

Four new deep-water flabelligerid species from Pacific Costa Rica (Annelida, Sedentaria, Flabelligeridae)

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Abstract

The discovery of four undescribed flabelligerid species from deep-water in Pacific Costa Rica resulted in the restriction of *Diplocirrus* Haase, 1915. As currently understood, *Diplocirrus* and *Pherusa* Oken, 1807 are separated after their morphological pattern. The species belonging in *Diplocirrus* have two types of branchiae, poorly developed cephalic cages and multiarticulate neurochaetae, whereas *Pherusa* species have branchiae of one type, well-developed cephalic cages and completely ankylosed neurochaetae. Benthic sampling and processing usually damage cephalic cages and if chaetae are completely broken, one could regard specimens without them, when they actually have it, but lost after sieving. Sampling using Alvin deep-sea submarine at methane seeps off Costa Rica resulted in some well-preserved specimens, and some of them fall between these two genera because they have well developed cephalic cages, and multiarticulate neurochaetae. *Saphobranchia* Chamberlin, 1919, with *Stylarioides longisetosa* von Marenzeller, 1890, as type species, is herein reinstated for some species previously included in *Diplocirrus*, restricted. The transferred species, including three ones newly described herein, have branchiae of a single type, long cephalic cage and body chaetae, and neurochaetae basally ankylosed and medially and distally articulated; some species currently included in *Diplocirrus* described from Arctic or deep water sediments are transferred into it. A key to identify all species in *Saphobranchia*, and another key to identify species in the restricted *Diplocirrus* are also included. The three new *Saphobranchia* species are *S. canela* n. sp., *S. ilya* n. sp. and *S. omorpha* n. sp. The fourth species belongs in *Lamispina* Salazar-Vallejo, 2014, and it is herein described as *L. polycerata* n. sp. after the presence of some long papillae along anterior margin of chaetiger 1.

Key words: *Diplocirrus*, *Lamispina*, *Pherusa*, *Saphobranchia*, ankylosed neurochaetae

Introduction

Haase (1915: 194) proposed *Diplocirrus* to incorporate some flabelligerid species provided with a swollen anterior region, multiarticulate neurochaetae and eight branchial filaments of two different types (hence the name): posterior filaments depressed, thicker; anterior filaments cirriform, thinner. The new genus included *D. glaucus* (Malmgren, 1867), *D. hirsutus* (Hansen, 1879), and *D. longisetosus* (von Marenzeller, 1890). Interestingly, Haase (1915: 194) separated these species into two groups because of the papillae, being single or grouped, by the articulation of neurochaetae (articles progressively long or long from bases), and by having what used to be regarded as nephridial (gonopodial) lobes. Then, *D. glaucus* was joined with *D. hirsutus*, whereas *D. longisetosus* was kept separated from them.

Chamberlin (1919: 397) overlooked Haase (1915) and proposed *Saphobranchia* with *Stylarioides longisetosus* von Marenzeller, 1890, as type species. A separate generic diagnosis was not provided but it is implicit in the key to flabelligerid genera (Chamberlin 1919: 396–397), and could be summarized as: Chaetigers 1–2 longer and stouter than following ones; body papillae short, coarse, sometimes sparse; all chaetae capillaries in notopodia and neuropodia; branchiae sessile, eight filaments, four long and four short.

Støp-Bowitz (1948: 7, key) was unaware of Chamberlin's monograph, and used the number of chaetae along the first few chaetigers as the basic feature to rearrange Haase's groups, such that *D. glaucus* was separated because of the presence of less than three chaetae per bundle in anterior chaetigers, whereas *D. hirsutus* and *D. longisetosus*

were grouped by having more abundant chaetae. Støp-Bowitz (1948: 27, 29, 32) provided detailed illustrations for these species and showed differences in their body shape. In *D. glaucus* the body is swollen anteriorly, and median and posterior segments are moniliform (Fig. 1A), whereas in *D. hirsutus* (Fig. 1E) and *D. normani* (McIntosh, 1908) (Fig. 1C) the body is club-shaped. Neurochaetal articulation pattern provides an additional difference, and this was shown in the original illustrations. For *D. glaucus*, Malmgren (1867, Pl. 13, Fig. 78D) showed that neurochaetae were articulated throughout its length (Fig. 1B). In *D. hirsutus*, Hansen (1879, Pl. 8, Fig. 4) showed that articulations differ along chaetae, with longer, clearly articulated ones in medial and distal regions, with a basal region with shorter ones (as shown in Fig. 1D). For *D. longisetosus*, von Marenzeller (1890, Pl. 1, Fig. 3) illustrated two complete neurochaetae showing barely defined (ankylosed) articles basally, and better developed ones medially and distally. The chaeta illustrated by Støp-Bowitz (1948) corresponds to *D. normani* and shows medial and distal regions (Fig. 1F).

These differences are relevant and their combination is herein used for separating some species currently included in *Diplocirrus* (restricted below) and transferring them into *Saphobranchia* Chamberlin, 1919, reinstated. In the revision of *Diplocirrus* Salazar-Vallejo & Buzhinskaja (2011: 9, key), *Saphobranchia* was regarded as a junior synonym of *Diplocirrus*, following Hartman (1959: 419), and Fauchald (1977: 117), and they avoided emphasizing cephalic cage features because of the condition of many specimens, although the size of chaetae to body width, and the extent of ankylosed chaetal regions were used for sorting out similar species. On the other hand, in separating these two species groups currently in *Diplocirrus*, *Saphobranchia* is the only name available for those species having branchia of a single type, and neurochaetae basally ankylosed; despite the fact they somehow resemble the body pattern shown by *Pherusa* Oken, 1807 (Fig. 1G), they differ because in the latter neurochaetae are completely ankylosed in median and posterior chaetigers (Fig. 1H), whereas in *Saphobranchia* they are ankylosed basally, and articulate medially and distally.

In this contribution, *Saphobranchia* is reinstated to accommodate some species matching the original proposal and amended below for including species provided with abundant, long cephalic cage chaetae, eight cirriform branchiae, and neurochaetae basally ankylosed and medially and distally articulated. *Saphobranchia* species were described from Arctic or deep water environments and are currently included in *Diplocirrus*, such as *D. hirsutus* (Hansen, 1882), *D. longisetosus* (von Marenzeller, 1890), *D. micans* Fauchald, 1972, *D. normani* (McIntosh, 1908), and *D. octobranchus* (Hartman, 1965). A key to identify these species is also included. Further, a key to species of *Diplocirrus* as herein restricted is also included. Further, four new species are described from off Pacific Costa Rica; three new species are described in *Saphobranchia*: *S. canela* n. sp., *S. ilya* n. sp., and *S. omorpha* n. sp. A fourth species is described in *Lamispina* Salazar-Vallejo, 2014: *L. polycerata* n. sp.

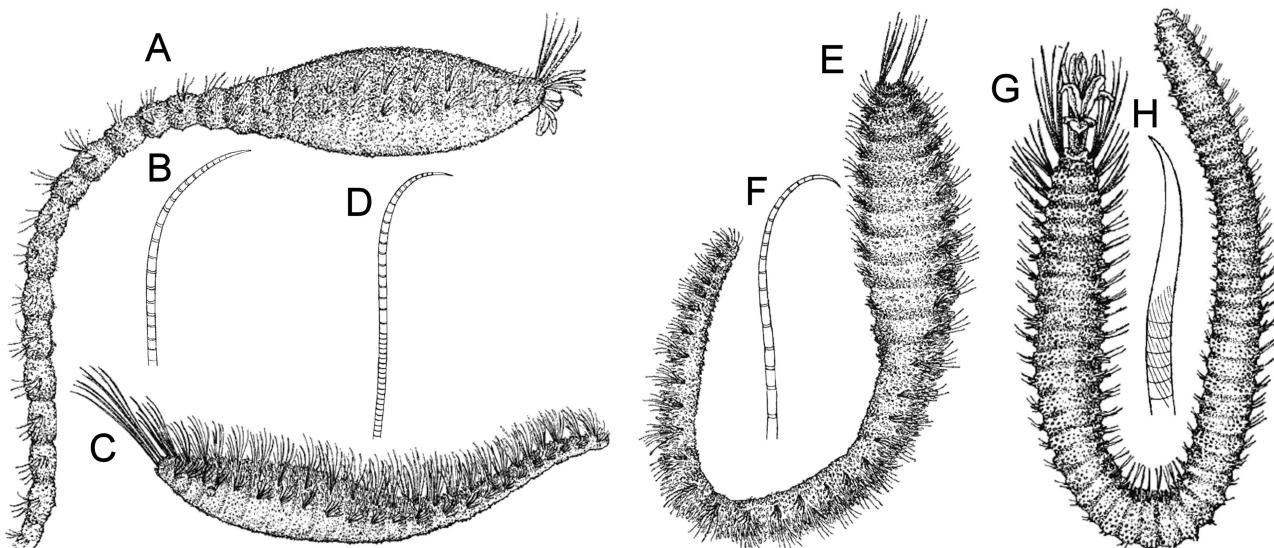


FIGURE 1. Carl Støp Bowitz (1948) illustrations for some flabelligerids. A. *Diplocirrus glaucus* (Malmgren, 1867), right lateral view. B. Same, neurochaeta. C. *D. normani* (McIntosh, 1908), left lateral view. D. Same, neurochaeta. E. *D. hirsutus* (Hansen, 1882), ventral view turning lateral view in posterior region. F. Same, medial and distal neurochaetal regions. G. *Pherusa plumosa* (Müller, 1776), ventral view. H. Same, neurochaeta (approved reproduction by University Museum of Bergen, 24 Jun. 2020).

Material and methods

Sampling. Specimens were collected with the Human Occupied Vehicle (HOV) Alvin during R/V Atlantis cruises AT15-44 (2009), AT15-59 (2010), and AT42-03 (2018) to several methane seep localities off the Costa Rican Pacific coasts. Live specimens were relaxed with 7% MgCl₂ in fresh water and photographed using a Leica MZ8 or MZ9.5 stereomicroscope with a Canon EOS Rebel T3i or T6i attachment. Morphological vouchers were fixed in 10% formaldehyde in seawater for approximately 24 hours and then rinsed and transferred to 50% ethanol for archival. Posterior fragments or whole individuals were preserved in 95% ethanol for molecular analysis. Type and voucher specimens are deposited in the Benthic Invertebrate Collection, Annelida, Scripps Institution of Oceanography (SIO-BIC), University of California, San Diego, CA, U.S.A. GenBank accession codes are inserted in brackets for barcoded specimens.

