gub	23	23	30	25				
dv					805	672	839	758
V					76	75	83	77
da	820	872	928	900	951	767	989	882
abd	32	32	36	34	27	24	29	26
t	93	98	111	104	111	93	114	105
tmr	13	8	12	10	18	17	19	18
a	23.9	22.6	24.5	23.5	12.7	10.9	14.4	12.3
b	5.8	6	6.7	6.3	5.8	5.5	7.1	6.1
c	9.8	9.4	10.1	9.7	9.6	8.8	9.8	9.4
a(ar)					25.3	19.6	27	23.2

ETYMOLOGY

ovisetosum refers to the fact that the eggs are attached to long somatic setae.

MEASUREMENTS

Table 1 & 2.

DESCRIPTION

Males

(Fig. 1; Plate 1). Cylindrical body with distinct head capsule and conical tail (Fig. 1B, Plate 1A). Numerous, slender and clear body annuli with a multi-layered cuticle. Slender lateral alae extending from about the 30th annule posterior to the head capsule, as far as the region of the spicules (the alae fade out anterior to the cloaca); they consist of a lateral raising of each body annule, but without interdigitations of these annuli at the level of the lateral alae. Somatic setae in eight longitudinal rows in the pharyngeal region, in six rows further along the body. Long, slender somatic setae most of the time alternating with tiny ones (which are not higher than the thickness of the cuticle; Fig. 1A). In the posterior body region (last third), the ventro-lateral row of somatic setae of each side splits in two (Plate 1A,F) close rows: the more ventrally located setae are long, strong and firm (ten to fifteen setae oriented in a way one would expect of the supporting setae of species of the family Epsilonematidae; here they probably render support during copulation); the more lateral setae are short and blunt (hard to distinguish). In the same region there are no long ventral somatic setae but instead there are ten short spine-like setae ('pre-cloacal sup-

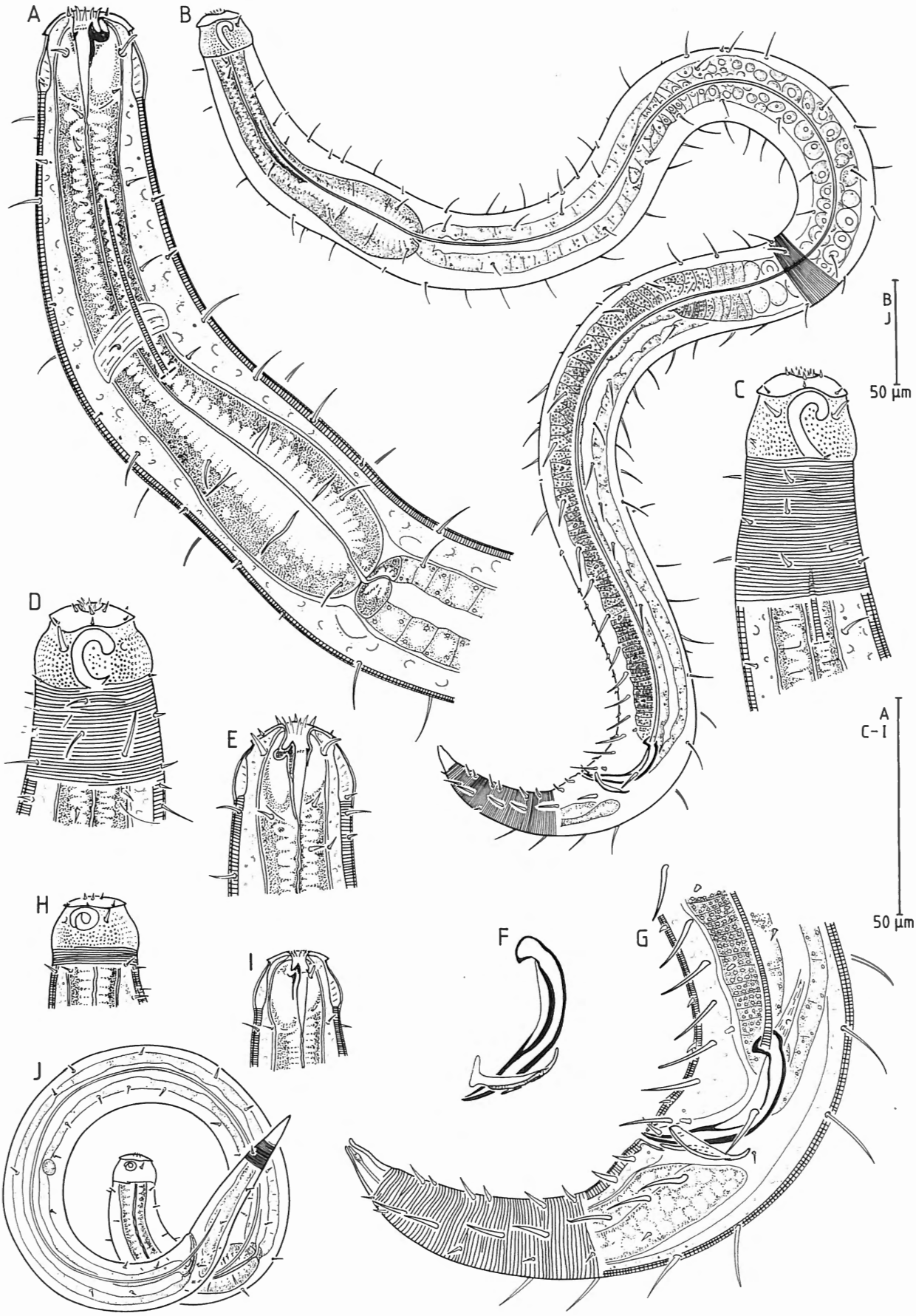

Fig. 1. – *Psammonema ovisetosum* gen. et sp.n. – A: Holotype male (σ_1), pharyngeal region; B: σ_1, habitus; C: σ_1, head capsule; D: Paratype male (σ_2), left view on head capsule; E: σ_2, right view on buccal cavity; F: Paratype male (σ_3), spicule and gubernaculum; G: σ_1, tail; H: J_{II}, head capsule; I: J_{II}, buccal cavity; J: J_{II}, habitus.

Table 2: Psammonema ovisetosum *gen. et sp.n. (measurements in μm)*

	J_{IV}			J_{III}		J_{II}	
	n=7			n=2		n=2	
	min	max	avg				
L	843	989	880	692	800	503	562
cs	4	6	5	4	6	3	5
dcs	4	7	5	6	7	6	5
amph %	36	46	42	39	47	42	46
aw	8	10	9	7	9	7	7
hw	21	24	22	18	19	17	15
dnr	66	74	70	56	73	59	57
ph	134	144	141	120	143	111	111
mbdph	39	44	42	36	39	29	32
mbd	40	57	48	35	37	27	31
bdnr	37	42	39	32	34	28	29
bdcs	20	24	22	18	20	18	17
da	742	889	782	598	700	429	476
abd	27	36	30	24	26	19	20
t	88	108	98	92	99	73	86
tmr	14	19	17	17	20	17	17
a	16	22	18	20	22	19	18
b	5.9	6.9	6.3	5.8	5.6	4.5	5.1
c	7.9	10	9	7.5	8.1	6.9	7.7

plements'; Fig. 1B,G). The last pair of latero-ventral 'supporting' somatic setae is followed by a pair of short, firm pre-cloacal setae (Fig. 1G). Following on these, there are eight pairs of short and strong latero-ventral somatic setae on the tail. At the level of the spicules there is an extra pair of firm lateral somatic setae, which is also followed by seven or eight pairs laterally on the tail (Fig. 1G). In total the tail shows seven longitudinal rows of somatic setae: a pair of latero-ventral rows of firm somatic setae, a pair of lateral rows of longer firm setae, a pair of dorso-lateral rows of small setae and a single dorsal row of long and slender setae.

Head capsule (Fig. 1C,D; Plate 1B,D,E) consists of two regions: the labial region with its six internal and six external labial sensillae, 'sits' as a helmet on the main (posterior or second) region of the head capsule which carries the four cephalic setae and the amphids. S.E.M. pictures reveal the presence of a crown of fringes around the mouth at the level of the internal labial setae (not clear with light microscope; Plate 1B). The extra thick inner layer of the main region of the head capsule is ornamented with numerous pores (vacuoles; Fig. 1C,D) which do not show superficially (Plate 1E). Four cephalic setae located at the anterior half of the amphids, at the transition of the narrower anterior and wider mid of the second region of the head capsule (Fig. 1C,D). Large open loop-shaped fovea amphidialis extending along the entire length of the second region of the head capsule, often filled by the corpus gelatum (Plate 1B,D). The first small somatic setae just behind the head capsule, can be shifted anteriorly into the interannual space between head capsule and first body annule or even onto the posterior edge of the head capsule, so giving the impression that some specimens have two to four 'additional setae' but as they do not occur in all specimens and show the same position as the following somatic setae in the pharyngeal region, they are not regarded to be real subcephalic setae and so not typical for the genus (as presence and number of subcephalic setae often is a genus character). The holotype male has two single (*i.e.* not paired) small latero-ventral spines posteriorly on the left side of the head capsule (Fig. 1C). Stoma with a crown cheilorhabdia in the cheilostome; a circle of tiny denticles, a large and strong dorsal tooth and two small subventral teeth in the esophastome (Fig. 1A,E). Cylindrical pharynx with slightly prolonged tripartite, muscular endbulb (Fig. 1A); lumen cuticle thin,

sometimes somewhat more pronounced in the endbulb. The two partitions are clear in the endbulb, but not in its lumen cuticle.
Reproductive system monorchic. Long testis located at the left side of and also ventrally to the intestine. Long vas deferens (Fig. 1B). Spicules arcuate, thickly cuticularized with beak-shaped capitulum and clear velum; gubernaculum with strange lateral parts which stretch out around the spicules (Fig. 1F). Ten to fourteen ventral pre-cloacal supplements (spine-shaped setae; Fig. 1B,G).
Caudal glands extending as far as the gubernaculum or spicules; valve in spinneret clear (Fig. 1G). Tail with seven rows of somatic setae and short non-annulated tail end; on S.E.M. pictures (Plate 1C) a few inconspicuous, tiny pores are visible on the non-annulated tail end, these are not clearly seen by means of the light microscope; a pair of latero-dorsal short somatic setae is present just posterior to the last tail annule.

Females
(Fig. 2; Plate 2, 3). Body cylindrical with enlarged posterior region in which the reproductive system is located; slender conical tail (Fig. 2B,G; Plate 2A, 3C). Body cuticle with numerous, slender annuli and lateral alae (Plate 3B). Lateral alae extend from about the 40th annule posterior to the head capsule as far as the enlarged body region of the reproductive system (at the level of the antepudendum) where it is interrupted, posterior to the vulva (at level of postpudendum) it turns up again and stops anterior to the anus (Fig. 2B,G; Plate 3C). In a few specimens, this second part of the lateral alae, posterior to the vulva, is not present.
Somatic setae arranged in eight longitudinal rows in the pharyngeal region, in seven rows in the region posterior to the pharynx and anterior to the enlarged body region, in eight rows at the level of the enlarged body region, and in four rows on the tail. There are three different types of somatic setae in females: (1) slender 'normal' somatic setae (9-14μm long, 1μm wide; Fig. 2C) alternating with tiny ones in the pharyngeal region, arranged in a ventro-ventral pair, a ventro-lateral pair, a dorso-lateral and dorso-dorsal pair of longitudinal rows; (2) posterior to the pharyngeal region and anterior to the enlarged body region the setae of the two ventro-lateral rows and single ventral row are very long and firm (32-36μm long, 2-4μm wide; Fig. 2B; Plate 2E) and are specialised in holding the eggs attached to the female's ventral body side as a kind of brood-protection; the two dorso-dorsal rows and two dorso-lateral rows show 'normal' somatic setae; (3) the third kind of somatic setae is located in the enlarged posterior body region, these are strong thorn-like setae (13-18μm long (ave 15), 2-4μm wide (ave 4); Fig. 2B,G; Plate 2C,F) arranged in two dorso-dorsal rows, two dorso-lateral rows, two ventro-lateral and two ventro-ventral longitudinal rows; between vulva and anus these last two rows become a single row again. On the tail there are two ventro-lateral and two dorso-lateral rows of short, slim somatic setae. Ecto-symbiotic organisms (see 'Morphology') can occur along the body surface, when present most of them are located in the pharyngeal region.
Head capsule as in males (Fig. 2A,D; Plate 2B,D); six inner and six slightly smaller outer labial setae on the helmet-shaped anterior part, crown of fringes at the level of the inner labial setae (Plate 3D); four cephalic setae located just anterior to or at the mid-level of the amphids, cephalic setae are hollow and are open distally with a pore (Plate 2D); large cryptospiral to closed loop-shaped (sexual dimorphism; Fig. 2D, 2A) fovea amphidialis located at the anterior edge of the main region of the head capsule (Plate 2B); head capsule ornamented with numerous pores in the deeper layers of the cuticle. As in males, in some specimens the first somatic setae can be shifted forward onto the posterior edge of the head capsule resulting in four 'additional' setae, two ventro-ventrally and two dorso-dorsally.
Stoma with crown of cheilorhabdia, followed by a prominent dorsal tooth (6μm), two small (1-2μm) subventral teeth and a circle of denticles (Fig 2C,E). Pharynx with muscular, cylindrical corpus and prolonged, tripartite endbulb (Fig. 2C); thin lumen cuticle. Broad cardia.
Slit-like vulva (Plate 3A) located in the posterior body region (V=75-83%). Short vagina vera thickly cuticularized, provided with a small sphincter muscle; longer vagina uterina also with thick cuticle and large sphincter muscle. Reproductive system located within the enlarged posterior body region; didelphic, amphidelphic with reflected ovaries; in some specimens the antepudendum is located at the right side of the intestine, postpudendum at the left; in other specimens both branches are located at the left of the intestine; uterus is situated ventrally to the intestine. Sperm cells present, located distally and ventrally against the uterus wall, probably incorporated within it. Eggs of different developing stages are attached in two latero-ventral rows to the mid body region by means of special setae (Fig. 2B; Plate 2E): brood protection, a phenomenon where females carry their eggs along after they have left the reproductive system. Females can carry up to ten eggs. The eggs measure up to 49-53μm in length and 43-44μm in width.
Slender conical tail with only few slender somatic setae. Caudal glands extend as far as the intestine (Fig. 2G). Valve in spinneret clear. Non-annulated tail end with a pair of latero-dorsal setae just posterior to the last tail annule.

