

# Scale-worms (Polychaeta, Polynoidae) associated with chaetopterid worms (Polychaeta, Chaetopteridae), with description of a new genus and species

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Three species of scale-worms inhabiting chaetopterid tubes have been found during routine studies of benthic communities. *Anotochaetonoe michelbhaudi* gen. et sp. nov. occurred in the E Atlantic off Congo in association with *Spiochaetopterus* sp. and *Phyllochaetopterus* sp. It has a relatively short body (fewer than 50 segments); elytra in posterior part of the body arranged on chaetigers 23, 26, 29, 32, 34, 37, 40, 43, 46, present to posterior end; achaetous notopodia; neuropodia long, with longer subtriangular prechaetal lobes and shorter postchaetal lobes rounded distally; upper neurochaetae unidentate and lower bidentate; globular ciliated papillae present between ventral cirri and ventral basis of neuropodia. *Lepidasthenia brunnea* occurred in the Mediterranean Sea off the French coast both free-living and in association with *Phyllochaetopterus* sp. *Ophthalmonoe pettiboneae* was found in Vietnam (South China Sea) in association with *Chaetopterus* sp. This is the second finding of the species. The characteristics of the associations between chaetopterid genera and symbiotic polychaetes are discussed.

**Keywords:** Symbiosis; Chaetopteridae; scale-worms; new genera; new species.

**Running head:** New scale-worms symbionts of Chaetopteridae

## Introduction

Routine assessments of marine biodiversity usually focus on free-living organisms (which are easy to detect and collect). However, a very rich and diverse fauna living in association with other animals (i.e. symbionts) co-exists in the same habitats, usually

being cryptic. Accordingly, this fauna tends to remain virtually unknown, especially in tropical and deep waters.

Among marine animals, the class Polychaeta includes one of the highest number of symbiotic species, with more than 370 symbionts according to Martin and Britayev (1998). Symbiotic polychaetes are associated with nearly all main taxa of marine metazoans (excluding flatworms, nemerteans and nematodes) and even with protozoans. However, they clearly prefer organisms providing them with good shelter, such as burrowing or tube-dwelling animals (viz. sipunculids, balanoglossids, tubicolous polychaetes). The durable and long tubes of chaetopterid worms (Polychaeta, Chaetopteridae) probably offer one of the most "comfortable" habitats for symbiotic polychaetes (Petersen & Britayev 1997) and shelter at least 17 species of facultative and obligate polychaete species (Martin & Britayev 1998).

During studies of the structure of bottom communities performed by the authors along the coasts of Congo (Atlantic Ocean), France (Mediterranean Sea) and Vietnam (South China Sea), three species of scaleworms inhabiting chaetopterid tubes were found. The first one, namely *Anotochaetonoe michelbhaudi*, is herein described as a new genus and species, and the types have been deposited in the collection of the 'Museo Nacional de Ciencias Naturales' (MNCN) of Madrid. The second species has been identified as *Lepidasthenia brunnea* Day, 1960, which was also recorded as a chaetopterid symbiont from *Phyllochaetopterus* sp. in South Africa (Day 1967). In the Mediterranean, *L. brunnea* has only been reported as free-living (Barnich & Fiege 2003). The species is, thus, reported for the first time in association with chaetopterids in the Mediterranean and its description is completed with previously unknown details of the pharyngeal structure. The specimens are deposited in the collection of the second author. The third species is *Ophthalmonoe pettiboneae* Petersen and Britayev, 1997, which was described on the basis of a single male specimen associated with *Chaetopterus appendiculatus* Grube, 1874 from Banda Sea, Indonesia (Petersen & Britayev 1997). In addition to enlarging the known area of its distribution, the discovery of several Vietnamese specimens allowed completion of its description and to confirm its symbiotic mode of life. These specimens are deposited in the collection of the first author.

## Material and methods

The sediments off Congo (Emeraude and N’Kossa petrol fields) and France (Nice) containing the symbiotic polynoids were sampled using a Van Veen grab (35 x 42 x 90 cm, about 0.1 m<sup>2</sup> per grab). The grab contents were mixed in a sufficiently large container, and then sieved out on board by pouring the contents through a 1 mm mesh sieve. The retained sediment was then transferred to a plastic bag, fixed with a 4% formaldehyde/seawater solution, stained with Rose Bengal and stored until sorted. An initial sorting was done under a stereomicroscope (Zeiss Stemi 2000-C) to separate the chaetopterid tubes, which were then counted to express their densities as number of individuals per m<sup>2</sup>. All specimens in tubes were preserved in 70% ethanol. In the case of the single chaetopterid tube found in N’Kossa, the specimen was separated ‘in vivo’ from the sieve. The host and the symbiont were then extracted from the tube by gently blowing inside, anaesthetised with some drops of alcohol, fixed with 4% formaldehyde/seawater solution and preserved in 70% alcohol.

The specimens of *Ophthalmonoe* were collected in Nhatrang Bay in southern Vietnam in June 2004. Host animals were dug by SCUBA diver at 10-12 m depth. While still under the water hosts were put into plastic bags, each specimen separately, to prevent loss of symbionts. Colour pictures of living animals were made under water with Nikon 90 photo camera inside a Sea & Sea NX-90 hermetic box.

In the laboratory, the length and width were measured, and the number of chaetigers was counted under the binocular microscope Zeiss Stemi 2000. The sex of the worms was determined after partially dissecting them to analyze the obtained fluid extracts under a Nikon Eclipse E200 microscope. The drawings were prepared with a microscope, Olympus CX40, equipped with a drawing tube.

Light micrographs of preserved specimens were made with a Zeiss Axioplan (body) and a Zeiss Stemi 2000-c (chaetae) stereomicroscopes equipped with the SPOT hardware and software (SP100 KAF1400 digital camera and software version 2.1.) from Diagnostic Instruments Inc.

## Results

### Family Polynoidae Malmgren, 1867

### Subfamily Lepidastheniinae Pettibone, 1989

### Genus *Anotochaetonoë* gen. nov.

**Type species.** *Anotochaetonoë michelbhaudi*, new species, by original designation herein. Gender: feminine.

**Diagnosis.** Body truncated anteriorly and gradually tapering posteriorly, convex dorsally and flattened ventrally, with up to 20 pairs of elytra and up to 47 chaetigers. Elytra on prominent elytophores, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32, 34, 37, 40, 43, 46, reaching the end of body. Dorsal surface without prominent tubercles.

