Nematol. medit. (1995), 23: 217-234

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FOUR NEW SPECIES OF THE GENUS *RHIGONEMA* COBB, 1898 (NEMATODA: RHIGONEMATIDA: RHIGONEMATIDAE) PARASITIC IN DIPLOPODS FROM PAPUA NEW GUINEA

by
D. J. HUNT

Summary. Four new species of *Rhigonema* Cobb, 1898, *R. acrulocantha* sp. n., *R. tomentosum* sp. n., *R. tribonophora* sp. n. and *R. villosum* sp. n. from the intestine of two unidentified species of giant diplopod (Diplopoda; Spirobolida) from Papua New Guinea are described and illustrated. Three of the species possess a vaginal diverticulum whereas *R. tribonophora* sp. n. has a long, anteriorly directed and then doubly reflexed, ovejector. *R. acrulocantha* sp. n. is unique amongst nominal *Rhigonema* species because of the highly developed pilose region extending from the head to the beginning of the tail in both sexes, the microtrichs being heavily cuticularized and spiniform. *R. tomentosum* sp. n. and *R. villosum* sp. n. are similar, yet morphologically distinct and from different hosts and may represent sibling species. SEM studies of the *en face* and pilose regions of three of the species are presented.

During December, 1982 a number of giant millipedes representing two species were collected in Papua New Guinea by J. A. Sutherland, preserved in 2% formalin and forwarded to the International Institute of Parasitology. Dissection of the alimentary tract revealed a rich nematode fauna with undescribed representatives from the Rhigonematida in particular, but also from the Oxyurida. This paper continues a series describing the new species and new genera found in two species of those diplopods (Hunt and Sutherland, 1984; Hunt and Sutherland, 1985; Hunt, 1993; Hunt, 1994 a, b, c, d) and deals with the members of the genus *Rhigonema* Cobb, 1898.

Materials and methods

Specimens for study by light microscopy were post-fixed in TAF, transferred to a 5% glycerol in water solution and processed to anhydrous glycerol over four or five days via a slow evaporation technique at 40 °C. Measurements are given in the form: mean ± standard deviation (range). Some specimens were used for studies of the *en face* view or dissected in order to elucidate structural details of the female genital tract, particularly that of the ovejector, the type of which is of crucial importance. Several selected specimens from three of the four species were utilized for SEM studies after being dehydrated through a graded series of ethanol, critical point dried with CO_2, mounted on stubs and sputter coated with a 750 Å layer of gold. They were examined at an accelerating voltage of either 10 or 25 kV.

Descriptions

*RHIGONEMA ACRULOCANTHA** sp. n.

(Figs 1, 2, 3)

Female (n=10): L = 4.05±0.34 (3.61-4.63) mm; width = 276±17 (257-302) µm; oesophagus =

* Derived from the Greek words *acrulos* and *acanthos*, meaning curled spines or prickles and referring to the form of the microtrichs.

346±46 (273-423) µm; basal bulb (height x width) = 75±8.0 x 120±9.9 µm; anal body width = 83±7.0 (72-96) µm; tail = 0.77±0.06 (0.62-0.83) mm; head to vulva = 1.84±0.22 (1.62-2.27) mm; a = 14.7 (13.2-16.1); b = 11.7 (9.6-14.2); c = 5.3 (4.3-6.2); c' = 9.2 (7.6-10.2); V = 45.4 (42.9-49.1).

Male (n=10): L = 3.57±0.23 (3.26-3.87) mm; width = 219±22 (189-250) µm; oesophagus = 312±23 (283-358) µm; basal bulb (height x width) = 67±7.2 x 105±17.2 µm; anal body width = 71±8.4 (59-88) µm; tail = 0.64±0.05 (0.55-0.70) mm; left spicule (n=8) = 380±54 (299-449) µm; right spicule (n=8) = 380±50 (299-449) µm; a = 16.3 (15.2-17.6); b = 11.4 (10.1-12.8); c = 5.5 (5.0-7.1); c' = 9.1 (7.5-10.1).

Holotype female: L = 4.46 mm; width = 288 µm; oesophagus = 423 µm; anal body width = 88 µm; tail = 0.79 mm; head to vulva = 2.09 mm; a = 15.5; b = 10.5; c = 5.3; c' = 9.0; V = 46.8.

Adults: medium sized nematodes ranging from about 3.6 to 4.6 mm in length for female and 3.2 to 3.9 mm for male. Cephalic region heavily cuticularized; consisting of broad, relatively high, cephalic cap followed by narrower cephalic collar. Cephalic cap circular in *en face* view and bearing four mammilliform papillae, two subdorsal and two subventral with amphids located laterally at junction of cap and cephalic collar. Cuticle with fine transverse striae, strongly spinose from cephalic collar to beginning of tail. Spinose region, which represents an extreme development of typical *Rhigonema* pilosity, comprises numerous, strongly cuticularized, robust spines (= microtrichs) spaced along posterior margin of striae; anteriormost spines about 40-45 µm long with tips reflexed. Further posterior, spines more robust and not reflexed, being curved, retrorse and more adpressed. In posterior third of a female, spines about 45-50 µm long with 10-12 µm diameter, suboval bases. Oral opening triradiate; equilateral in form; dorsal and two subventral sectors of equal development. Three cuticularized plates articulate to form jawlike apparatus at anterior end of oesophagus; dorsal and two subventral plates being of equal development and bearing a number of teeth and cuticular ridges. One specimen appeared to have been swallowing an eccrinid, the holdfast end of the organism protruding from the oral aperture. Oesophagus typical of genus, comprising a powerful, muscular, cylindrical corpus; redundant isthmus and powerful basal bulb broadest in the anterior third and then tapering towards oesophago-intestinal junction. Axial cuticularized rods around lumen of corpus finely striated anteriorly. Basal bulb anchored to body wall by muscles attached to its broadest point. Three large cardia extend from bulb into intestine. Intestinal cells packed with granules. Nerve ring encircles corpus at about its mid-point. Excretory pore located just anterior to corpus/basal bulb junction. Brown-tinted arcade cells forming palisade around oesophagus near anterior end.

Female: spines of similar form all around circumference of body (cf. male); terminating ventrally at anus and extending slightly further posterior dorsally, but ending before subulate portion of tail. A short break in ventral spination occurring at vulva. Vulva in form of broad, transverse slit located in anterior half of body (V = 45); usually with brown deposit around aperture. Vagina comprising a powerful sphincter muscle and a muscular, thick-walled *vagina vera* which leads to a capacious vaginal diverticulum. Common uterus extending posteriorly from vaginal diverticulum before reflexing and dividing into anterior and posterior uteri. Diverticulum, common uterus and uterine branches containing elongate spermatids in single specimen dissected. Genital tracts amphididelphic, reflexed with rounded spermatozoa visible in spermatheca of each tract. Genital tract conforming to Type 4 of Adamson (1987a). Genital tracts containing relatively few (<30), ovoid eggs with smooth, thick-walled, shells. Uterine eggs (n=10) measure 119±3.2 x 87±5.2 µm in

