Fundam. appl. Nematol., 1998, **21** (3), 281-297

Rhigonematida from New Britain diplopods. 1. The genus *Carnoya* Gilson, 1898 (Ransomnematoidea: Carnoyidae) with descriptions of three new species

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Accepted for publication 21 July 1997.

Summary – The genus *Carnoya* Gilson, 1898 is defined and the nominal species listed. Three new species are described from spirobolid diplopods from the island of New Britain and illustrated with the aid of SEM. *C. caputbulla* sp. n. is characterized by the female cephalic region having an offset, knob-like annule; by the form and distribution of the female cervical spines; the form of the broad lateral alae in the female; the form of the lateral alae in the male; a reduced complement of eleven papillae and their disposition; the annulation of the unarmed male cervical region and the extremely long tail and broad annules in both sexes. *C. posterovulva* sp. n. is characterized by the knob-like cervical annule in the female; the uniquely posterior position of the vulva; the cervical spination in the female; the disposition of the reduced complement of eleven male copulatory papillae; the annulation of the male cervical region; the male possessing a single cervical spine collar bearing about sixteen, well separated, spines and by the extremely long tail and broad annules in both sexes. *C. janiceae* sp. n. is characterized by the female cephalic region lacking an offset, knob-like annule; by the form and distribution of the female cervical spines; the form of the broad lateral alae in the female; the undulation of the lateral alae at cloacal level in the male; the disposition of the thirteen male papillae; the annulation of the unarmed male cervical region and the long tail and broad annules in both sexes. The taxonomy of the genus and the value of certain morphological characters are discussed and the species from the Americas and the Australasian/Pacific region compared and contrasted. © Orstom/Elsevier, Paris

Résumé – ***Rhigonematidae de Diplopodes de Nouvelle-Bretagne. 1. Le genre* Carnoya *Gilson, 1898 (Ransomnematoidea : Carnoyidae) et description de trois espèces nouvelles*** – Le genre *Carnoya* Gilson, 1898 est défini et une liste de ses espèces nominales établie. Trois nouvelles espèces extraites de Diplopodes Spirobolides provenant de l'île de Nouvelle-Bretagne sont décrites et illustrées, y compris au MEB. *C. caputbulla* sp. n. est caractérisé par la région céphalique femelle présentant un anneau en bouton, la forme et la répartition des épines cervicales femelles, la forme des larges ailes de la femelle et celle des ailes du mâle, le faible nombre (onze) de papilles réduites supplémentaires et leur répartition, l'annélation de la région cervicale du mâle laquelle n'est par renforcée, la queue extrêmement longue et les larges anneaux chez les deux sexes. *C. posterovulva* sp. n. est caractérisé par l'anneau cervical en bouton de la femelle, la position postérieure unique de la vulve, la présence d'épines cervicales chez la femelle, la position des onze papilles copulatrices réduites, l'annélation de la région cervicale du mâle, la présence d'un seul collier céphalique de seize épines bien séparées chez le mâle, la queue extrêmement longue et les larges anneaux chez les deux sexes. *C. janiceae* sp. n. est caractérisé par la région céphalique femelle sans anneau en bouton, la forme et la répartition des épines cervicales chez la femelle, la forme des larges ailes de la femelle, l'ondulation des ailes latérales au niveau du cloaque chez le mâle, la disposition des treize papilles mâles, l'annélation de la région cervicale du mâle, laquelle n'est pas renforcée, la longue queue et les larges anneaux chez les deux sexes. La taxinomie du genre et la valeur de certains caractères morphologiques sont discutées et les espèces des Amériques et de la région Australasie/Pacifique sont comparées et différenciées. © Orstom/Elsevier, Paris

Keywords: *Carnoya*, diplopods, morphology, New Britain, nematodes, new species, SEM.

In 1996, the second author made two collections of spirobolid diplopods (Diplopoda: Spirobolida) from New Britain. Fixed material of a slender greyish-brown diplopod about 10-12 cm long and of narrow cross section was collected at Kerevat in early 1996 and live material of two species of diplopod was obtained from three sites in western New Britain in November 1996. One of these latter species appeared to be the same as the Kerevat material whereas the other was black and yellow banded (the terminal seven or eight segments being entirely black) with pinkish-orange legs and antennae, about 10 cm long and of a considerably more robust body form. Descriptions in this paper are based on material from both collections, although most of the measurements were derived from nematodes from the freshly killed diplopods of the November collection as they were better preserved. Diplopods were killed by decapita-

tion and dissected immediately on arrival at the International Institute of Parasitology, St Albans and the nematodes from the gut picked out, killed with hot water (60°C) and fixed in TAF.

Rhigonematids of several genera (*Rhigonema* Cobb, 1898, *Heth* Cobb, 1898, *Carnoya* Gilson, 1898, *Ransomnema* Artigas, 1926, *Ichthyocephaloides* Hunt & Sutherland, 1984, *Zalophora* Hunt, 1994) were obtained, mostly representing new species. Other oxyurid nematodes encountered included *Desmicola* Basir, 1956, *Travassosinema* Rao, 1958, *Coronostoma* Rao, 1958 and a new genus, currently of uncertain placement. This paper describes the new members of the Carnoyidae. Males were assigned to females on a combination of unique association, relative size, similarity in lateral ala development and relative abundance. Permanent mounts were made in glycerine after dehydration via a slow evaporation technique. Selected specimens for SEM study were postfixed overnight in 1% osmium tetraoxide, dehydrated through a graded series of ethanol, critical point dried and sputter coated with gold. The specimens were examined at an accelerating voltage of 10 kV.

The family Carnoyidae comprises a handful of morphologically unusual genera found in the gut of a variety of millipede hosts. All known members of the family are monoxenous parasites of subtropical and tropical diplopods and have been recorded from South America and the West Indies, Africa, India, Australasia and the Pacific region. The type genus and species, *Carnoya vitiensis*, was described by Gilson (1898) from Fiji and was remarkable because of the rings of posteriorly directed spines in the cervical region of the female. Subsequent to this paper a further twelve species of *Carnoya* were described, mostly from South America (Artigas, 1926; Dollfus, 1952; Adamson, 1984, 1985), but also from either the West Indies (Adamson, 1984; Adamson & Van Waerebeke, 1985; Spiridonov, 1989) or Papua New Guinea (Hunt & Sutherland, 1984). The genus was last diagnosed by Adamson (1984), since when a number of additional species have been described and the morphological characterisation expanded. Accordingly, a full diagnosis of the genus is provided herein together with a list of the nominal species and the descriptions of the additional three new species proposed. Characters of taxonomic importance are discussed and the morphology of the Australasian forms compared to that of the American species.

Genus *Carnoya* Gilson, 1898

Diagnosis

Carnoyidae. Small nematodes about 1 to 3 mm long. Sexually dimorphic in cervical region. Body dorsoventrally flattened or rounded in cross section. Lateral alae narrow, very broad or absent. Body annulation fine or extremely broad.

Female: Cephalic region either knob-like and separated from rest of body by a narrow, strongly annulated neck region or more evenly tapering and lacking the offset knob-like region. Lateral alae usually starting just posterior to cervical spine collars and extending to about anal level or beyond. Oral opening hexagonal or polygonal. Buccal cavity consisting of a short, thick walled capsule containing one or two sets of teeth and a long, tubular portion surrounded by anterior oesophageal tissue. Oesophagus initially very narrow with transverse striae, rapidly expanding to a cylindroid corpus, offset at both ends. Isthmus long, narrow, leading to the spheroid basal bulb. Cervical region with a number of transverse rows of spines of varying appearance. Vulva usually in anterior half of the body (as measured from head to anus), rarely posteriorly and may be median or subventral in position, often on the left side of the body, but may be on the right. Vagina long, muscular, usually directed posteriorly (anteriorly in one species) to the common uterus. Two ovaries directed anteriorly. Eggs few in number, large and thin shelled. Tail long to very long, subulate.

Male: Cephalic region with one dorsal and two subventral lips. Buccal cavity initially subtriangular, then tubular and thin walled leading to a thick walled section tapering towards the oesophageal lumen. Posterior portion of buccal capsule may have three cuticular projections, one dorsal and two subventral. Cervical spines present either as a single or double spiny collar or as numerous transverse rows of minute spines, or entirely absent. Oesophagus comprising a long, narrow, tubular section leading to a short, well defined isthmus and a spheroid basal bulb. Spicules paired, separate, similar. Gubernaculum prominent, boat shaped, lacking a dorsal hole. Copulatory papillae typically numbering thirteen (occasionally eleven), arranged as a single median papilla on anterior cloacal lip, at least one pair precloacal with another two pairs either precloacal or at cloacal level and three (rarely two) pairs postcloacal, the last pair being on the tail spike. Tail long to very long, subulate.

Type species

C. vitiensis Gilson, 1898

Other species

C. caputbulla sp. n.
C. dollfusi Adamson, 1984
C. dubia Dollfus, 1952*
C. fimbriata Hunt & Sutherland, 1984

* *C. dubia* is known only from the male holotype and was redescribed by Adamson (1984).

