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The genus *Laxus* Cobb, 1894 (Stilbonematinae: Nematoda): Description of two new species with ectosymbiotic chemoautotrophic bacteria

Jörg A. Ott, Monika Bauer-Nebelsick, and Veronica Novotny

Institute of Zoology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

Abstract.—Two new species of free-living marine nematodes belonging to the genus *Laxus* Cobb, 1894, *L. oneistus* and *L. cosmopolitus,* are described from shallow subtidal sands in the Belize Barrier Reef and the Adriatic Sea. Both species are covered by ectosymbiotic chemoautotrophic sulfur-oxidizing bacteria. The genus *Laxus* is redefined and *Catanema cobbi* Inglis, 1967 transferred to this genus. For *L. oneistus,* biometrical data for juvenile stages are given.

The Stilbonematinae are a subfamily within the family Desmodoridae (order Desmodorida), characterized by an obligate ectosymbiosis with sulfur-oxidizing chemolithoautotrophic bacteria covering their cuticle in a manner that is characteristic for the genus, and even the species (Ott et al. 1991, Polz et al. 1992). The complex glandular sense organ described by Nebelsick et al. (1992) has so far been found only in the Stilbonematinae and is absent in species of other genera within the Desmodoridae, such as *Acanthopharynx* Marion, 1870, *Desmodora* DeMan, 1889 and *Spirinia* Gerlach, 1963 (M. Bauer-Nebelsick, pers. comm.). This is the only morphological autapomorphic character so far known to indicate the monophyly of this taxon. Otherwise, only a few common features unite the group, most of them being negative characters, such as the lack of a buccal armature.

The high variability regarding a number of taxonomically important characters, such as the amphid or the structure of cuticular reinforcement of the anterior end ("cephalic capsule," see Urbancik 1994) complicates assessment of the relationship of the Stilbonematinae with other subfamilies of the desmodorids and between the various known genera. It is, therefore, difficult to decide whether some characters have developed or have been modified (reduced) independently more than once. There is, for example, a tendency towards the development of an enlarged muscular portion at the anterior end of the pharynx, which in the genera *Robbea* Gerlach, 1956 and *Catanema* Cobb, 1920 is highly developed and found in all species, whereas in other genera (*Leptonemella* Cobb, 1920; *Eubostrichus* Greeff, 1869) it is only apparent in a few species. The reduction of the fovea of the amphid from the usual spiral shape to just a porus from which the corpus gelatum usually protrudes seems to have occurred independently at least three times (in the genera *Leptonemella, Stilbonema* Cobb, 1920 and *Catanema*).

In addition, the type species of several genera (e.g., *Laxus, Catanema, Leptonemella, Eubostrichus*) are either inadequately described or have features that are the exception rather than the rule in the subsequently described members of the genus. Liberal synonymization has contributed the rest of the problems.

During studies of the ecology and ecophysiology of the symbiosis (Ott & Novak 1989, Schiemer et al. 1990, Ott et al. 1991) using material from the Caribbean and the

Mediterranean Sea, a number of species new to science have been used and have been designated preliminary names. These animals, designated "sp. 1" or "sp. 2," need to be described and formally named. In addition, collections have been made by the authors in various other locations. Two species from these collections belong—in our opinion—to the genus *Laxus,* which was described by Cobb (1894) from specimens coming from sand in the Bay of Naples (*L. contortus*) and Port Jackson, New South Wales (*L. longus*). Although subsequent authors (Gerlach 1963a, Wieser & Hopper 1967, Hopper & Cefalu 1973) have classified this genus as doubtful, we have reasons to believe that we can assign our animals to Cobb's genus and can attempt a redefinition of this taxon.

Material and Methods

Sediment was collected in buckets by hand and the animals extracted by shaking aliquots of sediment in seawater and decanting the supernatant through a 63-μm screen. In some cases a $MgCl_2$ solution isotonic to seawater was used as an anaesthetic. Quantitative samples were taken with cores having an internal diameter of 3.5 cm down to a depth of 10 cm.

For light microscopy the animals were fixed in 4% formaldehyde, transferred in glycerol:water 1:9 and slowly evaporated before mounting in pure glycerol on microscopic slides. Drawings and measurements were made on a Reichert Diavar, Reichert Polyvar or Leitz Diaplan, all equipped with a camera lucida. Nomarski interference contrast photos were made on the Reichert Polyvar.

For scanning electron microscopy (SEM) specimens were fixed in 2.5% glutaraldehyde in 0.1M sodium cacodylate buffer (pH 7.2) isotonic to sea water and postfixed in 2% OsO_4 over night. After dehydration in a graded ethanol series they were critical point dried, coated with gold and examined with a JEOL JSM-35 CF.

Semithin sections were cut on a Reichert Ultracut from specimens fixed for transmission electron microscopy (TEM) according to Eisenman & Alfert (1982) and embedded in Spurr epoxy resin, stained with toluidin blue and photographed on a Reichert Polyvar.

Type material has been deposited in the Natural History Museum Vienna, Evertebrata Varia Collection (NHMW-EV).

Laxus oneistus, new species
Figs. 1–4, Table 1

Catanema sp. in Ott & Novak 1989, Schiemer et al. 1990, Polz et al. 1992, Ott et al. 1991, Nebelsick et al. 1992.

Holotype: male, NHMW-EV Nr.3406
L = 8.82 mm a = 193 b = 77 c = 130

Allotype: female, NHMW-EV Nr.3407
L = 8.40 mm a = 168 b = 75 c = 130

Paratypes: male, NHMW-EV Nr.3408
L = 6.89 mm a = 156 b = 58 c = 99

male, NHMW-EV Nr.3409
L = 9.94 mm a = 202 b = 76 c = 99

male, NHMW-EV Nr.3410
L = 10.25 mm a = 195 b = 78 c = 144

male, NHMW-EV Nr.3411
L = 9.50 mm a = 181 b = 81 c = 140

female, NHMW-EV Nr.3412
L = 9.79 mm a = 222 b = 73 c = 122

female, NHMW-EV Nr.3413
L = 8.91 mm a = 175 b = 79 c = 117

female, NHMW-EV Nr.3414
L = 9.83 mm a = 200 b = 77 c = 145

Etymology.—from the greek *oneistos,* meaning "most useful," because of its value as an experimental animal during ecological and ecophysiological studies.

Type locality.—Carrie Bow Cay, Belize, Caribbean Sea; coarse, poorly-sorted, coralline sand at the northern tip of the island; 0.2 to 0.5 m depth.

Extremely slender worms, with a cylin-

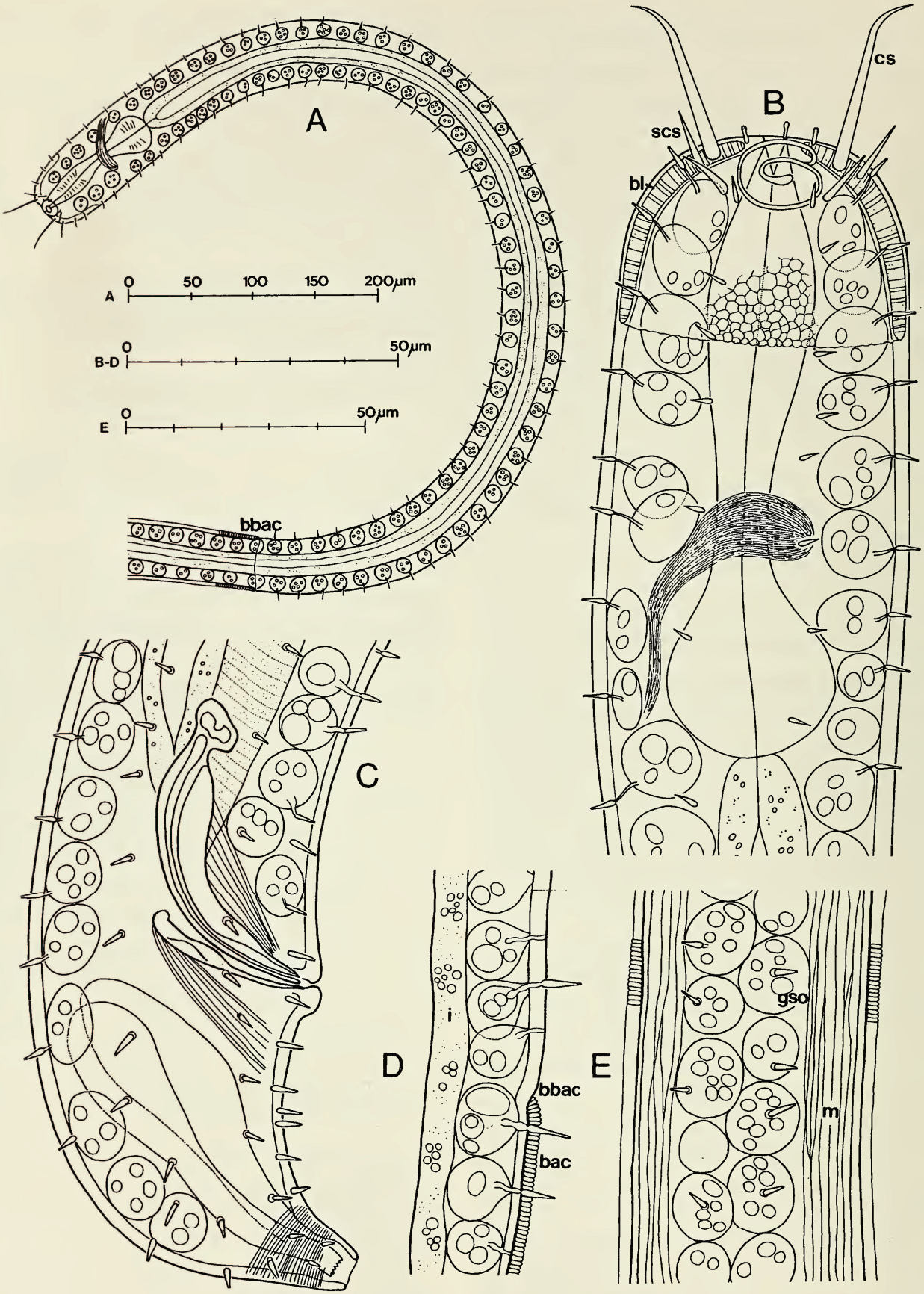

Fig. 1. *Laxus oneistus*, male, holotype. A. Anterior body region, lateral view. B. Anterior end and pharyngeal region. C. Posterior end with spicular apparatus and tail containing caudal glands. D. Beginning of bacterial coat showing reduction of body diameter. E. Midbody region showing longitudinal muscles and two sublateral rows of glandular sensory organs. A–E, lateral views. Abbreviations:am, amphid; bac, ectosymbiotic bacteria;

