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Redescription of *Polarsternium plumosum* (Ivanov, 1957) comb.n. (Annelida: Siboglinidae), with a taxonomic key to the species of the genus

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ABSTRACT: *Siboglinum plumosum* Ivanov, 1957 was originally described from a single specimen, the holotype collected in the Sea of Okhotsk at a depth of 194 m. Since then, the species has been repeatedly reported from the same and adjacent regions at depths of 119–387 m, but no data on its morphological variability have been available. Moreover, published information suggests that the holotype is highly incomplete and the original description contains major gaps. In this study, both the holotype of *S. plumosum* and several specimens from material recently collected near the type locality in the Sea of Okhotsk have been examined. These specimens lack papillae in the anterior (metameric) region of the trunk, bearing instead two continuous epidermal-muscular ridges. Multicellular glands in each ridge are arranged in at least two rows, increasing to 4–5 rows in the anteriormost portion of the trunk. This combination of characters does not fit the generic diagnosis of *Siboglinum*, but fully conforms to the diagnostic characters of *Polarsternium*. Consequently, the new combination *Polarsternium plumosum* (Ivanov, 1957) is proposed, with a full redescription of the species and illustrations of its morphological characters. The diagnosis of the genus *Polarsternium* is emended, key characters of all known species of the genus are summarised in a table, and an identification key to these species is presented for the first time.
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KEY WORDS: Pogonophora, morphology, systematics, identification key, *Siboglinum*, Sea of Okhotsk.

Переописание *Polarsternium plumosum* (Ivanov, 1957) comb.n. (Annelida: Siboglinidae) с определительным ключом для видов рода

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РЕЗЮМЕ: *Siboglinum plumosum* Ivanov, 1957 был первоначально описан по единственному экземпляру — голотипу, собранному в Охотском море на глубине 194 м. С тех пор вид неоднократно отмечался в этом же и смежных районах на глубинах 119–387 м, однако данные о его морфологической изменчивости отсутствуют. Более того, опубликованные данные свидетельствуют о крайней неполноте голотипа и наличии

существенных пробелов в первоначальном описании. В настоящем исследовании были изучены как голотип *S. plumosum*, так и несколько экземпляров из материала, недавно собранного вблизи типового местонахождения в Охотском море. У этих экземпляров отсутствуют папиллы в передней (метамерной) части туловища, вместо них имеются два сплошных эпидермально-мускульных валика. Многоклеточные железы в каждом валике расположены как минимум в два ряда, увеличиваясь до 4–5 рядов в самой передней части туловища. Эта комбинация признаков не соответствует родовому диагнозу *Siboglinum*, но полностью соответствует диагностическим признакам *Polarsternium*. В связи с этим предлагается новая комбинация *Polarsternium plumosum* (Ivanov, 1957) с полным переописанием вида и иллюстрациями его морфологических признаков. Диагноз рода *Polarsternium* исправлен, ключевые признаки всех известных видов рода сведены в таблицу, и впервые представлен определительный ключ для этих видов.
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КЛЮЧЕВЫЕ СЛОВА: Pogonophora, морфология, систематика, определительный ключ, *Siboglinum*, Охотское море.

Introduction

Siboglinidae Caullery, 1914 also known as Pogonophora, is a small group of sessile, predominantly deep-sea annelids first discovered over a century ago. Their most distinctive features are the absence of a digestive tract, reliance on endosymbiotic nutrition, occurrence in hydrogen sulphide- and methane-rich habitats, and a complex taxonomic history. All members of this group are currently classified within a single family, Siboglinidae, under the annelid subclass Sedentaria (Rousset *et al*., 2004; Struck, 2019), but, in our view, this classification does not adequately reflect the true ingroup diversity of pogonophorans. A number of internal lineages, formerly recognized as separate taxa ranging from families to subclasses (Ivanov, 1963, 1991, 1994 and others), have now lost their formal taxonomic status, despite being morphologically identifiable and recoverable through cladistic analyses (Schulze, 2003). A recent attempt to address this problem for vestimentiferans (Karaseva *et al.*, 2016) has resulted in the proposal to introduce infra- and subfamilial ranks into the taxonomy of Siboglinidae in general and vestimentiferans in particular. This approach, however, leads to an overly cumbersome system and is especially impractical for frenulate pogonophorans, where at least two taxonomic levels (families and orders) exist between the genera and the proposed higher taxon (subfamily Frenulata), both of which can be substantiated by morphological and cladistic data. Thus, for the purposes of description and comparative phylogenetic analysis of the pogonophoran taxonomic system, we prefer to continue using certain historically recognised taxa as clade names on the siboglinid phylogenetic tree.

The genus *Siboglinum* Caullery, 1914 currently comprises 72 species, accounting for more than half of all species within the clade Frenulata and approximately 30% of all siboglinids. This genus has the most complicated taxonomic composition among all siboglinid genera. *Siboglinum* belongs to the clade (formerly family) Siboglinidae s.str., whose principal diagnostic characters are the presence of more or less developed papillae, rather than continuous ridges, in the anterior trunk region and the arrangement of multicellular glands in this region in one or incipiently two irregular rows on each side of the dorsal furrow (Fig. 1). Despite their considerable morphological diversity, all *Siboglinum* species share one distinguishing trait — the presence of a single tentacle. The only other known single-tentacled genera, *Unibrachium* Southward, 1972 and *Polarsternium* Smirnov, 1999, belong to the oligobrachiid lineage and differ from *Siboglinum* in having continuous ridges and multiserial arrangement of multicellular glands in the anterior trunk region (Southward, 1972, 1975; Smirnov,

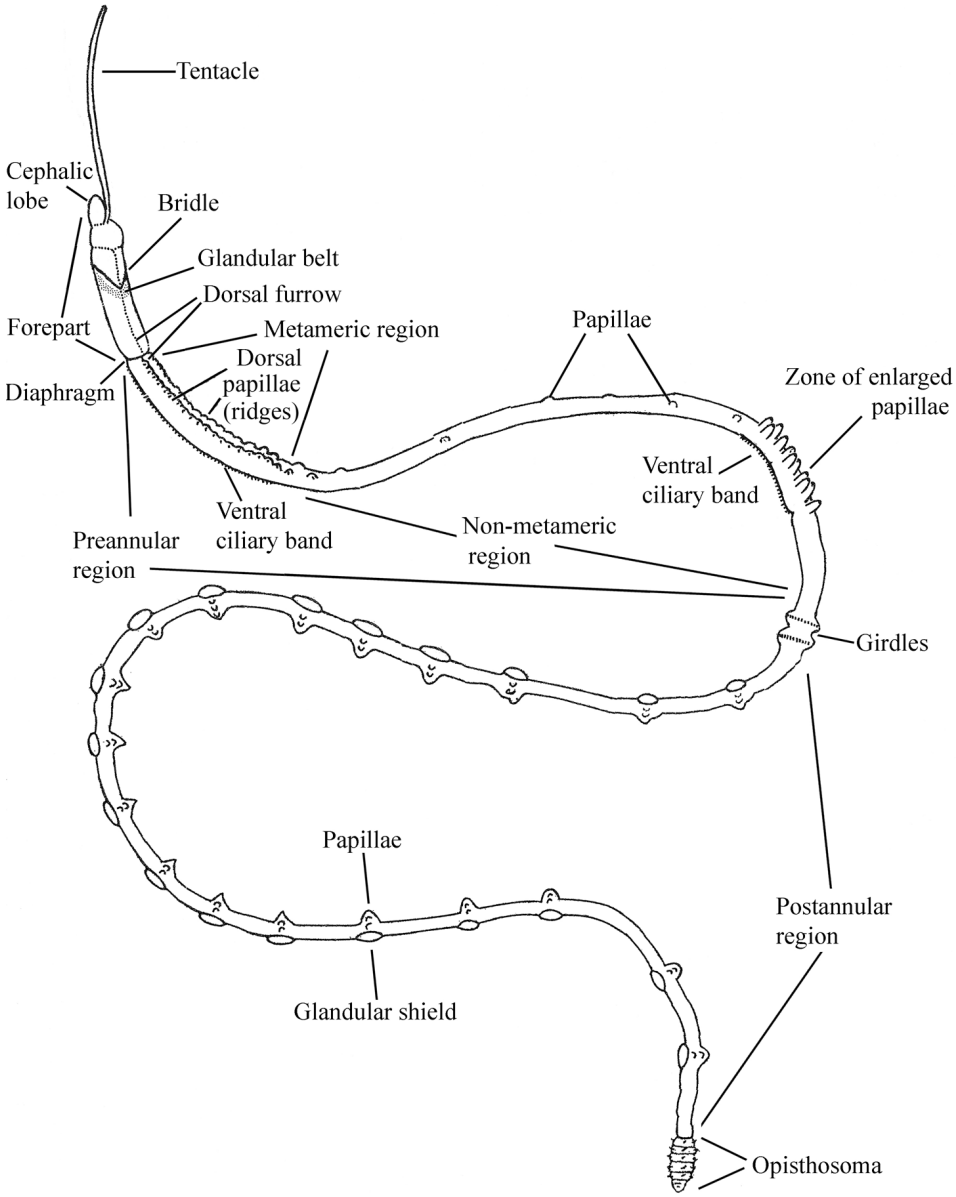

Fig. 1. Schematic view showing the general morphology and body regionalization pattern of *Siboglinum* species. Modifed from Southward (1980).

1999, 2005). Representatives of *Unibrachium* also exhibit several highly distinctive traits, including a unique structure of the bridle and cephalic lobe, an unusually elongated forepart, and a large body size. Species of *Polarsternium* most closely resemble typical representatives of the central oligobrachiid genus *Oligobrachia* Ivanov, 1957, except for the presence of a single tentacle, and they are readily distinguishable from those of *Siboglinum* in the morphology of the anterior trunk region. Five species of *Polarsternium* have been described to date, all having an exclusively polar distribution: one from the Arctic (Laptev Sea) and four from the Antarctic (Scotia Sea,

Weddell Sea, and adjacent areas of the Atlantic sector of the Southern Ocean).