Prostomium bilobed, wider than long, without cephalic peaks, with two palps and three antennae. Ceratophore of median antenna inserted in the anterior notch, ceratophores of lateral antennae inserted termino-ventrally on distal end of prostomium, not converging mid-ventrally (arranged in parallel). Tentaculophores lateral to the prostomium, achaetous, each with one pair of dorsal and ventral tentacular cirri. Buccal segment without nuchal fold; with a prominent conical facial tubercle; ventral buccal cirri longer than following ones. Proboscis with nine pairs of papillae and two pairs of jaws.

Parapodia relatively long, sub-biramous, without notochaetae. Notopodia achaetous, reduced to digitiform protrusion. Neuropodia deeply incised dorsally and ventrally, with longer subtriangular prechaetal lobes, and shorter, distally rounded postchaetal lobes; tips of acicula not penetrating epidermis. Neurochaetae straight to falcate, with rows of spines distally and unidentate knob-like or bidentate tip. Dorsal cirri present on segments without elytra; cirrophores short, cylindrical; styles smooth, tapering gradually to filiform tips, with a marked alternation in length. Ventral cirri short, gradually tapering, smooth. Globular ciliated papillae present ventrally between ventral cirri and basis of neuropodia. Pygidium with terminal anus and long, smooth anal cirri. Known only as symbionts of chaetopterid worms.

**Etymology.** from Latin, *a* – without, *notochaetae*, + *noe*, to refer to a polynoid worm without notochaetae.

**Remarks.** There are several polynoid genera without notochaetae, most of them belonging to the subfamily Lepidastheniinae (Barnich & Fiege 2004). Among them, only *Alentiana* is close to *Anotochaetonoe* in having fewer than 50 segments. However, they differ in: (1) the arrangement of elytra in posterior part of the body: on chaetigers 23, 26, 29, 32, 34, 37... (*Anotochaetonoe*) or 23, 26, 29, 32, 34, 36, 37... (*Alentiana*); (2) in the shape of neuropodia: long, with longer subtriangular prechaetal lobes and shorter, distally rounded postchaetal lobes (*Anotochaetonoe*) or relatively short with both lobes rounded (*Alentiana*). *Anotochaetonoe* resembles the long-bodied genus *Telolepidasthenia* in the arrangement of elytra on segments 23, 26, 29, 32, 34, 37; in the presence of globular ciliated papillae on the lower margin of neuropodia and in their life habits as symbionts with chaetopterid worms. However in the new genus, the number of chaetigers is fewer than 50, neuropodia have longer, subtriangular prechaetal lobes and shorter, distally rounded postchaetal lobes, and neurochaetae have unidentate and bidentate tips, while *Telolepidasthenia* has more than 60 chaetigers, neuropodia with both lobes rounded and neurochaetae with entire tips.

***Anotochaetonoe michelbaudi* sp. nov.**

(Figures 1-5)

**Type locality.** N’Kossa petrol field (5°16.52’ S, 11° 33.87’) coast of Congo.

**Material examined.** 1). Holotype (MNCN 16.01/10388) inside the tube of *Phyllochaetopterus* sp.: Atlantic Ocean, coast of Congo, N’Kossa petrol field, st. 13(3), 5°16.52’ S, 11° 33.87’ E, sandy silt, 180 m depth, 11 April 2003, one specimen. 2). Paratype (MNCN 16.01/10389) inside the tube of *Spiochaetopterus* sp.: Atlantic Ocean, coast of Congo, Emeraude petrol field, st. 1, 4°59.41’ S, 11° 45.01’ E, 70 m depth, silt, 15 November 1999.

**Etymology.** The species name *michelbaudi* refers to the polychaete taxonomist, biologist, and ecologist Dr. Michel Baud from the Observatoire Océanologique of Banyuls (CNRS, France) to acknowledge his insightful contributions to the general knowledge of polychaetes, especially chaetopterids, and to the present study in particular.

**Description.** Body truncate anteriorly, gradually tapering posteriorly, convex dorsally and flattened ventrally, holotype with 20 pairs of elytra and 47 segments; paratype with 18 pairs of elytra and 41 segments; holotype 14 mm long and 1.0 mm wide without parapodia, paratype 10.5 mm long and 0.3 mm wide without parapodia, both specimens 2 mm wide with parapodia (Figure 1A).

Prostomium hexagonal, bilobed, wider than long, without cephalic peaks, median notch a V-shaped gap between anterior ends of superior prostomial lobes, filled by median ceratophore (Figures 1B, 1C; 2A). Two pairs of large dark brown eyes, ovate or round in shape, the anterior pair larger than the posterior one; anterior eyes located immediately in front of widest part of prostomium, positioned laterally and orientated antero-laterally; posterior eyes smaller, at posterior edge of prostomium in its widest part, orientated dorsally; eyes of a pair (i.e. anterior or posterior) separated by one eye-diameter or less. Median antenna as long as lateral ones (holotype) or 1.5 times longer (paratype), 2.5 (holotype) or 4.5 times longer than prostomium (paratype), inserted anteriorly in median notch, with relatively long conical ceratophores. Lateral antennae inserted termino-ventrally on distal end of prostomium, slightly ventrally to median antenna, with relatively long cylindrical ceratophores not converging mid-ventrally (i.e. parallel). All antennae gradually tapering, smooth. Palps stout, conical, gradually tapering, 1.5 times longer than antennae and 4.5 times longer than prostomium in holotype, missing in paratype, smooth.

First segment not visible dorsally; tentaculophores long, achaetous, but with aciculae; two pairs of tentacular cirri, very long, slightly exceeding in length the median antenna (paratype) or 1.3 times longer (holotype); dorsal and ventral tentacular cirri similar in length or dorsal ones slightly longer than ventral ones, smooth (Figures 1D; 2C). Buccal segment without nuchal fold; with prominent conical facial tubercle; mouth surrounded by two lateral, cushion shaped lips and lobular ventral and dorsal lips

consisting of nine or ten lobes, more prominent in median parts of the lips (Figure 1F); with subbiramous parapodia and one pair of ventral cirri, shorter than ventral tentacular cirri and substantially longer than ventral cirri of subsequent segments, gradually tapering, smooth; pharynx with nine dorsal and nine ventral large terminal papillae and two pairs of brown jaws (Figure 1E).

Elytra up to 20 pairs on chaetigers 2, 4, 5, 7, alternating on segments to 23, 26, 29, 32, 34, 37, 40, 43, 46; present to posterior end. Most elytra still in place in both specimens, relatively small, slightly overlapping antero-posteriorly, covering dorsum in anterior fourth (Figure 2A) but with mid-dorsal area uncovered on most of the body. All elytra oval, slightly folded along the external margin, delicate, smooth except for some scarce, irregularly distributed micropapillae, transparent, with light brown pigmentation arranged in polygonal units in anterior part of elytron (Figure 3A-C); intensity of pigmentation decreasing along the body from anterior to posterior end.

