

Revision of *Buskiella* McIntosh, 1885 (including *Flota* Hartman, 1967), and description of its trifold organ (Polychaeta: Flotidae)

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ABSTRACT: The species included in both *Buskiella* McIntosh, 1885, and *Flota* Hartman, 1967 are revised on the basis of type and non-type materials, as well as on published accounts. Both genera are synonyms and the former has priority; the species included are *B. abyssorum* McIntosh, 1885, *B. flabelligera* (Hartman, 1967) comb.n., and *B. vitjasi* (Buzhinskaya, 1977) comb.n. Two other species previously included in the genus (*B. borealis* Hartman, 1965 and *B. minuta* Amoureux, 1986) are non-pelagic flabelligerids belonging elsewhere. The three *Buskiella* species are re-described, and an identification key is included. Further, the trifold organ is being described in details for the first time; this unique organ is neither a palp nor a branchial radiole. A similar structure has been reported in *Paralvinella* Desbruyères & Laubier, 1982. The independent status of Flotidae has been challenged, but its oligomery (body with few segments), trifold organ, and nervous system are unique, so this status deserves to be retained.

KEY WORDS: Pelagic polychaetes, abyssal fauna, Central Atlantic, Northern Pacific, Southern Pacific, taxonomy, Typhloscolecidae, Alvinellidae.

Ревизия *Buskiella* McIntosh, 1885 (включая *Flota* Hartman, 1967) с описанием трехраздельных органов (Polychaeta: Flotidae)

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РЕЗЮМЕ: Проведена ревизия пелагических полихет из родов *Buskiella* McIntosh, 1885 и *Flota* Hartman, 1967 с использованием типового и нетипового материала. Род *Flota* является младшим синонимом *Buskiella*. В род *Buskiella* включены следующие виды: *B. abyssorum* McIntosh, 1885, *B. flabelligera* (Hartman, 1967) comb.n. and *B. vitjasi* (Buzhinskaya, 1977) comb. n. Два других вида, ранее включаемые в род *Buskiella* (*B. borealis* Hartman, 1965 и *B. minuta* Amoureux, 1986) — донные флабеллигериды, принадлежащие к другим таксонам. Три вида *Buskiella* переописаны, предложен ключ для их определения. Впервые подробно

описаны трехраздельные органы; они не являются ни пальпами, ни жабрами, вероятно, это уникальные образования. Сходные структуры были описаны у *Paralvinella* Desbruyères & Laubier, 1982. Независимый статус семейства Flotidae вызывает сомнения, но такие признаки, как небольшое количество сегментов тела, трехраздельный орган, строение нервной системы дают основания для сохранения флотид как отдельного таксона.

КЛЮЧЕВЫЕ СЛОВА: Пелагические полихеты, абиссальная фауна, Центральная Атлантика, Северная Пацифика, таксономия, Typhloscolecidae, Alvinellidae.

Introduction

McIntosh (1885) studied some polychaete specimens collected in abyssal water off Sierra Leone and two other localities in the central South Atlantic Ocean. Combinations of several interesting morphological features in these polychaetes made him propose a new genus and species *Buskiella abyssorum*. The animals have elongate bodies with a thick cuticle, and their anterior ends carry trifid structures; the parapodia are few and carrying very long annulated chaetae. McIntosh thought that he had a benthic animal, although the extremely long chaetae could indicate a pelagic habitat. Mesnil (1899:84, footnote) was the first to suspect *Buskiella* was pelagic; later it was directly confirmed by Fauvel (1916b), and indirectly by Hartman (1967), when she proposed the name *Flota*.

Photos of living animals show that they are typically yellowish (bluish perhaps by the type of lighting employed) with transparent multi-articulated chaetae, have yellowish gonads placed in chaetigers 5–6, and a thin tunic. A specimen photographed in the East Pacific Rise, at 2500 m depth, is “the size of a sausage and swims by bending its stiff body from side to side, rowing with its bristles. Such worms are found only in very deep water, and have been seen from submersibles as deep as 6.5 km” (Batson, 2006). Karen Osborn who made many observations on living specimens had informed us that animals regularly reach a length of 12 cm. However, specimens suffer dramatic distortion when are not carefully relaxed — the body contracts while the tunic does not. This distortion would explain why the animals look so different to each other and from the living to the

preserved condition, especially regarding the thickness of the tunic, which becomes markedly wider in preserved specimens.

The taxonomic position of the pelagic flabelligerid-like polychaetes has been unstable. Heath (1930) proposed an independent family for *Poeobius* and regarded it as a link between the Echiura and Polychaeta, but as a member of the former. *Poeobius* was regarded as an aberrant annelid closely allied to sedentary polychaetes by Pickford (1947: 310–312), and later as closely allied to the Flabelligeridae by Hartman (1955: 53). This taxonomic position was confirmed using histological methods by Robbins (1965: 210), and recently by morphological (Rouse & Pleijel, 2003: 182–184) and molecular data (Burnette *et al.*, 2005: 218). On the other hand, *Buskiella* was described as a flabelligerid, while *Flota* was placed first in the same family, then integrated into a new family Fauveliopsidae Hartman, 1971, and later separated as an independent family, Flotidae, by Buzhinskaya (1996: 133–135). Family status of Flotidae was corroborated by Buzhinskaya (2006: 7–17).

The independent status for Flotidae has been challenged by Rouse & Pleijel (2003). They used 15 characters and 19 taxa to evaluate the affinities among cirratuliform polychaetes. For flotids, they regarded the trifid organ both as peristomial palps (charact. 1, state 0), and as branchiae arranged as an anterior cluster (charact. 5, state 4). These implications derived from comparative morphology may be correct, but are not based on a proper evaluation of the morphological features of the trifid organ since no histology or fine microscopical observations were employed. Therefore, in this paper we revise the species belonging to *Buskiella* and to

Flota on the basis of available material. Further, we present a detailed study of the trifold organ and try to define its function.

Materials and methods

Specimens were borrowed from several museums listed below. They were observed by light microscopy and some fragments were studied by histological methods and scanning electron microscopy. Some specimens were stained with methyl green, and photos were made with digital cameras with a microscope lens adapter in either dissecting or compound microscopes.

Acronyms

BMNH — Natural History Museum, London, UK;

DIZMSU — Department of Invertebrate Zoology, Moscow State University; Russia;

IOM — Institut Océanographique du Monaco, Monaco ;

IRFA — Institut de Recherche Fondamentale et Appliquée, Université Catholique de l'Ouest, Angers, France;

SIORAS — Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia;

USNM — National Museum of Natural History, Smithsonian Institution, Washington, USA;

ZIRAS — Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

Morphology

The morphological details of flotids have been based on a comparison with flabelligerids because they are closely allied. A short account follows to clarify the use of typical flabelligerid features. The eversible anterior end in most flabelligerids includes a tube-like siphon, which is rarely completely everted. Because the non-eversible anterior end sometimes resembles a hood and because it is shorter ventrally than dorsally, it is called a cephalic hood. Both taxa have a thick gelatinous layer or tunic surrounding the body. This hypertrophied epicuticle varies in thickness and stiffness, and in flabelligerids it may even include some sediment particles thus becoming a tough protective case

(Gunther, 1912: 23–26). This tunic may be regarded as an exoskeleton, similar to one present in arthropods (Borodin, 1929: 29–31), or in tunicates, with some internal differences that would explain their consistency. The calcified arthropod exoskeleton has some spines or setae running through it (Brusca & Brusca, 1990: 468, Fig. 4A, B); in tunicates, successive alternating reinforced layers may also have calcareous spicules as well as blood vessels (Ruppert & Barnes, 1996: 891, Fig. 17.21). In flabelligerids and flotids, the tunic is not calcified, body papillae run through it and although some may reach the outside, most remain inside providing some anchoring for it (Jourdan, 1887: 11–12).

Many flabelligerids live with its anterior part slightly exposed from the substrate. Thus, their few anterior chaetigers show some modifications and often have larger papillae. The dorsal surface of the first chaetiger has several modifications; it can be projected anteriorly, elevated dorsally or depressed, while its anterior margin can be papillated or smooth. Further, the anterior parapodia are often better developed and often have larger or more abundant papillae. These two features are not so well developed in flotids, perhaps due to the pelagic habitat and will not be detailed below.

Most flabelligerids have one pair of very long nephridia, running as two long sacs throughout the body, and opening besides the branchia in the anterior end (Gunther, 1912: 93–94; Schlieper, 1927: 369–373). Mature flabelligerids have gonads in few anterior chaetigers, which are not connected to nephridia; instead, the gonads drive the gametes outside of the body generally by paired ventrolateral lobes placed in one or two anterior chaetigers. Regrettably, they have been traditionally referred to as nephridial papillae (e.g. Hartmann-Schröder, 1996: 413). Thus, the ventral lobes present in mature flabelligerids, frequently in chaetigers 4–5, should be referred as gonopodial lobes. Because of their relative position, we are tentatively regarding the ventral lobes in flotids as gonopodial, not nephridial, but this deserves histological confirmation. Buzhinskaja (2006: 14) described female gonad on V and VI chaetigers in *Flota*

vitjasi but did not indicate connection of this gonad with papillae on IV chaetiger. In the parapodia many short simple capillaries are often not exposed at all, or perhaps only very distal tapering tips may be visible. These capillaries are the functional equivalents to aciculae, as originally stated by Schlieper (1927: 333).