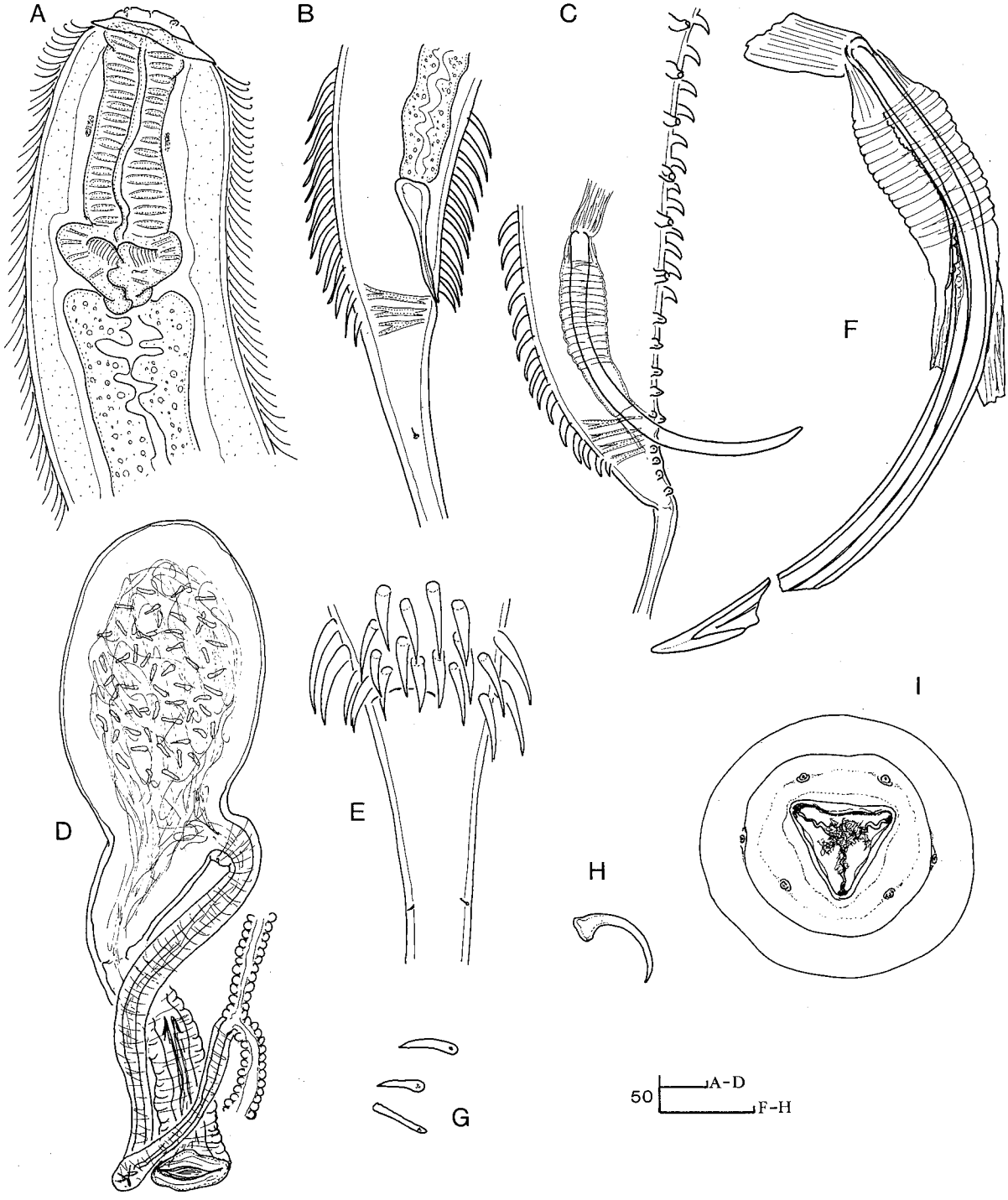

Fig. 1 - *Rhigonema acrulocantha* sp. n. A: oesophagus; B, E: female tail - lateral and ventral views; C: male tail; D: ovejector structure (dissected); F: male spicule (dissected, broken near tip); G: sperm from the vaginal diverticulum; H: spiniform microtrich from the posterior region; I: *en face*, schematic.

size; contents showing no signs of differentiation. Tail of medium length, conoid at first and then tapering evenly to subulate terminus. Phasmids located on subulate portion near its junction with conoid section of tail. Anterior lip slightly overhanging anus. Posterior anal lip not salient.

Male: exhibiting sexual dimorphism in body spination. In about posterior 40% of body, spines of midventral region becoming shorter, less adpressed and more sparse. Basal region of each spine thicker, distal section being more anteriorly-convex and subconical in form. Spines absent for short distance ventrally prior to cloaca and between cloaca and subulate portion of tail. Spines stop dorsally and laterally just before subulate portion of tail. Spicules paired, about 380 μm long, similar in size and appearance and ventrally arcuate. Spicule retractor muscles attached to head of each spicule and extending anteriorly before attaching to lateral body walls. Powerful spicule protractor muscles sheathing proximal region of each protracted spicule; sheath exhibiting circular muscle fibres for much of its length. Anteriorly, sheath attached to spicule head by longitudinal muscles whereas posteriorly strong longitudinal muscles run from sheath to subdorsal walls of tail. Copulatory papillae totalling 31 in number. There are eleven precloacal pairs; posteriormost three pairs normal in size and appearance whereas those located anteriad in pilose region become increasingly higher and barrel-shaped, almost matching spines in height. Single papilla occuring midventrally on anterior cloacal lip. Postcloacal papillae comprise four pairs, all located subventrally. Caudal alae absent.

Tail initially short, dorsally convex conoid and then with long subulate process continuing line of ventral contour.

Juveniles: spination less dense than that of adults; anterior spines well spaced, more robust and of highly unusual form with a long, attenuated distal process reflexed towards cephalic region (Fig. 2A, B). Spination extending from cephalic collar to beginning of tail.

Notes. 1) Because of the density of the spination over the entire body, the internal structures of this species are difficult to discern. Details of the oesophagus, female genital system and male spicules are mostly based on a dissected worm of each sex.

2) A few totally spined juveniles strongly resembling the juveniles of this species were also found amongst the gut fauna of the other, 'large grey', diplopod from Papua New Guinea. Whether these nematodes represented the same, or another, species is not known. Unusually, no adults were found, possibly indicating that the juveniles belonged to *R. acrulocantha* sp. n. and that conditions were unsuitable for establishment in this host.

Type host and locality

Posterior intestine of a 10 cm long, black and gold banded diplopod (? *Polyconoceras* sp.) collected by J. A. Sutherland at Bubia ARC, Lae, Morobe Province, Papua New Guinea. Several juveniles, possibly of this species, were also found in the gut of the other species of diplopod reported upon in this paper.

Diagnosis and relationships

Rhigonema acrulocantha sp. n. is characterized by the entire body in both sexes being covered in spinose microtrichs, these being exceptionally robust and of unusual form. The female genital tract has a short vaginal diverticulum and a common uterus which then divides into the two uteri, one running anteriorly and the other posteriorly; such an arrangement conforming to Type 4 of Adamson (1987a). The male spicules are long and there are 31 copulatory papillae, eleven pairs of which are precloacal. All the postcloacal papillae are subventral.