Body without prominent dorsal tubercles. Dorsum of body segments without distinct transverse ciliary bands. Parapodia relatively long, sub-biramous; notopodia achaetous, reduced with digitiform protrusion located on the anterodorsal side of larger neuropodia and acicular tips confined inside lobes (Figure 4A, 4B). Dorsal cirri attached to posterodorsal side of neuropodia, with short, cylindrical cirrophores and styles smooth, tapering gradually to filiform tips (Figure 4B), as long as or slightly longer than parapodia with chaetae.

Neuropodia deeply incised dorsally and ventrally, with longer subtriangular prechaetal lobes, and shorter, distally rounded postchaetal lobes (Figure 4C). Fourteen to 28 neurochaetae per bundle, increasing in number from posterior to anterior chaetigers; dorsal-most neurochaetae long, straight, slender, with a long serrated section (16-22 rows of spines), gradually tapering to nearly filiform entire, knob-like tip with a minute distal spherical swelling; rows of spines largest, most conspicuous at the basis of the serrated section, smaller and closer together distally (Figure 2D); middle neurochaetae with relatively shorter serrated section, bidentate, with small secondary tooth and slightly curved tips (Figure 2E); lower neurochaetae stouter, shorter, with a few rows of spines (10-12) and slightly curved, clearly bidentate tips and secondary tooth slender and orientated in parallel to the axis of the chaeta (Figure 2F).

Ventral cirri from the third chaetiger to the end of the body short, gradually tapering, smooth (Figure 4A-C). A single row of two to four globular ciliated papillae (Figure 4D) extends from the ventral cirri to the ventral basis of parapodia (Figures 4A,B). Pygidium with dorso-terminal anus and two pygidial cirri, located below anus, relatively long, comparable in length with dorsal cirri in the last segments, smooth (Figure 2B).

**Coloration.** Body of alcohol preserved specimens whitish, without prominent pigmentation except for a light brown patch on the posterior part of prostomium, on the dorsal surface of the four anterior chaetigers and on the distal part of the pharynx, and prominent dark spots at the basis of the pharyngeal papillae.

**Biology.** The species is here reported as a symbiont of the chaetopterid species *Spiochaetopterus* sp. and *Phyllochaetopterus* sp. The two specimens were located inside the host tube, with the dorsum in contact with the body of the host (Figure 5A, 5B). Only one symbiont inhabited each host tube. Both host species were very abundant in the studied area, especially in the vicinity of Emeraude petrol field, reaching up 150 ind. per m<sup>2</sup> for *Spiochaetopterus* sp. and 307 ind. per m<sup>2</sup> for *Phyllochaetopterus* sp. However, the infestation prevalence was very low. The transparent *Spiochaetopterus* tubes allowed direct check for the presence of symbionts, but only one symbiont was found for a population of more than 200 host tubes. The parchment-like tubes of *Phyllochaetopterus* were opaque, preventing the direct checking for symbionts inside. However, the dissection of about 40 host tubes only revealed the presence of a single symbiont. The symbionts inhabited silt and silty sand sediments between 70 m and 180 m depth.

**Distribution.** Tropical East Atlantic, coast of Congo.

*Lepidasthenia brunnea* Day, 1960.

(Figure 6)

*Lepidasthenia brunnea*: Barnich and Fiege 2003: 88, fig.45A-H (synonymy).

**Material examined.** Mediterranean Sea, Ligurian Sea, coast of Nice, st. 20, 43° 38.90'N 7°13.85'E, 85 m depth, silt, 2 April 2004, 1 specimen inside the tube of *Phyllochaetopterus* sp.; st. 12, 43°39.43'N 7°14.43'E, 129 m depth, silt, 4 April 2004, 1 specimen, free-living.

**Taxonomic remarks.** Our specimens are in general accordance with the original description (Day 1960) and the description of Mediterranean specimens by Barnich and Fiege (2003) except in having nearly invisible eyes, deeply hidden inside the prostomial tissue. They have 22 to 40 pairs of elytra and 56 to 81 chaetigers, measuring 4.2 – 4.8 cm long, 2 - 2.5 mm wide without parapodia and 4.7 - 5.2 mm wide with parapodia and chaetae. Buccal segment with a large facial tubercle; pharynx with nine dorsal and nine ventral large terminal papillae with prominent dark spots, two subdistal lateral folds and two pairs of large brown jaws (Figure 6A,B). Elytra smooth, semitransparent, with brown pigmentation in postero-medial part, without micropapillae (Figure 6D,E).

**Biology.** The smaller specimen was found inside the tube of *Phyllochaetopterus* sp. (Figure 6C). The larger specimen was found in the same area, but free-living on muddy bottoms like all previously reported Mediterranean specimens Barnich & Fiege (2003). On the coast of South Africa, *L. brunnea* has been recorded both as free-living and in association with *Phyllochaetopterus* sp. (Day 1967).

**Distribution.** Mediterranean, North East Atlantic, coast of South Africa.

#### **Subfamily Polynoinae Kinberg, 1856**

#### ***Ophthalmonoe pettiboneae* Petersen and Britayev, 1997**

(Figs.7-8)

*Ophthalmonoe pettiboneae* Petersen and Britayev 1997: 266-272, figures 1-3.

**Type locality.** Banda Sea, Indonesia.

**Material examined.** South China Sea, Bay of Nhatrang, western point of Tre Island, 8-12 m, sandy silt, 29 June 2004, 2 specimens in the tubes of *Chaetopterus* sp., collected by I. Marin.

**Description.** Body relatively short, wide and flat, truncate anteriorly and gradually tapering posteriorly, with 19 pairs of elytra, with 44-46 segments, 2.6 - 3 mm wide without parapodia, 10 - 10.5 mm wide with parapodia and chaetae, 19 and 27 mm long.

