

Re-description of some enigmatic genera of Syllidae (Phyllodocida: Polychaeta)

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Several type series of unusual and poorly known genera of Syllidae have been examined. New diagnoses for the following genera and re-descriptions of their type species are provided: Anguillosyllis, Clavisyllis, Lamellisyllis and Nuchalosyllis; Brachysyllis, previously synonymized with Dioplosyllis, is herein considered to be a valid taxon. The species Brachysyllis infuscata is also re-described. Three genera are considered to be non-valid taxa: Braniella, synonymous with Anguillosyllis; Alluaudella, synonymous with Odontosyllis; and Exogonella, synonymous with Parexogone. Their type species herein are re-described and assigned to their corresponding valid genus. Finally, Exogonoides is considered nomina dubia since its relationships with other syllids could not be established. Keys to species of Anguillosyllis and Brachysyllis are also included.

Keywords: re-description, synonymies, key to species, generic diagnoses

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INTRODUCTION

The family Syllidae is one of the most diverse families of Polychaeta; according to San Martín (2003) the family has more than 50 genera and 700 valid species, although in recent years this number has rapidly increased with the discovery of new genera and species (San Martín, 2002, 2005; San Martín & López, 2003; San Martín & Hutchings, 2006; San Martín *et al.*, 2007). Syllidae are currently divided into four subfamilies: Syllinae Grube, 1850; Exogoninae Langerhans, 1879; Eusyllinae Malaquin, 1893; and Autolytinae Langerhans, 1879. These subfamilies were diagnosed based on a few characteristics. For example, Exogoninae are characterized by having totally or partially fused palps, one or two pairs of tentacular cirri, and short smooth dorsal cirri; Autolytinae by having nuchal epaulettes and the absence of ventral cirri; Syllinae by having articulated antennae and dorsal cirri; and Eusyllinae by having smooth or pseudo-articulated antennae and dorsal cirri. Reproductive modes were also taken into account in the separation of these subfamilies; Eusyllinae and Exogoninae are mostly epigamic, while Syllinae and Autolytinae are mostly schizogamic (San Martín, 2003).

Notwithstanding the above, several authors have considered that the subfamilies within Syllidae could have been created solely for practical reasons, and some of them might not represent true monophyletic groups (Fauchald, 1977; Nygren, 1999; Glasby, 2000; Pleijel, 2001; Nygren & Sundberg, 2003; San Martín, 2003). In addition, the separation between these subfamilies is based only on very few features, and in several cases the reproductive mode is unknown. Furthermore, several features are common between subfamilies.

Currently, we are involved in a global revision of the family Syllidae within the scope of a global phylogenetic scenario. For

this purpose it is necessary to establish whether genera are valid or in fact conflictive in taxonomic terms. In this context, the main objective of the present study is to revise the type series of intriguing genera with features unique to their family, and/or showing a mixture of features that define several subfamilies. These puzzling genera are *Alluaudella* Gravier, 1905, *Anguillosyllis* Day, 1963, *Brachysyllis* Imajima & Hartman, 1964, *Braniella* Hartman, 1964, *Clavisyllis* Knox, 1957, *Exogonella* Hartman, 1961, *Exogonoides* Day, 1963, *Lamellisyllis* Day, 1960 and *Nuchalosyllis* Rullier & Amoureux, 1979. All these genera have been revised; some are re-described accepting their taxonomic status, whereas others are synonymized with other genera.

MATERIALS AND METHODS

Material examined is located at different institutions. Some specimens were studied during visits to the Muséum National d'Histoire Naturelle, Paris (MNHN), the Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB), and the Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH). Other specimens were taken on loan from different institutions, such as the Natural History Museum of London (NHML), the Smithsonian Institution (USNM), the Natural History Museum of Los Angeles County (NHMLAC), the South African Museum, Cape Town (SAM), the National Institute of Water and Atmosphere Research, New Zealand (NIWA) and the Universidad de La Laguna, Tenerife, Canary Islands (UL), and later examined at the Universidad Autónoma de Madrid (UAM).

Examinations were made using stereomicroscopes and optical microscopes provided by the respective institutions. Drawings were made to scale, with a camera lucida drawing tube attached to each optical microscope. The studied specimen of *Clavisyllis alternata* Knox, 1957 was critical point dried and subsequently coated with 102 Å of gold and

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examined under a Philips XL30 electronic microscope, connected to an EDAX DX4i analyser at SIDI (Servicio Interdepartamental de Investigación, UAM). One segment of *Brachysyllis infuscata* (Ehlers, 1901) was critical point dried and then coated with 80% of gold and 20% of palladium and examined using a LEO 1450 VP electronic microscope at the ZMB. The width of specimens was measured at the level of proventricle, excluding parapodia.

Most studied material were holotypes, these were old and fragile and, unfortunately, it proved impossible to distinguish several features due to the poor state of preservation; in these cases the information provided by the original descriptions was taken into account. In addition to this, dissection of certain holotypes proved impossible due to the unique nature of the material.

RESULTS

SYSTEMATICS

Genus *Anguillosyllis* Day, 1963

Anguillosyllis Day, 1963: 400.

Braniella Hartman, 1965: 72–73.

DIAGNOSIS

Body small, meiofaunal. Prostomium with three small antennae and two palps; palps elongated, fused, with a distal notch, more or less marked. Without eyes. One pair of papilliform tentacular cirri. Antennae and tentacular cirri minute, papilliform. Dorsal cirri long, filiform, coiled over dorsum. Ventral cirri present, digitiform, inserted medially to distally. Parapodia relatively long, triangular, with a short prechaetal and elongated postchaetal lobe. Compound chaetae heterogomph, with elongated, slender blades. Pharyngeal tooth absent. Proventricle barrel-shaped.

TYPE SPECIES

Anguillosyllis capensis Day, 1963.

REMARKS

Day (1963) placed *Anguillosyllis* within the subfamily Exogoninae because of the complete fusion of palps and the presence of a single pair of tentacular cirri (a common feature in several Exogoninae genera). Day (1967) and later, Böggemann & Purschke (2005) maintained this genus within Exogoninae. However, *Anguillosyllis* is far from being a typical Exogoninae, since it lacks a pharyngeal tooth and the dorsal cirri are long and filiform; common features in several Eusyllinae species. However, the fusion of palps and the presence of minute, papilliform antennae and a single pair of tentacular cirri are diagnostic of this subfamily. Unfortunately, its reproductive mode is totally unknown. This information would be extremely useful in order to determine the relationships of this genus with other Syllidae. Strictly, *Anguillosyllis* has intermediate morphological characteristics between Exogoninae and Eusyllinae.

The genus *Braniella* Hartman, 1965 has the same diagnosis as *Anguillosyllis*: fused palps (at least for more than half of their lengths), papilliform antennae, a single pair of small tentacular cirri, long and smooth dorsal cirri, digitiform ventral cirri (medially to distally inserted on parapodia), enlarged parapodial lobes, compound heterogomph chaetae and also

the absence of a pharyngeal tooth. Therefore, *Braniella* is considered herein synonymous with *Anguillosyllis*.

All the known species of this genus live in the deep sea (183–5500 m). The elongated postchaetal lobes are quite translucent, with fine walls, likely acting as branchiae.

Key to species

1. Palps fused only on basal half. Posterior parapodial lobe short, similar in shape and length to anterior lobe. Dorsal cirri on chaetiger 2 present. *Anguillosyllis palpata*
— Palps fused almost all their lengths. Posterior parapodial lobes elongated, distinctly longer than anterior lobes.
..... 2
2. Palps relatively short and broad, fused all along their lengths. Postchaetal lobes triangular. Ventral cirri proximally to medially inserted on parapodia, digitiform. Dorsal cirri on chaetiger 2 absent.
..... *Anguillosyllis pupa*
— Palps elongated, triangular, with a distal notch. Postchaetal lobes digitiform, distinctly long. Ventral cirri short, papilliform, almost distally inserted on parapodia. Dorsal cirri on chaetiger 2 present.
..... *Anguillosyllis capensis*

Anguillosyllis capensis Day, 1963

(Figure 1)

Anguillosyllis capensis Day, 1963: 400–401, figure 5a–d. Day, 1967: 271, figure 12.10z–zzz. Böggemann & Purschke, 2005: 222–223, figure 1.

MATERIAL EXAMINED

Holotype: NHML 1963.1.29, Agulhas Bank, South Africa, 34°51'S 28°4'E, 183 m, sand.

DESCRIPTION

Holotype incomplete; antennae, tentacular and dorsal cirri detached, 1.5 mm long, 0.7 mm wide, with six segments. No sign of pigmentation. Prostomium oval, broader than long. Palps tapered, longer than prostomium, fused for over half of their length, one of them without distal end (Figure 1A). Eyes absent. Antennae lost (three club-shaped antennae, *vide* Day, 1963). Peristomium shorter than subsequent segments, with a pair of tentacular cirri, papilliform (Figure 1A). Segments becoming wider towards posterior end, more than twice as broad as long in last segments. All dorsal cirri lost (long and slender, without any sign of annulation, often twisted and coiled, *vide* Day, 1963). Ventral cirri digitiform, inserted distally on parapodia, not reaching parapodial lobes (Figure 1B & C). Parapodia with one long, triangular posterior lobe (Figure 1B) (retractile, *vide* Day, 1963) and short, papilliform anterior lobe (Figure 1C). Numerous compound, heterogomph chaetae per parapodium, with long and slender blades, unidentate, decreasing in length from dorsal (98 µm) to ventral (48 µm), with minute and fine spines on cutting edge of blades (Figure 1D). Shafts smooth. Aciculae not visible by transparency. Pharynx through four segments (with six distal papillae, *vide* Day, 1963). Pharyngeal tooth absent. Proventricle broad, barrel-shaped, through three segments, and about 25–30 muscle cell-rows.

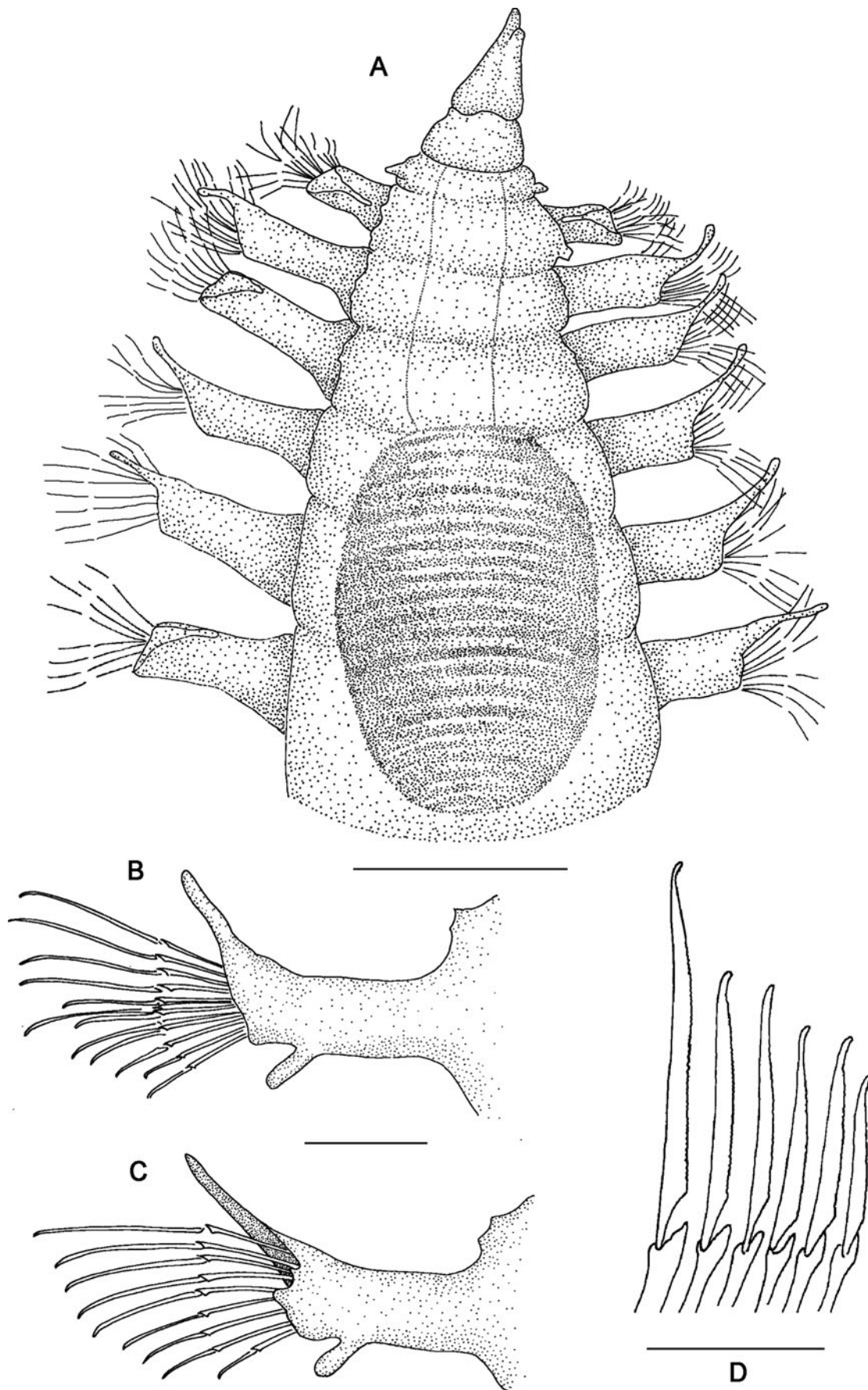


Fig. 1. *Anguillosyllis capensis*. Holotype. (A) Anterior end, dorsal view; (B) midbody parapodium, posterior view; (C) midbody parapodium, anterior view; and (D) midbody chaetae. Scale bars: A, 0.4 mm; B & C, 98 μ m; D, 48 μ m.

