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A new Entoprocta species from the northwestern Weddell Sea shelf (Southern Ocean), its soft-sediment habitat and possible polychaete hosts

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Abstract

Rare meiofauna taxa are often indicators of specific environmental conditions. A new and rare species of Entoprocta from the Southern Ocean, its abundance, habitat and possible commensal relationship with Polychaeta are presented. During the RV *Polarstern* expedition PS118 (2019) to the northwestern Weddell Sea, sediment samples were taken with a multicorer. The species of the family Loxosomatidae was discovered in the meiofauna size fraction of samples of only one of three investigated stations (413–415 m depth). *Loxosomella sigridae* sp. nov. is a solitary, medium-sized entoproct (total length up to 773 µm). Decisive characters of the adult include twelve tentacles, an aborally situated Y-shaped cell row, paired accessory gland cells along the foot groove and smooth adhesive papillae at the tip of the foot. The reproductive cycle of *Loxosomella sigridae* sp. nov. has a sexual and an asexual phase via larvae and bud-carrying individuals, respectively. We present confocal laser-scanning images of both developmental stages. Integrative methods are used to describe the habitat of *Loxosomella sigridae* sp. nov. and gain insight in its relationship to possible host organisms. We discuss co-occurring polychaete families and their ecology and conclude that Cirratulidae and/or Paraonidae may most likely be the hosts of *Loxosomella sigridae* sp. nov.

Keywords Kamptozoa · Taxonomy · Meiobenthos · Infaunal lifestyle · Southern Ocean · Continental shelf

Introduction

Benthic research on the Southern Ocean shelf often focusses on megafauna (animals > 10 mm) using data obtained from seabed imaging or samples collected by dredging (Gutt et al. 2016, 2019). To obtain the smaller macrofauna (0.5–10 mm) sediments are collected using different kinds of box corers (Glover et al. 2008; Pineda-Metz and Gerdes 2018) or multi- and megacorers (Mincks and Smith 2007; Glover et al. 2008). Subsequent sample treatment typically follows protocols aimed at extracting specific taxa or faunal size

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classes, for example, by using sieves with mesh sizes of 100, 300, or 500 μ m (Mincks and Smith 2007; Glover et al. 2008; Pineda-Metz and Gerdes 2018). Important components of the endobenthic communities are often not sampled or are excluded from the collected material by the techniques used. Among the neglected groups are bacteria protists and metazoans of the meiofaunal size class, which range from 32 μ m to 500 or 1000 μ m, depending on the definition (Soltwedel 2000). However, these small metazoans are numerous and play a crucial role in the decomposition of organic matter and the remineralisation of nutrients (Schratzberger and Ingels 2018).

In our study, we concentrated on the meiofauna. Under favourable environmental conditions, abundant meiofaunal taxa such as Copepoda may reach more than 10 times higher individual numbers than under adverse conditions. The abundance of Copepoda, for example, distinguished benthic communities between different Antarctic shelf regions (Veit-Köhler et al. 2018). And rare yet key taxa also reliably indicate differences between regions: Tardigrada (up to max. 20 individuals per 10 cm⁻²) were among the groups that



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separated sites in the southeastern Weddell Sea from stations at the Antarctic Peninsula (Säring et al. 2022). Here, we focus on the taxon Entoprocta, a group that is rarely reported from the Southern Ocean. Firstly, this "rarity" may be due to the small number of studies from the Antarctic that have dealt with these animals (see below). Secondly, "rare" taxa should be included in biodiversity studies and community analyses because their presence and abundance frequently indicate changes in environmental conditions (Säring et al. 2022). Herein, we focus on a new species of the for the Southern Ocean understudied phylum Entoprocta (Nitsche, 1869).

Entoprocta are small, mainly marine, colonial or solitary invertebrate animals that have been reported from different water depths world-wide (Nielsen 2016; Borisanova et al. 2018; WoRMS Editorial Board 2024). They are characterised by a horseshoe-shaped crown of tentacles (lophophore) surrounding an atrium in which the U-shaped gut starts and ends. Therefore, Nitsche (1869) established the name "Ento" procta. Their body (calyx) tapers towards a stalk (peduncle) which ends in a sucking disc or a complex foot organ with which they attach to the substratum. Sexually produced larvae often develop in the atrium before they are released to a short pelagic phase. Additionally, asexual reproduction by budding is common (Nielsen 2020). The majority of the known solitary Entoprocta are commensal symbionts that are associated to specific hosts. The hosts provide shelter and water currents for feeding and respiration. Possible host organisms belong to Sipuncula, Bryozoa, Porifera, Crustacea, Echinodermata or Ascidia. However, Polychaeta or their tubes are by far the most common hosts or habitats for species of these small suspension feeders (Nielsen 1989).