Juveniles
(Fig. 1H-I, 2F). All four juvenile stages were found.

Fourth stage juveniles
General body shape, body annuli and shape of somatic setae similar to males; head capsule and fovea amphidialis similar to females; long conical tail.
Lateral alae present, extending from about mid-way the pharynx to about the twentieth annule (or further) posterior to the anus. Somatic setae in six longitudinal

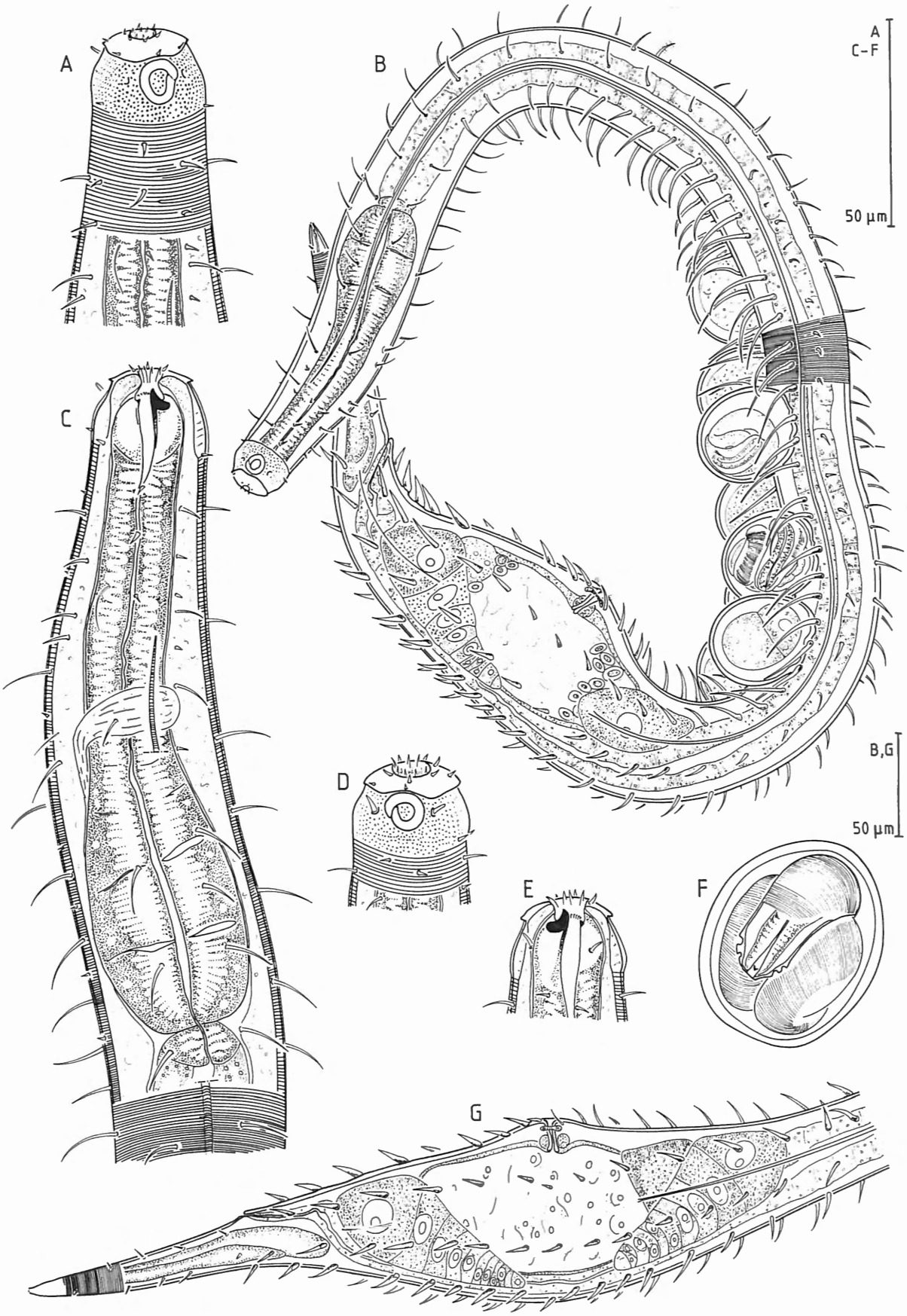

Fig. 2. – *Psammonema ovisetosum* gen. et sp.n. – A: Allotype female ($♀_1$), head capsule; B: $♀_1$, habitus; C: $♀_1$, pharyngeal region; D: Paratype female ($♀_2$), head capsule; E: $♀_2$, buccal cavity; F: Egg with J_I, attached to $♀_1$; G: Paratype female ($♀_3$), reproductive system ($♀_3$: also used for S.E.M. pictures).

rows, in four on the tail; a pair of latero-dorsal small somatic setae on the non-annulated tail end.
Head capsule, labial sensillae, position of cephalic setae, shape and position of the fovea amphidialis similar to females. Buccal cavity as in adults. Long cylindrical pharynx with prolonged muscular tripartite endbulb, lumen cuticle thin; the two partitions are clear in the endbulb itself but not in its lumen cuticle.
Male reproductive system of early J_{IV}'s is observed as a slender string of cells extending from the rectum to the anterior half of the body where the string is broader and germ cells (spermatogonia) are visible. Spicules and gubernaculum not present, but the cells which will form them are.
Female reproductive system of an early J_{IV}: didelphic uteri aligned by cylindrical cells, reflected ovaries in which germ cells are clearly present. Three pairs of cells align the future vagina uterina; the area where the vagina vera will be formed is indicated by a brownish granular pigmentation; the vaginal lumen is visible.
In late J_{IV}'s the adult reproductive system is completely developed.
Tail with well developed caudal gland cells, extending as far as the rectum. Valve in spinneret clear.

Third stage juveniles
Body shape, annuli and tail as in fourth stage juveniles.
Somatic setae slightly smaller than in J_{IV}, arranged in six longitudinal rows. Lateral alae present, raised only in the posterior part of the body or not at all; alae extend from the level of the posterior half of the pharynx to posterior to the anus.
Shape of the slightly shorter head capsule and position of labial setae similar to females, head capsule ornamented with pores but less pronounced. Four cephalic setae located at or just posterior to the mid-level of the fovea amphidialis. Large cryptospiral amphids located at the anterior edge of the main head region, extending as far as the middle of the rostral length. No subcephalic setae.
Buccal cavity as in adults. Pharyngeal tripartite endbulb slightly shorter than in J_{IV}.
Genital primordium in an early, probably female, J_{III} consists out of a group of cells. In an older, male, J_{III} the genital primordium is a slender string of cells (individual cells not distinct) located in the posterior half of the body extending as far as the rectum.

Second stage juveniles
(Fig. 1H-J). Cylindrical body with well set off head capsule and long conical tail (Fig. 1J). Numerous slender annuli. Slender lateral alae extending from the pharyngeal region as far as the tail region. Somatic setae in six rows in the pharyngeal region; posterior to it the ventral row is missing in one specimen (not present or all setae broken off?); in another specimen both dorsal and ventral row are lacking posterior to the pharyngeal region.
Shape of head capsule as in J_{III}; cephalic setae located posterior to the mid level of the fovea amphidialis. Large cryptospiral amphids (Fig. 1H) located anteriorly on the head capsule.
Buccal cavity as in adults. Long cylindrical pharynx with muscular, not prolonged, bipartite endbulb.
Genital primordium consists out of two round cells.

First stage juveniles
First stage juveniles were only found inside eggs, which are attached to the female body; so only few morphological features are commented.
Body with fine annuli. Somatic setae might be present (not certain). Lateral alae not observed.
Head capsule present, ornamented with vacuoles; large amphids.
Buccal cavity with large dorsal tooth; rest is unclear. Long cylindrical pharynx with round endbulb.

Diagnosis
Psammonema ovisetosum gen. et sp.n. is characterized by the combination of the following characters: shape of its head capsule with the helmet-like lip region; shape and anterior position of the amphids and the sexual dimorphism of the amphids; lateral alae which start anterior to the nerve ring in adults. Males are characterized by the shape of their spicules and conspicuous lateral parts of the gubernaculum; by the pair of latero-ventral rows of 'supporting' setae anterior to the cloaca. Females are characterized by three types of somatic setae; by the posterior position of the vulva and by the presence of a kind of brood-protection unknown up to now, namely: special, long setae embrace the eggs.

Discussion
Hitherto, brood protection within Desmodoridae has been reported by OTT (1976) for *Croconema ovigerum* OTT, 1976, and by GOURBAULT & VINCX (1990) for *Croconema otti* GOURBAULT & VINCX, 1990, and *Pseudochromadora incubans* GOURBAULT & VINCX, 1990. In both *Croconema* species, the same kind of brood protection mechanism was found: a single row of eggs is attached to the lateral side of the female's body with embryos within, which seem to have been fertilized at the same time. OTT (1976) suggested that the eggs are attached by the use of some adhesive substance as, quote, 'the body setae in the area where the eggs are carried neither seem to be different from the strong somatic setae of the rest of the body, nor are special glands or pore structure apparent in this region', unquote. In *Pseudochromadora incubans*, the mechanism is somewhat different: quote, 'a string of up to three eggs at different stages is attached to the modified prevulval region', unquote (GOURBAULT & VINCX, 1990); again there are no special setae involved in the attachment of the eggs. In *Psammonema ovisetosum* sp.n. we find a brood pro-

tection mechanism unknown up to now, where two rows of eggs at different developmental stages are held ventrolaterally to the mid body region by means of special, long setae.

Genus **Pseudochromadora** DADAY, 1889

Pseudochromadora coomansi sp.n.
(Fig 3, 4; Plate 4, 5; Table 3, 4)

TYPE SPECIMENS

29 ♂♂; 33 ♀♀; 60 JJ.
Holotype male: slide RIT 468 (KBIN)
Paratypes: allotype female: slide RIT 469 (KBIN). Other paratypes: slides RIT 469-470 (KBIN; 4♂,10♀♀,5J), BN 268-269 (MNHN; 6♂♂,1♀,11J), 1995.129-131 (BMNH; 2♂♂,1J), 3822 (ZIRUG; 1♀), 10281 (MBRUG; 1♂,3J).

TYPE LOCALITY

Kenya, Gazi (1-8-1989). Mouth of the Gazi Creek: samples of coarse sandy sediments taken on the sandbank in front of and on the beach behind *Sonneratia* bushes.

ETYMOLOGY

This species has been named in honour of Prof. Dr. A. Coomans.

MEASUREMENTS

See Table 3 & 4.

Table 3: Pseudochromadora coomansi *sp.n. (measurements in* µm)

	Hol.♂	Par♂♂			All.♀	Par♀♀		
		n=7				n=7		
		min	max	avg		min	max	avg
L	814	787	933	865	847	800	948	862
cs	7	4	7	6	6	4	7	5
dcs	5	4	7	6	8	4	8	6
amph %	32	29	33	31	27	24	30	26
aw	8	8	8	8	7	7	8	7
lpt(max)	4	4	6	5				
dnr	66	54	78	69	70	61	73	68
ph	123	107	136	124	125	109	135	125
mbdph	37	37	40	39	41	37	40	39
mbd	42	38	46	42	57	43	54	49
bdnr	33	33	37	35	36	32	36	35
bdcs	21	21	22	22	23	20	24	22
spic	42	38	47	42				
gub	22	23	26	24				
dv					501	490	584	526
V					59	59	63	61
da	717	672	816	753	737	692	827	754
abd	30	28	32	29	23	22	25	23
t	98	108	134	122	112	96	122	109
tmr	24	22	29	27	28	24	31	27
a	19.4	17.9	22.3	20.4	14.9	14.8	21.5	17.9
b	6.6	6.3	8.3	7	6.8	5.9	8	6.9
c	8.3	6.7	8.2	7.1	7.6	7.4	8.8	7.9

Table 4: Pseudochromadora coomansi *sp.n. (measurements in* μm)

	J4			J3			J2			J1		
	n=7			n=7			n=5			n=3		
	min	max	avg	min	max	avg	min	max	avg	min	max	avg
L	685	890	763	564	757	662	431	633	533	251	400	332
cs	6	7	6	3	7	5	5	6	5	3	7	5
dcs	4	8	6	3	7	5	2	8	5	4	6	5
amph %	23	30	26	25	31	28	23	27	25	26	28	27
aw	6	7	6	6	7	6	5	6	5	4	5	4
hw	23	26	24	19	24	22	19	25	22	14	19	16
dnr	63	79	70	59	70	64	47	63	57	50	50	50
ph	107	124	115	104	114	109	79	106	95	71	81	78
mbdph	35	42	38	32	34	33	28	33	31	20	25	23
mbd	32	43	38	26	32	30	23	29	27	15	19	17
bdnr	32	40	36	28	32	30	27	32	30	23		
bdcs	18	20	19	17	19	18	14	17	16	13	14	13
da	605	782	658	478	647	568	359	557	459	201	337	274
abd	19	28	25	19	23	21	17	23	20	13	17	15
t	87	119	104	83	108	92	74	94	82	50	63	57
tmr	21	27	23	19	26	22	17	21	19	12	13	13
a	17	25	20	19	27	22	19	22	20	17	22	19
b	6.1	7.4	6.7	5.3	7	6.1	5.3	6.2	5.6	3.5	4.6	4.2
c	6	8.3	7.4	6.7	8.4	7.2	5.8	7.2	6.5	5	6.3	5.7

DESCRIPTION

Males

(Fig. 3; Plate 4). Robust, cylindrical body with large head capsule, bent pharyngeal region (Plate 4D), and elongated cylindrico-conical tail (Fig. 3A). Thick body cuticle with well developed broad body annuli (diameter = 2μm) and distinct interannual spaces (1-2μm). Body annuli are ornamented with a long, slim vacuole (visible as a long slit, Fig. 3F); with exception of the last few tail annuli (Fig. 3E); this ornamentation is one of the deeper layers of the cuticle. One pair of lateral alae is present (Fig. 3A; Plate 4E). They are formed by the local raising of interdigitations of the body annuli (Fig. 3F); they extend from about the 83rd body annule (counted laterally), starting posterior to the pharynx, as far as the level of the first postcloacal thorns.