REMARKS

Böggemann & Purschke (2005) found several specimens of this species in the Angola basin and they could distinguish 1–4 aciculae within parapodia (with pointed tips) and 9–10 distal pharyngeal papillae. They also described a pair of smooth anal cirri similar in length and shape to dorsal cirri and one additional median anal papilla. This species has been found at depths between 183 and 5449 m.

DISTRIBUTION

Cape Agulhas, South Africa and Angola Basin, Angola.

Anguillosyllis pupa (Hartman, 1965) comb. nov.
(Figure 2)

Braniella pupa Hartman, 1965: 72–73, pl. 8. Hartman & Fauchald, 1971: 51.

MATERIAL EXAMINED

One specimen ZMH P-13585, off New England, 400–500 m. One specimen USMN 103505, North Atlantic Ocean, USA, Georges Bank, Northern Slope.

DESCRIPTION

Holotype complete, 1.5 mm long, 0.4 mm wide, with ten segments. Body broad with tapering ends, no signs of colour pattern. Prostomium broader than long. Antennae papilliform (median one detached). Palps triangular, longer than proventricle, completely fused, with dorsal groove. Eyes absent. Three short papilliform antennae inserted in a straight row on posterior half of prostomium (Figure 2A). Peristomium shorter than subsequent segments, with one pair of short, papilliform tentacular cirri, smaller than antennae (Figure 2A). Dorsal cirri smooth, long and coiled, most of them detached. Dorsal cirri on chaetiger 2 absent (*vide* Hartman, 1965). Ventral cirri digitiform, medially inserted on parapodia, not reaching level of tips of parapodial lobes. One long, triangular posterior lobe (Figure 2B). Numerous compound, heterogomph chaetae per parapodium. Dorsal blades long, pseudo-spinigers (95 µm), decreasing in length to ventral falcigers, falciger like (10 µm), all unidentate (Figure 2C). Fine and short spines on cutting edge of blades. Shafts smooth. Pygidium conical, with two anal cirri and distal cilia (*vide* Hartman, 1965). Pharynx through four segments without pharyngeal tooth. Distal papillae on pharynx not observed. Proventricle almost spherical, through three segments, with about 20–25 muscle cell-rows.

REMARKS

Hartman (1965) did not describe the fine spines along the cutting edge of the blades. This species has been found at depths between 400 and 4892 m.

DISTRIBUTION

Off New England, north-eastern South America.

Anguillosyllis palpata (Hartman, 1967) comb. nov.

Braniella palpata Hartman, 1967: 55, pl. 14.

MATERIAL EXAMINED

One specimen ZMH P-24133, Antarctic Ocean, Weddell Sea.

REMARKS

Anguillosyllis palpata has long triangular palps fused at their basal half, papilliform antennae and only one pair of papilliform tentacular cirri. Ventral cirri are medially inserted to parapodia. Anterior and posterior parapodial lobes are present. The pharyngeal tooth is absent. The species was well described and illustrated by Hartman (1967). Found at depths between 383 and 3770 m.

DISTRIBUTION

Antarctic Ocean and nearby areas (Cape Horn, Drake Passage, Weddell Sea).

Genus *Brachysyllis* Imajima & Hartman, 1964

Brachysyllis Imajima & Hartman, 1964: 108.

DIAGNOSIS

Body large, macrofaunal, with 13 chaetigers plus a pre-anal achaetous segment. Segments more or less trapezoidal. Palps long, free at bases, with a subdistal small papilla. Prostomium with four eyes. Nuchal organs as ciliary rows. Rows of transversal cilia covering dorsum and ventrum. Antennae, and tentacular, anal and dorsal cirri long, filiform and smooth. Ventral cirri long, filiform, inserted proximally to parapodia. Parapodia elongate, with a triangular pre-chaetal lobe, dorsally located. Compound chaetae falcigerous, blades bidentate, dorsal and ventral simple chaetae absent. Aciculae bending distally. Pharynx wide, straight, with a large anterior dorsal tooth and an incomplete ventral arc of small denticles (5–6), surrounded by a crown of distal pharyngeal papillae. Proventricle rectangular, shorter than pharynx. Reproduction by epigamy.

TYPE SPECIES

Brachysyllis japonica Imajima & Hartman, 1964.

REMARKS

Imajima & Hartman (1964) described *Brachysyllis* as a new genus and *B. japonica* as the type species. They assigned the previously described species *Amblyosyllis infuscata* Ehlers, 1901 to this genus. Later, *Brachysyllis* was synonymized with *Dioplosyllis* Gidholm, 1962 by Imajima (1966). Mueller & Fauchald (1976) presented a table with features of the four species tentatively belonging to *Dioplosyllis*: *D. cirrosa* Gidholm, 1962, *D. infuscata*, *D. japonica* and *D. broadi* Mueller & Fauchald, 1976. Afterwards, *D. broadi* was considered synonymous with *D. lagunae* (Hartman, 1961) by Kudenov & Harris (1995) and Perkins (1981) described a new species of this genus, *D. octodentata* Perkins, 1981. Another species described as *Dioplosyllis* (*D. tridentata* Kudenov & Harris, 1995) does not agree with the diagnosis of this genus and will be assigned to another genus in a future work.

However, we consider that there are enough differences to maintain *Brachysyllis* and *Dioplosyllis* as two different genera since the five species, until the moment belonging to *Dioplosyllis*, can be easily divided into two clear groups. The first group includes the species *B. infuscata*, *B. japonica* and *D. lagunae*, which have a short body, with a fixed number of chaetigers (13 in all known species) plus one achaetous, pre-anal segment; segments more or less trapezoidal; palps totally free at bases, with a subdistal papilla; ventral cirri long, filiform and proximally located on parapodia;

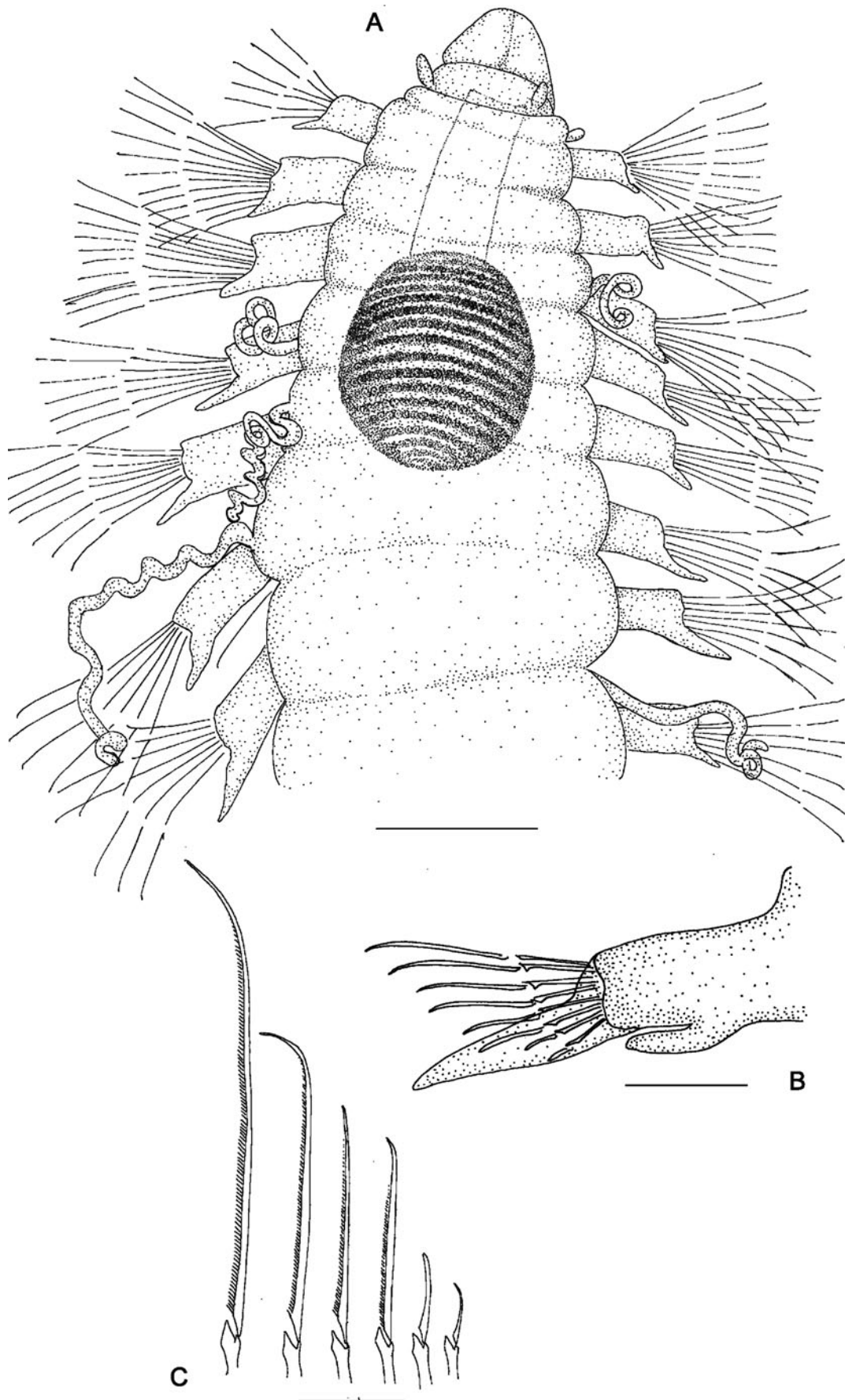


Fig. 2. *Anguillosyllis pupa* comb. nov. P.13585. (A) Anterior end, dorsal view; (B) midbody parapodium, anterior view; and (C) midbody chaetae. Scale bars: A, 0.2 mm; B, 74 μ m; C, 20 μ m.

and numerous aciculae (around 5), which are distally acute and curved (Imajima & Hartman, 1964; Mueller & Fauchald, 1976). The second group includes *D. cirrosa* and *D. octodentata*, which have a long body, with numerous rectangular segments (50–63), without pre-anal achaetous segment, palps fused at bases without subdistal papillae, ventral cirri short, digitiform, distally inserted and 1–2 aciculae distally truncated (Gidholm, 1962; Perkins, 1981). The type series of *D. cirrosa* has been lost, but we have examined specimens identified as *D. octodentata* from the Canary Islands (Núñez & San Martín, 1992) and have been able to check these differences. In addition to the morphological differences, the first group apparently has a distribution restricted to the Pacific Ocean (*B. infuscata* in Chile; *B. japonica* in Japan; and *B. lagunae* in California), and the second group is only known from the Atlantic Ocean (*D. cirrosa* in the north-eastern Atlantic and Mediterranean; *D. octodentata* in the Gulf of México, and the Canary Islands). Consequently, we consider *Brachysyllis* as a valid taxon, including *B. japonica*, *B. infuscata*, and *B. lagunae* and *Dioplosyllis* only comprising two species: *D. cirrosa* and *D. octodentata*.