The phylum Entoprocta includes four families, among them the Loxosomatidae Hincks, 1880 which comprise the two genera *Loxosoma* Keferstein, 1862 and *Loxosomella* Mortensen, 1911 (Nielsen 2010). Of these, *Loxosomella* has the most species, with more than 120 described. Continued interest in taxonomic work resulted in 27 new *Loxosomella* species described since the year 2000 (WoRMS Editorial Board 2024). However, Borisanova et al. (2018) point out that there are still geographical areas where no or only few studies on entoprocts have been conducted, including the Southern Ocean.

Until now, only the two studies by Franzén (1973) and Emschermann (1993) have focussed on *Loxosomella* species found in the Antarctic. The fact that Franzén (1973) was able to analyse samples collected during the 1901–1903 Swedish Antarctic Expedition highlights the importance of well-curated museum collections. Apart from locations in subantarctic regions, he reported two species from the northwestern Weddell Sea (NW WS; for geographical locations see Fig. 1). *Loxosomella compressa* Nielsen & Ryland,

1961 subsp. *antarctica* Franzén was found south of Seymour Island on a polynoid scale worm. North of Joinville Island is the type locality and the only known site where approximately 700 individuals of *Loxosomella antarctica* Franzén, 1973 were found on a single ophiuroid host.

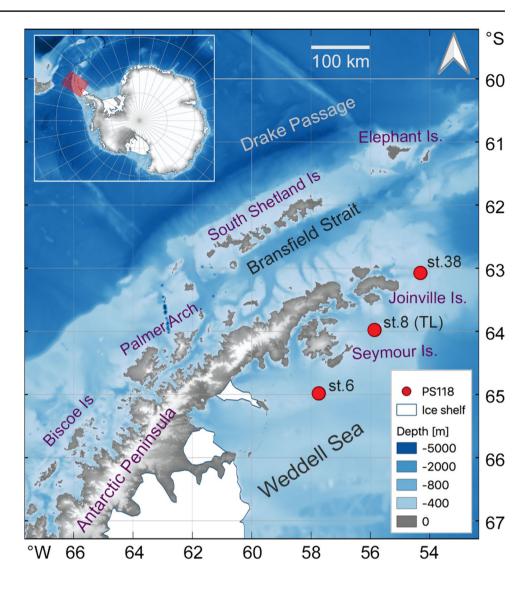
Emschermann (1993) reported 7 Loxosomella species from two Antarctic expeditions in the summer of 1989/1990. During RV *Meteor* expedition M XI-4, 15 stations were sampled along the western side of the Antarctic Peninsula (AP), including South Shetland and Biscoe Islands, Palmer Archipelago and Bransfield Strait (Fig. 1). RV Polarstern expedition ANT-VIII-5 contributed 28 stations in the SW and SE WS. At AP Loxosomella tonsoria Emschermann, 1993 was found on ampharetid polychaetes. At AP and in the southeastern (SE) WS, L. antarctica was collected from ophiurids and aphroditid polychaetes and Loxosomella varians Nielsen, 1964 from nephthyid polychaetes. L. compressa antarctica lives on polynoid polychaetes at AP and in the southwestern (SW) and SE WS. Loxosomella antedonis Mortensen, 1911 was found on aphroditid polychaetes in the SW and SE WS. Finally, Loxosomella brochobola Emschermann, 1993 and Loxosomella seirvoini Emschermann, 1993 are only known from the SE WS where they were collected from bryozoans and sipunculid annelids, respectively.

For a study on the diversity and function of meiofauna and macroinfauna in Southern Ocean soft sediments, we investigated samples from the northwestern Weddell Sea collected during RV Polarstern expedition PS118 in 2019 (Witte et al. 2019; Fig. 1). In the sediment fractions that were inspected for meiofauna, several individuals of a new species of Loxosomella were found. As of now, only two free-living meiofaunal Entoprocta species are known (Nielsen, 2020): Loxosoma isolata Salvini-Plawen, 1968 and Loxosomella vancouverensis Rundell & Leander, 2012 which inhabit coarse sands in shallow waters. L. isolata was described from Rovini (Croatia; Salvini-Plawen, 1968) and L. vancouverensis from Vancouver Island (Canada; Rundell and Leander 2012). Additionally, several other to date undescribed meiofaunal Entoprocta species have been found on the Florida coast, the Northern Adriatic and the French Atlantic coast (Nielsen 2020). However, truly meiofaunal Loxosomatidae are the exception and Polychaeta and/or their tubes and burrows are the preferred hosts/habitats of solitary species. Nielsen (1964) lists polychaete families such as Aphroditidae, Capitellidae, Maldanidae, Pectinariidae, Polynoidae and Sigalionidae as typical hosts for Loxosomatidae.