Firm, broad somatic setae (2-7μm long) arranged in six longitudinal rows: a single dorsal row, a single ventral row, a dorso-lateral pair and a ventro-lateral pair. Ventral setae between copulatory thorns and cloaca are somewhat thorn-shaped (Plate 4E). On the tail, they are arranged in four rows (no dorsal, no ventral row). Next to the postcloacal thorns, there is a latero-ventral pair of short, very firm, broad setae. Many of these probably are connected with hypodermal gland cells, (especially the ventral row of somatic setae), these glands could secrete a gluten on which the sometimes numerous ecto-symbiotic organisms (Cyanobacteria or Bacteria) 'feed'. The ecto-symbiotic organisms on the cuticle (when present) sometimes are so slim they could easily be mistaken for fine, hair-like setae.

Broad, well developed head capsule (Fig. 3B,C; Plate 4A) ornamented with numerous small dimples; head capsule exist out of two regions: a shorter anterior retractable lip region (Fig. 3B) and a larger posterior, thickly cuticularized (extra thick inner layer) region on which the amphids are located; the transition between the two regions is sometimes marked by a suture (more distinct in females and juveniles than in males). Six inner and six outer labial setae located on the anterior region of the head capsule; the four cephalic setae are situated at the level of the transition (suture) between anterior and posterior part of the head capsule; no subcephalic setae (Plate 4A). Unispiral fovea amphidialis.

Buccal cavity with large dorsal tooth and two tiny subventral teeth. Cylindrical pharynx with slightly enlarged buccal bulb and large, bipartite (one partition), muscular

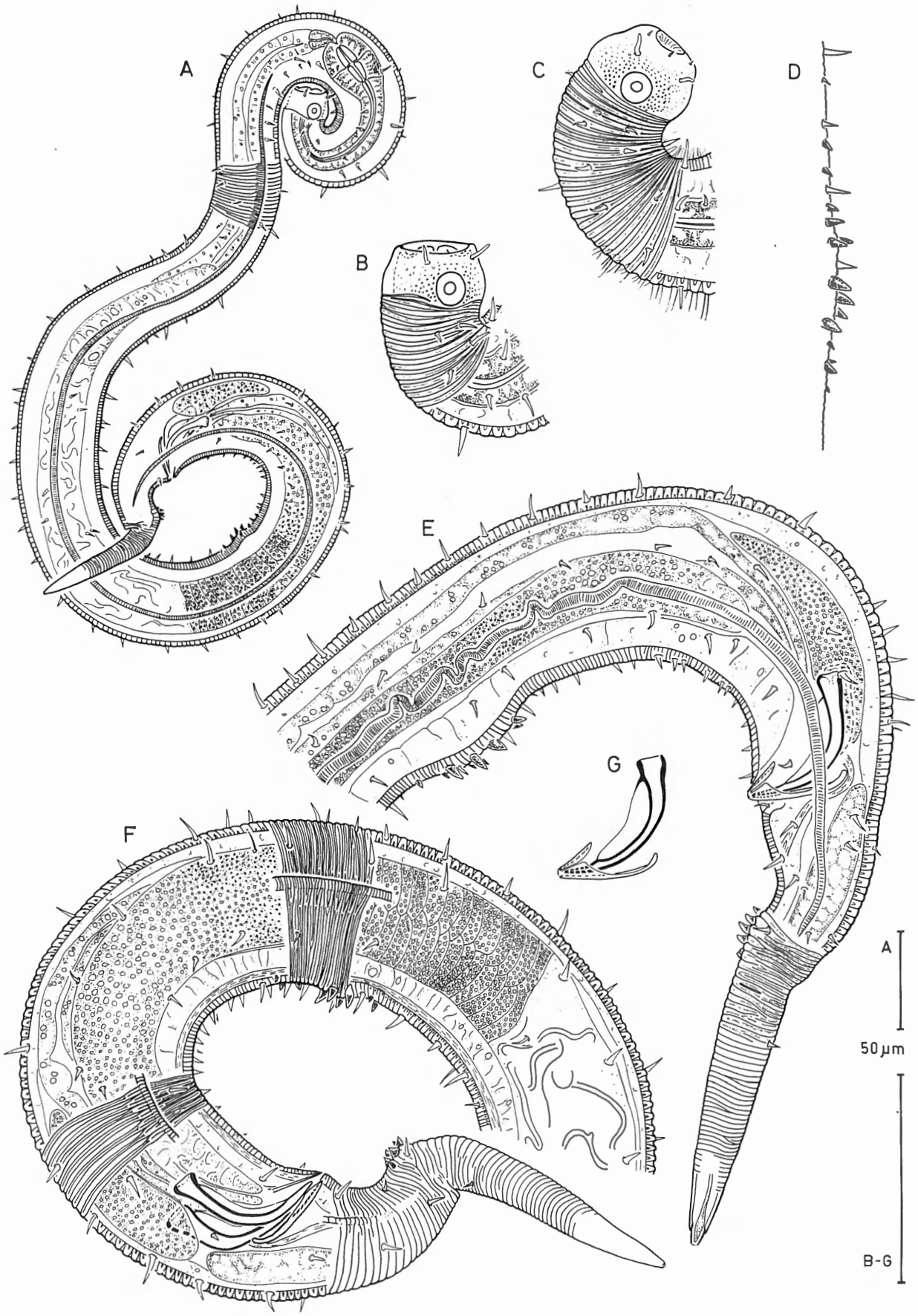

Fig. 3. – *Pseudochromadora coomansi* sp.n. – A: Habitus of holotype male (σ'_1); B: Head capsule of σ'_1; C: Head capsule of paratype male (σ'_2); D: Copulatory thorns of σ'_2; E: Tail of σ'_3; F: Tail of σ'_1; G: Spicule and gubernaculum of σ'_4.

endbulb; lumen strongly cuticularized (Fig. 3A). Cardia 8-11μm long.
Reproductive system monorchic. Testis located at the right and ventral side of the intestine. Spicules arcuate, no capitulum, instead the calamus is funnel-shaped; thin velum. Gubernaculum complex: distal, lateral parts meet with a capitulum, located in the anterior wall of the cloaca (Fig. 3G), forming a funnel through which the spicules protrude (Plate 4F). Nine to fourteen copulatory thorns of different sizes (2-6μm) arranged in a group (Fig. 3F; Plate 4B,E) or in a more stretched ventral (subventral) row (Fig. 3D). In a few males (not in holotype) this ventral row is rostrally continued (and in one specimen even caudally) in a ventral row of tiny thorns (1μm), one thorn occurring every four to ten annuli. On the tail there is a ventral group of postcloacal thorns (six, seldom more; Fig. 3E,F; Plate 4C,F); arranged in a ventral row of three to four thorns sided by some ventro-ventral thorns. Latero-ventrally immediately next to these postcloacal thorns, there is a pair of broad, heavy somatic setae.
Caudal glands extending up to the gubernaculum. Valve in spinneret clear; non-annulated tail-end not punctuated.

Females
(Fig. 4A-C; Plate 5). Body shape (Plate 4A), annuli, ornamentation and pattern of somatic setae as in males. Lateral alae extending from 80-90th annule posterior to the head capsule as far as the sixth to the tenth annule posterior to the anus. Body sometimes covered with ectosymbiotic organisms (more than in males; Plate 5D).
Broad head capsule, anterior part slightly shorter than posterior part; six inner and six outer labial setae (Plate 5B). Four cephalic setae located at the transition (suture faintly visible) between anterior and posterior region of the head capsule. No subcephalic setae. Unispiral fovea amphidialis located at the posterior edge of the head capsule (Fig. 4A). Head capsule ornamented with a large number of small vacuoles.
Buccal cavity with large, strongly cuticularized dorsal teeth and minute ventral tooth (or two subventral teeth; to small to see clearly). Pharynx with buccal bulb, cylindrical corpus and muscular, bipartite terminal bulb, with thickly cuticularized lumen (Fig. 4C). Cardia 6-11μm long. Ventrally, in the anterior part of the body, there are many hypodermal gland cells; also in this region the ventral somatic setae are built heavier compared to these along the rest of the body. The intestine is located dorsally and at the left (or right, depending on the specimen) of the reproductive system.
Reproductive system didelphic, amphidelphic with reflected ovaries (Fig. 4B). In some females, reflected ovaries are so long, that the ovary of the antepudendum extends posterior to the vulva and vice versa. Slit-shaped vulva (Plate 5E), slender vagina.
Tail with seven pairs of somatic setae (four latero-dorsal pairs and three ventro-lateral pairs).

Juveniles
Fourth stage juvenile
(Fig. 4K,L; Plate 5C,F). Body shape as in adults. Body annuli ornamented with slit-like vacuoles; interannule spaces longer than annuli. Lateral alae as in adults (Plate 5F). Somatic setae in six longitudinal rows, but in fewer numbers per row than in adults. Somatic setae are slimmer than in adults.
Suture between anterior and posterior region of head capsule clearly visible.
Four cephalic setae located in front of suture. Head capsule ornamented with numerous vacuoles (Fig. 4C). Unispiral fovea amphidialis. Buccal cavity, teeth and pharynx as in adults.
Genital primordium of young female: in an early fourth stage juvenile (Fig. 4K) both branches of uteri and ovaries (not reflected) are present together with two groups of cells aligning the vagina (lumen present).
Late fourth stage juveniles show a moulting female (ovaries not necessarily reflected).
Genital primordium of young male; in an early fourth stage juvenile there is a ventral slender string of cells extending from the body middle as far as the cloaca. Late fourth stage juveniles show moulting males with clear spermatocytes but not necessarily clear spicules.

Third stage juveniles
(Fig. 4I,J). Body shape, annuli, ornamentations, lateral alae, pattern of somatic setae, head capsule (Fig. 4I) and pharynx (terminal bulb bipartite) as in fourth stage juveniles.
Genital primordium of early third stage juveniles confined to a group of a few cells (Fig. 4J) located from ventrally to subventrally of the intestine.
Genital primordium of late third stage juveniles: young females with a string of cells but without cells aligning a lumen for the vagina. Young males show a slender string of cells in the posterior half of the body but that does not reach the cloacal region (posterior end of genital primordium located up to 70μm in front of the anus.

