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On the genera *Obainia* Adamson, 1983 and *Xustrostoma* Adamson & Van Waerebeke, 1984 (Nematoda : Rhigonematidae), with proposal of *Obainia pachnephorus* sp. n. from Ivory Coast

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Summary – The genera *Obainia* Adamson, 1983 and *Xustrostoma* Adamson & Van Waerebeke, 1984, rhigonematid parasites of diplopods, are reviewed and discussed. Both genera are diagnosed and a list of nominal species, together with their hosts and distribution, provided. *Obainia* is regarded as comprising two groups distinguished on the morphology of the cephalic and oesophageal regions and widely differing zoogeographic distributions. Within the Rhigonematidae, the development of the oral aperture from the presumed primitive triangular pattern of *Rhigonema* Cobb, 1898 towards a dorso-ventral slit, as found in *Obainia* and *Xustrostoma,* may have occurred independantly at a number of foci. *O. pachnephorus* sp. n. from a spirostreptid diplopod from Ivory Coast is described and illustrated and differentiated from *O. petteri* Adamson & Van Waerebeke, 1985, its closest relative, and the other members of the genus. Additional data are given for *X. stenoboli* Van Waerebeke, 1988, found for only the second time and parasitic in *Dactylobolus bivirgatus* (Karsch, 1881) Golovatch & Korsós, 1992 from Ile Picard, Aldabra. SEM studies of both genera are presented for the first time, particular emphasis being placed on the structure and modification of the buccal region.

Résumé – ***Au sujet des genres* Obainia *Adamson, 1983 et* Xustrostoma *Adamson & Van Waerebeke, 1984 (Nematoda : Rhigonematidae), et proposition de* Obainia pachnephorus *sp. n. provenant de Côte d'Ivoire*** – Les genres *Obainia* Adamson, 1983 et *Xustrostoma* Adamson & Van Waerebeke, 1984, Rhigonematides parasites de diplopodes, sont revus et discutés. Des diagnoses sont proposées pour les deux genres, avec la liste des espèces nominales, leurs hôtes et leur répartition. *Obainia* est considéré comme comprenant deux groupes différents par la morphologie des régions céphaliques et oesophagiennes et par leur répartition zoogéographique. Chez les Rhigonematidae, l'évolution de l'ouverture buccale, de la forme triangulaire, supposée primitive chez *Rhigonema* Cobb, 1898 vers une forme en fente dorso-ventrale comme chez *Obainia* et *Xustrostoma,* pourrait s'être effectué indépendamment dans un certain nombre de localisations. *O. pachnephorus* sp. n., originaire d'un diplopode spirostreptide de Côte d'Ivoire, est décrit et différencié de l'espèce la plus proche, *O. petteri* Adamson & Van Waerebeke, 1985, et des autres espèces du genre. Des données complémentaires sont fournies pour *X. stenoboli* Van Waerebeke, 1988, espèce trouvée pour la deuxième fois seulement parasitant *Dactylobolus bivirgatus* (Karsch, 1881) Golovatch & Korsós, 1992 dans l'île Picard, Aldabra. Les résultats de l'étude en microscopie électronique à balayage des deux genres sont présentés pour la première fois, une attention particulière étant portée à la structure et aux modifications de la région buccale.

Key-words : diplopods, new species, *Obainia,* SEM, taxonomy, *Xustrostoma.*

In the last decade or so, the Rhigonematidae, a family of monoxenous parasites of tropical and subtropical diplopods exhibiting divers forms, has received considerable attention with several new genera and many new species being proposed. Two of these genera, namely *Obainia* Adamson, 1983 and *Xustrostoma* Adamson & Van Waerebeke, 1984 are of particular interest because of the transformation of the oral aperture from the presumed ancestral equilateral triangle form, as found in the type genus *Rhigonema* Cobb, 1898, through an isosceles triangle with a reduced and modified dorsal sector in *Xustrostoma* to a dorsoventral slit with the dorsal sector atrophied as in *Obainia.*

Fixed material from : 1) the unusually small spirobolid *Dactylobolus bivirgatus* (Karsch, 1881) Golovatch & Korsós, 1992 [syn. *Spirobolus bivirgatus* Karsch, 1881; *Stenobolus bivirgatus* (Karsch, 1881)], collected from Ile Picard, Aldabra by Dr V. W. Spaull in 1974; and 2) an undetermined spirostreptid collected in Ivory Coast in October, 1987 by Dr D. Moore, contained one species of *Xustrostoma* and *Obainia* respectively. Examination of these nematodes showed that the Aldabra species corresponded well to the original description of *X. stenoboli* Van Waerebeke, 1988. The original description of this species was based on six males and eight females from the island of Nossi-Bé of the North West coast of Madagascar (Van Waerebeke, 1988), the material also coming from *D. bivirgatus.* The Ivory Coast material described herein is close to *O. petteri* Adamson & Van Waerebeke, 1985, which was described from *Pachybolus laminatus,* also from the Ivory Coast (Adamson & Van

