Nematologica 40 (1994): 78-105, © E. J. Brill, Leiden

EPSILONEMATIDAE (NEMATODA: DESMODOROIDEA) FROM THE EAST AFRICAN COAST, WITH A DISCUSSION ON THE EXTERNAL MORPHOLOGY OF CUTICULAR APPENDAGES

BY

D. VERSCHELDE & M. VINCX

Zoology Institute, Marine Biology Section, K.L. Ledeganckstraat 35, B 9000 Gent, Belgium

Morphological features of the cuticular appendages, such as spines, thorns, setae and flaps are described on the basis of SEM pictures of three new and three known species of the Epsilonematidae from East African coasts.

Epsilonema espeeli sp.n. is characterized by the presence of six subcephalic setae and a large number of hair-like spines on the dorsal body side; males are characterized by three pairs of copulatory thorns, three precloacal thorns and an anal tube; females have a large citucular flap covering the vulva. *Metepsilonema iuvenisspinosum* sp.n. is characterized by its small size, ornamentation and shape of the body annules, conspicuous inversions in direction of the body annules (3 dorsal inversions and 1 ventral inversion), oval amphid, 4 pairs of supporting setae of which the third pair is the longest one in the males and the last pair the longest one in the female, length of the spicules and the subdorsal spines on the female (and juveniles) tail. *Perepsilonema ritae* sp.n. is characterised by sexual dimorphism in: amphidial shape (slit-like in the males, spiral in the females), number of subcephalic setae (8 in the males, 6 in the females), ornamentation of the body annules, sudden broadening of the body just behind the ventral body curvature and a slender annule posterior to the ventral body curvature. Males have large copulatory thorns and slender spicules.

Additional morphological information on *Epsilonema parvospina* Decraemer, 1982, *Metepsilonema bermudae* Lorenzen, 1973 and *Perepsilonema kellyae* Gourbault & Decraemer, 1988 is presented and important external characteristics are illustrated with SEM pictures.

The external morphology of the ambulatory setae is compared between specimens of the Epsilonematidae and one species of Draconematidae (*Dracograllus eira* (Inglis, 1968)).

Keywords: marine nematodes, systematics, morphology

Epsilonematidae are small nematodes with an epsilon-shaped body, thick body cuticle and well developed body annules; most genera carry different modified cuticular appendages such as ambulatory setae (except for the genus *Perepsilonema* Lorenzen, 1973), additional supporting setae and thorn-like cuticular structures.

Morphological features of the cuticular appendages are described on the basis of SEM pictures of three new, and of three known species of the Epsilonematidae from East African coasts.

This paper results from benthic research in Kenyan coastal biotopes in cooperation with the Kenyan-Belgian project (organised by the Free University of Brussels, Belgium and by the Kenyan Marine Fisheries and Research Institute, Mombasa, Kenya) (Verschelde & Vincx, 1992).

MATERIALS AND METHODS

Benthic samples were taken using a core of 3.5 cm diam pushed into the sediment up to 20 cm depth. The samples were fixed in warm (70°C) 4% formalin-seawater solution. Nematodes were transferred to pure glycerine by the method of Seinhorst (1959). Drawings were made with the aid of a camera lucida on a Leitz Dialux 20EB. SEM pictures were taken from formalin fixed animals, stained in OsO_4, dehydrated, dried and coated with 200-250 Å gold (SEM: JEOL JSM 840).

Type and other specimens are deposited in the nematode collections of the Zoology Institute of the University of Ghent (ZIRUG), in the Marine Biology section of the Zoology Institute of the University of Ghent (MBRUG) and in the National Museum of Natural History of Paris, France (MNHN).

ABBREVIATIONS USED IN TEXT:

ABD : body diameter at level of anus
Amph % : diameter of amphid as a percentage of the corresponding head diameter
Asl : length of the anteriormost seta ambulatoria of the external subventral row
ant : length of the anal tube
cs : length of cephalic setae
dcs : distance from rostrum edge to cephalic setae
gub : length of gubernaculum
lct : length of copulatory thorns
lpt : length of precloacal thorns
mbd : maximum body diameter of posterior body region
(mbd) : minimum body diameter
mbd/(mbd) : maximum body diamter divided by minimum body diameter
mbd ph : body diameter at level of pharyngeal bulb
N : number of body rings
ph : length of pharynx
spic : length of spicule, measured along the arc
SSph : length of subdorsal somatic setae in pharyngeal region
tmr : length of non-annulated tail region

All measurements are in µm.

MORPHOLOGY AND DESCRIPTIONS

Epsilonema espeeli sp.n.

(Figs. 1, 2 & 3; Table I)

Measurements: see Table I.

Males: Body clearly epsilon-shaped; over the whole length almost equally

wide. Body annules equally shaped (2 µm wide), ornamented with a row of very small round vacuoles situated closely next to one another. Inversion in direction of body annules is situated dorsally between the fifth and sixth body annule anterior to the ventral body curvature, ventrally between fifth and sixth annule posterior to the dorsal body curvature.

In the pharyngeal region, somatic setae in five longitudinal rows (one subventral pair, one subdorsal pair and one single dorsal row). Six rows of somatic setae are present posterior to the ventral curvature. Setae ambulatoriae with distally bent tips (Fig. 2F), arranged in four longitudinal rows with six to seven setae per row. At the level of the last setae ambulatoriae there are three pairs (sometimes four pairs) of copulatory thorns; between the second of third pair of copulatory thorns there is a medioventral seta ambulatoria (Fig. 1A, 2B). In a few cases there are two or three single copulatory thorns implanted in front of the paired ones. A group of three precloacal thorns (one pair followed by a single ventral one) situated eleven to thirteen annules in front of the cloaca (Fig. 2B). Following the external row of setae ambulatoriae and anterior to the cloaca, there are four pairs of short and slender supporting setae. Paratype males have one pair of precloacal and two pairs of postcloacal setae located subventrally (Fig. 2B; these setae are not very clear in the holotype). There is a ventral field of short flattened spines extending from dorsal body curvature to the mid-level of the region of the setae ambulatoriae (Fig. 2A,F). Posterior to the ventral body curvature there is a dorsal to subdorsal field of long hair-like spines (Fig. 2A,B,E; in Fig. 1 not all spines are drawn). Hair-like spines consist of protrusions of the posterior edge of the culticular body annules (Fig. 2E,F).

Slender rostrum with four cephalic (length: 10 µm) and six subcephalic setae (length: 6-10 µm; Fig. 2C,D). Lip sensilles not visible because of the withdrawn lip region in all examined specimens. Cephalic setae situated at the mid-level of the rostrum (Fig. 2D). The cephalic and subcephalic setae end funnel-shaped (only distinct in SEM, Fig. 2C,D). Spiral amphidial fovea, ventrally whirled (1.5 turns).

Buccal cavity small, teeth not distinct. Lip region withdrawn. Long and slender pharynx, clearly bent, large muscular end-bulb, no mid-bulb; cardia (4 µm) surrounded by the first intestinal cells. Cloaca with anal tube (Fig. 1A, 2B).

Testis extends to the dorsal body curvature; a narrowing indicates the beginning of the vas deferens. Spicules strongly arched; capitulum and velum well developed. Gubernaculum slender, extended dorsally.

Tail with twelve annules, plus four to five partial annules on the dorsal side of the non-annulated tail end. Caudal glands not distinct.

Females: Body shape, ornamentation of the body annules, pattern of somatic setae similar to those of males. Setae ambulatoriae in four longitudinal rows of four to six setae, situated in front of the vulva; one more ventral seta ambulatoria posterior to the vulva. Between setae ambulatoriae and anus there are two or three pairs of supporting setae which are somewhat longer than the setae

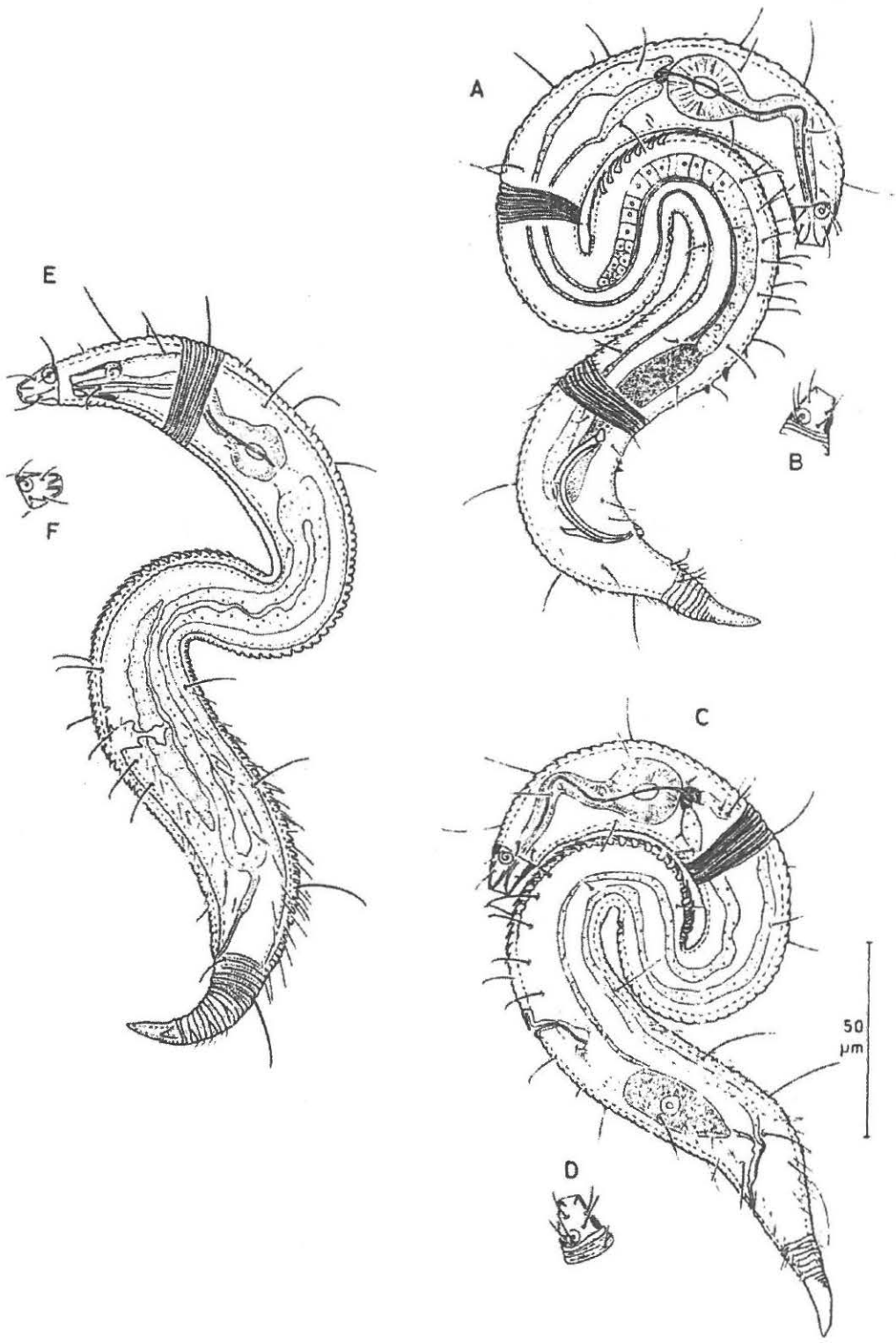

Fig. 1. *Epsilonema espeeli* sp.n. A. Habitus holotype male; B. Head holotype male; C. Habitus allotype female; D. Head allotype female; E. Habitus paratype juvenile, young female; F. Head of juvenile (E).