Preserved specimens were carefully cleaned by brushing off sediment particles. They were observed and photographed in Zeiss stereo and compound microscopes. Measurements for specimens include their body length, cephalic cage length, body width (about chaetiger 10), and number of chaetigers. Gonads were examined by a small puncture in the body wall for removing a gonad fragment, then fragments were mounted in a slide for observation, and then returned to the specimen. Digital photos were made with a Canon T3i and an adapter for microscopes. Series of photos were compressed with HeliconFocus, and arranged as plates with PaintShop Pro X9. *Saphobranchia* species are presented below in alphabetical sequence, but *Lamispina* will be presented first and then, *Diplocirrus* is being restricted, its emended diagnosis and key to species precede the corresponding diagnosis for *Saphobranchia*, reinstated, and its key to species.

Results

Order Flabelligerida Pettibone, 1982

Family Flabelligeridae de Saint-Joseph, 1894

Lamispina Salazar-Vallejo, 2014

Lamispina Salazar-Vallejo, 2014: 38.

Type species: *Stylarioides schmidtii* Annenkova-Chlopina, 1924, by original designation.

Diagnosis. Flabelligerids with body cylindrical, tapered posteriorly. Cephalic cage variable, often well-developed. Branchiae cirriform, eight filaments, four arranged in a continuous posterior row, and two lateral groups each with two filaments. Body papillae cylindrical, capitate, sometimes with adhering sediment particles or forming projections, arranged in irregular bands, or completely covered by the tunic. Medial chaetigers with long, distally foliose neurochaetae (lamispines), often as long as body width; tips usually paler, soft, flexible.

Distribution. *Lamispina* species are present in subtropical to cold-temperate waters, from shallow water to about 3300 m.

Lamispina polycerata n. sp.

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Figures 2; 3; 8A, B

Diagnosis. *Lamispina* with few sand particles along dorsum; cephalic cage chaetae barely longer than body width; anterior margin of chaetiger 1 with 5–6 long, horn-shaped papillae; lamispines longer than body width, tips falcate, tapered.

Type material. Holotype (SIO A9842), AD 4987, Mound 12 West (08°55'51.60"N, 84°18'46.80"W), 999 m, 2 Nov. 2018, E. Cordes & E Cowell, coll. [MW172256].

Description. Holotype (SIO A9842), an anterior fragment, bent dorsally, now broken into two pieces; anterior region bent dorsally, ventrolaterally expanded medially, 6.5 mm long, 1.3 mm wide, cephalic cage chaetae 2 mm long, 16 chaetigers (Figs 2A; 8A, B); posterior region 5 mm long, 1 mm wide, 11 chaetigers. Body pale, truncate

anteriorly, tapered posteriorly. Tunic with a few sand particles adhering to papillae; papillae conical, mucronate, stiff; sand particles on median to posterior regions, not on anterior region. Dorsum with two transverse series of large papillae, four larger, forming longitudinal rows, at least along anterior chaetigers, posterior chaetigers with only two larger middorsal papillae rows. Venter with smaller conical papillae, 2–3 transverse rows per segment along a few anterior chaetigers, up to five rows per segment in median, and up to eight rows per segment in posterior chaetigers.

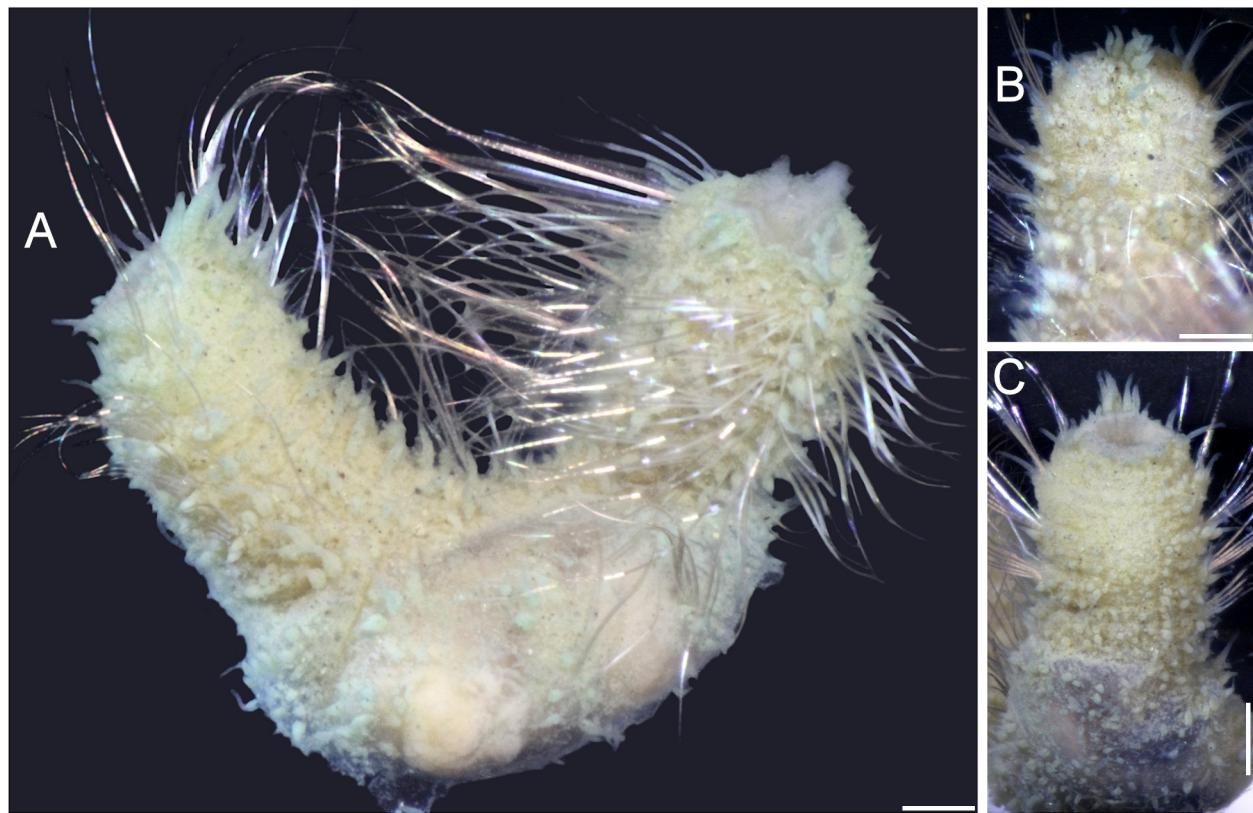


FIGURE 2. *Lamispina polycerata* n. sp., holotype (SIO A9842). A. Anterior fragment, left lateral view (anterior end to the left). B. Anterior end, dorsal view. C. Same, ventral view. Scale bars.- A: 0.38 mm, B–C: 0.47 mm.

Cephalic cage chaetae slightly longer than body width; chaetigers 1–2 involved in cephalic cage with longer chaetae. Chaetiger 1 apparently damaged, with three notochaetae and one neurochaetae per side; chaetiger 2 with two notochaetae and seven neurochaetae. Chaetiger 3 with shorter chaetae, two notochaetae and seven neurochaetae, directed laterally.

Anterior end not observed in holotype; not dissected to avoid further damage. Living specimen (Fig. 8A) with palps pale, branchiae brownish, blunt or slightly tapered. Palps twice wider than branchiae and slightly longer than them. Other features unknown.

Anterior dorsal margin of chaetiger 1 papillose, papillae conical, middorsally with 5–6 larger ones (Figs 2B, C; 3A), middorsal papillae longest. Chaetigers 1–3 progressively longer. Chaetal transition from cephalic cage neurochaetae to body neurochaetae abrupt; lamispines present from chaetiger 4. Gonopodial lobes not seen (Fig. 2C).

Parapodia low transverse folds (Fig. 3B), more projected along posterior chaetigers. Notopodia dorsolateral, neuropodia ventrolateral. Notopodia with a longer basal papilla. Neuropodia with 2–3 longer papillae per segment.

Median notochaetae multiarticulated capillaries in fan-shaped bundles, up to 14 per side, longest ones twice longer than body width; articles ankylosed basally, medially 2–3 times longer than wide, progressively longer distally; tips straight (Fig. 3C). Neurochaetae in transverse rows, six per bundle, longest ones longer than body width; subdistally widened, tips falcate, acute (Fig. 3D).

Posterior region with parapodia slightly more projected laterally (Fig. 3E). Notochaetae and neurochaetae in fan-shaped bundles.

Posterior end processed for molecular studies; living specimen with posterior region tapered, chaetae progressively smaller (Fig. 8B); pygidium with anus terminal.

Etymology. The epithet is made by combining the Greek words for many (*polýs*) and horns (*kérata*), becoming latinised to *polycerata*. This indicates the 5–6 horn-like larger papillae positioned over the anterior margin of first chaetiger. The specific name is regarded as a noun in apposition (ICZN 1999, Art. 31.2).

Remarks. *Lamispina polycerata* n. sp. belongs in the species group having sand or other foreign particles on their tunic, together with *L. ammophila* Jimi & Kajihara, 2018 from Japan, *L. amoureuxi* Salazar-Vallejo, 2014 from the northeastern Atlantic, and *L. keeli* Salazar-Vallejo, 2014 from the Gulf of Mexico. The latter differs by having sediment particles concentrated mid-dorsally, and lamispines with bifid tips, whereas *L. polycerata* and the other two species have sediment particles throughout their dorsum, and lamispines with entire tips. In *L. ammophila*, the cephalic cage chaetae are 1.5–2.0 times longer than body width, whereas in *L. amoureuxi* and *L. polycerata* they are shorter, slightly longer than body width. The main differences are that in *L. polycerata* sand particles are few and concentrated along median and posterior chaetigers, and median chaetigers have lamispines longer than body width, whereas sand particles are abundant, and lamispines are shorter than body width in *L. ammophila* and *L. amoureuxi*.