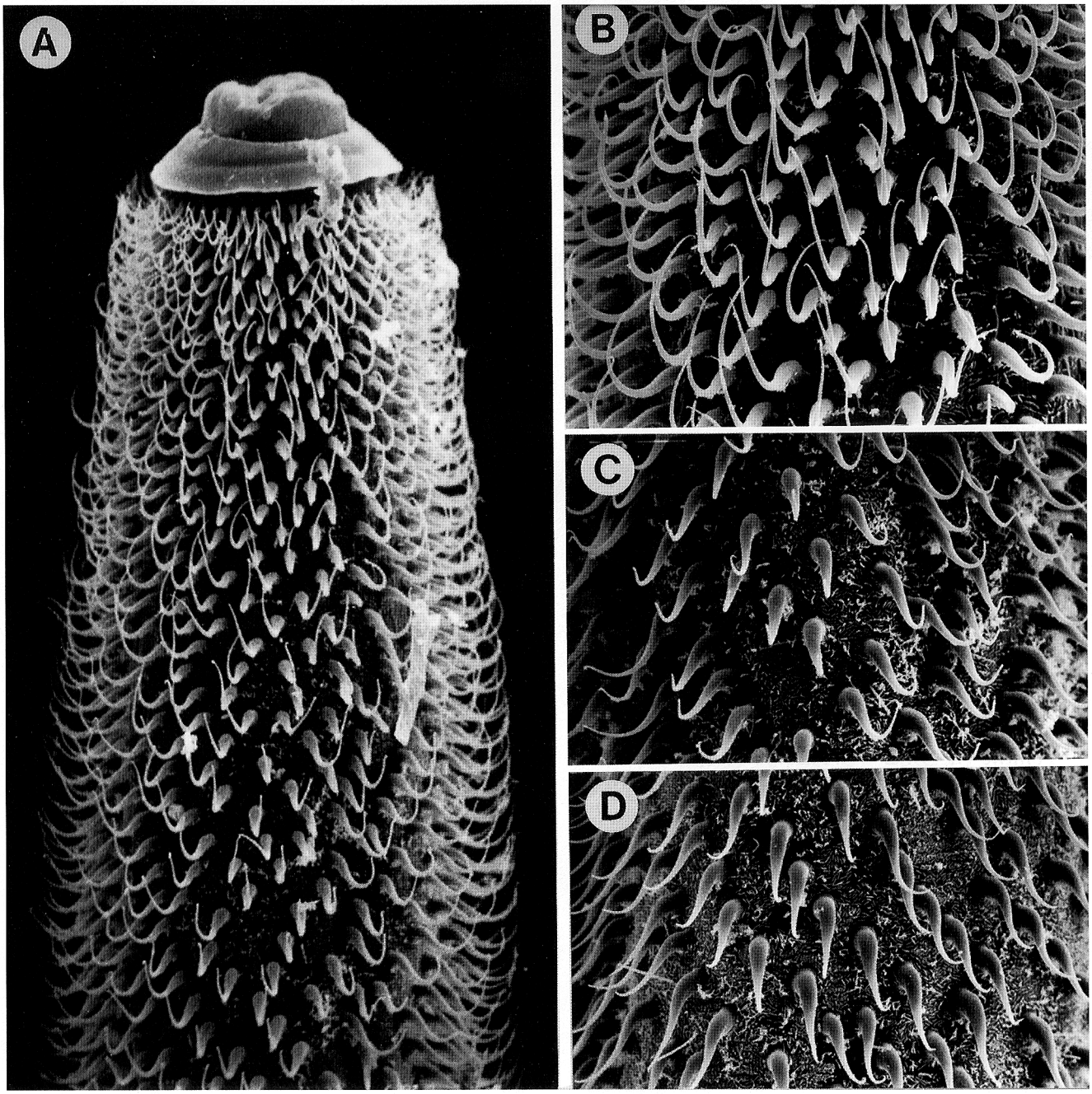

Fig. 2 - *R. acrulocantha* sp. n. SEM studies of juvenile. A: cervical region; B, C, D: microtrich development from just behind cephalic collar to near the anus.

The development and extent of the spinose microtrichs is unique amongst the nominal species of *Rhigonema* Cobb, 1898, although I have seen material of a similarly spined species, comprising poorly preserved juveniles and a female, from a polydesmid diplopod collected by M. Pierce in Sulawesi. This suggests that either *R. acrulocantha* sp. n. has a broader distribution than the island of New Guinea or, more probably, that a species cluster exists in the region.

Type material

Holotype female, nine paratype females and ten paratype males (slide numbers T504/3/1 to T504/3/12) in the type collection of the International Institute of Parasitology, St Albans, Herts., UK.

*RHIGONEMA TOMENTOSUM** sp. n.

(Figs 4, 5)

Female (n=5): L = 5.45±0.30 (5.13-5.91) mm; width = 327±32 (288-354) µm; oesophagus = 532±22 (501-554) µm; basal bulb (height x width) = 114±10.3 x 152±10.9 µm; anal body width = 88±14 (68-107) µm; tail = 1.05±0.08 (0.95-1.17) mm; head to vulva = 2.64±0.28 (2.27-3.01) mm; a = 16.7 (15.6-18.2); b = 10.2 (9.5-10.8); c = 5.2 (4.7-5.6); c' = 11.9 (9.9-14.5); V = 48.4 (44.3-54.6).

Male (n=8): L = 4.64±0.33 (4.27-5.29) mm; width = 257±38 (208-309) µm; oesophagus = 489±27 (449-536) µm; basal bulb (height x width) = 98±9.4 x 142±8.2 µm; anal body width = 88±10.2 (75-104) µm; tail = 0.85±0.11 (0.68-0.99) mm; left spicule = 559±71 (445-624) µm; right spicule = 553±46 (470-601) µm; a = 18.1 (15.2-21.3); b = 9.5 (8.8-10.7); c = 5.4 (4.5-6.6); c' = 9.7 (7.3-12.3).

Holotype female: L = 5.91 mm; width = 351 µm; oesophagus = 546 µm; anal body width = 107 µm; tail = 1.06 mm; head to vulva = 2.82 mm; a = 16.8; b = 10.8; c = 5.6; c' = 9.9; V = 47.7.

Adults: medium to long nematodes ranging from about 5.1 mm to over 5.9 mm in length for female and 4.2 to 5.3 mm for male. Cephalic region heavily cuticularized, consisting of broad cephalic cap followed by well developed cephalic collar with free margin undulating. Cephalic cap circular in *en face* view and bearing four mammilliform papillae, two subdorsal and two subventral with amphids located laterally at junction of cap and cephalic collar. Cuticle with fine transverse striae, densely pilose with delicate microtrichs from cephalic collar for about 2 to 2.5 oesophagus lengths posteriorly. Microtrichs long (about 20 - 22 µm near collar) and dense anteriorly, becoming shorter, adpressed and more widely spaced posteriorly, often with reflexed tips. Oral opening triradiate; equilateral in form; dorsal and two subventral sectors being of equal development. Three cuticularized plates articulate to form jawlike apparatus at anterior end of oesophagus; dorsal and two subventral plates of equal development and bearing a number of teeth and cuticular ridges. Oesophagus typical of genus, comprising powerful, muscular, cylindrical corpus; redundant isthmus and powerful, basal bulb, broadest in anterior third and tapering towards oesophago-intestinal junction. Basal bulb anchored to body wall by muscles attached to its broadest point. Three large cardia extending from bulb into intestine. Intestinal cells packed with granules. Nerve ring encircling corpus at about its mid-point. Excretory pore just anterior to corpus/basal bulb junction. Brown-tinted arcade cells forming palisade around oesophagus near anterior end.

Female: vulva open, in form of broad, transverse slit and located in median region of body (V = 48). Vagina comprising powerful

* Derived from the Latin *tomentosus*, meaning densely covered with hairs.