C. guantanamera Spiridonov, 1989*
C. janiceae sp. n.
C. kermarreci Adamson & Van Waerebeke, 1985
C. mackintoshae Adamson, 1985
C. martiniquensis Adamson, 1984
C. paradubia Adamson, 1984
C. perbella Hunt & Sutherland, 1984
C. posterovulva sp. n.
C. pyramboia Artigas, 1926**
C. strobilina Hunt & Sutherland, 1984
C. venezuelensis Adamson, 1984

DISTRIBUTION

South America (Brazil, Paraguay, Venezuela), West Indies (Cuba, Guadeloupe, Martinique), Fiji, Papua New Guinea, New Britain, Sulawesi (Hunt, unpubl.).

HOSTS

Intestine of Rhinocricidae, order Spirobolida (*Anadenobolus*, *Rhinocricus* and other unidentified genera).

BIONOMICS

Unknown, although they probably feed on the microbial flora in the gut. The intestine immediately posterior to the basal bulb is expanded to form a ventriculus which is offset from the rest of the gut by a constriction. The gut usually contains a relatively small amount of fine particulate material of indeterminate nature, although spores, some apparently empty, as large as 8 × 5 µm do occur (pers. observ.). The majority of this material is to be seen in the ventricular region. Eggs will embryonate and hatch in tapwater, the first stage juveniles then moulting to the second, presumably the infective, stage (Spiridonov, 1989).

DESCRIPTIONS

As pointed out by Hunt and Sutherland (1984), there are difficulties in accurately measuring the usual morphometric parameters in these animals because of their ability to telescope the large annules, particularly in the cervical region of the female and the tendency for the body to become even more dorso-ventrally flattened during processing. In many females, particularly those with the knob-like cephalic region, the entire cervical region can become highly contracted and the cephalic region withdrawn into the body. This makes measurement of the female oesophagus both difficult and inaccurate as the isthmus, which may comprise 20-25% or more of the oesophagus length in fully relaxed specimens, may be so folded as to apparently disappear, the corpus and basal bulb being virtually contiguous. For these reasons the body width is not recorded herein and the fully relaxed oesophagus state, when it occurs, is indicated separately in the measurements. Measurement of the male spicules and gubernaculum can also be inaccurate as the males, at least of the Australasian species, often die straight and, being slightly dorso-ventrally flattened with broad lateral alae, usually present the dorsal or ventral surface uppermost when mounted. Spicules and gubernacula measured in this way are substantially shorter than when measured laterally along the median line. Characterization of the species in this group should be focussed more on morphological features such as the cephalic region, cervical annulation and spination, type of somatic annulation, form and extent of the lateral alae, vulval position, disposition of the male copulatory papillae and form of the spicules and gubernaculum. The most useful ratios are V, V′ and c. The SEM is a very useful tool in elucidating the cervical spination, the full potential of which as a species character has yet to be realized.

*Carnoya caputbulla** sp. n.

(Figs 1, 2, 3)

MEASUREMENTS

Holotype (female; anterior region extended): L = 1.83 mm; L′ = 0.90 mm; head to posterior end of stoma = 66 µm; corpus = 75 µm; isthmus = 60 µm; basal bulb = 58 µm; total oesophagus length = 259 µm; anterior end to vulva = 490 µm; vulva to anus = 410 µm; tail = 927 µm; b = 7.1; c = 2.0; V = 27; V′ = 54.

Females (anterior region extended; paratypes; n = 7): L = 1.70 ± 0.12 (1.48-1.84) mm; L′ = 0.84 ± 0.05 (0.73-0.89) mm; head to posterior end of stoma = 68 ± 4.2 (63-76) µm; corpus = 79 ± 1.4 (76-80) µm; isthmus = 61 ± 3.1 (56-66) µm; basal bulb = 56 ± 2.2 (53-60) µm; total oesophagus length = 264 ± 6.2 (256-273) µm; anterior end to vulva = 480 ± 29 (427-523) µm; vulva to anus = 361 ± 24 (308-381) µm; tail = 857 ± 71 (745-950) µm; b = 6.0 (5.7-6.8); c = 2.0 (1.9-2.1); V = 28 (27-29); V′ = 57 (56-59).

Females (anterior region contracted); population from Kerevat (n = 5): L = 1.52 ± 0.07 (1.47-1.64) mm; L′ = 0.71 ± 0.04 (0.68-0.76) mm; head to posterior end of stoma = 56 ± 9 (40-62) µm; corpus = 76

* *C. guantanamera* was originally distinguished from all other species by having numerous (about twenty) cervical spine rows in the male (Spiridonov, 1989). However, virtually all of the species proposed by Adamson (1984, 1985) have multiple spine rows, a fact apparently overlooked by Spiridonov as he did quote the Adamson's papers. From the description the male appears to have a highly unusual arrangement of the copulatory papillae, but this needs to be confirmed.

** *C. pyramboia* types are lost (see Kloss, 1965, who also gives additional data).

* Specific epithet derived from the Latin, *bulla* = knob and *caput* = head, and referring to the knob-like head.

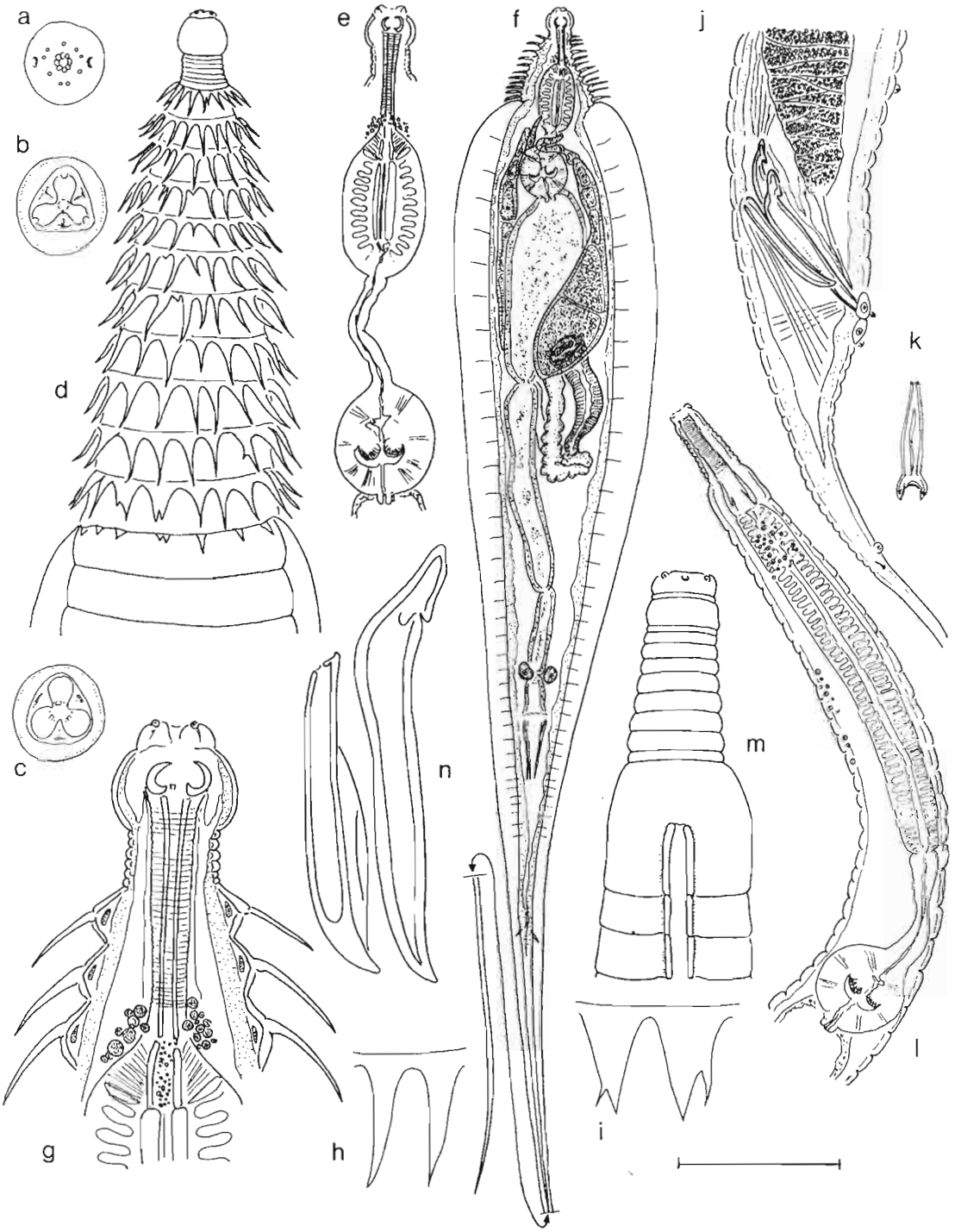

Fig. 1. Carnoya caputbulla *sp. n. Female: A-I. A: En face; B, C: Optical sections through anterior stoma; D: Cervical region, surface view; E: Oesophagus; F: Entire worm, dorsal view; G: Stoma and anterior oesophagus; H, I: Cervical spines. Male: J-N. J: Posterior region, lateral view; K: Gubernaculum, ventral view; L: Oesophagus; M: Cervical region, surface view; N: Spicule and gubernaculum. (Scale bars: F = 170 µm; D, E, J, K, L = 85 µm; A, B, C, G, H, I, M, N = 35 µm).*