On the other hand, if *L. polycerata* would be regarded as without sand particles, especially after finding only the anterior region, it would be joined with other three species having papillae stiff or conical and lamispines falcate, subdistally widened: *L. carrerai* Salazar-Vallejo, 2014 from the NE Pacific, *L. gymnopapillata* (Hartmann-Schröder, 1965) from the SE Pacific, and *L. horsti* (Haswell, 1892) from southern Australia. The main difference would be that in *L. polycerata* the cephalic cage chaetae are slightly longer than body width, whereas the other species have them 2–6 times longer.

Distribution. Only known from the type locality, off Pacific Costa Rica.

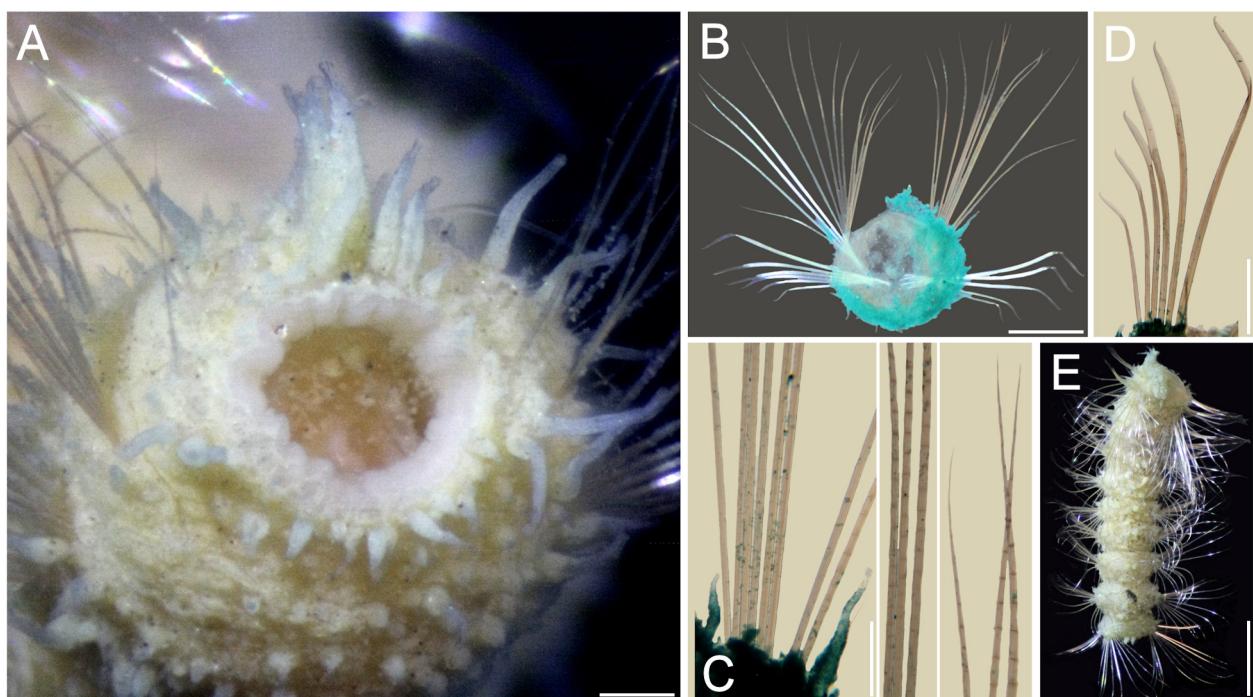


FIGURE 3. *Lamispina polycerata* n. sp., holotype (SIO A9842). A. Anterior end, frontal view. B. Chaetiger 17, transverse section, posterior view. C. Right parapodium. Notochaetal basal, medial and distal regions. D. Left parapodium, neurochaetae. E. Posterior fragment, dorsal view. Scale bars.- A: 0.15 mm, B: 0.56 mm, C: 0.20 mm, D: 0.25 mm, E: 1.25 mm.

Diplocirrus Haase, 1915, restricted

Diplocirrus: Salazar-Vallejo & Buzhinskaja, 2011 (partim).

Type species: *Trophonia glauca* Malmgren, 1867, by original designation.

Diagnosis (emended). Flabelligerids with body swollen anteriorly, median and posterior regions cylindrical, often with constrictions between successive segments (moniliform). Cephalic cage made by chaetiger 1, with three or less chaetae per bundle, fragile. Integument thin, usually with short papillae, with mud particles or free of them.

Branchial plate with eight branchial filaments of two types, anterior filaments cirriform and posterior filaments depressed, with longitudinal ridges. Parapodia never projected laterally. Notochaetae and neurochaetae sparse, usually smaller than body width. Neurochaetae completely multiarticulated.

Remarks. Støp-Bowitz (1948: 7) used the size of cephalic cage chaetae and papillae for separating *Diplocirrus* species, such that the type species, *D. glaucus* (Malmgren, 1867) has a few chaetae along the first few chaetigers, and short papillae, whereas *D. hirsutus* (Hansen, 1882) and *D. longisetosus* (von Marenzeller, 1890), have more chaetae, and longer papillae. Because specimens can be damaged, especially by breaking chaetae, Støp-Bowitz approach was not followed in the revision of the genus (Salazar-Vallejo & Buzhinskaja 2011). As benthic sampling is being done more carefully, better preserved specimens would allow for an extended use of the cephalic cage development. However, the size of chaetae along median chaetigers is more emphasized because they are less frequently broken by sieving or similar processing of benthic samples.

Saphobranchia Chamberlin, 1919, reinstated, resembles *Pherusa* Oken, 1807 by having very long cephalic cage chaetae (2–3 times longer than body width), and scarce papillae along body; it also resembles some species of *Lamispina* Salazar-Vallejo, 2014 by having very long chaetae in median chaetigers (twice as body width). However, it differs from *Pherusa* because *Saphobranchia* has neurochaetae basally ancylosed, and medially and distally articulate, whereas *Pherusa* and *Lamispina* have them completely ancylosed, shorter and falcate in the former, longer and distally foliose in the latter. *Saphobranchia* resembles *Diplocirrus* by having multiarticulate neurochaetae, but in *Saphobranchia* the cephalic cage has more chaetae, and in median segments chaetal basal section is ancylosed, whereas in *Diplocirrus* there are a few chaetae in cephalic cage, and neurochaetae are completely articulated. The type of branchial filaments, size of chaetae, together with the presence of a basal ancylosed section in neurochaetae, and the development of the cephalic cage chaetae are the main characters that support the removal of some *Diplocirrus* species, and the recognition of *Saphobranchia* as a distinct genus.

As currently understood, *Diplocirrus* includes 22 species having cephalic cage chaetae variably developed, abundant small body papillae, or scarce ones along body, branchial filaments of two types and neurochaetae usually multiarticulate along their length, or with a basal section ancylosed (Darbyshire & Mackie 2009, Salazar-Vallejo & Buzhinskaja 2011, Teixeira *et al.* 2015, Jimi *et al.* 2017). Six of the species are herein transferred to *Saphobranchia* and are newly combined by having long chaetae, neurochaetae basally articulate, usually well-developed cephalic cage, and branchial filaments of one type: *S. acasi* (Teixeira, Rizzo & Santos, 2015) n. comb., *S. hirsuta* (Hansen, 1882) n. comb., *S. longisetosa* (von Marenzeller, 1890), *S. micans* (Fauchald, 1972) n. comb., *S. normani* (McIntosh, 1908) n. comb., and *S. octobranchia* (Hartman, 1965) n. comb. Consequently, *Diplocirrus* is restricted and below is a key to species. *Saphobranchia* species can be separated as indicated in the separate key below.

Distribution. Arctic, Antarctic, and deep water environments in the northwestern and southwestern Atlantic, and central eastern Pacific.

Key to species of *Diplocirrus* Haase, 1915, restricted

(modified from Jimi *et al.* 2017)

1	Body papillae abundant, short, giving a velvety appearance	2
-	Body papillae scarce, long, tunic looks bare	<i>Diplocirrus</i> sp. Sri Lanka
2(1)	Body without sand particles	3
-	Body with sand particles	11
3(2)	Ventrolateral gonopores present in some anterior chaetigers	4
-	Ventrolateral gonopores absent	9
4(3)	First chaetiger with long chaetae, about half as long as body width; caruncle posteriorly expanded	<i>D. erythroporus</i> Gallardo, 1968 Vietnam
-	Anterior end with short chaetae, 1/3–1/5 as long as body width; caruncle posteriorly tapered	5
5(4)	Branchiae with lamellae	6
-	Branchia without lamellae	7