Nevertheless, both genera appear to be closely related, since they share similar shape of palps, segments and ciliated parapodia, very long, filiform dorsal cirri, and significantly a very similar pharyngeal armature. Other genera with similar pharyngeal armature (a mid-dorsal tooth and a ventral arc of denticles) are *Eusyllis* Malmgren, 1867, and *Miscellania* Martín, Alós & Sardá, 1990. *Miscellania* is much smaller, meiofaunal, it has antennae with distal swelling, and its dorsal cirri are small, similar to those of the Exogoninae. *Eusyllis* has shorter dorsal cirri, pseudo-articulated in some species, with numerous denticles on the pharyngeal rim and the ventral cirri are short and digitiform (San Martín, 2003).

Brachysyllis is similar to *Amblyosyllis* in having the long dorsal cirri, often coiled over the dorsum, invariable number of chaetigers, with a pre-anal achaetous segment, segments more or less trapezoidal, and the presence of an elongated parapodial lobe. However, *Brachysyllis* is different in the pharyngeal armature (*Amblyosyllis* possesses a complete trepan, though lacks a mid-dorsal tooth and a crown of soft papillae), ventral cirri (short, triangular in *Amblyosyllis*) and the absence of nuchal epaulettes. Besides, *Amblyosyllis* has a long and coiled pharynx, while *Brachysyllis* likely has a straight pharynx. The latter character could not be observed since the dissection of the holotype was not possible.

The three previously described *Brachysyllis* species seem to be very similar to each other and could be synonyms. Coming to a reliable conclusion would require the re-examination of types of these species together with a detailed study of new, well-preserved material.

Key to species

1. Pharyngeal armature composed by a ventral arc with six small teeth and one large tooth dorsally located.
 *Brachysyllis japonica*
 — Pharyngeal armature composed by a ventral arc with five small teeth and one large tooth dorsally located.
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2. Compound chaetae bidentate with distal and proximal teeth large and rounded, both similar in size.

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 *Brachysyllis lagunae*
 — Compound chaetae bidentate with proximal tooth pointed, distal tooth larger than proximal one.

 *Brachysyllis infuscata*

Brachysyllis infuscata (Ehlers, 1901)
 (Figures 3 & 4)

Amblyosyllis infuscata Ehlers, 1901a: 258–259. Ehlers, 1901b: 100–102, pl. 11, figures 4–9. Augener, 1922: 188–189.

Brachysyllis infuscata Imajima & Hartman, 1964: 110.

Dioplosyllis infuscata Mueller & Fauchald, 1976: 21 (table).

MATERIAL EXAMINED

Holotype: ZMB 6742, Juan Fernández, Chile, 36.5 m.

DESCRIPTION

Holotype incomplete, fragmented in several pieces, anterior fragment with six segments, 4.5 mm long, 1.5 mm wide. Fourteen segments, 15.5 mm long (whole body length and segments *vide* Ehlers, 1901b). Body fragile; greyish brown. Segments trapezoidal, with transversal, pigmented grooves with clumps of cilia, also present in parapodia (Figures 3A & 4B–D). Prostomium oval, with four eyes in trapezoidal arrangement difficult to distinguish (Figure 3A). Antennae lost, lateral ones inserted on anterior margin of prostomium, median inserted in the middle of prostomium, between anterior pair of eyes. Palps completely free, divergent, ventrally folded, twice as long as prostomium, with one small lateral papilla on subdistal end (Figure 3A). Peristomium shorter than subsequent segments, with two pairs of smooth, long tentacular cirri (only present on one side), dorsal one longer than ventral. Most of dorsal cirri lacking, present ones very long, as long as 5–6 segments (Figure 3A), smooth with small granular material inside. Parapodial lobes long, half midbody segment width, conical in shape, with conical prechaetal lobe, distally pointed and postchaetal lobe shorter and distally truncate (Figure 3D). Ventral cirri long, digitiform, inserted on proximal half of parapodia, with orange granular material inside (Figures 3D & 4A), nearly twice as long as parapodia. Parapodia with about 20 compound, heterogomph chaetae, blades distinctly bidentate, with short spines on cutting edge of blades (Figures 3E & 4E–H). Within fascicle, blades decreasing in length from dorsal (88 µm) to ventral (42 µm). Distal part of fangs with two tips (Figure 3E). Five straight aciculae per parapodia, some ending in a thin tip bending distally (Figure 3C). Pygidium lost. Pharynx shape not visible. Several crowns of structures on anterior part of the pharynx; a crown of ten distal papillae, a crown of large cilia and five internal conical teeth (Figure 3B). Pharyngeal tooth not clearly observed (large and conical *vide* Ehlers, 1901b, pl. 11, figure 7). Proventricle extending through two segments, with about 50–60 muscle cell-rows.

REMARKS

The species was described with only one large mid-dorsal pharyngeal tooth (Ehlers, 1901b), but later Augener (1922) described it with an additional incomplete arc of five small teeth. The pharyngeal opening also exhibits a crown of long cilia, not previously described. Another characteristic not

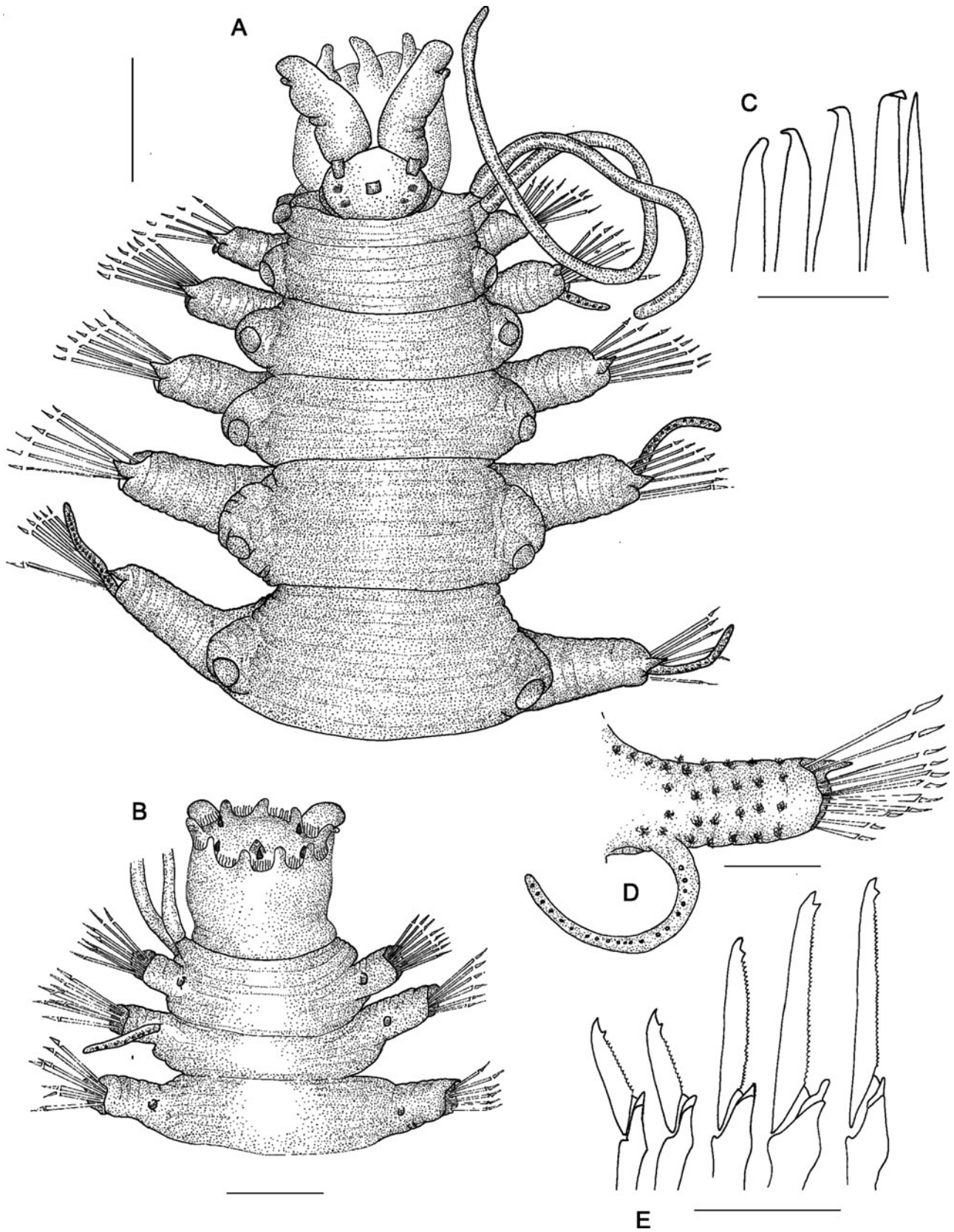


Fig. 3. *Brachysyllis infuscata*. (A) Anterior end, dorsal view; (B) everted pharynx, ventral view; (C) midbody aciculae; (D) midbody parapodium, posterior view; and (E) midbody falcigers. Scale bars: A & B, 0.7 mm; C & E, 50 μ m; D, 0.3 mm.

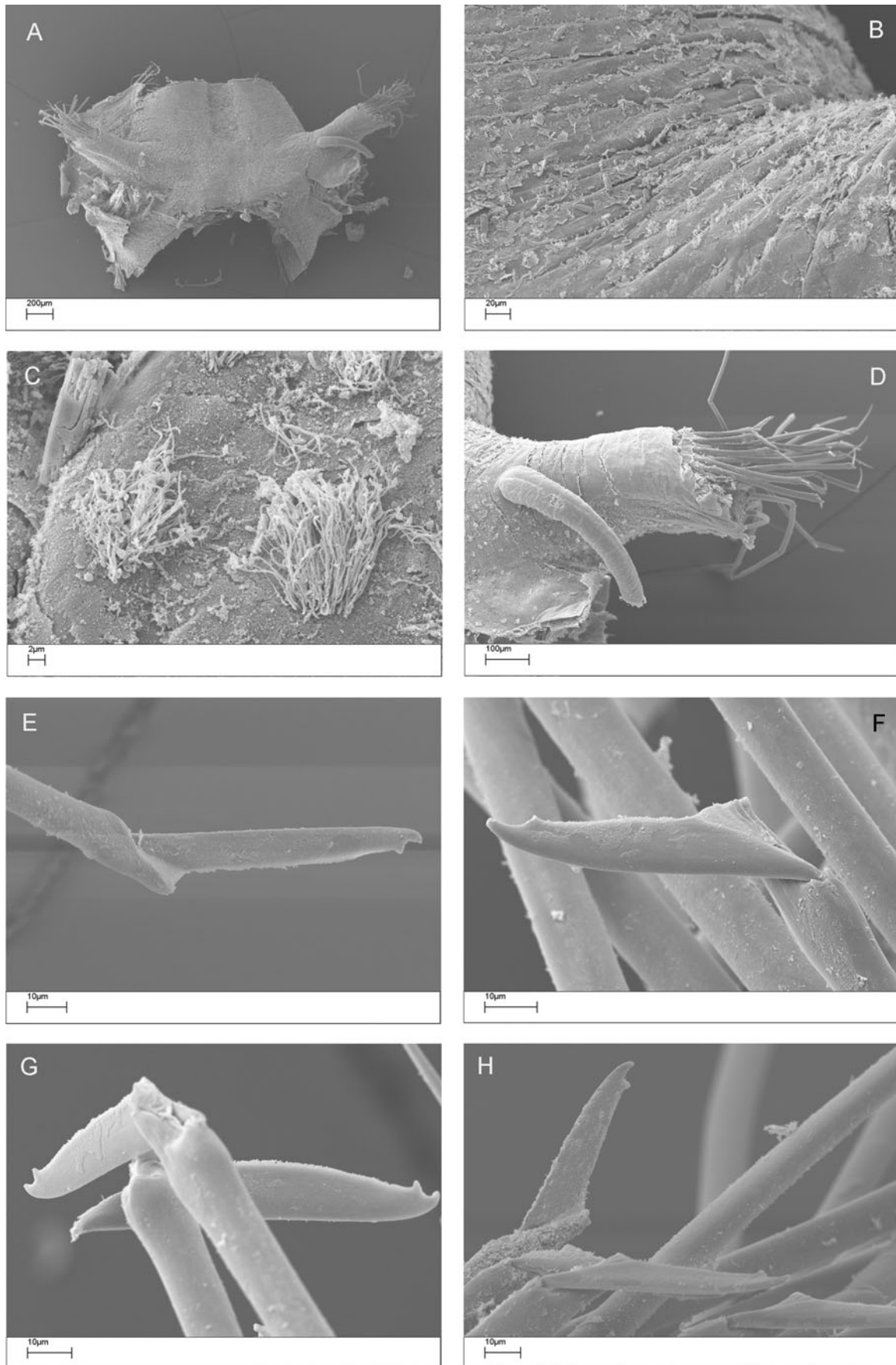


Fig. 4. *Brachysyllis infuscata*. Scanning electron microscopy. (A) Midbody segment, ventral view; (B) body surface, midbody segment; (C) clumps of cilia, midbody segment; (D) midbody parapodium; and (E–H) midbody falcigers.

previously described is the presence of transverse grooves with clumps of cilia along the body surface. Nuchal organs could not be studied since they are a difficult characteristic to observe in preserved material; however, the absence of nuchal epaulettes was noted. Other species of the genus were described with nuchal organs on ciliary ridges (Mueller & Fauchald, 1976). These ciliary ridges are probably grooves, more evaginated than usual in syllids, otherwise, the presence of nuchal organs on ridges would be a unique characteristic in Syllidae.