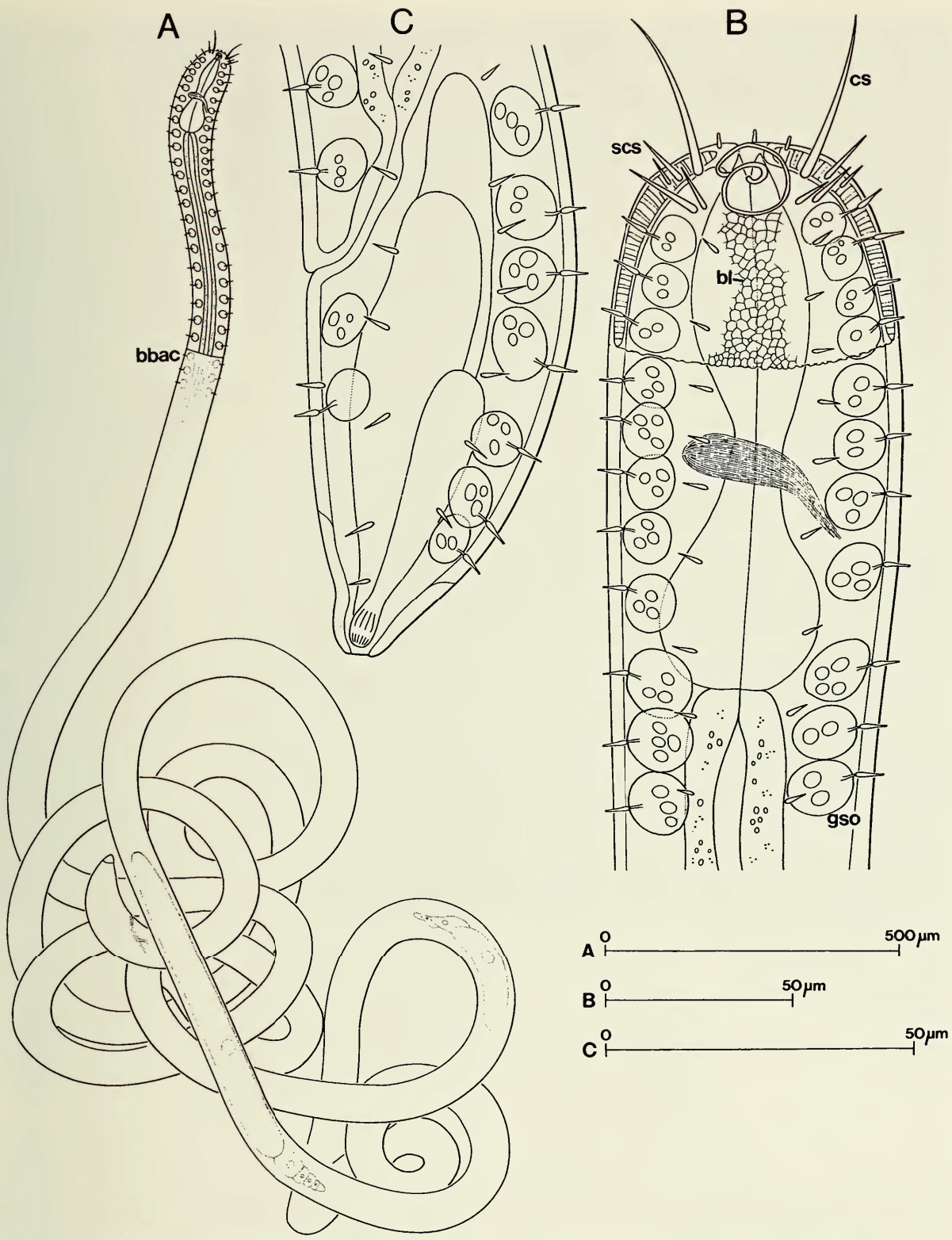

Fig. 2. *Laxus oneistus,* female, allotype. A. Total view. B. Anterior end and pharyngeal region. C. Tail. A–C, lateral views. (For abbrevations see Fig. 1.)

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bbac, begin of bacterial coat; bl, block layer; ca, cardia; cg, corpus gelatum; cgso, concentration of gso; cs, cephalic sensillae; cut, cuticula; de, ductus ejaculatorius: fa, fovea amphidialis; fp, fingerprint region; gr, granules of gso; gso, glandular sense organ; gu, gubernaculum; i, intestine; m, longitudinal muscles; nr, nerve ring; ov, egg; ovr, ovary; re, rectum; rs, receptaculum seminis; scs, subcephalic setae; sp, spiculum; ss, somatic setae; te, testis; ut, uterus; vu, vulva.

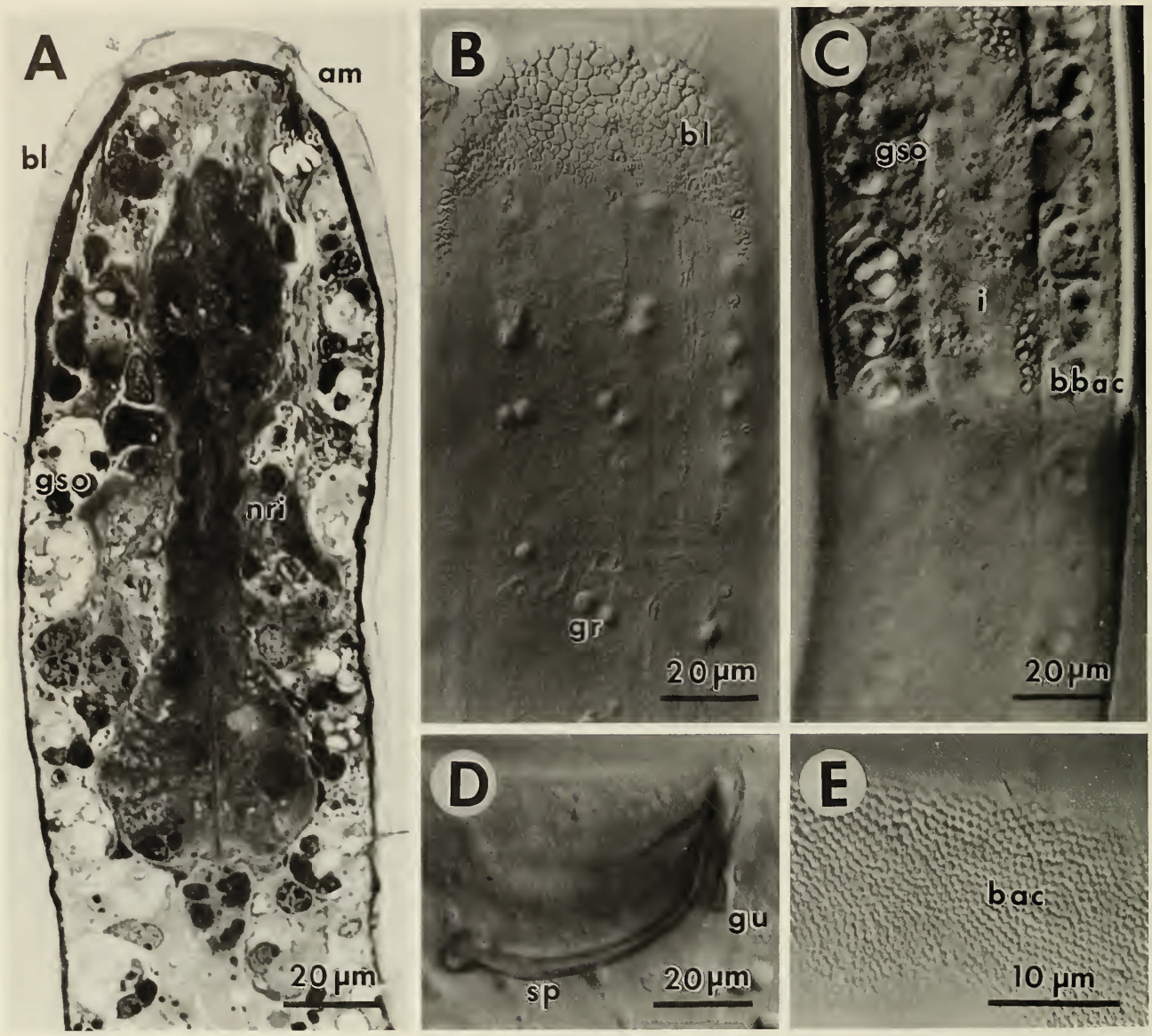

Fig. 3. *Laxus oneistus.* A. Anterior end and pharyngeal region showing the block layer of the cephalic capsule, the tripartite pharynx and several glandular sensory organs. Light microphotograph of a semithin section stained with toluidin blue. B–E. Nomarski interference contrast microphotographs of whole-mounts in glycerol. B. Anterior end showing cephalic capsule with block layers and granules in glandular sense organs. C. Beginning of bacterial coat. D. Spicular apparatus. E. Surface view of bacterial coat. (For abbrevations see Fig. 1.)

drical body. Body covered with radially arranged, rod-shaped bacteria (2.1 × 0.6 µm) except for the anterior region (Figs. 1A, 2A, 3C, E, 4F, G) which appears clear. Bacteria-covered remainder of the body white in incident and dark in transmitted light. Bacteria-free portion is 1010–1090 µm (8–9 times the pharynx length) in males, but only 340–500 µm (3–3.6 times the pharynx length) in females (Fig. 2A). Anterior region containing pharynx slightly swollen (Figs. 1A, B, 2A, B), maximum body diameter at