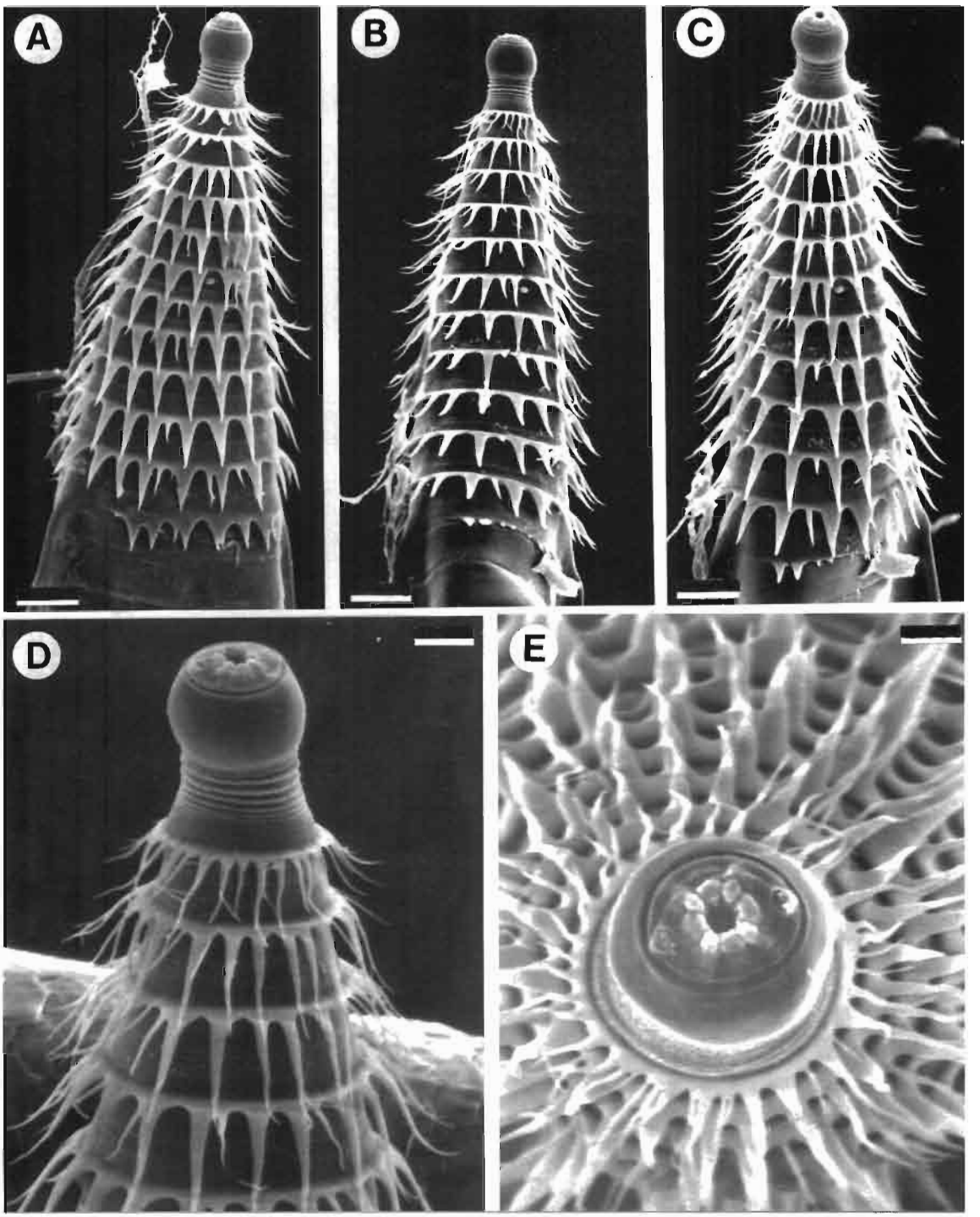

Fig. 2. Carnoya caputbulla *sp. n. Female. A-D: Cervical region; E: En face view. (Scale bars: A, C = 25 μm; B = 28 μm; D = 11 μm; E = 6 μm).*

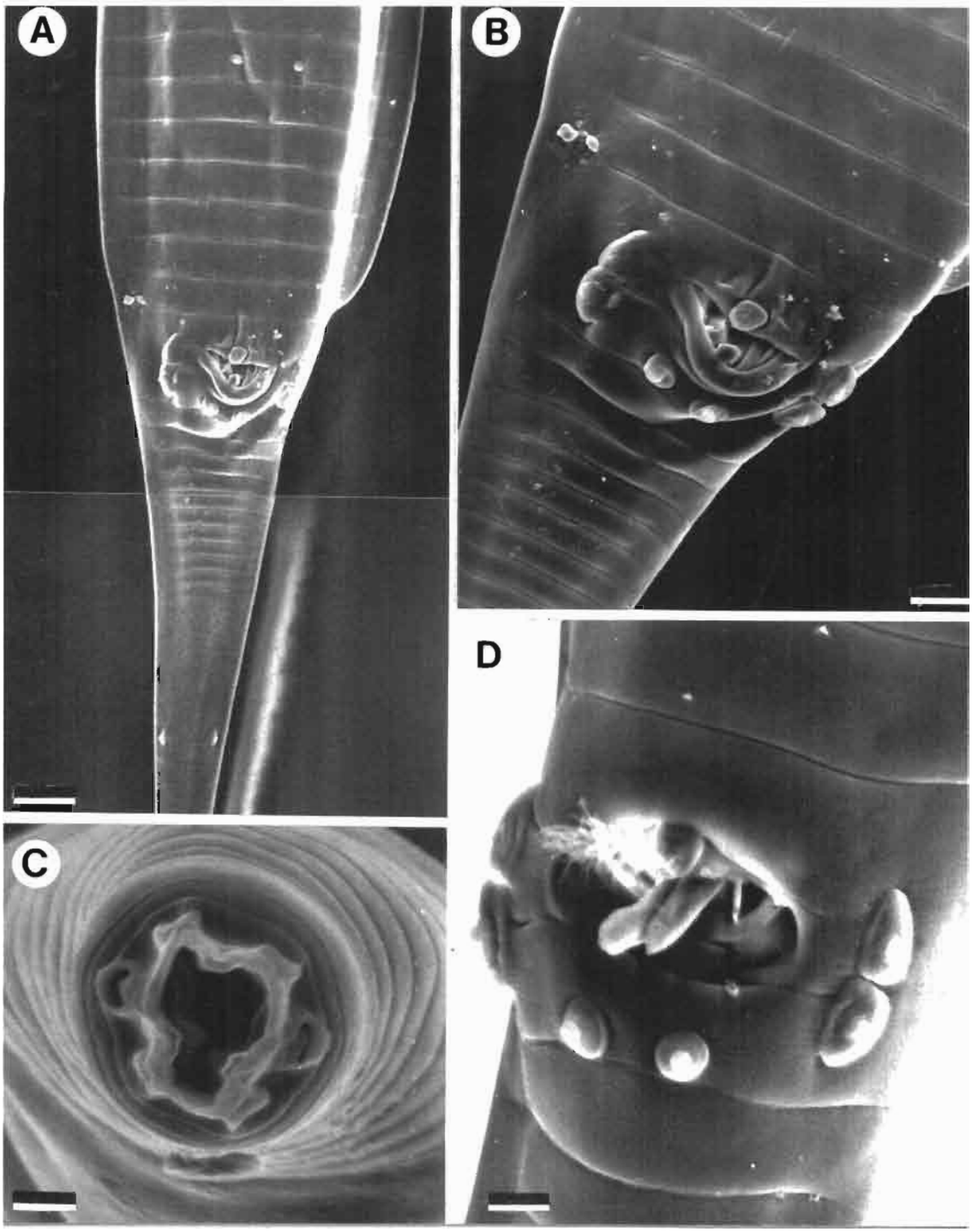

Fig. 3. Carnoya caputbulla *sp. n. Male. A: Posterior region showing all papillae; B, D: Cloacal region; C: En face view. (Scale bars: A = 25 µm; B = 12.5 µm; C = 2.6 µm; D = 6 µm).*

± 3.4 (73-81) µm; isthmus = 62 ± 8.3 (51-73) µm; basal bulb = 53 ± 3.6 (48-58) µm; total oesophagus length = 246 ± 21 (212-263) µm; anterior end to vulva = 326 ± 28 (298-367) µm; vulva to anus = 380 ± 16 (354-397) µm; tail = 819 ± 43 (775-880) µm; b = 6.2 (5.9-6.9); c = 1.9 (1.8-1.9); V = 21 (20-23); V′ = 46 (44-49).

Males (lateral mounts), (paratypes; n = 11): L (n = 10) = 1.38 ± 0.04 (1.30-1.46) mm; L′ = 0.76 ± 0.03 (0.68-0.80) mm; head to posterior end of stoma = 70 ± 6 (60-76) µm; corpus = 217 ± 6 (206-225) µm; isthmus = 61 ± 6.5 (46-70) µm; basal bulb = 52 ± 4 (50-60) µm; total oesophagus length = 400 ± 12 (378-412) µm; tail (n = 10) = 629 ± 24 (596-680) µm; spicule (n = 9) = 98 ± 7.3 (90-111) µm; gubernaculum (n = 9) = 69 ± 3.9 (63-75) µm; b = 3.5 (3.2-3.7); c = 2.2 (2.1-2.3).