Waerebeke, 1985), but differs in several significant aspects and is proposed as a new species. This paper also provides additional data on *X. stenoboli*. SEM studies of the cephalic region of both these intriguing genera are provided for the first time.

Materials and methods

Specimens for study by light microscopy were postfixed in TAF (7 ml 40 % formaldehyde; 2 ml triethanolamine; 91 ml distilled water), transferred to a 5 % glycerol in water solution and processed to anhydrous glycerol over 4 or 5 days via a slow evaporation technique at 40 °C. Some specimens were used for studies of the *en face* view or dissected to elucidate structural details of the female genital tract, particularly that of the ovejector, the type of which is of crucial importance in the taxonomy of this family. Several selected specimens from each 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 10 kV. Measurements are given in the form : mean ± standard deviation (range).

Genus *Obainia* Adamson, 1983

Diagnosis

Rhigonematidae. Medium sized to large nematodes ranging from 3.3 to 10.8 mm long. Cephalic region laterally compressed; oral aperture a dorsoventrally elongate slit. Cuticle with fine transverse striae bearing delicate microtrichs extending down body and eventually regressing to form transverse rows of cuticular ridges. Dorsal jawpiece extremely reduced in type and other African species; subventrals dentate and almost parallel to one another for most of their length, but species from New Caledonia with dorsal jawpiece not so reduced and subventrals more divergent. Corpus short and stout, longitudinally compressed; isthmus absent. Basal bulb hypertrophied, occupying over 50 % of oesophageal length in type and other African species, but not in atypical species from New Caledonia. Vagina lacking diverticulum, but typically expanding anteriorly to form large sac or chamber before narrowing and dividing into two uteri. Ovejector corresponding to Type 2 of Adamson (1987), of variable length; exceptionally long in West African species, but much shorter in those from Madagascar and New Caledonia. Genital tracts two, containing numerous thick shelled eggs. Spicules similar, arcuate, with small, weak, gubernaculum reportedly present. Copulatory papillae 23 in number arranged as four pairs plus a single papilla anterior to cloaca and seven pairs post-cloacal of which three pairs are latero-ventral or subdorsal in position.

Type species

O. gabonensis Adamson, 1983.

Other species

O. adamsoni Van Waerebeke, 1986.
O. chazeaui Van Waerebeke, 1991.
O. neocaledoniae Van Waerebeke, 1991.
O. pachnephorus sp. n.
O. petteri Adamson & Van Waeebeke, 1985.

Hosts and distribution

O. gabonensis was found in the gut of a *Pachybolus* sp. in Gabon, *O. petteri* in *Pachybolus laminatus* from Ivory Coast, *O. adamsoni* in an undetermined millipede from Madagascar and *O. chazeaui* and *O. neocaledoniae* in *Spirobolellus* sp. from New Caledonia. These records are mostly from members of the Pachybolidae in the Spirobolida. The host of *O. pachnephorus* sp. n. is an unidentified spirostreptid from Ivory Coast.

Discussion

As presently understood, *Obainia* contains two distinct groups of species which differ in the degree to which the dorsal jawpiece is reduced and the extent to which the oesophagus is longitudinally compressed with concomitant hypertrophy of the basal bulb. The first group contains *O. gabonensis* (the type species), *O. adamsoni, O. petteri* and *O. pachnephorus* sp. n. All have the dorsal jawpiece reduced to a vestigial structure so that the opposing faces of the subventral jawpieces run virtually parallel to one another for most of their length, the oesophagus being markedly compressed with a hypertrophied basal bulb. *O. adamsoni,* from Madagascar, differs from the three West African species primarily in having a much shorter and less developed ovejector, a slightly less compressed oesophagus and a slightly less reduced dorsal jawpiece. Thus, three similar species of this group are reported from equatorial West Africa (Gabon, Ivory Coast) with an outlying species from Madagascar showing signs of morphological divergence.