Siboglinum plumosum Ivanov, 1957 was one of the many pogonophoran species described by A.V. Ivanov from the Sea of Okhotsk during the early period of research on this group. Since its original description, this species has been retained within the genus *Siboglinum*, distinguished from other congeners primarily by its large body size. However, the original description of the species was based only on a single incomplete specimen and two fragments of empty tubes, which left many aspects of its morphology unknown (Ivanov, 1957). Recently collected material from the Sea of Okhotsk has now filled most of the gaps in the original description and provides sufficient grounds for excluding this species not only from the genus *Siboglinum*, but also from the entire clade Siboglinidae s.str.

Material and methods

All available material of *S. plumosum* was examined, including the type specimen housed in the pogonophoran collection of the Zoological Institute of the Russian Academy of Sciences (ZIN RAS). Specimens were collected between 1949 and 2023 at six stations in the Sea of Okhotsk by the RVs *Vityaz*, *Akademik M.A. Lavrentiev*, and *Professor Multanovsky*, using "Ocean" and "Van Veen" grab samplers and a "Sigsbee" trawl, at depths of 119–387 m. In total, over 50 specimens and several dozen empty tubes were available for study.

The type material was initially fixed in 4% formaldehyde and subsequently transferred to 70% ethanol. Some of the remaining material was pre-treated with 7% $MgCl_2$, fixed in 4% formaldehyde in seawater at 4°C for 8–10 hours, rinsed three times and transferred to 70% ethanol.

For scanning electron microscopy (SEM), specimens were fixed in 4% paraformaldehyde in 0.1 M phosphate-buffered saline (PBS), rinsed in PBS, and stored in PBS containing 0.05% NaN_3. To examine fine surface structures, fragments of four specimens were cleaned of mucus on a shaker through two alternating incubations in 20% ethanol and 16% glycerol in ethanol (6–12 hours each). Following this treatment, samples were dehydrated through an ascending ethanol series (50–100%) and acetone, critical-point dried, mounted on stubs, and sputter-coated with platinum. SEM images were obtained using a Quanta 250 scanning electron microscope (FEI, Netherlands) and then processed using Adobe Photoshop CS2 (USA). Micrographs of whole animals and tubes were taken with an Olympus MVX 10 macroscope (Olympus, Tokyo, Japan). All collected material is deposited in the Zoological Institute of the Russian Academy of Sciences, St Petersburg, under voucher number ZIN HN1.

ABBREVIATIONS: ZIN RAS — Zoological Institute of the Russian Academy of Sciences; D_f — diameter of forepart; L_f — length of forepart; L_f/D_f — forepart length and diameter ratio; L_{cl}/D_f — cephalic lobe length and forepart diameter ratio; D_t — diameter of tentacle; D_t/D_f — tentacle and forepart diameters ratio; D_{tb} — diameter of tube; st — station; cr — cruise; RV — Research Vessel.

Results

Taxonomy

Family Siboglinidae Caullery, 1914
Genus *Polarsternium* Smirnov, 1999

Type species: *Polarsternium rugellosum* Smirnov, 1999 (redescribed Smirnov, 2005).

DIAGNOSIS. (modified after Smirnov, 1999, 2014a). Tentacle: 1. Cephalic lobe without funnel. Forepart short (L_f/D_f ~5.8); glandular epidermis, if distinguishable, forms belt posterior, sometimes also anterior, to bridle. Groove anterior to bridle, if present, circular. Multicellular glands on forepart usually visible in transmitted light. Bridle keels straight, narrow, occasionally thickened on dorsal body side. Glandular epidermal patches on trunk form bands flanking multicellular gland regions on muscular ridges and sometimes rings encircling duct openings of these glands. Chaetal girdles: 2 or 3. Spermatophores wingless, sometimes with additional filament. Tube usually pale and relatively transparent. Rings variable; interspaces between rings not concave.

Polarsternium plumosum (Ivanov, 1957) **comb.n.**
Figs 2–10; Table 1.

Siboglinum plumosum: 456–461, 491, 495–497, Figs 28–30, 5; type locality: Sea of Okhotsk; Ivanov, 1960a: 1607, 1612, 1613; Ivanov, 1960b: 5, 12, 14, 27, 92, 96, 105, 128, 134, 136, 140–142, 145, 196, 265, Figs 19, 87, 103, 104; Ivanov, 1963: 12–14, 29, 31, 121, 128, 142, 180, 189, 192, 197–200, 202, 299, 306, 459, Figs 19B, 103, 104; Smirnov, 2013: 76; Smirnov, 2014b: 52, 54, 55; Karaseva *et al.*, 2019: 2, 3, fig. 1; Karaseva *et al.*, 2020: 2, 3, Figs 2, 3; Skalon *et al.,* 2024: 1–10, Figs 1A, 2–4;

MATERIAL EXAMINED. **Type material**. RV *Vityaz*, 2 cr.; st. 110; 15.09.1949; Sea of Okhotsk east of Nabil Bay (Sakhalin Island) 52°N, 144°3′E; "Ocean" bottom grab; 194 m; mud; one specimen and two fragments of empty tubes. Holotype ZIN HN1. RV *Vityaz*, 12 cr.; st. 1892; 1952; Sea of Okhotsk; "Sigsbee" trawl; 318–342 m; mud; three empty tubes;

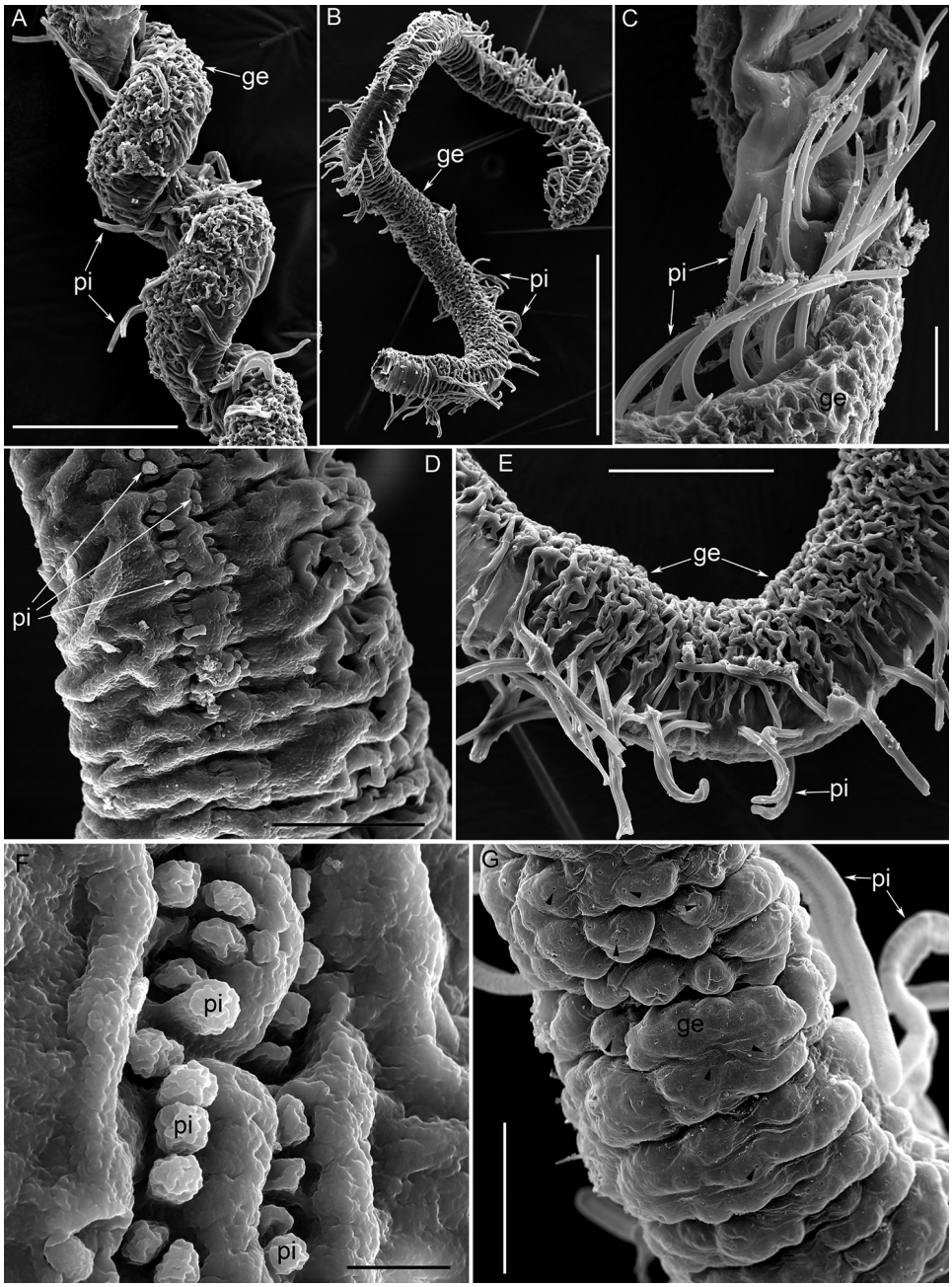

Fig. 2. *Polarsternium plumosum* comb.n. SEM micrographs of new material. A, B — tentacle, middle part, general view; C — tentacle, distal part, showing two dense rows of fully developed pinnules; D, F — tentacle, basal part, showing rudimentary pinnules; E — tentacle, middle part, showing glandular epidermis ventrally and pinnules dorsally; G — same, showing glandular epidermis with numerous openings (*arrowheads*) of unicellular glands.

Abbreviations: ge — glandular epidermis; pi — pinnules. Scale bars: A — 200 μm; B — 400 μm; C, E — 100 μm; D, G — 50 μm; F — 10 μm.