Second stage juveniles
(Fig. 4F-H). Cylindrical body with bent pharyngeal region and long tail. Slender body annuli (no ornamentations visible) with broad interannual spaces. From the 80th to 90th annule posterior to the head capsule as far as the eight to tenth annule posterior to the anus, the body annuli show lateral interdigitations (Fig. 4G) which do not rise above the surrounding body cuticle (in early second stage juveniles) so they can not be regarded as lateral alae; in late second stage juveniles these lateral interdigitations can be slightly risen but here it is due to the underlying lateral alae of the third stage juvenile. Somatic setae in four longitudinal rows (a dorsolateral pair and a ventrolateral pair) with only few setae per row.
Rounded head capsule (Fig. 4F,G) with obvious suture between anterior and thicker posterior part, six inner and

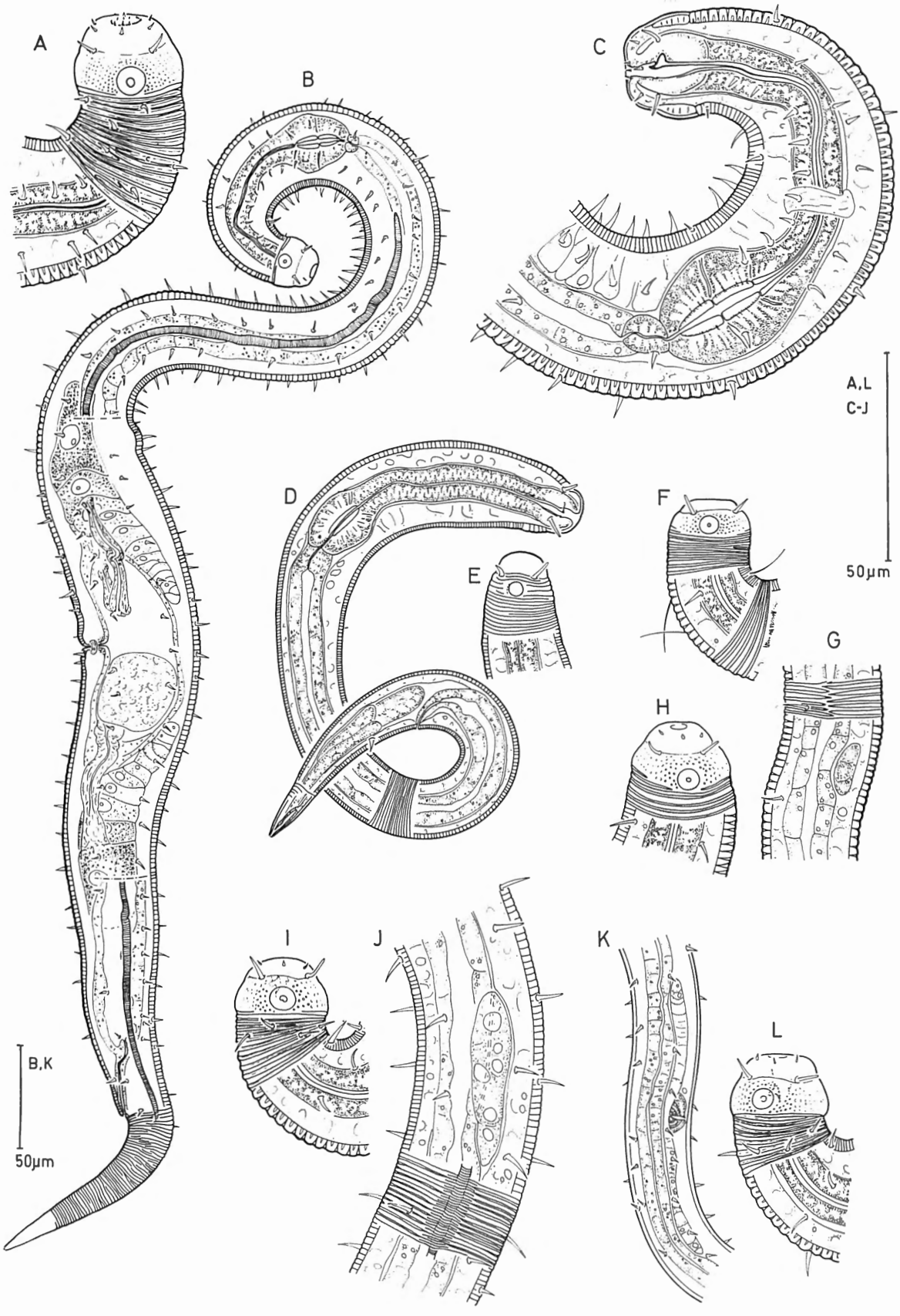

Fig. 4. – *Pseudochromadora coomansi* sp.n. – A: Head capsule of allotype female (♀$_1$); B: Habitus of ♀$_1$; C: Pharyngeal region of ♀$_1$; D: Habitus of J_I; E: Head capsule of J_I; F: Head capsule of $J_{II\,1}$; G: Genital primordium of $J_{II\,1}$; H: Head capsule of $J_{II\,2}$; I: Head capsule of J_{III}; J: Genital primordium of J_{III}; K: Genital primordium of J_{IV}; L: Head capsule of J_{IV}.

six outer labial setae, four cephalic setae located just in front of the suture, head capsule ornamented with numerous vacuoles. Large unispiral amphid with small central spot.
Buccal cavity with large dorsal and tiny ventral tooth. Pharynx with slender buccal bulb, cylindrical corpus and rounded terminal bulb, in which partitions can be observed, in the muscle tissue but not in the lumen cuticle. Genital primordium confined to a group of three cells in early second stage juveniles (Fig. 4G) and to a group of a few cells in late second stage juveniles.

First stage juveniles
(Fig. 4D,E). Fine, parallel body annuli with clear, broad (slim in early first stage juveniles) interannular spaces; no lateral alae; only a very few annuli on body and tail show little interdigitations.
No rows of somatic setae, except for a single or a pair of somatic setae latero-ventrally on the tail: if it is a pair they stand on a different level. A late first stage juvenile has also one lateral pair of somatic setae posterior to the pharyngeal terminal bulb.
No head capsule as is found in second and later stages: the anterior labial region is not annulated, body annuli start at the four cephalic setae (Fig. 4E); cephalic setae are located on the first or between first and second body annule; annuli surrounding the amphids are broad and have a thickened cuticle (posterior to these, annuli are slim and cuticle is also less thick; Fig. 4E).
Buccal cavity with large dorsal tooth and small (one or two, not clear; Fig. 4D) subventral tooth.
No genital primordium visible in early first stage juveniles; in a late first stage juvenile one or two flattened cells are visible.
Tail with one or a pair of somatic setae (Fig. 4D).

Diagnosis
Pseudochromadora coomansi sp.n. is characterized by its large number of broad somatic setae; its broad head capsule with shorter anterior part, its faint suture between anterior and posterior region of the head capsule; by the position of its cephalic setae; its large, heavily sclerotized dorsal tooth; its pharyngeal terminal bulb with clearly partitioned lumen cuticle, its numerous hypodermal gland cells. Males are characterized by their spicules which lack a capitulum (funnel-shaped calamus) but have a well developed velum.

Differential diagnosis
Pseudochromadora coomansi sp.n. resembles *Pseudochromadora cazca* GERLACH, 1956 but can be distinguished on basis of the combination of the following characters: shape of the head capsule (head capsule of *P. cazca* exists out of two equally sized broad annuli), position of the cephalic setae (cephalic setae of *P. cazca* located midway on the anterior part of the head capsule), shape of the male spicules (spicules of *P. cazca* have a capitulum but no velum), and the complex gubernaculum (gubernaculum of males of *P. cazca* has no capitulum).

Pseudochromadora buccobulbosa sp.n.
(Fig. 5-8; Table 5, 6)

TYPE SPECIMENS

45 males, 47 females, 66 juveniles.
Holotype male: slide RIT 471 (KBIN)
Paratypes: allotype female: slide RIT 472 (KBIN). Other paratypes: slides RIT 471 (KBIN; 4♂♂, 8♀♀, 6J), 1995.132-143 (BMNH; 2♂♂, 1♀, 9J), BN 270 (MNHN; 6♂♂, 9♀♀, 5J), 3822 (ZIRUG; 5♂♂, 2♀♀, 8J), 10282 (MBRUG; 7♂♂, 4♀♀, 14J).

TYPE LOCALITY

Kenya, Gazi, 10/08/1989: sandy sediment sample taken near the flood-tide between *Bruguiera* and *Sonneratia* bushes, nearby the field-lab hut (Fishermen's harbour).

ETYMOLOGY

Name referring to the well developed buccal bulb.

MEASUREMENTS

See Table 5 & 6.

DESCRIPTION

Males
(Fig. 5). Robust, cylindrical body with well developed head capsule, bent pharyngeal region, lateral alae, and cylindrico-conical tail, all typical for the genus. Thick, multi-layered (hyalin epicuticle) body cuticle with conspicuous annuli and interannual spaces. Each body annule is ornamented with a slit-like vacuole, present in the deeper layers of the cuticle (Fig. 5B), with exception of the tail annuli posterior to the post-cloacal thorns. Lateral alae extend from the fifteenth to twentieth body annule posterior to the pharyngeal endbulb as far as the tail, a few annuli in front of the post-cloacal thorns; they are formed by an uprising of the interdigitations of the body annuli, there each annule splits in (normally) two or sometimes three interdigitations (Fig. 5A,B,F); cross sections of these alae reveal that there is a cavity under the risen ala which still is separated from the epidermis by the substratum of the cuticle. Firm, broad somatic setae arranged in six longitudinal rows of alternating long and short setae: single ventral row, single dorsal row, a ventro-lateral pair and a dorso-lateral pair. Most of the ventral

Table 5: Pseudochromadora buccobulbosa *sp.n. (measurements in* μm)

	Hol.♂	Par♂♂			All.♀	Par♀♀		
		n=7				n=7		
		min	max	avg		min	max	avg
L	672	617	756	699	667	672	778	709
cs		5	7	6	7	4	8	6
dcs	6	5	8	6	5	4	8	6
amph %	27	23	28	25	24	19	25	23
aw	8	6	8	7	7	6	7	7
hw	28	27	28	28	28	27	30	28
dnr	78	74	86	78	80	69	85	78
ph	124	119	141	130	128	117	133	125
mbdph	30	30	32	31	31	30	32	31
mbd	31	31	36	34	42	38	42	41
bdnr	30	28	31	30	30	28	32	30
bdcs	22	21	23	22	23	21	25	23
spic	47	31	43	39				
gub	16	13	18	15				
dv					389	389	450	409
V					58	56	60	58
da	583	522	650	600	578	595	689	629
abd	23	23	26	25	19	18	21	20
t	95	94	106	101	90	71	95	86
tmr	19	21	26	24	26	21	24	23
a	21.7	19	22.1	20.5	15.9	16	18.5	17.5
b	5.4	5.2	5.6	5.4	5.2	5.4	6	5.7
c	7.1	6.5	7.3	6.9	7.4	7.5	9.5	8.2

somatic setae between copulatory thorns and cloaca have a thorn-like shape (Fig. 5F). On the tail there are two pairs of dorso-lateral (holotype $♂_1$) or ventro-lateral (in some paratype ♂♂) somatic setae: one pair anterior to and the second pair posterior to the post-cloacal thorns; a third pair of blunt, broad and hollow setae is located ventro-ventrally right next to the post-cloacal thorns (Fig. 5F,K). A ventral row of small thorns (also present in females) extending from the region posterior to the pharyngeal bulb as far as the copulatory thorns. Some specimens carry ecto-symbiotic organisms on their cuticle.

Well developed head capsule, consisting out of two regions: a shorter anterior, retractable lip region and a larger posterior region with an extra layer of thick cuticle. Transition between the two layers is aligned by a faint line. The anterior region of the head capsule carries the six inner and six outer labial setae; four cephalic setae are located just in front of (or at) the transition between anterior and posterior region of the head capsule. The thick second (posterior) region of the head capsule is ornamented with numerous pores (located in deeper layers of the cuticle) and carries the ventrally whirled amphids. Shape of the amphids (sexual dimorphism) varies between unispiral and closed loop-shaped: there is a large central spot and the posterior edge of the fovea is open (Fig. 5C,G). At the posterior edge of the head capsule, there are four 'additional setae', they are located at the edge of a first partial annule (Fig. 5C,G), and are not regarded as proper subcephalic setae (having no subcephalic setae is regarded to be a genus character).

Buccal cavity possibly with cheilorhabdia (not clear), very large dorsal tooth, a unique cuticular dorsal plug anterior to it, and two minute subventral teeth. The dorsal plug seems to be functionally associated with the large dorsal tooth (Fig. 5B,D,E; positioning and grasping of pennate diatoms for feeding?). Cylindrical pharynx with prominent buccal bulb (*cfr.* name) and bipartite terminal bulb;