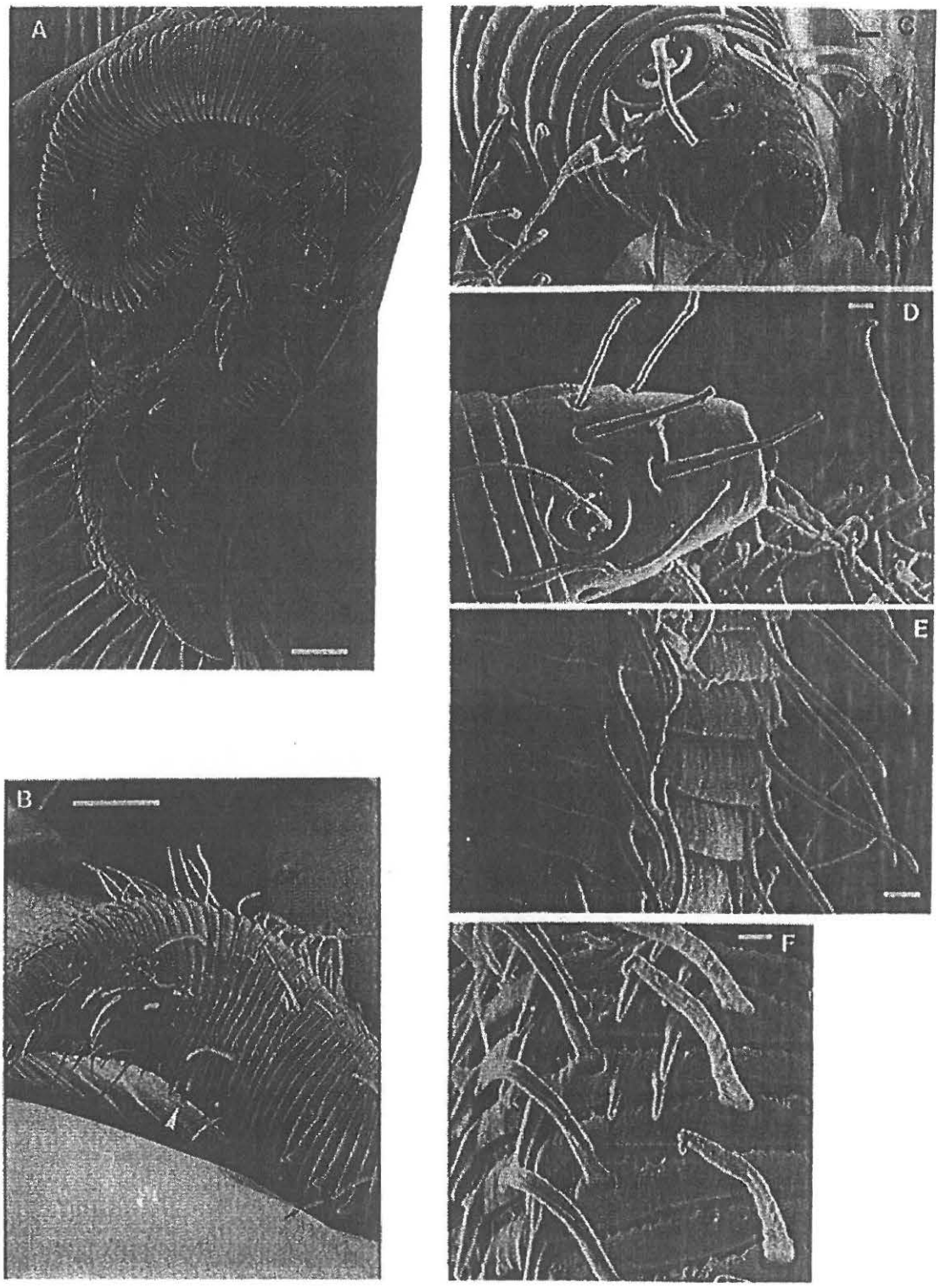

Fig. 2. *Epsilonema espeeli* sp.n. Paratype male. A. Habitus; B. Subventral view of the posterior part of the body (arrowhead indicates precloacal thorns; arrow indicates the medioventral seta ambulatoria between the copulatory thorns); C. Head region, frontal view; D. Head region, lateral view; E. Hair-like spines on the dorsal body side; F. Ambulatory setae. (Scale bars indicate: 10 µm in A, B; 1 µm in C-F.)

TABLE I

Measurements of Epsilonema espeeli *sp.n.*

	Holotype ♂	Paratype ♂♂ n = 7	Paratype ♀♀ n = 8	$J4_{♂}$ n = 1	$J4_{♀}$ n = 1
L	367	324-351 (339)	306-344 (327)	310	299
N	146	144-152 (147)	143-151 (148)	164	157
cs	10	6-9 (7)	6-8 (7)	7	7
Amph %	39	38-40 (39)	33-41 (38)	34	31
SSph	14	12-16 (14)	12-16 (14)	17	12
Asl	12	11-12 (11)	10-15 (12)	11	13
ph	72	65-69 (67)	64-69 (66)		
mbd	23	24-26 (25)	25-29 (28)	29	—
(mbd)	20	17-20 (19)	17-20 (18)	22	28
mbd ph	23	22-25 (23)	22-25 (23)	27	26
mbd/(mbd)	1.2	1.3-1.4 (1.3)	1.4-1.7 (1.6)	1.3	1.4
spic	44	43-46 (45)			
gub	15	15-18 (17)			
V			62-66 (64)		
ABD	18	16-18 (17)	14-17 (16)	18	14
tail	42	32-39 (36)	36-42 (38)	39	39
tmr	15	13-16 (15)	12-16 (15)	13	12
dcs	4	4-5 (4)	4-6 (5)	4	4
a	16	12-14.5 (11.6)	11.1-13 (11.6)	10.7	10.7
b	5.1	5-5.6 (5.1)	4.9-5.6 (4.9)		
c	8.7	9-10.3 (9.4)	7.7-9.3 (8.6)	7.9	7.7

(measurements in µm)

ambulatoriae, also longer than supporting setae of the male (males: supporting setae shorter than setae ambulatoriae). A ventral to subventral field of spines extends from dorsal body curvature to anus; the spines are more densely packed in the region anterior to the setae ambulatoriae and more spread in the region posterior to the setae ambulatoriae (Fig. 3A,D,F). A dorsal to subdorsal field of longer hair-like spines extends from ventral body curvature to non-annulated tail end.

Four cephalic and six subcephalic setae; fovea amphidialis as in male. No tooth visible in buccal cavity.

Vulva almost completely covered by a broad flap (Fig. 1B; Fig. 3B,C,D); the vulval flap has different shapes depending on the individual: sometimes the flap is undivided with a straight border, but in numerous cases the flap is split into two or several smaller slits. Vagina with thickly cuticularised vagina vera and muscular vagina uterina; vagina is always caudally bent. Reproductive system didelphic, amphidelphic with reflexed ovaries (not clear in allotype). Anus without anal tube.

Tail with twelve to fourteen annules; non-annulated tail end has dorsally four to five partial annules.

Juveniles: First, second and third juvenile stage not found.

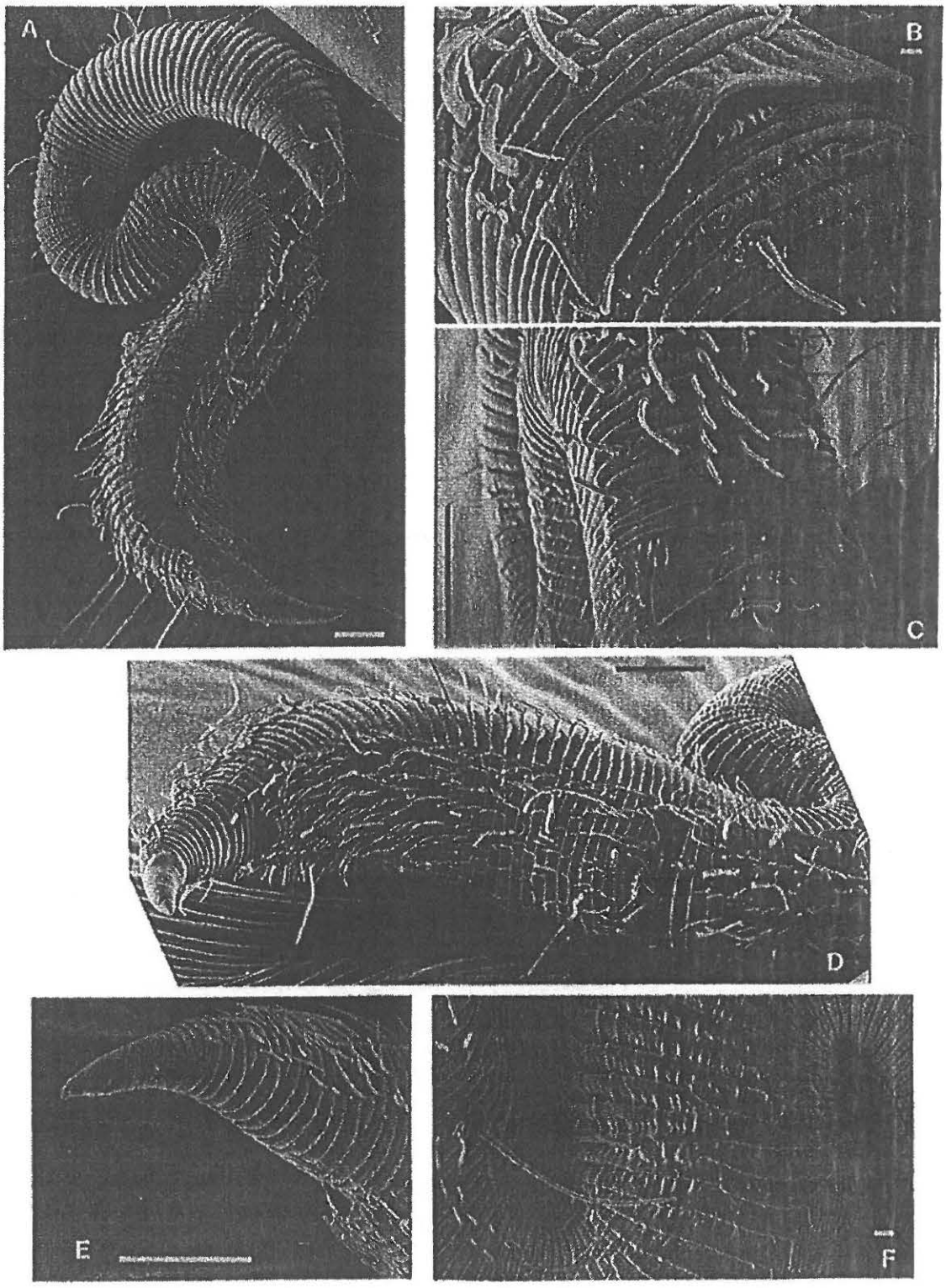

Fig. 3. *Epsilonema espeeli* sp.n. Paratype female. A. Habitus; B. Vulval flap; C. Vulval flap; D. Ventral view of the posterior part of the body; E. Subventral view of the tail: F. Inversion in the cuticular annules. (Scale bars indicate: 10 µm in A, C, D, E; 1 µm in B, F.)