In the second group, comprising *O. chazeaui* and *O. neocaledoniae,* the dorsal jawpiece, although reduced, is still substantial; the opposing faces of the subventral jawpieces run at more of an angle to one another rather than being parallel and the oesophagus is of more normal form, lacking the overall longitudinal compression and the extreme hypertrophy of the basal bulb. This group has a different and widely separated distribution from the African representatives, both species coming from New Caledonia in Australasia. Because of the less evolved oesophagus and jawpiece arrangement, Van Waerebeke (1991) regarded the second group as being the most primitive nominal species of *Obainia* and closer to *Rhigonema* Cobb, 1898, the most widely distributed (reported from Africa, the Americas, Asia, Australasia, Pacific islands) and presumed ancestral genus in the

Rhigonematidae. Van Waerebeke (1991) viewed *O. adamsoni* as an intermediate stage between the forms from New Caledonia and those from equatorial West Africa, a view which raises vexing questions as to the place of origin of the genus (the current locations have been separated for over 100 million years) and the manner of its subsequent dispersal. It is, perhaps, more likely that at least two distinct lineages are represented in *Obainia (sensu lato)* as the evolution of the buccal cavity from the (presumed) ancestral equilateral triangle of *Rhigonema* towards a dorsoventral slit has occurred in two other rhigonematid genera; *Xustrostoma* Adamson & Van Waerebeke, 1984 (two species recorded from Madagascar and Aldabra in the Indian Ocean) and *Zalophora* Hunt, 1994 (one species from Papua New Guinea and another, undescribed species, from the nearby island of Sulawesi). In both these genera the oesophagus has also been compressed, the former genus also showing hypertrophy of the basal bulb although in *Zalophora* it is predominantly the corpus which is enlarged.

Thus, in the broad distribution occupied by *Rhigonema,* the presumed ancestral genus, our current knowledge suggests that there is a tendency to evolve away from the primitive buccal characteristics of *Rhigonema* towards a more specialized dorsoventral slit. This evolution involves radiation, each species cluster being reproductively isolated and endemic to geographically separated enclaves. Such a process, occuring independently at a number of foci, is presumably a niche diversification strategy, possibly in response to trophic competititon within a species flock. An alternative, if less plausible, explanation for the observed zoogeographic distribution could be that a widespread ancestral form, with a laterally compressed oral aperture already evolved, existed (presumably sympatrically with *Rhigonema*) before the breakup of Gondwanaland, subsequently suffering differential extinction to leave the relict faunal pattern observed today.

In either scenario, assuming that other species with more intermediate character suites are not found, generic status may well be appropriate at a later date for those *Obainia (sensu lato),* geographically separated and morphologically atypical, from New Caledonia.

Obainia pachnephorus* **sp. n.**

(Figs 1, 2)

MEASUREMENTS

Female (n = 6): L = 7.27 ± 0.73 (5.98-8.22) mm; width = 292 ± 47 (221-345) µm; œsophagus = 287 ± 17 (267-312) µm; basal bulb (height × width) = 168 ± 11 (156-184) × 175 ± 4.4 (169-182) µm; tail = 322 ± 24 (289-361) µm; anal body width = 104 ± 24 (98-111) µm; head to vulva = 4.56 ± 0.57 (3.46-5.08) mm; a = 24.9 (20.9-29.7); b = 25.3 (21.4-27.1); c = 22.6 (18.2-25.8); c′ = 3.1 (2.9-3.4); V = 62.7 (57.8-65.9).

Male (n = 6): L = 5.44 ± 0.22 (5.19-5.78) mm; width = 219 ± 10 (198-226) µm; oesophagus = 277 ± 37 (231-309) µm; basal bulb (height × width) = 148 ± 10 (133-163) × 150 ± 10 (140-167) µm; tail = 272 ± 32 (231-306) µm; anal body width = 143 ± 18 (127-176) µm; left spicule = 326 ± 27 (280-361) µm; right spicule = 334 ± 34 (280-367) µm; a = 24.8 (23.2-26.6); b = 19.6 (17.0-23.9); c = 20.0 (17.8-24.4); c′ = 1.9 (1.5-2.1).

Holotype (female) : L = 8.22 mm; width = 296 µm; oesophagus = 312 µm; anal body width = 107 µm; tail = 361 µm; head to vulva = 5.08 mm; a = 27.8; b = 26.3; c = 22.8; c′ = 3.4; V = 61.8.