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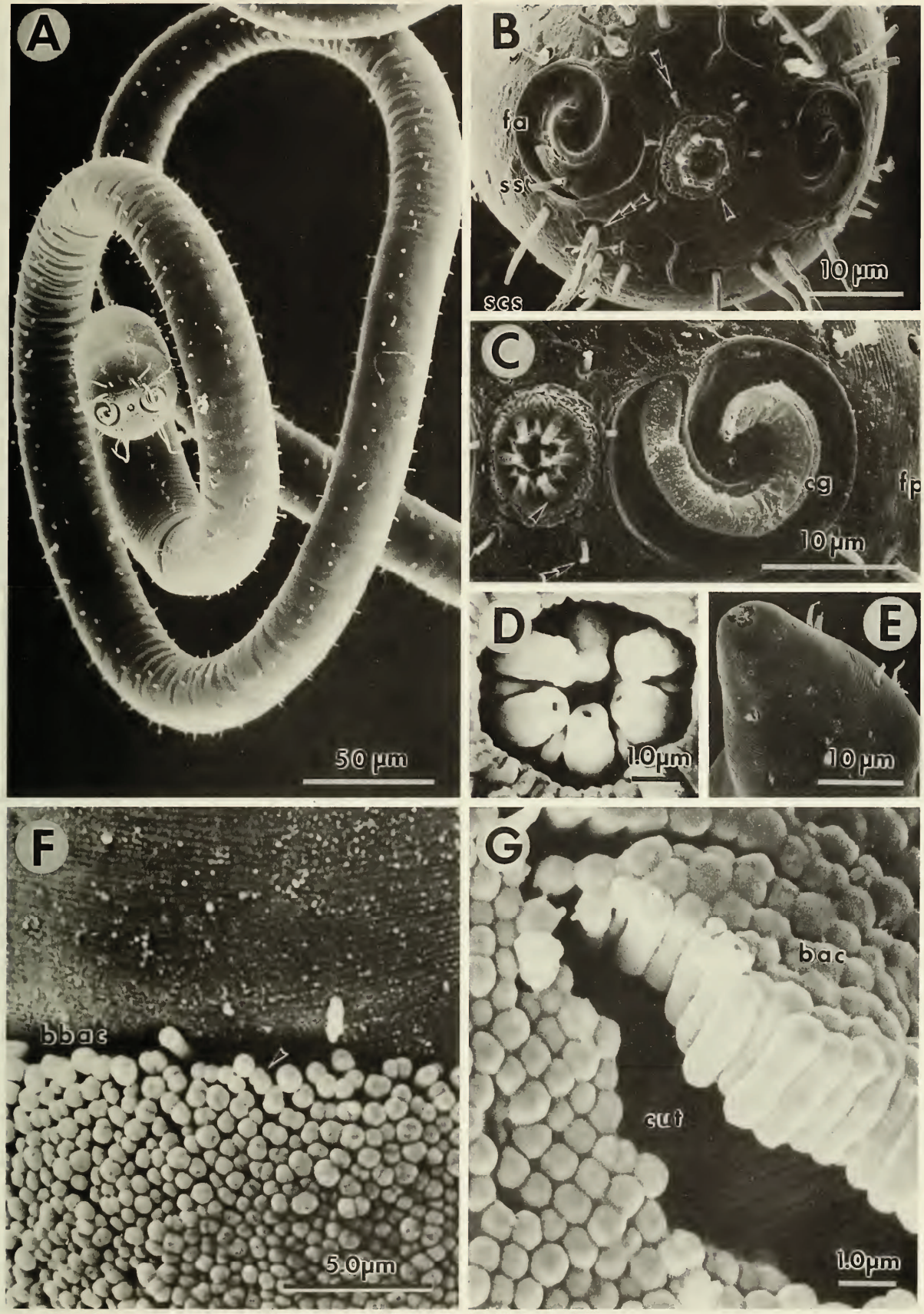
Fig. 4. *Laxus oneistus.* SEM photographs. A. Anterior body region with bacterial coat removed showing rows of somatic setae. B. *En-face* view of anterior end showing the three circles of cephalic sensillae (6 + 6 + 4), 8 subcephalic setae, the first circle of 8 somatic setae and the amphids. The mouth opening protrudes slightly



exposing the first circle of cephalic sensillae. C. *En-face* view of amphid with corpus gelatum surrounded by cuticular "fingerprint region." D. Close-up of first circle of cephalic sensillae showing terminal pores. E. Tip of tail with openings of caudal glands. F. Transition between bacteria-free and bacteria-coated region. G. Rod-shaped bacteria on cuticle. (For abbrevations see Fig. 1.)

Table 1.—Biometrical data for selected characters of the type specimens in *Laxus oneistus* ($n = 10$) and *L. cosmopolitus* ($n = 8$). All measurements are in μm.

Character	*L. oneistus*	*L. cosmopolitus*
Diameter at end of cc.	52.5–66.1	42.4–49.2
Mid-body diameter	44.1–52.5	49.2–55.9
Diameter at anus	50.1–61.0	42.4–56.1
Amphid width	13.6–20.3	11.9–15.3
Amphid (cbd)	27.1–42.4	35.6–37.3
Nerve ring (dfae)	66.1–83.1	84.8–110.2
Nerve ring (cbd)	52.5–69.5	47.5–59.3
Pharynx length	112.0–134.0	141.0–168.0
Bulbus width	28.8–40.7	28.8–32.2
Bulbus (cbd)	52.5–67.8	47.5–54.2
Vulva (dfae)	4290.0–4450.0	3644–5847.0
Vulva (% body length)	51.5–56.0	60.3–72.3
Spiculum length	67.8–89.8	67.8–84.8
Gubernaculum length	32.2–35.6	35.6–50.9
Tail length	64.4–79.7	84.8–113.0

dfae = distance from anterior end.
cbd = corresponding body diameter.

level of nerve ring. Body diameter is practically constant from a short distance posterior to end of pharynx all the way to the anus. This midbody diameter has been used to calculate *a.* Tail is conical, 1.4–1.5 anal diameters long in both sexes, curved ventrally in males (Fig. 1C), nearly straight in females (Fig. 2C).

Cuticle faintly annulated (Figs. 1C, 4E, F, G); annuli 0.25 μm wide. Annulation in the head region irregular forming a characteristic "fingerprint" pattern (Fig. 4C). Cephalic capsule consisting of a special layer of blocks of a homogeneous material, giving the anterior end a reticulated appearance if one focusses slightly below the surface (Figs. 1B, 2B, 3A, B). Tip of tail free of annulations and caudal glands open terminally through a complicated pore complex (Fig. 4E, see also Nebelsick et al. 1992: fig. 2). Cuticle 3 μm thick in bacteria-free body region. Cuticle thins at the beginning of bacterial coat and body diameter becomes smaller to an extent that the bacterial coat does not increase the overall thickness of the animal (Figs. 1D, 4F). Eight rows (four sublateral, four submedian) of somatic setae (5 μm long) in anterior body region (Figs. 1B, 2B) are outlets of glandular sense organs (*gso,* Nebelsick et al. 1992) which lie in double rows in lateral (Fig. 1E), dorsal, and ventral positions. Posterior to end of pharynx ventral and dorsal double rows of *gso* merge gradually into a single row each. Consequently only six rows of setae (four sublateral, one mediodorsal and one medioventral) and *gso* are present over most of the body. Near posterior end the submedian rows become distinct from each other again (Fig. 1C). Cephalic sensillae consist of a circle of six blunt papillae with apical openings surrounding the mouth opening (Fig. 4B, C), often appearing retracted and not visible from the outside except in *en-face* view (Fig. 4D). Second circle formed by six short setae (2.2 μm) with swollen tips, the third by four long, conical setae (32–35 μm). A circle of eight subcephalic setae, 10–13 μm long, apparently not connected to glandular sensory organs is flanked by first circle of regular somatic setae. Two or three more circles of eight setae

Table 2.—*Laxus oneistus*. Distribution of males, females and juveniles in 10 cores.

Core #	Males	Females	Juveniles
1	10	17	6
2	19	24	3
3	1	2	7
4	5	4	4
5	27	26	30
6	6	7	5
7	38	28	6
8	7	6	2
9	1	7	19
10	—	1	4
Total	114	122	86

situated on the reinforced cuticle of the head. Amphids close to the anterior end consisting of a simple ventrally wound spiral.

Buccal cavity small and tubular, tri-partite pharynx consisting of a distinctly swollen corpus occupying almost the anterior half, twice as wide as the isthmus, and a round terminal bulb leading into intestine without cardia (Figs. 1B, 2B, 3A). Isthmus and bulb occupy approximately 30 and 24% of pharynx length, respectively. Nerve ring encircling isthmus approximately at two-thirds of the length of the pharynx. No ventral gland or excretory pore seen.

Single testis in males at 39–46% of body length. Spicula cephalate proximally, arcuate, with a velum (Figs. 1C, 3D), about one anal diameter long (chord) or up to 1.3 anal diameters (arch). Gubernaculum simple, with a dorsally directed apophysis. Ovaries paired, symmetrical, antidromous reflexed, uteri containing extremely long (up to 620 μm) ova. Vulva at 51–56% of body length.

Diagnosis.—Characters of the genus; corpus occupying anterior 46% of the pharynx, twice as wide as the isthmus, bulbus 24% of pharynx length; subcephalic setae ca. 40% of the length of the cephalic setae; annulation very faint; coat of bacterial symbionts begins at a distinct level several hundred microns behind the anterior end.

Biometry of developmental stages.—Ten

Table 3.—*Laxus oneistus*. Biometrical data for juvenile stages (j) 1 + 2, 3 and 4, males, females and pooled adults from the cores (only 61 adults included).