Fourth juvenile stage: body shape, ornamentation of the body annules, pattern of somatic setae similar to female. Setae ambulatoriae in four longitudinal rows: sublateral rows with five to six setae, subventral rows with two to three setae. Hair-like spines, present dorsally and ventrally, in smaller numbers.

Rostrum short with four cephalic and six subcephalic setae.

Reproductive system of juvenile male consisting out of a group of cells (testis) located at the level of the setae ambulatoriae, which extends further as far as the rectum as a narrow string (vas deferens). Spicules present. Reproductive system of juvenile female didelphic, amphidelphic, ovaries not clear. Vulva and vagina clear.

Diagnosis: *Epsilonema espeeli* sp.n. is characterized by the position of the cephalic setae (at the middle of the rostrum), six subcephalic setae and hair-like spines in the posterior half of the body; males are characterized by three pairs of copulatory thorns, three precloacal thorns and an anal tube; females have a large flap covering the vulva.

Differential diagnosis: *Epsilonema espeeli* sp.n. differs from most *Epsilonema* species by the number of subcephalic setae: six (as in *E. lasium*) compared with eight in all other *Epsilonema* species.

The males of *E. espeeli* sp.n. closely resemble *E. lasium* Lorenzen, 1973 but differ from it by the smaller copulatory thorns, presence of an anal tube (*E. lasium* has paracloacal thorns) and the larger number of hair-like spines on the dorsal side, larger body and larger spicules (*E. lasium*: spic. of type specimens = 25 µm; specimens from Guadeloupe = 35-38 µm). Females of *E. espeeli* sp.n. are larger (327 µm) than those of *E. lasium* (230-290 µm); they do not have a field of thorn-like spines between setae ambulatoriae (normal and hair-like spines are present); they have a conspicuous prevulval flap which consists of a protrusion of the anterior edge of the vagina vera.

Type specimens: 8 males, 8 females and 2 juveniles. Holotype male: slide n° 3583, allotype female: slide n° 3584, paratype juvenile: slide n° 3619, in the collection of ZIRUG. Other paratypes (2 ♀♀): slide n° BN 197 are added to the collection of MNHN

Type locality: Kenya, Gazi (01-08-1989). Mouth of the Gazi Creek river, beach in the vicinity of *Sonneratia* vegetation.

Etymology: This species is named in honour of Dr. Marc Espeel.

Epsilonema parvospina Decraemer, 1982

Males: The two specimens largely agree with the original description of the type specimens of Papua New Guinea (Decraemer, 1982).

A few differences in characteristics and measurements compared with the type material are noted: the Kenyan specimens are slightly larger (L = 344-369 µm; mbd = 22-23 µm, (mbd) = 15-16 µm) than the type specimens (L =

295-350 µm), although they have fewer body annules (N = 124-125 compared to 138 (mean value)). Four longitudinal rows of seven to eleven setae ambulatoriae (Asl = 9-11 µm). The most posterior setae ambulatoriae of the subventral rows are situated at the level of the third copulatory thorn. Posterior to the sublateral setae ambulatoriae, there are four supporting setae, followed by three postcloacal somatic setae. Cephalic setae posteriorly shifted (cs = 7-9 µm; dcs = 4 µm), almost reaching the mid-level of the rostrum (length of rostrum = 11 µm); large amphid almost unispiral (spiral little more than one whirl; amph % = 47-48 µm). Pharynx with strong, muscular end-bulb and very small mid-bulb (ph = 63-68 µm, mbd ph = 23-24 µm, SSph = 17-18 µm).

One testis beginning posterior to the dorsal body curvature; spicules 30-34 µm; short gubernaculum (4 µm) which is less bent than the gubernaculum of the type specimens.

Body width at level of cloaca 15-17 µm. Tail (38-41 µm) with nine annules, ventrally counted; non-annulated tail tip (tmr = 16 µm) is dorsally provided with five half annules.

Specimens: Two males: slide 3557 (ZIRUG).
Locality: Kenya, Malindi, 04-08-1988, Watamu Reserve; coarse coral sand.

Metepsilonema iuvenisspinosum sp.n.

(Figs. 4, 5; Table II)

Measurements: see Table II

Males: Body epsilon-shaped, small and slender. Body annules with specific shape and vacuolar ornamentation: in the pharyngeal region the annules (width = 2 µm, laterally measured) are ornamented with a mosaic of bubble-shaped vacuoles; from the sixth annule in front, to the eight annule behind the dorsal body curvature the annules are broader (3 µm) with an inconspicuous ornamentation of tiny vacuoles; in the region of the ventral body curvature there are very slim annules (1 µm) with broader inter-annular spaces (Fig. 5D); from the seventh annule posterior to the ventral body curvature to the cloaca, the annules are somewhat broader again (2 µm) and ornamented with a row of small bubble-shaped vacuoles; the tail annules are broader (2.5 µm) and ornamented with tiny vacuoles. This ornamentation is one of the deeper layers of the cuticula; there is no superficial ornamentation (Fig. 5F). Dorsally there are three and ventrally one inversions in direction of the body annules (Fig. 4A, see arrows): a first dorsal inversion in the fifth annule behind the rostrum, this annule has a protruding anterior and posterior edge which is characteristic for the species; the second dorsal inversion is located in the dorsal body curvature; third dorsal inversion is located just in front of the ventral body curvature; the only ventral inversion of the body annules is located ventrally is the dorsal body curvature.

TABLE II

Measurements of Metepsilonema iuvenisspinosum *sp.n.*

	Holotype ♂	Paratype ♂♂ n = 7	Paratype ♀♀ n = 8	J3
L	225	216-241 (224)	204-219 (211)	180
N	85	84-86 (85)	85-87 (87)	82
cs	3	3-5 (4)	2-4 (4)	
amph %	27	25-37 (31)	25-31 (29)	33
SSph	10	10-13 (11)	9-11 (10)	6
Asl	6	7-9 (8)	6-8 (8)	4
ph	49	46-51 (49)	47-49 (48)	41
mbd	18	15-19 (17)	20-22 (21)	17
(mbd)	9	7-9 (8)	7-9 (8)	9
mbd ph	20	18-20 (19)	19-21 (20)	18
mbd/(mbd)	2	1.9-2.6 (2.3)	2.2-2.8 (2.5)	1.9
spic	16	15-18 (17)		
gub	4	5-6 (5)		
V			72-74 (74)	
ABD	12	11-12 (12)	10-11 (11)	6
tail	20	10-22 (21)	19-22 (21)	12
tmr	9	10-11 (11)	10-12 (11)	4
dcs	3	3-4 (4)	2-4 (3)	2
a	12.5	12.1-14.7 (13.0)	9.3-10.3 (9.9)	10.6
b	4.5	4.6-5.3 (4.6)	4.6-4.8 (4.6)	4.4
c	11.3	9.8-11.5 (10.5)	9.5-10.5 (10.2)	15

(measurements in µm)

Setae ambulatoriae in four longitudinal rows of eight setae which are not knicked or only knicked at their base. Posterior to the setae ambulatoriae, there are 4 pairs of supporting setae located ventro-laterally: the third supporting seta is 1.7 to 2.1 times longer than the other three supporting setae; between first and second supporting setae there are two body annules, between second and third nine and between third and fourth supporting setae there are five body annules (Fig. 4A). Posterior to ventral body curvature there is a lateral row of four somatic setae; dorsally on the fifth and twelfth annule anterior to the tail, there are two long, single somatic setae (Fig. 4A).

Rostrum with four cephalic and two subcephalic setae; a few specimens have one or two more inconspicuous, additional (subcephalic) setae dorsally on the rostrum (Fig. 5B,E). Fovea amphidialis oval-shaped.

Stoma small, teeth not distinct. Pharynx with small mid-bulb and round, muscular end-bulb. Small cardia (2 µm). Cloaca without anal tube.

Single testis broad, surrounds the intestine from both sides; it reaches the fifth annule posterior to ventral body curvature; large, oval sperm cells; short spicules strongly arched; gubernaculum plate-shaped.

Tail with five annules; caudal glands not distinct.

Females: Body shape, pattern and ornamentation of body annules similar to

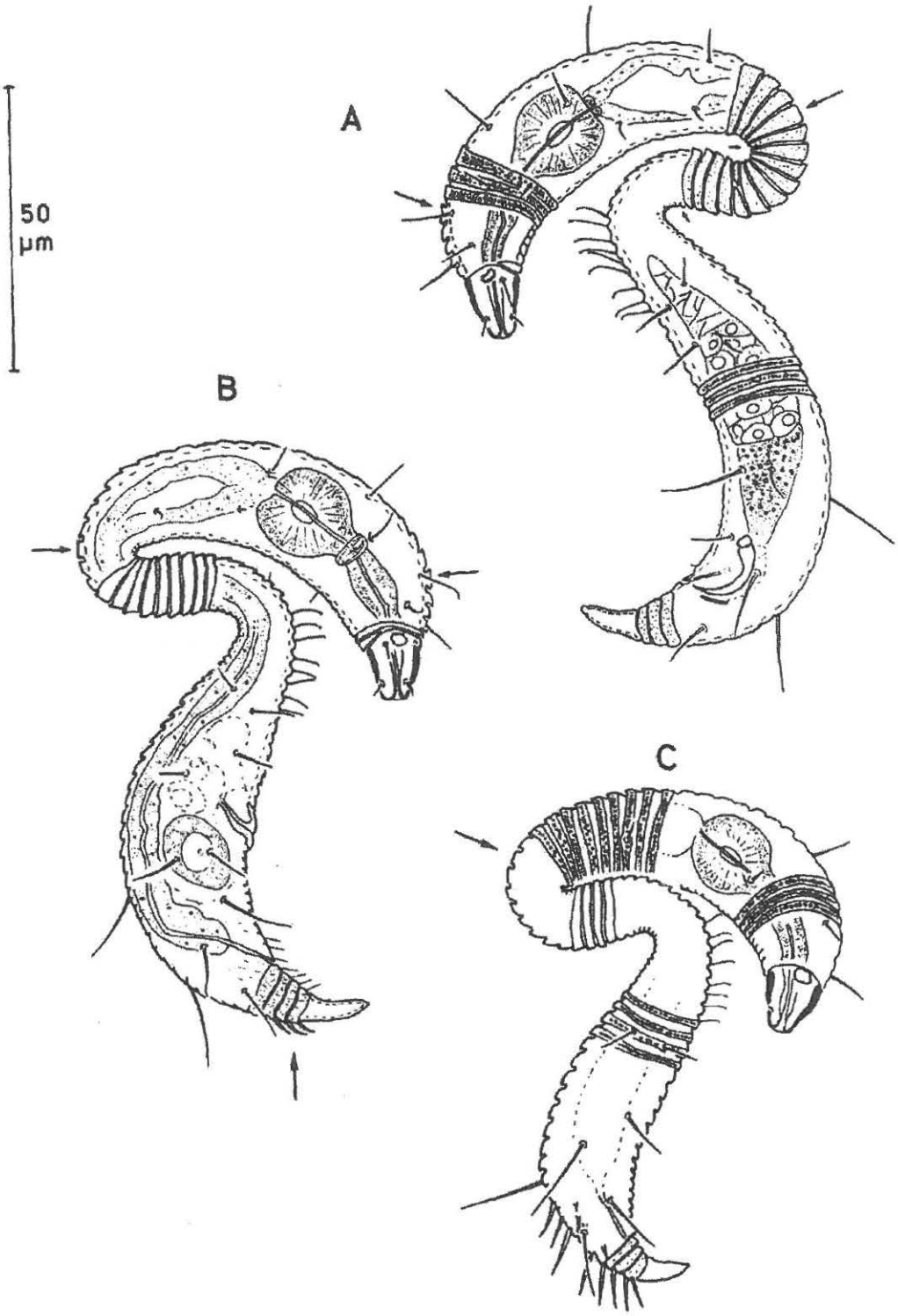

Fig. 4. *Metepsilonema iuvenisspinosum* sp.n. A. Habitus holotype male; B. Habitus allotype female; C. Habitus paratype juvenile.