6(5)	Median chaetigers with neurochaetae tapered, 22–25 articles, and tip delicately falcate; cirriform branchiae with lamellae along basal 1/4–1/5 of each filament	<i>D. branchiatus</i> (Rullier, 1965) Australia
-	Median chaetigers with neurochaetae barely tapered, 8–11 articles, and tip markedly falcate; cirriform branchiae with lamellae along basal 1/3–1/2 of each filament	<i>D. nicolaji</i> (Buzhinskaja, 1994) Russia, Japan
7(5)	Dorsal branchiae as long as ventral ones; caruncle shorter than palp scar	<i>D. mamoi</i> Jimi, Fujiwara & Kajihara, 2017 Japan
-	Dorsal branchiae shorter than ventral ones; caruncle longer than palp scar	<i>D. asamushiensis</i> Jimi, Fujiwara & Kajihara, 2017 Japan
8(3)	Papillae digitate, longer than wide; chaetiger 1 with notochaetae fragile, if complete, as long as body width	9
-	Papillae hemispherical, about as long as wide; cephalic cage chaetae shorter than body width	10
9(8)	Median chaetigers with neurochaetae with articles slightly longer than wide; body brownish	
-		<i>D. capensis</i> Day, 1961 South Africa
-	Median chaetigers with neurochaetae with articles 4–6 times longer than wide; body yellowish	
-		<i>D. imajimai</i> Jimi, Fujiwara & Kajihara, 2017 Japan
10(8)	Median chaetigers with 5–6 neurochaetae, shorter than notochaetae, with articles 2.0–2.5 times longer than wide	
-		<i>D. kudenovi</i> Salazar-Vallejo & Buzhinskaja, 2011 Eastern Pacific Ocean
-	Median chaetigers with 2–3 neurochaetae, about as long as notochaetae, with articles 7–8 times longer than wide	
-		<i>D. stopbowitzi</i> Darbyshire & Mackie, 2009 Southern Irish Sea
11(2)	Anterior chaetigers barely wider than following ones	12
-	Anterior chaetigers swollen, much wider than following ones	13
12(11)	Some lateral papillae twice as long as in chaetal lobes	
-	Lateral papillae shorter	<i>D. rugosus</i> Teixeira, Rizzo & Santos, 2015 Brazil
-		<i>Diplocirrus</i> sp. Morocco
13(11)	Lateral papillae 1/25–1/5 as long as longest notochaetae	14
-	Lateral papillae 1/3–5/6 as long as longest notochaetae	18
14(13)	Ventrolateral gonopores present	15
-	Ventrolateral gonopores absent	16
15(14)	Cephalic cage well developed (2/3 as long as body width)	
-	Cephalic cage poorly developed (1/4 as long as body width)	<i>D. ohtsukai</i> Jimi, Fujiwara & Kajihara, 2017 Japan
-		<i>D. salazarvallejoi</i> Teixeira, Rizzo & Santos, 2015 Brazil
16(14)	Cephalic cage well developed (as long as body width)	17
-	Cephalic cage poorly developed (1/3 as long as body width)	<i>D. tohokuensis</i> Jimi, Fujiwara & Kajihara, 2017 Japan
17(16)	Neurochaetal rounded projection present in each article	
-	Neurochaetal rounded projection absent	<i>D. toyoshioae</i> Jimi, Fujiwara & Kajihara, 2017 Japan
-		<i>D. glaucus</i> (Malmgren, 1867) Norway
18(13)	Lateral papillae in chaetal lobe short (1/3 as long as notochaeta); anterior part (roughly corresponding to chaetigers 1–3) not pigmented	
-	Lateral papillae in chaetal lobe long (5/6 as long as notochaeta); anterior part (chaetigers 1–3) with rusty pigments	<i>D. incognitus</i> Darbyshire & Mackie, 2009 South Africa
-		<i>D. seisuiæ</i> Jimi, Fujiwara & Kajihara, 2017 Japan

***Saphobranchia* Chamberlin, 1919 reinstated**

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Saphobranchia Chamberlin, 1919: 387 (key, etymology, type species).

Diplocirrus: Salazar-Vallejo & Buzhinskaja, 2011 (partim).

Type species. *Stylarioides longisetosus* von Marenzeller, 1890, by original designation.

Diagnosis. Flabelligerids with body anteriorly swollen, tapered posteriorly. Cephalic cage made by chaetigers 1–2 (rarely only chaetiger 1), with more than four chaetae per bundle. Integument thin with long papillae, each with mud particles. Branchial plate with eight branchial filaments of one type, cirriform. Parapodia sometimes laterally projected. Notochaetae and neurochaetae abundant, usually as long as body width, or longer. Neurochaetae basally ankylosed, medially and distally multiarticulate.

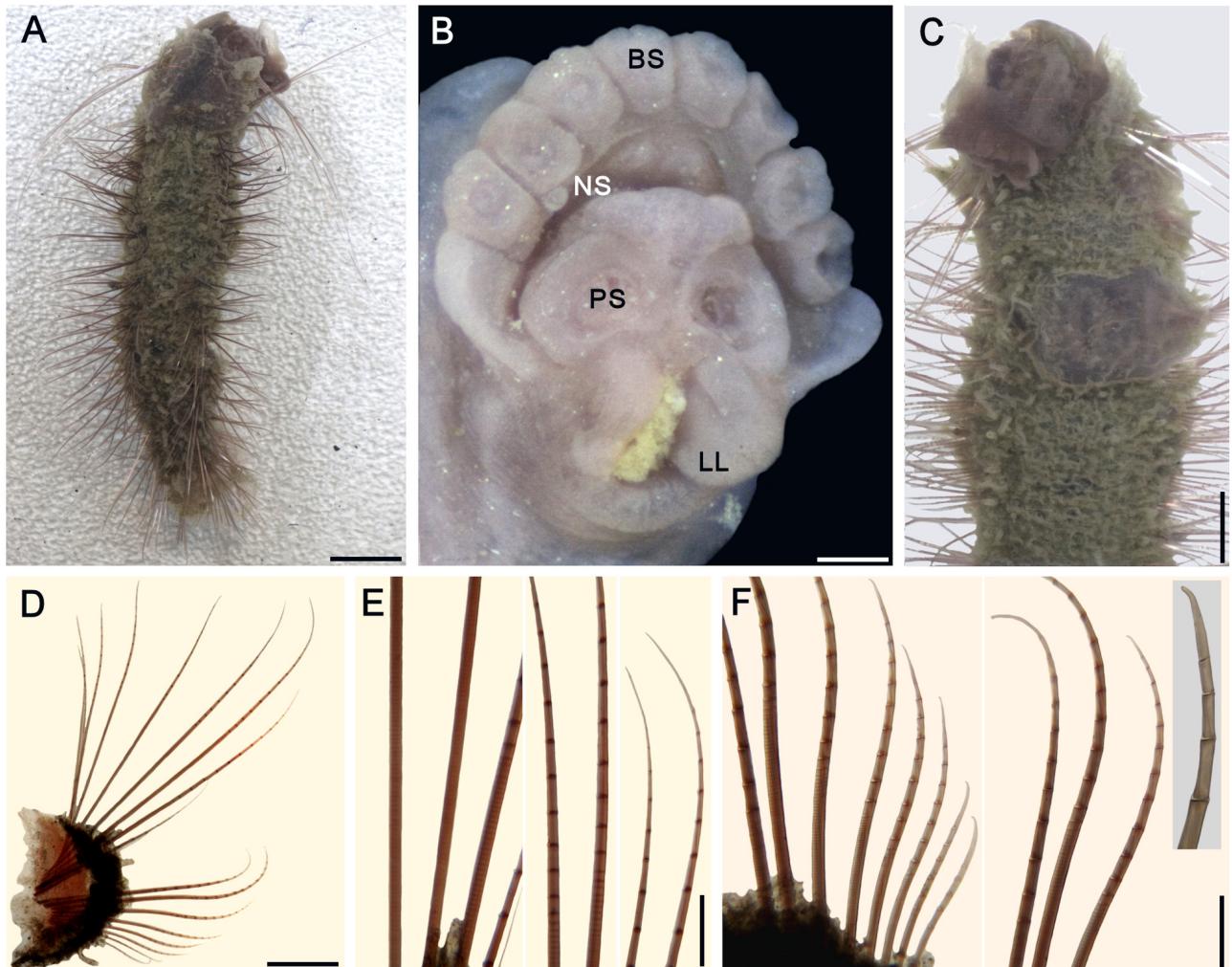


FIGURE 4. *Saphobranchia canela* n. sp., holotype (SIO A1332). A. Dorsal view. B. Anterior end, oblique frontal view (BS: branchial scar, LL: lateral lip, NS: Nephridial lobe scar, PS: palp scar). C. Anterior region, ventral view. D. Chaetiger 14, right parapodium, posterior view. E. Same, notochaetal basal, medial and distal regions. F. Same, neurochaetal basal and distal regions (inset: neurochaetal tip). Scale bars.- A: 1.1 mm, B: 150 μ m, C: 0.65 mm, D: 0.46 mm, E: 140 μ m, F: 0.8 mm.

Key to species of *Saphobranchia* Chamberlin, 1919 reinstated

(Modified from Salazar-Vallejo & Buzhinskaia 2011)

- 1 Body tunic without sand particles, or with a few sand and fine particles 2
- Body tunic with sand particles; median chaetigers with 7–8 notochaetae per bundle; neurochaetae with long articles distally 7
- 2(1) Median chaetigers with notochaetae as long as body width; papillae very long, single; neurochaetal tips falcate (body often reddish) *S. hirsuta* (Hansen, 1882) n. comb. Arctic and subarctic
- Median chaetigers with notochaetae longer than body width 3
- 3(2) Median neurochaetae with distal articles barely longer than wide, tips straight; gonopodial lobes present 4
- Median neurochaetae with most articles markedly longer than wide; no gonopodial lobes 5
- 4(3) Gonopodial lobes dark (papillae core and tip blackish); body papillae thick, digitate (body often grayish) *S. normani* (McIntosh, 1908) n. comb. Arctic and subarctic
- Gonopodial lobes pale; body papillae thin, filiform (body often pale) *S. longisetosa* (von Marenzeller, 1890) Gulf of Alaska

5(3)	Median chaetigers with neurochaetal tips falcate	6
–	Median chaetigers with neurochaetal tips straight, non-falcate	<i>S. omorpha</i> n. sp. Central eastern Pacific
6(5)	Median chaetigers neurochaetae with basal ancylosed region 1/2–1/3 chaetal length, medial and distal regions with articles 4–5 times longer than wide, barely shorter with a very slight reduction distally	<i>S. ilya</i> n. sp. Central eastern Pacific
–	Median chaetigers neurochaetae with basal ancylosed region 1/5–1/6 chaetal length, medial and distal regions with articles about twice longer than wide, progressively smaller	<i>S. micans</i> (Fauchald, 1972) n. comb. Central eastern Pacific
7(1)	Neurochaetal tips falcate	8
–	Neurochaetal tips straight	9
8(7)	Median chaetigers with notochaetae half as long as body width; median neuropodia with five neurochaetae per bundle; body wall and chaetae yellowish	<i>S. acafi</i> (Teixeira, Rizzo & Santos, 2015) n. comb.
–	Median chaetigers with notochaetae slightly longer than body width; median neuropodia with eight neurochaetae per bundle; body wall and chaetae cinnamon in colour	<i>S. canela</i> n. sp. Central eastern Pacific
9(7)	Sand particles restricted to the bases of papillae; neurochaetae with ancylosed region about 1/5 chaetal length	<i>S. octobranchia</i> (Hartman, 1965) n. comb. Northwestern Atlantic
–	Sand particles fixed along the papillae; neurochaetae with ancylosed region 1/2–1/3 chaetal length	<i>Saphobranchia</i> sp. Antarctica

***Saphobranchia canela* n. sp.**

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Figures 4; 8C–E

Diagnosis. *Saphobranchia* with tunic adhering sand particles, including dorsal papillae; median chaetigers with neurochaetal tips falcate, ancylosed region 1/2–1/3 chaetal length.