Results

Taxon descriptions

Family Flotidae Buzhinskaya, 1996

Flotidae Buzhinskaya, 1996: 141.

Type genus: *Flota* Hartman, 1967, by original designation. Junior synonym of *Buskiella* McIntosh, 1885 (see below).

DIAGNOSIS EMENDED. Pelagic oligomeric polychaetes with a thin tunic when alive, thick when preserved. Anterior end with paired trifold organs. Pharynx thick, eversible, unarmed. First chaetiger larger than second chaetiger, ventrally displaced in some species; other chaetigers lateral. Parapodia biramous, with long multiarticulated capillaries, articles very long. Nerve chord with multiple ganglia per segment. One or two pairs of gonopodial lobes, in the posterior ventral margins of chaetigers 3–4.

REMARKS. The family name is based on *Flota* and must be retained despite being formed after the name of a junior synonym (ICZN, 1999, Art. 40.1). The diagnosis for the family (Buzhinskaya, 1996: 141) has to be modified. Most diagnostic features are shared by flabelligerids: both families have similar epidermal papillae, tunic, cephalic hood, and chaetal structure. However, flotids have such unique features as trifold organs, modification of the nervous system, and oligomeric body.

Most polychaete taxonomists have regarded flabelligerid chaetae as multi-annulate or barred (Day, 1967: 652; Fauchald, 1977: 115; Fauvel, 1927: 112; Uschakov, 1955: 305, 1965: 282). This may apply to stiff, thicker neurochaetae in several genera such as *Brada* or *Pherusa*. However, members of all genera have at least notochaetae clearly articulated. Their chaetae are separated by transverse septa, each having a small deeper socket, which is restricted to a single longitudinal line, thus, chaetae bend in a single direction. Langerhans (1881, Fig. 14a) and Hansen (1878: 10, Pl. 8, Figs 3–4; 1882, Pl. 7, Fig. 8) illustrated the chaetae of what is now called *Diplocirrus*, showing the characteristic articulations. This was further explained and illustrated by Gunther

(1912: 40, Fig. 20) for *Flabelligera*, and by Schlieper (1927: 343, Fig. 14) for *Pherusa*. Thus, Costa (1843: 277), Grube (1878), Hansen (1881: 39, ff), and Mesnil (1899: 81) called flabelligerid chaetae articulated. After the revision of most available type material, this early conclusion is confirmed and flabelligerid chaetae should be now redefined. Their notochaetae are multiarticulate, at least distally, with articulations sometimes ill-defined (as fusiform transverse notched septae), and neurochaetae multiannulate (with short or invisible rings), or clearly compound (multiarticulate). The longest chaetae in flabelligerids are restricted to few anterior chaetigers and form what has been called the cephalic cage. These chaetae may have long articles and the articulations are poorly developed basal- and medially, and slightly better developed distally. Flotids have unusually long articles in their chaetae. The few chaetae that have been illustrated by McIntosh (1885) and Buzhinskaja (1977) do not show clear articulations despite their large size, and despite the very long article, but they are better developed basally. They seem to be stiff without bending or just slightly bending as the animal swims. Thus, flotids and flabelligerids have similar body chaetae, but those of flotids are extremely large, provided with very long articles, and have very poorly developed articulation restricted to the basal or medial parts while in flabelligerids the articulation tend to be better developed distally.

The distinguishing features of flotids in relation to flabelligerids, as indicated by Buzhinskaya (1996, 2006), are the lack of a cephalic cage, and the presence of paired trifold organs, multiple nerve ganglia per segment, and some peculiar oral tentacles. The lack of the cephalic cage was indicated by Hartman (1967: 126); the anterior end may be modified (broader than other chaetigers) and the contraction of the larger first parapodia may resemble the flabelligerid cephalic cage. However, this is an artifact of preservation because in living specimens most parapodia are lateral (Batson, 2006; K. Osborn, pers. comm.).

Another feature which deserves attention in flotids is the ventral displacement of second chaetiger in some species. Most flabelligerids have their first chaetiger dorsally displaced, even though there may be few or short chaetae, while the second chaetiger is lateral, resembling those present in succeeding chaetigers. In *Buskiella*, however, the displacement of the second chaetiger is not a preservation artifact because it is observed in some living animals (see http://www.exploretheabyss.com/photo/gallery/gallery/popups/worm_lr.htm).

The ventral nerve chord in flabelligerids has been illustrated for *Flabelligera* (de Quatrefages, 1849, Pl. 10, Fig. 1), *Pherusa* (Schlieper 1927: 375,

Fig. 58), *Diplocirrus* (Filippova *et al.*, 2003: 220, Figs 2C, 4, 5), and *Poeobius* (Heath, 1930: 241, Figs A, C, Pl. 1, Fig. 1, 4, Pl. 2, Fig. 10). The ganglia may be elongate but there is only one per segment, whereas in flotids they are duplicate, as originally shown by McIntosh (1885: 374, Pl. 45, Fig. 2). *Poeobius* is the only pelagic polychaete having only 11 pairs of ganglia, as in *Buskiella*, but in the former they are single, not double as in the latter. Since in most of the above flabelligerids the body has more segments, the multiple ganglia might indicate the fusion of successive segments. This duplication of the ventral nerve chord ganglia is unique.

The third feature for distinguishing flotids from flabelligerids is the large size with few chaetigers. They are oligomeric, having a body with up to 11 chaetigers, but can reach a very large size (over 100 mm). The largest known flabelligerids are *Flabelligera mundata* Gravier, reaching over 50 mm in length with about 25 chaetigers (Gravier, 1906: 537), and *Pycnoderma congoense* Grube, reaching 120 mm in length with about 100 chaetigers (Augener, 1918: 451). Other benthic polychaetes with a large body, but without many chaetigers include some species of *Aphrodita* (25–30 chaetigers, 10–20 cm), *Chloeia* (20 chaetigers, 10–12 cm), and *Hesione* (16 chaetigers, 6–8 cm) (Fauvel, 1953; SISV, pers. obs., MNHN, Paris). The oral tentacles are not found in the studied specimens (see below). They might be either a series of muscular filaments broken from the thick pharynx surface, or they might be true tentacles, but most likely belonging to another animal which could have been recently captured and partly ingested.

Nevertheless, the trifold organ is another unique feature. Taken this together with the lack of cephalic cage, the duplicate ventral ganglia, and the oligomeric condition, despite not being used in previous phylogenetic studies, they may warrant the independent family status for the Flotidae, although closely allied to flabelligerids. Because of the above reasons, we think Flotidae should be kept distinct from Flabelligeridae.

The family Flotidae Buzhinskaya, 1996 is defined by trifold organs, duplication of ventral nerve ganglia per segment, and by oligomeric body. It contains a single genus, *Buskiella* McIntosh, 1885 (including *Flota* Hartman, 1967), with three species: *B. abyssorum* McIntosh, 1885, *B. flabelligera* (Hartman, 1967) comb.n., and *B. vitjasi* (Buzhinskaya, 1977) comb.n.

Buskiella McIntosh, 1885

Buskiella McIntosh, 1885: 372; Fauchald, 1977: 116 (*partim*). Type species: *Buskiella abyssorum* McIntosh, 1885, by original designation.

Flota Hartman, 1967: 125; Fauchald, 1977: 118.

DIAGNOSIS EMENDED. Body cylindrical, tapering posteriorly, with 9–11 chaetigers; outer cuticle thick, soft, covering parapodia. Paired trifold organs on the anterior end. Pharynx thick, as wide as anterior end. First chaetiger large, lateral; second chaetiger short, sometimes directed ventrally. Chaetae include smooth and multiarticulate capillaries, articles very long. Abyssopelagic.

REMARKS. Fauvel (1916) studied the pelagic polychaetes collected from several localities during two oceanographic cruises. In the material collected from a station located between the Azores Islands and the Iberian Peninsula, using an oblique tow from 5,700 m, he found what he identified as *Buskiella abyssorum*. The outer cuticle was tougher than the one found in *Flabelligera*, and without sediment; further, one specimen had a single median palp, and another specimen had some lateral bands of short branchia-like filaments on the anterior end, as well as some rounded lobes in the pharynx. The notochaetae are longer than the neurochaetae, and that there were many companion chaetae in both rami; although Fauvel (1916) stressed the differences between his specimens and *B. abyssorum*, he regarded those as artifacts of preservation as well as a result of size differences.

Hartman (1967) erected *Flota* for some abyssopelagic flabelligerid-like polychaetes found off Chile. However, she (as well as other taxonomists after her) overlooked the paper by Fauvel (1916), where the pelagic habitat for *Buskiella* was suggested. Thus, she compared *Flota* to *Enigma* Betrem, 1925, and to *Poeobius* Heath, 1930. *Enigma terwilli* Betrem, 1925 is closely related to *Poeobius meseres* Heath, 1930, and may even belong to the same species. Furthermore, its type locality is Bay of Guayaquil, Ecuador (Hartman, 1967: 127), and there are some records for *P. meseres* from off Ecuador (McGowan, 1960: 132, Fig. 4). *Enigma*, however, is a junior homonym of a coleopteran insect, and despite the announcement of a forthcoming paper by the author, it never came out. Fauchald (1977: 117) regards *E. terwilli* as *incertae sedis*, but it might be eventually regarded as a senior synonym if its type material is found. However, these two genera lack parapodia and chaetae, and if different, they are more closely related to each other than to *Buskiella*.