DESCRIPTION

Adults : Medium sized to large nematodes. Cephalic region heavily cuticularized and comprising cephalic cap and collar, both showing strong lateral compression. Cephalic cap divided into dorsal sector with small, median lip-like development (similar to that reported for *O. adamsoni*), a subventral sector and two, more extensive, lateral sectors. Oral aperture modified from the primitive equilateral triangle arrangement to form a dorsoventrally elongate slit; dorsal sector highly reduced whilst cuticularized and dentate faces of subventral sectors are well developed, parallel and opposed. Four prominent mammilliform cephalic papillae, two subdorsal and two subventral. Amphids located dorsolaterally at groove marking junction of cap and collar. Cuticle with fine transverse striae bearing fine spines or microtrichs which apparently extend well into caudal region. Microtrichs longest immediately posterior to cephalic collar, becoming shorter thereafter until eventually reduced to transverse bands of contiguous longitudinal ridges. Corpus short and stout, longitudinally compressed; isthmus absent. Basal bulb hypertrophied, about as long as wide, occupying over 50 % of total oesophagus length and with modified, heavily cuticularized valve plates. Nerve ring obscure, located just anterior to basal bulb. Small excretory pore at junction of corpus and basal bulb; leading to vesiculate duct. Prominent valve-like formation present in anterior intestinal lumen about three oesophageal lengths behind basal bulb with a row of four coelomocytes about a body width further posterior and another tetrad more posterior still.

Female : Vulva post-median, body narrowing ventrally posterior to vulva. Vulval opening a transverse slit covered by pronounced vulval flap. Brown deposit present around flap, apparently plugging vulval opening.

* From the Greek *pachne* = frost and *phoreus* = to bear, a fanciful reference to the frosted appearance of the anterior region of the worm.