DISTRIBUTION

Juan Fernández, Chile.

Genus *Clavisyllis* Knox, 1957

Clavisyllis Knox, 1957: 493.

DIAGNOSIS

A macrofaunal species, body long, thick. Prostomium with four eyes, three antennae and two palps. Palps fused at base, ventrally directed. Peristomium with two pairs of tentacular cirri. Two prominent, long, sinuous nuchal epaulettes, together with single, digitiform nuchal cirrus. Antennae, tentacular and dorsal cirri large, ovoid, inflated, with distinct cirrophores; ventral cirri ovoid. Compound heterogomph falcigers with blades having long spines on cutting edges. Pharynx and proventricle of similar length; anterior margin of pharynx with a mid-dorsal tooth and a crown of soft papillae. Proventricle barrel-shaped.

TYPE SPECIES

Clavisyllis alternata Knox, 1957. Type series lost.

REMARKS

Knox (1957) could not assign this genus to any subfamily. He found some similarities with Exogoninae in terms of the shape of cirri and with Autolytinae given the presence of nuchal epaulettes. The genus also has some common features with *Amblyosyllis* (currently located within Eusyllinae) and *Lamellisyllis*, such as the presence of parapodial lobes and nuchal epaulettes. The presence of single nuchal cirri between nuchal epaulettes is unique in Syllidae. Only one species is known from this genus, *Clavisyllis alternata*. The holotype has been lost and there is only one specimen identified as *Clavisyllis alternata*.

Clavisyllis alternata Knox, 1957
(Figures 5 & 6)

Clavisyllis alternata Knox, 1957: 493–496, figures 1–3.

MATERIAL EXAMINED

One specimen NIWA 4067, New Zealand, North Island, port of New Plymouth, 39°09'18"S 174°05'70"E, 8 m, 17 April 2002.

DESCRIPTION

Specimen complete, 13 mm long, 1 mm wide, fragmented, with 61 segments. Live specimen orange, eyes red (*vide* Knox, 1957). Preserved specimen with whitish body, brownish parapodia and dorsal cirri. Body strongly arched, broad, tapering posteriorly. Prostomium rounded, with two pairs of large,

oval eyes, in a trapezoidal arrangement; posterior pair slightly larger than anterior ones (Figure 5A). Palps ventrally folded (Figure 5B), fused at their base, as long as prostomium. Antennae, tentacular and dorsal cirri with cylindrical ceratophores or cirrophores and distal, ovoid and inflated ceratostyles or cirrostyles, respectively (Figures 5A & 6A, B). Ceratostyles and cirrostyles with a reticulate surface (Figure 6B & E). Lateral antennae inserted on anterior end of prostomium, median antenna inserted on middle of prostomium, between posterior pair of eyes (Figures 5A & 6A, B). Nuchal epaulettes arising from posterior end of prostomium, sinuous and long, attached through their length to dorsum, reaching to chaetiger 8, with rows of cilia on lateral side and clumps of cilia covering dorsal side (Figures 5A & 6A–D). A short, digitiform nuchal cirrus present between nuchal epaulettes, inserted on posterior end of prostomium, reaching chaetiger 2 (Figure 5A). Peristomium shorter than subsequent segments, covered by nuchal epaulettes; difficult to see dorsally. Two pairs of tentacular cirri, dorsal pair larger than ventral ones. Dorsal cirri similar to dorsal tentacular cirri, alternating in their point of insertion and size over dorsum (Figure 5A). Dorsal cirri more dorsally inserted and smaller than those inserted more laterally (Figure 5A). Ventral cirri conical, not reaching tips of parapodial lobes (Figure 5D). Parapodia with a large stout rounded lobe projecting dorsally to chaetal bundle (Figure 5D). About 30 compound, heterogomph chaetae per parapodium. Anterior and posterior blades short (29–32 µm), bidentate, both teeth similar in size and length; short spines basally on cutting edge; long spines distally surpassing distal teeth (Figures 5C & 6F, G). One acicula per parapodia, straight and distally pointed (Figure 5D). Dorsal and simple chaetae not seen. Pygidium conical with two anal cirri similar to dorsal cirri. Pharynx straight, shorter than proventricle, with ten distal papillae and a pharyngeal tooth long and conical, anteriorly located (Figure 5E). Proventricle through three segments, with about 45 muscle cell-rows.

DISTRIBUTION

New Zealand (North Island, port of New Plymouth and type locality: Menzis Bay, Banks Peninsula on *Sertularia*).

Genus *Lamellisyllis* Day, 1960

Lamellisyllis Day, 1960: 319.

DIAGNOSIS

A macrofaunal species, body long, thick. Prostomium with four eyes, three lamella-shaped or foliaceous antennae and two palps fused at base. Two pairs of tentacular cirri, dorsal pair foliaceous, ventral pair cirriform. Two prominent nuchal epaulettes. Dorsal cirri large, ovoid and foliaceous, with distinct cirrophores; ventral cirri ovoid. Compound heterogomph falcigers with blades having long spines on cutting edge. Pharynx longer than proventricle. Proventricle barrel-shaped.

TYPE SPECIES

Lamellisyllis comans Day, 1960.

REMARKS

Although Day (1960, 1967) considered that there was only one pair of tentacular cirri, the re-examination of type material revealed that there are in fact two pairs of tentacular cirri on

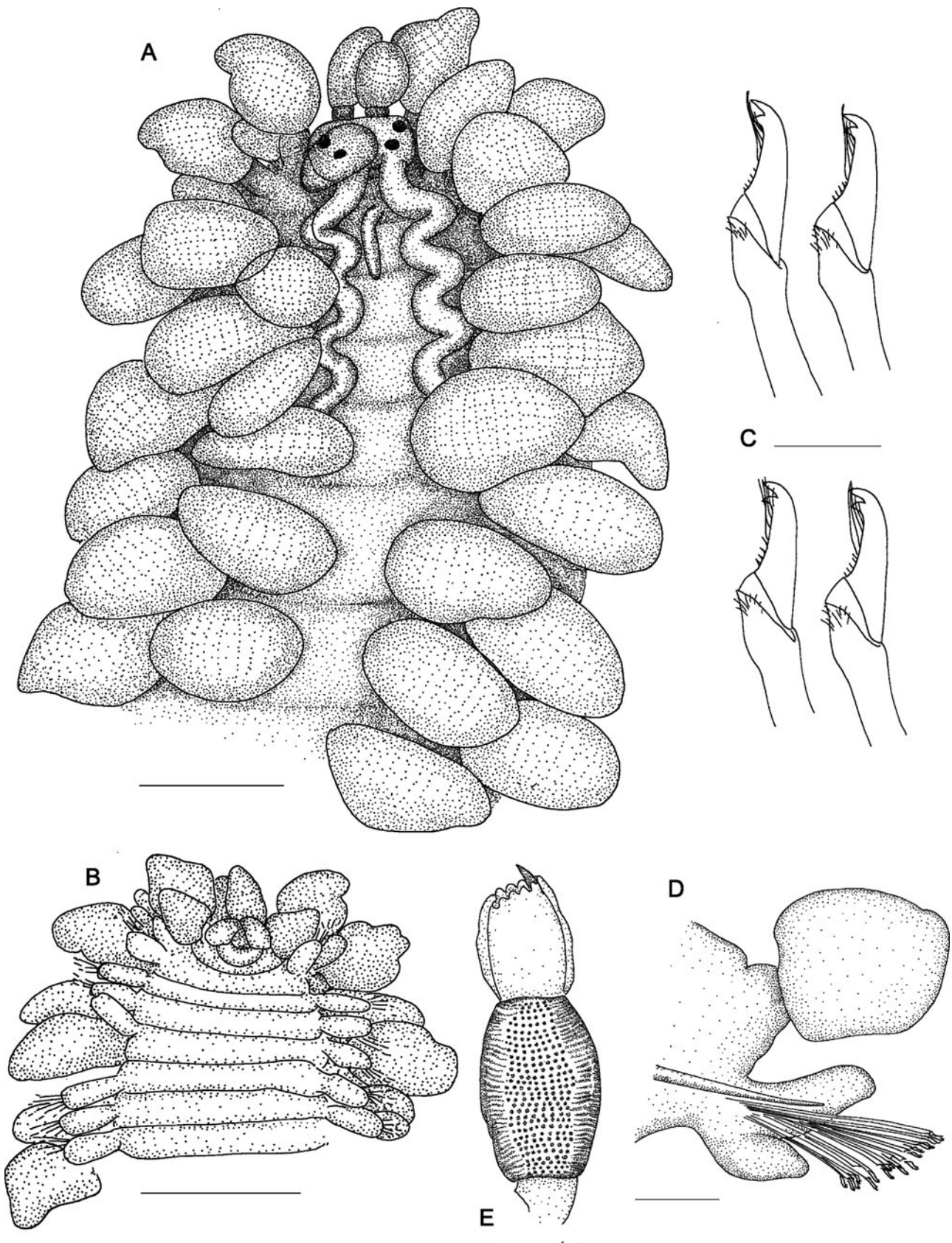


Fig. 5. *Clavisyllis alternata*. (A) Anterior end, dorsal view; (B) anterior end, ventral view; (C) midbody falcigers; (D) midbody parapodium, anterior view; and (E) pharynx and proventricle. Scale bars: A, 0.4 mm; B, 0.8 mm; C, 20 μ m; D, 0.2 mm; E, 0.5 mm.