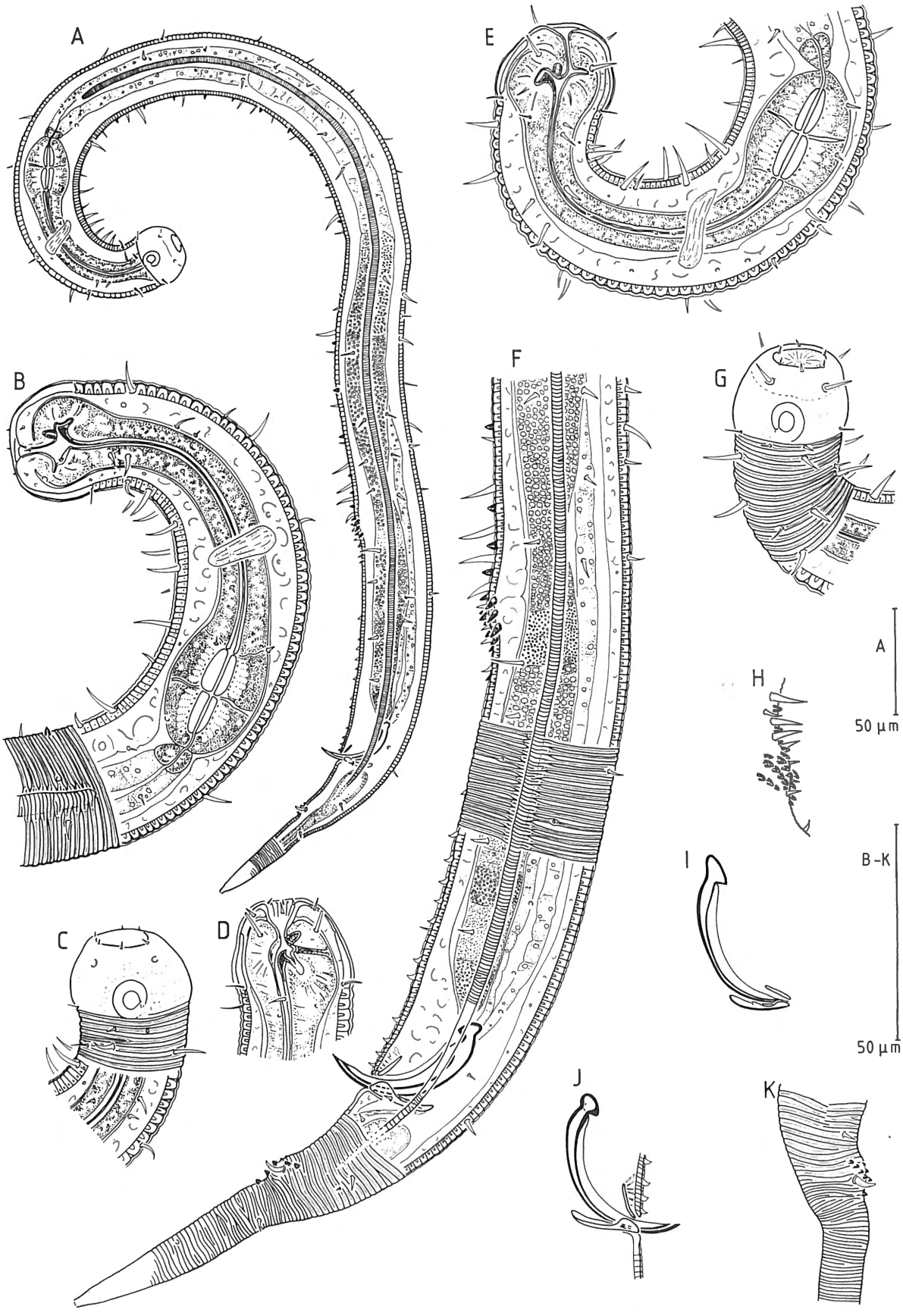

Fig. 5. – *Pseudochromadora buccobulbosa* sp.n. – A: Holotype male (σ_1), habitus; B: σ_1, pharyngeal region; C: σ_1, head capsule; D: Paratype male (σ_2), buccal bulb; E: Paratype male (σ_3), pharyngeal region; F: σ_1, posterior body region; G: σ_3, head capsule; H: Paratype male (σ_4), copulatory thorns; I: σ_4, spicule and gubernaculum; J: σ_1, spicule and gubernaculum; K: σ_4, postcloacal thorns.

Table 6: Pseudochromadora buccobulbosa *sp.n.* *(measurements in* μm)

	J4			J3			J2			J1		
	n=7			n=7			n=7			n=4		
	min	max	avg	min	max	avg	min	max	avg	min	max	avg
L	589	683	637	489	617	531	283	389	346	250	267	262
cs	6	7	7	5	7	6	5	5	5	4	5	5
dcs	3	8	6	4	9	5	3	7	5	4	5	5
amph %	21	25	23	20	27	23	17	23	21	18	25	21
aw	6	6	6	5	6	6	3	5	4	3	4	3
hw	22	29	25	22	26	24	18	22	19	15	17	16
dnr	60	80	70	50	68	62	45	57	52	40	45	43
ph	106	122	114	95	113	104	77	91	85	71	76	73
mbdph	29	36	32	26	29	28	20	26	23	17	18	18
mbd	29	39	33	24	27	26	15	23	20	14	15	15
bdnr	29	34	31	25	28	27	21	26	23	17	19	18
bdcs	19	22	21	18	23	20	15	19	16	13	14	13
da	517	605	555	417	495	445	233	328	288	211	222	214
abd	18	21	20	12	19	17	11	15	14	10	12	11
t	74	95	84	59	82	71	50	66	58	39	55	47
tmr	18	22	20	11	21	17	13	18	15	11	13	12
a	16	22	20	18	23	21	16	19	18	17	19	18
b	5.2	5.8	5.6	4.3	6.4	5.1	3.7	4.4	4.1	3.4	3.7	3.6
c	7	8.6	7.6	6.7	8.7	7.5	5.4	7.3	6	4.9	6.4	5.7

pharyngeal lumen thickly cuticularized with conspicuous valves in the terminal bulb (Fig. 5B,E). Large cardia (9-15μm). Intestinal cells filled with many greenish lipid droplets (indication of diatom feeding); intestine followed by a rectal valve and rectum with fine cuticular alignment. Reproductive system monorchic. Anterior part of the testis located at the left side of the intestine, vas deferens located ventrally to the intestine (Fig 5F). Hyalin sperm cells not clear; vas deferens distinct. Spicules arcuate with birds-head shaped capitulum, thickly cuticularized lamina (body), and clear, slender velum (Fig. 5I,J). Gubernaculum with capitulum (Fig. 5I,J). A ventral to ventroventral group of up to twenty (or more) copulatory thorns (Fig. 5F,H) located anterior to the spicules; a ventral group of smaller post-cloacal thorns, accompanied by a pair of firm, broad setae, on the tail (Fig. 5K).
Caudal glands extending as far as gubernaculum and spicules. Tail with short non-annulated tail end and clear spinneret.

Females
(Fig. 6,7 & 8A,B). General body shape, cuticle, ornamentation and shape of body annuli, pattern of somatic setae, digestive system and tail shape similar as in males.
Lateral alae starting slightly further posterior to the pharyngeal endbulb, compared to males, and extend as far as the first few tail annuli.
A ventral row of five to ten small thorns located anterior to the vulva (extending from about the fortieth annule posterior to the level of the beginning of the lateral alae, as far as the vulva); a small number of females also show two to five small ventral thorns located on the first few annuli posterior to the vulva.
Head capsule with six inner and six outer labial lipsensillae, four cephalic setae and sometimes four to five additional subcephalic setae located on a partial annule posteriorly on the head capsule (Fig. 6C); unispiral to almost cryptospiral amphids (Fig. 6C, 8A). Deeper cuticle of the posterior part of the head capsule thick, and with numerous small pores.
Buccal cavity and teeth as in males. Pharynx with prominent buccal bulb and muscular, bipartite endbulb. In many specimens some pseudocoelomocytes can by seen along the intestine. Some of the pseudocoelomocytes, located near the uterus, show large crystalloid inclusions.
Reproductive system didelphic, amphidelphic with short reflected ovaries; in most specimens located at the left of

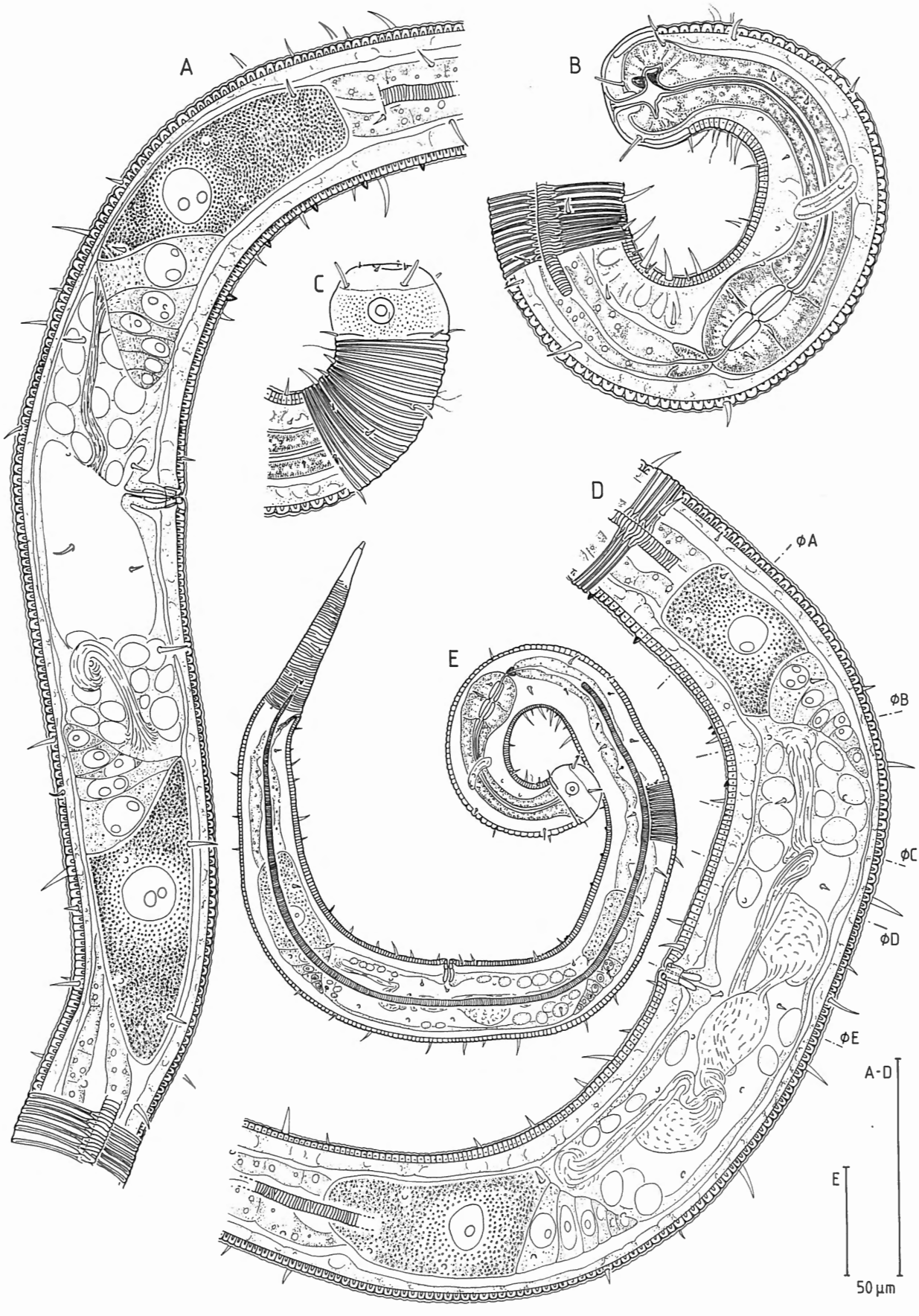

Fig. 6. – *Pseudochromadora buccobulbosa* sp.n. – A: Paratype female (φ_2), reproductive system; B: Allotype female (φ_1), pharyngeal region; C: φ_1, head capsule; D: φ_1, reproductive system (with asigned areas of the cross sections of Fig. 7); E: φ_1, habitus.

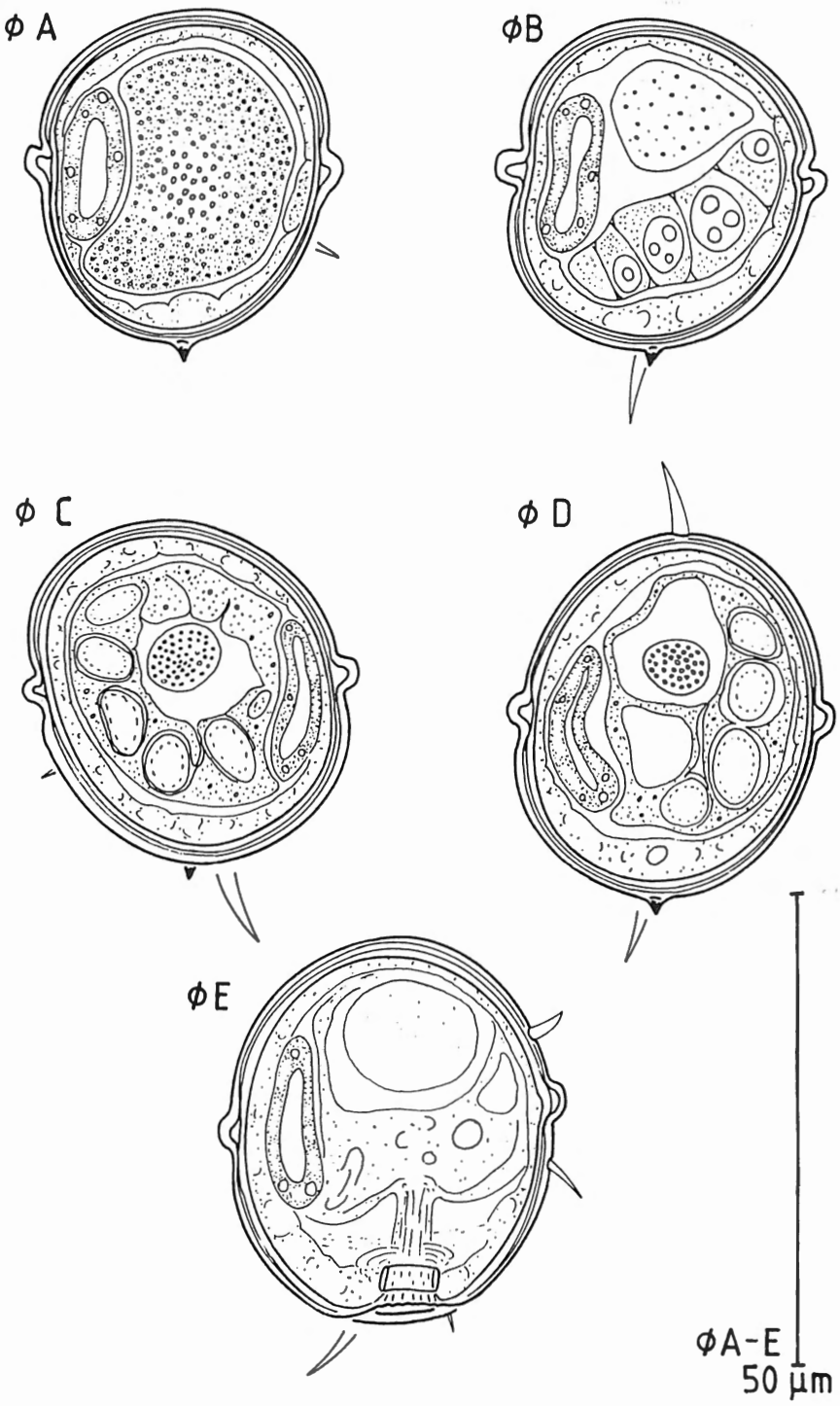

Fig. 7. – *Pseudochromadora buccobulbosa* sp.n. – Paratype female (♀$_3$). – ∅A: Cross section through anterior ovary, frontal view; ∅B: Cross section through anterior ovary tip, frontal view; ∅C: Cross section through distal end of uterus, rear view; ∅D: Cross section through uterus, frontal view; ∅E: Cross section at level of vagina, frontal view.

the intestine, in others at the right. Most specimens have the two ovaries reflected to the dorsal side, but in some one ovary is reflected to the ventral side. The nuclei of the oocytes have two to six nucleoli. Slit-like vulva, short but clear vagina vera and slightly muscular vagina uterina. At both distal ends of the uterus, hyalin sperm cells are embedded in the uterus wall, in which way the uterus wall functions as a kind of spermatheca (Fig. 6A,D). At both ends within the uterus, a hyalin cord can be seen (Fig. 6A), which in some specimens even runs through the entire uterus (Fig. 6D, 7∅A-∅E; a similar structure was also seen in the uterus of females of a new *Echinodesmodora* species, VERSCHELDE & VINCX (submitted)); cross sections (Fig. 7) reveal that in some areas this cord is attached

to the uterus wall (Fig. 7E), and remains free in the lumen along the rest of its length. There is no evidence towards function or purpose of these cords, but maybe they have a feeding function for the sperm cells or they could give guidance to the sperm cells so these can find their way and reach the distal parts of the uterus, or they could contribute to the building of the eggshells.
Caudal glands extending dorsally above the rectum. Slender cylindrico-conical tail; last half (or third) of the tail annuli without inner ornamentation; slender non-annulated tail end; clear valve in spinneret.