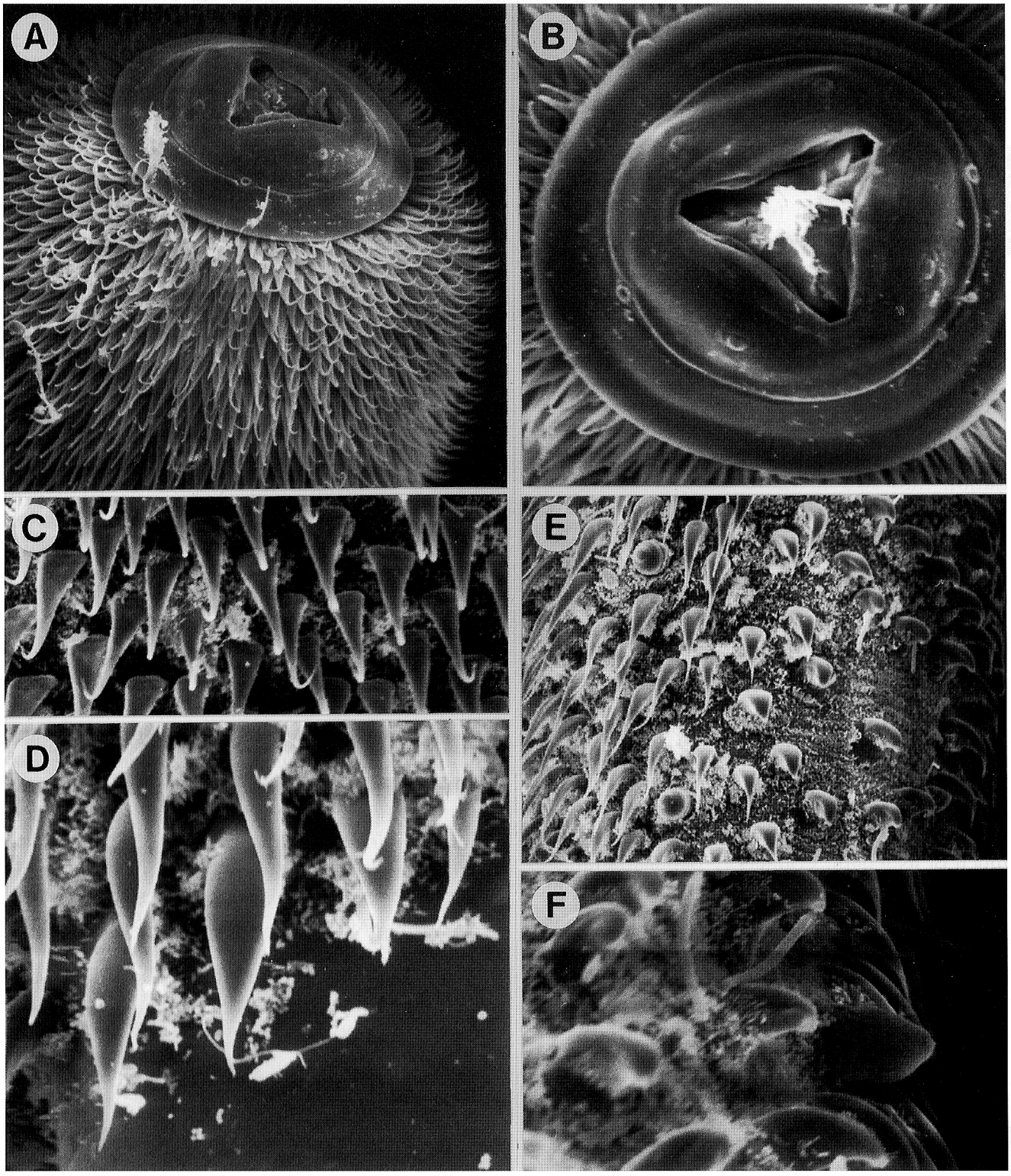

Fig. 3 - *R. acrulocantha* sp. n. SEM studies of adult. A: anterior region; B: *en face*; C: microtrichs in mid body region; D: microtrichs at their termination near the female anus; E: subventral view of male precloacal region showing change in shape and distribution of microtrichs and copulatory papillae; F: one of the elongate precloacal copulatory papillae.

sphincter muscle and an anteriorly directed, muscular, thick-walled vagina leading to vaginal diverticulum. Common uterus extending posteriorly from vaginal diverticulum before reflexing near vulva and then dividing into anterior and posterior uteri. Vaginal diverticulum extending anteriorly for about 250 µm from junction with common uterus and containing fibrous-like material. Genital tracts amphididelphic, reflexed with rounded spermatozoa visible in spermatheca of each tract. Genital tract conforming to Type 4 of Adamson (1987a). Genital tracts containing numerous (>30), ovoid eggs with smooth, thick-walled, shells. Uterine eggs (n=10) measuring 95±5.4 x 67±3.9 µm in size; contents showing signs of differentiation into two or more cells in vicinity of common uterus. Tail very long, conoid at first and then tapering evenly to a long, subulate portion with finely rounded terminus. Phasmids occuring on subulate portion, just posterior to conoid section of tail. Anterior anal lip slightly overhanging anus. Posterior anal lip not salient.

Male: spicules long, of similar size, ventrally arcuate with thin cuticular velum along distal part of ventral limb, although this does not extend to tip. Well developed protractor muscles sheathing proximal section of spicules; sheath with clearly marked circular muscle fibres for much of its length. Copulatory papillae arranged as nine to thirteen precloacal pairs plus single midventral papilla on anterior cloacal lip and four subventral postcloacal pairs. Bursa and gubernaculum absent. Tail long, dorsally convex-conoid and then ventrally subulate; dorsal contour of subulate section offset at its junction with conoid part.

Type host and locality

Posterior intestine of a 15 cm long, grey millepede collected by J. A. Sutherland at Bubia ARC, Lae, Morobe Province, Papua New Guinea.

Diagnosis and relationships

R. tomentosum sp. n. is characterized by: the densely pilose anterior region; the Type 4 genital system; the long spicules; nine to thirteen precloacal pairs of copulatory papillae; all four pairs of postcloacal papillae arranged subventrally and the tail shape in both sexes.

A vaginal diverticulum is reported for the following species: *R. africana* Dollfus, 1964; *R. acrulocantha* sp. n.; *R. alvarengai* Travassos *et* Kloss, 1960; *R. carlosi* Adamson, 1987 (1987b); *R. critesi* Ramírez, 1974; *R. infecta* Leidy, (1849) (= *R. nigella* Thomas, 1930); *R. lanceacauda* Hunt, 1981; *R. longecaudatum* Dollfus, 1952; *R. pinguilabellum* Hunt, 1981; *R. villosum* sp. n.; *R. subtruncatum* Dollfus, 1952; *R. thysanophora* Crites, 1965; *R. truncatum* Artigas, 1926; *R. zealandica* Clark, 1978. Of these, only *R. acrulocantha* sp. n., *R. villosum* sp. n. and *R. zealandica* are recorded from the same geographic region as *R. tomentosum* sp. n., the remainder emanating from either the Americas or Africa. *R. tomentosum* sp. n. differs from *R. zealandica* in that the uteri fuse to form a common uterus before joining the vagina at the vagina/diverticulum junction, whereas in the latter species both uteri apparently join the vagina separately (ie. Type 3 of Adamson, 1987a). *R. tomentosum* sp. n. is easily distinguished from *R. acrulocantha* sp. n. by the unique spination of the latter and from *R. villosum* sp. n., its closest relative, in having the pilose region comprising longer microtrichs which extend posteriorly for about 2 - 2.5 oesophagus lengths as opposed to one. *R. tomentosum* sp. n. and *R. villosum* sp. n. may well be sibling species differing in host and relatively few, yet consistent, morphological characters.

Type material

Holotype female, four paratype females and eight paratype males (slide numbers T504/7/1 to T504/7/4) in the type collection of the International Institute of Parasitology, St Albans, Herts., UK.