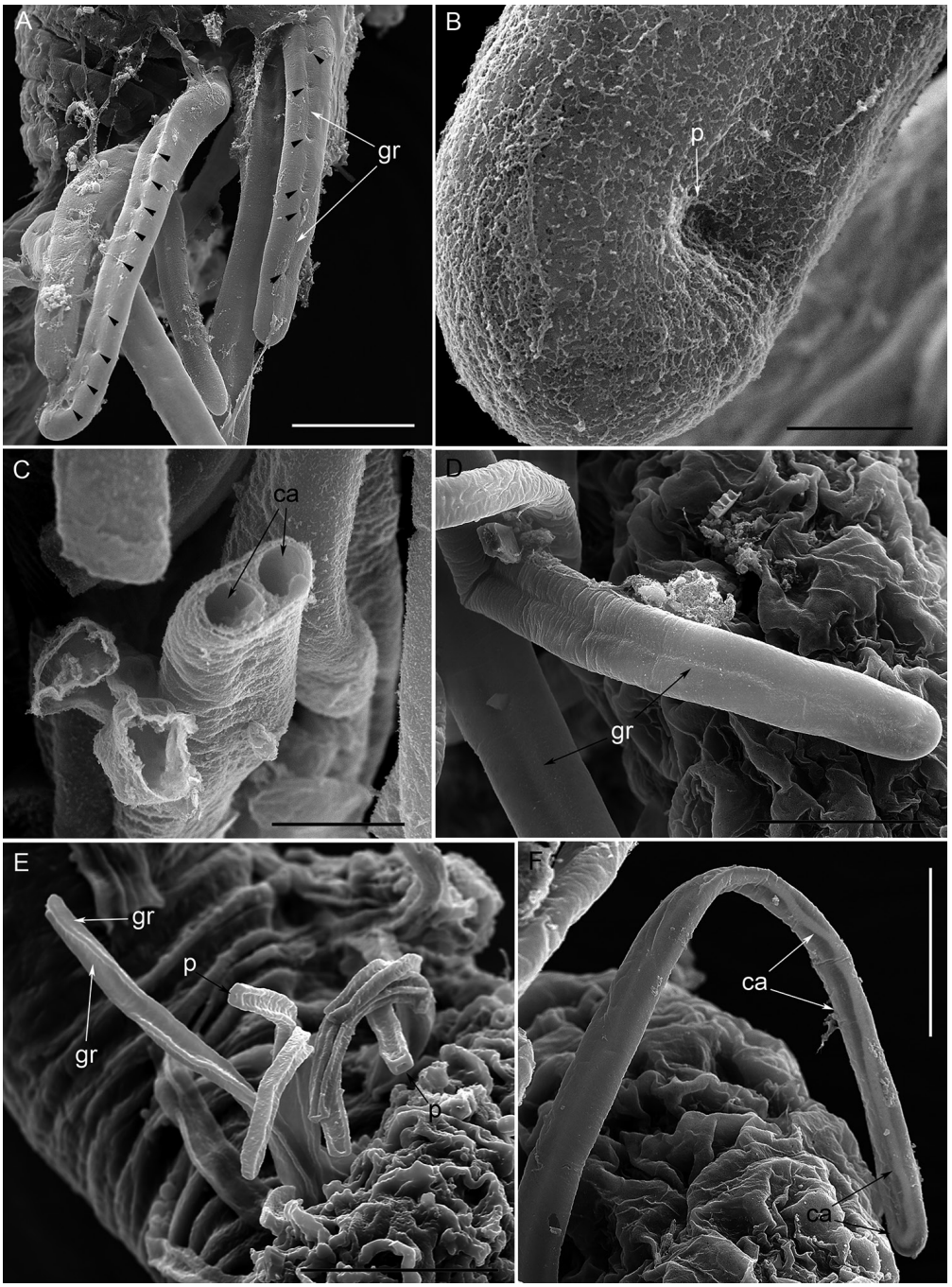

Fig. 3. *Polarsternium plumosum* comb.n. SEM micrographs of new material . A — pinnules, showing a groove on one side with a chain of pits (*arrowheads*); B — pinnule tip at higher magnification, with a pit; C — pinnule in section, showing two blood capillaries; D — pinnules, showing a groove on one side without pits; E — pinnules, showing grooves on both sides and terminal pits; F — pinnule, showing a loop of blood capillaries. Abbreviations: ca — capillary; gr — groove, p — pit. Scale bars: A, E — 50 μm; B — 5 μm; C — 10 μm; D, F — 40 μm.

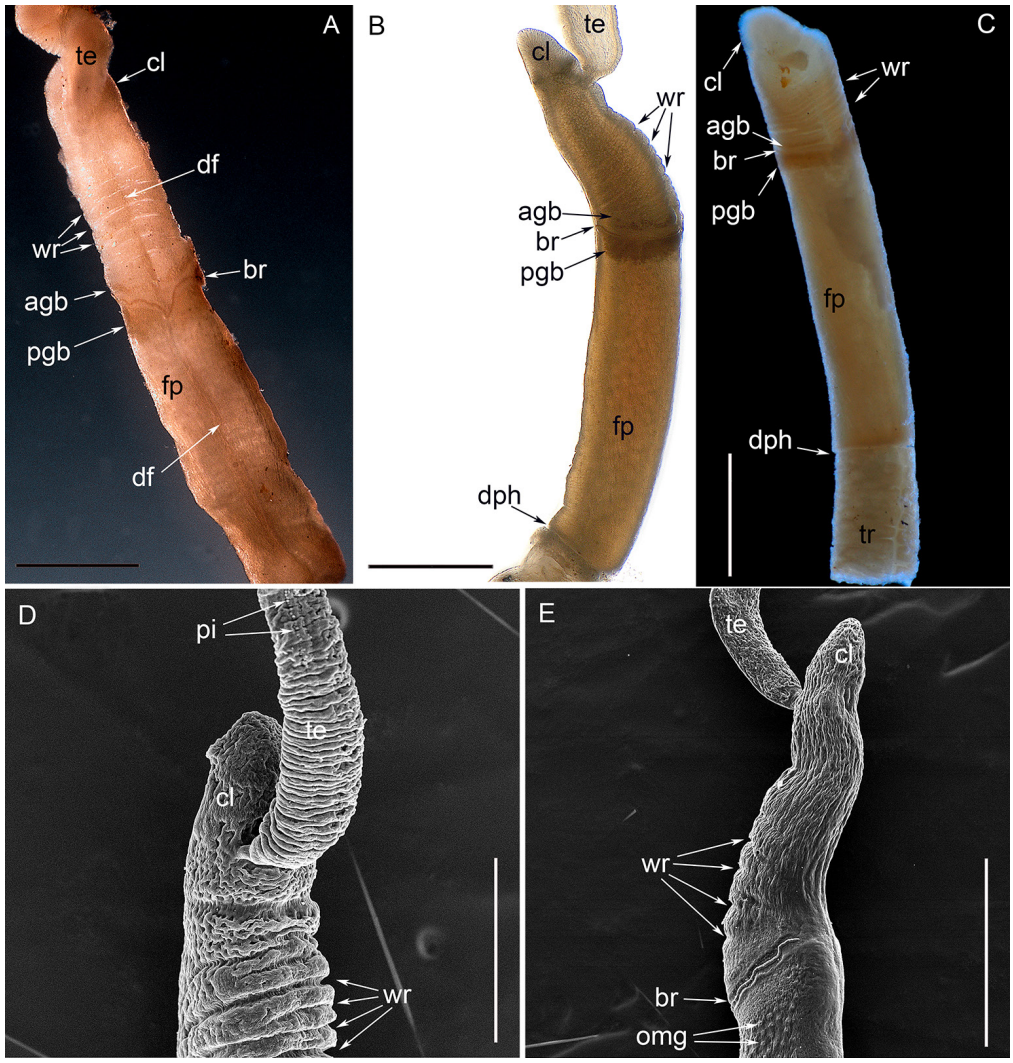

Fig. 4. *Polarsternium plumosum* comb.n. Light (A–C) and SEM (D, E) micrographs of new material (A, B, D, E) and holotype (C). A — forepart, dorsal view; B, E — same, lateral view; C — same, ventral view; D — anterior part of forepart, dorso-lateral view.
Abbreviations: agb — anterior glandular belt; br — bridle, cl — cephalic lobe; df — dorsal furrow; dph — diaphragm; fp — forepart; omg — opening of multicellular gland; pgb — posterior glandular belt; pi — pinnules; te — tentacle; tr — trunk; wr — wrinkles. Scale bars: A–C, E — 0.5 mm; D — 0.3 mm.

st. 1849; 1952; Sea of Okhotsk; 119–124 m; "Sigsbee" trawl; mud; one fragment of empty tube.

Additional material. RV *Akademik M.A. Lavrentiev*, 28 cr.; st. Lv 28–16–2; 16.08.1998; Sea of Okhotsk off northern Sakhalin Island 54°22′66″–21′36″N, 143°59′5″–4″E; "Sigsbee" trawl; 382–387 m; mud, cold methane seep; two empty tubes. RV *Professor Multanovsky*, st. KP4–22; 12.08.2022; Sea of Okhotsk off the eastern coast of Sakhalin Island 51°32′5″N, 144°25′3″E; "Van Veen" bottom grab; 274 m; silty sand with stones; 23 specimens and 12 empty tubes; st. KP4–23; 24.07.2023; Sea of Okhotsk off the eastern coast of Sakhalin Island 51°32′5″N, 144°25′3″E; "Van Veen" bottom grab; 281 m; silty sand with stones; about 50 specimens and a few dozen fragments of empty tubes (NCBI nucleotide accession number OR551480.1). LSID urn:lsid:zoobank.org:pub:CDDFF661-07DA-4542-BDF7-9BA5E99F02DB

MORPHOLOGICAL RE-ASSESSMENT. Tentacle typically coiled into tight spiral, very thick