Juveniles
(Fig. 8; note that not all cephalic setae were drawn in Fig. 8 I,J, and M as some setae were broken off and insertion pores were unclear). All four juvenile stages were found.

Fourth stage juveniles
(Fig. 8C,D,O). Body shape, ornamentations and shape of annuli, position of lateral alae and tail similar to adults. At the level of the lateral alae, part of the body annuli split in two and interdigitate, and part of them do not split and just raise up in the ala.
Slender somatic setae (compared to the firm, broad setae in adults) arranged in six longitudinal rows.
Shape of the head capsule as in adults. Six inner and six outer labial setae, four cephalic setae located posteriorly on the anterior region of the head capsule. Fovea amphidialis unispiral, located laterally in the middle of the posterior region of the head capsule; no subcephalic setae.
Esophastome with conspicuous dorsal plug in front of the large dorsal tooth, and two tiny subventral teeth. Pharynx with prominent buccal bulb, cylindrical corpus and muscular, bipartite terminal bulb. Pharyngeal lumen thickly cuticularized, with clear cuticular valves in the terminal bulb. Cardia 5-9μm.
Genital primordium of a female fourth stage juvenile is characterized by a string of cells of which both distal ends are swollen, and the presence of two ventral groups of (three) cells, located halfway the genital primordium, which will form the vagina (Fig. 8O).
Genital primordium of male fourth stage juveniles consists out of a slender string of cells which extends almost as far as the cloacal region; dorsally to the rectum, cells group up to form spicules and gubernaculum.

Third stage juveniles
(Fig. 8E-G, 8P-Q). General body shape, body annuli, lateral alae, pattern of (the even more) slender somatic setae, head capsule, amphids, buccal cavity with teeth, pharynx and tail shape similar as in fourth stage juveniles. Cardia 6-10μm.
Genital primordium of early third stage juveniles consists out of a somewhat stretched group of cells (Fig. 8P).
Genital primordium of later female third stage juveniles consists out of a short string of cells of which the distal ends are slightly swollen; no vaginal cells visible.
Genital primordium of male third stage juveniles consists out of a slender, short string of cells which does not extend further towards to the cloaca; dorsally to the rectum a few cells indicate the forming and future position of the spicules.

Second stage juveniles: (Fig. 8I-K,R). Slender body. Slender annuli, with ornamentation, and broad interannual spaces. Lateral alae present, but in early second stage juveniles only slightly raised above the surrounding cuticle, in late second stage juveniles somewhat more pronounced; only few annuli split and interdigitate at the level of the lateral alae. Some ecto-symbiotic organisms present along the body.
Fine somatic setae arranged in six longitudinal rows of only a few setae.
Head capsule with six inner and six outer labial setae; four cephalic setae located on the posterior edge of the anterior region of the head capsule. Unispiral amphids with small central spot located midway the posterior region of the head capsule. Posterior region of the head capsule with extra thick inner cuticle and ornamented with small pores. The head capsule of one second stage juvenile shows four short partial annuli on its left ventro-lateral side (Fig. 8I); this can be regarded as a reminder of one of the evolutionary transitional processes that occurred in Desmodoroidea when nematodes probably evolved from having no head capsule (annulation starting anterior to the amphids) to having one.
Buccal cavity with dorsal plug followed by a large dorsal tooth; subventral teeth not visible. Slender cylindrical pharynx with large buccal bulb and round, bipartite terminal bulb with clear cuticular valves. Cardia 4-7μm.
Genital primordium consists out of a small round (group of) cell(s?) (Fig. 8R).
Slender cylindrico-conical tail with clear valve in spinneret.

First stage juveniles
(Fig. 8L-N). Slender body with well developed annuli (with clear ornamentation) but very fine interannual spaces. No lateral alae. No somatic setae.
Head capsule with short posterior region. Lip region protrudable, inner and outer labial setae present. Four cephalic setae located at the anterior edge of the posterior region of the head capsule; circular amphids; thick inner cuticle of second region of the head capsule ornamented with numerous pores.
Buccal cavity with cheilorhabdia, cuticular dorsal plug, dorsal tooth and two tiny subventral teeth (Fig. 8L). Long cylindrical pharynx with large buccal bulb and round, bipartite terminal bulb. Pharyngeal lumen cuticular with valves in terminal bulb (Fig. 8N). Cardia 4μm.
Genital primordium not observed, probably consisting out of one cell.
Long cylindrico-conical tail with fine spinneret.

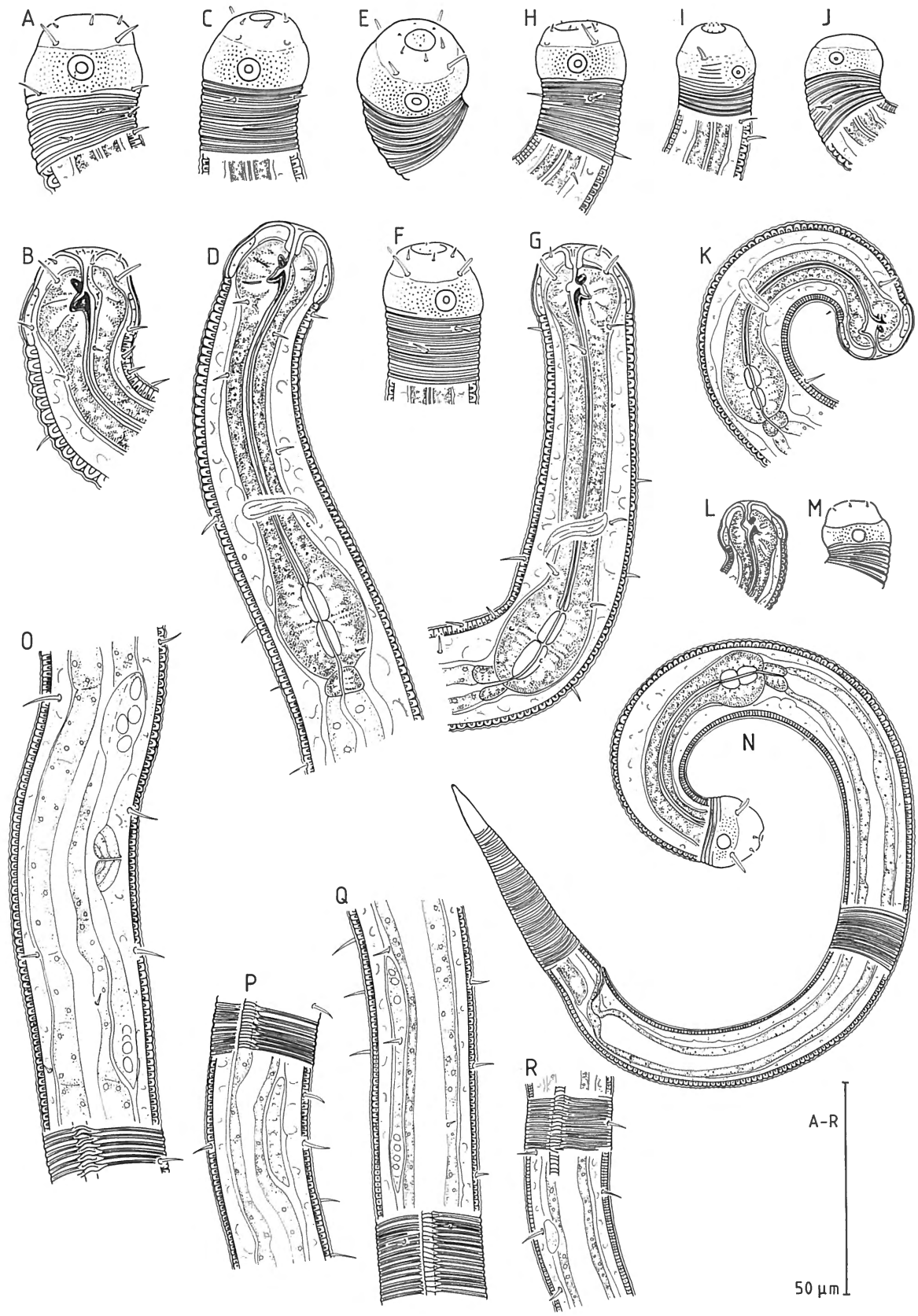

Fig. 8. – *Pseudochromadora buccobulbosa* sp.n. – A: ♀ 2, head capsule; B: ♀ 2, buccal bulb; C: Fourth stage juvenile (J_{IV}), head capsule; D: J_{IV}, pharyngeal region; E: Third stage juvenile ($J_{III\ 1}$), head capsule; F: $J_{III\ 2}$, head capsule; G: $J_{III\ 2}$, pharyngeal region; H: Second stage juvenile ($J_{II\ 1}$), head capsule; I: $J_{II\ 2}$, head capsule; J: $J_{II\ 3}$, head capsule; K: $J_{II\ 3}$; pharyngeal region; L: First stage juvenile ($J_{I\ 1}$), buccal cavity; M: $J_{I\ 1}$, head capsule; N: $J_{I\ 2}$, habitus; O: J_{IV}, reproductive system; P: $J_{III\ 1}$, reproductive system; Q: $J_{III\ 3}$, reproductive system; R: $J_{II\ 1}$, reproductive system.

Diagnosis

Pseudochromadora buccobulbosa sp.n. is characterized by the combination of the following characters: large muscular buccal bulb, stoma with a conspicuous cuticular dorsal plug and broad dorsal tooth, and sexual dimorphism in shape of the amphids. Males are characterized by their large number of copulatory thorns and spicules with birds-head shaped capitulum.

Differential diagnosis

Pseudochromadora buccobulbosa sp.n. somewhat resembles *P. coomansi* sp.n. but can easily be distinguished from it by combination of the following characters: large buccal bulb with cuticular dorsal plug (small buccal bulb without dorsal plug in *P. coomansi* sp.n.), shape of the amphids (unispiral in both sexes in *P. coomansi* sp.n.), and presence of a ventral row of small thorns (absent in *P. coomansi* sp.n.). Males can be distinguished by the birds-head shaped capitulum of the spicules (no capitulum in *P. coomansi* sp.n.), and by the number and shape of the copulatory thorns (fewer but larger in *P. coomansi* sp.n.).

Morphology

Ecto-symbiotic organisms

Many specimens of the two new species of *Pseudochromadora* DADAY, 1889 are covered with ecto-symbiotic organisms. Such organisms have already been sited and studied many times in Stilbonematinae by OTT and colleagues (OTT & NOVAK, 1989). The organisms found here, on the *Pseudochromadora* specimens, are fine hair-like structures, which (seen by means of light microscope) do not seem to be multicellular. Seen by means of Scanning Electron microscope, the organisms show to be filiform with a swollen distal end (Plate 5D).

It has been suggested to us by one of the referees that the organisms we observed on the *Pseudochromadora* specimens could also be parasites, or fungi penetrating moribund nematodes, or even bacteria which originated by contamination in the course of preparation, instead of being ecto-symbiotic organisms. All three possibilities are highly improbable because of the following arguments:

(1) To what parasites are concerned, there is little or no previous evidence or literature to such phenomenon occurring with parasites of such habitus, especially within the Desmodoroidea.

(2) The organisms cannot be (parasitic) fungi penetrating moribund nematodes, as all specimens that would be 'infected', are in good preserved condition and show no deterioration or decomposition, which is the case when fungi penetrate, what so ever.