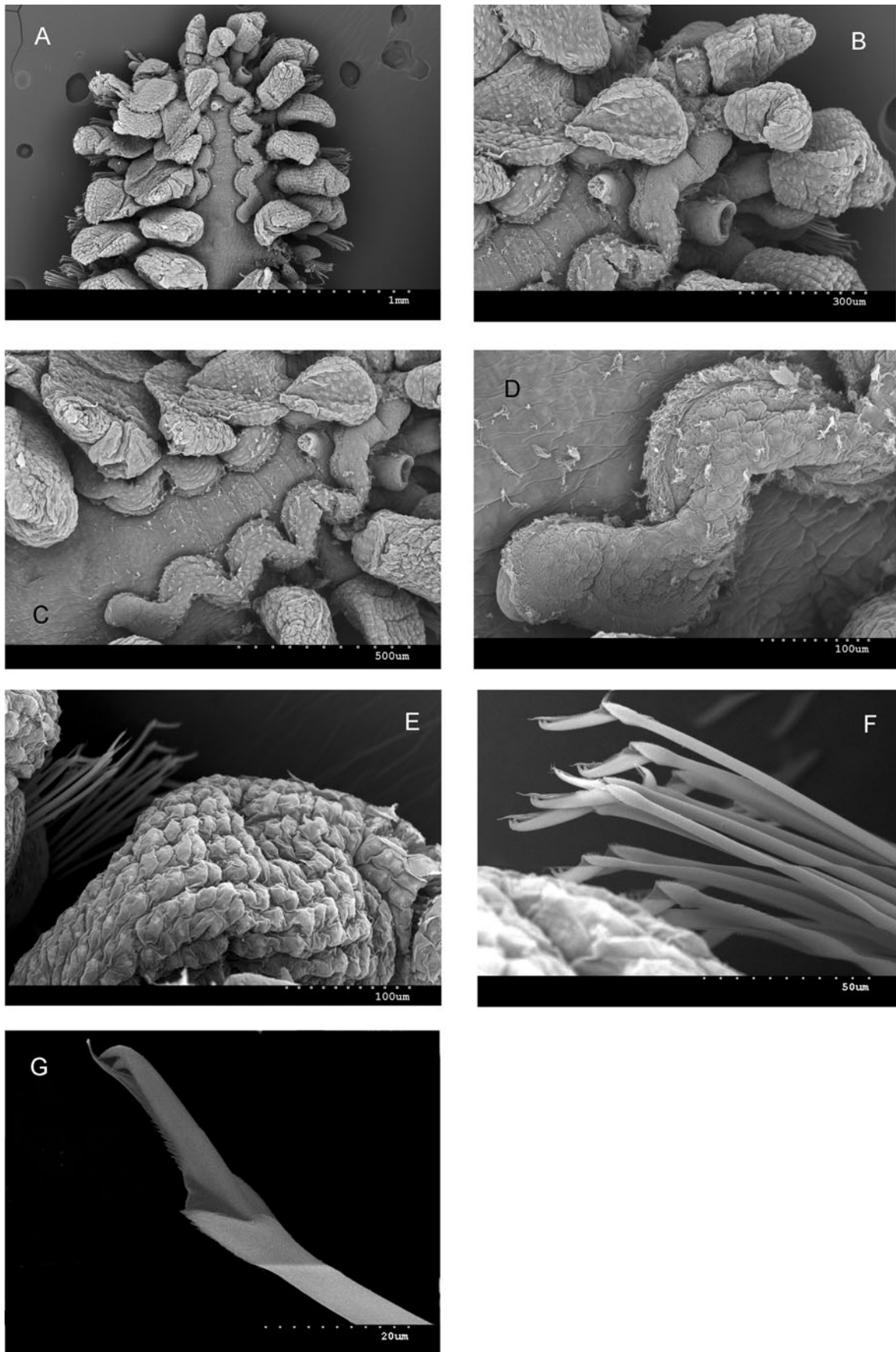


Fig. 6. *Clavisyllis alternata*. Scanning electron microscopy. (A & B) Anterior end, dorsal view; (C & D) nuchal epaulettes; (E) dorsal cirrus, midbody chaetiger; and (F & G) midbody falcigers.

peristomium. The genus was previously placed within Autolytinae because of the presence of nuchal epaulettes, although it was suggested that there could be a subfamily for this genus together with *Clavisyllis* (Day, 1960). The only known species of this genus, *Lamellisyllis comans*, presents similarities with *Clavisyllis alternata*. Both species have unusual dorsal cirri, foliaceous in *Lamellisyllis* and inflated in *Clavisyllis*, nuchal epaulettes and developed parapodial lobes. These latter two features are also present in *Amblyosyllis*. Members of Autolytinae, in general, also have nuchal epaulettes. The holotype has eggs within posterior segments (see below) and this evidence could suggest that this species reproduces itself epigamically. If the reproductive mode could be confirmed, it would suggest a closer relationship with Eusyllinae rather than Autolytinae. The genus has only one species, with one specimen.

Lamellisyllis comans Day, 1960
(Figure 7)

Lamellisyllis comans Day, 1960: 319, figure 7f–i. Day, 1967: 257.

MATERIAL EXAMINED

Holotype: SAM A20924. False Bay, South Africa, 8–12 m.

DESCRIPTION

Holotype complete, 8 mm long, 1 mm wide, with 50 segments. Body pale, dorso-ventrally flattened, with tapering ends. Prostomium dorsally covered by dorsal tentacular cirri, rounded, wider than long. Four eyes in rectangular arrangement, all similar in size (Figure 7A). Palps triangular, longer than prostomium, fused at base (Figure 7B). Three foliaceous antennae, lateral pair arising from anterior margin of prostomium, median one inserted on middle of prostomium (Figure 7A). Two grooved, finger-like nuchal organs diverging from posterior margin of prostomium towards laterals of chaetiger 3 (Figure 7A). Peristomium with two pairs of tentacular cirri, dorsal ones foliaceous, dorsally covering prostomium and peristomium, ventral ones with cylindrical cirrophore and digitiform cirrostyle (Figure 7B). Dorsal cirri foliaceous and flattened, oval to circular (Figure 7A & H). Ventral cirri conical, exceeding length of parapodial lobes (Figure 7H). Parapodia with a triangular, dorsal parapodial lobe distally located (Figure 7H). Parapodia with about 20 compound, heterogomph chaetae, decreasing in number and size towards posterior part of body. Blades bidentate, both teeth similar in size and length, long spines on edge, distal ones long, reaching distal teeth (Figure 7D & G). Anterior blades all similar in length (63 µm) posterior ones decreasing in length on the fascicle from dorsal blades (60 µm) to ventral ones (37 µm). Single acicula per parapodium, straight and distally pointed (Figure 7H). Posterior parapodia with one dorsal simple chaeta, unidentate, distally rounded (Figure 7F), and one ventral simple chaeta bidentate, with distal tooth longer than proximal one; with spines subdistally, with one larger spine (Figure 7E). Pygidium rounded with two anal cirri foliaceous, smaller than dorsal cirri (Figure 7C). Pharynx straight, through six segments (Figure 7A). Distal papillae and pharyngeal tooth not observed (one anterior dorsal tooth *vide* Day, 1960). Proventricle barrel-shaped, through 3–4 segments

(Figure 7A), with about 20 muscle cell-rows. Female holotype with numerous oocytes within body.

DISTRIBUTION

False Bay, South Africa.

Genus *Nuchalosyllis* Rullier & Amoureux, 1979

Nuchalosyllis Rullier & Amoureux, 1979: 164.

DIAGNOSIS

Body long, ribbon shaped, with numerous segments. Prostomium with two pairs of eyes and three antennae anteriorly located. Palps triangular, fused at base. Two pairs of tentacular cirri. Antennae, tentacular, dorsal and anal cirri distinctly articulated. A pair of prominent nuchal epaulettes, with several transversal lamellae. Parapodia conical, with enlarged, triangular prechaetal lobes. Ventral cirri conical, exceeding parapodial lobe. Compound chaetae, heterogomph falcigers. Pharynx with a large anterior dorsal tooth and a crown of ten distal pharyngeal papillae. Reproduction by schizogamy.

TYPE SPECIES

Nuchalosyllis lamellicornis Rullier & Amoureux, 1979.

REMARKS

Nuchalosyllis has a feature that makes it different from any other genera of Syllidae; the comb-like shape of the nuchal epaulettes. Nuchal epaulettes are typical in most of the genera of Autolytinae (which lack ventral cirri) but they are also present in *Amblyosyllis*, *Clavisyllis* and *Lamellisyllis*, the former currently located within Eusyllinae and the latter two with uncertain position; all of them with distinct ventral cirri. *Nuchalosyllis* may be related to these species, however their epaulettes are unique (with several lamellae) and its reproduction is schizogamic. The reproductive mode could suggest that the species may well belong to or may well be related to the subfamily Syllinae. *Nuchalosyllis lamellicornis* closely resembles *Trypanosyllis* in having numerous segments and a ribbon-like body. However, *Nuchalosyllis* does not possess a trepan, characteristic feature of *Trypanosyllis*, and its nuchal organs are markedly different. The genus has only one species, with one specimen.

Nuchalosyllis lamellicornis Rullier & Amoureux, 1979
(Figure 8)

Nuchalosyllis lamellicornis Rullier & Amoureux, 1979: 164–166, figure 6.

MATERIAL EXAMINED

Holotype: MNHN 1302, Brazil, near Salvador, 44–60 m, sand with stones and broken shells.

DESCRIPTION

Holotype fragmented, anterior part 27 mm long, 1.8 mm wide with 125 segments and posterior part 22 mm long and 124 segments; stolon developing on posterior end (Figure 8F). Body dorso-ventrally flattened, pale yellow to orange without colour markings. Cirrophores markedly pigmented in orange. Antennae and tentacular cirri weakly pigmented in pale yellow. Dorsal cirri with bright yellow to

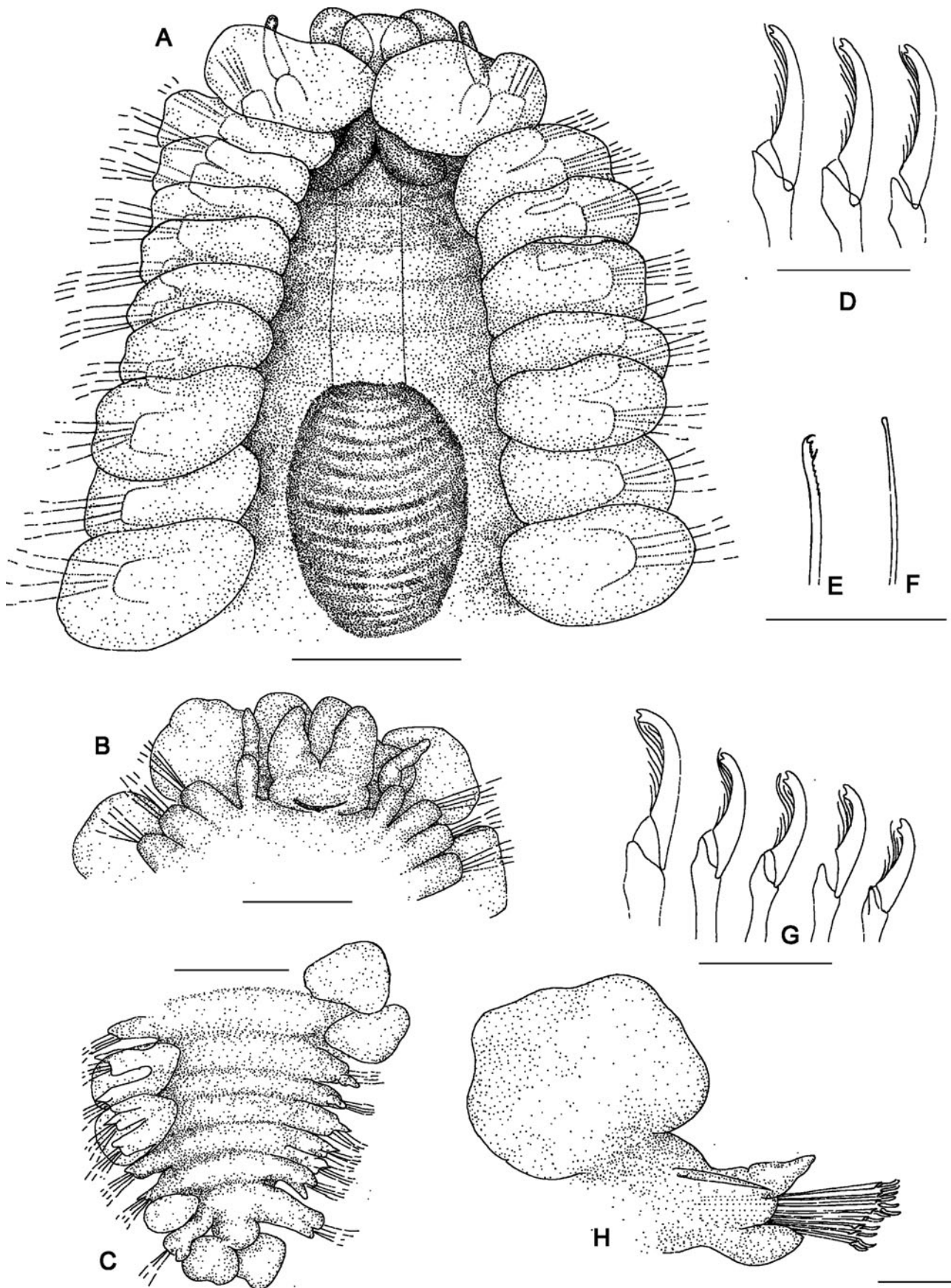


Fig. 7. *Lamellisyllis comans*. (A) Anterior end, dorsal view; (B) anterior end, ventral view; (C) posterior end, dorsal view; (D) anterior falcigers; (E) dorsal simple chaeta, posterior parapodium; (F) ventral simple chaeta, posterior parapodium; (G) posterior falcigers; and (H) midbody parapodium, anterior view. Scale bars: A & C, 0.5 mm; B & H, 0.4 mm; D–G, 48 μ m.