As currently redefined, the species included in *Buskiella* are *B. abyssorum* McIntosh, 1885, *B. flabelligera* (Hartman, 1967) n. comb., and *B. vitjasi* (Buzhinskaya, 1977) n. comb. Two other species described within this genus belong elsewhere. *B. borealis* Hartman, 1965, is a benthic species which resembles *Pycnoderma* Grube, 1877, or *Trophonilla* Caullery, 1944, and *B. minuta* Amoureux, 1986, is more closely allied to *Piromis* Kinberg, 1867. The generic definition by Fauchald (1977: 116) included

B. borealis, and that explains why the branchiae were regarded as abundant and placed on a triangular membrane, which rather resembles *Piromis*, rather than *Buskiella* or *Flota*, as then known. Further, some details are missing in the original description of *Buskiella*, and the type materials include specimens in varying degrees of deterioration. A redescription and the designation of a lectotype for *Buskiella abyssorum* is presented below to help clarify questions regarding its morphology.

The main distinguishing features to separate the three species of *Buskiella* are the relative number of gonopodial lobes (one pair in *B. vitjasi*; two pairs in the other species), and their relative shape (blunt digitate in *B. abyssorum*, tapering cirriform in *B. flabelligera*). The gonopodial lobes are covered and protected by the thick cuticle, and their number and relative shape are herein regarded as useful features, since they are useful in separating some flabelligerid species (Støp-Bowitz, 1948: 33). Further, the relative shape of the trifold organ, despite its exposure and often eroded state, might be used to separate the species in two groups, by the relative position of the lateral branches in relation to the central lobe. Thus, in *B. vitjasi*, the trifold organ has the lateral lobes rising from the central lobe, while in the two other species the lateral lobes have a more basal position, such that they look as if they were stemming from the body wall. However, because the trifold organ is more easily damaged, its usefulness needs some validation based upon additional better fixed and preserved specimens.

KEY TO SPECIES OF *BUSKIELLA* McINTOSH, 1885

1. Gonopodial lobes in chaetigers 3 and 4 (trifold organs with lateral lobes stemming from the anterior region, not from the central lobe) ... 2
 - Gonopodial lobes only in chaetiger 4 (trifold organ with lateral lobes stemming from central one, lateral branches thin)
 - *B. vitjasi* (Buzhinskaya, 1977), comb. n.
2. Gonopodial lobes blunt digitate, not pointed
 - *B. abyssorum* McIntosh, 1885
- Gonopodial lobes tapering cirriform, not blunt ...
 - *B. flabelligera* (Hartman, 1967), comb. n.

Buskiella abyssorum McIntosh, 1885

Figs 1, 2, 5.

Buskiella abyssorum McIntosh, 1885: 372–374, Pl. 45, Figs 1–2, Pl. 23A, Figs 15–18; Fauvel, 1916: 113–115, Pl. 8, Fig. 6, Pl. 9 (*non Buskiella*), Figs 15–18 (redescrip. *partim*).

TYPE MATERIAL. Central Atlantic Ocean. Lectotype: BMNH 1885.12.1.265, and paralectotypes collected off Sierra Leone, RV Challenger, Stat. 101 (05°48' N,

14°20' W), dredge hauled from 4500 m (2500 fathoms), 19.VIII.1873. Two paralectotypes (BMNH-McIntosh coll. 1921.5.1.2657), collected off Tristan da Cunha, R/V Challenger, Stat. 333 (05°48' N, 14°20' W), dredge hauled from 3645 m (2025 fathoms), 13.III.1876 (one median fragment, another very long median fragment without cuticle; 73 mm long excluding the everted gut, 10 mm wide by chaetiger 1, 11 chaetigers, trifold organ paired).

ADDITIONAL MATERIAL. One posterior fragment (BMNH-85.12.1.266), R/V Challenger, Stat. 106 (01°47' N, 24°26' W), 3330 m (1850 fathoms), 25.VIII.1873 (it has an oblique cut, 3–4 chaetigers). One damaged specimen (MOM-181438) collected during Monaco Campaign 1909, Stat. 2875 (43°04'30" N, 19°42' W), tow 0–5,700 m, 8.VIII.1909 (anterior fragment, 17 mm long, 2 chaetigers and anterior gut; trifold organ paired; the dark filamentoid structures in the gut is the stomach's anterior end, corrugated, torn off after contraction; they are not tentacles). Some fragments (MOM-181438), collected in the same station (they are typhlosolecids, close to *Travisiopsis*, see below). Three slides from the same *Buskiella* specimen (IRFA-89, -90, -90') with fragments of tunic and parapodia, chaetae broken. One specimen (SIORAS), R/V M. Keldysh, Stat. 4355, polygon Broken Spur (29°10.67' N, 43°10.38' W), 25.VI.2002, oblique tow 2960 – 650 m, bottom depth: 3000 m.

DESCRIPTION. Lectotype complete (Figs 1B, 2A), distorted, anteriorly swollen, tapering posteriorly, cylindrical; body pale brown, slightly darker anteriorly, surface smooth, with a transparent thick tunic, mostly free from sediment particles, posteriorly damaged, with foreign particles; 32 mm long, 4 mm wide (chaetiger 3), first chaetiger chaetae 13 mm long (most chaetal tips broken), 9 chaetigers (some without chaetae).

Anterior end eroded. Cephalic hood not seen (present in SIORAS specimen, Fig. 5B). Prostomium damaged in the lectotype (Fig. 1C, D). Prostomium a very low cone (in paralectotype BMNH 1885.12.1.265), anteriorly rounded. Trifold organ paired, right one better preserved, left one damaged (Fig. 1D, and in another fragment); all lobes thick, tapering; median lobe thicker, lateral ones stemming from the ventral side of the base, twice as long in fresh material, now sub-equal. Lateral lips well developed, dorsal and ventral lips shorter (Figs 1D). Pharynx thick (Fig. 2C), internal surface smooth, connecting to a dark stomach.

First chaetiger larger than the remaining; chaetae at least 1/3 as long as body, or 3 times longer than body width (Figs 1A, B, 2A). Chaetae arranged in short rows, notochaetae arranged in two short transverse rows, now contracted and distorted. There are 16+8 (on each row) notochaetae and 16 neurochaetae, the latter slightly thicker. Chaetiger 2 smaller, difficult to detect because of distortion. Posterior chaetigers larger, decreasing in size posteriorly. All remaining chaetae long multiarticulated capillaries. Ventral gonopodial lobes small, digitate, in posterior margins of chaetigers 3 and 4 (Fig. 2B).

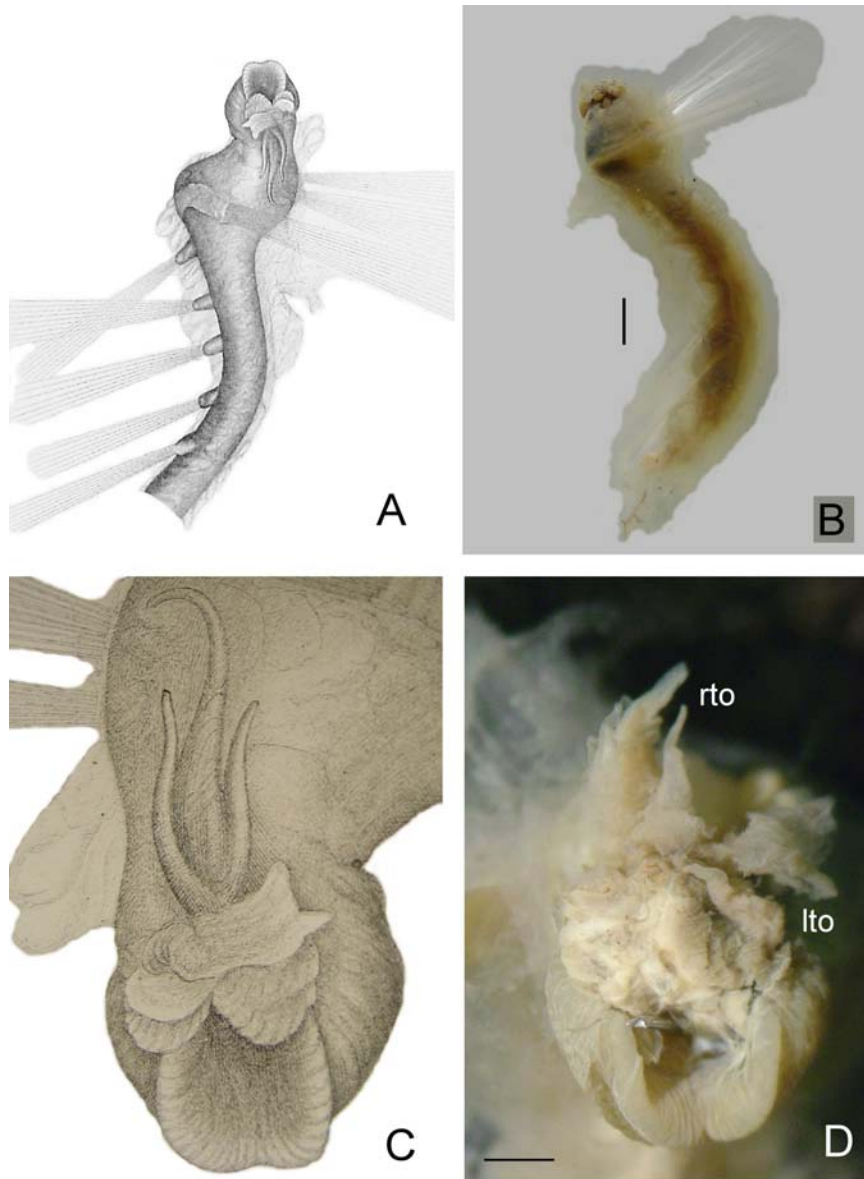


Fig. 1. *Buskiella abyssorum* McIntosh, 1885, lectotype; A, C — original drawing by McIntosh (1885, Pl. 45, Fig. 1).