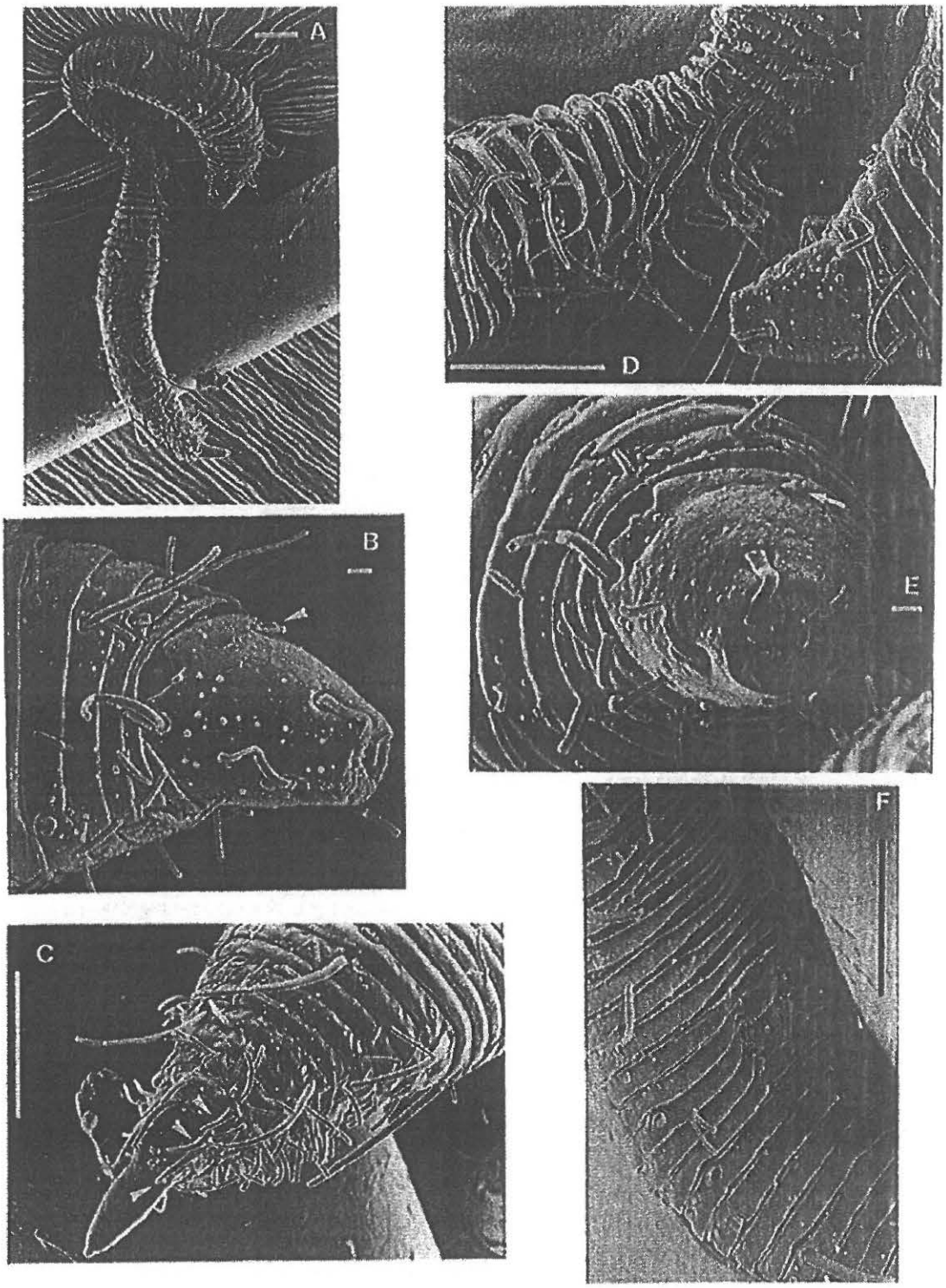

Fig. 5. *Metepsilonema iuvenisspinosum* sp.n. Paratype female. A. Habitus; B. Rostrum-lateral view (arrow indicates the subdorsal subcephalic seta); C. Dorsal view of the tail; D. Ambulatory setae; E. Head end, frontal view (arrow indicates the subdorsal subcephalic seta); F. Vulva. (Scale bars indicate: 10 µm in A, C, D, F; 1 µm in B, E.)

those of males, except for the broad body annules from third annule anterior to dorsal curvature to tenth annule posterior to dorsal curvature, which have no ornamentation. Inversion in direction of body annules (Fig. 4B; third dorsal inversion is difficult to localize) pattern of somatic setae and setae ambulatoriae (four rows of eight to nine setae) similar to males. Four pairs of supporting setae of which the fourth seta (contrary to the third in males) is the longest one. Characteristic are the three pairs of short, thick spines subdorsally on the last annules of the tail (Figs. 4B, 5C).

Rostrum with four cephalic setae and two subcephalic setae; sometimes one or two tiny subdorsal subcephalic setae. Fovea amphidialis rounder and slightly larger than in males (sexual dimorphism). Pharynx with small mid-bulb and strong, muscular end-bulb; nerve-ring situated just in front of end-bulb.

Vagina vera well developed, slightly bent anteriorly; reproductive system didelphic, amphidelphic with reflexed ovaries (not visible in allotype).

Tail with four annules; laterally and ventrally there are a large number of micro-organisms (Figs. 4B; 5A,C).

Juvenile: This probably is a third stage juvenile, due to the three rows of setae ambulatoriae and three pairs of supporting setae. Body-shape, body annules and ornamentation of annules similar to adults. First dorsal inversion in direction of body annules is absent; second dorsal inversion as in adults (Fig. 4C), and third difficult to distinguish.

Setae ambulatoriae in three longitudinal rows of four to five setae. Three pairs of supporting setae which gain in length from first to third: third supporting seta is 2.2 times as long as the first and 1.4 times as long as the second.

Rostrum probably with four cephalic setae (although only the subventral inplantation pore is distinct, Fig. 4C), no subcephalic setae. Fovea amphidialis as in female. Subdorsally on the last ten body annules, there are twelve pairs of long spines, of which five pairs stand in a longitudinal row. Intestine and genital primordium not clear.

Diagnosis: *Metepsilonema iuvenisspinosum* sp.n. is characterized by its small size (L = 204-241 µm), ornamentation and shape of the body annules, conspicuous inversions in direction of the body annules (3 dorsal inversions and 1 ventral inversion), oval amphid with sexual dimorphism, 4 pairs of supporting setae of which the third pair is the longest one in the males and the last pair the longest one in the female, length of the spicules (15-18 µm) and the subdorsal spines on the female and juvenile tail.

Differential diagnosis: *Metepsilonema iuvenisspinosum* sp.n. can hardly be confused with any other *Metepsilonema* species because of its body length, shape of its body annules and length of spicules. *M. iuvenisspinosum* sp.n. clearly differs from the other smaller species of the genus, in shape of the amphid and length of the spicules: *M. acanthum* Clasing, 1984 (spic = 24 µm), *M. callosum* Lorenzen, 1973 (spic = 40-45 µm) and *M. striatulum* Decraemer & Gourbault, 1990 (spic = 22-29 µm) all have a large spiral amphid.

M. iuvenisspinosum resembles *M. clasingae* Decraemer & Gourbault, 1989, *M. limbatum* Lorenzen, 1973 and *M. magdae* Decraemer & Gourbault, 1989, but can easily be distinguished from them: males of *M. clasingae* have well developed subdorsal spines extending from the level of the testis to the tail, such spines are also found in females and juveniles; *M. limbatum* differs in shape and ornamentation of the body annules (annules ornamented with square vacuoles), supporting setae, shape and size of spicules (spic = 27 µm); males of *M. magdae* have a large loop-shaped amphid, females and juveniles have a unispiral amphid and small spiny projections dorsally in the posterior body region.

Subdorsal additional (subcephalic) setae, although not considered as characteristic of the genus (Lorenzen, 1973) are until now found in *Metepsilonema bermudae* (see also below) and *M. iuvenisspinosum* sp.n. The genus diagnosis of *Metepsilonema* has to be extended for the number of setae on the rostrum: two subcephalic setae are always present and 1 or 2 additional dorsal setae may be present on the rostrum. The presence of spines on the lateral and dorsal surface of the posterior body region of females and juveniles (and not of males) has so far only been mentioned in *Bathyepsilonema dermoglyphum* Gourbault & Decraemer, 1987. Less pronounced than in *M. iuvenisspinosum*, females and juveniles of *M. magdae* also have small spiny projections dorsally in the posterior body region which are absent in males; but this is not the same as in *M. iuvenisspinosum* where the juvenile has a number of large spines which are absent in both adults.

Type specimens: 8 males, 8 females and 1 juvenile. Holotype male: slide n° 3585, allotype female: slide n° 3586, paratype juvenile: slide n° 3587 in the collection of ZIRUG. Other paratype: slide n° BN 198 (1♂, 3♀ in the collection of MNHN and slide n° 10278 (2♂, 1♀) in the collection of MBRUG.

Type locality: Kenya, Mombasa, Nyali Beach: 31-07-1989.

Etymology: From Latin: iuvenis = young man; spinosus, -a, -um: spiny. The specific name "*iuvenisspinosum*" alludes to the presence of long, subdorsal spines in the juveniles which are absent in adults.