DESCRIPTION

Adults: Small nematodes, females about 1.5-1.85 mm long, males 1.3-1.46 mm long. Sexually dimorphic in cervical region. Body slightly dorsoventrally flattened in unmounted females and males. Heat relaxed females dying almost straight with cervical region usually extended; males either C-shaped or slightly ventrally arcuate.

Female: Cephalic region knob-like, about 28 (25-30) µm wide, heavily cuticularized and separated from rest of body by a narrow neck region of seven or eight annules, the three annules in the middle being broader. There are four cephalic papillae and two lateral amphids. Broad lateral alae present, up to about 45-50 µm high; starting in the region of the basal bulb and extending to about anal level before tapering smoothly into the tail. Body annules broad, about 27-30 µm apart. Oral opening octagonal and surrounded by eight lobes arranged as one dorsal, two subdorsal, two lateral, two subventral and one ventral. Buccal cavity consisting of a short, thick walled capsule about 16 (15-18) µm deep, formed from smooth cuticle and containing one dorsal and two subventral teeth and a long tubular portion about 40 µm long surrounded by the anterior oesophageal tissue. Oesophagus initially very narrow with prominent transverse striations about 0.7 µm apart, rapidly expanding to the cylindroid corpus, offset at both ends. Isthmus long, narrow, leading to the spheroid basal bulb. Nerve ring just anterior to corpus. Cervical region with eleven complete transverse rows of spines and one incomplete row at the level where the lateral alae commence. This last row may be better developed on the dorsal side. The first collar comprises about 32 spines with filamentous tips, but the number is variable due to some spines sharing the same base. Individual spines are relatively few in number (about eighteen in the penultimate ring) large, evenly tapering to fine, filamentous points and with broad, non-contiguous bases in the more posterior collars. Some spines are bifurcate, usually terminally, but occasionally at some distance from the tip. Spines forming the last ring are much shorter than those of preceeding rings. There are multiple fine transverse striae between the anteriormost spine collars. Vulva transversely oval, often covered by a brownish plaque, located at about midway between head and anus (about eight-nine annules posterior to the commencement of alae) and may be median or slightly left subventral in position. Vagina long, muscular, directed posteriorly to a common uterus. Two ovaries directed anteriorly; germinal zones extending to, or slightly in excess of, basal bulb level. Eggs few in number, large and thin shelled. Tail initially conoid; attenuating to a very long subulate process. Conspicuous phasmids located about two to three anal body widths behind crescentic anus.

Male: Cephalic region with one dorsal and two subventral lips. Four cephalic papillae, a pair of lateral amphids and six minute papilla-like structures around oral opening. Buccal cavity initially subtriangular, then tubular and thin walled leading to a thick walled section tapering towards oesophageal lumen. Posterior portion of buccal capsule with three simple cuticular projections, one dorsal and two subventral. Cervical region with ten or eleven annules before the broad annule on which the alae commence, the second being larger than the others and the first and last smaller. Cervical spines absent. Lateral alae relatively broad, abruptly narrowing to body contour at cloacal level. Body annules broad, perhaps 22 µm apart dorsally and 17 µm apart ventrally on a specimen dying in the typical C-shape. Oesophagus comprising a long, narrow, tubular section leading to a short, well defined isthmus and a spheroid basal bulb. Spicules paired, separate, isomorphic and isometric. Gubernaculum prominent, boat shaped, lacking a dorsal hole; a ventral keel locates between the spicules and distal flanges clasp the spicule shafts on either side. Copulatory papillae numbering eleven, arranged as one precloacal pair at eight-nine annules anterior to cloaca, plus a single median papilla on anterior cloacal lip, two pairs in tandem at cloacal level, each papilla being on a raised platform about 13-14 µm long, one subventral pair (with duplex nerve endings) on first annule posterior to cloaca and one subventral pair on tail spike. Tail long, subulate.

TYPE HOST AND LOCALITY

Type population from posterior intestine of the slender diplopod from Kimbé, New Britain. Also found in the same species of diplopod from Kerevat, New Britain.

TYPE MATERIAL

Holotype female, eight paratype females and seven paratype males in the type collection of the International Institute of Parasitology, St. Albans, UK and four paratype females and four paratype males in the nematode type collection at the Muséum National d'Histoire Naturelle, Paris, France.

DIAGNOSIS AND RELATIONSHIPS

C. caputbulla sp. n. is characterized by the female cephalic region having an offset, knob-like cervical annule; by the form and distribution of the female cervical spines; the form of the broad lateral alae in the female; the form of the lateral alae in the male; a reduced complement of eleven copulatory papillae and their disposition; the annulation of the unarmed male cervical region and the extremely long tail and broad annules in both sexes. The combination of very long tail and broad annules in both sexes immediately distinguishes *C. caputbulla* sp. n. from all of the American species and the long tail from *C. vitiensis* from Fiji. In having a knob-like cephalic region this species resembles *C. posterovulva* sp. n. and *C. strobilina*. It can be readily distinguished from the former by the anterior position of the vulva, the disposition of the male papillae (particularly the position of the precloacal pair and the arrangement of the two adcloacal pairs) and the form of the male cervical region, particularly the lack of a cervical spine collar and in having the second postcephalic annule larger than the others (spine collar with sixteen spines and all cervical annules about the same size in *C. posterovulva* sp. n.). From *C. strobilina* it differs in having the vulva located on annules eight or nine posterior to the commencement of the lateral alae as opposed to five to eight; smaller spicules (90-111 *vs* 118-137 µm); number (eleven *vs* thirteen) and disposition of the male papillae; male cervical region with ten or eleven annules as opposed to five.

*Carnoya posterovulva** sp. n.

(Figs 4; 5A, B)

MEASUREMENTS

Holotype (female; anterior region partially contracted): L = 2.35 mm; L′ = 1.11 mm; head to posterior end of stoma = 67 µm; corpus = 97 µm; isthmus (contracted) = 18 µm; basal bulb = 70 µm; total oesophagus length = 252 µm; anterior end to vulva = 800 µm; vulva to anus = 307 µm; tail = 1241 µm; b = 9.3; c = 1.9; V = 34.1; V′ = 72.3.

Females, anterior region contracted, (paratypes; n = 5): L = 2.06 ± 0.07 (1.97-2.14) mm; ; L′ = 1.0 ± 0.08 (0.92-1.09) mm; head to posterior end of stoma (n = 3) = 66 ± 5.5 (62-72) µm; corpus = 95 ± 4.9 (89-100) µm; isthmus = 60-80 µm (when outstretched); basal bulb = 72 ± 9.3 (63-84) µm; total oesophagus length = 286 ± 38 (242-310) µm; anterior end to vulva = 768 ± 72 (667-840) µm; vulva to anus = 231 ± 23 (206-253) µm; tail = 1056 ± 51 (987-1127) µm; b = 7.4 (6.9-8.6); c = 1.9 (1.9-2.1); V = 37 (34-40); V′ = 77 (73-79).

Male (paratype; n = 1): L = 1.39 mm; L' = 0.89 mm; head to posterior end of stoma = 37 µm; corpus = 117 µm; isthmus = 23 µm; basal bulb = 30 µm; total oesophagus length = 207 µm; tail = 500 µm; spicule = 145 µm; gubernaculum = 92 µm; b = 6.7; c = 2.8.

DESCRIPTION

Adults: Small, plump nematodes, females about 2-2.4 mm long; male 1.4 mm long. Sexually dimorphic in cervical region. Body slightly dorsoventrally flattened in unmounted females and broader towards the posteriorly located vulva. Heat relaxed females tend to die straight, although the cervical region is usually strongly contracted making measurement of oesophageal structures, particularly the highly folded isthmus both inaccurate or impossible (in fully relaxed females isthmus 60-80 µm long and forming a considerable proportion of the total oesophagus length). The solitary male dying in a C shape.

Female: First annule of cephalic region offset, knob-like, about 30 µm in diameter; formed from thick, smooth cuticle lacking transverse striae and separated from rest of body by a narrow neck region divided into three-four prominent annules and several smaller ones. Lateral alae well developed, about 40-50 µm high, starting in region of basal bulb and tapering gently into tail cuticle. Body with very broad annules, 26-30 µm apart at midbody. Oral opening irregularly hexagonal and surrounded by four cephalic papillae and a pair of lateral amphids. In en face view the oral opening surrounded by nine refractive rods arranged as a single dorsal, two pairs of subdorsal, two single subventral and a ventral pair. These representing the tips of supporting cuticular rods emanating from three cuticular plates (= chevron shaped pieces of Adamson, 1985) arranged as one dorsal and two subventral, each rod at the two extremities of each plate being almost contiguous with those of adjacent plates, thus giving rise to the alternation of single and paired rods seen in apical view. Buccal cavity consisting of a short, thick walled capsule (formed from smooth cuticle) containing one dorsal and two subventral teeth and a long tubular portion surrounded by the anterior oesophageal tissue. Oesophagus initially very narrow with prominent transverse striations, rapidly expanding to the cylindroid corpus, offset at both ends. Isthmus narrow, often strongly contracted and leading to

* The specific epithet refers to the posterior position of the vulva, a unique feature in the genus to date.