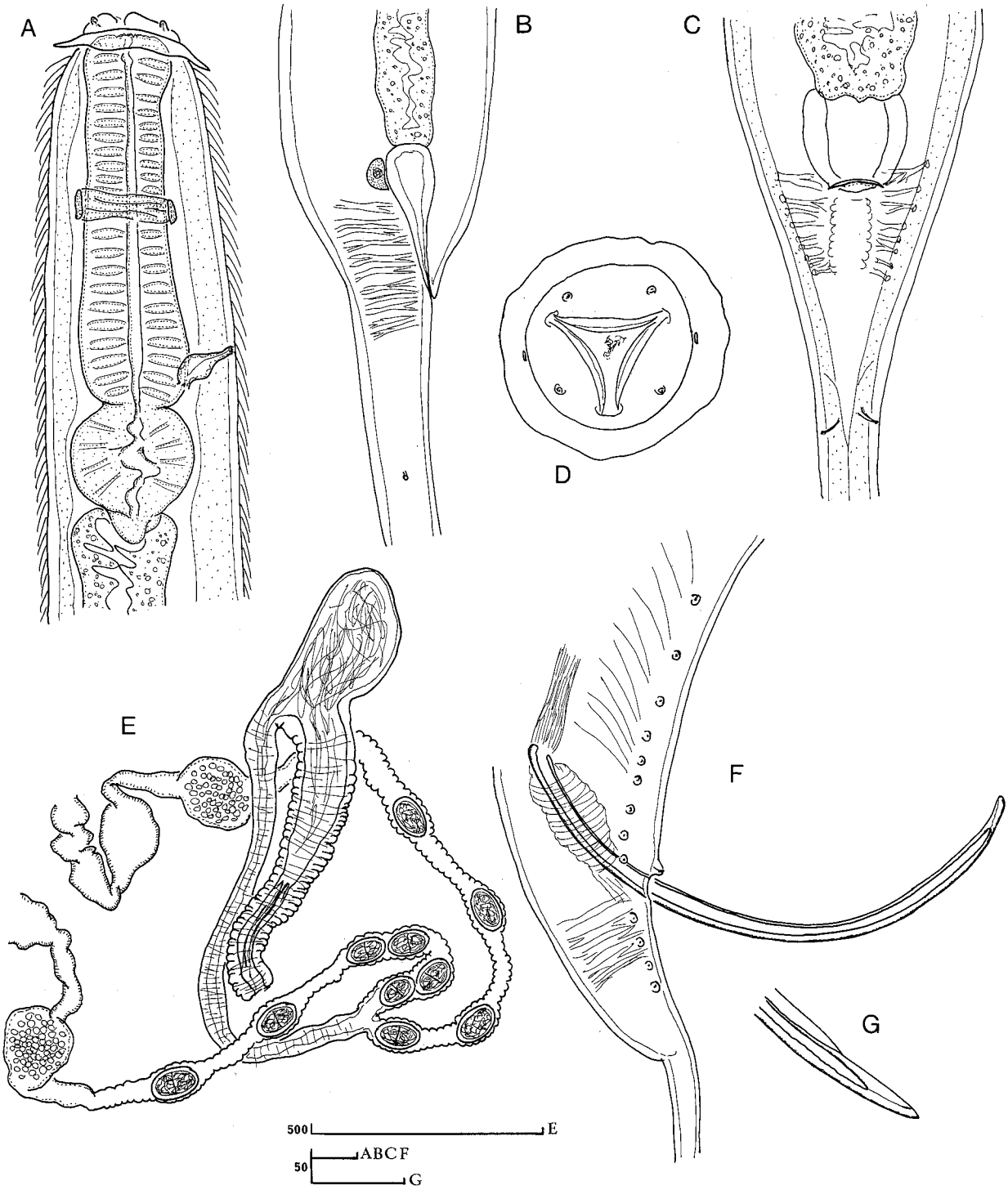

Fig. 4 - *Rhigonema tomentosum* sp. n. A: oesophagus; B, C: female tail - lateral and ventral views; D: *en face*, schematic; E: ovejector structure (dissected); F: male tail region; G: spicule tip.

*RHIGONEMA TRIBONOPHORA** sp. n.

(Figs 6, 7)

Female (n=10): L = 4.81±0.71 (3.72-5.65) mm; width = 275±64 (192-403) µm; oesophagus = 390±21 (361-419) µm; basal bulb (height x width) = 86±8.6 x 138±14.7 µm; anal body width = 87±18 (59-107) µm; tail = 0.54±0.03 (0.48-0.58) mm; head to vulva = 2.56±0.37 (1.95-3.01) mm; a = 17.5 (14.0-19.4); b = 12.3 (10.3-13.6); c = 9.0 (7.5-10.8); c' = 6.2 (5.0-8.2); V = 53.2 (50.6-58.4).

Male (n=11): L = 4.16±0.54 (3.12-5.16) mm; width = 241±44 (185-302) µm; oesophagus = 336±33 (270-393) µm; basal bulb (height x width) = 78±6.7 x 135±11.8 µm; anal body width = 85±14 (68-104) µm; tail = 0.34±0.05 (0.25-0.41) mm; left spicule (n=10) = 213±10.9 (192-231) µm; right spicule (n=10) = 213±17.0 (176-234) µm; a = 17.2 (16.0-20.1); b = 12.4 (10.1-14.6); c = 12.3 (9.6-16.2); c' = 4.0 (3.4-5.0).

Holotype female: L = 5.65 mm; width = 403 µm; oesophagus = 390 µm; anal body width = 87 µm; tail = 0.53 mm; head to vulva = 3.01 mm; a = 14.0; b = 13.5; c = 10.6; c' = 5.1; V = 53.3.

Adults: medium to long nematodes ranging from about 3.7 mm to over 5.6 mm in length for female and 3.1 to 5.2 mm for male. Cephalic region heavily cuticularized, consisting of broad cephalic cap followed by narrower cephalic collar. Cephalic cap circular in *en face* view and bearing four mammilliform papillae, two subdorsal and two subventral with amphids located laterally at junction of cap and cephalic collar. Cuticle with fine transverse striae, shortly pilose from cephalic collar for about one oesophagus lenght posteriorly. Oral opening triradiate; equilateral in form; dorsal and two subventral sectors of equal development. Three cuticularized plates articulating to form jawlike apparatus at anterior end of oesophagus with dorsal and two subventral plates of equal development and bearing a number of teeth and cuticular ridges. Oesophagus typical of genus, comprising powerful, muscular, cylindrical corpus; redundant isthmus and powerful, basal bulb broadest in anterior third and then tapering towards oesophago-intestinal junction. Basal bulb anchored to body wall by muscles attached to its broadest point. Three large cardia extending from bulb into intestine. Intestinal cells packed with granules. Nerve ring encircling corpus at about its mid-point. Excretory pore slightly anterior to corpus/basal bulb junction. Arcade cells forming palisade around oesophagus near anterior end.

Female: vulva open; in the form of broad, transverse slit and located in median region of body (V = 53). Vagina comprising sphincter muscle and an anteriorly directed, muscular, thick-walled *vagina vera* leading to a long, thinner walled, *vagina uterina* reflexed posteriorly to about vulval level and then flexed anteriorly for some distance before dividing into two uteri. Vaginal diverticulum absent. Genital tracts amphididelphic, reflexed with rounded spermatozoa visible in irregular, offset spermatheca of each tract. Genital system, although having two flexures in vagina, conforming to Type 2 of Adamson (1987a). Genital tracts containing few to numerous (10-50), ovoid eggs with smooth, thick-walled, shells. Uterine eggs (n=10) measuring 93±3.5 x 68±4.7 µm in size; contents showing signs of differentiation into two or more cells in more mature females. Tail long, conoid at first and then tapering evenly, except for a dorsal sinuosity, to a subulate proces. Posterior anal lip not salient.

Male: spicules relatively short, of similar size, ventrally arcuate with thin cuticular velum on ventral limb. Cuticle patterned with numerous small refractive dots. Spicule protractor muscles sheathing proximal region of spicules. Copulatory papillae arranged as five, more usually six, precloacal subventral pairs plus single midventral papilla on anterior cloacal lip and four subventral postcloacal pairs, making 19 or 21 in to-

* Derived from the Greek words *Itribonos* and *phorus*, meaning bearing a threadbare robe or cloak; a whimsical reference to the relatively scant pilosity of this worm.