Metepsilonema bermudae Lorenzen, 1973

(Figs 6, 10B)

Measurements: see Table III

Additional information:

Males: The specimens found in Kenya are smaller than the type specimens (231 µm compared with 280 µm in the type material) and specimens found in Guadeloupe (L = 260-320 µm, Decraemer & Gourbault, 1989) although they have an equal number of body annules (N = 92). The described ornamentation of the body annules ("a well cuticularized anterior and posterior border with a

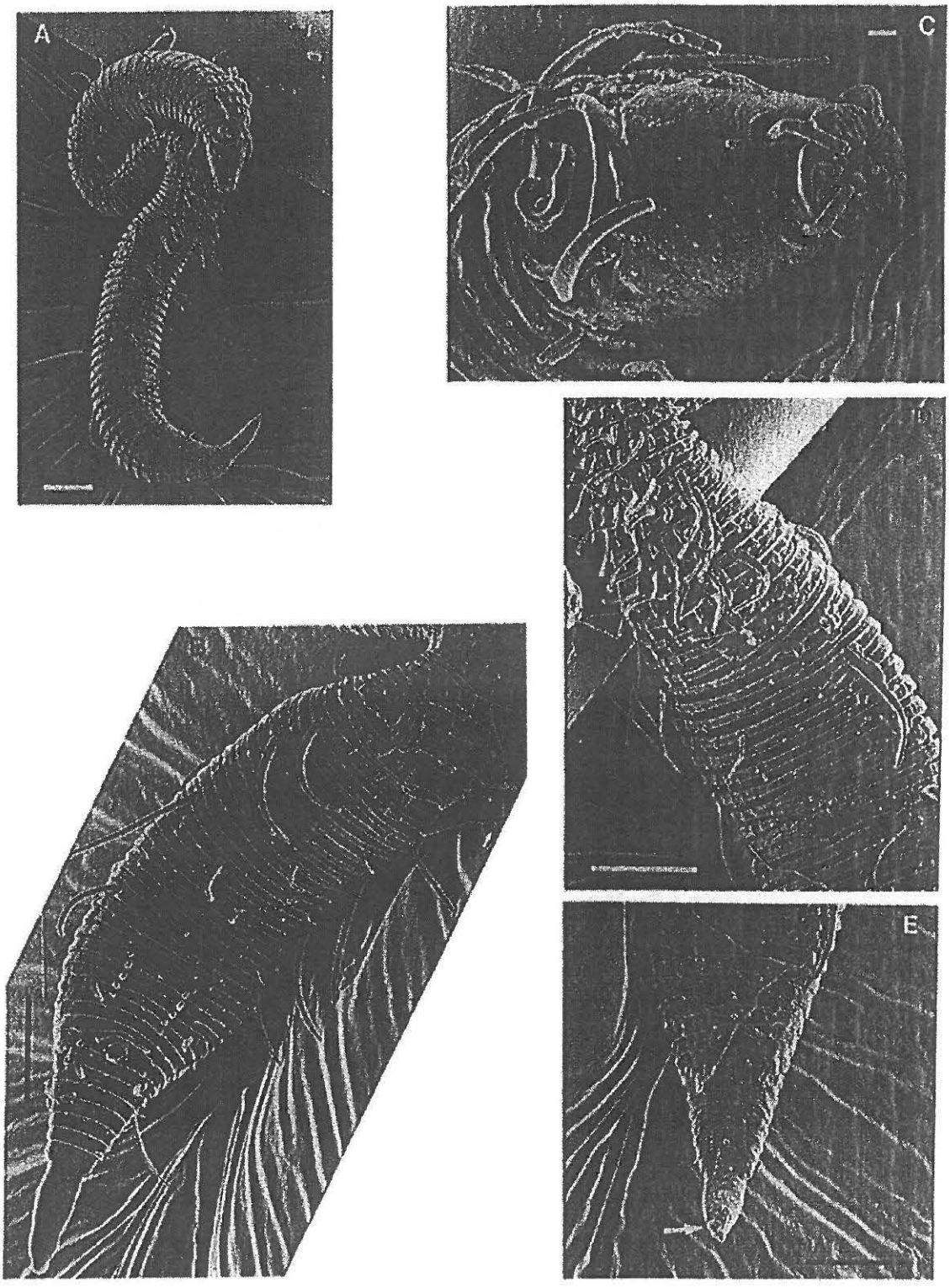

Fig. 6. *Metepsilonema bermudae* Lorenzen, 1973. A. Habitus male; B. Ventral view posterior end male (arrowhead indicates precloacal knotty thorns); C. Rostrum male; D. Ventral view of field of spines, ambulatory setae and vulva, female; E. Tail region, ventral view, female. (Scale bars indicate: 10 µm in A, B, D, E; 1 µm in C.)

TABLE III

Measurements of Metepsilonema bermudae *Lorenzen, 1973*

	♂♂ n = 7	♀♀ n = 7	J_4 n = 1
L	206-244 (231)	200-238 (225)	220
N	89-96 (92)	88-92 (90)	77
cs	4-7 (5)	4-7 (4)	4
Amph %	39-47 (45)	25-41 (34)	33
SSph	10-13 (12)	10-12 (11)	9
Asl	8-10 (9)	7-10 (9)	9
ph	48-54 (51)	44-55 (51)	54
mbd	20-22 (21)	22-26 (24)	22
(mbd)	10-12 (11)	9-12 (10)	11
mbd ph	20-21 (21)	20-22 (22)	22
mbd/(mbd)	1.8-2.2 (2.0)	2.1-2.5 (2.4)	2
spic	23-26 (24)		
gub	6-9 (7)		
V		68-70 (68)	
ABD	13-15 (14)	11-14 (13)	15
tail	25-30 (27)	21-29 (25)	30
tmr	10-15 (12)	12-14 (13)	12
dcs	2-4 (3)	1-3 (2)	2
a	9.4-11.8 (10.7)	7.7-10.3 (9.3)	10
b	4.1-5.0 (4.4)	4.2-5.2 (4.5)	4.1
c	7.8-9.0	8.0-10.3 (8.9)	7.3

(measurements in µm)

weak zone in between" in Lorenzen (1973)) is one of the deeper layers of the cuticle.

In the pharyngeal region and region between dorsal and ventral body curvature there is also a superficial ornamentation of the body annules: in the pharyngeal region annules are ornamented with a row of shallow dimples (Fig. 6A,C), in the body region between dorsal and ventral curvature these dimples are more rectangular and distinct (Fig. 6A). Setae ambulatoriae have distal bifid tips (Fig. 10B). Males show five pairs of small precloacal thorns and one or two pairs of very small paracloacal thorns (Fig. 6B). These observations are new for the species.

Ventral to subventral field of small spines extending from dorsal body curvature to last setae ambulatoriae (Fig. 6A); dorsal field of small spines extending from ventral body curvature to tail, as described in type specimens and others from Guadeloupe.

Head capsule with two cephalic and two subcephalic setae; dorsally on the rostrum there are also two single additional (subcephalic) setae (Fig. 6C), which were also described by Lorenzen but are not thought to be characteristic of the genus. Large fovea amphidialis (amph % = 39-47%, compared to 38% in the type specimens; Fig. 6A,C) as in specimens from Guadeloupe.

Broad, short, arched spicules; gubernaculum straight. One spinneret in tail tip not obvious.

Females: Ventral to subventral field of spines extending from dorsal body curvature to last setae ambulatoriae (Fig. 6D). Fovea amphidialis smaller than that of males (amph %: 34%, compared to 28% in type specimens of Bermuda). The vulva is a small slit-like opening in between two annules (Fig. 6D). Note the difference in shape of the male cloaca (Fig. 6B) and the female anus (Fig. 6E): in males the posterior border of the cloaca is probably continuously connected with the gubernaculum of the male. Two somatic setae are located near the single spinneret (Fig. 6E).

Fourth juvenile: Body shape similar to that of adults. Setae ambulatoriae in four longitudinal rows of respectively 6-4-4-7 setae. Ventral field of spines not visible; dorsal field of spines posterior to ventral body curvature inconspicuous. Rostrum with four cephalic setae; no paired subcephalic setae but one single dorsal seta is present. Fovea amphidialis similar to that of females. Pharynx less bent compared with that of adults.

Specimens: 19 males, 13 females, 6 juveniles. Gazi specimens: slides n° 10270-10273 in the collection of MBRUG; Nyali Beach specimens: slide n° BN 198 (1♂, 1♀, 1 juv.) in the collection of MNHN, slide n° 10278 (2♀, 2 juv.) in the collection of MBRUG.

Locality: Kenya, Gazi: 07-08-1989; Kenya Beach: 31-07-1989; coarse coral sand.

Perepsilonema ritae sp.n.

(Figs 7, 8; Table IV)

Measurements: see Table IV.

Males: Body epsilon-shaped; broad pharyngeal region; posterior to ventral curvature the body widens suddenly (Fig. 7A). Broad body annules (3 µm) ornamented with a row of large, square vacuoles situated in the deeper layers of the cuticle; superficially no ornamentation (Fig. 8A,C), except for a ventral field of ridges in the pharyngeal region and one posterior to the ventral body curvature (Fig. 8D). Six of the eight males had, at the level of the copulatory thorns, a typical slender annule which has no ornamentation (Fig. 7A; the slender annule is missing in the male in Fig. 8D). Dorsal and ventral inversion in direction of the body annules is located at the annule of the second pair of copulatory thorns. Few somatic setae are present, arranged in six longitudinal rows, most of them in the pharyngeal region.

Ventral field of tiny spines in the region between dorsal and ventral body curvature, which can only be seen in SEM pictures (Fig. 8A). Subdorsally on tail five pairs of small spines. Two pairs of somatic setae on non-annulated tail end (Fig. 8B,E).