Stage	*n*	Length			a		b		c		
		Mean	*SD*	Range	Mean	*SD*	Range	Mean	*SD*	Mean	*SD*	Range
j 1 +2	39	1.93	0.55	1.08–2.92	51.2	13.1	29.8–88.0	22.1	5.7	13.9–35.6	29.8	6.9	13.6–44.3
j 3	27	3.75	0.55	3.05–4.91	86.8	15.8	68.0–135.0	37.1	6.6	26.6–49.3	53.6	9.2	37.2–71.0
j 4	20	5.81	0.50	5.09–6.86	124.0	16.2	93.7–154.1	54.4	5.7	44.1–64.4	78.6	16.8	46.8–109.4
Males	21	6.86	0.90	5.36–8.71	134.3	18.1	101.6–161.1	61.7	9.3	42.4–75.9	93.0	12.8	75.8–125.3
Females	40	7.19	1.06	5.18–9.36	130.9	22.2	91.9–176.4	66.6	14.2	36.4–99.0	94.0	19.2	56.0–132.8
Adults	61	7.08	1.02	5.18–9.36	132.0	20.9	91.9–176.4	64.8	12.7	36.4–99.0	93.7	17.2	56.0–132.8

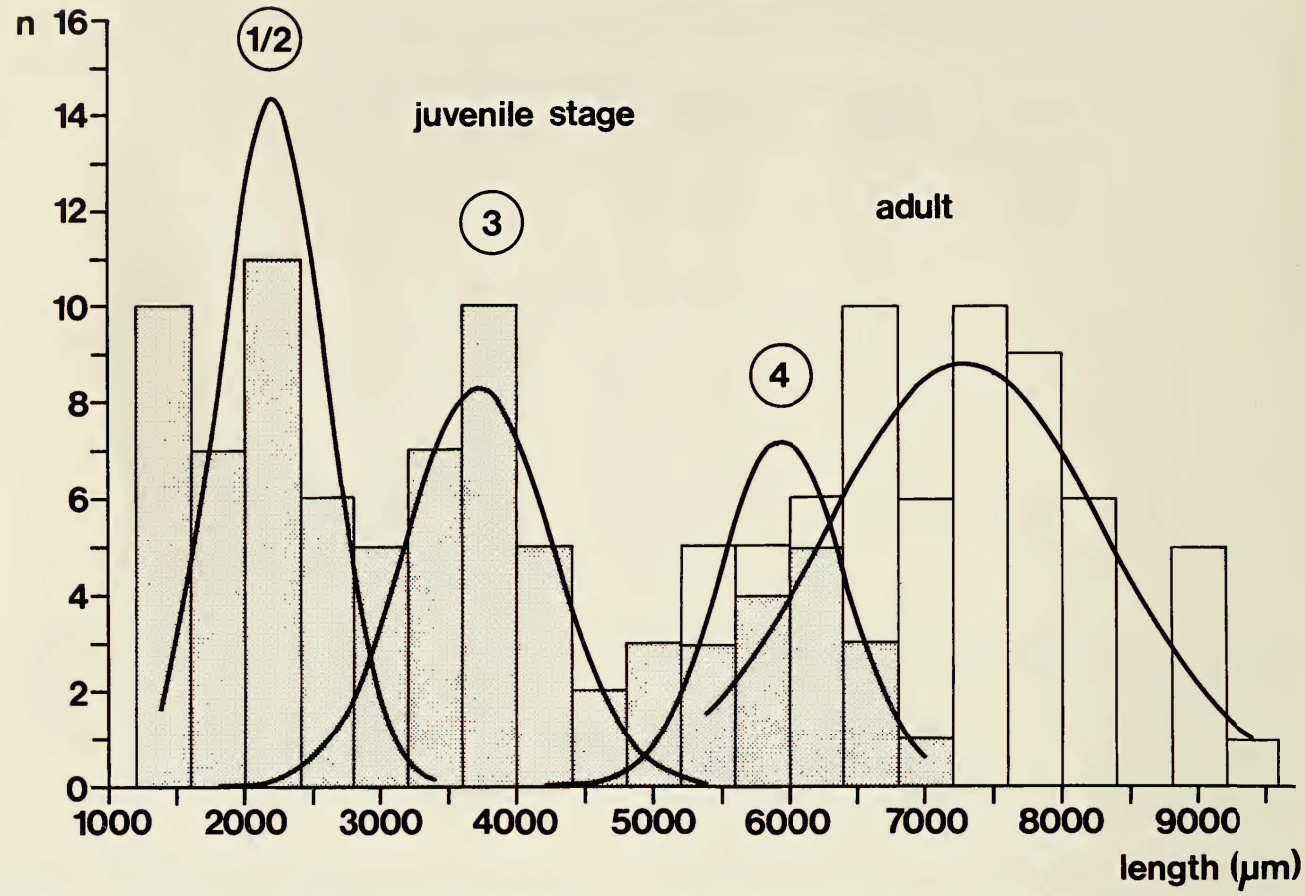


Fig. 5. *Laxus oneistus*. Size-frequency plot of juveniles (shaded) and adults (white). Separation of juvenile stages 1/2, 3 and 4 by fitting normal distributions using Bhattacharaya's method (Elefan).

quantitative cores taken in 1991 contained a total of 322 specimens, 236 of which were adults (114 males, 122 females) (Table 2). The 86 juveniles ranged in size from 1.1 mm to 6.9 mm (Table 3). A size frequency plot (Fig. 5) revealed four modes among the juveniles. Bhattacharaya's method for separating frequency distributions, however, gave only three normal distributions. We interpret these as the pooled stages 1 and 2, stage 3 and stage 4 juveniles. The stage 4 juveniles length distribution strongly overlaps with that of the adults. The statistical method used was unable to separate stage 4 juveniles by length from the adults, which were identified by the presence of fully developed gonads and treated separately.

Plotting *a* (body length divided by maximum body width) against length (Fig. 6) shows that juveniles become progressively more slender during growth. With the adult molt the worms become stouter, especially the females due to the development of the gonads. The midbody region elongates more strongly during growth than either the pharynx and the tail as is evident from plots of *b* (body length divided by pharynx length) or *c* (body length divided by tail length) against body length (Figs. 7, 8). The index c shows little correlation to body size in adult males probably due to different degrees of curvature of the tail.

Remarks.—*Laxus oneistus* is extremely common in subtidal coarse sands in the Belize Barrier Reef system, from just below the waterline to at least 7 m depth. It inhabits the deeper, microxic to anoxic sediment layers. By migration through the chemocline it exposes its symbiontic bacteria alternately to sulfide and oxygen. The

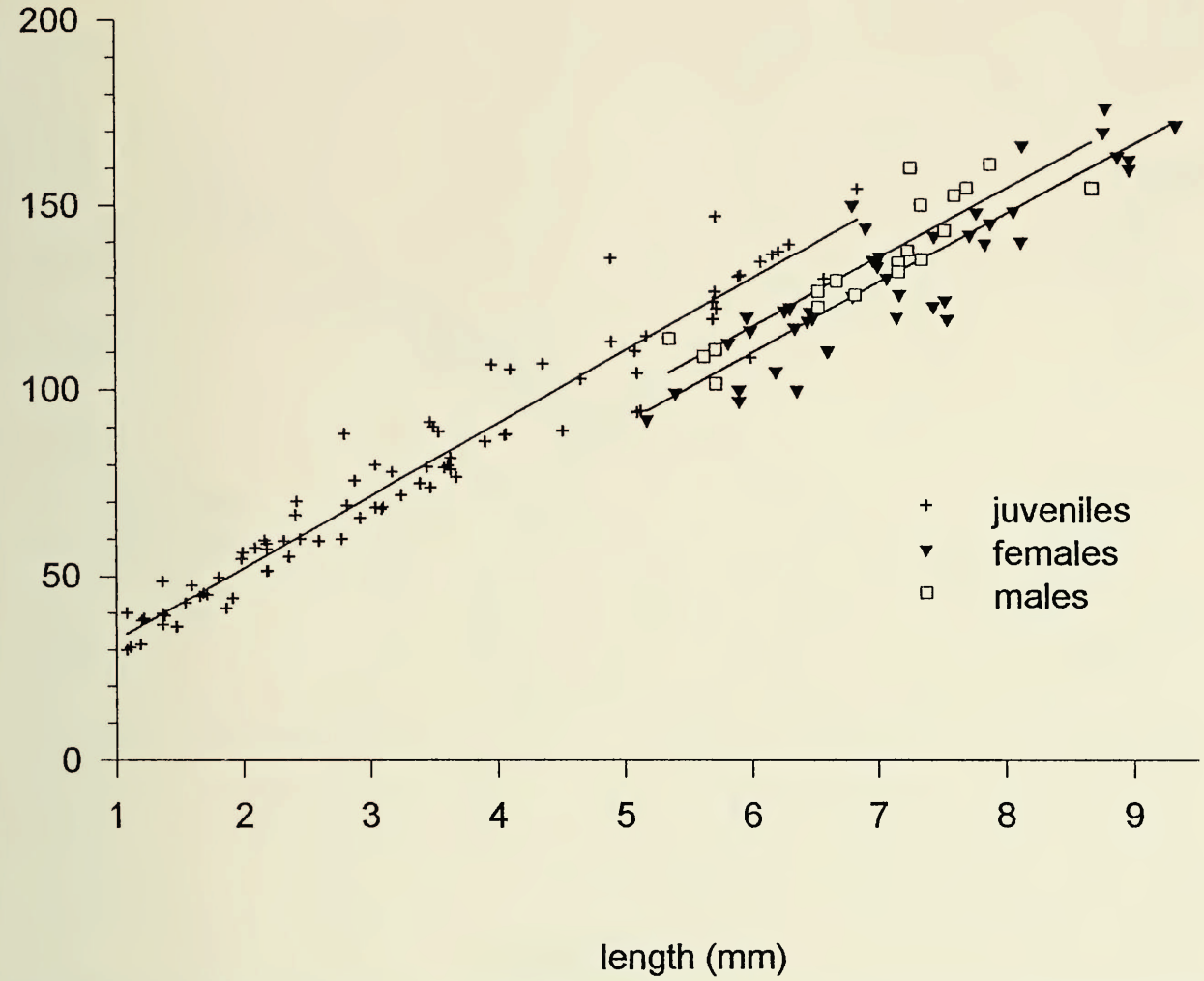


Fig. 6. *Laxus oneistus.* Biometry of development: Relationship between body length and ratio *a* (body length/maximum body width). Linear regression.

chemoautotrophic bacteria constitute probably the main bulk of the food for these worms (for details of the biology see Ott and Novak, 1989 and Ott et al., 1991). When extracted from the sediment it tends to curl up its body except for the anteriormost part (Fig. 2A). It is very thigmotactic and in dishes forms tightly knotted aggregations with conspecifics or other long nematodes from which only the anterior parts protrude executing elegant undulating movements.