A — in dorsal view; C — anterior end, ventral view, enlarged (and inverted); Lectotype: B — complete specimen (notice the reduced size of anterior end and the body twisting); D — anterior end, ventral view; notice the reduced size of the trifid organ (rto — right, lto — left), and the lack of any well-defined epistomal membranes. Scales: B — 2 mm; D — 500 μ m.

Рис. 1. *Buskiella abyssorum* McIntosh, 1885, лектотип; A, C — оригинальный рисунок МакИнтоша (McIntosh, 1885, Pl. 45, Fig. 1).

A — общий вид со спины; C — передний конец, вид спереди; B, D — тот же экземпляр, фото. B — общий вид (передний конец меньше по размеру, чем на рисунке; тело перекручено); D — передний конец, вид спереди; трехраздельный орган меньше, чем на рисунке (rto — правый, lto — левый), нет никакой мембраны надо ртом. Масштаб: B — 2 мм; D — 500 мкм.

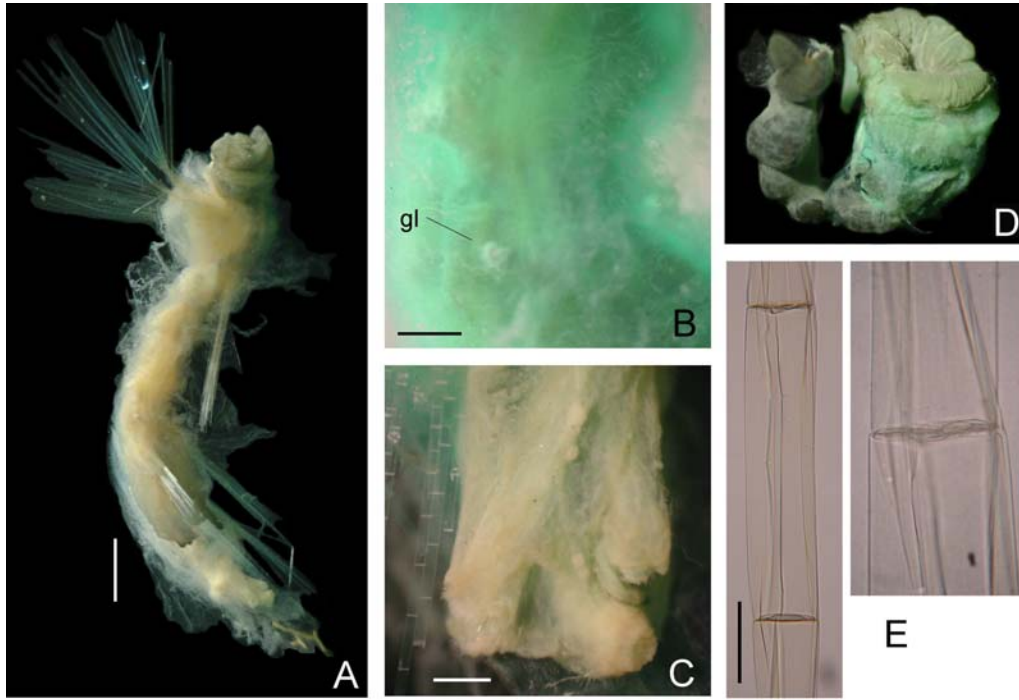


Fig. 2. *Buskiella abyssorum* McIntosh, 1885, lectotype.

A — entire animal, ventral view showing the reduced number of chaetigers and body distortion; B — chaetigers 3–4, ventral view, showing gonopodial lobes (gl); C — posterior end, ventral view; notice the swollen ventral ganglionic sites, and the muscular elevated anus, as well as some chaetae; Same, paralectotype: D — pharynx and stomach from another paralectotype; E — another paralectotype, multiarticulated chaetae and details of articulation (note the lateral constriction). Scales A — 500 μ m; B — 125 μ m; C — 63 μ m; D — 18 μ m.

Рис. 2. *Buskiella abyssorum* McIntosh, 1885, лектотип.

А — общий вид с брюшной стороны; В — щетинконосные сегменты 3–4, вид с брюшной стороны, видны гоноподияльные лопасти (gl); С — задний конец, вид с брюшной стороны; видны выступающие ганглии брюшной нервной цепочки, мускулистый пигидий, щетинки; D — паралектотип, глотка и желудок; E — другой паралектотип, членистые щетинки и детали сочленения. Масштаб: А — 500 мкм; В — 125 мкм; С — 63 мкм; D — 18 мкм.

Parapodia well developed, lateral, rounded muscular lobes; median neuropodia ventrolateral. Noto- and neuropodia fused almost completely, chaetal lobes flat, long. Median notochaetae arranged in a short tuft, folded over the body, oblique to body axis. All notochaetae very long, multiarticulated capillaries, median articles very long (3–4 times longer than wide), becoming longer distally, about 20 chaetae per bundle, 2–3 times longer than body width (most broken). Neurochaetae all multiarticulated capillaries, slightly thicker than notochaetae, arranged in a curved line, about 10 per bundle; all with long articles (Fig. 2E).

Posterior end damaged, almost separated from the remainder of the body, with smaller parapodia (Fig. 2C); pygidium slightly swollen, anus terminal, no anal cirri.

REMARKS. *Buskiella abyssorum* McIntosh, 1885 resembles *B. flabelligera* (Hartman, 1967) n.

comb. Their main difference relies on the shape of their gonopodial lobes; thus, they are digitate in *B. abyssorum* but in *B. flabelligera* they are cirriform and tapering.

A lectotype is herein designated because it was the only complete specimen in the type series, despite the fact of being distorted and having a much damaged left trifold organ; most syntypes are in poor condition, being either fragments or pieces of the digestive system. After ICZN (1999, Art. 74, Recomm. 74B), the lectotype has been selected based upon the original description and illustration. The paralectotypes (BMNH-McIntosh coll. 1921.5.1. 2657) include very long fragments (up to 97 mm). Since the lectotype is complete with 9 chaetigers (32 mm long), and a paralectotype is much longer with 11 chaetigers (73 mm long), with very long posterior chaetigers, there is a variable degree of contraction if both specimens had a similar size when alive.

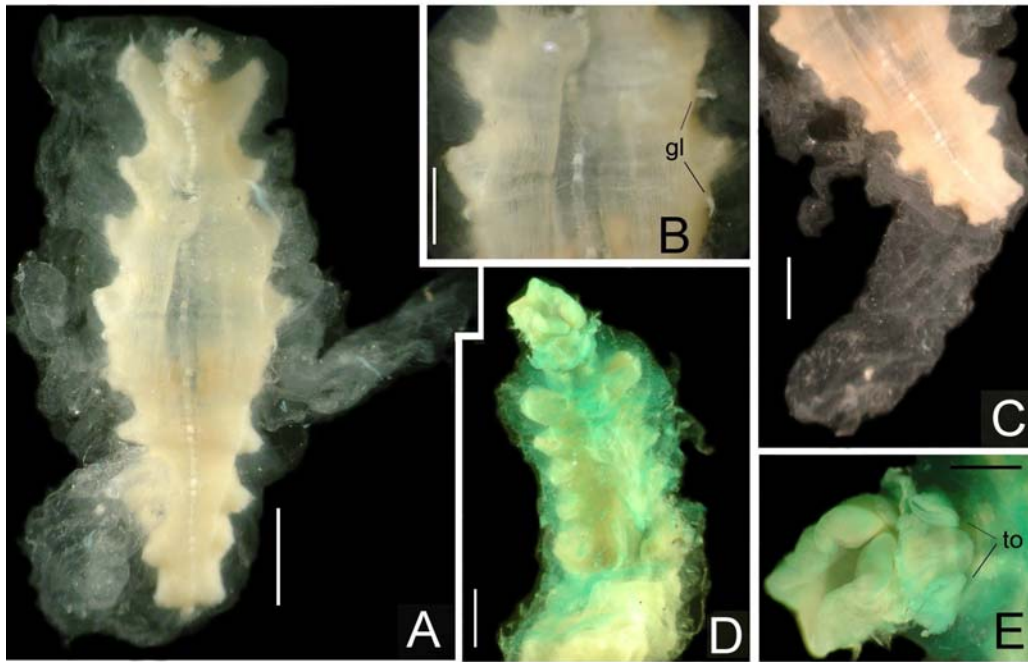


Fig. 3. *Buskiella flabelligera* (Hartman, 1967), comb.n., holotype.