Therefore, the aim of this study is to contribute to the knowledge of understudied Antarctic taxa with the description of the new solitary entoproct species *Loxosomella sigridae* sp. nov. An environmental characterisation of its sampling locality in the northwestern Weddell Sea is given. Further, members of polychaete families inhabiting the same sediment horizons are presented and their possible



Fig. 1 Map of the northern part of the Antarctic Peninsula and the northwestern Weddell Sea. Upper left: overview map of the Antarctic indicates location of detailed map (red frame). Stations (st.) visited during RV Polarstern expedition PS118 are represented by red dots. TL=type locality where Loxosomella sigridae sp. n. was found (for coordinates see Table 1). Map created by Leon Hoffman using QGIS (2022) and bathymetry from GEBCO (IOC, IHO, BODC 1994)



relationship to and ecological importance for the new species are discussed.

Material and methods

Sampling and sample treatment

During RV *Polarstern* expedition PS118 (09.02.–10.04.2019) to the northwestern Weddell Sea, sediment samples were taken for meiofaunal analysis using a Multicorer MUC10 equipped with eight polycarbonate cores (inner diameter 94 mm, surface area of 69.4 cm²; Fig. 1, Table 1; Witte et al. 2019). Throughout the text, cores are designated with a combined identifier consisting of "station-deployment-core" number based on the information given in Table 1.

From the sediment cores, subsamples were extracted for sediment analyses, which reduced the available surface area per core to 66.4 cm². All sediment cores were sliced into 1-cm sections for the first five centimetres and stored in a borax-buffered 4% formaldehyde-seawater solution. Cores from station 6 deployment no. 2 were split in half due to sampling constraints. At the home institute, samples from stations 6, 8 and 38 were washed with 20- μ m filtered tap water over three stacked sieves with 1000, 500, and 32- μ m mesh sizes. All available material of the size fractions > 1000 μ m and 500-1000 μ m was used for macrofauna determination (including Polychaeta, see below).

The 32–500 µm sediment fraction was used for meiofauna analyses and centrifuged with a colloidal silica polymer (Levasil® 200/40, Akzo Nobel Pulp and Performance) as a flotation medium. Kaolin was added to hold back heavier particles during decantation (McIntyre and Warwick 1984). Every sample was centrifuged three times for 6 min at 4000 rpm. After each iteration, the supernatant containing organic matter and fauna was decanted over a 32-µm sieve, rinsed with filtered tap water and



Table 1 Sediment samples were collected with the multicorer during RV *Polarstern* expedition PS118 (09.02.–10.04.2019) to the northwestern Weddell Sea. Cores from three stations were used for this study. Information on deployment and core numbers, sampling date, water depth and coordinates are given according to Witte et al. (2019). Individual numbers of *Loxosomella sigridae* sp. nov., Copepoda and Nematoda (as representatives of the two most abundant meiofauna taxa) found in each core are expressed per 10 cm²

(0-5 cm sediment depth). Sediment cores were sliced in 1-cm steps (0-1, 1-2, 2-3, 3-4, 4-5 cm horizons). Amount of sediment available/analysed per core/sediment horizon (expressed as surface area): $W=\text{whole core }(66.4 \text{ cm}^2)$, $H=\text{half }(32.7 \text{ cm}^2)$, $H=\text{permonent}(16.6 \text{ cm}^2)$. For macrofauna (including Polychaeta) whole cores were analysed (except for cores from station-deployment 6-2, see material and methods section). In the following, cores are designated with a combined identifier consisting of "station-deployment-core" number

Station	Deployment	Core no	Sampling date	Depth [m]	Coordinates	Analysed surface	Individual densities per 10 cm ^{2 a)}			
no	no					per sediment horizon	L. sigri- dae sp. nov.	Copepoda	Nematoda	
6	2	6; 18	05.03.2019	423	64° 58.724' S 57° 46.379' W	all horizons: H	0; 0	100.6; 138.3	2400.5; 2633.0	
6	3	11; 14	05.03.2019	425	64° 58.612' S 57° 46.363' W	all horizons: W	0; 0	114.4; 102.2	4196.0; 3318.1	
8	5	6	11.03.2019	413	63° 58.264' S 55° 54.322' W	0–2 cm: ¹ / ₄ 3–5 cm: W	2.1	277.4	3006.8	
8	7	3	11.03.2019	415	63° 57.882' S 55° 54.469' W	0–2 cm: ¹ / ₄ 3–5 cm: W	3.6	247.9	3670.9	
8	7	7	11.03.2019	415	63° 57.882' S 55° 54.469' W	0–2 cm: ¹ / ₄ 3–5 cm: W	0.5	186.0	2813.3	
38	3	15; 16	22.03.2019	427	63° 04.480' S 54° 20.226' W	0–2 cm: ¹ / ₄ 3–5 cm: W	0; 0	884.7; 940.4	3441.5; 4582.5	
38	3	21	22.03.2019	427	63° 04.480' S 54° 20.226' W	all horizons: W	0	926.4	3348.9	