Prostomium nearly rectangular in shape, slightly wider than long, without cephalic peaks; prostomial lobes well-separated by a shallow groove and a deep V-shaped median notch (Figure 7A). Two pairs of large, dark black eyes, round in shape, with the anterior pair slightly larger than the posterior one; anterior eyes in the frontal edge of prostomium and directed anteriorly, visible through a thin dorsal prostomial cuticle; posterior eyes located dorso-laterally on the widest part of prostomium, near posterior edge of prostomium and orientated dorso-posteriorly; eyes of each pair (i.e. anterior or posterior) separated by more than one eye-diameter; both pairs with conspicuous oval lenses. Median antenna more than twice longer than prostomium, cylindrical, with slightly tapering tip; ceratophore relatively short, massive, conical, placed in the notch between prostomial lobes; two dark pigmented longitudinal lateral bands, spreading distally and covering tip of antenna completely. Lateral antennae inserted ventrally to prostomial lobes and slightly ventral to median antenna; short, cylindrical, tapering slightly at the tips, with a light brownish pigmentation at their basis; ceratophores short, converging mid-ventrally, but well-separated by the ceratophore of median antennae. All antennae smooth. Palps more than five times longer than prostomium, conical, gradually tapering, smooth, without pigmentation.

First segment indistinct dorsally; tentaculophores relatively short, thick, achaetous, but with acicula; two pairs of tentacular cirri, slightly longer than prostomium, smooth; dorsal cirri with one longitudinal pigmented band on posterior surface. Buccal segment without nuchal fold; without prominent facial tubercle; mouth surrounded by two lateral relatively small lips, large ventral lip and small dorsal lip consisting of three prominent lobules (Figure 7B); with biramous parapodia, smaller than the following ones, with one pair of relatively long ventral (buccal) cirri reaching

the end of parapodium, twice longer than ventral cirri of subsequent segments, conical, gradually tapering, smooth and arising from the basis of neuropodia (Figure 8A ).

Elytra 19 pairs, on chaetigers 2, 4, 5, alternating to 23, then on 26, 29, 32, 35, 38, 41, 42; last two to four segments cirrigerous, without elytra. Most elytra missing, except in anterior-most and posterior-most regions, relatively large, overlapping antero-posteriorly, covering or not the dorsum in anterior region, depending on the specimen (Figure 7A,E), but with mid-dorsal area always covered in posterior-most region; all elytra basically oval, but markedly irregular in outline, folded along external margin, delicate, smooth except for some scarce irregularly distributed micropapillae (Figure 7D), semi-transparent, with narrow dark brown rim along mid-dorsal and posterior margins, with small distinct notch after the pigmented rim ends, where each elytron surrounds the dorsal cirrus of the following segment (Figure 7C). Pigmentation intensity similar in all elytra along the body (Figure 7E).

Body without prominent dorsal tubercles. Dorsal surface with one conspicuous transverse dark-brown band across the middle of each segment, slightly wider mid-dorsally in anterior segments (Figure 7A). Pigmented band on cirrigerous segments reaching basis of cirrophores and continuing on posterior side of cirrophores and dorsal cirri (Figure 8B,D). Dark band on elytrigerous segments always in the middle, reaching top of elytriphores. Segment 5 with oval, mid-dorsal black spot posterior to transverse band (Figure 7A). Body non-pigmented ventrally. Transverse ciliary bands absent (at least indistinct under stereomicroscope).

Parapodia relatively long, biramous; notopodia, small, conical, located at the antero-dorsal side of neuropodia; dorsal cirri attached to postero-dorsal side of parapodia, with relatively massive, cylindrical, short cirrophores (Figure 8B-D). Styles smooth, cylindrical, tapering gradually to filiform tips (Figure 8B,D), alternating in length from similar (or slightly shorter than) to longer than parapodia with chaetae. Dorsal cirri on cirrigerous segments 3 and 6 short, on segment 8 long, on 10 short, then alternating long and short up to the end of the body. Long cirri with dark longitudinal pigmented bands, covering completely the cirri on their terminal fourth section; short cirri with less intense pigmented bands, not reaching their tips.

Neuropodia longer and wider than notopodia, with row of cilia along ventral side. Prechaetal neuropodial lobe elongated, nearly digitiform, substantially longer than the

triangular postchaetal lobe (Figure 8B,D). Distal region of postchaetal lobes with diffuse brown pigmentation, slightly more intense dorsally.

Notochaetae arranged in a fan-shaped bundle orientated nearly horizontally, virtually all of them on the same level, numerous, increasing in number from 70 (chaetiger 2) to more than 150 (chaetiger 20), more slender than neurochaetae, fine, long, capillaries, smooth (at least serration indistinct under 1000x with immersion oil).

Neurochaetae numerous, increasing in number from more than 80 (chaetiger 2) to more than 240 (chaetiger 20), stout, nearly cylindrical, some chaetae slightly expanded in distal hooded part; tips hooded, blunt and nearly rounded, with internal part slightly curved and unidentate; with rows of narrow petaloid spines, smaller and closer together distally; number of rows increasing from ventral-most (14 – 26) to dorsal-most notochoetae (up to 87) (Figure 8E ).

Ventral cirri from the second chaetiger to the end of the body; relatively long at the second chaetiger (Figure 8A); on subsequent segments, located on the first third of the neuropodia, at the same level as notopodia, being twice or more shorter than prechaetal lobes, conical, gradually tapering, smooth (Figure 8B-D); ventral cirri without coloration.

Anus dorso-terminal, two pygidial cirri, located below anus, slightly longer than last pair of dorsal cirri.

**Coloration.** The worms preserved in alcohol have distinctive pigmentation on the dorsal surface. The body is basically light brownish and has a conspicuous transverse dark-brown or black band crossing each segment. On segment 5, there is an additional characteristic oval, mid-dorsal, black spot posterior to the transverse band (Figure 7A ). The longest dorsal cirri have more intense dark pigmentation than the smaller ones. The ventral body surface is always non-pigmented. In living worms, the coloration is brighter and a transverse white band in front of the dorsal segmental dark brown band becomes visible in some chaetigers. A similar white pigmentation is also conspicuous on dorsal cirri, antennae, and external margins of elytra (Figure 7E ).

**Taxonomic remarks.** The discovery of the Vietnamese specimens confirmed the number of elytra and segments reported for the holotype and contributed to the

description of the species with some important characteristics. In particular, the structure of the buccal lips, which was not originally described since the pharynx of the holotype was fully everted, and the alternation in length of the dorsal cirri. These features are useful additions to the specific diagnosis. The new specimens agree in general with the holotype description, but it is necessary to mention several minute differences. The prostomium of the holotype is nearly hexagonal, instead of rectangular, as in the Vietnamese specimens. However, the pharynx of the holotype is fully extended so this may have changed the shape of the prostomium. According to Petersen and Britayev (1997) “neurochaetae... becoming slightly broader at point where hood begins; ...internal part of chaetae unidentate”. In the Vietnamese specimens, the distal part of most neurochaetae is cylindrical, without any extension, and the internal part of the chaetal tips is unidentate and slightly curved. Moreover, the rows of spines in notochaetae were indistinct even under a magnification of 1000x (with immersion oil), as well as the transverse ciliary bands described in the holotype (under binocular microscope). However, we suggest that these slight differences probably reflect an intra-specific variation in the species morphology and/or the quality of the optics employed. The pigmentation pattern of Vietnamese specimens also agrees with that of the holotype and seems to be a remarkable species-specific characteristic of *O. pettiboneae*, confirming the differences in pigmentation between *O. pettiboneae* and *O. tonkinika* (Uschacov 1992) as suggested by Petersen and Britayev (1997).