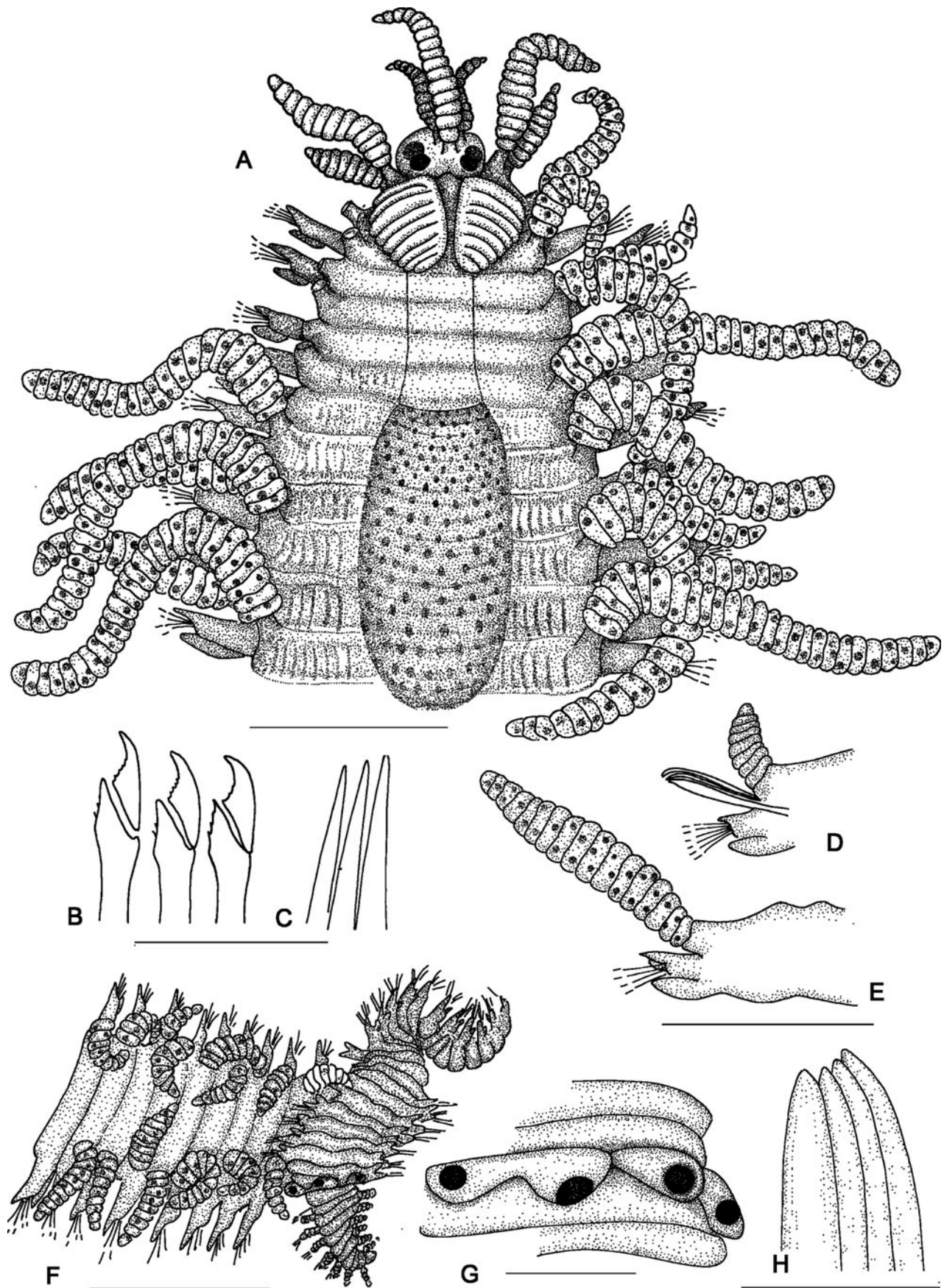


Fig. 8. *Nuchalosyllis lamellicornis*. (A) Anterior end, dorsal view; (B) midbody falcigers; (C) midbody aciculae; (D) parapodium of stolon, anterior view; (E) midbody parapodium, anterior view; (F) posterior end in regeneration and stolon, dorsal view; (G) prostomium of developing stolon; and (H) natatory chaetae. Scale bars: A, 1 mm; B, C & H, 48 μ m; D & E, 1.8 mm; F, 1.2 mm; G, 0.2 mm.

orange granular material inside (Figure 8A). Transversal grooves and crests on dorsal surface of midbody segments towards posterior ones. Prostomium oval, slightly wider than long; two pairs of dark reddish eyes in open trapezoidal arrangement; anterior pair larger than posterior ones. Median antenna emerging from anterior part of prostomium, between anterior pair of eyes, with relatively short ceratophore and 15 articles. Lateral antennae inserted anteriorly to median one in the middle of prostomium with short ceratophores, shorter than median antenna with ten articles (Figure 8A). Palps conical, similar in length to prostomium, free or very basally fused, ventrally folded and not visible dorsally. Large nuchal epaulettes, arising from posterior end of prostomium, with about 7–8 transversal lamellae (Figure 8A). Peristomium relatively short, with an anterior lobe covering posterior part of prostomium. Two pairs of tentacular cirri; cirrophores well developed, dorsal pair with about 15 articles, ventral pair shorter, with about ten articles. Anterior and midbody dorsal cirri thick, originating on distinct cirrophores, alternately long and short. Long dorsal cirri longer than body width; with about 20–30 articles; inserted dorso-laterally. Short dorsal cirri with about 15 articles, inserted more ventrally than long cirri (Figure 8A & E). Posterior dorsal cirri similar to anterior ones but shorter, with about 10–15 articles (Figure 8F). Ventral cirri lanceolate, anterior ones longer than parapodial lobes, slightly decreasing in length towards posterior segments. Parapodia conical, with a long triangular to digitiform prechaetal lobe inserted on dorsal position and one smaller, oval postchaetal lobe ventrally inserted (Figure 8F). Anterior parapodia with 12–15 compound falciger chaetae. Blades unidentate, smooth or with small, short, thin spines on cutting edge of blades, 24 µm long (Figure 8B). Posterior parapodia with ten falcigers similar in shape and length to anterior ones. Dorsal and ventral simple chaetae not observed. Three straight and pointed aciculae per parapodia (Figure 8C). Pharynx through seven segments, proventricle through six segments, with about 30 muscle cell-rows (Figure 8A). Pharyngeal tooth located on anterior part of pharynx, large and conical, surrounded by a crown of ten papillae. Pygidium in regeneration, conical, without anal cirri (Figure 9F).

STOLON

Sexual reproduction by stolons formed by posterior budding, stolon beginning on chaetiger 290. Fully developed stolon complete with 37 chaetigers (Figure 8F). Attachment of stolon to parental specimen directly on dorsal surface, parental specimen ventrally regenerating posterior end (Figure 8F). Stolon with yellowish to orange body, dorsal cirri partially pigmented in orange. Stolon's head in development, visible in ventral position. Two pairs of eyes on lateral sides of prostomium on two cephalic lobes, dark reddish; posterior pair larger than anterior one (Figure 8F, G). Palps reduced or absent. Dorsal cirri with 5–6 articles, cirrophores well developed. Ventral cirri slightly longer than parapodia lobes, digitiform to lanceolate (Figure 8D). Conical neuropodia with pre- and postchaetal lobes with about five unidentate falcigers (Figure 8D). Wide and long notochaetae, laceolate in shape, in many cases fused along their length forming paleae (Figure 8D & H).

DISTRIBUTION

Brazil.

Genus *Odontosyllis* Claparède, 1863;

Odontosyllis Claparède, 1863: 47. San Martín & Hutchings, 2006: 281–282.

Alluaudella Gravier, 1905: 372.

TYPE SPECIES

Syllis fulgurans Audouin & Milne-Edwards, 1833.

DIAGNOSIS

(Modified from San Martín & Hutchings, 2006.) Body of variable size, 5–10 mm in length, with numerous cylindrical segments. Prostomium with four eyes, and sometimes a pair of anterior eyespots. Three antennae. Palps broad, free for almost all their length, fused basally. Peristomium usually reduced dorsally; two pairs of tentacular cirri. Occipital flap present, usually well developed, covering peristomium dorsally and prostomium partially. Nuchal organs as two ciliated grooves between prostomium and peristomium, sometimes extending to lateral areas of prostomium. Dorsal cirri elongated, smooth, distally tapered, but sometimes short or indistinctly articulated. Parapodia usually with pre- and postchaetal lobes. Ventral cirri digitiform to pillow-shaped. Compound chaetae heterogomph, usually with shafts distally spinose. Dorsal and ventral simple chaetae present on some parapodia. Pharynx short, distinctly shorter than proventricle, provided with a few teeth, directed backwards, pharyngeal mid-dorsal tooth absent; pharynx when not everted situated posteriorly to chaetiger 1. Proventricle usually long and wide and massive. Pygidium with two anal cirri. Reproduction by epigamy; epigamic specimens sometimes strongly modified and phosphorescent.

REMARKS

San Martín & Hutchings (2006) suggested that *Alluaudella* could be synonymous with *Odontosyllis*, however, they could not revise the type series. In their paper, they provide a complete list of synonymies. The genera *Fauvelia* Gravier, 1900; *Atelesyllis* Pruvot, 1930; *Eurymedusa* Kinberg, 1865 and *Synpalposyllis* Hartmann-Schröder, 1983 may well be synonymous with *Odontosyllis* too, their type series however, have been lost or they consist only in one juvenile without clear diagnostic features (e.g. in *Synpalposyllis*).

Odontosyllis madagascariensis (Gravier, 1905) comb. nov.
(Figure 9)

Alluaudella madagascariensis Gravier, 1905: 372–376, figures 1–5. Day, 1967: 279, 278.

MATERIAL EXAMINED

Holotype: MNHN 279 and two paratypes MNHN280, Madagascar, Fort Dauphin, coll. by Allan, 1 January 1901.

ADDITIONAL MATERIAL EXAMINED

Alluaudella longocirrata Murad & Mohamad, 1973. Holotype: NHML 1971.43, Kuwait, Al-Najafa, 29°16'N 48°05'E, intertidal in rock cleft, 1 August 1969.