Type material. Holotype (SIO A1332), Alvin dive 4502, Costa Rica Mound 12 (08°55'40.80" N, 84°18'46.80" W), 1000 m, 23 Feb. 2009, G. Rouse & D. Huang, coll. [MW172257]. Paratypes: One specimen (SIO A1321), Alvin dive 4501, Costa Rica Mound 12 (08°55'48.00" N, 84°18'46.80" W), 1008 m, 22 Feb. 2009, G. Rouse & D. Huang, coll. [MW172258]. One specimen (SIO A1939), Alvin dive 4589, Mound 12 (08°55'48.00" N, 84°18'43.20" W), 998–1018 m, 10 Jan. 2010, G. Rouse, coll. [MW172259]. An anterior fragment (SIO A9607), Alvin dive 4974, black slurp, Mound 12 (08°55'48.00" N, 84°18'46.80" W), 996 m, 20 Oct. 2018, L. Levin & K. Metcalfe, coll. One specimen (SIO A9909), Alvin dive 4989 RedSlurp, Jaco Scar (09°07'04.80" N, 84°50'24.00" W), 1785 m, 4 Nov. 2018, L. Levin & D. Casagrande, coll. [MW172260, MW172261, two specimens sequenced].

Description. Holotype (SIO A1332), mature female, anterior fragment, brownish; chaetae cinnamon in colour. Body tapered, markedly contracted, introvert exposed, directed ventrally, anterior body wall eroded, venter anteriorly and posteriorly eroded, expanded (Fig. 4A); dorsum with sand particles, looks tuberculate; 9 mm long, 2 mm wide, cephalic cage chaetae 5 mm long, 21 chaetigers.

Tunic papillated, sediment particles include sand and silt, adherent along body and papillae (Fig. 8C). Dorsum with 2–3 transverse rows of papillae per segment, most damaged after removal of sand particles, two larger papillae in a row close to mid-dorsal line. Single larger blunt conical papillae in central notopodial fascicle, one inter-ramal, and another below neurochaetal fascicle (Fig. 4D). Venter with smaller, digitate papillae, 5–6 alternating rows per segment (Fig. 8D).

Anterior end exposed, slightly eroded, appendages detached (Fig. 4B). Branchiae marginal, eight scars of similar diameter. Palps size proportion to branchiae unknown. Nephridial lobe scars visible below bases of second lowermost branchiae. Prostomium slightly projected, caruncle short, reaching branchial plate. Eyes not seen. Upper and lower lips reduced, lateral lips massive, projected laterally. Living specimen with eight cirriform, branchial filaments of similar thickness, half as wide as palps, and slightly longer than them (Fig. 8E).

Cephalic cage chaetae 2.5 times longer than body width. Chaetigers 1–2 forming cephalic cage, distorted; right chaetae of chaetiger 1 directed posteriorly, those of chaetiger 2 directed anteriorly; chaetiger 3 with chaetae directed laterally, notochaetae 1/2–2/3 as long as those in previous chaetigers. Chaetae arranged in short rows, dorsolateral fan-shaped fascicles from chaetiger 3 to end of fragment.

Chaetiger 1 with six notochaetae and three neurochaetae per side, longest ones basally to medially ancylosed, distally articulated, shorter ones completely articulated, articles 4–6 times longer than wide, progressively longer.

Chaetiger 2 with four notochaetae, and seven shorter neurochaetae, notochaetae 2/3 as long as those of chaetiger 1, ancylosed section progressively shorter in smaller chaetae; neurochaetae shorter, thicker than those of chaetiger 1, similar to those present in posterior chaetigers, 2–3 times longer than wide, slightly longer distally.

Anterior dorsal margin of chaetiger 1 eroded, without tunic, with two larger tapered papillae. Chaetigers 1–4 distorted, chaetigers 1–2 expanded, twice longer than following ones. No chaetal transition from cephalic cage chaetae to body chaetae; all neurochaetae multiarticulate. Gonopodial lobes not seen (Fig. 4C). Oocytes inside ovary, cinnamon in colour, no oil droplets between oocytes, each about 60–80 μm in diameter.

Parapodia poorly developed, chaetae emerge from body wall. Parapodia lateral; median neuropodia ventrolateral. Notopodia with a larger central conical papilla, slightly larger than interramal papilla (Fig. 4D); neuropodia with a large, digitate basal papillae (conical before removal of sediment particles).

Median notochaetae arranged in short transverse rows, chaetal fascicles fan-shaped, directed dorsally, slightly longer than body width. All notochaetae multiarticulate capillaries; 9–10 per bundle, central notochaetae with basally ancylosed region half as long as total chaetae, 1–2 median articles twice longer than wide, then 4–5 times longer than wide, progressively longer distally, tips straight (Fig. 4E). Neurochaetae 2/3 as long as body width; 8 per bundle, ancylosed region 2/5–1/3 total length (Fig. 4F), 1–2 median articles as long as wide, or slightly longer than wide, progressively longer up to 3–4 times longer than wide subdistally; tips falcate (Fig. 4F, inset).

Posterior region unknown.

Etymology. The specific epithet is from the Spanish word for cinnamon, *canela*, and indicates the cinnamon colour of chaetae and body wall. The Spanish word comes from the French *canelle*, or from the Italian *canella*, both meaning ‘small cane’ and in Spanish refers to the cinnamon tree cortex that, once dried, twists around itself forming small canes. The specific name is regarded as a noun in apposition (ICZN 1999, Art. 31.2).

Variation. An anterior fragment from the type locality (SIO A1321) 5 mm long, 1 mm wide, 16 chaetigers, cephalic cage chaetae broken 1 mm long. It has integument brownish, tunic partially eroded, a few sand particles in posterior segments; many chaetae broken including those of chaetigers 1–2; anterior end fully exposed, partially eroded, cephalic appendages lost; gonopodial lobes not seen. A small specimen from the type locality (SIO A1939) has the anterior end fully exposed, appendages detached, ventral pharyngeal organ everted, without posterior end; 15 mm long, 2 mm wide, 27 chaetigers. Anterior chaetigers damaged, many chaetae broken, cephalic cage chaetae 2.5 mm long, tunic granulose with sand particles; gonopodial lobes not seen. Median chaetigers have slightly less notochaetae, same number of neurochaetae, but body wall and chaetae are paler. The interramal papillae is as long as 1/5 notochaetal, or 2/5 neurochaetal length. Another fragment (SIO A9607) distorted, anterior end exposed, slightly eroded, cephalic appendages lost; 6 mm long, 1.8 mm wide, 10 chaetigers. Cephalic cage chaetae 6.5 mm long; chaetiger 1 with seven notochaetae and five neurochaetae; chaetiger 2 with 5–7 notochaetae, 2/3 as long as those of chaetiger 1, and 6–7 neurochaetae, about 1/3 as long as those of chaetiger 1. Chaetiger 3 with smaller chaetae, neurochaetae directed laterally. Gonopodial lobes not seen. Another paratype (SIO A9909) is almost complete, integument brownish, tunic with sand particles. Body anteriorly swollen, twisted medially, tapered posteriorly; 14 mm long, 2 mm wide (widest by chaetigers 5–6, 2.5 mm), cephalic cage 4 mm long, 29 chaetigers. Chaetigers 1–2 lateral, chaetiger 1 with five notochaetae, 3–4 neurochaetae; chaetiger 2 with three notochaetae half as long as those in chaetiger 1, and 5–6 neurochaetae directed anteriorly. Anterior end visible but not exposed, appendages detached. Median chaetigers with seven notochaetae and eight neurochaetae per bundle; reduced in size and number posteriorly.

Remarks. *Saphobranchia canela* n. sp. resembles *S. acafi* (Teixeira, Rizzo & Santos, 2015) n. comb., because they have sand particles along body, median chaetigers with 7–8 notochaetae per bundle, and neurochaetae with long articles distally. Their main differences are the length of notochaetae, the number of neurochaetae along median chaetigers, and the pigmentation of body wall and chaetae. In *S. canela*, the notochaetae are longer than body width, there are eight neurochaetae per bundle, and body wall and chaetae are cinnamon in colour, whereas in *S. acafi* notochaetae are half as long as body width, there are five neurochaetae per bundle, and body wall and chaetae are yellowish.

On the other hand, *S. canela* n. sp. differs from the two other newly described species: *S. ilya* n. sp. and *S. omorpha* n. sp. especially because of the body wall and chaetal pigmentation, being brownish, or cinnamon in colour in the former species, because the two other species have a pale body wall, and paler chaetae.

Distribution. Off Pacific Costa Rica in 998–1785 m depth.