**Biology.** The species lives symbiotically inside the tubes of a chaetopterid polychaete belonging to the genus *Chaetopterus* (Figure 7E). Each studied chaetopterid tube contained one symbiont. The two Vietnamese specimens are females and contained oocytes of 95 to 130  $\mu\text{m}$  in greatest diameter (mean value 116 $\mu\text{m}$ , n=13), with large (about 55  $\mu\text{m}$  in diameter) spherical nucleus and small (about 11  $\mu\text{m}$  in diameter) nucleolus. The spermatozoa of *O. pettiboneae* belong to a primitive type, with rounded head of about 1.3  $\mu\text{m}$  in diameter (Petersen & Britayev 1997). Both features are usually linked to a broadcast reproductive strategy (Thorson 1950; Rouse 1999).

The Vietnamese specimens of *Ophalmonoe pettiboneae* shared the host tube with two other symbiotic species, an unidentified carapid fish and a porcellanid crab belonging to the genus *Pachycheles*.

**Distribution.** Coasts of Ambon Island (Indonesia, Banda Sea) and Tre Island (Bay of Nhatrang, South coast of Vietnam, South China Sea). Known only as symbiont of *Chaetopterus* sp., collected from 8-12 m depth in silty sand sediments.

## Discussion

A total of 19 species of polychaetes, including *Anotochaetoneo chaetoptera*, is currently known in association with chaetopterids [see Martin & Britayev (1998) for a full list]. According to Fauchald (1977), the number of species belonging to each of the four genera is very different, with *Phyllochaetopterus* including more than 40%, *Spiochaetopterus* and *Mesochaetopterus* both including slightly more than 27% each one, and *Chaetopterus* being monotypic (Figure 9). Even assuming the incompleteness of the currently known number of chaetopterid species, a general trend can be clearly identified when analysing the number of symbionts associated with each chaetopterid genus: most of them are associated with *Chaetopterus* (42%) and *Phyllochaetopterus* (32%), while only 26% are found together with *Mesochaetopterus* (16%) and *Spiochaetopterus* (10%) (Figure 9). Several different factors may explain this peculiar distribution. The possible correspondence between the differences in species diversity among host genera and the diversity of symbionts could be supposed, but certainly these two trends seem to be virtually opposite. Thus, more reliable explanation may be linked to differences in size and morphology of hosts and host tubes, trophic-functional behaviour and geographical distribution.

The genus *Chaetopterus*, which harbours the most diverse symbiotic fauna, includes large worms inhabiting parchment-like tubes. They may reach more than 1 m in length and 2.5 cm in diameter (*Chaetopterus* specimens from the Sea of Japan, T. A. Britayev, personal observations). They are unique within the family in having U-shaped tubes with both ends opening at the ground surface, and in showing a very powerful system of tube ventilation (MacGinitie 1939; Barnes 1965). Both characteristics appear to favour the presence of symbionts. The two equi-functional openings (i.e. they may be used indistinctly for inhalation or excretion, as the worms are able to turn 180° inside

the tubes), as well as the strong inhalant/exhalant current, may facilitate the process of symbionts entering the host tubes at different stages of their life cycles. Moreover, the powerful water current produced by the peristaltic contraction of the mid-body piston-like segments supplies enough oxygen and food particles not only to support the host itself but for several co-existing symbiont individuals often belonging to different species as well. In fact, the occurrence of several symbiotic species sharing the same host individual seems to be common, and this includes relatively large animals such as pinnotherid or porcellanid crabs and carapid fish (Petersen & Britayev 1997; Britayev 1993; this paper).

The other three genera of Chaetopteridae have trophic-functional behaviour similar to *Chaetopterus*, although some of them may filtrate directly from the water column with the help of tentacles instead of using mucus bags (e.g. *Mesochaetopterus* sp., D. Martin personal observations). Conversely, all them are similar in having relatively uniform tube-building structures, distinct from that of *Chaetopterus* (Sendall et al 1995; Barnes 1965). In spite of some differences in tube building material, all three genera have one tube end opening at the ground level and the other more or less deep within the sediment, probably reflecting different tube ventilation or pellets' disposal procedures (Barnes 1965). Moreover, the tubes tend to be relatively narrow, even for the largest known *Mesochaetopterus* species. For instance, *M. taylori* measures more than 2 m long and less than 1 cm wide (Sendall et al 1995; MacGinitie & MacGinitie 1968) and *Mesochaetopterus* sp. may reach more than 2.5 m long and about 0.7 cm wide (D. Martin, unpublished results). A normal width/length ratio in *Spiochaetopterus solotarius* is 0.6/100 mm (Bhaud et al 1994), while the width/length *Phyllochaetopterus* sp. may range from 0.2/20 cm (Congo) to 0.6/>30 cm (France) as found by D. Martin.

The species of both *Spiochaetopterus* and *Mesochaetopterus* may be considered as cosmopolitan, while *Phyllochaetopterus* tends to be widespread in subtropical and tropical waters (M. Bhaud, personal communication). This distinction does not agree with the fact that the latter also differs from the former two in harbouring more symbiotic species. On the contrary, excluding *Chaetopterus*, there seems to be a clear relationship between intra-generic host species diversity and symbionts diversity, both being higher in *Phyllochaetopterus* and uniformly low for the other two genera (Figure 9).

According to our preliminary data, the diversity of symbiotic polychaete species associated with each chaetopterid genus is related to: 1) the trophic-functional behaviour and tube structure, *Chaetopterus* being distinct from the other three genera, and 2) the intra-generic species diversity. However, explanation of the characteristics of the Chaetopteridae as hosts of symbiotic polychaete is still not clear enough and, thus, this seems to be an interesting subject for further studies. Special attention should be addressed to the increasing evidence that most chaetopterid species formerly reported as cosmopolitan are, in fact, complexes of several species, each of them with restricted biogeographical distributions. Studies of chaetopterid behaviour will also contribute but, certainly, the most relevant approach would be to analyze the host/symbiont relationships in vivo.