DESCRIPTION

Body broad anteriorly, tapered posteriorly. Holotype is fragmented in two parts, 8 mm long in total with 51 segments, anterior end 3 mm long, 1 mm wide. Two paratypes, with

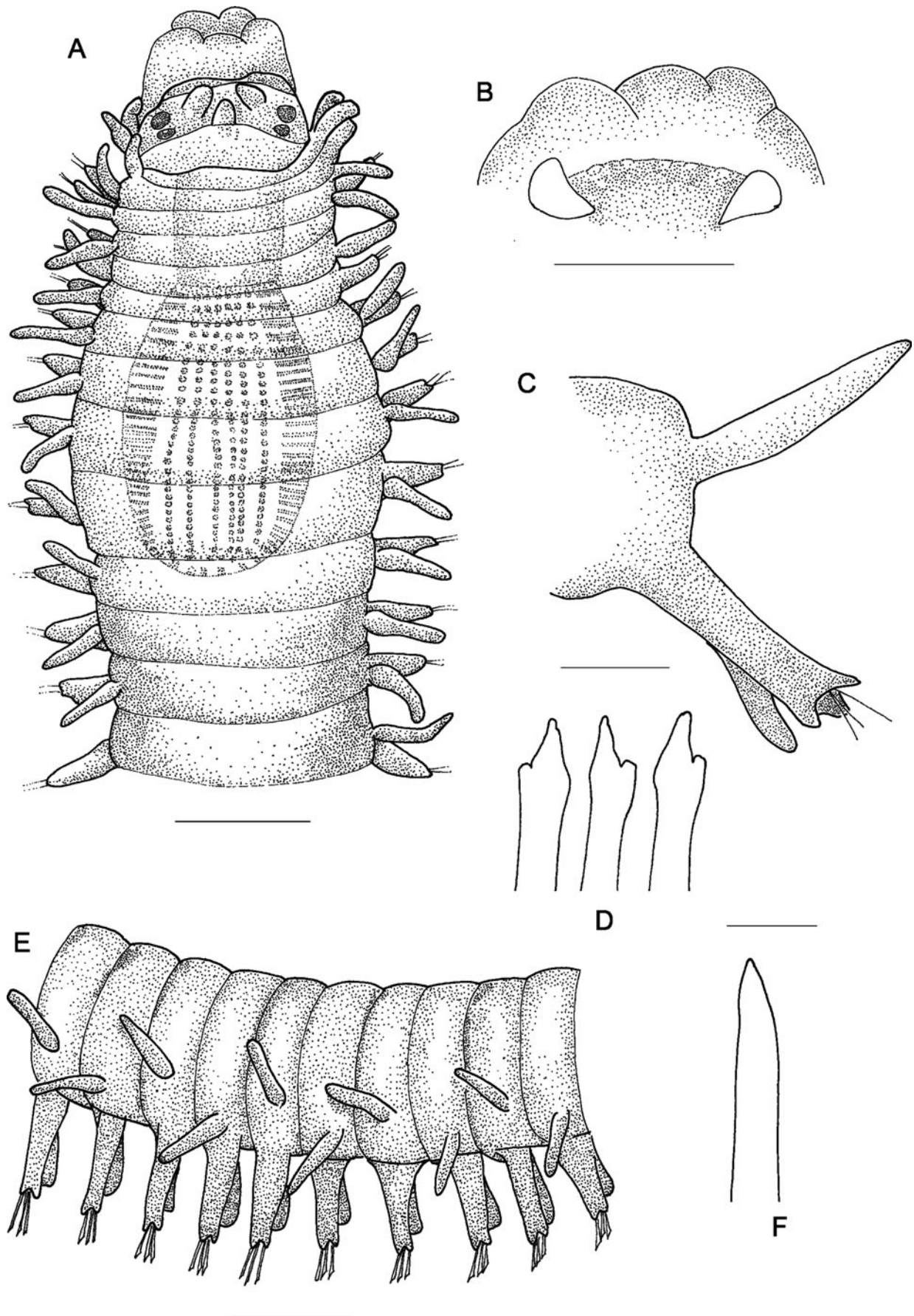


Fig. 9. *Odontosyllis madagascarensis* comb. nov. (A) Anterior end, dorsal view; (B) lateral plates on pharynx; (C) midbody parapodium, anterior view; (D) midbody chaetae; (E) midbody segments, lateral view; and (F) midbody acicula. Scale bars: A & E, 0.5 mm; B, 0.25 mm; C, 0.15 mm; D & F, 12.5 μ m.

several fragments, 5 mm and 3 mm long, both 0.9 mm wide. Colour pattern consisting of transversal black or dark brownish bands on posterior end of each segment and black spots irregularly distributed over dorsum of anterior segments. Some paratypes without colour pattern. Dorsum of body markedly arched. Prostomium oval, large; four eyes in open trapezoidal arrangement; median antenna short, conical, shorter than prostomium, originating between posterior eyes (Figure 9A). Lateral antennae short and conical, similar in length to median one, originating near anterior margin of prostomium, close to median antenna (Figure 9A). Palps reduced, shorter than prostomium, ventrally folded. Nuchal organs as two ciliated pits between prostomium and peristomium. Peristomium dorsally reduced. Large occipital flap covering posterior part of prostomium. Tentacular cirri digitiform, both similar in size, longer than antennae (Figure 9A). Dorsal cirri more elongated than antennae and tentacular cirri, shorter than half of body width, as long as parapodial lobe on anterior segments, half longer than parapodial lobe on posterior segments (Figure 9A & E). Dorsal cirri alternating in their insertion and orientation, those arising from dorsal position directed dorsally; those arising from ventral position directed ventrally (Figure 9E). Parapodial lobes elongated, lateroventrally directed, almost rectangular, with one prechaetal lobe and two postchaetal lobes, anterior one slightly longer than posterior ones (Figure 9C). Progressively, posterior parapodia becoming more elongated, parapodial lobes more distinct. Ventral cirri digitiform, not reaching or extending beyond parapodial lobes (Figure 9C); 12 simple chaetae per parapodia, apparently shafts of compound chaetae (Figure 9D). Ventral simple chaetae on posterior parapodia, thin, smooth. Dorsal simple chaetae not observed. Parapodia with one pointed acicula (Figure 9F). Pharynx short and wide, through 2–3 segments (Figure 9A), with two lateral plates (Figure 9B). Proventricle wide, short, barrel-shaped slightly longer than pharynx, through about five segments (Figure 9A), with 35 muscle cell-rows in paratype, not visible in the holotype. Pygidium missing on the examined specimens.

REMARKS

Gravier (1905) and later Day (1967) considered that this species lacked ventral cirri and principally because of this characteristic, they placed it in a new genus. After detailed examination, we saw ventral cirri on each parapodium, inserted on the proximal half of parapodia and in many cases joined to the parapodia, though possibly fused during the preservation process. Gravier (1905) dissected one paratype and described the terminal part of the pharynx with papillae but he did not observe any kind of armature. After examining the dissected paratype we agree that it is difficult to observe any teeth, but two lateral plates, common in the trepan of *Odontosyllis*, were evident. Another characteristic mentioned in the previous descriptions was the presence of spherical tentacular cirri. However, the tentacular cirri are bent in the holotype. In a dorsal view they seem to be oval but in a lateral position it is possible to appreciate its distal part. They are slightly shorter than the dorsal cirri but the difference in length is not significant. Finally the chaetae were described as simple chaetae, although Day (1967) considered them as shafts without blades, which were probably lost. We agree with the latter hypothesis since they are quite similar in shape to common shafts of Syllidae. None of the

specimens present blades but the type series consists only in the holotype and two paratypes plus several fragments, therefore it is quite possible that all of them have lost their blades.

The studied species shares several diagnostic characteristics with *Odontosyllis*: presence of an occipital flap, shape and length of dorsal and ventral cirri, elongated parapodia with several long pre- and postchaetal lobes, lateral plates in the pharynx and probably teeth, short and spherical proventricle and short and considerably wide pharynx. Although the presence of the typical trepan of *Odontosyllis* was not clearly observed, we consider that there are enough similarities to assign this species to genus *Odontosyllis*. The only other species of the genus, *A. longocirrata*, was synonymized with *O. freycinetensis* by San Martín & Hutchings (2006). The holotype of this species also lacked a complete trepan but San Martín & Hutchings (2006) argued that the specimen was a juvenile and this characteristic might not be present in juvenile individuals. This too, might be the explanation for the absence of teeth in *O. madagascariensis* since the specimens were all small (3–8 mm) (adult specimens in *Odontosyllis* are generally 20–40 mm long). *Odontosyllis freycinetensis* is also similar to *O. madagascariensis* in the colour pattern and long parapodia, however, its dorsal cirri are not inserted at different levels, as they are in *O. madagascariensis*. Other similar species of *Odontosyllis* are *O. annulatus* (Hartmann-Schröder, 1979) and *O. globulocirrata* Hartmann-Schröder, 1981, both from Australia. *Odontosyllis annulatus* was originally described without ventral cirri as Gravier (1905) described *O. madagascariensis*; however, it has ventral cirri distally inserted and practically fused to parapodia (San Martín & Hutchings, 2006). Both species are different principally because ventral cirri and parapodia in *O. annulatus* are considerably shorter. *Odontosyllis globulocirrata* is similar to *O. madagascariensis* in the presence of dorsal cirri inserted alternatively at different levels on each segment. Besides, the specimen dissected by San Martín & Hutchings (2006) did not have a trepan. Nevertheless, they are remarkably different in the shape and size of dorsal cirri, which are spherical in *O. globulocirrata*.

DISTRIBUTION

Madagascar.

Genus *Parexogone* (Mesnil & Caullery, 1918)

Parexogone Mesnil & Caullery, 1918: 125. San Martín, 2005: 108.

Exogonella Hartman, 1961: 74.

TYPE SPECIES

Paedophylax hebes Webster & Benedict, 1884.

DIAGNOSIS

Modified from San Martín (2005). Body small, meiofaunal, surface smooth. Prostomium with three antennae; usually four eyes, sometimes also with two eye spots. Palps well developed, completely fused to each other or with terminal notch. Single pair of minute tentacular cirri. Dorsal cirri usually small, papilliform to oval, present on all segments or absent on chaetiger 2 in adults of some species. Compound chaetae with heterogomph articulations, falcigers all similar in shape and blade length, sometimes pseudospinigers with simple

shaft tips, blades relatively similar to falcigers but longer. Dorsal simple chaetae similar throughout body, tips unidentate or bidentate, with both teeth similar. Ventral simple chaetae on posterior parapodia. Two usually long anal cirri present. Pharynx with anterior margin surrounded by soft lobes, with anterior tooth. Mature females carrying eggs ventrally, developing to embryos and juveniles, lacking capillary notochaetae (natatory chaetae); mature males with long natatory chaetae; some species viviparous.

REMARKS

Parexogone was initially considered to be a subgenus of *Exogone* Örsted, 1845 by San Martín (1991). It was later promoted to a genus by Böggemann & Westheide (2004).

Parexogone brunnea (Hartman, 1961)
(Figure 10)

Exogonella brunnea Hartman, 1961: 74–75, pl. 8, figures 1–5; 1965: 430, 431.

MATERIAL EXAMINED

Holotype: NHMLAC 14,811, Point Vicente, San Pedro area, Southern California, shelf and slope depths, in sediments of black mixed silt and sand.

DESCRIPTION

Body small, cylindrical, holotype complete 4 mm long, and 0.3 mm wide, with 48 segments. Prostomium ovate to rectangular, wider than long; eyes not observed (four small eyes spots in the posterior half of prostomium, *vide* Hartman, 1961); antennae short, papilliform, all similar in size. Median antenna inserted on posterior part of prostomium and partially covered by peristomium, slightly posteriorly located. Palps broad, longer than prostomium, fused along their length, anterior end bluntly conical (Figure 10A). Peristomium shorter than subsequent segments, covering dorsally posterior part of prostomium; tentacular cirri papilliform, similar to lateral antennae. Dorsal cirri on all segments, papilliform similar in size and shape to tentacular cirri and antennae (Figure 10A). Ventral cirri papilliform, not reaching tips of parapodial lobes. Anterior chaetigers with six compound chaetae, two pseudospinigers with elongate blades (32 μm), unidentate, distal tooth larger than proximal one; blades with long, erect, fine spines on cutting edge (Figure 10C); four falcigers with short blades (6 μm), unidentate, with fine spines on proximal side of cutting edge (Figure 10D). Posterior parapodia with four compound chaetae; one pseudospiniger, shorter than anterior ones (19 μm); four falcigers (6 μm). Dorsal simple chaeta on posterior-most parapodium, straight, unidentate (Figure 10E). Ventral simple chaetae not observed. Pygidium conical, with two spherical anal cirri, larger than dorsal cirri and antennae (Figure 10B). Pharynx through six segments; pharyngeal tooth conical, on anterior edge (Figure 10A). Proventricle short, through 4–5 segments (Figure 10A), muscle cell-rows not clearly visible.