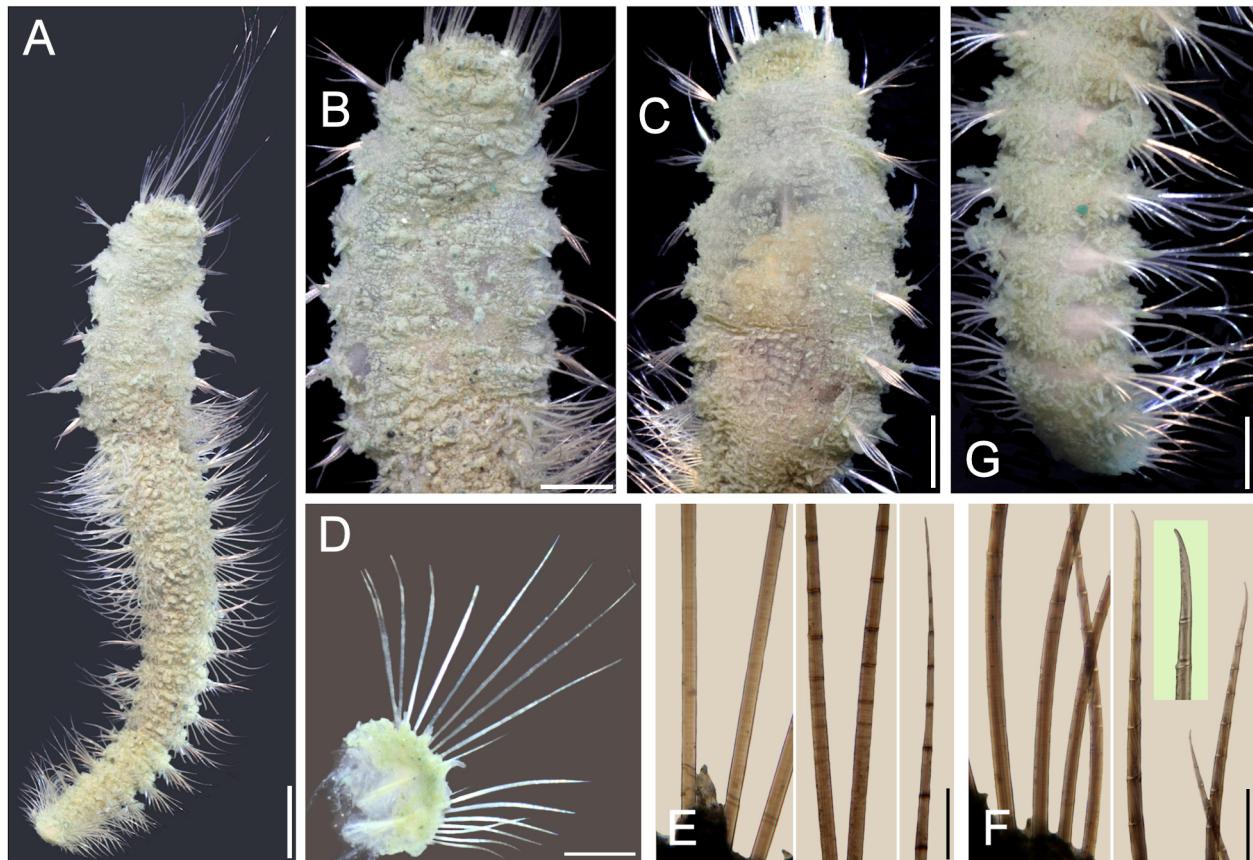


FIGURE 5. *Saphobranchia ilys* n. sp., holotype (SIO A9605). A. Dorsal view. B. Anterior region, dorsal view. C. Anterior region, ventral view. D. Chaetiger 14, right parapodium, posterior view. E. Same, notochaetal basal, medial and distal sections. F. Same, neurochaetal basal and distal sections (inset: neurochaetal tip). G. Posterior region, ventral view. Scale bars.- A: 2.1 mm, B: 1.1 mm, C: 1.5 mm, D: 0.65 mm, E, F: 17 μ m, G: 0.7 mm.

***Saphobranchia ilys* n. sp.**

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Figures 5, 8F, G

Diagnosis. *Saphobranchia* with tunic without sand particles; median chaetigers with notochaetae longer than body width; neurochaetae with tips falcate, basal ancylosed region $\frac{1}{2}$ - $\frac{1}{3}$ chaetal length, articles 4–5 times longer than wide; no gonopodial lobes.

Type material. Holotype (SIO A9605), CR18-0028, Alvin dive 4973 slurp, Jaco Scar ($09^{\circ}07'04.80''$ N, $84^{\circ}50'24.00''$ W), 1795 m, 19 Oct. 2018, V. Orphan & N. Gallo, coll. [MW172262]. Paratypes: Two fragments (SIO A9725), one anterior, one posterior, probably from same specimen, Alvin dive 4977, mussel pot 2, Jaco Scar ($09^{\circ}07'04.80''$ N, $84^{\circ}50'24.00''$ W), 1783 m, 23 Oct. 2018, E. Cordes & J. Klein, coll.

Description. Holotype (SIO A9605) mature female, without pygidium, greenish. Body anteriorly swollen, slightly bent laterally, tapered posteriorly (Figs 5A; 8F); 31 mm long, 2.5 mm wide (widest by chaetigers 5–6, 4 mm), cephalic cage 8 mm long, 31 chaetigers.

Tunic papillated, sediment particles mostly fine, adherent along body, and few larger sand particles, especially dorsally, and some dorsal papillae basally swollen (Fig. 5B). Venter with digitate to conical papillae, 3–4 times longer than wide. Papillae short, about 1/5–1/10 as long as notochaetae, about five rows per chaetiger, especially visible in median and posterior chaetigers, anterior dorsal surface slightly eroded. Venter with smaller papillae, digitate, about five rows per chaetiger (Fig. 8G).

Anterior end features not visible; not dissected to avoid further damage.

Cephalic cage chaetae 2–3 times longer than body width. Chaetigers 1–2 forming cephalic cage, chaetae direct-

ed anteriorly; chaetiger 3 with less chaetae, notochaetae about half as long as those of chaetiger 2. Chaetae arranged in short rows, dorsolateral thin fascicles along chaetigers 4–7, in fan-shaped fascicles posteriorly.

Chaetiger 1 with 7–8 notochaetae, 3–4 neurochaetae, longest ones basally ancylosed, medially and distally articulated, shorter ones completely articulated, articles 3–4 times longer than wide medially, progressively longer distally. Chaetiger 2 with three thinner notochaetae, 2/3 as long as those of chaetiger 1, ancylosed section progressively shorter in smaller chaetae; neurochaetae shorter, 1/3 as long as those of chaetiger 1, articles 3–4 times longer than wide medially, progressively longer distally. Chaetigers 3–7 damaged, most chaetae broken.

Anterior dorsal margin of chaetiger 1 with 2 larger, conical papillae. Chaetigers 1–4 progressively longer. No chaetal transition from cephalic cage to body chaetae; all neurochaetae multiarticulate. Gonopodial lobes not seen (Fig. 5C). Oocytes seen in an ovary fragment, with oil droplets between them, each about 80–100 μm in diameter.

Parapodia poorly developed, chaetae emerge from body wall. Parapodia lateral; median neuropodia ventrolateral. Notopodia with a larger, digitate postchaetal conical to digitate papillae along chaetigers 3–8; other notopodia and neuropodia with a few short papillae, each about as long as 1/5–1/10 notochaetal length (Fig. 5D).

Median notochaetae arranged in short transverse rows, chaetal fascicles fan-shaped, directed dorsally, up to twice longer than body width. All notochaetae multiarticulate capillaries; 9–10 per bundle, central notochaetae with basally ancylosed region up to half total length, basal chaetae fully articulated; articles 4–5 times longer than wide, becoming longer distally; tips straight (Fig. 5E). Neurochaetae about as long as body width; 7–8 per bundle, ancylosed region 1/2–2/5 total length, medially with articles 3–4 times longer than wide, progressively shorter distally; tips falcate (Fig. 5F, inset).

Posterior region cylindrical (Fig. 5G), posterior end unknown.

Etymology. The specific name is the Greek word for mud, feminine, is because of the presence of fine sediment particles in the tunic and covering papillae, as opposed to having sand particles on them. The specific name is regarded as a noun in apposition (ICZN 1999, Art. 31.2).

Variation. A paratype (SIO A 9725) is 8 mm long, 2.8 mm wide, 10 chaetigers; anteriormost left chaetigers removed, integument with fine sediment particles making dorsal papillae look digitate to conical; epizoic organisms on chaetae making them look pilose. Cephalic cage chaetae 6 mm long; chaetiger 1 with eight notochaetae and seven neurochaetae; chaetiger 2 with eight notochaetae, 4/5 as long as those of chaetiger 1, and seven neurochaetae, half as long as those of chaetiger 1. Chaetiger 3 with smaller chaetae, neurochaetae directed laterally. Posterior fragment with seven chaetigers, 4 mm long, 1.4 mm wide.

Remarks. *Saphobranchia ilya* n. sp. resembles *S. micans* (Fauchald, 1972) n. comb. from Western Mexico because they have long papillae, giving integument an hirsute appearance, by having a few sand particles along body, notochaetae far longer than body width in median chaetigers, and neurochaetae with articles longer than wide. They differ in neurochaetal features in median chaetigers. In *S. ilya* n. sp. articles are 4–5 times longer than wide, with a very slight reduction distally, and the ancylosed region is 1/2–1/3 chaetal length, whereas in *S. micans* they are progressively smaller, about twice longer than wide, and the ancylosed region is 1/5–1/6 chaetal length.

On the other hand, *S. ilya* n. sp. resembles *S. omorpha* n. sp. especially because both have pale body wall and brownish chaetae. They differ in the development of tunic papillae, associated sediment particles, parapodial development, and chaetal size in median chaetigers. In *S. ilya* n. sp. body wall is rugose because the dorsal papillae are short, blunt mainly with fine sediment and a few sand particles, parapodia are barely projected from the body wall, and chaetae are as long as body width. On the contrary, in *S. omorpha* n. sp. body wall is pilose because the fewer dorsal papillae are without sediment particles, or fine particles adhering forming a thin cover, parapodia are markedly projected laterally, and chaetae are up to 4 times longer than body width.

Distribution. Off Pacific Costa Rica, in 996–1784 m depth.

Saphobranchia omorpha n. sp.

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Figures 6, 7, 8H, I

Diagnosis. *Saphobranchia* with tunic without sand particles; median chaetigers with notochaetae longer than body width; neurochaetae with tips straight, basal ancylosed region 1/3 chaetal length, articles 4–6 times longer than wide; no gonopodial lobes.