Laxus cosmopolitus, new species

Synonym.—"undescribed genus from the Adriatic Sea" in Ott et al. 1991, "undescribed genus from the Mediterranean" in Polz et al. 1992, *Eubostrichus exilis* (Cobb, 1920) in Gerlach 1963a, probably *E. exilis* (Cobb, 1920) in Gerlach 1964

Holotype: male, NHMW-EV Nr.3415
L = 6.53 mm *a* = 133 *b* = 46 c = 59
Allotype: female, NHMW-EV Nr.3416
L = 7.71 mm *a* = 138 *b* = 45 *c* = 76
Paratypes: male, NHMW-EV Nr.3417
L = 6.01 mm *a* = 115 *b* = 42 *c* = 57
male, NHMW-EV Nr.3418
L = 6.99 mm *a* = 128 *b* = 45 *c* = 83
female, NHMW-EV Nr.3419
L = 7.29 mm *a* = 148 *b* = 48 *c* = 66
female, NHMW-EV Nr.3420
L = 6.22 mm *a* = 122 *b* = 42 *c* = 73
female, NHMW-EV Nr.3421

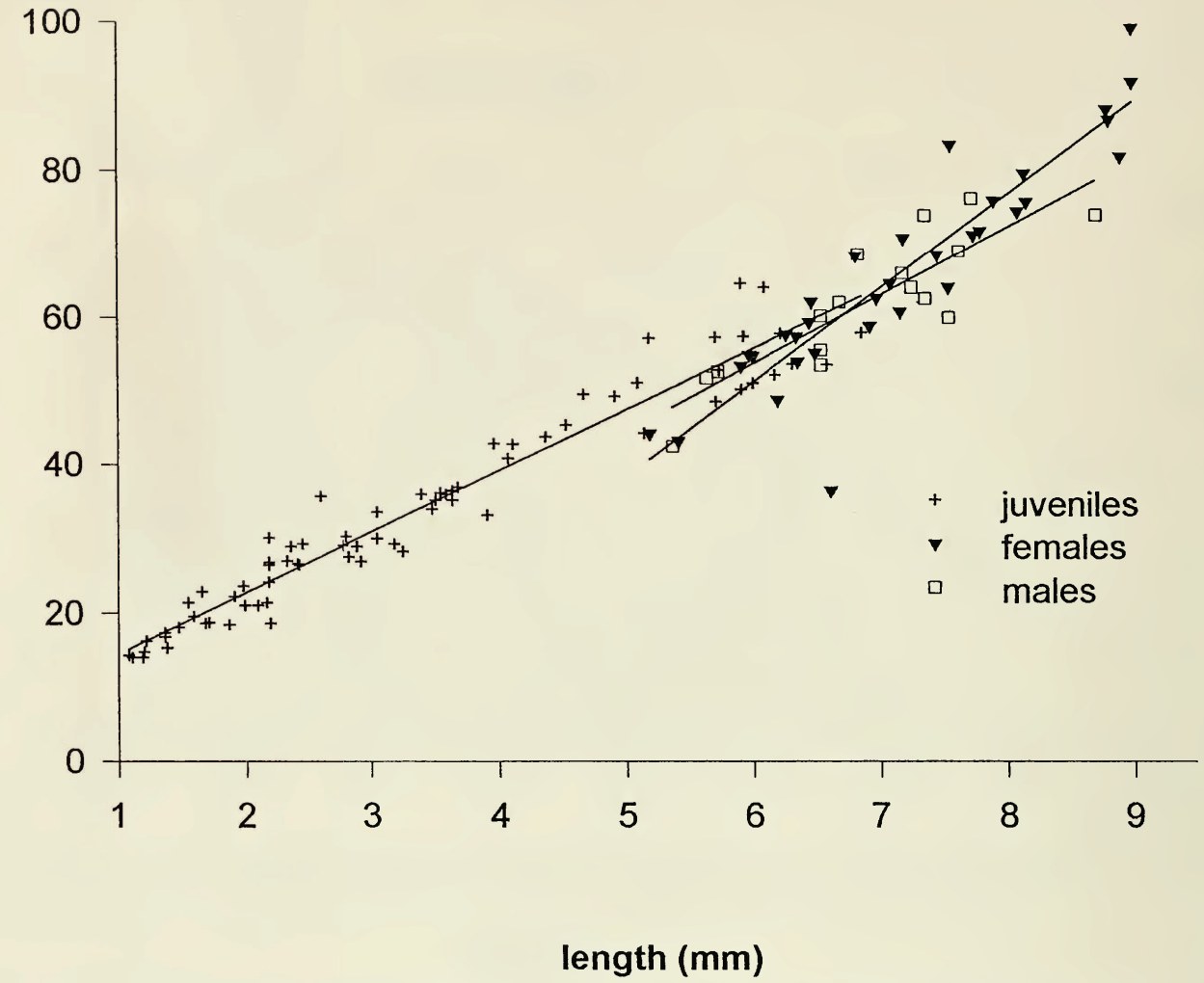


Fig. 7. *Laxus oneistus.* Biometry of development: Relationship between body length and ratio *b* (body length/pharynx length). Linear regression.

L = 7.97 mm a = 164 b = 42 c = 83
female, NHMW-EV Nr.3422
L = 9.07 mm a = 178 b = 61 c = 80

Etymology.—from the greek *kosmopolites,* meaning "citizen of the world," because of its wide distribution.

Type locality.—Bay of Vestar south of Rovinj, Croatia, Adriatic Sea, Mediterranean; moderately well sorted coarse calcareous sand in 3–4 m depth.

Cylindrical, long, robust worms (Figs. 9A, 10A), body completely covered by radially arranged rod shaped bacteria (1.8 × 0.7 μm) except for head and tip of tail (Figs. 9B, C, 10B, C, 11C–F, 12A, D), bacteria appearing white in incident and dark in transmitted light.

Cuticle distinctly annulated; annuli 1.3 μm wide; anterior end with "fingerprint"-pattern and cephalic capsule composed of a block layer similar but coarser than in the foregoing species. Eight rows of somatic setae (5 μm long) distinct in cervical region. After end of pharynx the two subventral and the two subdorsal rows merge as in the foregoing species. Males with a region of especially dense and large glandular sense organs (*gso*) ventrally starting at level of the end of pharynx extending 1.27 mm posteriad (Figs. 9A, 11A), a similar region of dense *gso* (0.9 mm long) in front of the cloaca (Fig. 9A). In females the *gso* denser in vulvar region than in remainder of body (Fig. 10D).

Arrangement of cephalic sensillae is similar to that in *L. oneistus.* First circle of six

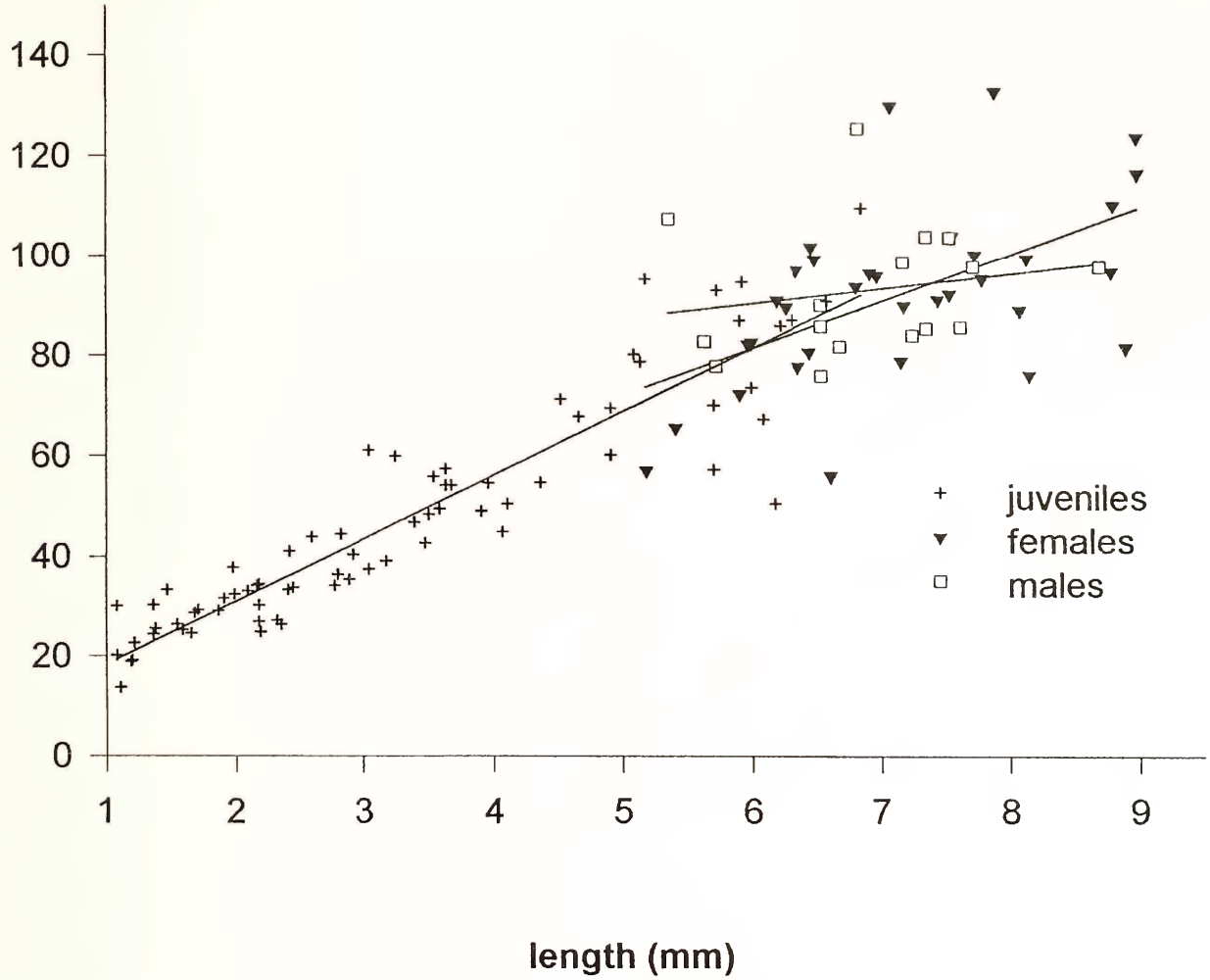


Fig. 8. *Laxus oneistus*. Biometry of development: Relationship between body length and ratio *c* (body length/tail length). Linear regression.

blunt papillae is in most cases retracted into mouth, second circle again consisting of six short setae with swollen ends (Figs. 12A, B). Four setae of the third circle 26–29 μm long. Eight subcephalic setae only slightly longer (7–8 μm) than setae of following three circles situated on cephalic capsule. Amphids ventrally wound spirals with 1.5 turns and deeply incised fovea (Fig. 12B).