A — ventral view, notice the large tunic and the breakage of the muscular body wall in chaetigers 3–5; B — same, chaetigers 3 and 4 enlarged showing gonopodial lobes (gl); C — same, posterior end, with tunic unfolded to show its original length; paratype: D — anterior fragment in dorsal view with everted pharynx, previously stained with methyl green; notice the more or less parallel body sides; E — same, close up of the anterior end showing the paired trifold organ (to) and the pharynx. Scales: A — 4 mm; B–D — 2 mm; E — 1 mm.

Рис. 3. *Buskiella flabelligera* (Hartman, 1967), comb.n., голотип.

A — вид с брюшной стороны, видна туника, стенка тела разорвана в районе 3–5-го сегментов; B — тот же экземпляр, щетинконосные сегменты 3 и 4, видны гоноподальные лопасти (gl); C — тот же экземпляр, задний конец, туника расправлена; D — паратип, передний конец, вид со спины, глотка вывернута, окраска метиленовым зеленым; видно, что края тела более-менее параллельны; E — тот же экземпляр, передний конец с парным трехраздельным органом (to) и глоткой. Масштаб: A — 4 мм; B–D — 2 мм; E — 1 мм.

The only other specimens of this species were recorded by Fauvel (1916). However, only one specimen deposited in the Monaco collections belongs in this species. The other anterior fragments belong to a typhloscolecid, close to *Travisioopsis*. It resembles *T. lumbricoides*, as recorded and illustrated by Støp-Bowitz (1992: 100–101, Fig. 36), by having globose parapodial cirri, but the anterior end is too damaged, and it is posteriorly tapered, not blunt. However, the Støp-Bowitz's record differs in several relevant morphological features (body shape, segment shape, and parapodial cirri) from *T. lumbricoides* Reibisch (1895: 57–57, Pl. 5, Figs 10–12). It might belong in another genus. Further, the specimens studied by Fauvel (1916) have finely papillate basal rings in the everted pharynx, and the frilled nuchal organ; the palpode is missing, probably after Fauvel's examination.

DISTRIBUTION. Abyssal waters in the central equatorial and northern Atlantic Ocean.

Buskiella flabelligera (Hartman, 1967),
comb.n.

Figs 3, 4, 6, 7.

Flota flabelligera Hartman, 1967: 125–127, Pl. 38.

TYPE MATERIAL. Southeastern Pacific Ocean. Holotype of *Flota flabelligera* (USNM-55548), and paratypes (USNM-55549), collected off Southwestern Chile, RV Eltanin, Stat. 190 (34°46'–35°05' S, 74°53'–74°29' W), 2891 m, 30.VIII.1962.

ADDITIONAL MATERIAL. One specimen (DIZM-SU-unnumb.) without collection locality information, perhaps collected off Chile.

REDESCRIPTION. Holotype complete (Fig. 3A), distorted, fusiform, mid-ventral body wall bro-

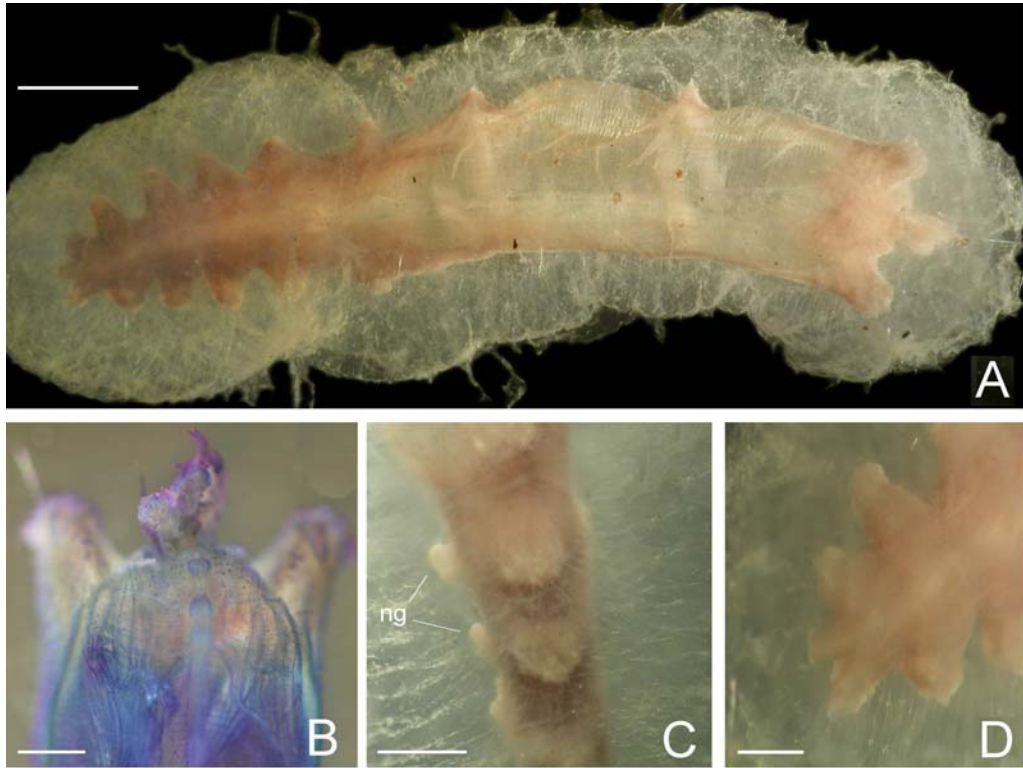


Fig. 4. *Buskiella flabelligera?* DIZMSU.

A — complete specimen in dorsal view, showing widened tunic and many elongate filiform papillae running through it, as well as thin circular muscle bands in the body wall; B — anterior end, ventral view, tunic removed, showing an impaired tridentate organ and ventral nerve ganglia (methyl blue staining), as well as two bundles of longitudinal muscles; C — posterior segments, lateral view, notice the papillae projecting from parapodia and globular exposed nerve ganglia (ng) on the ventral (left) side (due to body contraction); D — posterior end, dorsal view showing pygidium, parapodia and papillae in posterior segments. Scales: A — 1.5 mm; B–D — 370 μ m.

Рис. 4. *Buskiella flabelligera?* КЗБМГУ.

A — общий вид со спины, видна толстая туника и проходящие сквозь нее многочисленные нитевидные папиллы, стенка тела с тонкими кольцевыми мышечными волокнами; B — передний конец, вид с брюшной стороны, туника удалена, виден непарный трехраздельный орган, ганглии брюшной нервной цепочки и два пучка продольной мускулатуры (окраска метиленовым синим); C — задние сегменты, вид сбоку, видны папиллы, отходящие от параподий, и выступающие ганглии (ng) на брюшной стороне; D — задний конец, вид со спинной стороны, виден пигидий, параподии и папиллы на последних сегментах. Масштаб: A — 1,5 мм; B–D — 370 мкм.

ken by contraction (Fig. 3B), dorso-ventrally flat; body pale throughout, surface smooth, with a transparent thick tunic, without sediment particles, posteriorly elongated, without foreign particles; 22 mm long, 8 mm wide (excluding the tunic), most chaetae broken, 9 chaetigers.

Anterior end damaged in holotype. Cephalic hood as a short narrow tube with a single ring; margin smooth. Prostomium low cone. Tridentate organ paired, sessile (Fig. 3D, E), all lobes of about the same length; lateral lobes thin, middle one twice as wide as laterals. Dorsal lip short, lateral lips muscular, thick; ventral lip not seen. Pharynx thick (Fig.

3A, D, E), with small tubercles ventrally, internal surface smooth, connecting to a dark stomach.

First chaetiger larger than the rest; chaetae broken (Figs 3A, D). Length of chaetae in relation to total body length unknown. Chaetae in a tuft; only about three neurochaetae basis left, much thicker than notochaetal bases. Chaetiger 2 smaller, more ventrally directed. Posterior chaetigers larger, decreasing in size posteriorly. Ventral gonopodial lobes cirriform, tapering, in the posterior margin of chaetigers 3 and 4 (Fig. 3B).