(3) To what bacterial contamination during preparation is concerned: We have to state up front that on each one and the same slide, we mounted both sexes of the *Pseudochromadora* species together with other specimens of different nematode species and genera. The possibility of contamination occurring during preparation is minute and could only happen during the very short time that the animals remain in pure glycerine, after the transfer from formaldehyde (4%) by the method of SEINHORST (1959) and before they are mounted on COBB-slides (COBB, 1917). The developing of such large number of bacteria, as can be observed on the specimens (Plate 5D), in such short period of time is very unlikely. But the most important argument to reject the possibility of bacterial contamination is the following: when contamination through preparation would occur, there would be no possible reason for the bacteria to make a choice between the different nematode sexes or discriminate any nematode specimen or species present in one slide, and so there would be no reason for females of the *Pseudochromadora* species, present in the same slide as the males, to be more 'infected' by bacteria than the males, and most of all there would be no reason for the other nematode species, present in the same slide, not to be 'infected'.

Feeding habits

Species of both *Psammonema* gen. et sp.n. and *Pseudochromadora* DADAY, 1889 show a large dorsal tooth in the stoma. Furthermore, in the cells of the intestine of these species, many lipid droplets (indication towards the digestion of diatoms, a feature seen in many marine nematodes) are present.

The presence of such large dorsal tooth could indicate that these species are 'epistrate feeders' (WIESER, 1953). Such nematodes have been observed to feed on diatoms, other microalgae and Cyanobacteria. When these nematodes feed on diatoms, they either pierce them (the diatom is sucked against the lips) through with the dorsal tooth ('piercers'; NEHRING, 1992) or they grasp and hold the diatom within their stoma and than crack a hole in it with the dorsal tooth ('crackers'; NEHRING, 1992); in both cases the contents of the diatom is sucked out and the empty frustule is discarded, instead of swallowing the diatom at a whole. *Pseudochromadora buccobulbosa* sp.n. has, besides the large dorsal tooth, a dorsal 'plug' in its wide buccal bulb (Fig. 5D,E). This plug might 'articulate' with the dorsal tooth (or act as a bench on which the dorsal tooth can 'hammer'). The hypothesis is that *Pseudochromadora buccobulbosa* sp.n. can hold slender pennate diatoms between its dorsal plug and the dorsal tooth before breaking it open, so that *Pseudochromadora buccobulbosa* can be regarded as a 'cracker', feeding on pennate diatoms and possibly other microalgae.

As noted above, many specimens of *Pseudochromadora coomansi* sp.n. are covered with ecto-symbiotic organisms (Plate 5A,D). We also see that the firm somatic setae of this species are connected with epidermal gland cells. The idea is that the glands secrete a gluten on which the ecto-symbiotic organisms can feed (on the mucus itself or on organic particles that adhere to it; GERLACH, 1978) and therefore settle on the nematodes (gardening); the nematode on his turn than can feed on the ecto-symbiotic

organisms (perhaps in times of scarcity in its environment). The organisms are attached so well to their host's cuticle, that even ultrasonic washing (this technique is used to clean the nematodes before mounting for S.E.M. purposes) does not get them of.

The idea of some desmodorids, such as *Croconema* COBB, 1920, and *Desmodora* DE MAN, 1889, feeding on small organisms instead of engulfing larger detritus particles was already stated by Boucher (1972-73) as he argued that the labial structures of those desmodorids are too rigid to allow uptake of large particles.

The fact that these ecto-symbiotic organisms are present more abundantly in females than in males, suggests that they do not only serve as food for the adults, but possibly the female gardens the organisms to serve as food for her offspring (brood-care), a feature also BLOME & RIEMANN (1987) described earlier for *Desmodora schulzi* GERLACH, 1950.

Species of *Pseudochromadora* almost always have a conspicuous, nicely bent pharyngeal region (Fig. 3A, 4B,C, 6E; Plate 4D, 5A). It is also this region which shows the largest densities of ecto-symbiotic organisms (next to the tail region), and the most conspicuous epidermal gland cells. This suggests a link between the shape of the pharyngeal region and the gardening: a bent pharyngeal region make it more easy to graze in these (and more posterior) areas.

Ontogenetic transformations of some morphological characters

During ontogeny we see the c-value increasing (*Pseudochromadora coomansi* sp.n., J_I to J_{IV}: 5.7, 6.5, 7.2, 7.4; *Pseudochromadora buccobulbosa* sp.n., J_I to J_{IV}: 5.7, 6, 7.5, 7.6), meaning that the relative tail length shortens during that process (DE CONINCK, 1965). Based on the theory of the ontogenetic method (NELSON, 1978) we can state that within the Desmodoroidea, for the character 'tail', 'long' is a primitive (plesiomorphic) state and 'short' is a derived (apomorphic) state.

Looking at the juvenile series of *Pseudochromadora coomansi*, we can see a transformation going from an annulated (or partially -) head region (VERSCHELDE *et al.*, in press) to a fully developed head capsule (compare Fig. 4E with Fig. 4F,H; see also *Pseudochromadora buccobulbosa*, Fig. 8I). Therefore, it is hypothesized that, within the Desmodoroidea, the presence of an annulated head region is a primitive state and of a head capsule is a derived state.

Finally, we found that during ontogeny the amphids evolve from circular over unispiral with a tiny central spot towards unispiral with clear central spot (*Pseudochromadora buccobulbosa* sp.n., J_I to J_{VI}: Fig 8 M, J, H, C), and (in this case) showing sexual dimorphism in the adult faze (Fig. 5C). A similar case was discussed by LORENZEN (1984) for Axonolaimidae. So it is hypothesized that, within the Desmodoroidea, for the character 'amphids', 'circular' is a primitive state compared to 'unispiral' which is a more derived state and 'sexual dimorphism' even more derived. LORENZEN (1981) stated that circular amphids (apertura as large as fovea amphidialis) themselves are apomorphic for the Chromadoria compared to the primitive 'plectoid' amphids (apertura smaller then fovea amphidialis); indeed, plectoid amphids are sometimes seen in first stage juveniles of some species of the Epsilonematidae, and is even kept as the adult amphidial shape in *Metepsilonema iuvenisspinosum* VERSCHELDE & VINCX, 1994 (VERSCHELDE & VINCX, 1994). These conclusions on amphidial shape agree with the point of view of LORENZEN (1981) but are in contrast (this contrast was also mentioned by LORENZEN (1981)) with the assumed evolutionary pattern concerning amphidial shape of SCHUURMANS, STEKHOVEN and DE CONINCK (in DE CONINCK, 1965); they regard 'unispiral' as plesiomorphic and 'circular' and 'plectoid' as apomorphic, but presented no arguments in favour of their assumptions.

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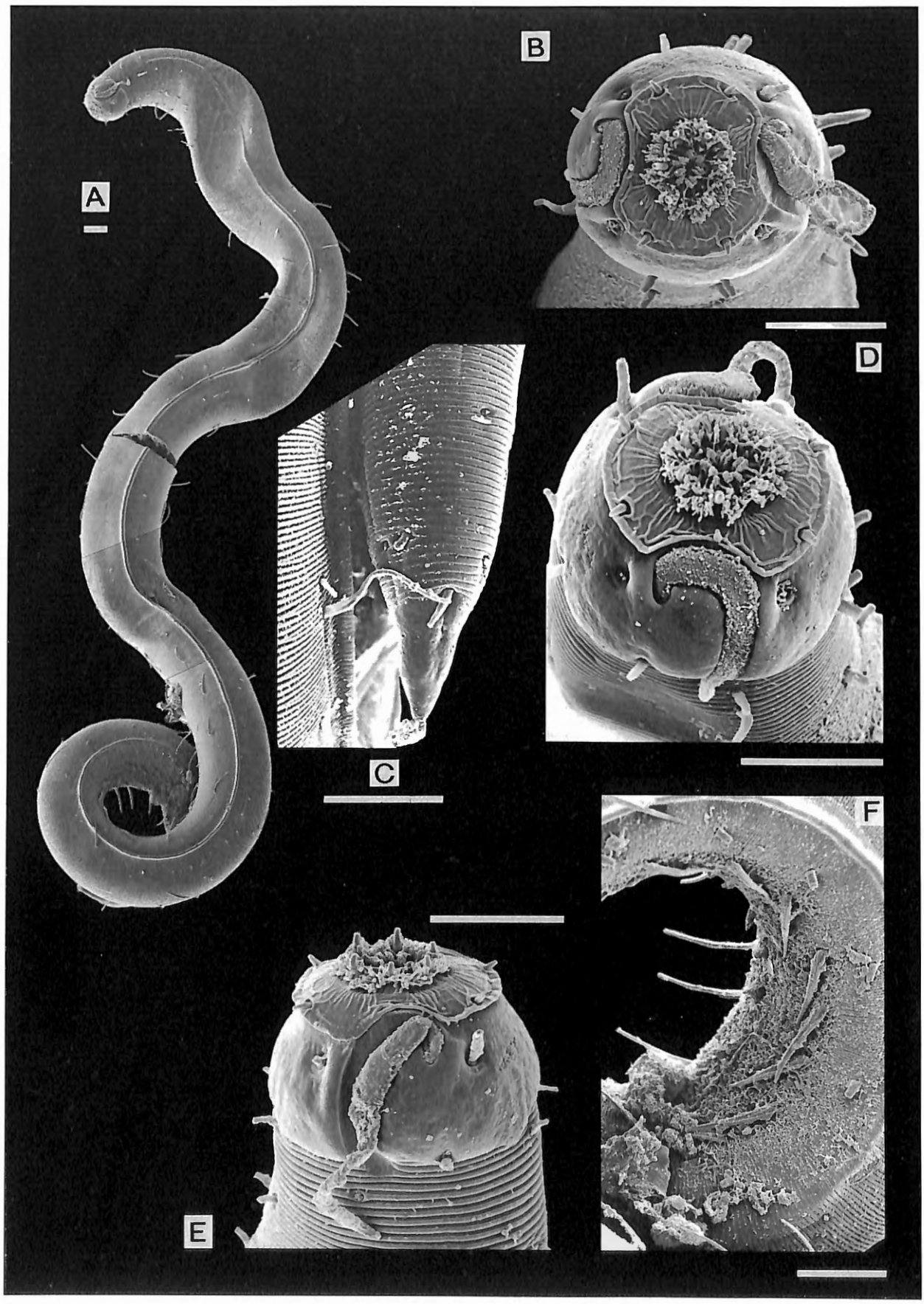

Plate 1. – *Psammonema ovisetosum* gen. et sp.n. Paratype male (σ'_4) – A: Habitus; B: Head capsule, frontal view; C: Tail; D: Head capsule, fronto-lateral view; E: Head capsule, lateral view; F: 'Supporting' somatic setae (Scale bars equal 10μm).

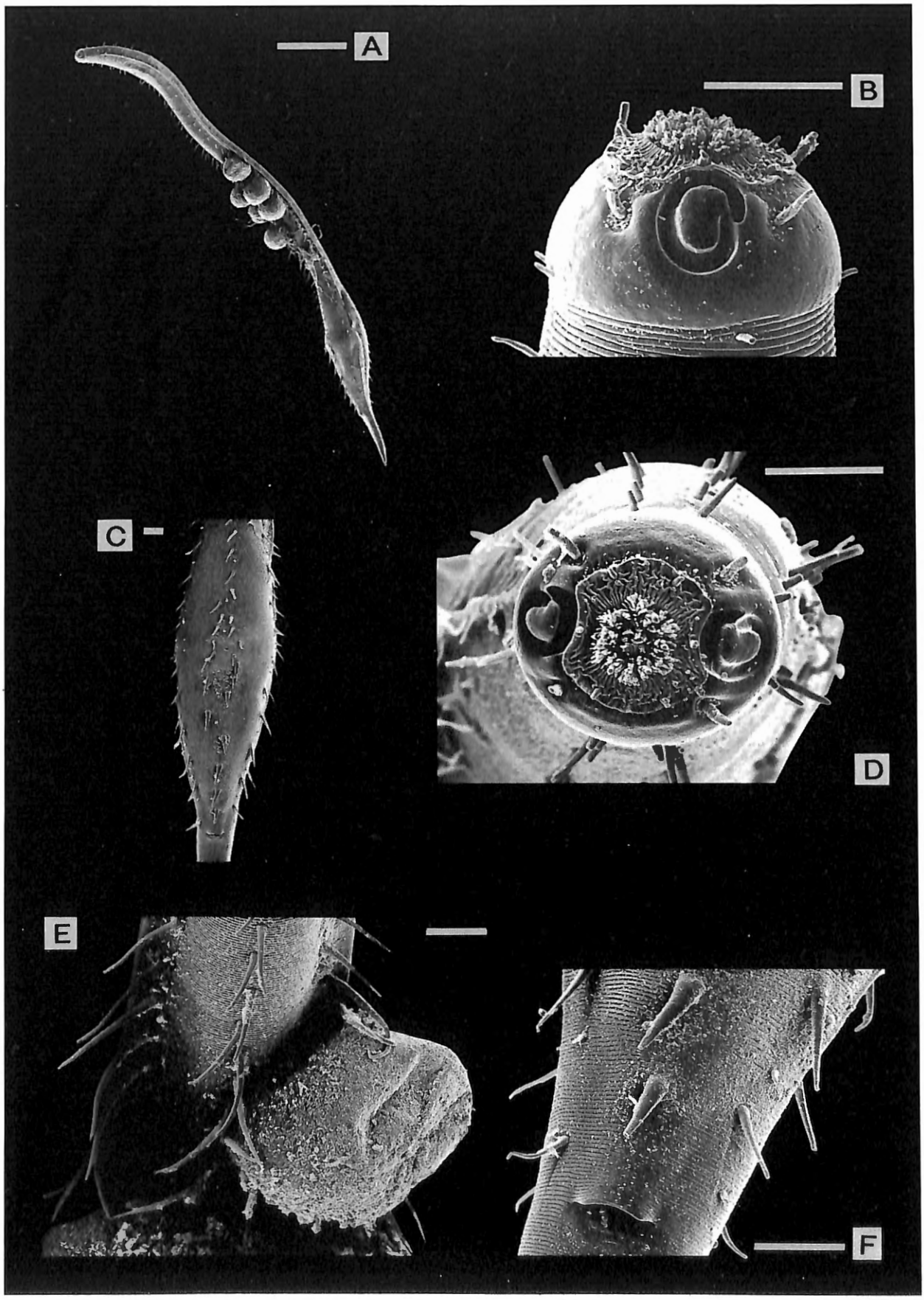

Plate 2. – *Psammonema ovisetosum* gen. et sp.n. Paratype female (♀$_3$) – A: Habitus; B: Head capsule, lateral view; C: Enlarged body region with vulva; D: Head region, frontal view; E: Egg held by special setae; F: Thorn-like setae in front of anus (Scale bar of A equals 100μm, of B-F 10μm).