Pharynx only slightly swollen in anterior half, forming a corpus 30–50% wider than isthmus, terminating in a round to pyriform bulb. Small cardium projects into intestine. Nerve ring encircling the isthmus. No excretory system seen.

Single testis in males begins at 38% of body length. Spicula 1.2 (chord) or 1.4–1.6 (arch) anal body diameters long, cephalate proximally, with a velum. Gubernaculum, with dorsally directed apophysis. Female gonads paired, ovaries symmetrical antidromous reflexed. Distinct *receptacula seminalis* visible at junction of ovaries and uteri. Vulva at 60–72% body length.

In addition to the type locality, *L. cosmopolitus* was also found near the Island of Tubya Al-Bauda, Bay of Safaga (Egypt, Red Sea) and at Biyadoo (Maldive Islands, Indian Ocean). The animals from these localities agree in most characters with the Mediterranean specimens. There are, however, a few consistent differences. With 6 to 9 mm body length ($\bar{X} = 7.22 \pm 1.0$ mm, $n = 8$) the specimens from Rovinj are significantly larger than those from Safaga (4.6–7.4 mm, $\bar{X} = 5.94 \pm 0.9$ mm, $n = 10$) and

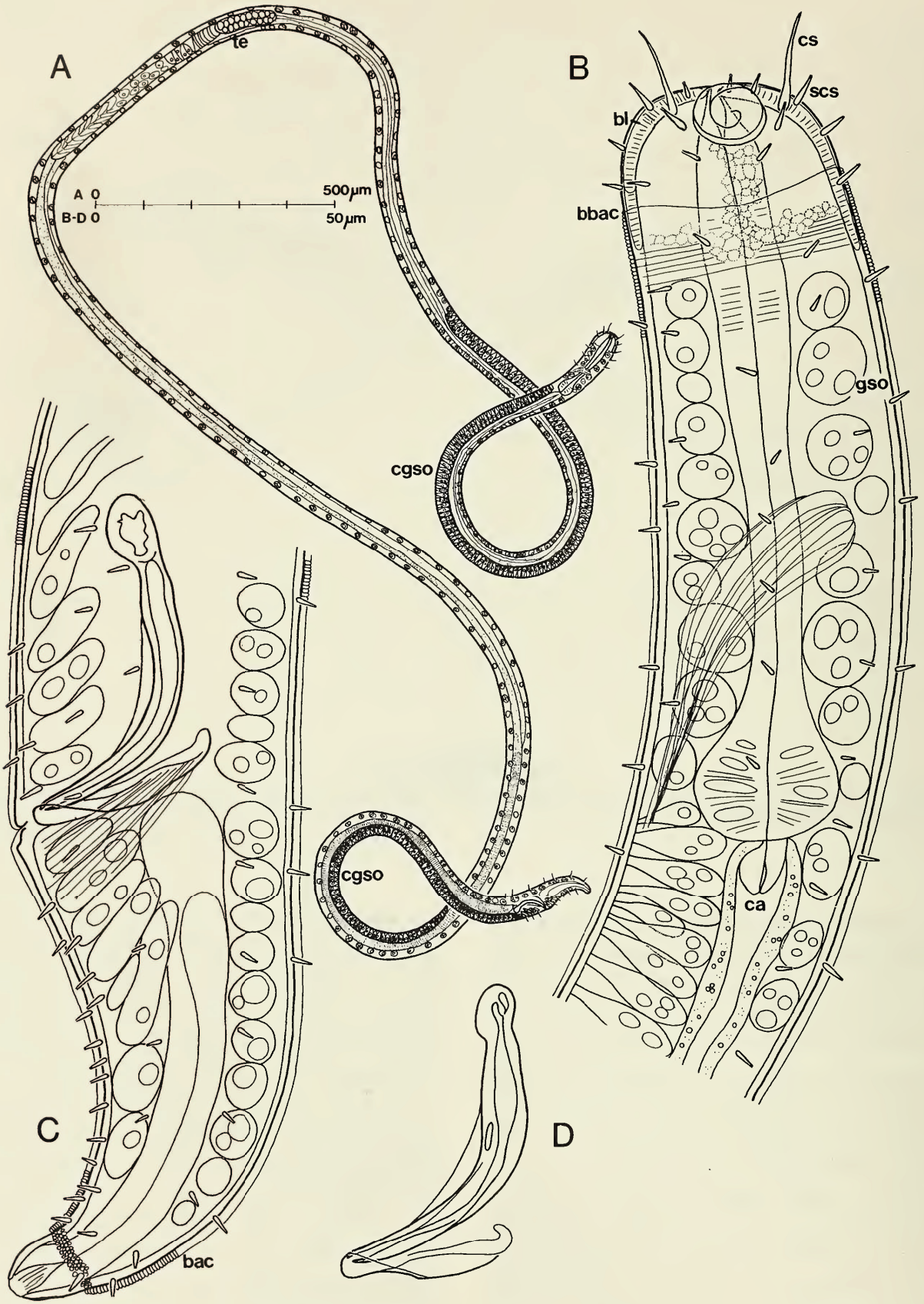


Fig. 9. A–C. *Laxus cosmopolitus,* male, holotype. A. Total view showing concentrations of *gso* ventrally in postpharyngeal and preanal region. B. Anterior end and pharyngeal region, showing cephalic capsule and pharynx. C. Posterior end with spicular apparatus and tail with caudal glands. D. Male, paratype. Spicular apparatus. A–D, lateral views. (For abbrevations see Fig. 1.)

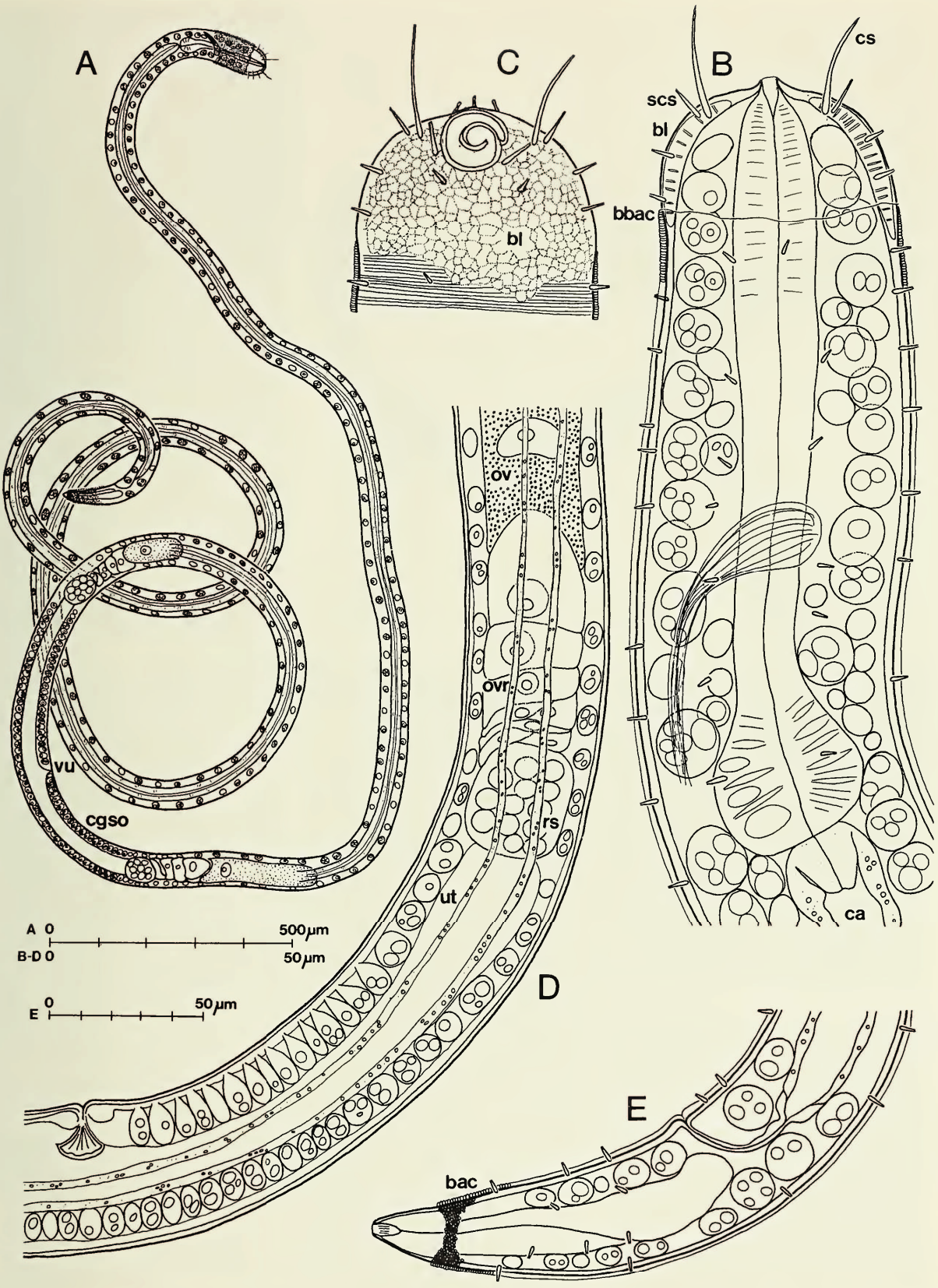


Fig. 10. *Laxus cosmopolitus,* female, allotype. A. Total view. B. Anterior end and pharyngeal region, optical section. C. Head, surface view showing amphid and honeycomb pattern of block layer. D. Vulvar region and part of anterior ovary. E. Tail with caudal glands. A–E, lateral views. (For abbrevations see Fig. 1.)