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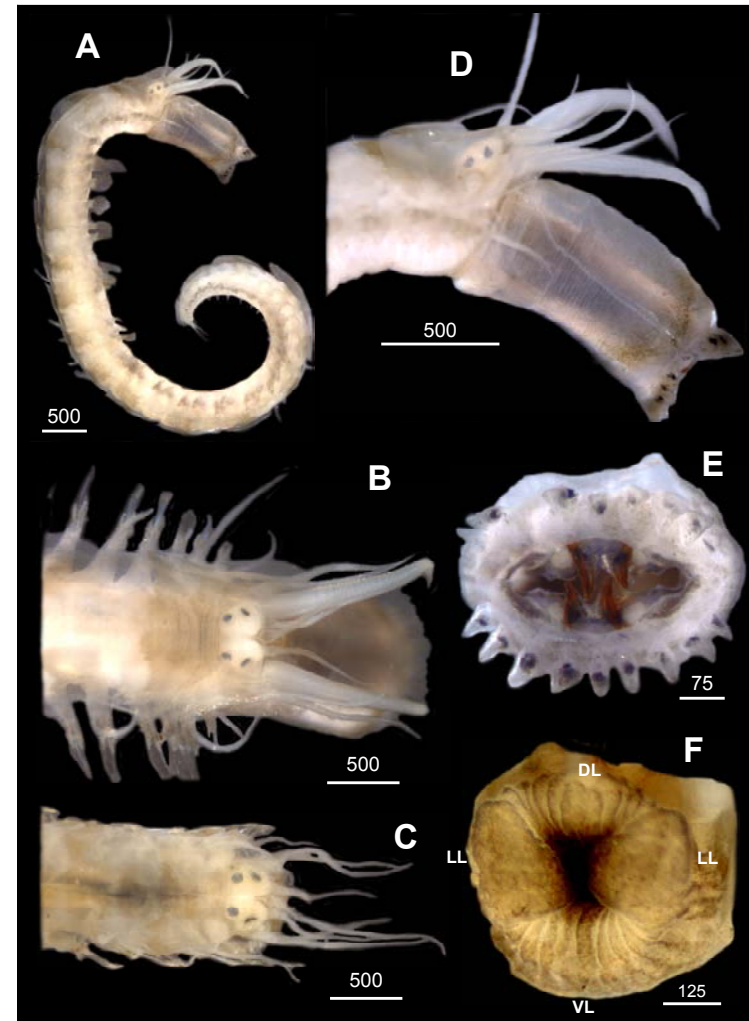


Figure 1. *Anotochaetonoe michelbaudi* gen. and sp. nov. (A) Whole worm, lateral view; (B, C) anterior end, dorsal view; (D) anterior end, lateral view; (E) terminal view of the pharynx, showing papillae and teeth; (F) terminal view of anterior end, showing the buccal lips. (A, B, D, E) Holotype; (C, F) paratype. DL, dorsal lip; LL, lateral lips; VL, ventral lip. Scale bars are in mm.

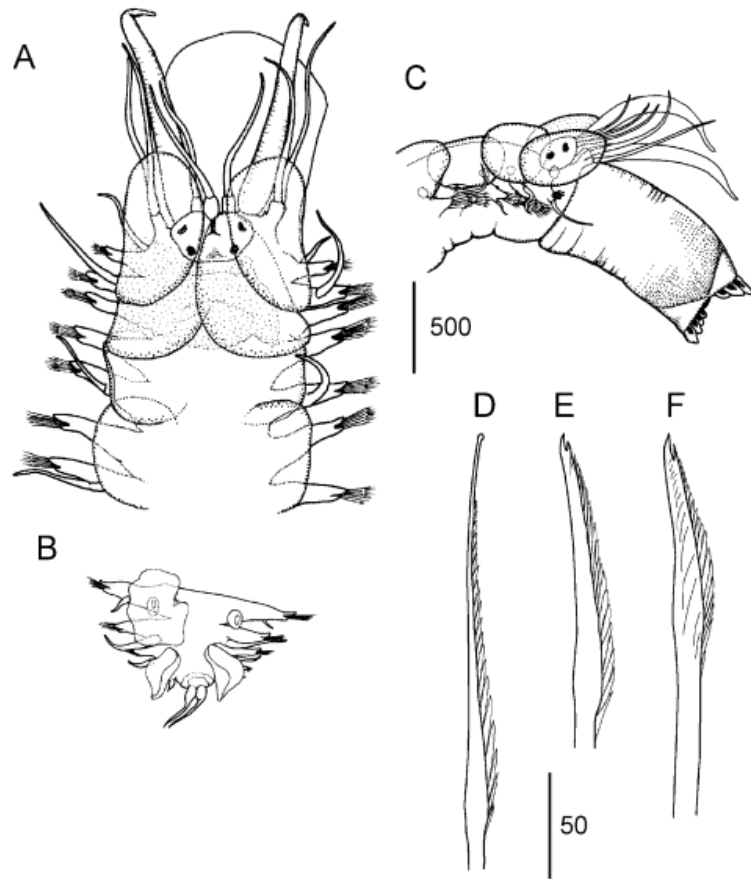


FIG. 2. *Anotochaetonoe michelbaudi* gen. et sp. nov. (a) Anterior end, dorsal view. (b) Anterior end, lateral view. (c) Posterior end, dorsal view. (d) Dorsal neurochaeta. (e) Middle neurochaeta. (f) Ventral neurochaeta; (a - f) holotype. Scale bars are in mm.