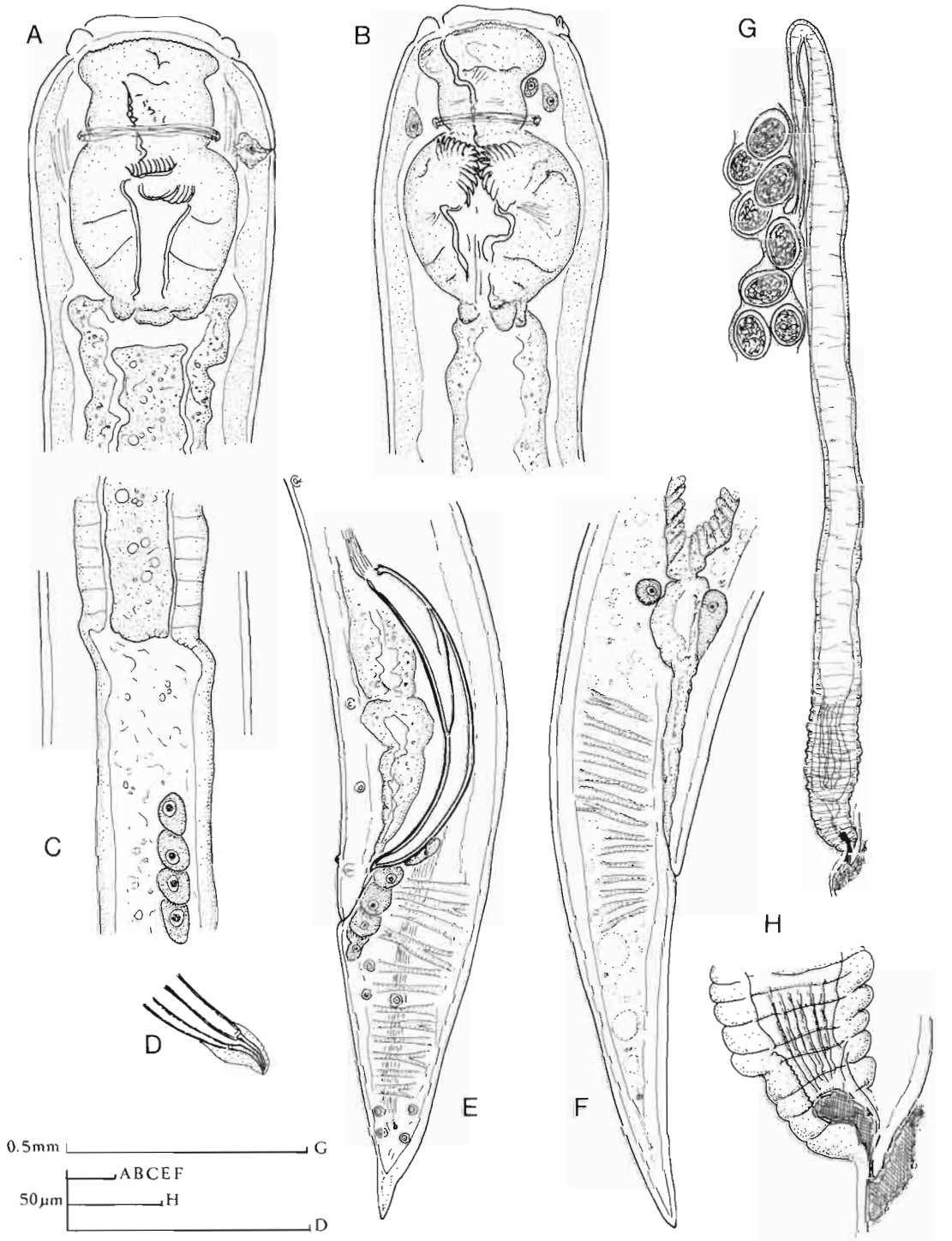

Fig. 1. Obainia pachnephorus *sp. n. A, B : Oesophagus; C : Valve-like structure in anterior intestine and tetrad of coelomocytes; D : Tip of spicules; E : Male tail; F : Female tail; G : Ovejector; H : Vulval region.*