Parapodia well developed, lateral, conical, truncate muscular lobes; median neuropodia ventrolater-

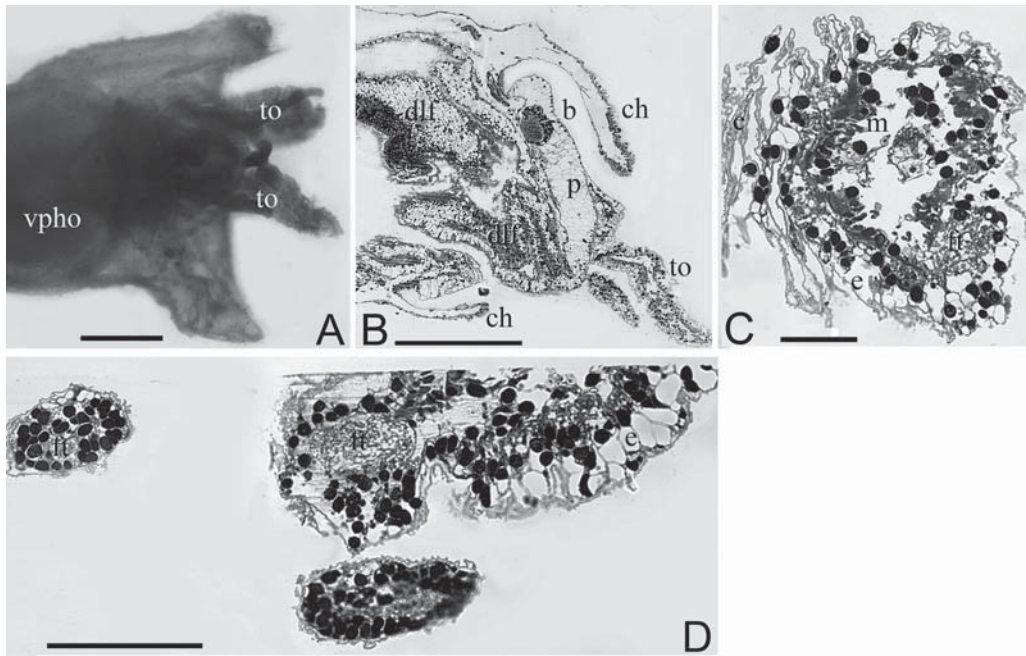


Fig. 5. *Buskiella abyssorum* McIntosh, 1887, SIORAS, light microscopy.

A — anterior end in ventral view, tunic removed, ventral pharyngeal organ visible through the body wall; B — same, parasagittal semi-thin section showing the anterior end appendices and ciliated glandular dorso-lateral folds covered by mucus (the frontal ones possibly eversible) are seen in the pharynx cavity; C–D — trifold organ, transversal semi-thin section: C — median part; D — median and two lateral parts (b — brain; ch — cephalic hood; dlf — dorso-lateral folds; e — epithelium; ft — fibrous tissue; m — muscles; p — prostomium; to — trifold organ; vpho — ventral pharyngeal organ). Scales: A, B — 500 μ m; C — 50 μ m; D — 100 μ m.

Рис. 5. *Buskiella abyssorum* McIntosh, 1887, ИО РАН, световая микроскопия.

A — передний конец, вид с брюшной стороны, туника удалена, сквозь стенку тела виден вентральный фарингеальный орган; B — тот же экземпляр, парасагиттальный полутонкий срез передней половины тела, виден трехраздельный орган, в глотке расположены реснично-железистые дорсо-латеральные лопасти, покрытые слизью (передние лопасти, вероятно, могут выворачиваться); C–D — трехраздельный орган, поперечный полутонкий срез: C — средняя лопасть; D — средняя и две боковые лопасти (b — мозг; ch — головной капюшон; dlf — дорсо-латеральные лопасти; e — эпителий; ft — волокнистая ткань; m — мышцы; p — простомий; to — трехраздельный орган; vpho — вентральный фарингеальный орган). Масштаб: A, B — 500 мкм; C — 50 мкм; D — 100 мкм.

al. Noto- and neuropodia fused (chaetal fascicles inside the parapodia reveal the external fusion). Median parapodia with notochaetal basis arranged in lateral tufts. Most chaetae broken; companion capillary chaetae distally articulated. Chaetal size unknown. Median neuropodia lateral. Neurochaetae only 2–3 left, few multiarticulated large chaetae per ramus; arranged as a tuft (revealed by cross section of parapodia).

Posterior end as a short tube (Fig. 3C), contracted (indicated by very long tunic remains); pygidium with anus terminal, without anal cirri.

REMARKS. The holotype of *Buskiella flabelligera* (Hartman, 1967) comb.n., is distorted by contraction; the mid-ventral body wall muscles are broken. It is most similar to *B. vitjasi* (Buzhinskaya

1977), comb.n., but *B. flabelligera* has a shorter cephalic hood, gonopodial lobes in chaetigers 3 and 4, not only in chaetiger 4, and the lateral lobes of its trifold organ are attached basally, over the anterior end, instead of being fixed over the median lobe (“pedunculate”) as in *B. vitjasi*. Further, *B. flabelligera* differs from *B. abyssorum* by the relative shape of the gonopodial lobes, being cirriform and tapering in *B. flabelligera*, and digitate in *B. abyssorum*. The most noticeable difference is the relative number of chaetae per fascicle, with *B. abyssorum* provided with abundant chaetae, while *B. flabelligera* has just few chaetae. However, this difference is likely to be due to some damage during sampling since in both species, the chaetal bases in parapodial lobes are very abundant. Other differences in relative body

shape and distortion are can be probably attributed to the type of collecting gear, as use of a plankton sampler seems to result in more significant damage of specimens, such as almost complete lack of chaetae in *B. flabelligera*.

The specimen without collecting information is tentatively attributed to this species, but because of this uncertainty we include here its main morphological features. The body is short, tapering posteriorly, encased in a semi-transparent thick tunic, without sediment particles (Fig. 4A); 12 mm long, 2.3 mm wide (excluding the tunic), with nine segments, probably all chaetigers. The epithelium is thin, transparent, wrinkled in the anterior region, and covered by abundant long, filiform papillae with one or two bulges (Fig. 4C, D). Longitudinal, oblique and circular muscles are visible through the cover.

Cephalic hood short. Prostomium inverted into the tunic, not seen. Trifid organ sessile; only right part remains (Fig. 4B). Its median branch is short, rounded, lateral branches twice as long and thinner, stemming from the ventral side of the base. All might be long structures but much contracted after fixation.

First chaetiger with most chaetae lost, companion chaetae visible by SEM (Fig. 7A, B); first chaetiger larger with a very thick chaetal lobe. Epithelium in anterior part wrinkled. Length of chaetae in relation to total body length unknown. Multiarticulated chaetae with articulation surface concave (one companion distally articulated chaetae fixed over it) (Fig. 7C). Companion notochaetae in a S-shaped pattern, neurochaetae in short transversal line (Fig. 7A,mB).

Second chaetiger as long as first one, third slightly shorter, subsequent segments short. Parapodia well-developed as long truncate conical muscular lobes, much contracted after fixation. Noto- and neuropodia almost completely fused. Posterior end as a short

tube (Fig. 4D); pygidium with anus terminal, without anal cirri.

Ventral nerve chord subepithelial, prominent above body wall (Fig. 4C), contains two paired ganglia per segment, excluding first and last segments. Three ganglia in the first segment, one pair seen near base of circum-oesophageal connectives (Fig. 6A), and one ganglion in last segment.

DISTRIBUTION. Off NW Concepcion, Chile, to Cape Horn, in 2800–4110 m, abyssopelagic.

Buskiella vitjasi (Buzhinskaya, 1977),
comb.n.

Flota vitjasi Buzhinskaya, 1977: 9–12, Figs 1, 2.

TYPE MATERIAL (Buzhinskaya 1977: 12). Northwestern Pacific Ocean: Holotype ZIRAS-43261, R/V 'Vityaz' (43°40' N, 149°31' E), 1.VII.1953, 6000 m, and paratype ZIRAS-43262, 46°11' N, 154°56' E, 23.V.1953, 4000 m. No type specimens available for examination; the re-description is based on translated and modified original description. Also two specimens in ZIRAS were not examined; both previously identified as *Planctoflabelligera pacifica* n. gen., n. sp. by Uschakov (R/V 'Vityaz', ZIRAS-11651: 5,760 m, 51°46.2' N, 161°48.2' E, and ZIRAS-11652: 5,700–0 m, 38°18.4' N, 143°55.0' E).

DESCRIPTION. Modified from Buzhinskaya (1977: 9–12). Holotype and paratype light brown, flat, with thick transparent tunic, penetrated by papillae. Tunic wrinkled; oblique skin folds on dorsum of each segment; similar folds ventrally on first and second segments. Papillae short, almost globular, or long-stalked, some medially swollen, penetrating tunic; 20–30 mm long, 4–8 mm wide, 9 chaetigers.