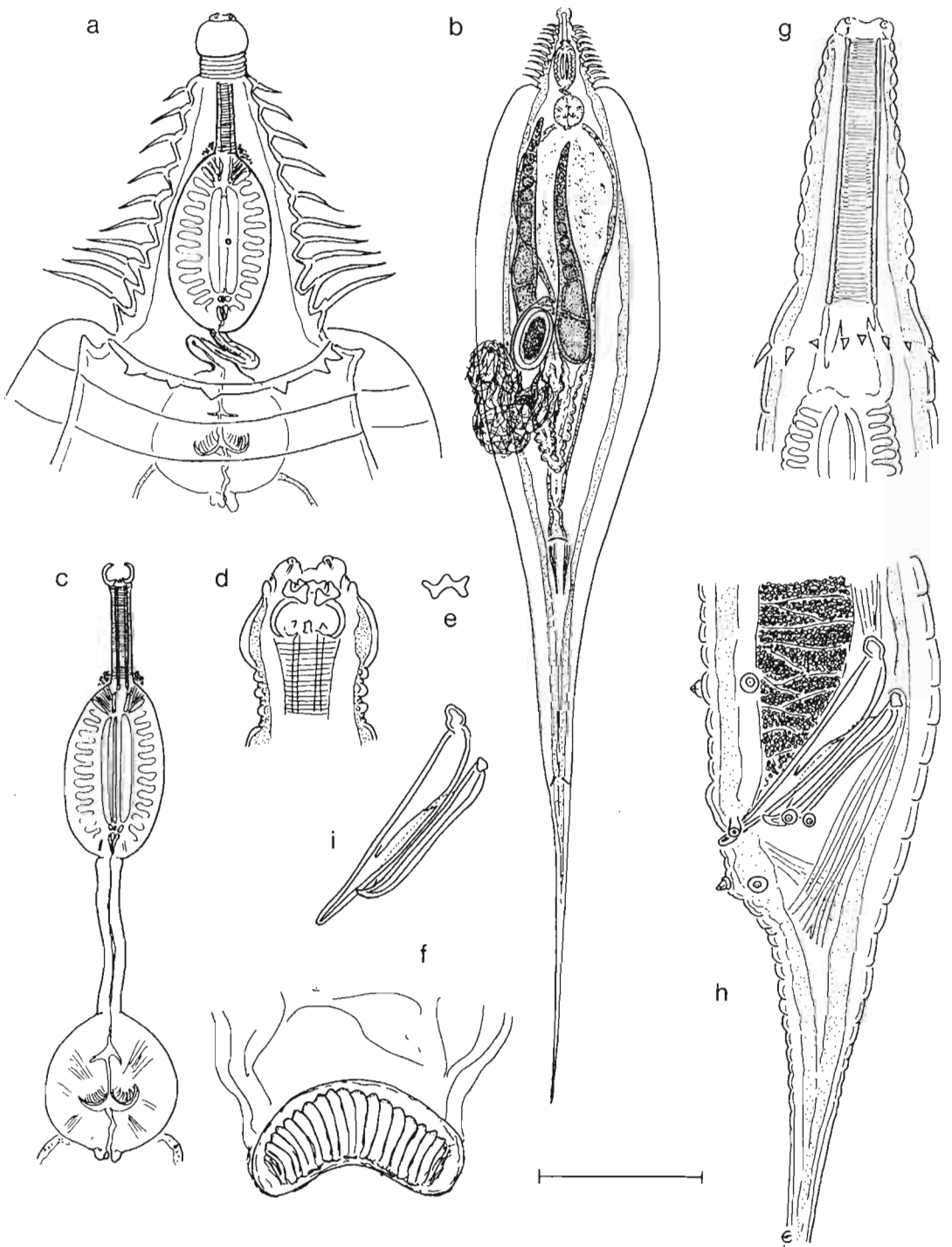

Fig. 4. Carnoya posterovulva *sp. n. Female: A-F. A: Cervical region, ventral view; B: Entire worm, ventral view; C: Oesophagus; D: Cephalic region, ventral view, showing three cuticular supports; E: Dorsal cuticular support from stoma; F: Vulval region, ventral view – Male: G-I. G: Cervical region and stoma; H: Posterior region, lateral view; I: Spicule and gubernaculum. (Scale bars: B = 345 µm; A, C, H, I = 85 µm; D, E, F, G = 35 µm).*

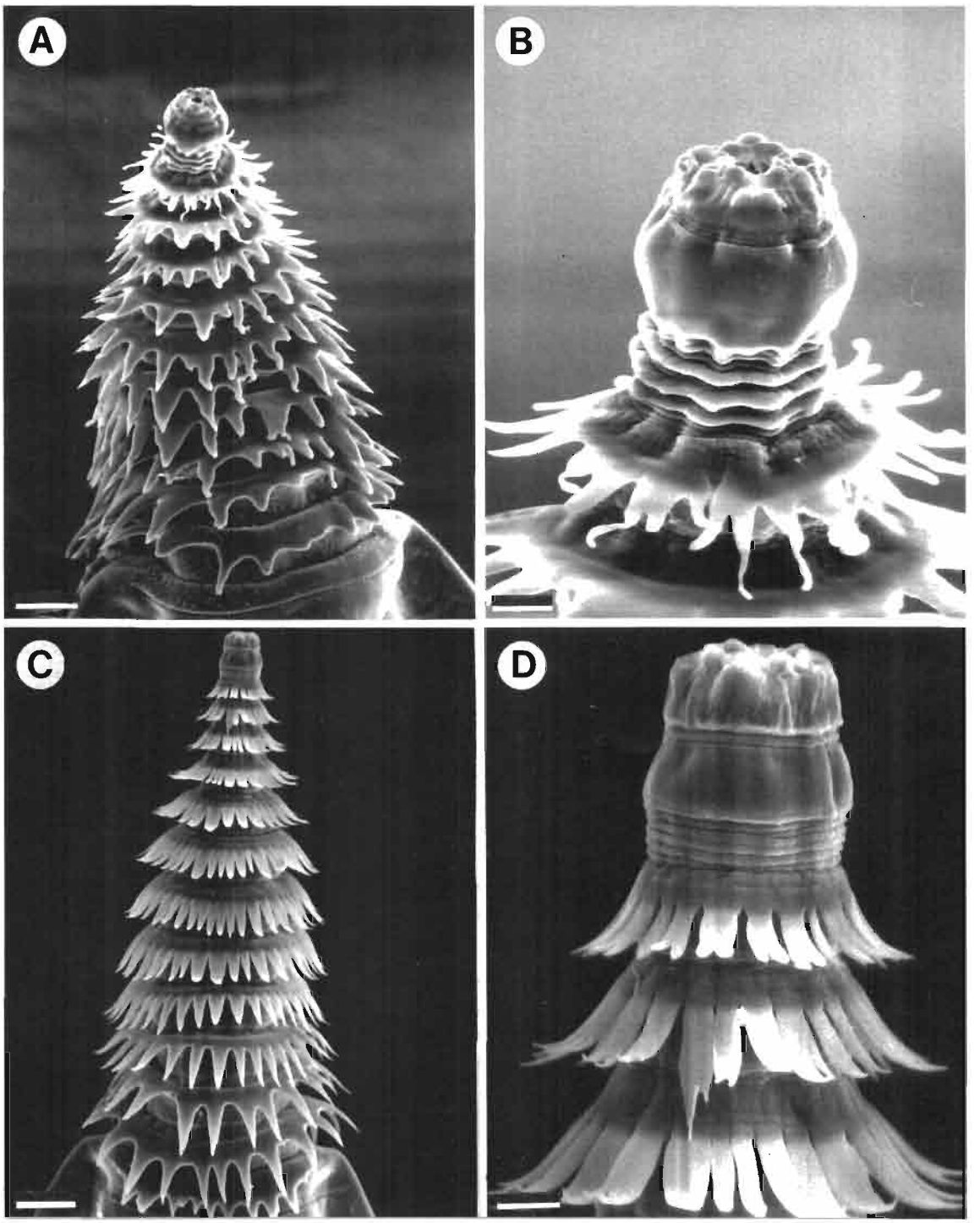

Fig. 5. Carnoya posterovulva *sp. n. Female. A: Cervical region; B: Cephalic region* - Carnoya janiceae *sp. n. C: Cervical region; D: Cephalic region. (Scale bars: A = 19 µm; B = 6 µm; C = 22 µm; D = 5 µm).*

the spheroid, valvate, basal bulb. Nerve ring located just anterior to corpus. Excretory pore obscure, located between spine collars six and seven. Anterior intestine expanded to form a ventriculus almost filling body width. Cervical region with ten complete transverse rows of dagger-like spines and an additional incomplete row at the commencement of the lateral alae. This last row may be spineless and represented by a thickened ridge of cuticle ventrally, but more usually has a few scattered, poorly developed spines. First spine collar with about 28-30 spines. Vulva about 50 µm across; with about eighteen rib-like structures when seen in ventral view and covered by a brownish plaque. Vulva obliquely angled to the body axis, in the posterior third of body (measured as head to anus) on about 24th annule posterior to last spine ring and right ventrolateral in position. Vagina broad and muscular, about 200 µm long, directed anteriorly; the common uterus being posteriorly directed before joining the two oviducts. Two ovaries directed anteriorly, one on either side of intestine and with reflexed tips. Uterine eggs few in number, large (130-133 × 75-78 µm) and thin shelled. Two specimens each having two eggs containing a fully embryonated juvenile folded about 3.75 times within the egg. Crescentic anus about ten annules posterior to vulva. Tail very long, subulate. Phasmids on subulate portion.