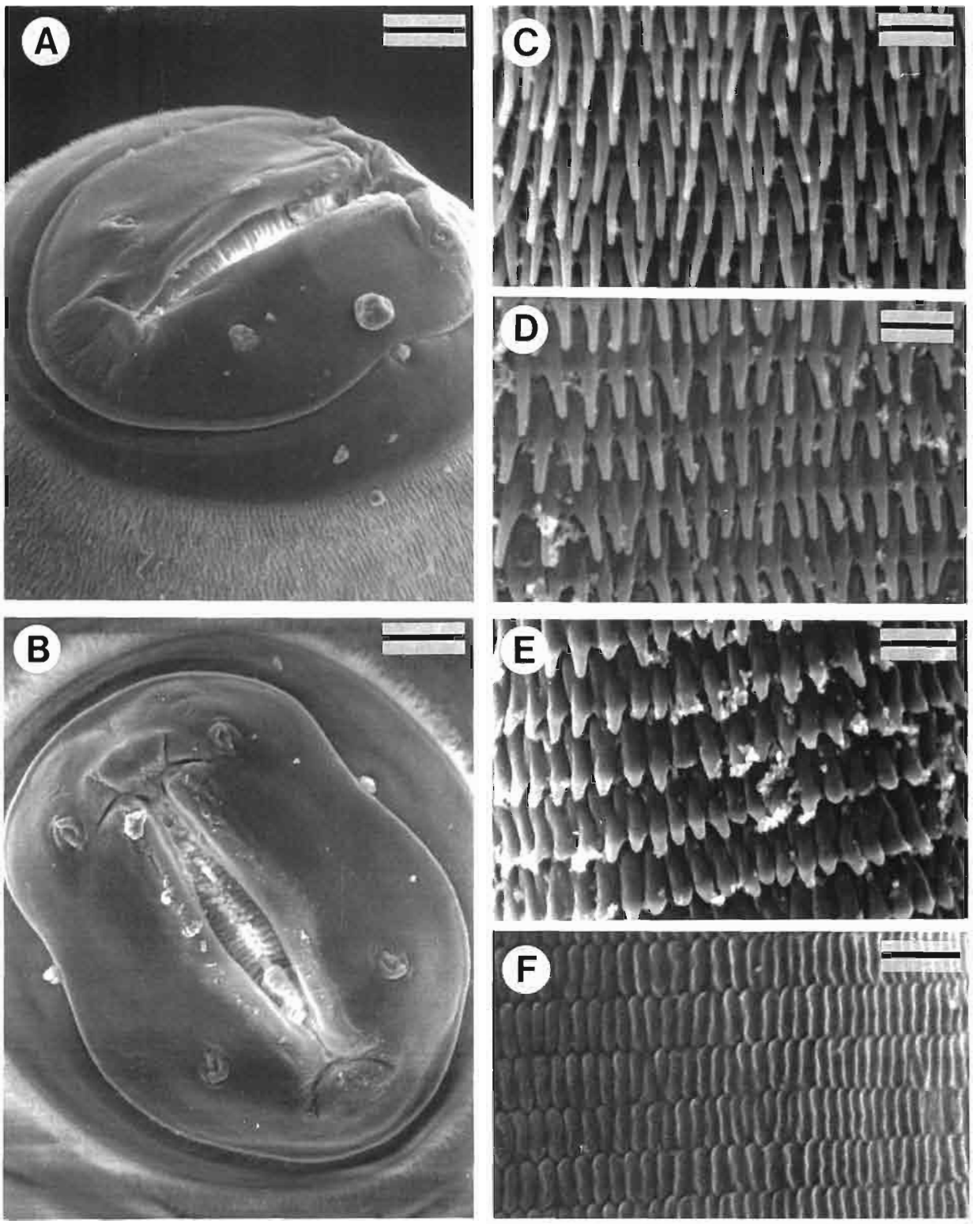

Fig. 2. Obainia pachnephorus *sp. n. SEM studies. A, B : Cephalic region; C-F : Microtrich development (sequential) from just behind the cephalic collar to near the tail.* (Scale bar : A, B = 10 μm; C, D, E, F : = 1 μm).

Vagina extremely long, initially with relatively short, thick-walled section with prominent circular muscles and then with much longer, expanded, thinner-walled section (the vaginal chamber) with less developed muscles which narrows and then flexes posteriorly for some distance before joining the two uteri. Vaginal diverticulum absent. Genital tract conforming to Type 2 of Adamson (1987). Few rounded sperm visible in reflexed portion of vagina and in uteri of some specimens. Genital tracts two, reflexed, each with an irregular spermatheca containing sperm. Genital tracts containing numerous, large, thick shelled (8-10 µm) eggs about 116 ± 8.3 × 80 ± 2.5 µm (n = 10) in size and, even in most mature females studied, almost entirely located anterior to vulva. Tail medium conoid, tapering evenly to terminus, phasmids being located at about level of distal third.

Male : Spicules slightly subequal in size, similar in form, arcuate, with a slightly recurved, dorsally directed distal tip bearing minute velum more highly developed on dorsal side. Copulatory papillae 23 in number : four pairs precloacal; single papilla on anterior cloacal lip; seven pairs postcloacal of which three pairs sublateral or subdorsal in position. Tail medium conoid with slightly offset, terminal, digitiform process. Phasmids located between last two pairs of papillae.

Remarks : Adamson and Van Waerebeke (1985) also recorded a very similar " valve-like formation " in the anterior intestine of *O. petteri*. The function of the feature is unclear.

TYPE HOST AND LOCALITY

Posterior intestine of an undetermined species of spirostreptid diplopod collected in Ivory Coast in October, 1987 during a field trip by Dr D. Moore of the International Institute of Biological Control, Silwood Park, Ascot, UK.

TYPE MATERIAL

Holotype female, three paratype females and four paratype males (slide numbers T519/1/1 to T519/1/5) in the type collection of the International Institute of Parasitology, St Albans, Herts., UK and two paratype females and two paratype males in the nematode type collection of Rothamsted Experimental Station, Harpenden, Herts., UK.

DIAGNOSIS AND RELATIONSHIPS

O. pachnephorus sp. n. is characterized by : comparatively short body length in both sexes; the occurrence of a small dorsal lip between the virtually parallel faces of the subventral jawpieces; compacted oesophagus with hypertrophied basal bulb; spicule length; voluminous vaginal chamber; vulval flap; tail length and shape.

It is closest to *O. petteri* Adamson & Van Waerebeke, 1985 yet differing in *i :* markedly shorter body length in both sexes (female 5.98-8.22 *vs* 9.63-10.56 mm; *ii :* male 5.19-5.78 *vs* 9.01-9.58 mm); *iii :* development of a small dorsal lip; differently shaped tail in the male and, presumably, the female (Adamson and Van Waerebeke (1985) did not specifically describe or illustrate the female tail for *O. petteri*, stating that the female was identical to the male in all respects except for sexual characters); *iv :* female tail longer in absolute length yet with smaller c ratio (289-361 *vs* 289-304 µm; *v :* c = 18.2-25.8 *vs* 31.7-36.2); *vi :* less voluminous vaginal chamber; *vii)* shorter spicules. *O. pachnephorus* sp. n. differs from *O. gabonensis* by *i :* shorter body length in both sexes (female 5.98-8.22 *vs* 10.21-10.84 mm; *ii :* male 5.19-5.78 *vs* 8.76-9.65 mm); *iii :* development of a small dorsal lip; *iv :* differently shaped tail and shorter spicules. It differs from *O. adamsoni* in having a much longer and more highly developed ovejector, more posterior vulva and a different tail shape in both sexes, this being particularly so in the male. The two species from New Caledonia, which are very similar to one another, are easily distinguished from *O. pachnephorus* sp. n. on the basis of the oesophagus being of more normal form and lacking extreme hypertrophy; the more developed dorsal jawpiece with the subventral jawpieces divergent instead of parallel and much shorter ovejector.