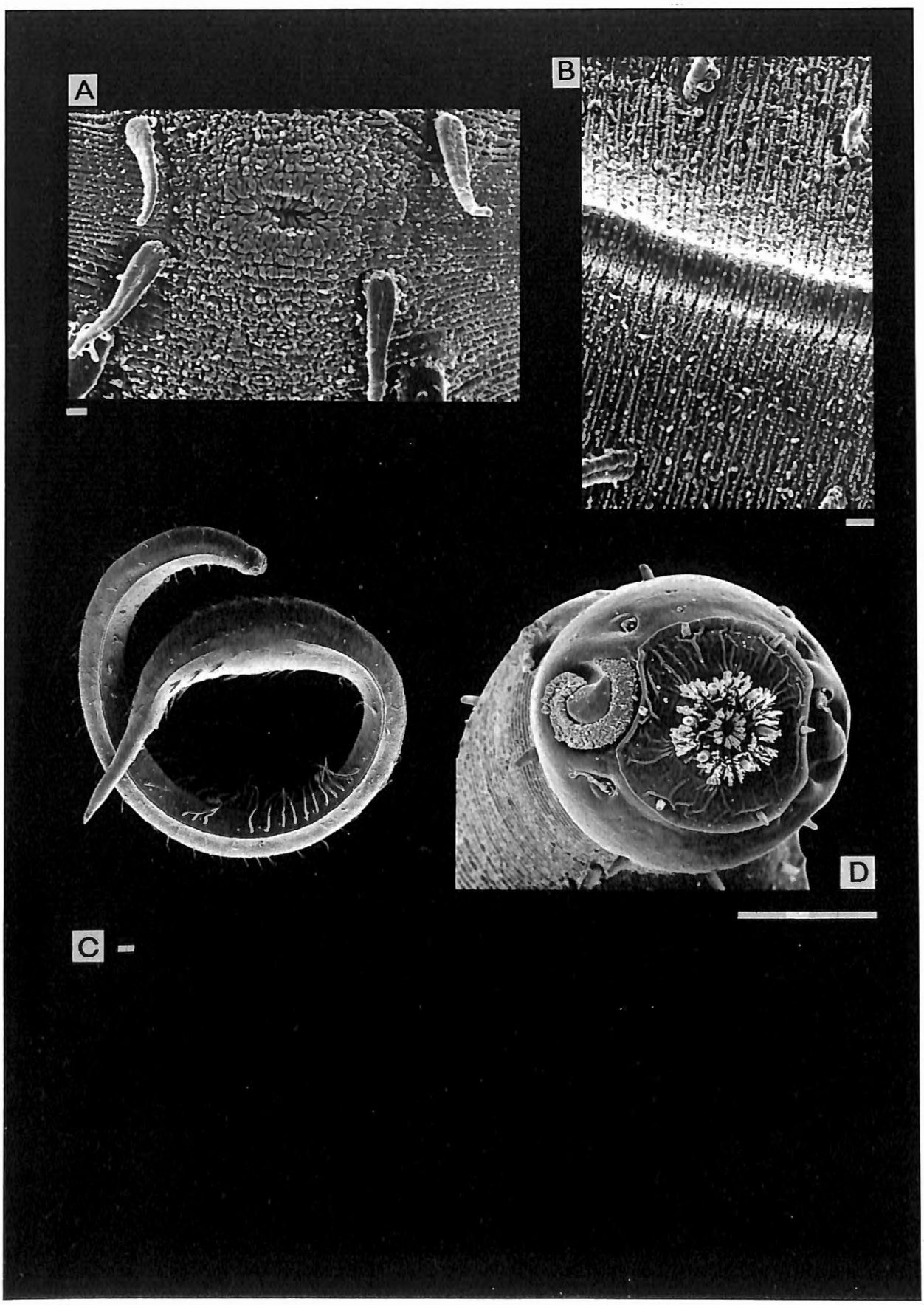

Plate 3. – *Psammonema ovisetosum* gen. et sp.n. – A: ♀$_3$, vulva; B: ♀$_3$, lateral ala; C: ♀$_4$, habitus; D: ♀$_5$, head region, frontal view (Scale bars of A,B equal 1μm, of C,D 10μm).

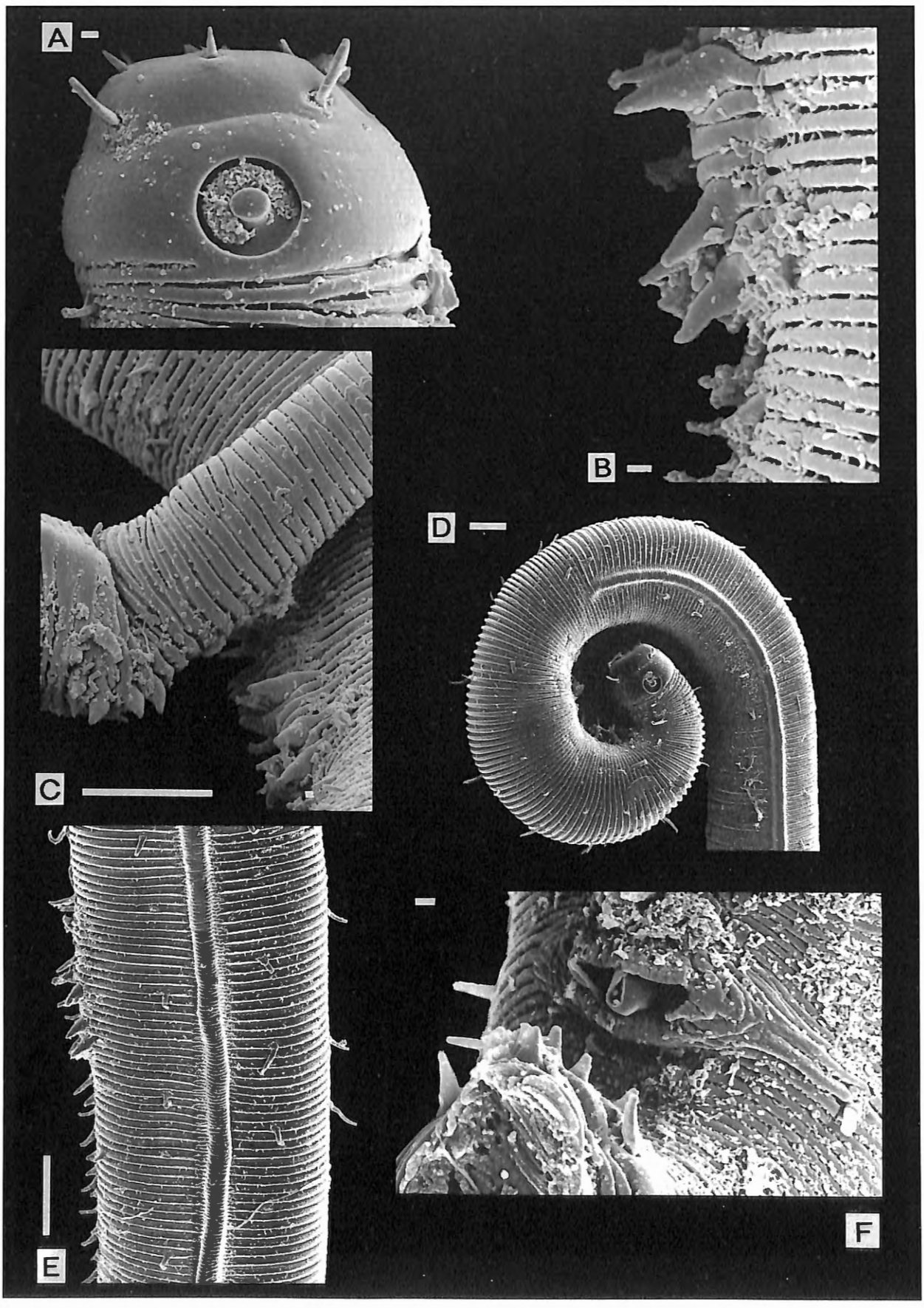

Plate 4. – *Pseudochromadora coomansi* sp.n. – A: ♂$_5$, head capsule; B: ♂$_5$, copulatory thorns; C: ♂$_5$, copulatory and post-cloacal thorns; D: ♂$_6$, pharyngeal region; E: ♂$_6$, body region with copulatory thorns; F: ♂$_6$, cloaca.

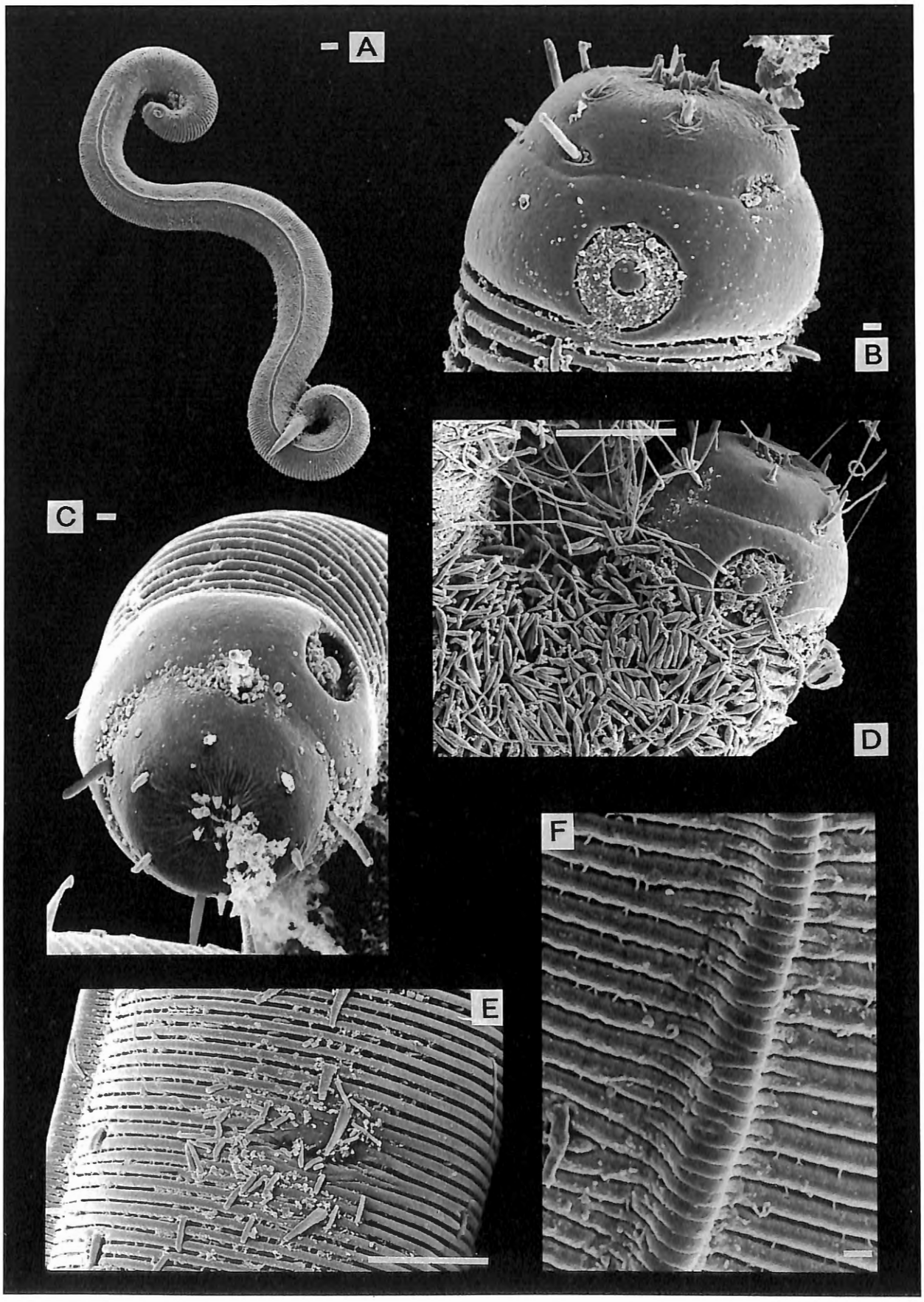

Plate 5. – *Pseudochromadora coomansi* sp.n. – A: ♀$_2$, habitus; B: ♀$_3$, head capsule; C: J_{IV}, head capsule; D: ♀$_4$, ecto-symbiotic organisms; E: ♀$_5$, vulva; F: J_{IV}, lateral ala.