Male: Cephalic region with one dorsal and two subventral lips; four cephalic papillae and a pair of lateral amphids. Buccal cavity initially subtriangular, then tubular and thin walled with finely striated cuticle leading to a thick walled section tapering towards the oesophageal lumen. Posterior portion of buccal capsule with three cuticular projections, one dorsal and two subventral, each terminating in a simple process. Body annules broad, about 22 µm wide dorsally at midbody. Cervical region narrow with about eleven annules before the broad annule bearing the spine collar and the commencement of the alae. Lateral alae prominent, commencing just behind cervical collar and tapering on to tail region. Cervical spines present as a single spiny collar bearing about sixteen, irregularly sized and arranged spines. Oesophagus comprising a long, relatively narrow, tubular section leading to a short, well defined isthmus and a spheroid basal bulb. Spicules paired, closely adpressed; isomorphic and isometric. Gubernaculum prominent, boat shaped, lacking a dorsal hole, with a midventral keel and distal flanges. Copulatory papillae numbering eleven, arranged as a single median papilla on anterior cloacal lip, a subventral precloacal pair about 33 µm (or five annules) anterior to cloaca, two pairs at cloacal level arranged in a transverse line, a subventral pair near posterior cloacal lip (this pair bears duplex nerve endings and presumably represents a fusion of the two pairs normally located in this position) and a subventral pair about 80 µm posterior to cloaca on subulate portion of tail, just anterior to phasmids. Tail long, subulate; terminus finely pointed.

TYPE HOST AND LOCALITY

Intestine of the more slender of the two spirobolid millipedes, collected at Hargy Estate, Bialla, New Britain in November, 1996. This species was only found once and in very low numbers (seven females, one of which was sacrificed for SEM studies, and one male). No other species of *Carnoya* was present in the host, although other nematodes in the gut included *Rhigonema* sp. n., *Ichthyocephaloides* sp. n., *Heth* sp. n., *Heth* cf. *zeuglocantha* Hunt, 1994, *Travassosinema*, *Desmicola* and an unusual new genus of oxyurid.

TYPE MATERIAL

Holotype female, three paratype females and one paratype male in the type collection of the International Institute of Parasitology, St Albans, UK and two paratype females in the Muséum National d'Histoire Naturelle, Paris, France.

DIAGNOSIS AND RELATIONSHIPS

Carnoya posterovulva sp. n. is characterized by the knob-like cephalic annule in the female; the uniquely posterior position of the vulva; the cervical spination in the female; the disposition of the reduced complement of eleven male copulatory papillae; the annulation of the male cervical region; the male possessing a single cervical spine collar bearing about sixteen, well separated, spines and by the extremely long tail and broad annules in both sexes. It can be distinguished from all other nominal species by the posterior vulva with the uterus running anteriorly as opposed to an anterior to median vulva with the uterus directed posteriorly. Under the SEM the cervical spine margins in the only female studied appear to be more irregular in appearance when compared to the other species from the Australasian area. This is not apparent under the light microscope and may be the result of distortion caused during the critical point drying stage of the preparation.

Carnoya janiceae* **sp. n.**

(Figs 5C; D 6, 7)

MEASUREMENTS

Holotype (female; anterior region extended): L = 1.85 mm; L′ = 0.97 mm; head to posterior end of stoma = 83 µm; corpus = 114 µm; isthmus = 88 µm; basal bulb = 78 µm; total oesophagus length = 363 µm; anterior end to vulva = 567 µm; vulva to anus

* Named in honour of Janice Sheldon in recognition of her excellent contributions to the scanning electron microscopy of rhigonematids.

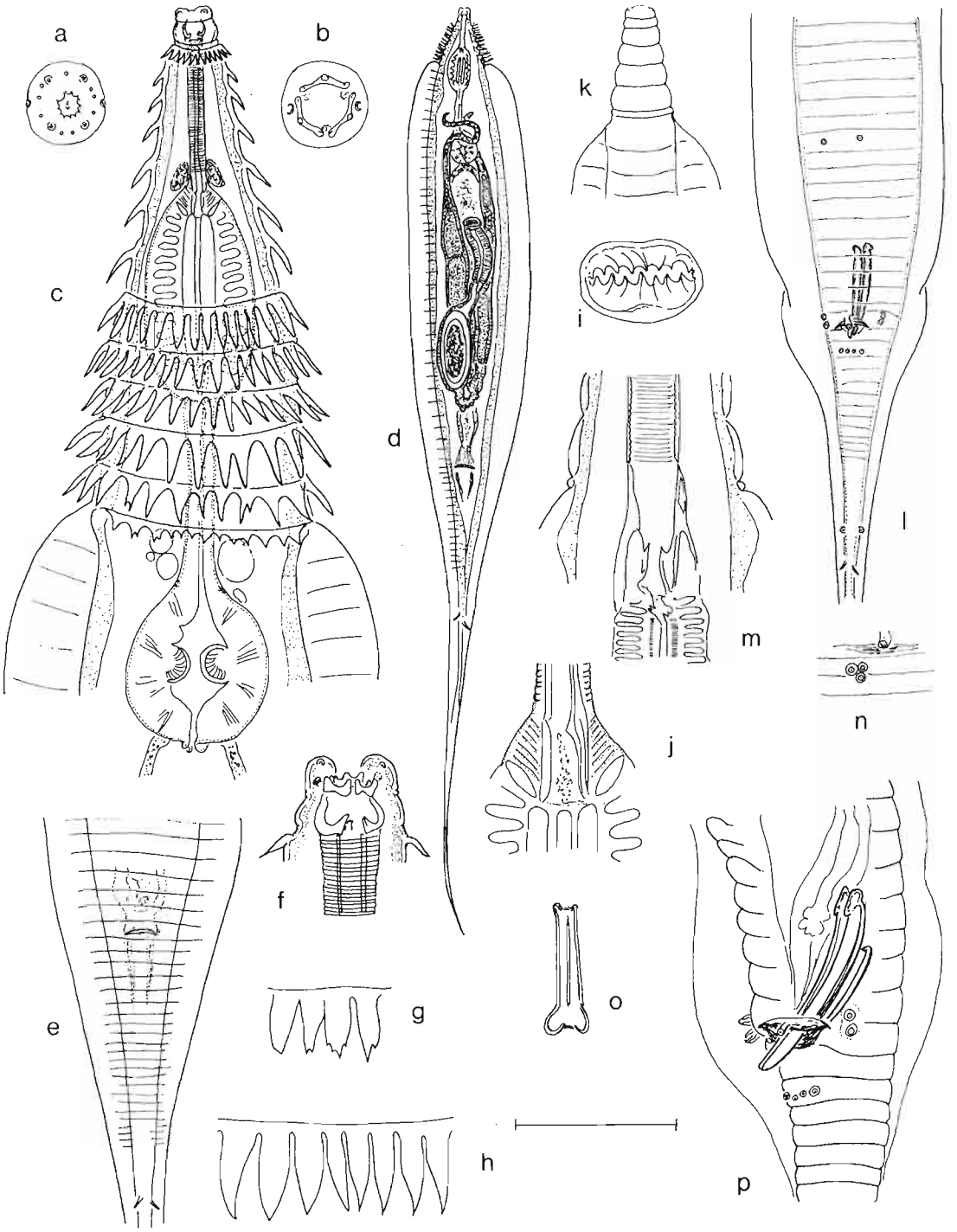

Fig. 6. Carnoya janiceae *sp. n. Female: A-J. A: En face; B: Optical section through stoma at level of the three cuticular supports; C: Cervical region; D: Entire worm, ventral view; E: Tail region, ventral view; F: Cephalic region; G, H: Cervical spines; I: Vulval region, ventral view; J: Junction of anterior oesophageal region with the corpus. Male: K-P. K: Cervical region, surface view; L: Posterior region, ventral view; M: Base of stoma; N: Unusual papillal arrangement posterior to cloaca; O: Gubernaculum, ventral view; P: Posterior region, ventrolateral view. (Scale bar: D = 345 µm; E, L = 170 µm; C, K, O, P = 85 µm; A, B, F, G, H, I, J, M, N = 35 µm).*