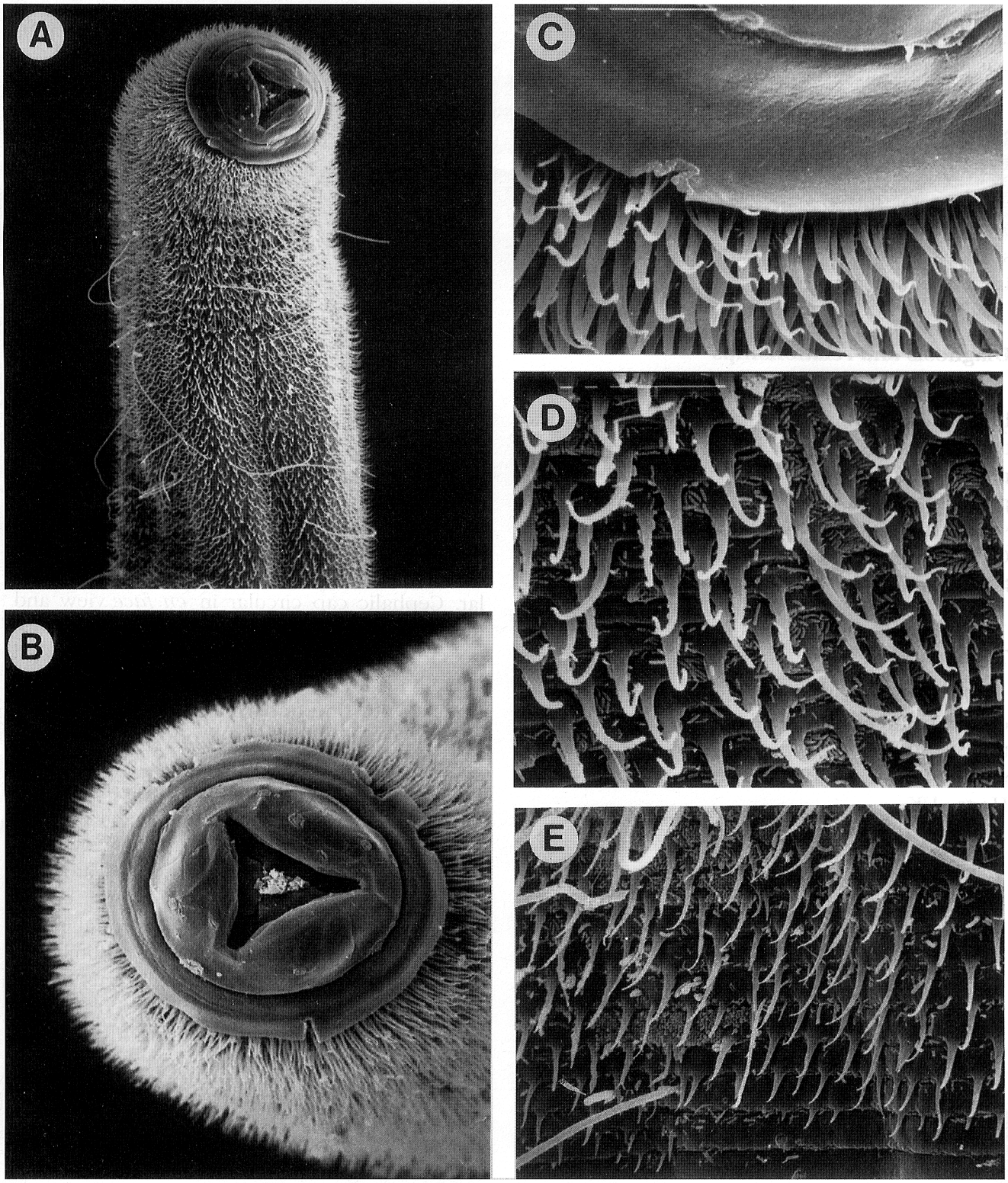

Fig. 5 - *R. tomentosum* sp. n. SEM studies. A: cervical region; B: *en face*; C: microtrichs immediately posterior to the cephalic collar; D, E: microtrichs further down the body and at their termination.

tal. Bursa and gubernaculum absent. Tail short, dorsally convex-conoid and then ventrally subulate.

Type host and locality

Posterior intestine of a 10 cm long, black and gold banded diplopod (?) *Polyconoceras* sp.) collected by J. A. Sutherland at Bubia ARC, Lae, Morobe Province, Papua New Guinea.

Diagnosis and relationships

R. tribonophora sp. n. is characterized by: long vagina with two flexures before joining the two uteri; pilosity restricted to the oesophageal region; short spicules; all paired copulatory papillae subventral in position; tail shape in both sexes. It is the only species from Papua New Guinea described herein to lack a vaginal diverticulum and to possess short spicules.

Type material

Holotype female, nine paratype females and eleven paratype males (slide numbers T504/8/1 to T504/8/6) in the type collection of the International Institute of Parasitology, St Albans, Herts., UK.

*RHIGONEMA VILLOSUM** sp. n.

(Fig. 8)

Female (n=11): L = 4.81±0.58 (3.61-5.85) mm; width = 253±37 (189-332) µm; oesophagus = 383±25 (348-445) µm; basal bulb (height x width) = 88±8.8 x 125±16.4 µm; anal body width = 98±7 (91-111) µm; tail = 0.86±0.08 (0.74-1.02) mm; head to vulva = 2.24±0.30 (1.85-2.84) mm; a = 19.0 (16.3-22.7); b = 12.5 (10.4-14.5); c = 5.6 (5.0-7.0); c' = 8.8 (7.5-11.2); V = 46.6 (42.9-51.6).

Male (n=12): L = 3.54±0.53 (2.57-4.41) mm; width = 163±37 (120-218) µm; oesophagus = 313±30 (263-354) µm; basal bulb (height x width) = 76±16.1 x 112±12.6 µm; anal body width = 81±18 (52-114) µm; tail = 0.52±0.07 (0.35-0.62) mm; left spicule = 474±44 (406-572) µm; right spicule = 468±46 (403-536) µm; a = 21.7 (16.5-31.5); b = 11.3 (8.7-13.2); c = 6.9 (4.6-9.0); c' = 6.4 (5.4-7.8).

Holotype female: L = 5.85 mm; width = 332 µm; oesophagus = 445 µm; anal body width = 111 µm; tail = 0.83 mm; head to vulva = 2.84 mm; a = 17.6; b = 13.1; c = 7.0; c' = 7.1; V = 48.6.

Adults: medium to long nematodes ranging from about 3.6 mm to over 5.8 mm in length for female and 2.6 to 4.4 mm for male. Cephalic region heavily cuticularized, consisting of broad cepalic cap followed by narrower cephalic collar. Cephalic cap circular in *en face* view and bearing four mammilliform papillae, two subdorsal and two subventral with amphids located laterally at junction of cap and cephalic collar. Cuticle with fine transverse striae, densely pilose near cephalic collar; pilosity becoming shorter and more sparse until it peters out about one oesophagus length posterior to collar. Oral opening triradiate; equilateral in form; dorsal and two subventral sectors of equal development. Three cuticularized plates articulating to form jawlike apparatus at anterior end of oesophagus; dorsal and two subventral plates of equal development and bearing a number of teeth and cuticular ridges. Oesophagus typical of genus, comprising powerful, muscular, cylindrical corpus; redundant isthmus and powerful, basal bulb, broadest in anterior third and then tapering towards oesophago-intestinal junction. Basal bulb anchored to body wall by muscles attached to its broadest point. Three large cardia extending from bulb into intestine. Intestinal cells packed with granules. Nerve ring encircling corpus at about its mid-point. Excretory

* Derived from the Latin *villosus*, meaning shaggy or hairy and referring to the pilosity.