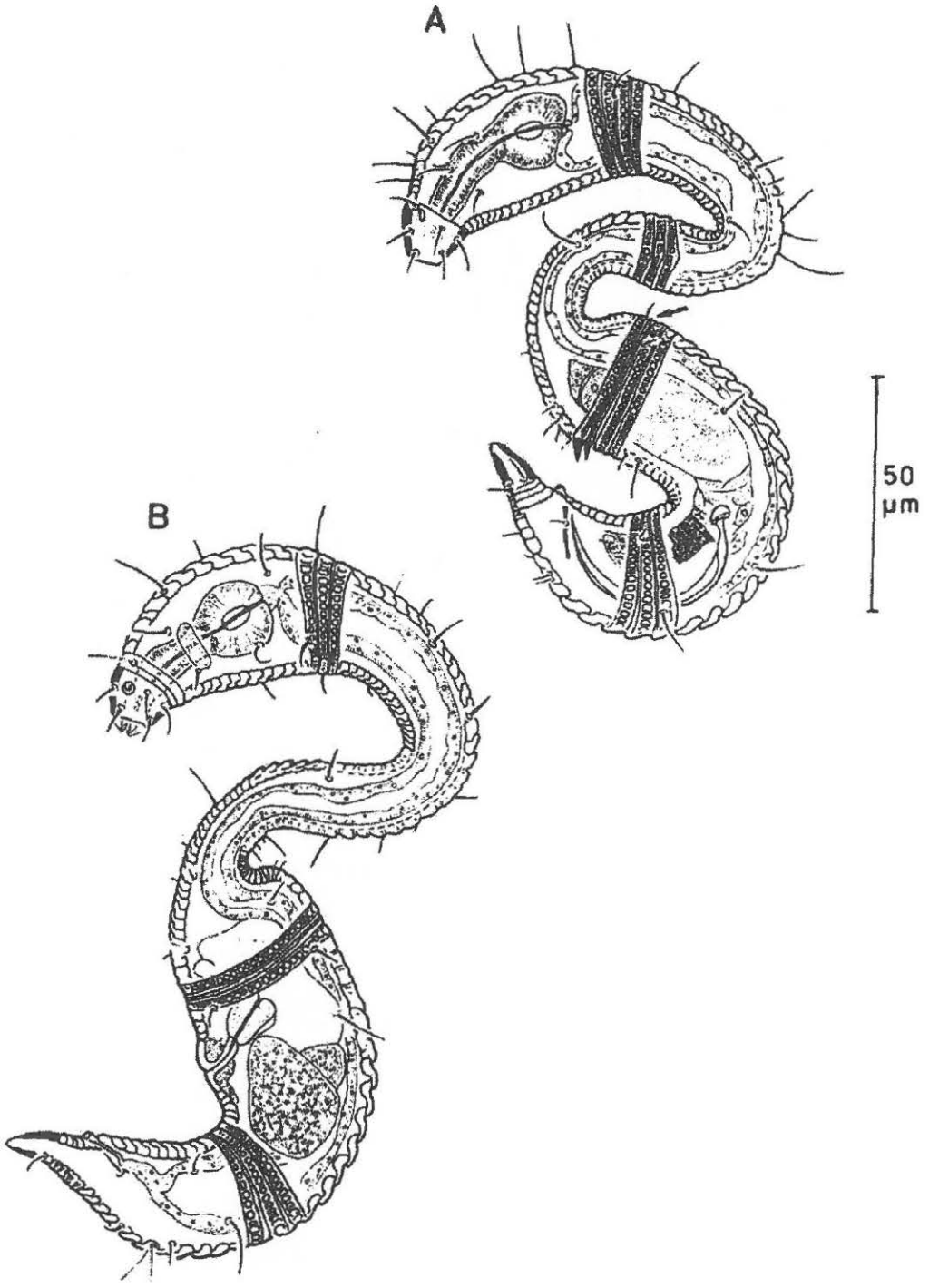

Fig. 7. *Perepsilonema ritae* sp.n. A. Habitus holotype male; B. Habitus allotype female.

Rostrum broad, strongly cuticularized; four cephalic and eight subcephalic setae. Fovea amphidialis small and straight, apertura amphidialis as a small pore (Fig. 8C).

Stoma not distinct. Short, broad pharynx with muscular end-bulb. Nerve ring located just in front of end-bulb. Small cardia (1 µm).

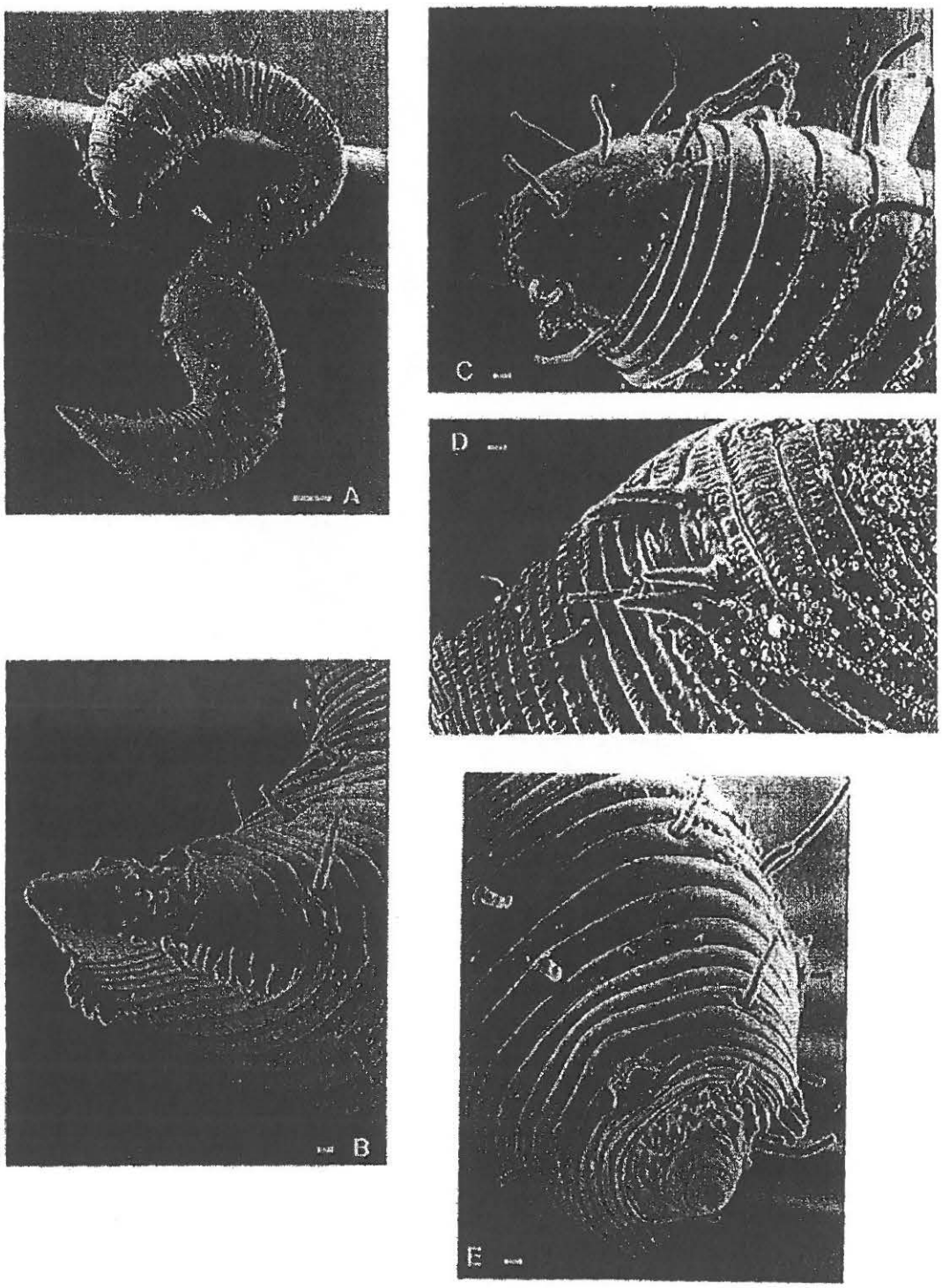

Fig. 8. *Perepsilonema ritae* sp.n. Paratype male. A. Habitus (arrowhead indicates ventral field of tiny spines); B. Tail, dorsal view; C. Head end, lateral view; D. Copulatory thorns; E. Anal tube and spinneret. (Scale bars indicate: 10 µm in A; 1 µm in B-E.)

TABLE IV

Measurements of Perepsilonema ritae *sp.n.*

	Holotype ♂	Paratype ♂♂ n = 7	Paratype ♀♀ n = 8
L	273	259-307 (280)	283-309 (294)
N	111	104-109 (106)	101-111 (107)
cs	6	4-6 (4)	4-5 (5)
Amph %	7	5-8 (5)	19-23 (22)
SSph	12	10-13 (12)	11-13 (12)
ant	2	1-3 (2)	1-2 (2)
ph	44	41-45 (43)	39-45 (43)
mbd	29	28-31 (29)	34-37 (35)
(mbd)	10	9-11 (10)	10-11 (10)
mbd ph	28	27-28 (28)	28-30 (29)
mbd/(mbd)	2.9	2.5-3.2 (2.9)	3.3-3.7 (3.5)
lct	4	4-5 (4)	
spic	58	52-56 (54)	
gub	11	12-14 (13)	
V			63-68 (66)
ABD	11	11-12 (11)	11-12 (12)
tail	20	16-20 (18)	17-18 (18)
tmr	10	9-10 (9)	9-10 (10)
dcs	2	1-2 (2)	1-2 (2)
a	9.4	9.1-10.3 (9.6)	8.0-9.1 (8.4)
b	6.2	6.2-7.1 (6.5)	6.7-7.4 (7)
c	15.2	13.6-17.2 (15.7)	15.7-18.2 (16.6)

(measurements in µm)

Two pairs of large copulatory thorns (4-5 µm; Fig. 8D). Broad testis extending to ventral body curvature. Spicules long, slender and strongly arched; club-shaped capitulum. Short but firm gubernaculum. Cloaca with anal tube.

Tail with five annules: spinneret probably with three groups of two pores (Fig. 8E).

Females: Body shape, shape and ornamentation of body annules, presence of a single slender annule posterior to ventral body curvature, inversion in direction of the body annules and pattern of somatic setae similar to those of males.

Only one pair of somatic setae on non-annulated tail end. Six pairs of small, subdorsal spines on tail annules.

Short, broad rostrum with four cephalic and six subcephalic setae (sexual dimorphism). Small, spiral (1.5 turns) fovea amphidialis. Cardia not clear. Vulva is a transverse slit-like opening. Short anal tube (1-2 µm).

Vagina consists of two parts: cuticularized vagina vera and heavy muscular vagina uterina; vagina slightly rostrally bent. Reproductive system didelphic, amphidelphic with reflexed ovaries.

Diagnosis: *Perepsilonema ritae* sp.n. is characterised by: amphidial shape (slit-like

in the males, spiral in the females), number of subcephalic setae (8 in the males, 6 in the females), by the ornamentation of the body annules, by the habitus with a sudden broadening of the body just behind the ventral body curvature and a slender annule posterior to the ventral body curvature (lacking in some specimens). Typical for males are the large copulatory thorns and slender spicules.

Differential diagnosis: *Perepsilonema ritae* sp.n. resembles *Perepsilonema trauci* Lorenzen, 1973 and *Perepsilonema kellyae* Gourbault & Decraemer, 1988; but differs from these by the amphidial shape, length and number of copulatory thorns (*P. trauci*: four pairs of copulatory thorns and three pairs of precloacal thorns; *P. kellyae*: one pair of large and four pairs of very small copulatory thorns followed by three precloacal thorns) and spicule length (*P. trauci*: 34-38 µm; *P. kellyae*: 42-48 µm).

Type specimens: 8 males, 8 females. Holotype male: slide n° 3588, allotype female: slide n° 3589 in the collection of ZIRUG. Other paratypes: slide n° BN 199 (7♂, 4♀) in the collection of MNHN (sample 13).

Type locality: Kenya, Gazi: 01-08-1989. Mid-edge of sandbank in the mouth of the Gazi Creek river.

Other localities: Kenya, Gazi: 02-08-1989. Upstream tip of sandbank in the mouth of the Gazi Creek river (sample 13). Kenya, Gazi: 10-08-1989. Mixed mangrove, between *Ceriops* trees (sample 28).

Etymology: Named in honour of Rita van Driessche, who did all the SEM preparations and took the SEM photographs.

Perepsilonema kellyae Gourbault & Decraemer, 1988

(Fig. 9, Table V)

Measurements: see Table V.

Additional information:

Males: The Kenyan specimens of *Perepsilonema kellyae* very much resemble the type specimens found in Guadeloupe (Gourbault & Decraemer, 1988). Apertura amphidialis is a longitudinal slit (Fig. 9A,B). One pair of larger copulatory thorns (3 µm) are followed by four to five pairs of smaller ones, as in type specimens. Two specimens were found in which the first pair of smaller copulatory thorns are enlarged so that there are two pairs of larger copulatory thorns; in this case, the first pair of copulatory thorns has a narrower base. Three pairs of short precloacal thorns; anteriormost pair may be larger (1 µm). Straight testis extending to the ventral body curvature. One specimen had a reflexed top of testis. Spicules as described in the type material, sometimes somewhat more arched. One specimen with protruded spicules was found; spicules turn sideways to the (left) lateral side.