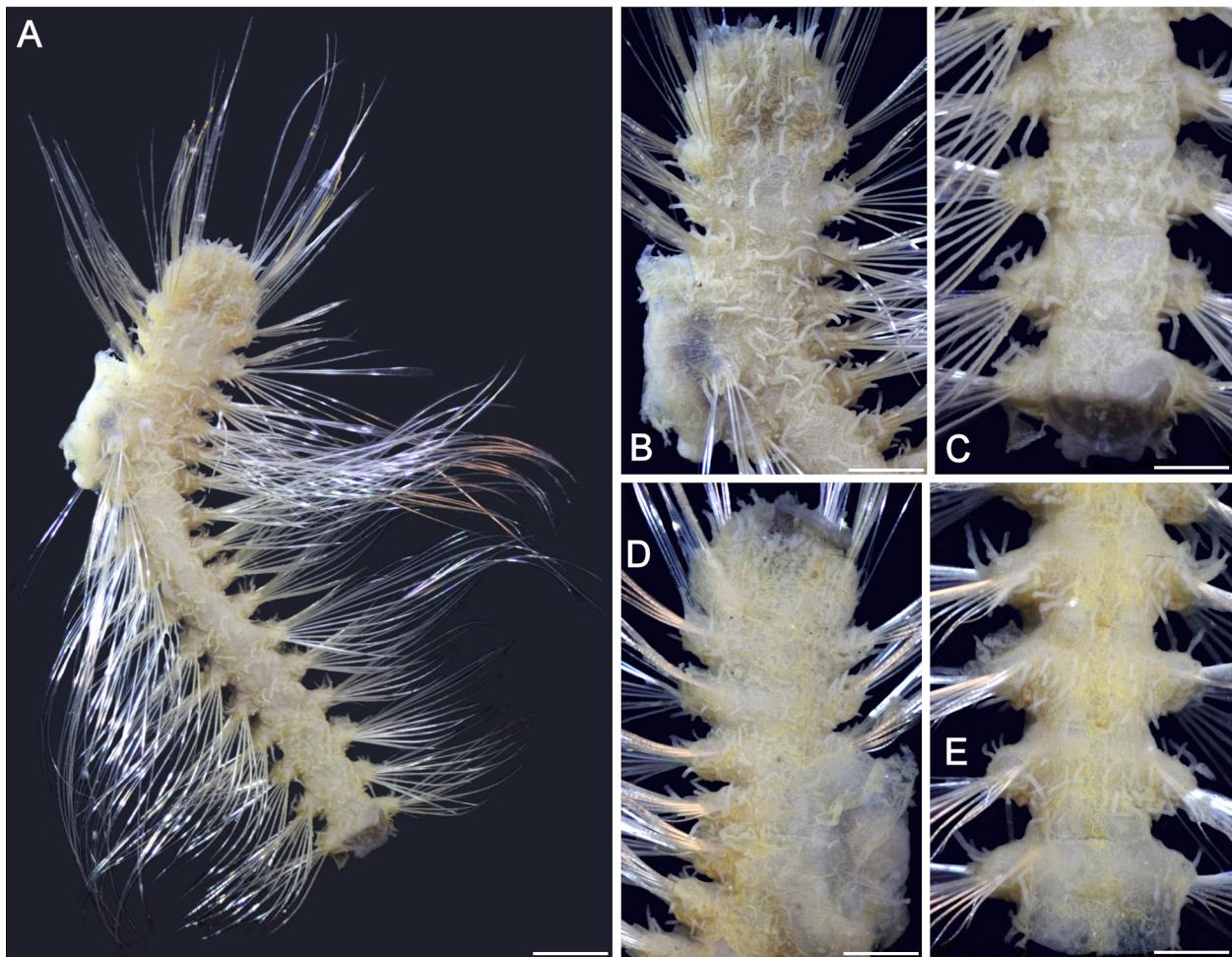


FIGURE 6. *Saphobranchia omorpha* n. sp., holotype (SIO A9595). A. Dorsal view. B. Anterior region, dorsal view. C. Last chaetigers, dorsal view. D. Anterior region, ventral view. E. Last chaetiger, ventral view. Scale bars.- A: 1.5 mm, B: 0.90 mm, C: 0.60 mm, D: 0.95 mm, E: 0.52 mm.

Type material. Holotype (SIO A9595), CR 18-0013, Alvin dive 4972, Jaco Scar ($09^{\circ}07'01.20''$ N, $84^{\circ}50'24.00''$ W), 1784 m, 18 Oct. 2018, G. Rouse & A. Hatch, coll. [MW172264].

Description. Holotype (SIO A9595) originally with 32 chaetigers (Fig. 8H), 12 posterior chaetigers removed for molecular studies; now without posterior region. Body pale, anteriorly swollen, slightly bent laterally, broken along left margins of chaetigers 5–8, tapered medially and posteriorly, anterior chaetigers with notochaetae up to 9 times longer than body width; body wall broken along left side in chaetigers 5–8 (Fig. 6A); 13 mm long, 1 mm wide (widest by chaetigers 7–8, 2.8 mm), cephalic cage chaetae 6 mm long, 20 chaetigers (last one removed for a slide).

Tunic thin, without sand particles; papillae long, in about three different lengths, up to 10 times longer than wide, sparse, variably eroded along body, dorsally and ventrally of similar shape, shorter and more abundant ventrally (Figs 6D; 8I), and surrounding chaetal bundle bases (Fig. 6C, E).

Anterior end features not seen; one palp barely exposed, brownish; not dissected to avoid further damage.

Cephalic cage chaetae 2–3 times longer than body width. Chaetigers 1–2 forming cephalic cage, chaetae directed anteriorly; chaetiger 3 with notochaetae directed anteriorly, neurochaetae directed laterally. Chaetae arranged in short rows, notochaetae dorsolateral along body.

Chaetiger 1 with 7–8 notochaetae, 3–4 neurochaetae, longest ones basally to medially ankylosed, shorter ones completely articulated, articles 3–4 times longer than wide medially, progressively longer distally. Chaetiger 2 with 7 thinner notochaetae, 4/5 as long as those of chaetiger 1 or of similar size, ankylosed region progressively shorter in smaller chaetae; neurochaetae thicker, 11–12 per bundle, some with adsorbed brownish particles along their length, articles 2–3 times longer than wide, slightly longer distally.

Anterior dorsal margin of chaetiger 1 with several papillae and two small blunt conical projections internal to notochaetae (Fig. 6B), also visible in chaetiger 2. Chaetigers 1–4 of similar length. No chaetal transition from cephalic cage to body chaetae; all neurochaetae multiarticulated. Gonopodial lobes not seen (Fig. 6D). Testis seen through broken body wall, confirmed by abundant spherical spermatids within gonad.

Parapodia laterally projected from body wall; parapodia lateral, median neuropodia ventrolateral. Notopodia and neuropodia surrounded by several cylindrical papillae (Fig. 7A); papillae covered by a very thin tunic (Fig. 7B), longest papillae about as 1/13 as long as longest notochaetae, or 1/11 as long as longest neurochaetae.

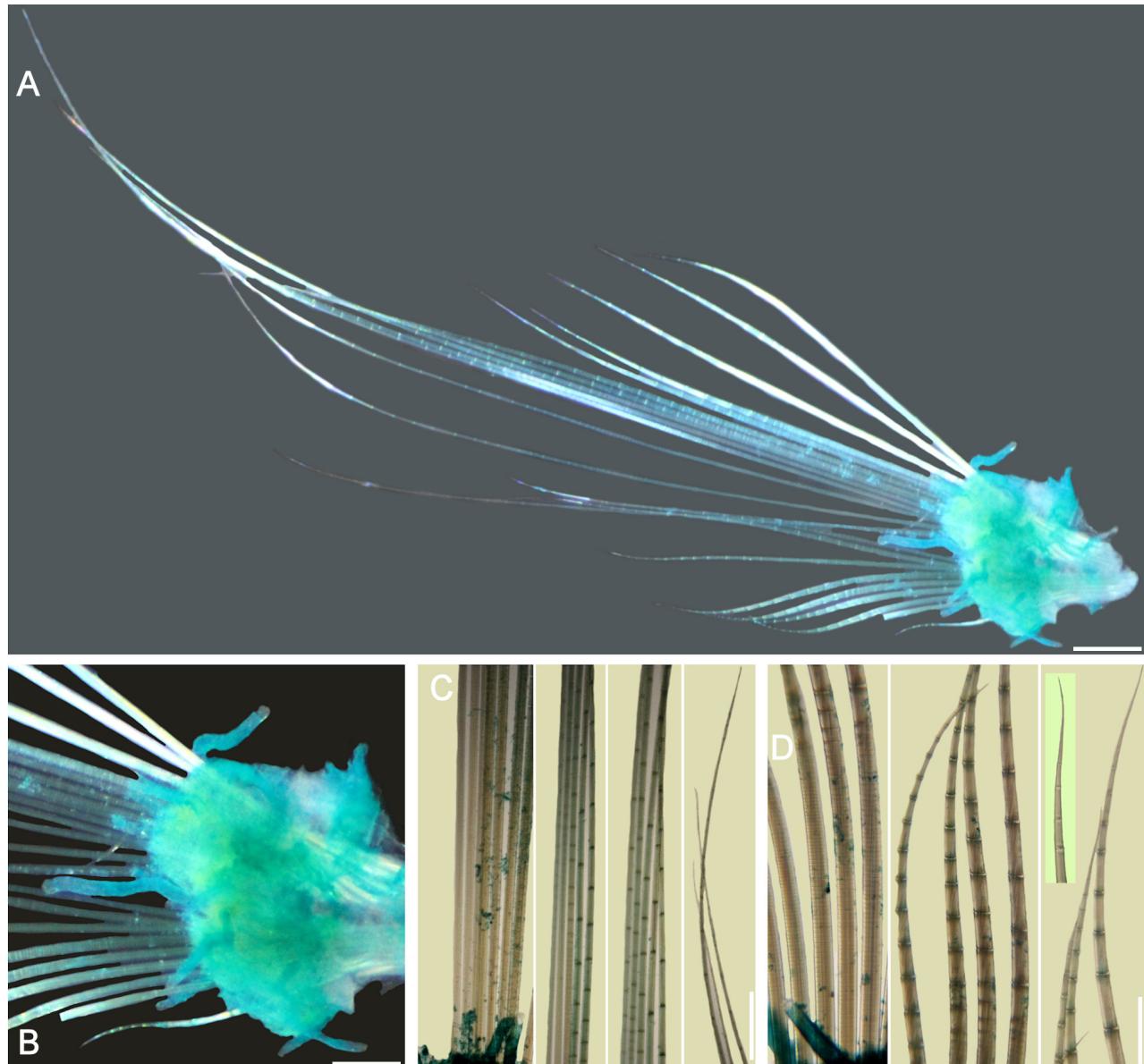


FIGURE 7. *Saphobranchia omorpha* n. sp., holotype (SIO A9595). A. Chaetiger 14, right parapodium, anterior view. B. Close up of parapodium. C. Central notochaetae, basal, medial and distal regions. D. Central neurochaetae, basal, medial and distal regions (inset: neurochaetal tip). Scale bars.- A: 0.36 mm, B: 0.21 mm, C: 35 μ m, D: 65 μ m.

Median notochaetae arranged in short transverse rows, chaetal fascicles fan-shaped, directed dorsally, at least 5 times longer than body width. All notochaetae multiarticulate capillaries; 14 per bundle, central notochaetae with basally ancylosed region about 1/3 chaetal length (Fig. 7C), basal notochaetae with a shorter ancylosed region, not fully articulated; articles 4–6 times longer than wide medially, progressively longer distally. Neurochaetae twice longer than body width, nine per bundle, central neurochaetae with ancylosed region 1/3 as long as chaetal length, medially with articles 3–4 times longer than wide, progressively longer distally (Fig. 7D), tips straight (Fig. 7D, inset).