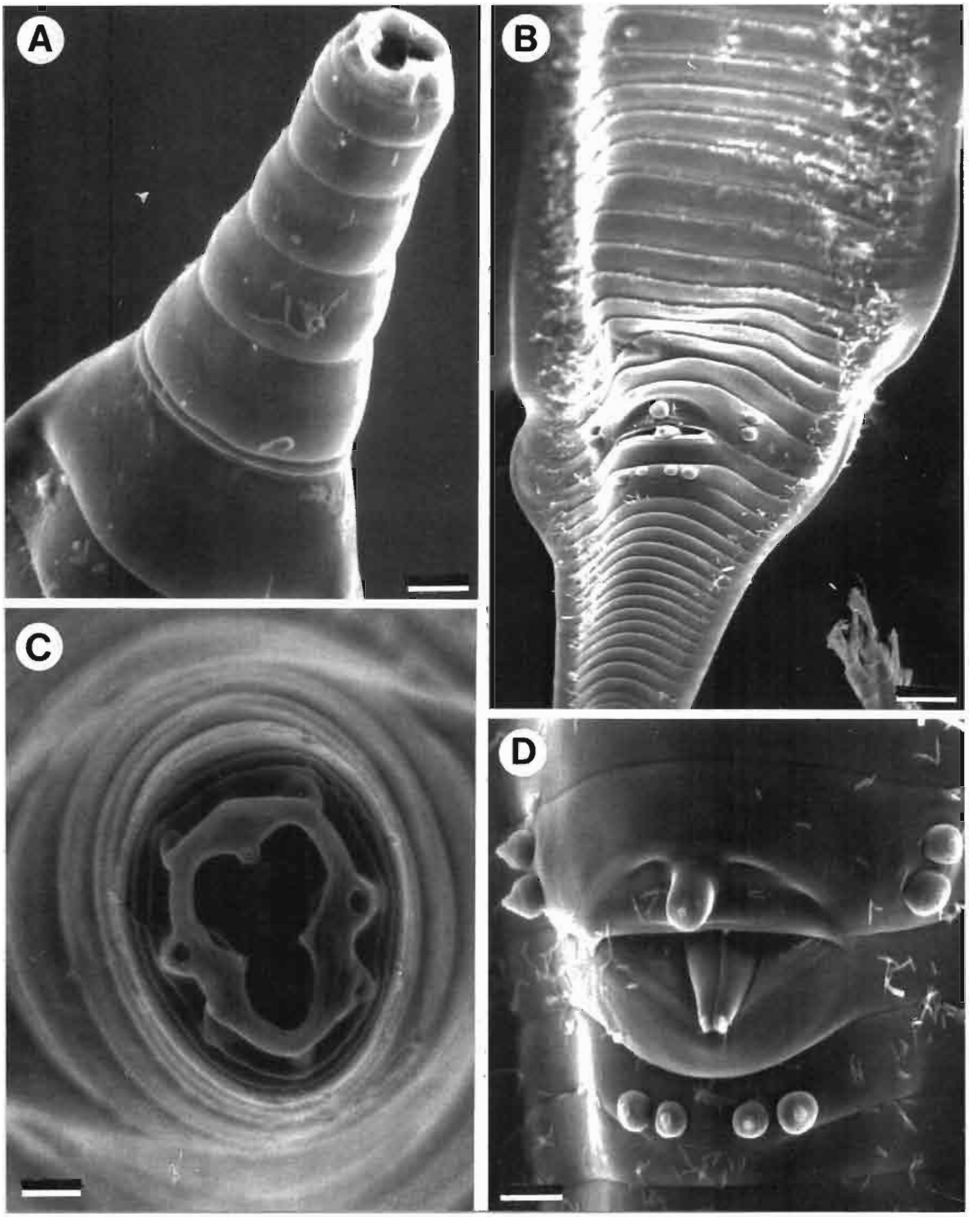

Fig. 7. Carnoya janiceae *sp. n. Male. A: Cervical region; B: Posterior region showing all papillae apart from the pair on the tail spike; C: En face view; D: Cloacal region. (Scale bars: A = 6 μm; B = 18.5 μm; C = 3 μm; D = 7 μm).*

= 407 µm; tail = 874 µm; b = 5.1; c = 2.1; V = 31; V′ = 58.

Females (anterior region extended; paratypes; n = 12): L = 1.97 ± 0.19 (1.69-2.35) mm; L′ = 1.0 ± 0.05 (0.89-1.17) mm; head to posterior end of stoma = 81 ± 2.6 (76-85) µm; corpus = 118 ± 2.9 (113-120) µm; isthmus = 94 ± 5.4 (86-101) µm; basal bulb = 81 ± 2.3 (75-83) µm; total oesophagus length = 374 ± 9.9 (350-384) µm; anterior end to vulva = 575 ± 38 (520-660) µm; vulva to anus = 421 ± 42 (354-407) µm; tail = 968 ± 111 (800-1187) µm; b = 5.3 (4.8-6.3); c = 2.0 (2.0-2.1); V = 29 (28-32); V′ = 58 (56-60).

Males (mostly ventral mounts; paratypes; n = 10): L = 1.66 ± 0.08 (1.57-1.77) mm; L′ = 0.91 ± 0.04 (0.85-0.97) mm; head to posterior end of stoma = 88 ± 2.3 (86-93) µm; corpus = 283 ± 12 (265-301) µm; isthmus = 64 ± 4.5 (56-71) µm; basal bulb = 66 ± 4.8 (60-73) µm; total oesophagus length = 501 ± 17 (477-531) µm; tail = 751 ± 37 (707-800) µm; spicule (ventral mounts, n = 8) = 103 ± 4.2 (96-108) µm; gubernaculum (ventral mounts, n = 7) = 57 ± 3.2 (51-60) µm; spicule (lateral mounts, n = 5) = 117 (113-120) µm; gubernaculum (lateral mounts, n = 5) = 66 (63-71) µm; b = 3.3 (3.2-3.6); c = 2.2 (2.2-2.3).

Description

Adults: Small, plump nematodes about 1.7-2.35 mm long in female and 1.57-1.77 mm in male. Sexually dimorphic in cervical region. Body slightly dorsoventrally flattened in unmounted females and with broad lateral alae. Males tend to die straight, resulting in ventral or dorsal mounts because of the broad alae.

Female: Cervical region tapering gently to truncate extremity, not offset or knob-like and about 22-25 µm wide immediately before head. Four cephalic papillae and a pair of lateral amphids. Lateral alae well developed, up to 37-40 µm high, starting just posterior to cervical spine collars and extending down body, eventually tapering into tail cuticle at some distance from anus. Body annules broad, strongly developed and about 16-22 µm apart in midbody region. Oral opening polygonal. Cephalic region supported by nine cuticular rods, three arising from a dorsal plate and the others from two subventral plates; these rods appearing as nine refractive dots arranged as three singles and three pairs in *en face* view. Buccal cavity consisting of a short, thick walled capsule, about 17-18 µm deep, containing basal teeth (two subventrals and a single, broader, dorsal tooth) and a longer, tubular section about 76-85 µm long surrounded by anterior oesophageal tissue. Oesophagus initially very narrow with prominent transverse striations about 0.7 µm apart, rapidly expanding to the cylindroid corpus, offset at both ends. Isthmus long, narrow, leading to the spheroid basal bulb. Cervical region with eleven or twelve complete transverse rows of spines plus one incomplete row at the commencement of the alae. Spines numerous, mostly parallel sided for much of their length and with contiguous bases, although the last two rows being more dagger-like and with separate bases; some spines shortly furcate in distal third; about twenty spines on the first collar, about 36 on the seventh and about twenty on the twelfth; spine length varying from about 8 µm on the first row to 28 µm on the twelfth. Vulva transversely oval with about seven or eight cuticularized teeth-like undulations proximally (*i.e.* nearest the point of attachment) and often covered by a brownish plaque. Vulva located at about midpoint of body as measured from head to anus (on about 18th to 22nd annule posterior to commencement of alae), slightly ventrolateral in position and on left side of body. Vagina initially with an undulate lumen, long, muscular, directed posteriorly to common uterus. Two ovaries directed anteriorly, their tips reaching to the basal bulb or beyond. Tail very long, subulate. Phasmids located about one third of distance down tail.

Male: Cephalic region with one dorsal and two subventral lips. Four cephalic papillae, a pair of lateral amphids and six minute papillae-like structures around the oral opening. Buccal cavity initially subtriangular, then tubular and thin walled leading to a thick walled section tapering towards the oesophageal lumen. Posterior portion of buccal capsule with three simple cuticular projections, one dorsal and two subventral. Cervical region with, from anterior to posterior, one shallow annule, four much broader annules and one very narrow annule just before broad annule on which lateral alae commence. Cervical spine collar absent. Lateral alae broad, extending from near cephalic extremity to cloacal level, there being a distinct undulation in alal contour just prior to cloaca, before tapering evenly into tail cuticle. Body annules broad. Oesophagus comprising a long, narrow, tubular section leading to a short, well defined isthmus and a spheroid basal bulb. Spicules paired, separate, closely adpressed, similar; when seen laterally (n = 5) spicules about 117 (113-120) µm long and gubernaculum 66 (63-71) µm long, *i.e.*, about 12-15% longer than dimensions from ventral mounts. Gubernaculum prominent, boat shaped, proximally bifid and lacking a dorsal hole; midventral keel and distal flanges present. Copulatory papillae numbering thirteen, arranged as a single median papilla on anterior cloacal lip, one subventral precloacal pair about twelve to sixteen annules anterior to cloaca, two subventral pairs in tandem on a slight protuberance at cloacal level (rarely one of these papillae can be missing), two subventral pairs arranged transversely on second annule posterior to cloacal lip and another subventral pair on tail spike. Anteriormost pair of precloacal papillae,

located about 200 µm anterior to cloaca, possibly on the same annule or, more commonly, one papilla, usually the left, possibly one annule more anterior. Postcloacal transverse row of four papillae showing some variation - in one specimen both papillae contiguous on right hand side, although still with separate tips and in another one papillae missing, the remaining three forming a triangle. Tail long, subulate. Phasmids located just posterior to last pair of papillae.