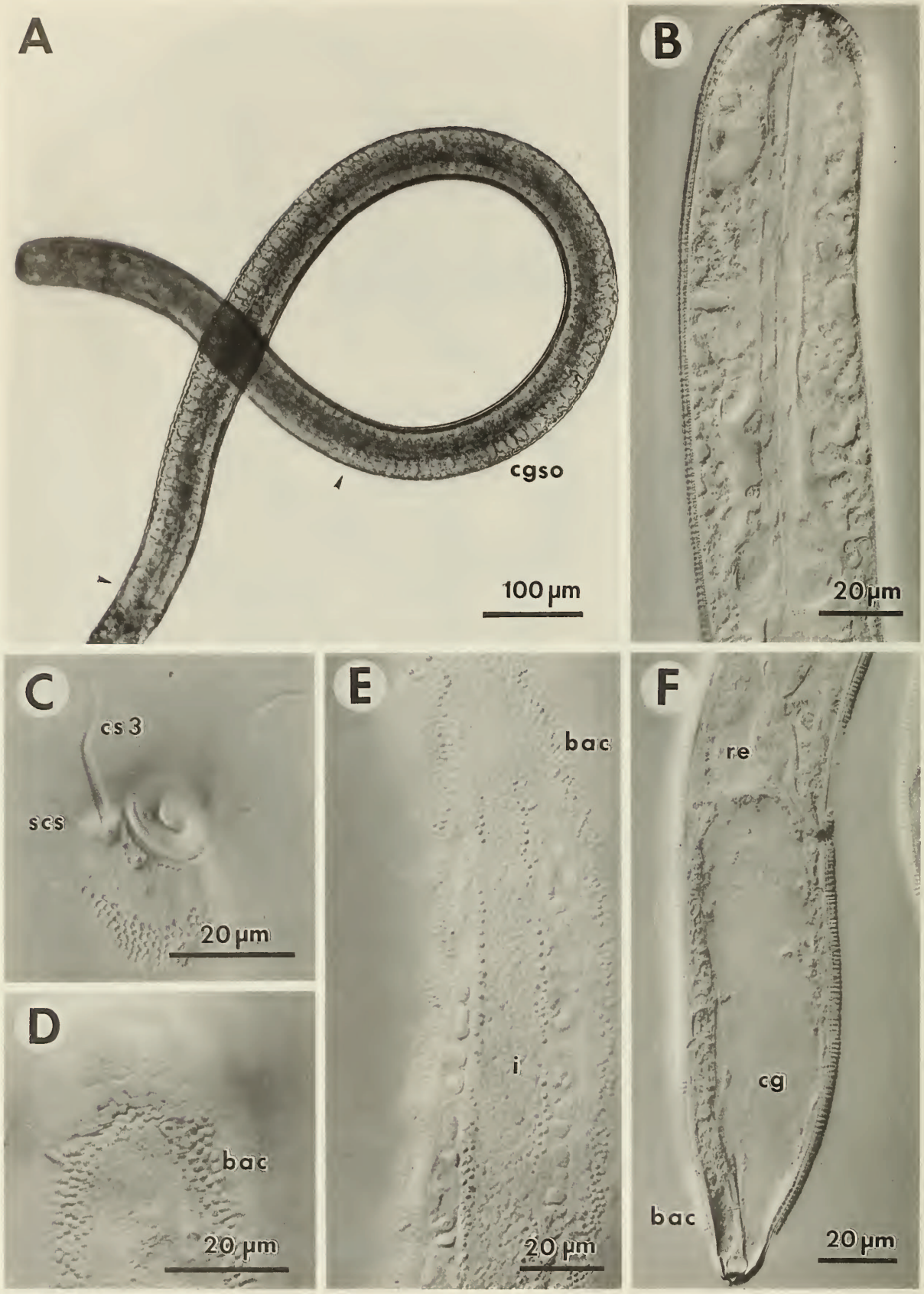


Fig. 11. *Laxus cosmopolitus,* Nomarski interference contrast microphotographs. A. Anterior body region showing concentration of *gso.* B. Anterior end and pharyngeal region. C. Head showing amphid, block layer of cephalic capsule and beginning of bacterial coat. D. Posterior end of cephalic capsule, annulated cuticle and microbial coat. E. Optical section through midgut region showing gut filled with bacteria similar to the ecto-symbiotic bacteria on the cuticle. F. Posterior end of female showing rectum, anus and caudal glands. (For abbrevations see Fig. 1.)

the Maldives (3.98–6.6 mm, $\bar{X}$ = 4.95 ± 0.85 mm, n = 8) (Kruskal-Wallis one-way analysis by ranks, P = 0.005, pairwise test of significance of differences after Conover 1980). The tail is strongly curved ventrally in males from Rovinj and regularely conical, in the Red Sea specimens it is almost straight, conical with a distinctly set-off cylindrical end part, whereas in the Maldives the tail is almost cylindrical over most of its length and narrows abruptly only near the tip. The two rows of subventral setae on the male tail are slender in the Rovinj specimens, stouter in those from the Red Sea and triangular thorns in males from the Maldives. The spicula in the Maldive males are more distinctly cephalate, less curved and have only a small velum (Fig. 13). Additional specimens provided by G. Boucher (Paris) from New Caledonia resemble the Red Sea animals.

Diagnosis.—Characters of the genus; corpus occupying 50% of the length of the pharynx, being 30–50% wider than the isthmus (34% of pharynx length), bulbus small (16%); subcephalic setae ca. 30% of length of cephalic setae; annulation relatively coarse (1.3 μm); concentration of glandular sense organs ventrally, in males in the postpharyngeal and praecloacal region, in females in the pre- and post-vulvar region; bacterial coat extends into region of cephalic capsule.

Remarks.—*Laxus cosmopolitus* is regularely found in coarse subtidal sand at the type locality and in several locations in the vicinity of Rovinj (Bay of Cisterna, Punta Croce). It is, however, never abundant. Both the Red Sea and the Maldive Island material comes from shallow subtidal coralline sand. The association of the worms with sulfidic sediments and the similarity between the bacteria found in the gut and on the cuticle together with their ultrastructure suggest a similar biology as in *L. oneistus*.

Discussion

The genus *Laxus* was proposed by Cobb in 1894 for two nematodes collected from such different regions of the world as the Gulf of Naples and the Australian coast. Although the description of the type species, *L. contortus*, is on the basis of a female only and is not accompanied by a figure, it is sufficiently precise to warrant the assumption, that it is congeneric with the second species, *L. longus*. In fact, Cobb himself designated the latter as the genotype in Stiles & Hassal (1905) (see also Baylis & Daubney 1926). This allows an identification on the genus level with our species described above. In particular, the genus *Laxus* is recognized by the special structure of the tripartite pharynx with its swollen corpus, which is not as clearly set off as in the genera *Catanema* Cobb, 1920 or *Robbea* Gerlach, 1956; the lack of cervical papillae (which distinguishes it from *Robbea*); and the spicular apparatus with a large cephalate spiculum having a velum in its distal half and a simple, slightly curved gubernaculum with a straight, dorsally directed apophysis (which distinguishes it from *Catanema*). Additional characters are the four long setae of the third circle of cephalic sensillae, which are flanked by shorter setae ("two setae of unequal size placed on each submedian line," Cobb 1894:415) and the presence of additional setae adding up to the eight elongated setae that constitute the first circle of somatic setae; the apparent lack of an excretory system; the shape and position of the amphid; the shape of the tail and the prominent rows of subventral setae pre- and postanally. Although none of the forgoing characters is unique for the genus, the combination is. Cobb's fig. 11/II also indicates the reinforcement of the cephalic cuticle by the block layer.

Laxus septentrionalis, described by Cobb in 1914 from Antarctica, however, does certainly not belong to this genus. Neither does the conical head nor the amphid depicted in the description resemble the foregoing species. The pharynx ("oesophagus" in Cobb's description) is explicitely described as "cylindroid," there is a distinct excretory