Cloacal tube (length = 1-2 µm) is built out of two half cuticular circles (Fig.

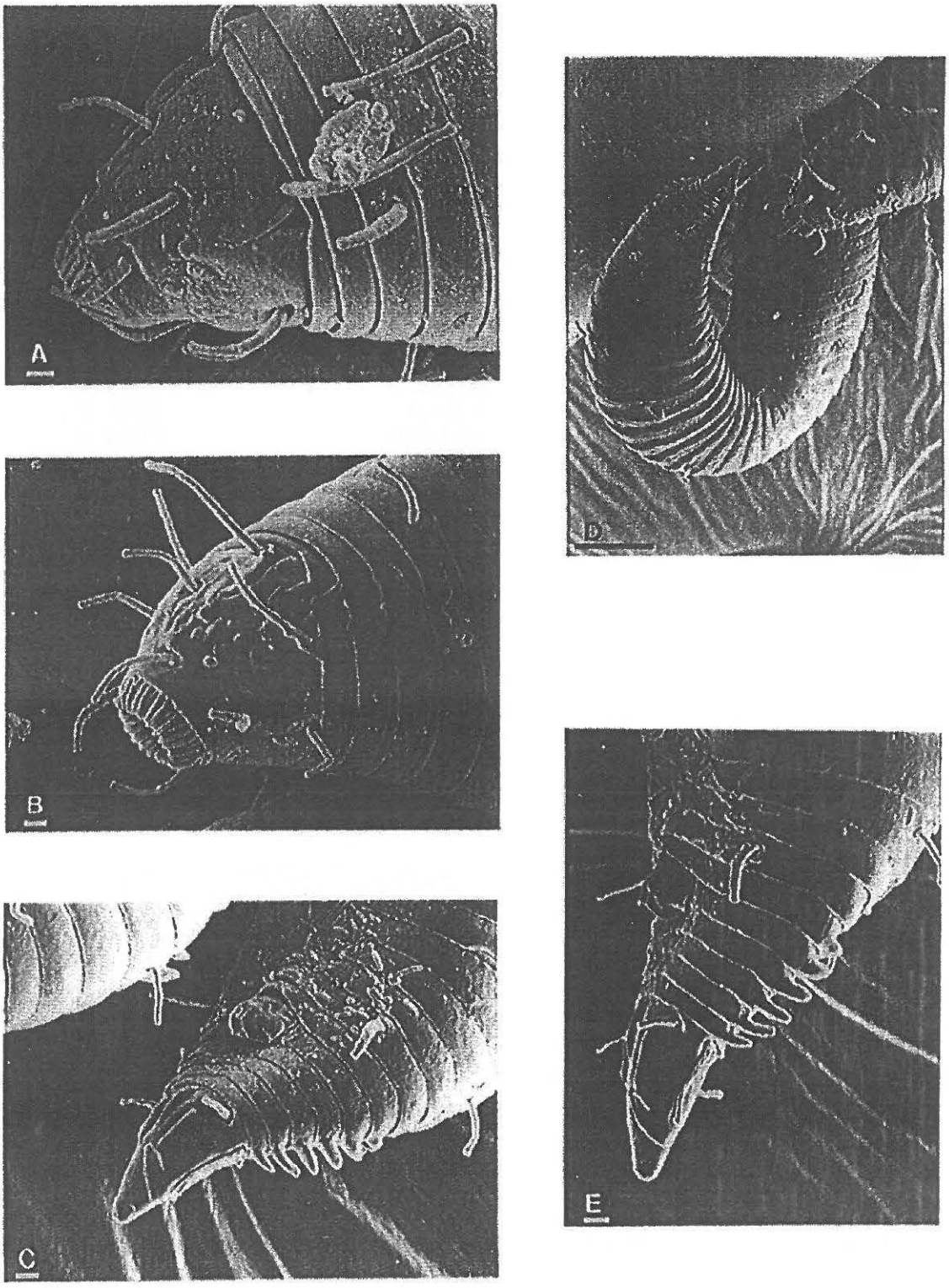

Fig. 9. *Perepsilonema kellyae* Gourbault & Decraemer, 1988. Male. A. Head end lateral view; B. Head end, subventral view; C. Anal tube; D. Posterior part, dorsal view of the tail; E. Lateral view of the tail. (Scale bars indicate: 10 µm in A, 1 µm B-E.)

TABLE V

Measurements of Perepsilonema kellyae *Gourbault & Decraemer, 1988*

	Males n = 7	Females n = 7
L	250-316 (264)	228-274 (249)
N	97-105 (101)	99-108 (103)
cs	5-6 (6)	4-6 (5)
Amph %	17-24 (20)	18-28 (22)
SSph	8-14 (11)	8-17 (11)
ant	1-2 (1)	1-3 (2)
ph	43-48 (45)	39-44 (43)
mbd	25-28 (26)	27-31 (29)
(mbd)	8-10 (9)	8-10 (9)
mbd ph	24-25 (24)	23-25 (25)
mbd/(mbd)	2.6-3.3 (2.9)	2.7-3.9 (3.2)
lct	2-3 (3)	
spic	40-55 (46)	
gub	8-12 (9)	
V		66-72 (70)
ABD	9-12 (10)	8-10 (10)
tail	14-18 (16)	14-15 (14)
tmr	7-9 (8)	7-9 (8)
dcs	1-2 (1)	1-1 (1)
a	9.8-12.2 (10.2)	7.8-10.1 (8.6)
b	5.3-7.0 (5.8)	5.3-6.2 (5.8)
c	14.0-18.6 (16.1)	16.3-19.6 (17.3)

(measurements in µm)

9C). Non-annulated tail end with three pairs of somatic setae (Fig. 9C,D,E).

Females: Fovea amphidialis spiral (1.5 turns), smaller than in type specimens. Vulva slit-shaped; vagina always bent anteriorly. Non-annulated tail end with two pairs of somatic setae.

Remark: In general it is accepted that during copulation the male spicules exit the cloaca perpendicular to the ventral body wall and that the female vagina can bend somewhat in case of arched spicules. This will be the case in many species. Another possibility for copulation is shown by a male of *Perepsilenoma kellyae* with protruding spicules which turn away along the lateral side of the body. The advantage of this rotation is clear considering the fact that if the long and arched spicules in *P. kellyae* protruded perpendicularly to the ventral body wall (as is the case in most of the nematodes; exception: *Daptonema williamsi*, cf. Vincx & Coomans, 1984) for their whole length, they would pierce the ventral side of the male (if they did not protrude for their whole length, one would expect shorter spicules). Females often have a heavily cuticularized vagina vera which is bent towards the rostral or caudal side but probably cannot bend enough in those cases where the spicules protrude perpendicular to the ventral

body wall of the male. In fact, if the spicules protrude and turn over to the lateral side, they match perfectly with the rostrally or caudally bent vagina vera.

A clear example of predation of epsilonematids was seen in a *Latronema* specimen which had an Epsilonematid species (probably a *Perepsilonema* species) in the intestine. The body cuticle of the epsilonematid was little damaged but the internal structures of the animal were already digested.

Specimens: 29 males, 37 females, 13 juveniles, slide n° 10274-10276 in the collection of MBRUG.

Locality: Kenya, Gazi: 07-08-1989. Under a *Bruguiera* tree near the flood line, in front of the field lab hut of the KMFRI, Mombasa.

DISCUSSION ON THE EXTERNAL MORPHOLOGY OF CUTICULAR APPENDAGES

Within the Epsilonematidae, numerous cuticular appendages have been described (e.g. Lorenzen, 1973) but so far confusion exists about the use of some terms. Therefore, the following description characterizes the different kinds of spines and setae and other typical cuticular appendages. These are illustrated for the first time with SEM micrographs. The following cuticular appendages occur in the Episonematidae: ridges, spines, thorns, setae, flaps. Several types of setae can be distinguished: "common" setae which are described as somatic setae and occur in the majority of nematodes and "derived" setae of which the cephalic-, subcephalic-, supporting and ambulatory setae are present within the Epsilonematidae.

Ridges are superficial, uprising cuticular ornamentations of the body annules, rostro-caudally on the annule (Fig. 10C).

Spines are noncellular, cuticular protrusions of the body annules (Maggenti, 1981) which, within the Epsilonematidae, are mostly protrusions of the posterior edge of the annules (Fig. 2E,F). They are not attached to any gland, nerve or muscle. Roughly three types of spines occur within the Epsilonematidae:

— (normal) spines: short, slender spines which are no longer than one width of the annules (Fig. 3F).

— thorn-like spines: same size as previous, but strongly built and with a broad base (Fig. 2F).

— hair-like spines: slim spines with the appearance of slender somatic setae (Fig. 2E), longer than one width of an annule.

In general it can be said that juveniles have no spines or setae which do not also occur in the adults. The juvenile of *M. iuvenisspinosum* sp.n. is an exception to this rule: the juvenile has a series of twelve pairs of long latero-dorsal spines on the posterior body (Fig. 4C), of which only the last three pairs are present in the female. It is hypothesised that as the juveniles are smaller than 200 µm they would have difficulty in coping with water current conditions in the environ-