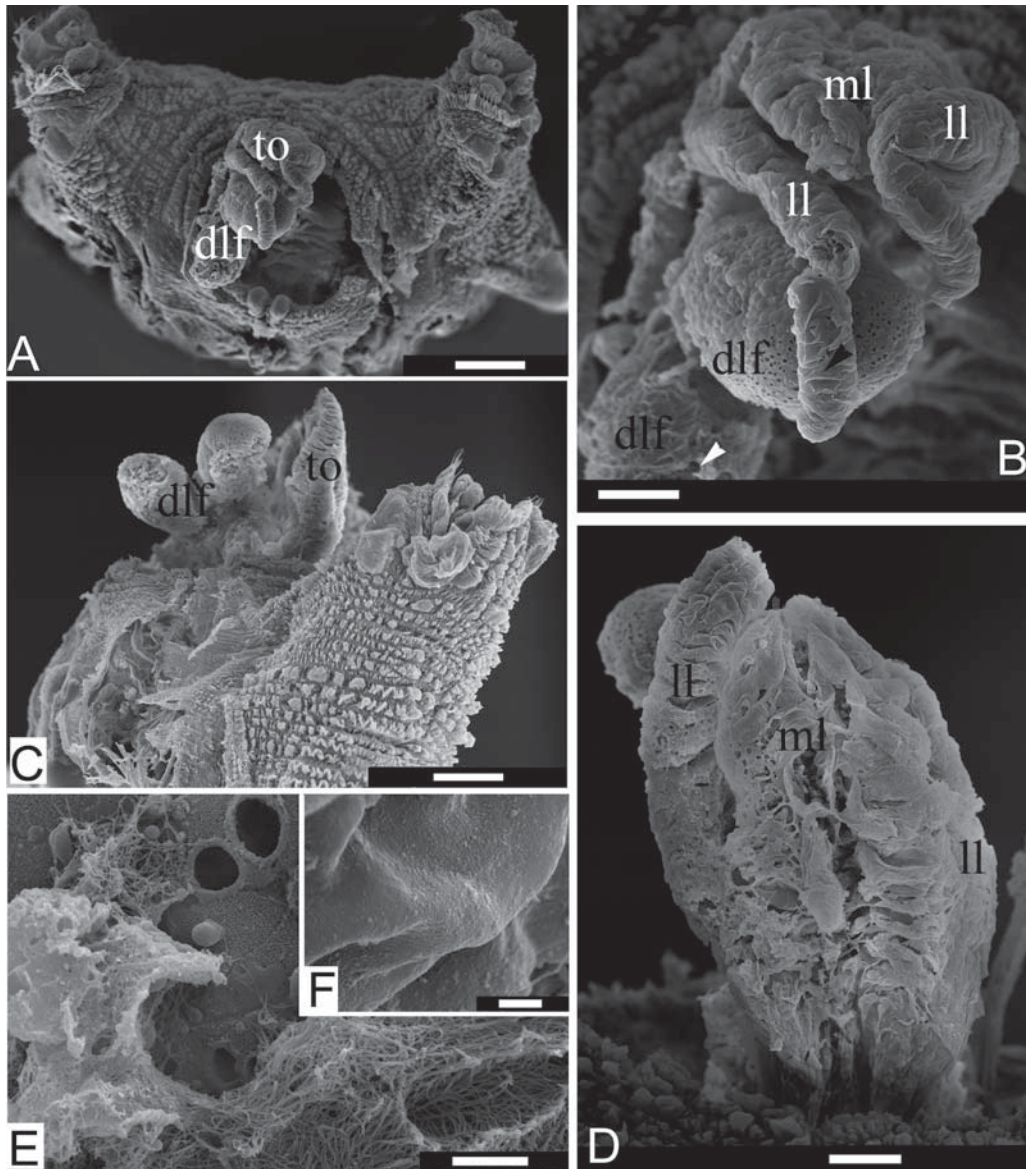
Prostomium round with paired trifid organs. Median lobe longer than lateral ones, all of about the same width. Peristomium elongated, forming a neck zone. First chaetiger enlarged, with thin transverse

Fig. 6. *Buskiella flabelligera*? DZIMSU: SEM.

A — anterior end in frontal view, tunic removed; notice the impaired (right) trifid organ, two everted dorso-lateral folds and enlarged first chaetiger, directed dorsally; B — same, close-up of the trifid organ and dorso-lateral folds; white arrowhead indicates enlarged area in E, and black arrowhead indicates enlarged area in F below; C — same as A, lateral view; D — trifid organ, dorsal view; E — ciliated — glandular epithelium of dorso-lateral folds; a thick mucous layer remains on the cilia, and large gland openings in the background; F — close-up of the epithelium of the lateral lobe of the trifid organ, notice that both cilia and gland openings are missing (dlf — dorso-lateral folds; ll — lateral lobe of the trifid organ; ml — median lobe of the trifid organ; to — trifid organ). Scales: A, C — 300 μm; B, D — 100 μm, E — 10 μm, F — 3 μm.

Рис. 6. *Buskiella flabelligera*? КЗБМГУ: СЭМ.

A — передний конец, вид спереди, туника удалена; виден непарный (правый) трехраздельный орган, две вывернутые дорсолатеральные лопасти и параподии первого сегмента, смещенные дорсально; B — тот же препарат, трехраздельный орган и дорсолатеральные лопасти; белая стрелка показывает увеличенный участок на фото E, черная стрелка показывает увеличенный участок на фото F; C — то же, что A, вид сбоку; D — трехраздельный орган, вид со спины; E — реснично-железистый эпителий дорсо-латеральных лопастей; на ресничках остался толстый слой слизи, видны крупные отверстия желез; F — эпителий латеральной лопасти трехраздельного органа, реснички и отверстия желез отсутствуют (dlf — дорсо-латеральная лопасти; ll — латеральная лопасть трехраздельного органа; ml — медиальная лопасть трехраздельного органа; to — трехраздельный орган). Масштаб: A, C — 300 мкм; B, D — 100 мкм, E — 10 мкм, F — 3 мкм.



brown bands. Parapodia biramous, first chaetiger directed forward, others directed laterally. All chaetae fragile transparent with long submerged ends, about 25 chaetae per bundle. All chaetae multiarticulated, most broken, articles longer basally, shorter distally; companion chaetae capillary, thinner, slightly emerging in each chaetiger lobe. In larger specimen chaetae remain in segments II, V, VI, VII; 12–13 chaetae per bundle, about 14 mm long, exceeding body width (including tunic). Gonopodial lobes in posterior margin of chaetiger 4, digitate. Posterior end cylindrical, anus terminal.

REMARKS. The original description of *Buskiella vitjasi* (Buzhinskaya, 1977) comb.n., was modified by Buzhinskaya (1996, 2006) to include oral tentacles. She stated that the pharynx has two groups of thin tentacles, attached dorso-laterally; each tentacle is hollow with a longitudinal ciliated groove. Specimens from which these tentacles were originally described were not available for this study and thus, their presence and nature could not be confirmed. No such tentacles were found on the examined specimens belonging to other species. Among the paratypes of *Buskiella flabelligera* (Hart-

man), there is only one small specimen with some filaments coming out of the mouth, but the anterior end is slightly damaged, and they look more like muscle fibers, not tentacles. Since none of the other specimens with everted pharynx had any such filaments, this cannot be regarded as a reliable feature for the species.

Other details (Buzhinskaya, 1996, 2006) were given for the feeding apparatus and nervous system. The trifold organ, which she called palps, was described as lacking a ciliated groove, and containing “large blood vessels, and probably performs respiratory and sensory functions.” Another peculiarity is very large ventral pharyngeal organ resembling bursa with pair of salivary glands at the posterior boundary. For the nervous system, she noticed three pairs of large ganglia on circumesophageal connectives, and then two pairs of segmental ganglia, each with a well-defined border between them. In addition to the whole nerve chord, there are smaller ganglionic bulges between each group of segmental ganglia. The original species name was made after regarding the ship’s name as a masculine noun, which might be incorrect since a vessel is a feminine in Latin, but this usage is followed herein.

DISTRIBUTION. Described from 4.000–6.000 m depth, off Kuril-Kamchatka trench, northwestern Pacific Ocean.

The trifold organ

Figs 5–7.

LIGHT MICROSCOPY. In *B. abyssorum* SIO-RAS specimen, both trifold organs are present (Fig. 5A), each with tapering lobes and the median lobe larger, twice as wide and long as the others. The lateral lobes are borne over the ventral base of the median lobe. The histological sections show that the cephalic hood is better developed dorsally, the prostomium wall consists of large polygonal vacuolated cells, and the trifold organ may be hollow (Fig. 5B). No nuchal organs were found.

The fine structure of the trifold organ (Fig. 5C, D) shows that the epithelium consists of highly vacuolated supportive cells with relatively large, dark nuclei, covered by a folded cuticle. Cilia or glandular cells were not observed. Under the epithelial layer, circular and longitudinal muscle bands are located. No blood vessels were found but some hollow areas may be indirect evidence for them. Between the epithelium and the muscle layers, some fibrous (or nerve) tissue is located subcentrally. The central part of the trifold organ lobes are hollow. The lateral lobes differ from the median by having smaller epithelial cells, by a reduced development of the musculature and inner cavity, and a higher proportion of fibrous tissue which occupies most of the cavity.

SEM. In what we have regarded as *B. flabelligera*, the trifold organ is sessile and only the right part remains (Fig. 6A). The median lobe is short and rounded, while the lateral lobes are twice as long and thinner, extending ventrally from the base (Fig. 6D). They all seem to be long structures but are shortened by contraction, probably due to fixation. Two rounded lobes (presumably everted dorso-lateral folds) are situated ventrally to the trifold organ (Fig. 6B, C). Their surface is ciliated, with numerous openings of glands (6–8 μm in diameter); however, the epithelium covering the trifold organ is smooth, covered by a folded cuticle (Fig. 6F).