Genus *Xustrostoma* Adamson & Van Waerebeke, 1984

DIAGNOSIS

Rhigonematidae. Small to medium sized nematodes about 2 to 4 mm long. Cephalic region laterally compressed; oral aperture dorsoventrally elongate in form of isosceles triangle. Cephalic cap and collar separated by groove, amphidial apertures located in groove. Transverse striae with microtrichs in anterior half of body. Cuticle lining of anterior lumen of corpus forming tripartite jawlike apparatus with one dorsal and two subventral sectors. Dorsal sector subtriangular in dorsal view and bearing spines that are larger and in alternating rows compared to those on subventral sectors which are smaller and arranged in transverse rows. Isthmus short; basal bulb hypertrophied, barrel shaped and occupying over half oesophageal length. Vagina lacking diverticulum. Genital tracts two, containing few (5-8) thick shelled eggs. Spicules similar, arcuate. Copulatory papillae numbering 23 : four precloacal pairs; single median precloacal papilla; seven postcloacal pairs.

TYPE SPECIES

X. margarettae Adamson & Van Waerebeke, 1984.

OTHER SPECIES

X. stenoboli Van Waerebeke, 1988.

HOSTS AND DISTRIBUTION

The type species came from the gut of a member of the Sphaeroteroidea (Glomerida) from Madagascar and the other species, *X. stenoboli*, from a spirobolid, *Dacty-*