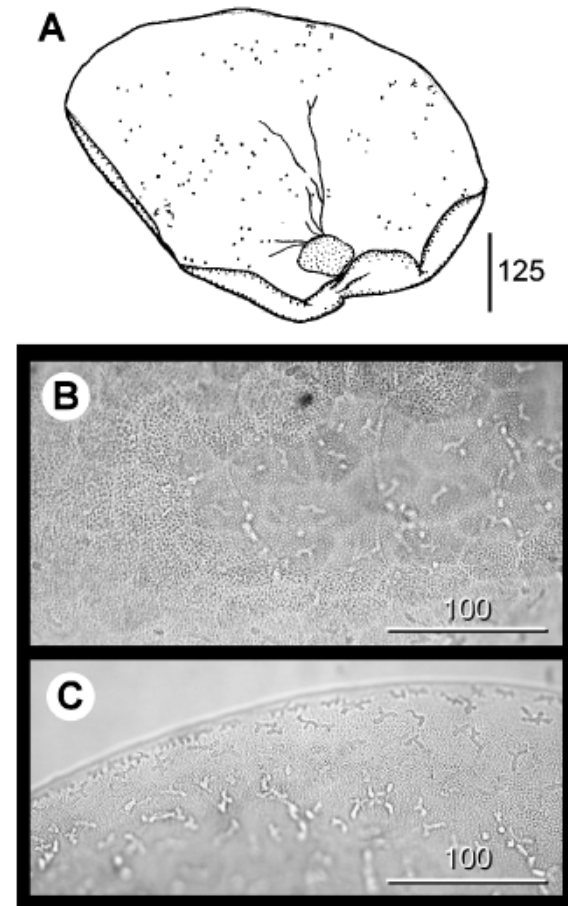


FIG. 3. *Anotochaetonoe michelbaudi* gen. et sp. nov. Elytron of paratype from unknown segment. (a) Entire view. (b) Detail of the structure of the dorsal surface showing the polygonal units of pigmentation. (c) Detail of the anterior edge. Scale bars are in mm.

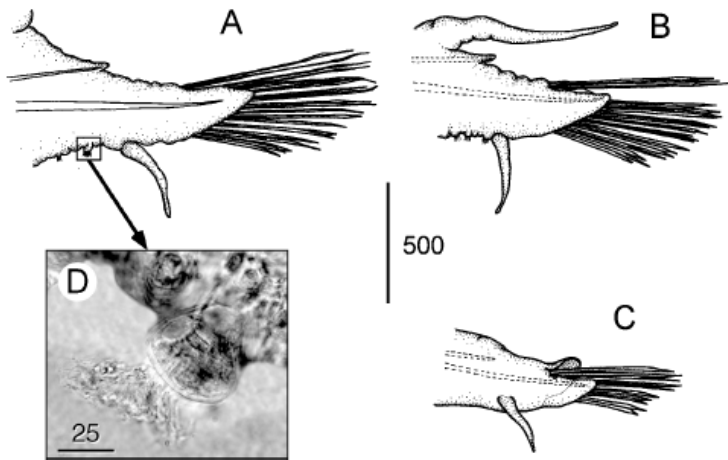


FIG. 4. *Anotochaetonoe michelbhaudi* gen. et sp. nov. Parapodia. (a) 14th cirrigerous chaetiger, anterior view with details of prechaetal lobe. (b) 15th elytrigerous chaetiger, anterior view. (c) 13th cirrigerous chaetiger, anterodorsal view. (d) Ciliated papilla from the ventral surface of neuropodia. (a, b) holotype; (c) paratype. Scale bars are in  $\mu\text{m}$ .

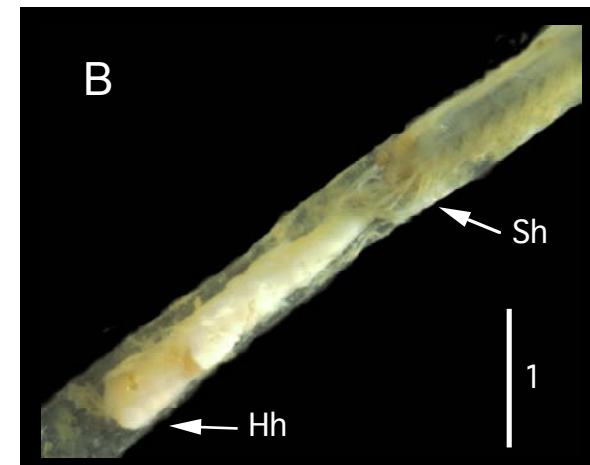
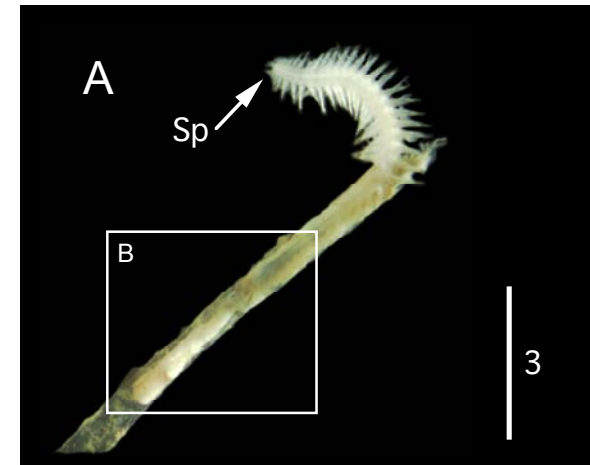


Figure 5. *Anotochaetonoe michelbhaudi* gen. and sp. nov. inside the tube of the host. (A) Posterior end protruding from the tube of the host; (B) anterior end of symbiont in contact with body of host. Hh, head of host; Sh, head of symbiont; Sp, pygidium of symbiont. Scale bars are in mm.

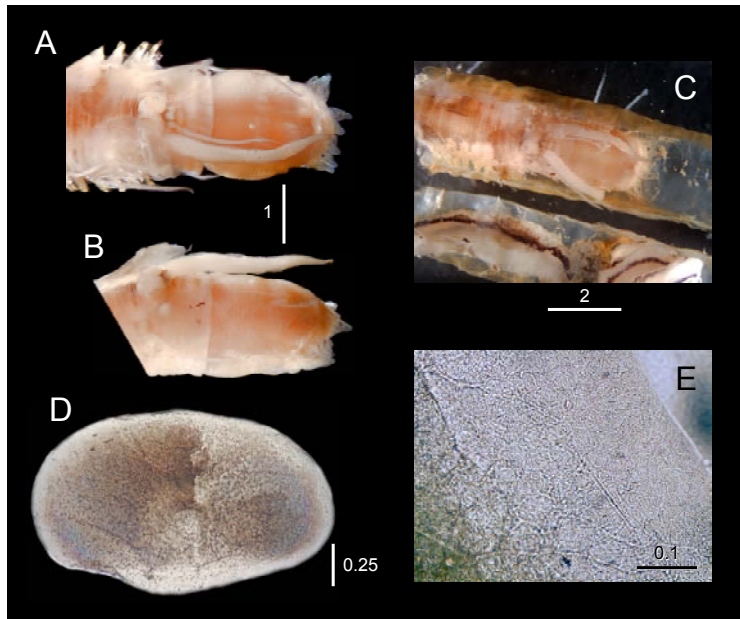


Figure 6. *Lepidasthenia brunnea*. (A) Anterior end, dorsal view; (B) anterior end, lateral view; (C) tube of the host cut to show the symbiont on one section (up) and the host tentacles in the other (down); (D) elytron; (E) detail of the external edge of elytron. Scale bars are in mm.