There are few detailed studies on the anatomical features of the flabelligerids anterior end. Spies (1975, Pls. 4–5) included some histological sections of the head appendages of *Flabelliderma* Hartman, 1969, and Gardiner (1988, Fig. 2.1D) provided some details on the branchial features of an unidentified flabelligerid (*Piromis?*). Thus, palps have a ciliated longitudinal furrow, and branchiae have abundant cilia and blood vessels. Since these features are not present in the trifold organs, they cannot be regarded as either palps or branchiae. However, trifold organs might have respiratory functions, just like coelobranchiae, since they have a hollow core. The trifold organs may yet be homologous with palps or branchiae but the function would have changed significantly enough to modify the features considered typical of each. The presence of fibrous tissue that may be nervous tissue, suggests the trifold organ may function in a sensory capacity. Histological works with TEM using better preserved specimens are necessary to determine the nature of this structure, as well as the homology of the trifold organ could be established by studying its innervation and early development.

Paired trifold non-ciliated appendages (“peribuccal tentacles”) are present in Alvinellidae Desbruyères & Laubier, 1980¹. Alvinellid trifold organs are found on the anterior end, together with numerous grooved tentacles. Each trifold organ is made of foliose projections and the lateral ones are marginally papillose; thus, differing from those found in flotids. Zal *et al.* (1994: 43, Fig. 1A), Jouin-Toulmond *et al.* (1997), and Zhadan *et al.* (2000) have indicated that they are restricted to males. Alvinellid trifold organs have been recorded in *Paralvinella grasslei* Desbruyères & Laubier (1982: 487, Fig. 1B,D; Desbruyères &

¹ This paper includes the proposal of Alvinellinae as a new subfamily (p. 268); after the Principle of Coordination in the family group—ICZN, 1999, Art. 36.1—this should be the date for the family as well. Holthe (1986: 112) used a previous report and gave 1979 as the publication date based upon another document; that report, however, may not be a formal publication for nomenclatural purposes and that would explain why the authors avoided including it in their references.

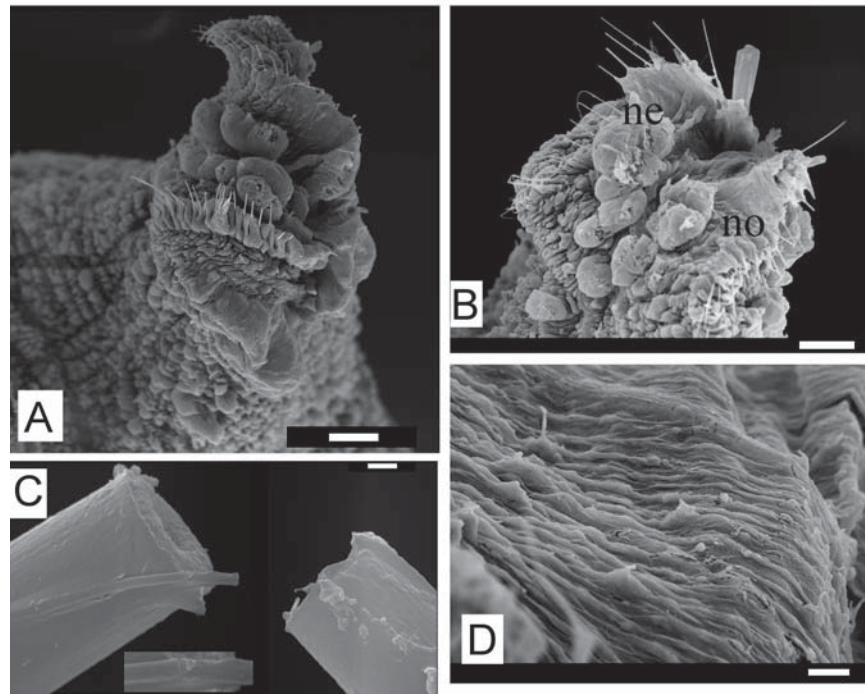


Fig. 7. *Buskiella flabelligera?* DZIMSU.

A — close up of the left parapodia from the first chaetiger, frontal view with notopodium above; thin filaments are companion chaetae; all annulated chaetae lost, their insertion sites are the fusiform depressions external to the companion chaetae; B — close up of the right parapodia from the first chaetiger, dorsal view; notice the mucus mass continued over the bases of companion chaetae, and a single base of a broken annulated neurochaeta; C — close-up of two fragments of a broken multiarticulate chaetae showing a smooth surface, and a broken articulate companion chaetae enlarged in insert (lack of a denticulated surface as in *Acrocirridae*); D — close-up of the ventral skin surface, notice the circular muscles project through the skin and base of damaged papillae (ne — neuropodium; no — notopodium). Scales: A, B — 100 μm ; C — 3 μm ; D — 30 μm .

Рис. 7. *Buskiella flabelligera?* КЗБМГУ.

A — левая параподия первого сегмента, вид спереди, нотоподия сверху; тонкие волокна — дополнительные щетинки; все членистые щетинки утрачены, места их прикрепления — веретеновидные углубления снаружи от дополнительных щетинок; B — правая параподия первого сегмента, вид со спины; видна слизь, покрывающая основания дополнительных щетинок, и сломанная членистая неврохета; C — фрагменты сломанной членистой щетинки, видно, что поверхность сочленения гладкая, а не зазубрена, как у *Acrocirridae*; на вставке — сломанная дополнительная щетинка (видно гладкое сочленение); D — поверхность тела с вентральной стороны, видны кольцевые мышцы и основания поврежденных папилл (ne — невроподия; no — нотоподия). Масштаб: A, B — 100 мкм; C — 3 мкм; D — 30 мкм.

Laubier, 1986: 2231, Fig. 7A–C), *P. palmiformis* Desbruyères & Laubier (1986: 2242, Figs 26–26), and *P. fijiensis* Desbruyères & Laubier (1993: 232, Fig. 5B). Other alvinellids may have single-lobed or bilobed non-ciliated organs; Desbruyères & Laubier (1993) have used their presence to separate subgenera of *Paralvinella*. Because of several rather marked differences between alvinellid and flotid trifid organs, these structures are herein regarded as a convergent feature.

According to Zal *et al.* (1994: 47), alvinellid trifid organs may play a role in pseudocopulation. We do not know whether studied *Buskiella* specimens are males or females, but trifid organs are present in all specimens. A reproductive role would be established by linking the gonads with the trifid organ, or by linking the trifid organs with a mechanical function during spawning or sperm transfer.

The trifid organs in flotids might need some internal support. Because there are hollow cells in

the *Buskiella abyssorum* epithelium, they might perform a supportive role, as it has been shown in Chaetopteridae where the tentacular epidermal cells may be occupied by a single large vacuole (Storch, 1988). No cartilaginous structures, such as those found in sabellids or other polychaetes, were found (Tovar-Hernández and Sosa-Rodríguez, 2006).

Dorsolateral ciliary folds are present in many polychaete families; they mostly occur as a pair of lateral eversible ciliary fields (Purschke & Tzetlin, 1996; Tzetlin & Purschke, 2005). These features have not been recently studied in flabelligerid polychaetes, but both Costa (1841: 278, Pl. 12, Fig. 2a), and Claparède (1869: 101, Pl. 25, Fig. 1) mentioned them. However, they found three eversible ciliated lobes in *Stylarioides monilifer* delle Chiaje (although the former renamed it as *Lophiocephala*); Costa called them antennae and Claparède called them “languettes ciliees”. We have noticed that the dorsolateral ciliary folds are also present in flatidids. However, the use of dorsolateral ciliary folds for microphagous feeding is only present in small epibenthic or interstitial species, or in juveniles of larger species. In the latter, some other types of microphagous feeding structures such as tentacles, and non-muscular axial proboscis, develop later during ontogeny (Tzetlin & Purschke, 2005). In *Buskiella*, these folds are eversible but relatively small, and it would be hardly useful for microphagous feeding in abyssopelagic layers. Thus, the more probable feeding modes are either forming a mucus net, macrophagy, or a combination of both.

Buzhinskaya (1996) suggested that the oral tentacles might produce a water flow and catch small food particles, while the ventral organ is used to catch larger particles. She supposed a combined breathing and sensory role for the trifid organ, and that the unique features in the nerve cord were connected with an intensification of the locomotion due to the transition to pelagic life. It has been shown that *Poebius* is neutrally buoyant and feeds by deploying a mucous net which, once it had accumulated some falling particles, it pulls into its mouth (Uttal & Buck, 1996: 335–336). The presence of developed eversible ciliated-glandular dorso-lateral folds in *B. flabelligera* and *B. abyssorum* may indicate a similar way of feeding. In this case, the trifid organs might be used for holding and manipulating the mucus net.

In comparison with *Poebius*, *Buskiella* has much better developed parapodia and has elongate chaetae, which might make it a better swimmer, although some direct observations indicate it is not a strong swimmer (K. Osborn, P. Batson pers. comm.). Further, the combination of a thick pharynx and dark stomach that might block potential ingested prey bioluminescence, would imply a predatory behavior, since this combination is also present in some other

bathypelagic animals. If this suggestion is eventually confirmed, it would explain the presence of some tentacles in the pharynx of *B. vitjasi*.

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