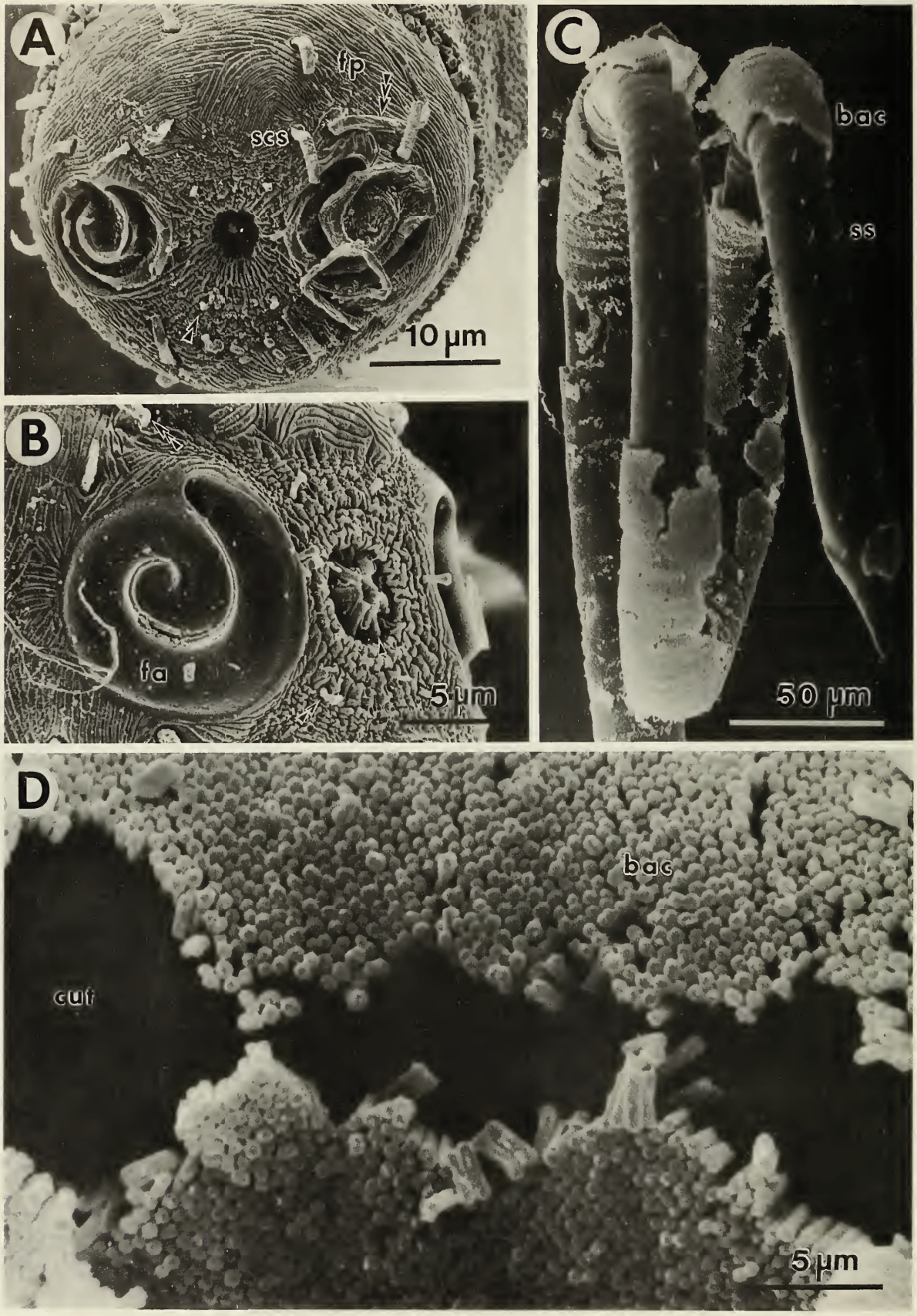


Fig. 12. *Laxus cosmopolitus,* SEM microphotographs. A. En-face view of anterior end showing fingerprint region, amphids, mouth opening surrounded by second circle of six cephalic sensillae (double arrow), third circle of four *cs* (triple arrow) and subcephalic setae. Note that bacterial coat reaches the fingerprint region. B. Close-up of amphid and mouth opening with first (single arrow), second (double arrow) and third circle (triple arrow) of *cs.* C. Posterior end of female showing rows of somatic setae. The disruption of the bacterial coat is an artefact

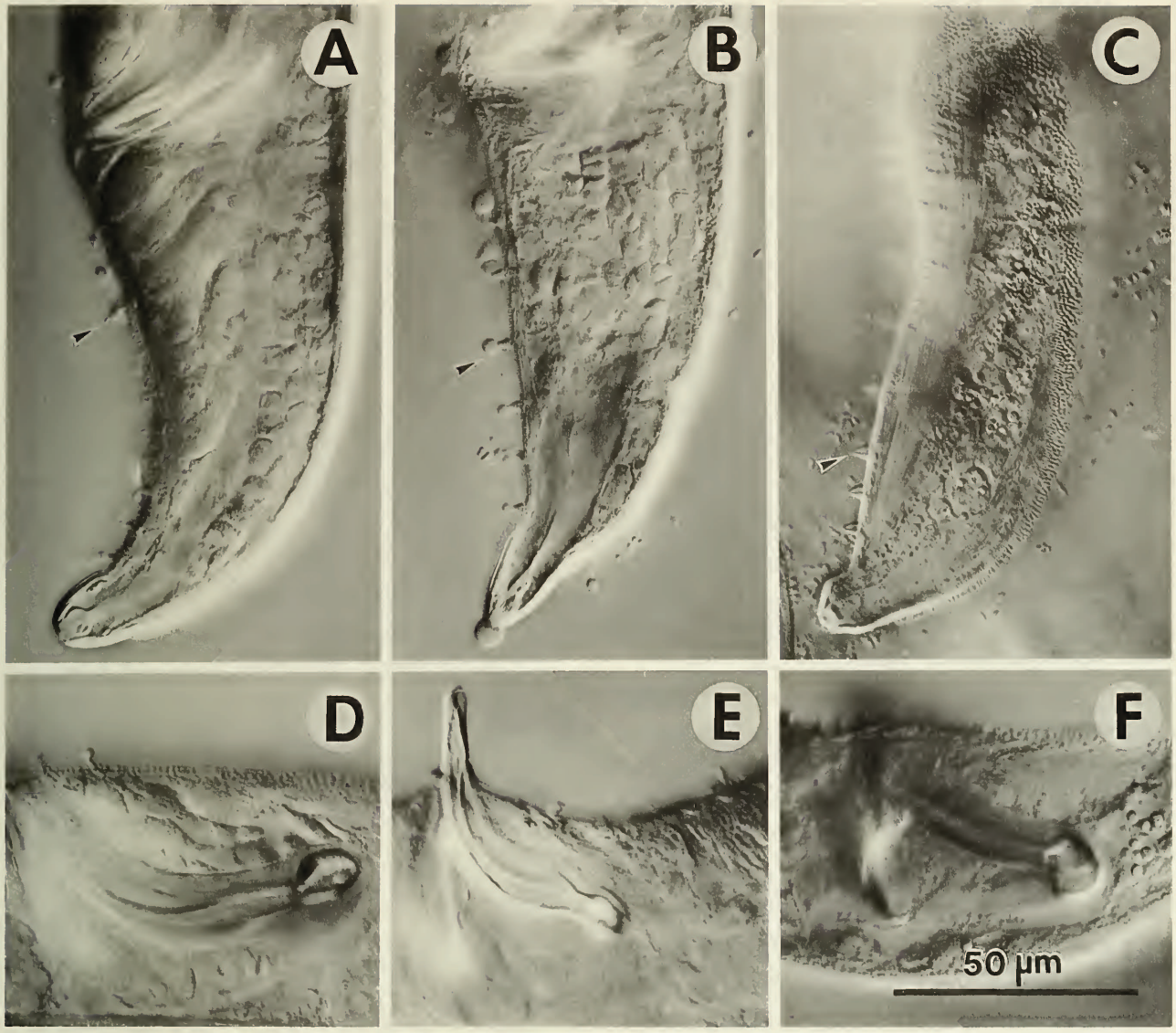


Fig. 13. *Laxus cosmopolitus,* Nomarski interference contrast microphotographs. Variations in the shape of the tail, postanal setae and spicular apparatus between male specimens from the Mediterranean Sea (A, D), the Red Sea (B, E) and the Maldive Islands (C, F). (For abbrevations see Fig. 1.)

system, and the gubernaculum is described to have an apophysis perpendicular to "the part which is applied to the spicula."

In contrast, *Catanema cobbi* Inglis, 1967 certainly has to be transferred to the genus *Laxus* on the basis of the special structure of the pharynx and the distinct block layer reinforcing the head cuticle. Inglis also mentiones that the annulation extends over the region of the block layer. It is very similar to *L. longus* because of the length of the first circle of eight setae and the relative proportions of the three regions of the pharynx, but differs in the number of postcloacal subventral setae (or "tube-like organs"). In the present state of knowledge and in the absence of type specimens it is better to refrain from synonymizing these two species.

The genus *Laxus* may be redefined as follows: Desmodoridae, Stilbonematinae, cu-

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of preparation. D. Close-up of bacterial coat in the midbody region showing closely packed rods standing perpendicular to the annulated surface of the cuticle. (For abbrevations see Fig. 1.)

ticle finely annulated, with "fingerprint" pattern on the anterior end. In this region a cephalic capsule is developed by a special "block-layer" inserted between the median and basal zone of the cuticle; pharynx tripartite, with a swollen corpus that is not distinctly set off from the isthmus; spicula curved, cephalate; gubernaculum without apophysis, straight to slightly S-shaped. Symbionts are rod-shaped bacteria arranged in a single layer in which the longitudinal axis of the microorganisms is perpendicular to the cuticle surface.

The following species belong to the genus: *Laxus longus* Cobb, 1894 (type species), *Laxus contortus* Cobb, 1894, *Laxus cobbi* (Inglis, 1967) (syn. *Catanema cobbi* Inglis, 1967), *Laxus oneistus* new species., *Laxus cosmopolitus* new species.

It is peculiar, that neither Cobb nor Inglis—both being keen observers—mention the bacterial ectosymbiosis. Most of the stilbonematids that have been described previously and practically all specimens in our collection (comprising all genera so far described) show the conspicuous and species-specific coat of microorganisms. Also, in Cobb's descriptions of the type species of the genera *Stilbonema, Leptonemella, Catanema* and *Laxonema* (Cobb 1920), no mention is made of the ectosymbionts. Especially in *Stilbonema* the multilayered bacterial coat cannot be overlooked. Since no type material exists, we cannot be sure whether the bacterial ectosymbiosis is absent in these species (which seems improbable), whether the bacteria had been lost during preparation, or whether they were deliberately ignored because the authors believed them to be contaminants.

The small proportion of juveniles in the collection is consistent with other indications of a slow development, low reproduction rate and longevity of adults in *L. oneistus*. Both juveniles and adults could be kept alive for up to three weeks in dishes during which time neither molting or egg-laying was observed.

There is a notable difference between the mean body length of the type specimens and the adults from the quantitative cores, the latter being significantly smaller. This could be an indication of seasonal or year to year variation in size (the type specimens were collected in May 1989, the cores were taken in February 1991). Another explanation could be an unconscious bias when choosing type specimens from qualitative collections where larger "representative" specimens may be preferentially selected. Therefore, size differences between haphazardly selected material and type specimens should not be overrated.

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