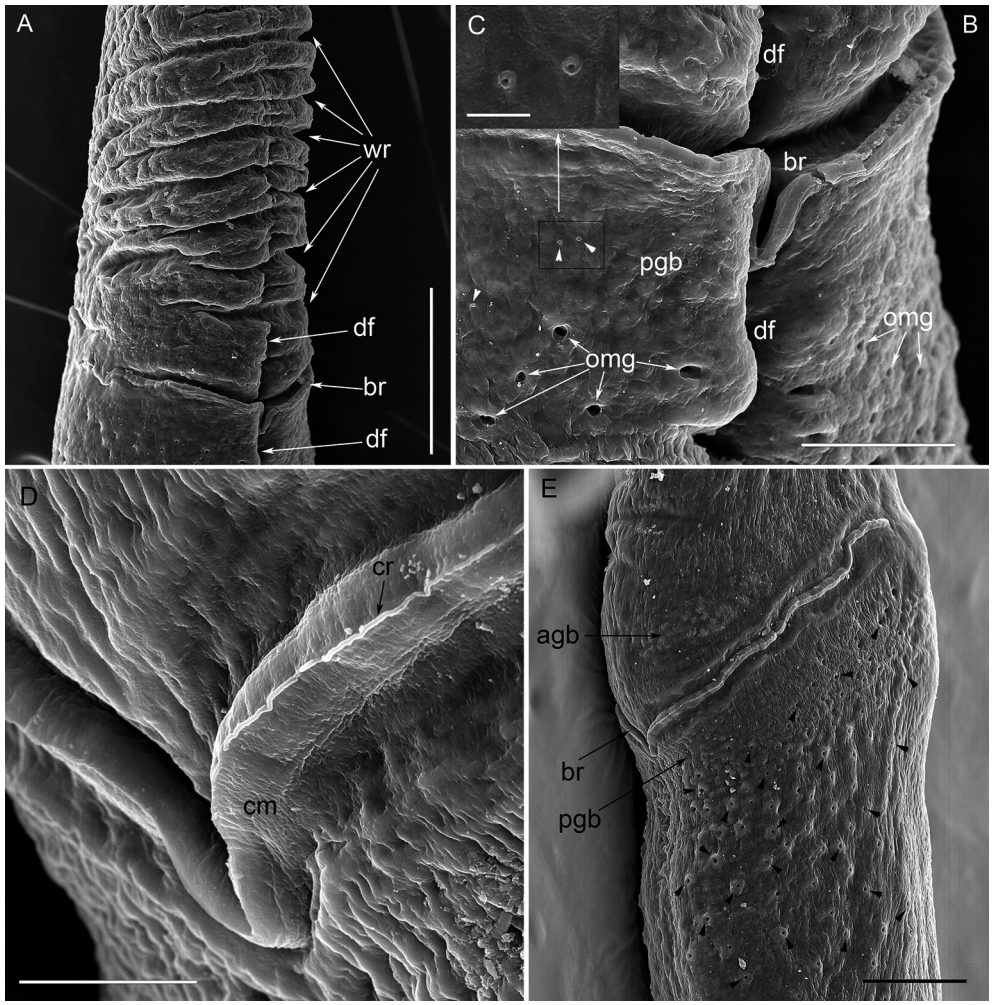

Fig. 5. *Polarsternium plumosum* comb.n. SEM micrographs of new material. A — prefrenular forepart region, dorso-lateral view; B — bridle area, showing large openings of multicellular glands and tiny openings (*arrowheads*) of unicellular glands, dorsal view; C — same, showing openings of unicellular glands at higher magnification; D — bridle keels at higher magnification, dorsal view; E — frenular and postfrenular forepart regions, showing glandular belts and numerous openings (*arrowheads*) of multicellular glands, lateral view. Abbreviations: agb — anterior glandular belt; br — bridle; cm — cuticular membrane; cr — cuticular ridge; df — dorsal furrow; omg — opening of multicellular gland; pgb — posterior glandular belt; wr — wrinkles. Scale bars: A — 200 μm; B — 50 μm; C — 5 μm; D — 20 μm; E — 100 μm.

(D_t 0.13–0.21 mm, D_t/D_f 0.39–0.65, mean ~0.5; in holotype D_t 0.21 mm; D_t/D_f 0.42), almost from base throughout entire length (up to 13 mm, in holotype up to 19.5 mm) covered with numerous folds of complex configuration, predominantly transverse (Fig. 2A, D, G). Pinnules long in middle and distal tentacle regions (up to 210 μm; in holotype up to 270 μm), but appear as short stumps 7–10 μm long in basal region, arranged in two closely spaced dense rows along entire tentacle (Fig. 2B–D, F). Scanning micrographs reveal a deep groove along one or occasionally both sides of many fully developed pinnules, extending from the base to the tip of the pinnule (Fig. 3D, E). Occasionally, a chain of pits is visible either within the groove or in its place, if the groove is absent (Fig. 3A, B). Distal ends of pinnules often bear a deep pit (Fig. 3E). In some scanning micrographs, internal structures are discernible in pinnules; for example, there are two blood capillaries forming a loop at the tip of the pinnule (Fig. 3C, F). Pinnules are located on inner

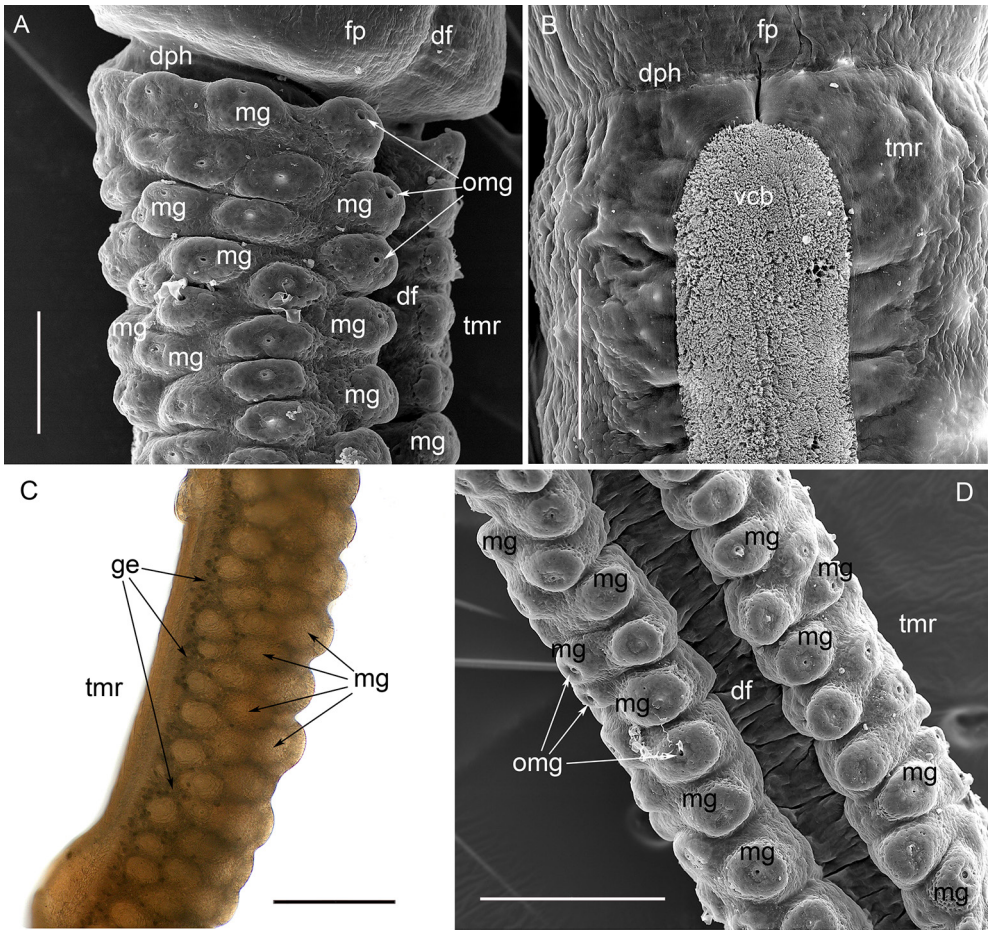

Fig. 6. *Polarsternium plumosum* comb.n. Light (C) and SEM (A, B, D) micrographs of new material. A — trunk metameric region, anterior part, dorso-lateral view; B — same, ventral view; C — same, lateral view; D — trunk metameric region, posterior part, dorsal view.
Abbreviations: df — dorsal furrow; dph — diaphragm; fp — forepart; ge — glandular epidermis; mg — multicellular gland; omg — opening of multicellular gland; tmr — trunk metameric region; vcb — ventral ciliary band. Scale bars: A, B — 100 μm; C — 500 μm; D — 200 μm.

(dorsal) side of tentacle spirals; opposite side (outer, ventral) with band of strongly folded epidermis, possibly glandular, parallel to pinnules; less pronounced in some specimens (Fig. 2C, E, G). Tentacle attached to forepart by slender stalk, slightly left of body midline in all new specimens, but not in holotype (Fig. 4A–D). Cephalic lobe small (L_{cl} 0.21–0.3 mm, L_{cl}/D_f 0.58–0.78, mean ~0.7), triangular; rounded in holotype (L_{cl} 0.3 mm, L_{cl}/D_f 0.6). Forepart relatively short (D_f 0.31–0.38 mm, L_f 1.82–2 mm, L_f/D_f ~6; in holotype D_f 0.5 mm, L_f 2.5 mm, L_f/D_f 5). Entire prefrenular forepart region covered with numerous, relatively deep folds and wrinkles (Figs 4A–D, E; 5A). This epidermal structure is consistent across all studied individuals at all fixation stages, including after the anaesthesia and in live observations. Glandular epidermis on forepart forms two belts: a prominent, broad, continuous, ventrally interrupted belt posterior to bridle and a poorly defined, narrow, fragmented, bilaterally interrupted belt anterior to bridle (Figs 4A, B; 5C, E). In the holotype, only the postfrenular belt is clearly distinguishable, interrupted on both sides of the body (Fig. 4C; Ivanov, 1963: fig. 103A, B). Bridle in anterior third of forepart; keels slender but distinct, brown, with median ridge, dorsally in close contact with each other (or fused), ventrally separated (Figs 4A, E; 5A, B, D, E). Holotype with distinctly interrupted dorsal ends of bridle; bridle oriented almost transversely (Fig. 4C; Ivanov, 1963: fig. 103A, B). Median dorsal furrow clearly defined