REMARKS

The monotypic genus *Exogonella* was described as a new taxon, as the species *E. brunnea* was reported to lack antennae and dorsal cirri. However, after a detailed study, we found that the holotype has three minute, papilliform antennae on the posterior part of the prostomium, and tentacular and dorsal

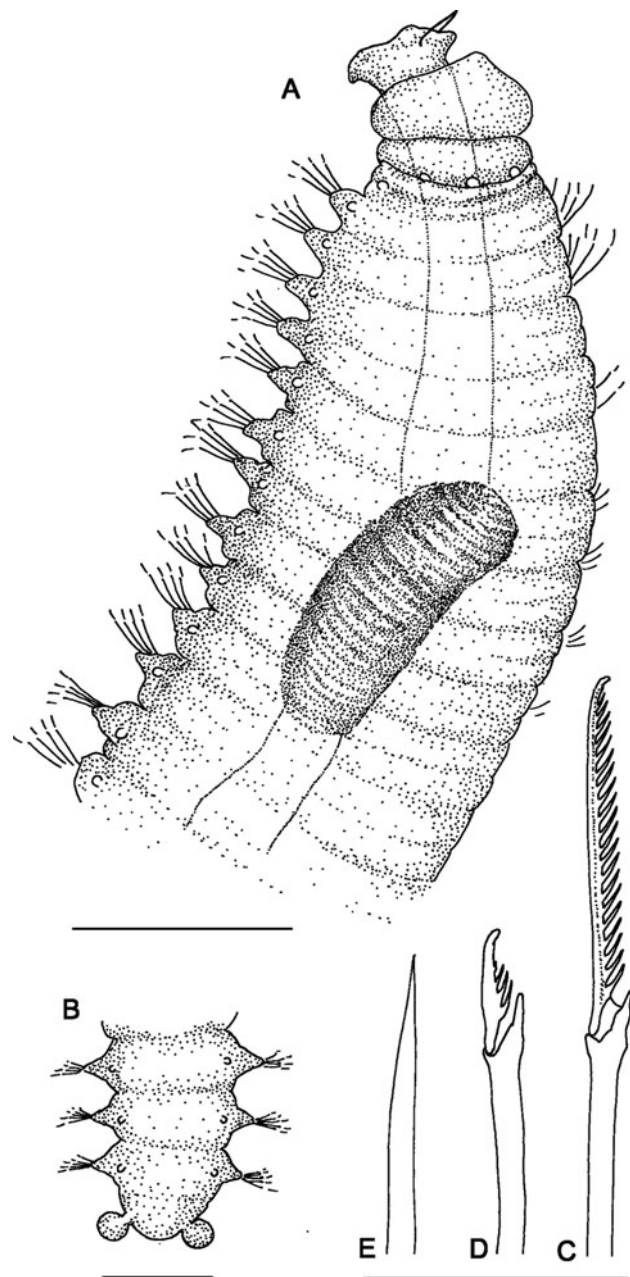


Fig. 10. *Parexogone brunnea* comb. nov. (A) Anterior end, dorsal view; (B) posterior end, dorsal view; (C) superior chaeta, anterior parapodium; (D) inferior chaeta, anterior parapodium; and (E) simple dorsal chaeta, anterior parapodium. Scale bars: A, 0.2 mm; B, 0.25 mm; C–E, 24 μm .

cirri similar to antennae on each parapodium. This species has similar characteristics to the *Parexogone* species and it is herein transferred to that genus. The eyes were not distinguished in this revision, probably due to the poor state of preservation.

DISTRIBUTION

Southern California.

Nomina dubia taxa

Exogonoides antennata Day, 1963
(Figure 11)

Exogonoides antennata Day, 1963: 403–404, text-figure 5 j–n. Day, 1967: 279, figure 12.11s–w.

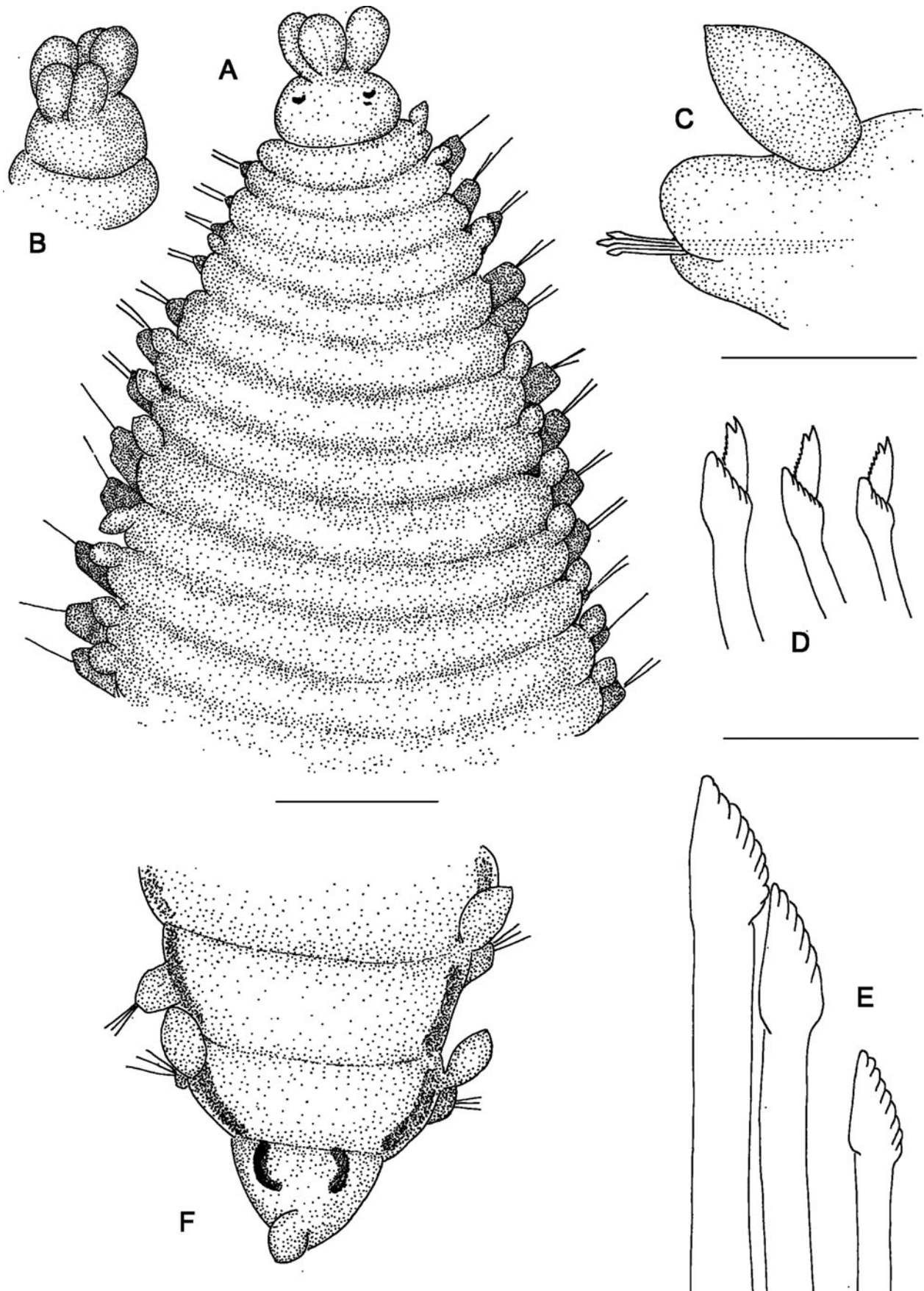


Fig. 11. *Exogonoides antennata* incertae-sedis. (A) Anterior end, dorsal view, holotype; (B) anterior end, ventral view, holotype; (C) midbody parapodium, anterior view, paratype; (D) anterior chaetae, holotype; (E) posterior chaetae, paratype; and (F) posterior end, dorsal view, paratype. Scale bars: A, B & F, 0.2 mm; C, 92 μm ; D & E, 20 μm .

MATERIAL EXAMINED

Holotype: NHML 1963.1.34, south coast of Cape Province, 34°02'1 23°28.4'E, 49 m, sand and rocks, 29 November 1960, coll. by Professor J.H. Day.

Paratype: NHML 1963.1.35, south coast of Cape Province, 34°02'S 23°28.4'E, 49 m, sand and rocks, 29 November 1960, coll. by Professor J.H. Day.

DESCRIPTION

Holotype anterior fragment with more than 200 segments, 35 mm long and 0.5 mm wide. Paratype posterior fragment. Body cylindrical, broad and slender, cream coloured with black vertical marks on dorso-lateral sides of posterior segments and pygidium (Figure 11F). Prostomium wider than long, elliptical. Two pairs of eyes, crescent-shaped; located on anterior half of prostomium; anterior pair larger than posterior one (Figure 11A). Ocular spots absent. Five anterior lobes, ovoids; three of them more dorsally located (antennae, *vide* Day, 1963) inserted on anterior part of prostomium, all similar in length. Remaining two lobes ventrally located (palps, *vide* Day 1963), shorter than dorsal ones, not visible dorsally, and not fused (Figure 11A & B). Peristomium similar in length to following segments. One pair of tentacular cirri, ovoid. Dorsal cirri spherical to ovoid, increasing in size towards posterior part. Ventral cirri fused to ventral margin of parapodia (Figure 11C). Holotype with three compound heterogomph chaetae per parapodium, with short blades (6–8 µm), bidentate, both teeth similar in size and fine spines on cutting edge of blades (Figure 11D). Paratype with three simple chaetae per parapodium, morphologically similar to shafts of chaetae of holotype, but they are larger and distally expanded, triangular with serration on cutting edge of blades (Figure 11E). Aciculae not seen. Pygidium conical with one anal cirri, ovoid, similar to dorsal cirri (Figure 11F). Pharynx and proventricle not present (holotype dissected) (pharynx through six segments and proventricle with 15 muscle cell-rows, trepan and pharyngeal tooth absent, *vide* Day, 1963).

REMARKS

Day (1963) considered this species similar to *Exogone* in the antennae, tentacular and dorsal cirri shape, although a possible similarity with *Autolytinae* was also suggested. In the original description, the holotype was considered to be an anterior fragment and the paratype a posterior fragment. We agree with this interpretation, and we add that both fragments could actually belong to the same animal, because the segment at which the holotype is fragmented coincides with the first segment of the paratype. Simple chaetae in posterior chaetigers seem to be the result of an enlargement of shafts and loss of blades. Although simple chaetae of several Syllidae species are supposed to have the same origin (e.g. *Syllis amica* Quatrefages, 1865, *Syllis ferrani* Alós & San Martín, 1987, *Opisthosyllis japonica* Imajima, 1966 and *Haplosyllis onthogorgicola* Martín, Núñez, Riera & Gil, 2002), chaetae of *Exogonoides* are different from those of any described species. Moreover, pharynx and proventricle could not be examined since they were not preserved after dissection, consequently possible similarities and differences with the common proventricle of Syllidae could not be assessed. As some characteristics are different from any other species of the family and as we could not check the presence of

a proventricle, we believe this taxon should be considered *nomina dubia*.

DISTRIBUTION

Agulhas Bank, South Africa.

DISCUSSION

The genera *Alluaudella*, *Braniella* and *Exogonella* are considered to be non-valid, they have been synonymized with *Odontosyllis*, *Anguillosyllis* and *Paraexogone*, respectively. Otherwise, *Brachysyllis* is considered herein as a valid genus, exhibiting clear differences from *Dioplosyllis*. The relationships between *Anguillosyllis*, *Clavissyllis*, *Brachysyllis*, *Lamellisyllis* and *Nuchalossyllis* and the rest of Syllidae still prove difficult to establish, despite their revision. These, in fact, show a combination of traits which do not fit the diagnosis of any of the traditionally recognized subfamilies.

Other recently described genera are also difficult to assign to any subfamily. For instance, *Nooralia* San Martín, 2002 possesses a peculiar system of brooding carrying eggs attached to dorsal chaetae. This genus was provisionally placed within Exogoninae, despite not fully coinciding with the diagnosis (San Martín, 2002). *Karroonsyllis* San Martín & López, 2003 is a genus with a mixture of traits typical of the Exogoninae and Syllidae subfamilies, and was provisionally placed within Syllinae due to the presence of articulated cirri (San Martín & López, 2003). *Paraopisthosyllis* Hartmann-Schröder, 1991 was provisionally assigned to Eusyllinae despite the fact that its dorsal cirri could be considered as articulated (with only one article), and its reproductive mode is still unknown (San Martín & Hutchings, 2006). Finally, *Murrindisyllis* San Martín, Aguado & Murray, 2007, is a recently described genus showing a combination of traits between Exogoninae and Eusyllinae (San Martín *et al.*, 2007). All these examples show that there are too many exceptions to the rule. There are few phylogenetic studies on Syllidae and they are principally focused in particular processes, such as reproductive modes (Nygren, 1999; Nygren & Sundberg, 2003) or in specific groups, e.g. *Autolytinae* (Nygren, 2004) or *Typosyllis* (Licher, 1999). These studies revealed that some of the traditional subfamilies, such as Eusyllinae, might be paraphyletic. However, these studies are still insufficient to reach a robust understanding of Syllidae as a whole. The combination of different techniques, methodologies and sources of data is becoming increasingly necessary in aiming to comprehend the biology of this group. Revisions of historical material, such as the one presented herein, shall also help shed new light in our understanding of the evolutionary paths taken by these fascinating animals.

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