TYPE HOST AND LOCALITY

Type population from posterior intestine of the slender diplopod from Kimbé, New Britain. Also found in the same species of diplopod from Balima, Bialla and Kerevat and from the robust black and yellow banded spirobolid from Kimbé and Balima, New Britain.

TYPE MATERIAL

Holotype female, eight paratype females and six paratype males in the type collection of the International Institute of Parasitology, St. Albans, UK and four paratype females and four paratype males in the Muséum National d'Histoire Naturelle, Paris, France.

DIAGNOSIS AND RELATIONSHIPS

C. janiceae sp. n. is characterized by the female cephalic region lacking an offset, knob-like annule; by the form and distribution of the female cervical spines; the form of the broad lateral alae in the female; the undulation of the lateral alae at cloacal level in the male; the disposition of the thirteen male papillae; the annulation of the unarmed male cervical region and the long tail and broad annules in both sexes. The exceptionally long tail and broad annules in both sexes immediately distinguishes this species from all the American species and the long tail from *C. vitiensis* from Fiji. It is closest in appearance to *C. fimbriata* and *C. perbella*, both being described from the neighbouring island of New Guinea. From *C. fimbriata* it differs principally in having smaller female body size (1.7-2.4 *vs* 2.8-3.15 mm); fewer female cervical spine collars (12-13 *vs* 18-19); smoothly tapering lateral alae in both sexes as opposed to sharply recurved to the body at anal level; male lacking a cervical spine collar (present in *C. fimbriata*) and disposition of the male papillae. From *C. perbella* it differs in having fewer female cervical spine collars (12-13 *vs* 14-17); vulva located 18-22 annules posterior to the commencement of the lateral alae as opposed to twelve-fourteen; smaller spicules (113-120 *vs* 129-149 µm); male lacking a cervical spine collar (present in *C. perbella*) and disposition of the male papillae.

Discussion

With the three new species described in this paper there are now seven nominal species from the Australasian/Pacific region compared to nine from the Americas. Comparing the species from the two major regions, regions separated for over 70 million years, reveals some consistent differences in morphology indicating the likelihood of at least two, possibly three, lineages.

FEMALE CEPHALIC REGION

The nominal species of the genus from the Australasian/Pacific regions show two types of cephalic region in the female.

Type 1 has the first annule behind the lip region markedly offset and knob-like. This inflated annule is smooth and lacks transverse striae. Following this annule is a sequence of about four to eight much smaller annules which allow the head region to be withdrawn into the body or extended and moved around. Posterior to this region are the rings of cervical spines, each ring bearing a small number of large, dagger-like spines tapering evenly to finely pointed tips and with well separated bases. The Type 1 cephalic region is recorded for the type species, *C. vitiensis* and for *C. strobilina*, *C. caputbulla* sp. n. and *C. posterovulva* sp. n.

Type 2 cephalic region lacks the expanded, smooth, knob-like annule and consist of a number of annules (up to seven-nine) of more or less equal diameter, but varying height. The cervical spine rows are formed from numerous spines with contiguous bases, each spine being parallel sided for much of its length before narrowing to the terminus. Such spines are typical of the majority of the spine rings, but the last few rings may show separated, irregularly arranged and more dagger-like spines. The Type 2 cephalic region is recorded for *C. perbella*, *C. fimbriata* and *C. janiceae* sp. n.

In general, the species from the Americas show affinities with Type 2 in the form of the cephalic region, although the spines appear to be more variable in form and distribution, *e.g.*, *C. martiniquensis* has numerous, small spines with separate bases (Adamson, 1984). The female cephalic region of *C. paradubia* is described as knob-like (Adamson, 1984), but this is a comparative term related to the American species, the cephalic region being neither as well developed nor separated from the remainder of the cervical region as in the Type 1 species from the Australasian/Pacific region and, in addition, being subdivided by several transverse striae.

FEMALE STOMA

The female stoma is supported by three cuticularized plates, one dorsal and two subventral, each with

three anteriorly directed rod-like extensions. These supports, the first clear indication of which was by Artigas (1926) in his drawing of *C. pyramboia*, were referred to as chevron-shaped pieces by Adamson (1985) and almost certainly occur in all species of the genus, although they may be obscure or difficult to interpret. The only other genera in the Carnoyidae where cuticularized pieces are reported to occur around the stoma are *Brumptaemilius* Dollfus, 1952 and *Raonema* Kloss, 1965, where three pairs are evident. The three chevron shaped pieces in *Carnoya* probably represent a development and fusion of these six supports.

Tail

The three species described from Papua New Guinea (Hunt & Sutherland, 1984) all share the characteristic of an unusually long tail which is as long as, or longer than, the rest of the body. The three new species proposed in this paper from the neighbouring island of New Britain also have exceedingly long tails, such a feature apparently being the normal condition for this part of the Australasian region where mean c ratios range from 1.9-2 (according to the illustration, the c ratio for the type species, *C. vitiensis*, from Fiji, is 2.9). In contrast, the tail in the species from the Americas is considerably shorter than the rest of the body, c ratios of 3.0-3.8 being recorded.

Lateral alae and annulation

In the South American/West Indian species the lateral alae are either narrow (*C. dubia*, *C. paradubia*, *C. martiniquensis*, *C. venezuelensis*); absent (*C. mackintoshae*) or described as "prominent, slightly inflated" (*C. kermarreci*) by Adamson and Van Waerebeke (1985), the alae measuring about 10-12 µm high as calculated from the illustration. The condition in *C. guantanamera* is described by Spiridonov (1989) as extending from the basal bulb to halfway along the body in the male, but there is no illustration of the feature. In the Australasian/Pacific species the situation is different as the alae are always broad and well developed, even when compared to *C. kermarreci*. This difference in alae development is apparently correlated with two other characters: cross sectional shape of the body and annulation. In the species from the Americas the body is stated to be more or less round in cross section (Adamson, 1984) and the body annules are numerous and small whereas in the Australasian/Pacific species the body is dorso-ventrally flattened in cross section (Gilson, 1898; Hunt & Sutherland, 1984) and in all nominal species the annules are few, but very broad. The shape of the body should be interpreted with some caution as to some extent the body flattening in the latter group is often exaggerated during processing, live specimens, particularly older, mature females, appearing more rounded with the dorso-ventral flattening becoming much more apparent during dehydration as the body tends to collapse dorsally and ventrally whilst being stiffened laterally by the strong alae. The pronounced annulation does appear to be consistent, however, for both males and females.

Copulatory papillae

There are typically thirteen papillae in the male arranged as a single midventral papilla on the anterior cloacal lip; three precloacal pairs and three postcloacal pairs. Of the precloacal papillae the most anterior pair is subventral and usually a considerable distance anterior to the cloaca, whilst the other two pairs are grouped near the cloaca in various arrangements. The inner pair often form a transverse line with the midventral papilla on the cloacal lip although they may be more anterior or even slightly posterior. The outer pair are usually more anterior than the inner pair (but posterior in *C. martiniquensis*) or join the transverse line on the cloacal lip (*C. guantanamera*). In the species from the Americas the first two postcloacal pairs usually form a transverse line just posterior to the cloaca, but in *C. dollfusi* and *C. mackintoshae* they are arranged well posterior to the cloaca and in tandem (*C. guantanamera* was uniquely reported as having the posterior papillae arranged as two transverse lines of three papillae each. This assertion would benefit from confirmation). The overall papillal arrangement of *C. pyramboia* is unclear from the original description (only two pairs were mentioned) and the types have been lost, but Artigas (1926) described one pair as being immediately posterior to the cloaca and another pair near where the tail starts to narrow (this *could* indicate a hypothetical projected total of only eleven papillae, but again requires confirmation). The arrangement in the species from Australasia/Pacific are broadly similar to those from the Americas, but two species have only eleven papillae, one of the postcloacal pairs being presumably fused with the other pair as duplex nerve endings are visible in the remaining pair. *C. strobilina* from Papua New Guinea has the first two pairs of postcloacal papillae arranged in tandem, but close together and near the cloaca (*cf. C. dollfusi* and *C. mackintoshae* from the Americas, where they are well separated and more posterior).

Male cervical spination

Males from the Americas either have no cervical spines (*C. dollfusi*, *C. kermarreci*, *C. mackintoshae*, *C. pyramboia*) or exhibit numerous minute spinelets arranged in multiple spine collars (13-70 rows, depending on species). Multiple spine collars are unique to the Americas. In contrast, those from the Australasian/Pacific region are either spineless or pos-

sess fewer, larger spines arranged as single or double collars, a feature unique to this region.

Although there is increasing evidence for consistent differences between species from the Americas and those from the Australasian/Pacific region, it is still too early to draw profound conclusions as to the taxonomic significance of such morphological trends. It is possible that molecular methodologies, currently under investigation, may clarify the position in the near future.

Acknowledgements

We thank Janice Sheldon for general technical assistance and for the SEM and photographic work.

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