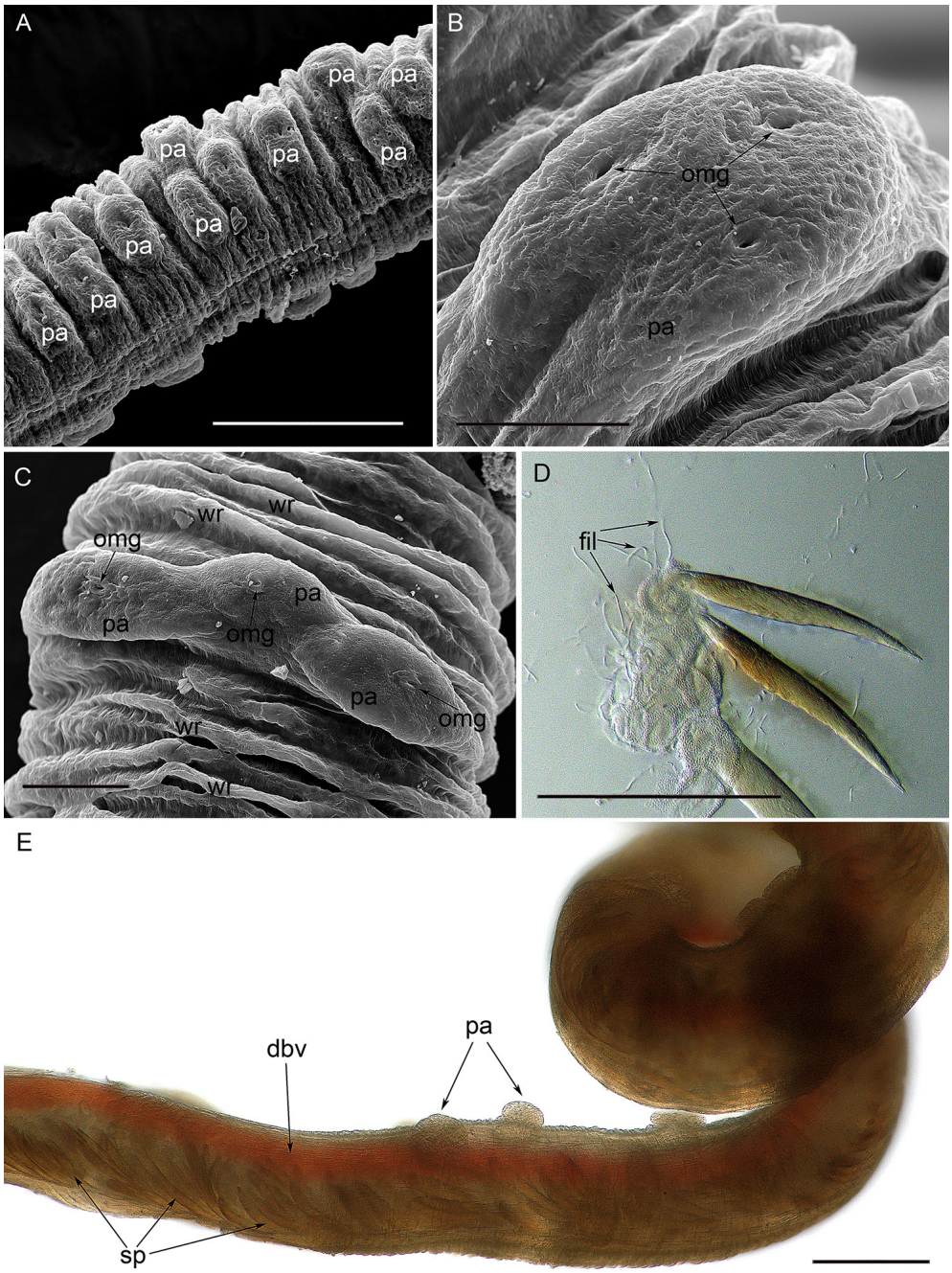

Fig. 7. *Polarsternium plumosum* comb.n. SEM (A–C) and light (D, E) micrographs of new material. A — trunk non-metameric region, ventro-lateral view; B — papilla with three openings of multicellular glands; C — three papillae with one opening of multicellular gland on each; D — spermatophores; E — part of non-metameric region, showing numerous spermatophores visible inside under transmitted light, lateral view. Abbreviations: dbv — dorsal blood vessel; fil — main filament; omg — opening of multicellular gland; pa — papilla; sp — spermatophore; wr — wrinkles. Scale bars: A — 200 µm; B — 40 µm; C — 50 µm; D — 300 µm; E — 500 µm.

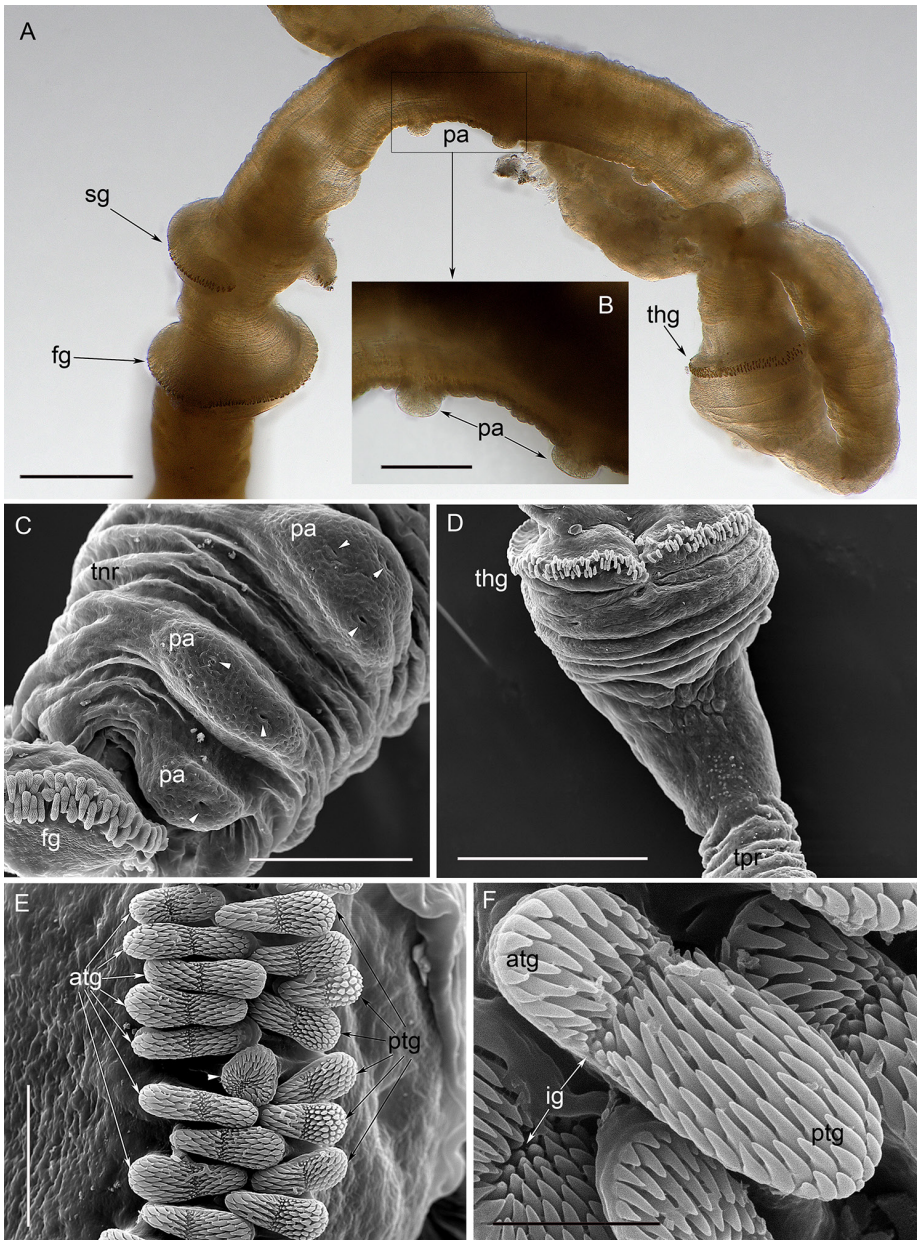

Fig. 8. *Polarsternium plumosum* comb.n. Light (A, B) and SEM (C–F) micrographs of new material. A — girdles of toothed chaetae, dorso-lateral view; B — papillae between girdles at higher magnification, lateral view; C — first anterior girdle with adjacent part of non-metameric region, showing papillae with openings (*arrowheads*) of multicellular glands, dorsal view; D — third (posterior) girdle with adjacent part of post-annular region, ventral view; E — part of third (posterior) girdle at higher magnification, showing rows of normal and abnormal (*arrowhead*) chaetae; F — heads of toothed chaetae, showing two opposite groups of denticles and intermediate minute denticles.

Abbreviations: atg — anterior teeth group; ig — intermediate zone; fg — first girdle; pa — papilla; ptg — posterior teeth group; sg — second girdle; thg — third girdle; tnr — trunk non-metameric region; tpr — trunk postannular region. Scale bars: A — 500 µm; B — 200 µm; C — 100 µm; D — 300 µm; E — 20 µm; F — 5 µm.