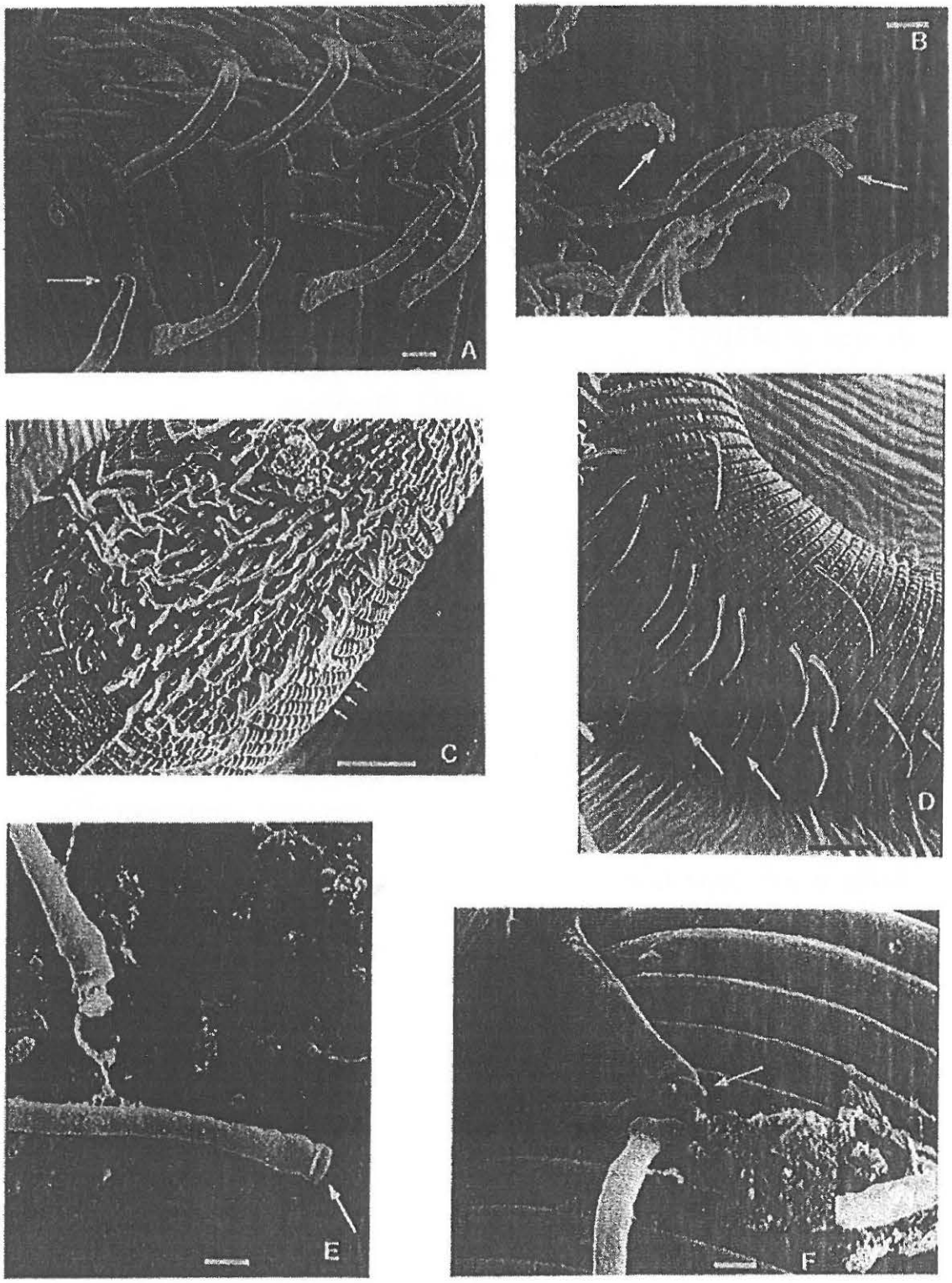

Fig. 10. Several types of setae ambulatoriae and adhesion tubes. A. *Epsilonema espeeli* sp.n.; B. *Metepsilonema bermudae* Lorenzen, 1973; C. *Polkepsilonema mombasae* Verschelde & Vincx, 1993; D. *Pternepsilonema servaesae* Verschelde & Vincx, 1993; E. *Dracograllus eira* (Inglis, 1968); F. *Dracograllus eira* (Inglis, 1968). (Scale bars indicate: 10 µm in C, D; 1 µm in A, B, E, F.)

ment in which they live and long spines prevent them from being washed out of their interstitial spaces; the larger adults (♂ = 224 µm, ♀ = 211 µm) would not encounter this problem and thus have no use for such spines.

Thorns are derived from spines. They have a broad, roundish base and are somewhat cone- or pyramid shaped. Special thorns are: (1) *copulatory thorns* (mostly a group of thorns located ventrally in the posterior region of the ambulatory setae (e.g. *E. espeeli* sp.n., Fig. 2B); (2) *precloacal thorns*: located in the area posterior to the copulatory thorns and anterior to the cloaca (e.g. *E. espeeli* sp.n., Fig. 2B); (3) *paracloacal thorns*: located beside, just in front of or just behind the cloaca (e.g. *Leptepsilonema richardi* Verschelde & Vincx, 1992). These three types of thorn occur only in males. Within the genus *Dracognomus* Allen & Noffsinger, 1978 subventral thorns occur on the non-annulated tail end. Dorsal thorns are described from both sexes in *Akanthepsilonema* Gourbault & Decraemer, 1991; *Polkepsilonema* Verschelde & Vincx, 1993 and in *Pternepsilonema* Verschelde & Vincx, 1993.

Setae are "sensory organs (sensillae) produced by specialized cells of the hypodermis" (Maggenti, 1981); they are connected with a nerve, gland cell or muscle. They emerge from the body cuticle through a pore.

(1) *Cephalic and subcephalic setae*: By means of light microscopy we can see that these setae are connected with nerves or probably with gland cells. On SEM pictures (Fig. 2C,D) of *Epsilonema espeeli* sp.n. we can see that the cephalic and subcephalic setae end funnel-shaped. If these setae are connected with gland cells, it could mean that in some species within the Epsilonematidae, the subcephalic setae have a similar use in locomotion as the cephalic adhesion tubes (CAT) of Draconematidae (Allen & Noffsinger, 1978).

(2) *Setae ambulatoriae*: Unlike the posterior adhesion tubes of Draconematidae (De Coninck, 1965; Maggenti, 1981) which are associated "with glands, muscles and nerves" and end in funnel-shaped suckers (Fig. 10E,F), the ambulatory setae of Epsilonematidae are not connected with any gland cells, their distal tip has no pore and is almost always bent forming a single claw (Fig. 10A) or a bifid claw (Fig. 10B,D). Compared with the other setae, they are heavily built and rostro-caudally flattened (Fig. 10A), which indicates that the ambulatory setae only, articulate in the rostro-caudal direction. The thick cuticle of the ambulatory setae could give an extra resilience and so an extra propulsion during locomotion, also it probably gives extra strength against the interstitial water currents.

The genus *Perepsilonema* is characterized by the absence of ambulatory setae and the curled up posterior body end. The dorsal side of the tail is always flattened and carries two latero-dorsal rows of thorns (Fig. 8B, 9E); the theory is that these thorns "replace" the ambulatory setae of the other genera of the Epsilonematidae and provide a grip on the substrate when the tail pushes on it during locomotion (Lorenzen, 1973).

(3) *Supporting setae*: Derived somatic setae, located ventrolaterally in 2 longitudi-

nal rows, most posterior to the external rows of ambulatory setae. They "support" the body (in balancing it) during locomotion on their ventral body side (Fig. 4A, 5A).

Vulval flap: Females of *Epsilonema espeeli* sp.n. have a cuticular flap which covers the vulva (Fig. 3B,C,D). This flap can differ in shape from specimen to specimen, from completely round to totally divided. The reason for these different shapes and also the function of the flap are obscure, but it may prevent dirt coming into the vulva (which is somewhat open).

The authors acknowledge logistic support for the research programme from the Kenyan Marine and Fisheries Research Institute in Mombasa (Kenya), the National Science Foundation of Belgium (FKFO 2.0043.88) and the EEC (TS2-240-C (GDF)). We are also grateful to Dr. A. Vanreusel, Dr. P. Aerts, Mrs. R. van Driessche, Mrs. W. Gijselinck and Ms Anneke Herman for helping in sampling and treatment of the material. We thank Dr. N. Gourbault for reading the *Résumé*.

RÉSUMÉ

Epsilonematidae (Nematoda: Desmodoroidea) des côtes d' Afrique de l'Est, discussion sur la morphologie des appendices cuticulaires

La morphologie des appendices cuticulaires, tels qu' épines, soies et opercule vulvaire d'Epsilonematidae, est étudie sur la base de clichés S.E.M. de six espèces, dont trois nouvelles. Leurs soies ambulatoires sont comparées aux tubes adhésifs d' une espèce de *Dracograllus* Allen & Noffsinger, 1978.

Epsilonema espeeli sp.n. est caractérisé par la présence de six soies subcéphaliques, de nombreuses épines subdorsales postérieures et d' un tube anal chez les mâles; les femelles ont un opercule vulvaire. *Metepsilonema iuvenisspinosum* sp.n. présente des anneaux remarquables de forme et ornementation cuticulaire, quatre paires de soies-support dont une deux fois plus longue que les autres; les femelles et juvéniles ont des épines subdorsales postérieures qui sont absentes chez les mâles. *Perepsilonema ritae* sp.n. est caractérisé par la forme des amphides, le nombre des soies subcéphaliques (huit chez les mâles, six chez les femelles), et l' élargissement brusque du corps juste en arrière de la courbure ventrale; les mâles ont de longues épines copulatoires.

Des données complémentaires sont fournies pour *Epsilonema parvospina* Decraemer, 1982, *Metepsilonema bermudae* Lorenzen, 1973 et *Perepsilonema kellyae* Gourbault & Decraemer, 1988.

REFERENCES

Allen, M. W. & Noffsinger, E. M. (1978). A revision of the marine nematodes of the superfamily Draconematoidea Filipjev, 1918 (Nematoda: Draconematina) *University of California Publications in Zoology* **109**, 1-133.

Clasing, E. (1984). Interstitielle Fauna von Galapagos. XXXII. Epsilonematidae (Nematodes). *Microfauna Marina* **1**, 149-189.

De Coninck, L. A. P. (1965). *Traité de Zoologie. Classe des Nématodes.* Grassé (ed), Masson et cte, **Tome IV, 2e fasc.**, 731 pp.

Decraemer, W. (1982). Draconematidae and Epsilonematidae (Nematoda) from Laing Island Papua New Guinea, with one new genus and three new species. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* **54**, 1-22.

Decraemer, W. & Gourbault, N. (1987). Marine nematodes from Guadeloupe and other Caribbean Islands. IV. The genus *Epsilonema* (Epsilonematidae). *Bulletin de l'Institut royal des Sciences naturelles de Belgique* **57**, 57-77.

DECRAEMER, W. & GOURBAULT, N. (1989). Marine nematods from Guadeloupe. IX. The Genus *Metepsilonema* (Epsilonematidae). *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* **59**, 25-38.

DECRAEMER, W. & GOURBAULT, N. (1990). Nématodes marins de Guadeloupe. X. Trois espèces nouvelles de *Metepsilonema* (Epsilonematidae) du group *callosum*. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4° sér., **12**, section A, n° 2, 385-400.

GOURBAULT, N. & DECRAEMER, W. (1987). Nématodes marins de Guadeloupe. VI. Les genres *Bathyepsilonema* et *Leptepsilonema* (Epsilonematidae). *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4° sér. **9**, 605-631.

GOURBAULT, N. & DECRAEMER, W. (1988). Nématodes marins de Guadeloupe VIII. Le genre *Perepsilonema* (Epsilonematidae). *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4° sér. **10**, section A n° 3, 535-551.

GOURBAULT, N. & DECRAEMER, W. (1991). A new genus and species of Epsilonematidae (Nematoda) from New Caledonia. *Zoologica Scripta* **20**, 315-319.

LORENZEN, S. (1973). Die Familie Epsilonematidae (Nematodes). *Mikrofauna des Meeresbodens*, **25**, 1-86.

LORENZEN, S. (1974). *Glochinema* nov. gen. (Nematodes, Epsilonematidae) aus Sudchile. *Mikrofauna des Meeresbodens*, **47**, 393-412.

MAGGENTI, A. R. (1981). *General Nematology*. Springer-Verlag: New York.

SEINHORST, J. W. (1959). A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. *Nematologica* **4**, 67-69.

VERSCHELDE, D. & VINCX, M. (1992). Freeliving marine nematodes from East African coasts. *Bathyepsilonema anulosum* sp.n. and *Leptepsilonema richardi* sp.n. *Hydrobiologia* **239**, 179-186.

VERSCHELDE, D. & VINCX, M. (1993). Freeliving marine nematodes (Desmodoroidea, Epsilonematidae) from East African coasts. *Polkepsilonema mombasae* gen. et sp.n. and *Pternepsilonema servaesae* gen. et sp.n. *Hydrobiologia* **257**, 129-142.

VINCX, M. & COOMANS, A. (1984). *Daptonema williamsi* sp.n. (Nematoda, Xyalidae) from the Solomon Islands. *Zoologica Scripta* **12**, 4, 237-244.

Accepted for publication: 30 October 1992