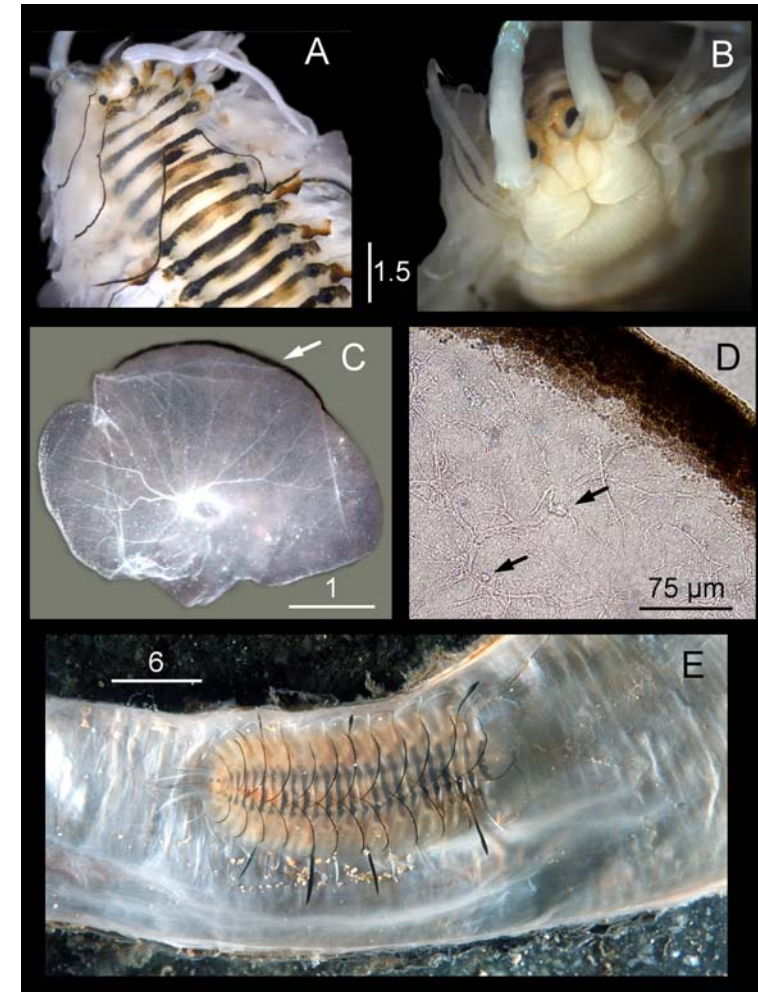


Figure 7. *Ophthalmonoe pettiboneae*. (A) Anterior end, dorsal view, showing both the pigmentation and the elytra arrangement; (B) terminal view of the anterior end, showing the buccal lips; (C) elytron; (D) detail of the surface of the elytron with micropapillae; (E) living worm (lacking the posterior end) inside the tube of the host. Scale bars are in mm (except D).

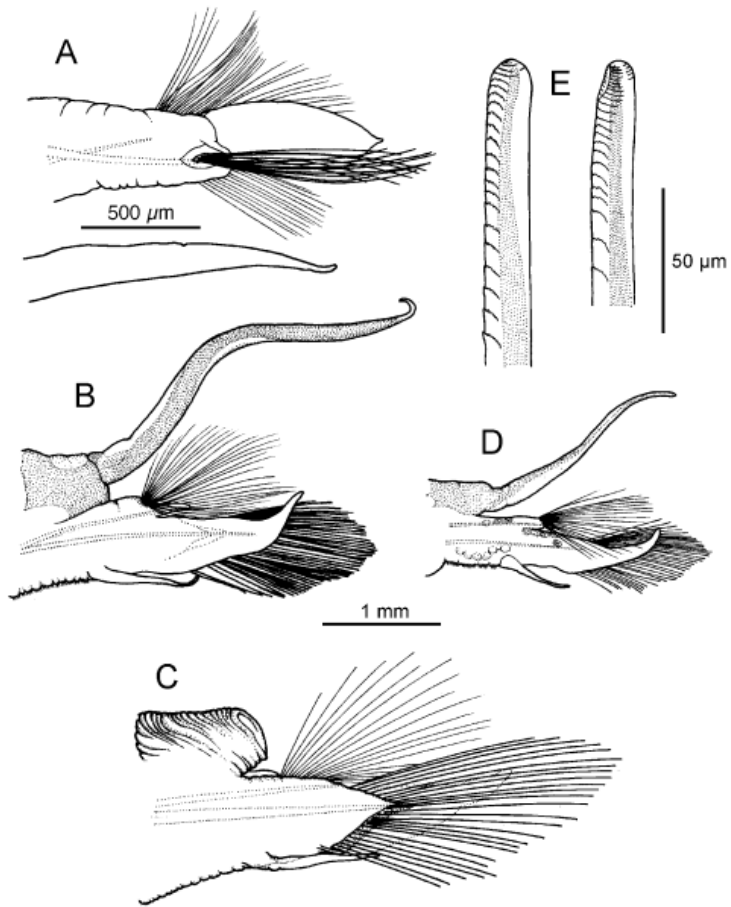


FIG. 8. *Ophthalmonoe pettiboneae*. Parapodia. (a) 2nd elytrigerous chaetiger (long ventral cirrus separated), ventral view. (b) 20th cirriferous chaetiger, anterior view showing the long, intensely pigmented dorsal cirrus. (c) 16th cirriferous chaetiger, posterior view, showing the short triangular postchaetal lobe. (d) 40th cirriferous chaetiger, anterior view showing the short dorsal cirrus. (e). - Tips of hooded neurochaeta.

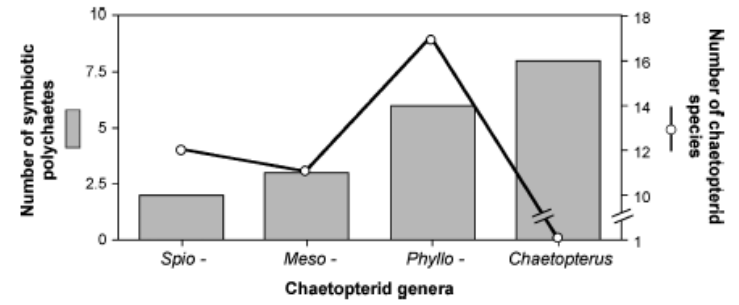


FIG. 9. Number of symbiotic polychaete species associated with Chaetopteridae in relation with the number of species of the four currently known genera of the family.