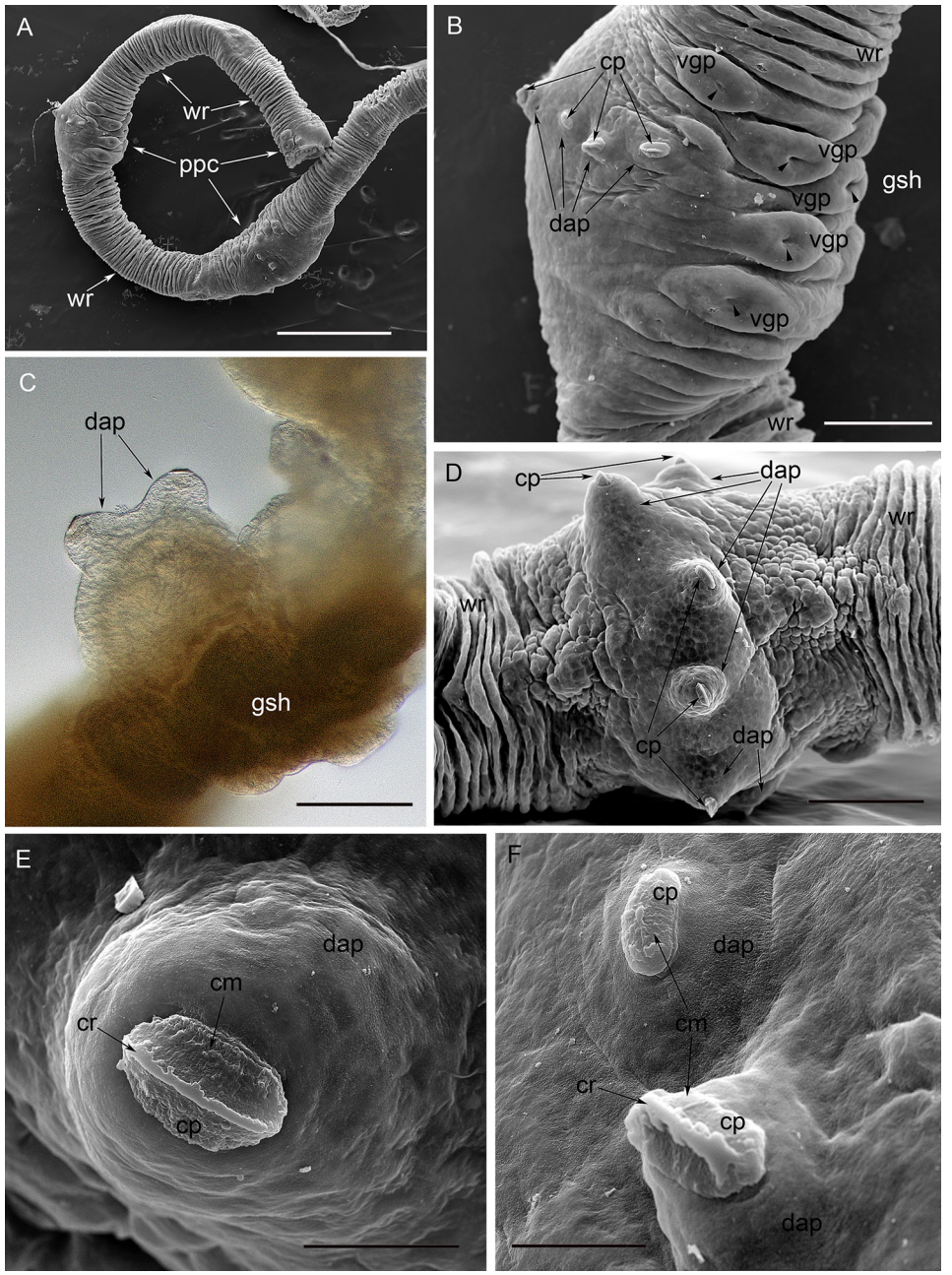

Fig. 9. *Polarsternium plumosum* comb.n. SEM (A, B, D–F) and light (C) micrographs of new material. A — trunk postannular region, dorso-lateral view; B — postannular complex, showing dorsal papillae with cuticular plaques and ventral papillae in glandular shield with openings (*arrowheads*) of multicellular glands, lateral view; C — same with two dorsal papillae opposed ventrally by glandular shield, lateral view; D — same with six dorsal papillae, dorsal view; E, F — cuticular plaques.

Abbreviations: cm — cuticular membrane; cp — cuticular plaque; cr — cuticular ridge; dap — dorsal armed papilla; gsh — glandular shield; ppc — postannular papillary complex; vgp — ventral glandular papilla; wr — wrinkles. Scale bars: A — 500 μm; B–D — 100 μm; E, F — 20 μm.

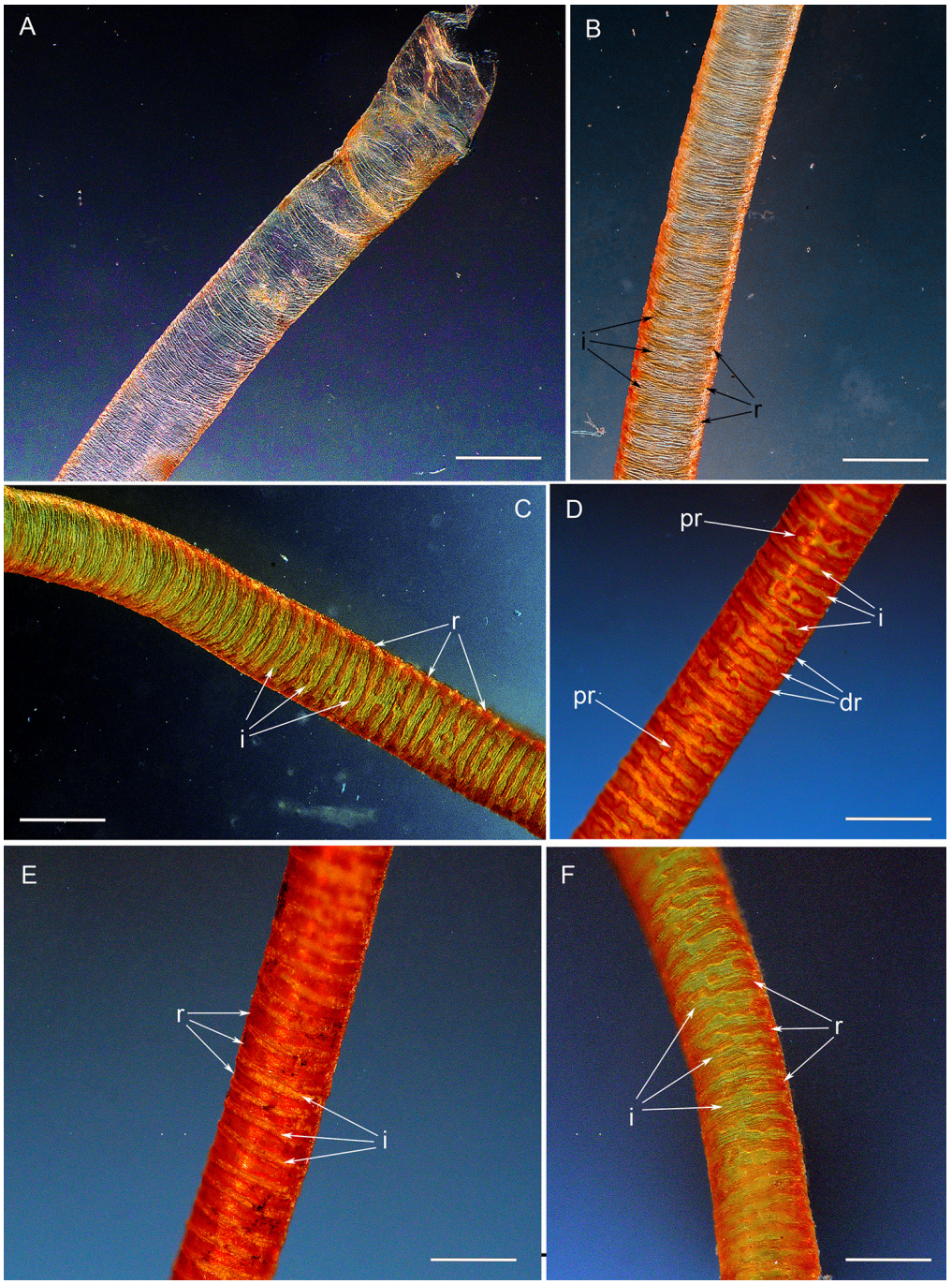

Fig. 10. *Polarsternium plumosum* comb.n. Light micrographs of new material. A — tube anteriormost filmy region; B — tube anterior region, showing rings appear gradually; C — same, showing gradual increase in ring irregularity; D — tube middle region, showing highly irregular rings; E — tube posterior region, showing more regular rings; F — tube posteriormost region, showing irregular vanishing rings.
Abbreviations: dr — double rings; r — rings; i — interspaces; pr — "perforations". Scale bars: A–F — 0.5 mm.

Table 1. Characteristics of the species of *Polarsternium*.

Species	*P. rugellosum*	*P. mirabile*	*P. evrikae*	*P. australe*	*P. magnum*	*P. plumosum*
Tube, diameter (mm)	0.3–0.5	0.18–0.19	0.25–0.3	0.15–0.29	0.47–0.55	0.48–0.68
Tube, segments	–	–	–	–	+ –	–
Tube, rings	+ regular single	–	+ regular single	+ regular double	+ irregular single	+ irregular single
Tentacle, character	thick, wrinkled	thin, smooth	thin, smooth	thin, smooth	thick, wrinkled	thick, wrinkled
Tentacle, position	left	median	median	Left	left	left
D_t/D_f, average	0.4	0.2	0.2	0.22	0.42	0.5
Pinnules	–	– (?)	1-2 rows	–	2-4 rows	2 rows
Pinnules, max length (μm)			140		280	270
L_{cl}/D_f, average	1.01	2.11	1.8	1.18	0.84	0.7
Forepart, diameter (mm)	0.3–0.37	0.14	0.21–0.24	0.11–0.23	0.43–0.44	0.31–0.5
L_f/D_f	6-7	5	4.5–5.5	3.5–8	7	5-6
Forepart, glandular patches	1 belt br (p)	–	1 belt br (p)	2 belts br (p), di	1 belt br (p)	2 belts br (a, p)
Postfrenular glandular belt fused d	+		+ –	+	+ –	+ –
Postfrenular glandular belt fused v	–		+	–	–	–
Bridle keels character	thin, yellowish	thick, yellow	thick, brown	thin, brownish	thin, brown	thin, brown
Bridle keels fused d	+ –	+	+	+	+	+ –
Bridle keels fused v	–	+	–	–	–	–
Trunk metameric part, glandular patches	bands	bands	rings, bands	rings, bands	rings, bands	rings, bands
Trunk anteriormost part, rows of multicellular glands in each ridge	4–5	4–5	3–4	3–4	4–5	3–5
Genital papillae	?	?	–	–	+	–
Enlarged papillae	~11, 2 rows	–	~30, 1–2 rows	–	–	–
Enlarged papillae, cuticular plaques, diameter (μm)	–		21–32			

Table 1 (continued).