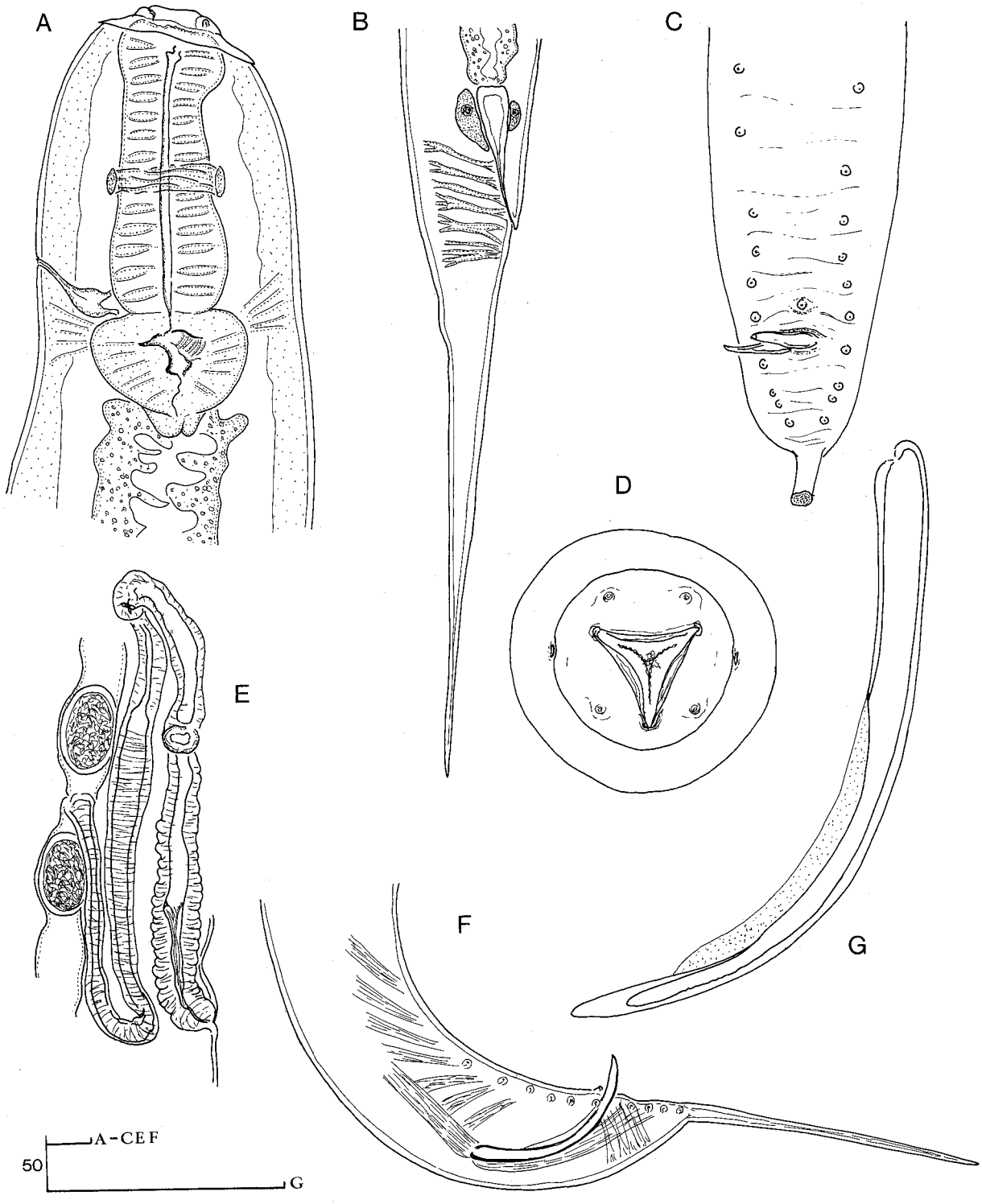

Fig. 6 - *Rhigonema tribonophora* sp. n. A: oesophagus; B: female tail; C: male tail, ventral view; D: *en face*, schematic; E: ovejector structure; F: male tail region; G: left spicule.

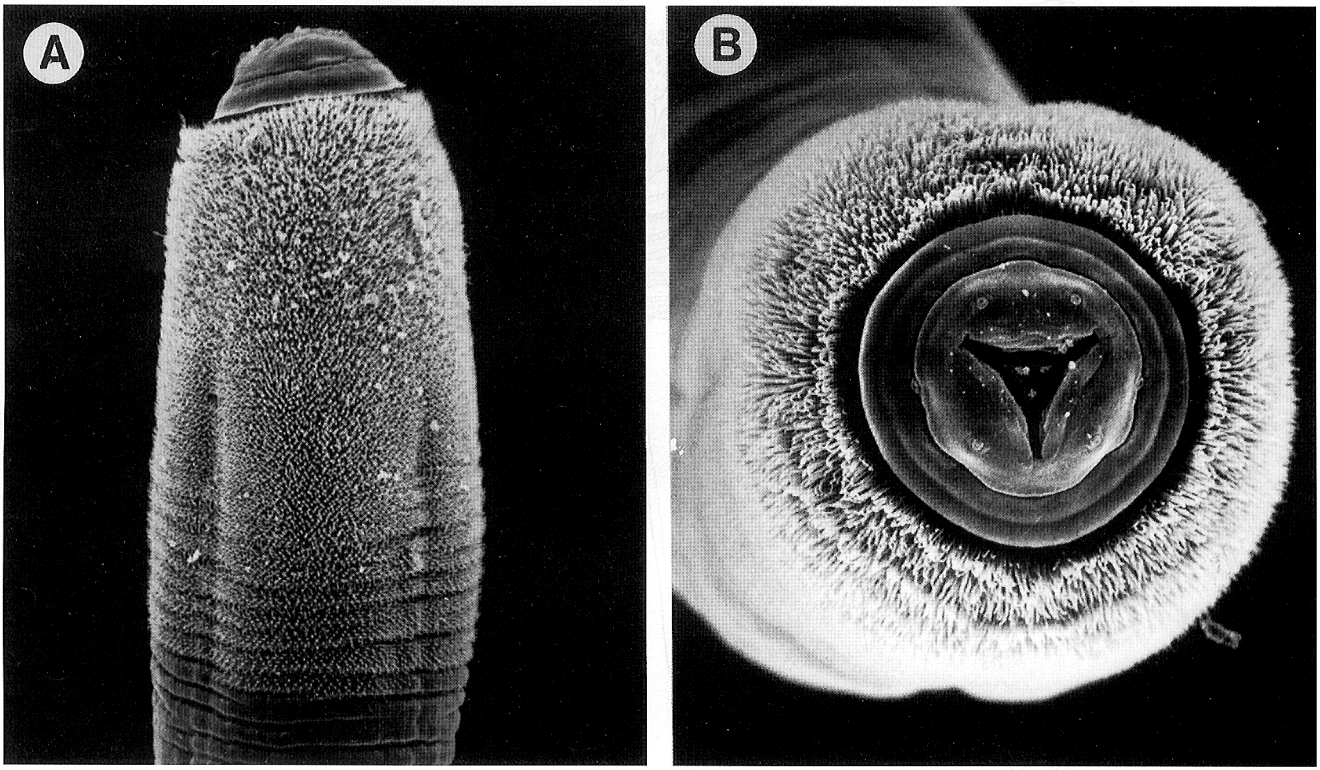

Fig. 7 - *R. tribonophora* sp. n. SEM studies. A: cervical region; B: *en face*.

pore just anterior to corpus/basal bulb junction. Arcade cells forming palisade around oesophagus near anterior end.

Female: vulva open, in form of broad, transverse slit located in median region of body (V = 46). Vagina comprising powerful sphincter muscle and an anteriorly directed, muscular, thick-walled vagina leading to long, thin-walled vaginal diverticulum. Long, common uterus extending posteriorly from about halfway along vaginal diverticulum to about vulval level before reflexing anteriorly for a short distance and dividing into anterior and posterior uteri. In a typical specimen, vagina measuring about 300 µm, vaginal diverticulum about 490 µm and common uterus about 600 µm in length. Genital tracts amphididelphic, reflexed with rounded spermatozoa visible in offset spermatheca of each tract. Genital tract conforming to Type 4 of Adamson (1987a). Each female containing relatively few (<30) ovoid eggs with smooth, thick-walled, shells. Uterine eggs (n=10) measuring 86±6.7 x 63±6.7 µm in size; contents showing no signs of differentiation. Tail long, tapering evenly to pointed terminus. Anterior lip slightly overhanging anus. Posterior anal lip not salient.

Male: spicules long, of similar size, ventrally arcuate with smooth capitulum continuing line of shaft. Protractor muscles strongly developed, forming sheath-like structure around proximal half of protracted spicules. Sheath marked by circular muscles with longitudinal muscles at proximal end attaching to spicule head and at distal end to subdorsal body wall of tail. Copulatory papillae arranged as nine to eleven subventral precloacal pairs plus single midventral papilla on anterior cloacal lip and four subventral postcloacal pairs, thus making 27 to 31 in