Posterior region cylindrical, tapered (seen in photos before cropping for molecular studies); pygidium unknown.

Etymology. The specific name is from the Greek *ómorphos*, beautiful, masculine, latinised and declined in feminine, for referring to the beauty of the specimen. The specific name is regarded as a noun in apposition (ICZN 1999, Art. 31.2).

Remarks. *Saphobranchia omorpha* n. sp. groups with *S. micans* (Fauchald, 1972) n. comb., and *S. ilys* n. sp. because their bodies do not have abundant sand particles adhered on tunic, and their notochaetae are longer than body width. Their main difference after the key above is the type of neurochaetal tips. In *S. omorpha* n. sp. they are straight whereas in *S. micans* and *S. ilys* n. sp., they are falcate. Another conspicuous difference is the size of chaetae, because in *S. omorpha* n. sp. they are very long, more than 10 times longer than body width, whereas in the two other species, they can be up to 5 times as long.

An additional comparison might be needed because *S. omorpha* n. sp. and *S. ilys* share pale body wall and brownish chaetae. As indicated above, their main differences are in the development of tunic papillae, associated sediment particles, parapodial development, and chaetal size in median chaetigers. *Saphobranchia omorpha* n. sp. has a pilose body wall because the scarce dorsal papillae lack sediment particles, or have fine particles forming a thin layer, parapodia are clearly projected laterally, and chaetae are up to 4 times longer than body width. On the contrary, *S. ilys* n. sp. has a rugose body wall because dorsal papillae are short, blunt mainly with fine sediment, and a few sand particles, parapodia are slightly projected from the body wall, and chaetae are as long as body width.

Distribution. Off Pacific Costa Rica, in 1784 m depth.



FIGURE 8. Living specimens. A. *Lamisipina polycerata* n. sp., holotype (SIO A9842), anterior fragment, left lateral view. B. Same, posterior fragment, dorsal view. C. *Saphobranchia canela* n. sp., holotype (SIO A1332), dorsal view. D. Same, ventral view. E. Same, anterior end, frontal view (Br: branchia, Pa: palp). F. *S. ilys* n. sp., holotype (SIO A 9605), dorsal view. G. Same, ventral view. H. *S. omorpha* n. sp., holotype (SIO A9595), dorsal view. I. Same, ventral view. Scale bars: A, B: 1.0 mm; C, D: 2.2 mm; E: 0.4 mm; F, G: 3.5 mm; H, I: 3.7 mm (Photos: Greg Rouse).

General Discussion

Morphology

Haase (1915) made the first taxonomic thorough analysis of the Flabelligeridae. In his key to species, he relied upon several diagnostic features such as the type of branchiae, papillae along the body, gonopodial lobes (then regarded as nephridial papillae), and chaetae. Støp-Bowitz (1948) enlarged the morphological features by including some other diagnostic ones; as a consequence, in his key to the Norwegian flabelligerids, he included the number of chaetae in first chaetigers, the tunic, the body shape, the types of chaetae along body, and the type of sediment particles adhered on body papillae. Further observations resulted in better refinement of several features as the type of branchiae or chaetae, such that the family now includes 27 genera and 182 species (Pamungkas *et al.* 2019).

Diplocirrus Haase, 1915, *Lamispina* Salazar-Vallejo, 2014, *Pherusa* Oken, 1807, and *Saphobranchia* Chamberlin, 1919, as herein reinstated, all have eight branchial filaments. *Lamispina* and *Pherusa* separate from the other two genera because their neurochaetae are ancylosed, in the former the distal portion is foliose and can be as long as body width, whereas in the latter they are often shorter than body width, and usually falcate.

On the other hand, *Saphobranchia* differs from *Diplocirrus* in four diagnostic features. First, in *Saphobranchia* there are more than three notochaetae in chaetiger 1, whereas there are up to three notochaetae in *Diplocirrus*. Second, *Saphobranchia* has large body wall papillae, giving an hirsute to rugose appearance to the body, whereas in *Diplocirrus* they are short, giving a velvety appearance. Third, in *Saphobranchia* all branchial filaments are of a single type, smooth (Fig. 8E), whereas in *Diplocirrus* there are two types: the posterior branchiae have longitudinal ridges and are basally fused to each other, and the anterior filaments are cirriform. Third, notochaetae are often longer than body width in *Saphobranchia*, whereas they are as long as body width in *Diplocirrus*.

The species of *Saphobranchia* can be separated, as indicated in the key above, after the sediment cover along the body, the size of notochaetae and neurochaetae regarding to body width, the number of neurochaetae, the size of articles along neurochaetae, and their tips, and the presence of gonopodial lobes.

The combination of these features helps sorting out the three species herein described: *Saphobranchia canela* n. sp. with a few notochaetae in first chaetigers, larger sand particles dorsally (Fig. 8C, D), against many chaetae in first chaetigers and mud particles dorsally in *S. ilya* n. sp. (Fig. 8F, G), and *S. omorpha* n. sp. (Fig. 8H, I). The size of notochaetae and neurochaetal tips are also different, with *S. omorpha* with extremely long chaetae, and tapered neurochaetae, whereas the two others have markedly shorter chaetae, and neurochaetal tips are falcate. Two additional features which have not been used to separate similar species in *Saphobranchia* are the body shape, and the length or parapodial lobes; most species have body tapered gradually decreasing in width posteriorly, with short parapodial lobes, but in *S. omorpha* the body is almost cylindrical with longer parapodial lobes. These differences are regarded as sufficient to separate similar species in *Saphobranchia* and this explains why they were described above. The fact they were carefully collected, sorted out, and relaxed before preservation does not allow regarding their differences as a result of distortion due to screening or preservation artifacts.

COI barcoding

These morphological differences among the new *Saphobranchia* species are not corroborated with COI sequences. Rouse (2020, 11 Jul. 2020, email) indicated that

“it is quite clear that *Saphobranchia omorpha* is *S. canela* from the COI data ... The COI sequences of the two holotypes differ by only 3 DNA bases. Did you consider that the *S. omorpha* may be an epitokous form? It is not clear at present if *S. ilya* may also be *S. canela* since one specimen is also only 4 bases difference from the *S. canela* holotype ... Also there is more DNA variation among the *S. canela* specimens than there is among the three nominal *Saphobranchia* new species.” This means COI barcodes only identify a single species, not three as indicated after their morphology and pigmentation patterns. The reasons for regarding the *Saphobranchia* specimens as three different species were indicated above but additional reasoning may be found below.

1) Barcodes sometimes fail for identifying species. The percentage informally reported for the three *Saphobranchia* species is low, indeed, but barcodes do not always match morphologically clearly separable species. This has been documented in mosquitoes (Hernández-Triana *et al.* 2013), curculionid beetles (Cognato *et al.* 2020), or

lepidopterans (Efetov *et al.* 2019). The recommendation is that if “barcodes fail to deliver species resolution or where they reveal taxonomic conflicts, detailed evaluations of additional specimens and additional gene regions will be necessary” (Schmidt *et al.* 2015).

2) Swimming and swarming have been documented for a few flabelligerids (Salazar-Vallejo 2019), notably members of *Flabelligera* Sars, 1829. Some of these records indicated that the thick tunic is lost before invading the water column, but those specimens were not illustrated. *Flabelliderma berkeleyorum* Salazar-Vallejo, 2007 does not have a thick tunic, and its notopodia and neuropodia are not transformed in comparison to other members of the same genus; notochaetal bundles are about half as long as body width, and neurochaetae are not replaced nor elongated, as would be expected in a typical body transformation during epitoky. Further, regarding *S. omorpha* as the epitoke of *S. canela* would involve a series of drastic body changes which are not documented anywhere among polychaetes undergoing full-body epitokal transformations. These are the features potentially associated with epitoky: First, the body becomes thinner, with longer parapodia and chaetae. Second, the papillae are sparser, longer, and without adherence for foreign particles. Third, the number of chaetae in chaetigers 1–2 is increased. Fourth, the neurochaetae with falcate tips would be replaced by tapered ones (some chaetal modifications show a similar trend for swimming). Nevertheless, after the evidence from *Flabesymbios commensalis* (Moore, 1909) where gonads become hypertrophied, in *S. omorpha* gonads were barely developed, rendering its regarding as an epitoke unlikely.

3) Besides epitokes, striking dimorphism is very rare among marine benthic annelids. Chances are that if the differences shown by the three new *Saphobranchia* species are not epitokal, they might be due to dimorphism. The most extreme case was documented for the White Sea spionid *Scolelepis laonicola* (Tzetlin, 1985). The male is a permanent ectoparasite of the female, and has lost all traces of its family or generic affiliations, such that it was described in a different family. These three morphological *Saphobranchia* species might eventually be shown to be part of a complex reproductive pattern or polymorphic condition. However, the information available about flabelligerid reproduction is rather scant, and differences in gonads (ovaries *vs.* testis) are easy to note, but they do not imply, in the few documented cases, any dimorphism beyond some pigmentation in the reproductive region.

In conclusion, it is likely that without the COI sequences, the *Saphobranchia* species herein described would probably be accepted after their morphological differences. However, it would be bad taxonomy to disregard the evidences once they are available, and this should apply to both, morphology and COI sequences. The newly described *Saphobranchia* species are sufficiently different on morphological grounds despite the high similarity in COI sequences.

Acknowledgments

Drs Charlotte Seid and Greg Rouse (SIO) kindly allowed me to study a small part of their wonderful collection of deep sea invertebrates. They barcoded the specimens and after their results, they also kindly questioned my earlier identifications, made me improve my routine practices during this endless confinement, and suggested some means to improve this contribution. Thanks also to the captain and crew of the R/V Atlantis, the pilots and technicians for the HOV Alvin, the cruise science parties, and chief scientists Lisa Levin (SIO) and Erik Cordes (Temple University). Specimen collection was funded by U.S. National Science Foundation (NSF grants OCE-0826254, OCE-0939557, OCE-1634172). The careful reading by Drs Alexandra Rizzo and Naoto Jimi resulted in an improved draft. Wagner Magalhães carefully edited this final draft.

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