Species	*P. rugellosum*	*P. mirabile*	*P. evrikae*	*P. australe*	*P. magnum*	*P. plumosum*
Postannular papillae in each row	5-7	4–5	?	2–3	2	2–6
Postannular cuticular plaques, diameter (μm)	24	24–27	?	13–14	40–45	16–27
Girdles region, papillae (number)	$p^3(1)$	–	?	$p^3(3–5)$	$p^3(1)$	$p^2(4–6)$
Girdles region cuticular plaques, diameter (μm)	30		?	13–14	–	–
First girdle fused d	–	–	?	–	+	+
First girdle fused v	+	–	?	+–	–	–
Second girdle fused d	+	–	?	+	–	–
Second girdle fused v	–	+	?	–	+	+
Third girdle fused d	–		?	–	–	+–
Third girdle fused v	–		?	+–	–	+–
Third girdle distance, mm	0.6–0.8	–	?	1.4–1.55	3.1	3.1
Chaetae, rows	1–2	1	?	1	1–2	1–3
Chaetae, size (μm)	17–20	13–19	?	13–17	17–24	13–18
Chaetae, anterior teeth area, %	33–43	21–26	?	40	40–50	45–55
Spermatophore, length (μm)	?	?	280–308	112–118	325–392	252–294
Spermatophore, additional Structures	?	?	ad fil	ad fil	ad fil, adh ves, lanc pr	–

Symbols: + — present; – — absent; +– — variable or poor development; ? — unknown; d — dorsal; v — ventral; a — anterior; p — posterior; br — bridle; di — diaphragm; p^2 — papillae between girdles; p^3 — papillae just behind girdles; ad fil — additional filament; adh ves — adhesive vesicles; lanc pr — lanceolate process.

Символы: + — присутствует; – — отсутствует; +– — изменчиво или слабо развито; ? — неизвестно; d — дорсальный; v — вентральный; a — передний; p — задний; br — уздечка; di — диафрагма; p^2 — папиллы между поясками; p^3 — папиллы сразу за поясками; ad fil — дополнительный филамент; adh ves — клейкие везикулы; lanc pr — ланцетовидный отросток.

on dorsal side of forepart, both anterior and posterior to bridle, extending to forepart-trunk boundary (diaphragm) (Figs 4A; 5A, B). The multicellular glands occupying the forepart coelom posterior to the bridle are not clearly visible in transmitted light, but their presence and arrangement is indicated by numerous gland duct openings, seen in SEM images on both sides of the dorsal furrow (Figs 4E; 5B, E). Annular groove (diaphragm) separating forepart and trunk well-defined; genital papillae absent. Papillae in anterior (metameric) trunk indistinct from continuous epidermal-muscular ridges in all specimens, including holotype. Multicellular glands within each ridge are densely packed in 3–5 rows and distinctly protruding; further posteriorly, their outlines become smoother and the number of rows reduces to 1–2 on each side of the dorsal furrow (Fig. 6A, C, D). Each gland is surrounded by a distinctly contrasting ring of glandular epidermis. The narrow glandular epidermal strips also flank the glandular region ventro-laterally (Fig. 6C). Glandular patches on trunk indistinct in holotype. The broad ventral ciliary band begins slightly posterior to the anterior trunk margin (from the diaphragm in the holotype), extending to the posterior end of the metameric region, whose boundary with the non-metameric trunk is indistinct dorsally (Fig. 6B; Ivanov, 1963: fig. 103A, B). Epidermal-muscular ridges with multicellular glands gradually fragment into discrete lobes resembling papillae; dorsal furrow and glandular strips disappear; epidermis becomes heavily wrinkled. Further posteriorly, at some distance, multicellular glands reappear within large, transversely elongated papillae, typically one, rarely up to four per papilla (Figs 7A–C; 8C). Papillae lack cuticular plaques; irregularly scattered over dorso-lateral surface. Zone of enlarged papillae absent. Three girdles of chaetae present, arranged according to standard scheme 2+1 (Fig. 8A). Distance between 2 anterior chaetal girdles and posterior girdle ~3.1 mm. 1st girdle dorsally fused, ventrally divided; 2nd girdle dorsally divided, ventrally fused; 3rd girdle nearly continuous in some specimens, with barely discernible bilateral interruptions (Fig. 8A, D). Chaetae 13–18 μm long, arranged in 1–2 rows in anterior girdles, up to 3 rows in posterior girdle (Fig. 8E). Anterior teeth group on chaetal heads well-developed, comparable in area (45–55% of head length) and size to posterior group. Narrow intermediate zone between teeth groups filled with minute denticles, oriented perpendicular to head axis (Fig. 8F). Several small, unarmed papillae are present dorsally between anterior and posterior girdles (Fig. 8B). Beginning at a pronounced constriction posterior to the girdles (Fig. 8D), the postannular trunk bears transverse rows of dorsal papillae (2–6 per row), situated at varying, sometimes considerable, distances from its anterior margin and opposed ventrally by the so-called glandular shields (Fig. 9A–D). These shields consist of aggregations of up to a dozen unarmed glandular papillae, morphologically similar to those of the non-metameric region but much smaller in size. As in the non-metameric region, each papilla typically contains a single multicellular gland. Dorsal papillae bear oval cuticular plaques (16–27 μm in diameter) with thickened median ridge (Fig. 9E, F). Regions of the postannular trunk not occupied by papillary aggregations or glandular shields are densely covered with numerous transverse folds (Fig. 9A, B, D). Opisthosoma torn off in all specimens. Spermatophores, measuring 252–294 μm in length and bearing a single main filament, were extracted from the reproductive tracts of several specimens (Fig. 7D, E). No additional structural elements were observed in the spermatophores. Tube thick-walled but flexible. Anterior filmy portion of tube up to 18 mm long, transparent, with sparse evenly spaced fibres (Fig. 10A). Segmentation absent. Rings typically appear gradually (Fig. 10B); however, in some tubes with abnormally short anterior ends, which were probably torn off and are now being rebuilt, the rings appear abruptly, already "perforated" and irregular in shape. Normally, rings initially regular, pale reddish, narrow (1/5–1/6 tube diameter) (Fig. 10C), but further posteriorly darken to reddish-brown and become highly irregular (especially in tube mid-region), with uneven edges, "perforations", and frequent anastomoses between rings and interspaces (Fig. 10D). Some rings appear double due to "perforation" and uneven colouration: central part lighter than margins. In posterior tube region, rings become paler and more regular (Fig. 10E), then irregular again and gradually vanish (Fig. 10F). Tube diameter 0.48–0.68 mm anteriorly; maximum length 27.5 cm.

REMARKS. The description of *S. plumosum* published by Ivanov (1957) and later supplemented by Smirnov (2014b) remains largely valid, except for certain morphological details of the anterior (metameric) trunk region, particularly those concerning the papillae and multicellular glands. Previously, this species was known only from short fragments of a single specimen and several empty tubes, leaving the morphology of the trunk from the non-metameric region to the postannular region completely undescribed. The newly collected material now fills these gaps. Re-examination of the type material partially confirms Ivanov's (1957, 1960b, 1963) conclusion that the holotype had undergone extreme contraction. This interpretation is supported by both meristic indices (L_t/D_t, L_{cl}/D_t, D_t/D_t) and qualitative characters (rounded cephalic lobe, transversely oriented bridle keels, dorsal interruptions in the bridle and postfrenular glandular belt, the anterior end of the ventral ciliary band coinciding with the forepart-trunk boundary, and the condition of the muscular ridges in the metameric trunk region). Contrary to Ivanov's (1957) interpretation, however, the numerous folds and wrinkles observed on the tentacle, in the prefrenular forepart region,

and, as shown in our study, in the non-metameric and postannular trunk regions, appear to be inherent characteristics of this species rather than contraction artefacts. It is also notable that the holotype is an exceptionally large specimen, exceeding all other individuals in our material in several morphometric parameters (D_f, L_f, D_{tb}, tentacle and pinnule length). This, however, does not cast any doubt on its specific identity. Ivanov's (1957) report of papillae in the metameric trunk region was erroneous and his fixation method prevented observation of several other anatomical traits, such as the presence of a prefrenular glandular belt and glandular patches on the trunk.

Of particular interest are the characteristics of the pinnules revealed by SEM. Although the unilateral and bilateral grooves, as well as the lateral and terminal pits observed on the pinnules, are likely artefacts of specimen preparation for SEM, their spatial arrangement clearly correlates with the internal structure of these extensions of epidermal tentacular cells, specifically, the presence of afferent and efferent blood capillaries that merge at the pinnule tip (Ivanov, 1963). It is also possible that the structural differences in the pinnules observed under SEM may to some extent reflect varying functional states of individual pinnules.

Among all species of the genus, *P. plumosum* comb. nov. appears to be most closely related to *P. magnum* Smirnov, 2005. Their phylogenetic affinity is supported by most morphometric characters of both species (most notably, a large diameter of the forepart and tube, a relatively short cephalic lobe, and a thick, wrinkled tentacle). The two species are also significantly similar in the morphology of the tube rings (very narrow and irregular), the presence of two rows of long pinnules on the tentacle, the absence of cuticular plaques on the papillae of both the non-metameric and annular trunk regions, the configuration of chaetal girdles, and the distance between the anterior and posterior girdles (Table 1). *P. plumosum* differs from *P. magnum* in the presence of an additional belt of glandular epidermis anterior to the bridle, the absence of a distinct boundary between the anterior (metameric) and posterior (non-metameric) regions of the preannular trunk, the twice smaller size of cuticular plaques on the papillae of the postannular region, a significantly shorter spermatophore, the absence of an accessory filament and other supplementary structures on the spermatophore, and the lack of tube segmentation and male genital papillae.