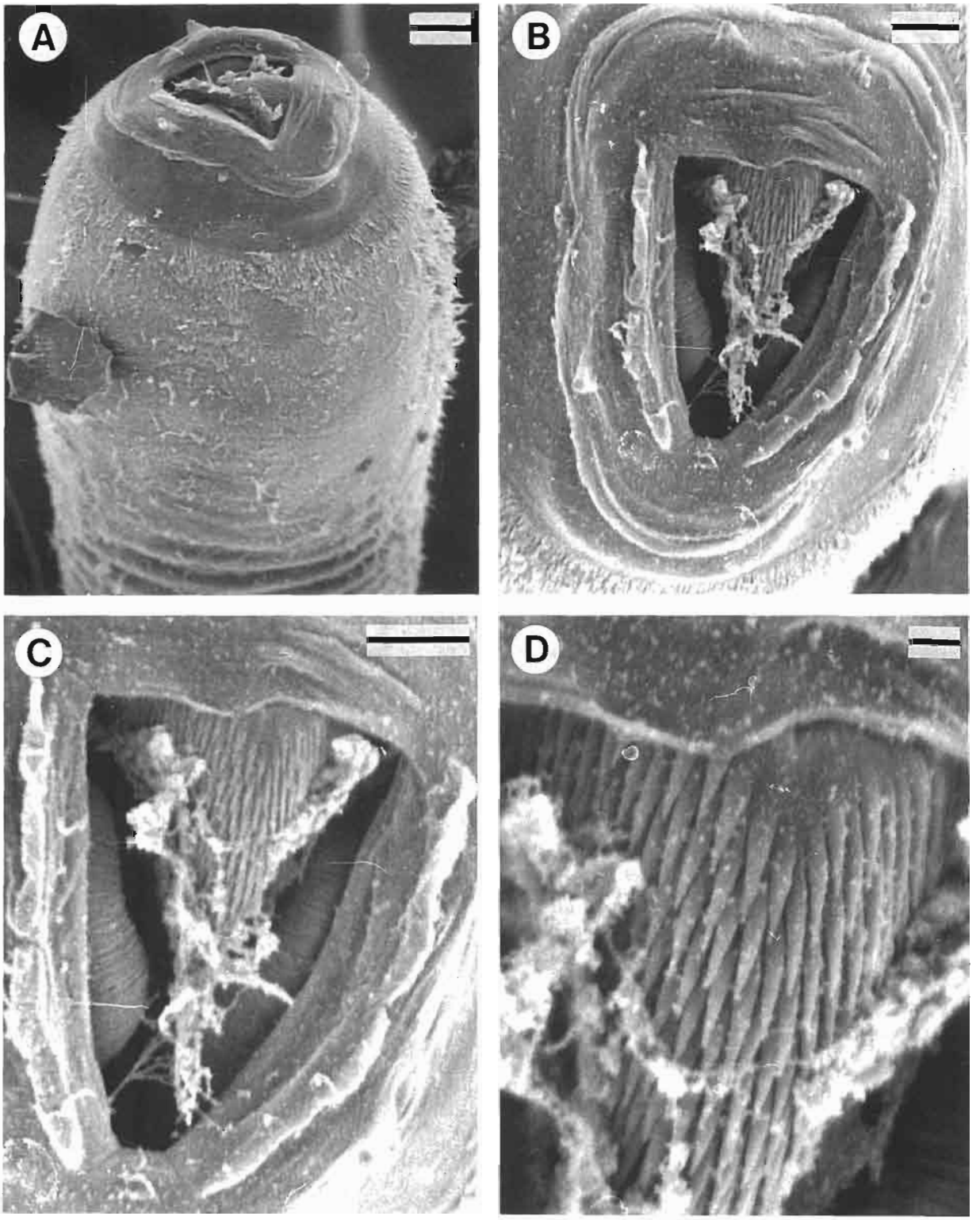

Fig. 3. Xustrostoma stenoboli *Van Waerebeke, 1988. SEM studies. A : Cervical region; B : En face; C : Oral aperture showing the dorsal and two subventral jawpieces; D : Dorsal jawpiece.* (Scale bar : A = 10 μm; B, C = 5 μm; D = 1 μm).

lobolus (= *Stenobolus*) *bivirgatus*, from Nossi-Bé, a small island just off the coast of Madagascar and from Aldabra in the Indian Ocean. The diplopod *D. bivirgatus* occurs on other islands in the Indian Ocean, being reported from the Comoro Islands (Karsch, 1881), Pemba Island (Attems, 1910) and the Seychelles Islands (Golovatch & Korsós, 1992) and it is reasonable to assume that its parasite, *X. stenoboli*, also shares this distribution. Golovatch and Korsós (1992) also comment on the strong Malagasy influence on the composition of the diplopod fauna of the Seychelles Islands.

Xustrostoma stenoboli Van Waerebeke, 1988
(Fig. 3)

MEASUREMENTS

Female (n = 10): L = 2.51 ± 0.28 (1.92-2.81) mm; width = 140 ± 13 (111-153) µm; oesophagus = 162 ± 5 (153-169) µm; basal bulb (height × width) = 96 ± 6 (85-104) × 103 ± 4 (98-111) µm; tail = 73 ± 7.4 (63-78) µm; anal body width = 56 ± 3 (52-59) µm; head to vulva = 1.35 ± 0.18 (1.02-1.65) mm; uterine eggs = 96 ± 3.8 (91-104) × 73 ± 2.6 (67-75) µm; a = 18.0 (16.7-20.5); b = 16.6 (11.8-17.2); c = 34.4 (28.0-43.8); c′ = 1.3 (1.2-1.5); V = 53.7 (51.0-58.9).

Male (n = 6): L = 2.33 ± 0.24 (2.04-2.66) mm; width = 121 ± 10 (104-133) µm; oesophagus = 151 ± 5.4 (143-156) µm; basal bulb (height × width) = 95 ± 5.8 (85-101) × 94 ± 1.8 (91-96) µm; tail = 96 ± 7.5 (85-107) µm; anal body width = 82 ± 8.1 (72-91) µm; left spicule = 161 ± 9.7 (153-179) µm; right spicule = 153 ± 8.1 (143-163) µm; a = 19.3 (16.4-22.1); b = 15.4 (14.0-17.1); c = 24.2 (21.1-29.9); c′ = 1.2 (1.0-1.3).

REMARKS

This population agrees very well, both morphologically and morphometrically, with the original description of the type population from the same host from the island of Nossi-Bé, Madagascar (Van Waerebeke, 1988). Although the material had been fixed for over 20 years and suffered from some surface disintegration of the cuticle, the SEM studies clearly show the structure of the spinose, tongue-like dorsal sector of the buccal armature (Fig. 3 B, C, D) and confirm the uniqueness of a genus which is intriguing both morphologically and because of its restricted distribution.

HOST AND LOCALITY

Intestine of *Dactylobolus bivirgatus* (Karsch, 1881) Golovatch & Korsós, 1992 collected on 23 February, 1974 from Ile Picard, Aldabra, Indian Ocean by Dr V. W. Spaull. The material was originally fixed in 5 % formalin. Voucher specimens are retained at the International Institute of Parasitology, St Albans.

Acknowledgements

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