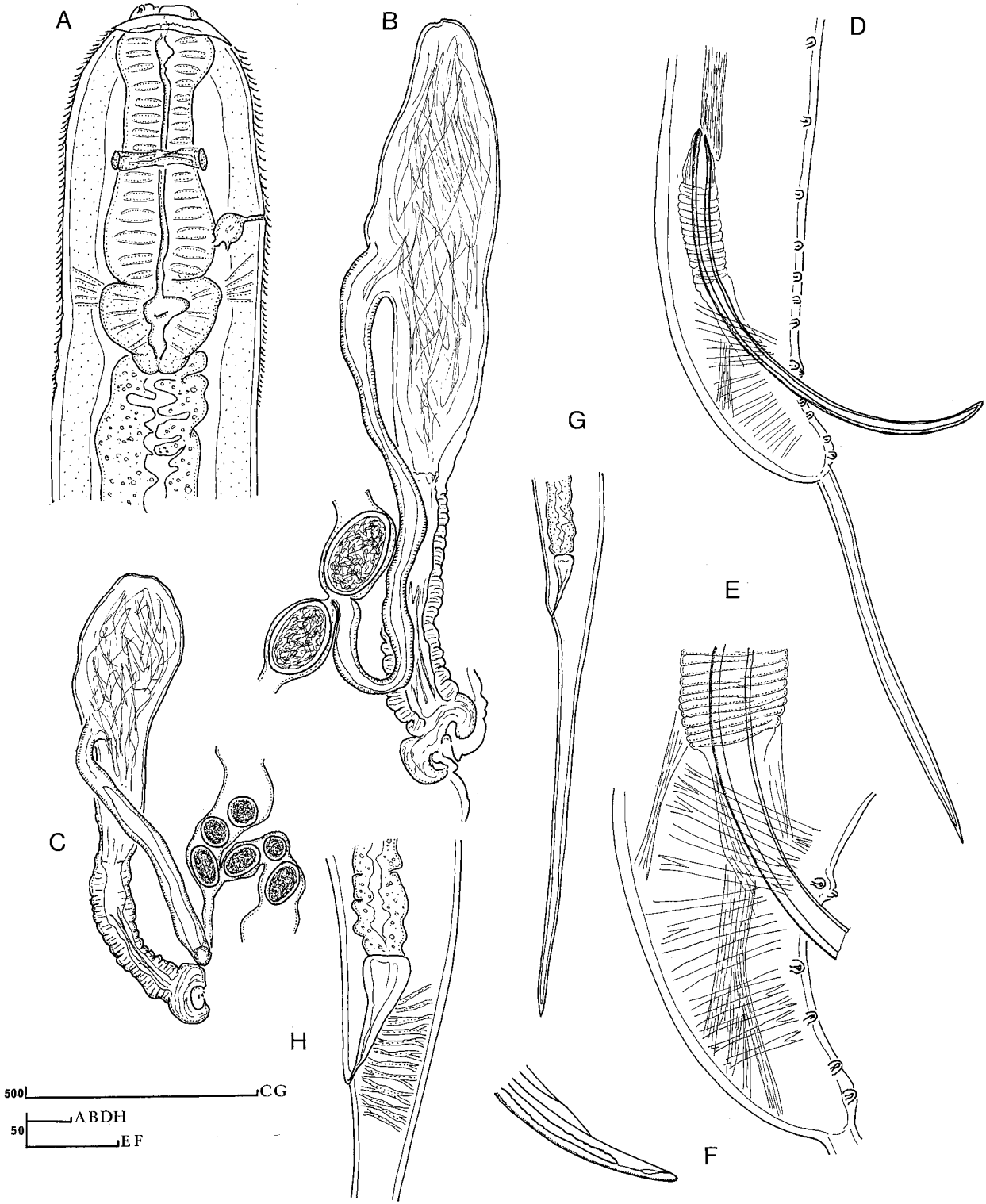

Fig. 8 - *Rhigonema villosum* sp. n. A: oesophagus; B, C: ovejector structure (C is dissected); D: male tail region; E: cloacal region; F: spicule tip; G: female tail; H: female anal region.

total. Bursa and gubernaculum absent. Tail initially dorsally convex-conoid and then with long subulate process which is clearly dorsally offset from conoid section of tail.

Type host and locality

Posterior intestine of a 10 cm long, black and gold banded diplopod (? *Polyconoceras* sp.) collected by J. A. Sutherland at Bubia ARC, Lae, Morobe Province, Papua New Guinea.

Diagnosis and relationships

R. villosum sp. n. is characterized by: female genital system having a long vaginal diverticulum with an elongate common uterus extending posteriorly from it before reflexing and dividing into the two uteri; long, evenly tapering female tail; long, similarly shaped and sized spicules; number and arrangement of the copulatory papillae; male tail shape and length.

A vaginal diverticulum is reported for the following species: *R. acrulocantha* sp. n.; *R. africana* Dollfus, 1964; *R. alvarengai* Travassos *et* Kloss, 1960; *R. carlosi* Adamson, 1987 (1987b); *R. critesi* Ramírez, 1974; *R. infecta* Leidy, (1849) (= *R. nigella* Thomas, 1931); *R. lanceacauda* Hunt, 1981; *R. longecaudatum* Dollfus, 1952; *R. pinguilabellum* Hunt, 1981; *R. subtruncatum* Dollfus, 1952; *R. thysanophora* Crites, 1965; *R. truncatum* Artigas, 1926; *R. tomentosum* sp. n.; *R. zealandica* Clark, 1978. Of these, only three species, *R. acrulocantha* sp. n., *R. tomentosum* sp. n. and *R. zealandica* share the same geographic area as *R. villosum* sp. n., the others being from the Americas or Africa. *R. villosum* sp. n. is closest to *R. tomentosum* sp. n. from which it can most easily be distinguished by: pilose region extending a shorter distance posteriorly (about one as opposed to 2 - 2.5 oesophagus lengths); shorter and more sparse microtrichs; differently shaped tail in both sexes. *R. acrulocantha* sp. n. is easily distinguished because of its unique pilosity extending from head to tail with the microtrichs being fewer in number, much larger and heavily cuticularized. *R. zealandica* differs in possessing a much smaller diverticulum with both uteri discharging separately into it; shorter tail in both sexes; shorter and differently shaped spicules; many fewer precloacal papillae.

Type material

Holotype female, ten paratype females and twelve paratype males (slide numbers T504/6/1 to T504/6/6) in the type collection of the International Institute of Parasitology, St Albans, Herts., UK.

Discussion

The genus *Rhigonema* is widely distributed through the tropical and subtropical regions which formerly constituted Gondwanaland, but contains at least two valid species from North America, presumably the result of a later northward migration. On the basis of the arrangement of the postcloacal copulatory papillae in the male, the genus can be divided into two broad groups: 1) those species with all such papillae arranged subventrally and 2), those species with several, typically three, pairs shifted to a sublateral/subdorsal position. The first group is recorded from the Americas, Australasia and the Pacific region and the second group from Africa and India with other species from Malaysia (Van Waerebeke, 1986), Myanmar (Hunt and Moore, 1995) and Vietnam (Hunt and Spiridonov, 1995). All the species described herein from Papua New Guinea conform to the general Australasian pattern and have all the postcloacal papillae located subventrally. Several undescribed species of *Rhigonema* from Sulawesi diplopods (Hunt, pers. obsv.) also share this arrangement. As *R. erringtoni* from the Malay

Peninsular has the typical Afro-Indian pattern (Van Waerebeke, 1986) and *R. modigliani* (Parona, 1896), a *species inquirenda* from the Mentawei Islands off the west coast of Sumatra, has only subventral papillae illustrated (Parona, 1896), it is reasonable to assume that somewhere in the Indonesian archipelago the two types of pattern meet and possibly coexist, although in this regard it should be borne in mind that the spirobolid family Rhinocricidae, members of which harbour the majority of the described rhigonematids, are distributed mainly to the east of the Wallace Line in the Indo-Australian region (Hoffman, 1982). As a consequence, it would be both interesting and instructive to examine material from the swarm of small islands situated east of the Sunda Platform in the vicinity of the Wallace Line and the Weber Line; an area where the migration of the Australasian-type fauna westwards meets the eastward migration of the Asiatic fauna.

This paper almost concludes the descriptions of new rhigonematid and oxyurid nematodes from just two species of Papua New Guinea diplopod. The oxyurids comprise *Travassosinema morobecola* Hunt, 1993 from the black and gold banded diplopod (Hunt, 1993) and representatives of *Coronostoma* and *Desmicola* in both millipede species. The rhigonematids, by far the most diverse and numerous inhabitants, are represented by three species of *Carnoya* (Hunt and Sutherland, 1985); two species of *Ichthyocephaloides* (Hunt and Sutherland, 1984; Hunt, 1994c); five species of *Heth* (Hunt, 1994a); a new genus and species of Rhigonematidae (Hunt, 1994b); four species of *Rhigonema* described herein; a new species of *Ransomnema* (Hunt, 1994d) and a new genus, presumed to be an ancestral form of *Heth*, with but a single species (unpublished) - some 17 new species and three new genera of Rhigonematida in all.

Diplopods have a strong tendency to speciate (Loomis and Schmitt, 1971) and to form endemic species swarms, particularly on islands, whilst Hoffman (1982) estimated that the approximately 10, 000 described species of millipede represented only a sixth of the actual world fauna. These factors, together with the small proportion of species investigated for nematodes so far, indicate the immense scope for further study, not only on the speciation within the group, but also on the ecology and niche partitioning of these fascinating nematodes.

Acknowledgements. I thank J. A. Sutherland for collecting the diplopods, Janet Machon and Janice Sheldon for the SEM work and Judith Ashurst for technical assistance.

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Accepted for publication on 30 May 1995.