DISCUSSION. When Smirnov (1999) established the genus *Polarsternium*, he proposed the following diagnostic characters: the presence of a single tentacle; distinct grooves separating the forepart from the trunk (diaphragm) and the cephalic lobe from the remainder of the forepart and delineating boundaries within the bridle area; the absence of papillae replaced by epidermal-muscular ridges in the anterior (metameric) trunk; a multiserial arrangement of multicellular glands within these ridges; and a non-segmented, ringed tube with a membranous anterior end. The subsequent description of two new species, *Polarsternium mirabile* Smirnov, 2005 and *P. magnum*, revealed variability in some of these traits, such as the presence of forepart grooves and the unsegmented nature of the tube, thus reducing their diagnostic significance (Smirnov, 2005).

Polarsternium belongs to the oligobrachiid stem of siboglinids, where its closest relatives are *Unibrachium*, *Oligobrachia*, and *Nereilinum* Ivanov, 1961. The principal distinguishing traits that differentiate these genera are the presence or absence of a funnel at the point of tentacle(s) attachment on the cephalic lobe; the relative length of the forepart; the shape of the groove in the bridle region; the morphology of the bridle; the visibility of multicellular glands in the forepart under transmitted light; the shape and distribution of glandular epidermal patches on the trunk; the number of chaetal girdles; and specific morphological traits of the spermatophores and tube (Smirnov, 2014a). Based on these criteria, Smirnov (2014a) revised the generic diagnosis of *Polarsternium*. However, newly acquired data on *S. plumosum* and its reassignment to *Polarsternium* necessitated further diagnostic amendments, particularly regarding the presence of an additional filament on the spermatophores and the arrangement of glandular patches on the forepart.

The highly incomplete original description by Ivanov (1957) has, until now, precluded a definitive resolution of the taxonomic position of *S. plumosum* within the genus. Ivanov considered this species to be closely related to the group of species resembling *S. ekmani* Jägersten, 1956, based on the presence of a pretentacular groove on the forepart, two rows of pinnules on the tentacle, and double ("perforated") rings on the tube (Ivanov, 1960b, 1963). Smirnov (2014b) subsequently attempted a detailed morphology-based revision of the genus, proposing a subgeneric classification comprising nine subgenera, including three monotypic ones, and providing an estimation of the taxonomic significance of their morphological traits. According to this classification, the most informative characters for subgeneric delimitation are the arrangement of glandular patches on the forepart; the presence and relative development of anterior teeth on the chaetal heads; the number, shape, and arrangement of chaetal girdles; the shape of the so-called segmental groove in the bridle area of the forepart; the length and structural details of the spermatophore; tube colour; the presence of segments (with or without rings) on the tube; the relative diameter of the tentacle; and the presence of pinnules on the tentacle. Smirnov (2014b) also described some morphological details of the tube in *S. plumosum*, based on newly collected material, which clarified to some extent the taxonomic placement of the species at that time. A previously undescribed long (17–18 mm) membranous portion with thin, collapsing fibrous walls, lacking any seg-

mentation, was found at the anterior end of the tube. This morphology of the tube precluded the inclusion of *S. plumosum* in the subgroup typified by *S. ekmani* (subgenus *Ekmanifilum* Smirnov, 2014), whose representatives are all characterised by segmented tubes. Although the structure of the girdles region and spermatophore in *S. plumosum* remained unknown at the time, the presence of a unsegmented, ringed, dark brown tube lacking a regular "perforation" pattern, a thick tentacle bearing two rows of pinnules, a circular groove anterior to the bridle, and the absence of longitudinal glandular bands on the forepart, led Smirnov to tentatively assign the species to the subgroup, whose type species is *S. weberi* Caullery, 1944 (subgenus *Siboglinum* Caullery, 1914). However, the holotype was not re-examined during that study and all tubes from the new material were, unfortunately, empty. New morphological data on *S. plumosum*, especially for the anterior trunk region (the absence of papillae and the presence of multiserial tubiparous glands), now support the transfer of *S. plumosum* to the genus *Polarsternium*. This genus belongs to a different frenulate lineage, Oligobrachiidae, to which another single-tentacled genus, *Unibrachium*, had already been previously assigned (Southward, 1972).

The molecular phylogeny of Siboglinidae in general and *Siboglinum* in particular remains insufficiently resolved to fully support morphological interpretations. Although the monophyly of siboglinids as a whole is not in doubt, internal relationships within the family, and among *Siboglinum* species, remain the subject of ongoing debate. Until recently, molecular data were available for only three of the 72 recognised species in this genus (Hilário *et al*., 2010; Li *et al*., 2015), but Skalon *et al.* (2024) have now published mitogenomic data for two additional siboglinid species, including *S. plumosum*. These data are fully consistent with previous phylogenies based on single genes and mitochondrial genomes, all of which indicate a distant relationship between *S. fiordicum* Webb, 1963 and *S. ekmani* and suggest that the genus *Siboglinum* is probably non-monophyletic (Halanych *et al*., 2001; Halanych, 2005).

In the phylogenetic analysis by Skalon *et al.* (2024), *S. plumosum* is recovered as the sister taxon of *S. ekmani.* According to the morphology-based classification, the remaining three species still in *Siboglinum* (*S. fiordicum*, *S. ekmani*, and *S. poseidoni* Flügel et Langhof, 1983) are placed in different subgenera and do not share any unique morphological characters (Smirnov, 2014b). Thus, the paraphyly of the genus *Siboglinum* is supported by both morphological and molecular evidence. However, since the internal relationships within the genus can be properly resolved only if molecular data are available from representatives of at least all recognised subgenera, the markedly divergent positions of *Siboglinum* species on molecular phylogenies can, at present, scarcely be regarded as sufficient justification for formally splitting the genus into several distinct genera. Overall, molecular data for frenulates remain fragmentary, preventing a clear understanding of evolutionary rates and divergence patterns within this group. This limitation is further illustrated by the phylogenetic position of *Oligobrachia dogieli* Ivanov, 1957, which Skalon *et al.* (2024) placed as the sister taxon of *S. fiordicum.* This position is distant from both other *Oligobrachia* species and from *S. plumosum*, and the latter species, despite lacking shared, distinct morphological traits with *S. ekmani*, nevertheless groups together with it in a single clade (Skalon *et al.,* 2024). In general, our results point to the need for a re-evaluation of morphological characters in frenulates and highlight the overall scarcity of molecular data for this enigmatic group of annelids.

Identification key to the species of *Polarsternium* (type localities in parentheses)

1 Bridle in posterior third of forepart, very strongly developed, with thick keels fused on both body sides and lying on prominent epidermal-muscular ridges. Groove separating forepart from trunk absent. Epidermal glandular patches on forepart absent. Tube without rings and segments .... *P. mirabile* (Scotia Sea)

– Bridle approximately in middle or anterior half of forepart; keels narrow, separated ventrally. Glandular patches on forepart present. Groove separating forepart from trunk well-developed. Tube ringed, sometimes also segmented 2

2 Zone of enlarged papillae present. Cuticular plaques in preannular and/or annular trunk region 21–33 μm across. Tube rings simple 3

– Zone of enlarged papillae absent. Cuticular plaques in preannular and/or annular trunk region, if present, not exceeding 15 μm across. Tube rings at least in its middle region double and/or "perforated" forming anastomosing patterns.....4

3 Pinnules absent. Tentacle attached significantly left of body midline. L_{cl}/D_f ~1. D_f 0.3–0.37 mm. L_f 2–2.1 mm. Glandular belt posterior to bridle dorsally fused, ventrally interrupted. Multicellular glands on forepart visible in transmitted light. Glandular epidermal rings around ducts of multicellular glands on trunk ridges absent. ~11 enlarged papillae... *P. rugellosum* (Laptev Sea)

– Pinnules present. Tentacle attached medially. L_{cl}/D_f ~1.8. D_f 0.21–0.24 mm. L_f 1.1–1.22 mm. Postfrenular glandular belt ventrally fused, dorsally interrupted. Multicellular glands on forepart not visible in transmitted light. Each duct of multicellular glands on trunk ridges encircled by epidermal glandular ring. ~30 enlarged papillae .... *P. evrikae* Smirnov, 2005 (Scotia Sea)

4 Pinnules absent. Two glandular belts on forepart: posterior to bridle and near diaphragm. Bridle in mid-forepart region. D_f 0.11–0.23 mm. L_f 0.6–1.32 mm. Distance between 2 anterior and 1 posterior girdles of chaetae 1.4–1.55 mm; 1st girdle dorsally interrupted, 2nd ventrally interrupted and dorsally fused. 3–5 papillae directly posterior to 3rd girdle. Spermatophores 112–118 μm long. Tube rings fairly regular: single in anterior tube region, double posteriorly. Ring width (single and double) ca. 1/2 tube diameter .... *P. australe* Smirnov, 2005 (Laurie Trench, Scotia Sea, Weddell Sea)

– Pinnules present. Glandular patches on forepart near diaphragm absent. Bridle significantly anterior to mid-forepart region. D_f 0.31–0.5 mm. L_f 1.8–3 mm. Distance between 2 anterior and 1 posterior girdles of chaetae ca. 3 mm; 1st girdle dorsally fused, 2nd dorsally interrupted and ventrally fused. Papilla immediately posterior to 3rd girdle, if present, solitary. Spermatophores 252–392 μm long. Tube rings single, narrow (1/5–1/6 tube diameter), mostly highly irregular (anastomosing and "perforated").....5

5 Glandular epidermis on forepart present only as postfrenular belt. Large genital papillae in males. Multicellular glands multiserial throughout entire metameric trunk region. Solitary papilla immediately posterior to 3rd girdle. Cuticular plaques in postannular region 40–45 μm across. Spermatophores 325–392 μm long..... .....*P. magnum* (Scotia Sea)

– Two glandular belts on forepart: anterior and posterior to bridle. Genital papillae absent. Multicellular glands multiserial only on anterior trunk; posteriorly, number of rows reduced to 1–2. Papillae immediately posterior to 3rd girdle absent. Cuticular plaques in postannular region 16–27 μm across. Spermatophores 252–294 μm long ..... *P. plumosum* (Sea of Okhotsk)

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Conflict of interest

The authors declare no conflicts of interest.

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