a) values for different cores separated by ";"

preserved again with 4% buffered formalin. Samples were stained with Rose Bengal in order to facilitate sorting. In core 38-3-21 (station-deployment-core no., see Table 1), an exceptionally high abundance of meiofauna organisms, especially Copepoda, was detected. Therefore, the first two sediment horizons, of the remaining cores from stations 8 and 38 were split into eight parts each using a Jensen splitter (Jensen 1982). Meiofauna organisms of two of these subsamples per slice were counted (aliquot representing $\frac{1}{4}$ core surface). Thus, the amount of sediment per core that was available and analysed varied and is expressed as respective surface area [W= whole core (66.4 cm²), H= half (32.7 cm²), $\frac{1}{4}$ = quarter of core (16.6 cm²); Table 1].

Table 2 Number of *Loxosomella sigridae* sp. nov. found in sediment layers of three cores collected at station 8 during RV *Polarstern* expedition PS118 (2019) to the northwestern Weddell Sea. Note the dif-

Meiofauna and Entoprocta

Meiofauna was counted and higher taxa identified under Leica Mz 12.5 and Mz 125 stereo microscopes according to the pictorial keys of Higgins and Thiel (1988) and Schmidt-Rhaesa (2020). All entoprocts were transferred to glycerine and mounted on slides. Specimens of *Loxosomella sigridae* sp. nov. were only found at station 8 (Fig. 1; Tables 1, 2).

Several specimens were stained with acid-fuchsin and Congo-red watery solution and imaged with a confocal laser-scanning microscope (CLSM; method modified after Michels and Büntzow 2010). These individuals were mounted on slides using corn syrup to avoid displacement during the scans. Scans were made with a Leica CTR 5000

fering amount of sediment that was inspected for the different sediment layers (see Table 1). Bold numbers: Total number of individuals found per core

Station-Deployment-Core no	0–1 cm	1–2 cm	2–3 cm	3–4 cm	4–5 cm	Total
8-5-6	0	0	6	7	1	14
8-7-3	3	2	1	1	2	9
8-7-7	0	0	0	3	0	3



(DZMB, Senckenberg am Meer) equipped with a Leica DM 5000 B microscope (400×magnification) and two visible light lasers (Argon and DPSS561). Maximum intensity projections were created with the Leica LAS software (Leica Microsystems) using image stacks. The final images were assembled and adjusted for colour, contrast and brightness using Adobe Photoshop CS 3 software. Inkscape v1.1 was used to assemble the figures. Line drawings were made from CLSM scans using a Wacom cintiq 16 tablet and Inkscape v1.2.

Polychaeta

Polychaeta were analysed from the > 1000-μm and 500-1000 μm sediment fractions. Individuals were determined to family level using taxonomic keys (Hartman 1964, 1976, 1996; Fauchald and Jumars 1979; Pettibone 1982; Hartmann-Schröder 1996; Hayward and Ryland 2017). Individuals found in the same sediment layers as specimens of *Loxosomella* were visually inspected for adhering Entoprocta. Polychaetes were stored in 4% buffered formalin. Information on polychaete life style was adapted from Rouse and Pleijel (2001).

Environmental characteristics

Sediment and water-column parameters were determined according to Säring et al. (2022). Environmental parameters relevant for the present study were: *Water column*—temperature near the sea bottom ($_{bottom}$ T), salinity near the sea bottom ($_{bottom}$ Sal); *sediment*—chlorophyll a content ($_{sed}$ Chl a), phaeopigment content ($_{sed}$ Phaeo), carbon:nitrogen ratio, content of silt&clay (<63 μ m), sand (63–500 μ m) and coarse

Table 3 Morphometrics of the type material (10 individuals) of *Lox-osomella sigridae* sp. nov. collected at station 8 during RV *Polarstern* expedition PS118 (2019) to the northwestern Weddell Sea. Number

sand (> 500 μ m) all averaged over the 0–5 cm layers of the respective sediment cores. Pigment and C/N_{molar} measurements were obtained from the same cores as the animal counts (Table 1), grain-size measurements were averaged from additional environmental cores, preferably from the same deployments where available.

Taxonomy

Phylum Entoprocta Nitsche, 1869.
Family Loxosomatidae Hincks, 1880
Genus Loxosomella Mortensen, 1911
Loxosomella sigridae Corus & Veit-Köhler sp. nov.
http://zoobank.org/urn:lsid:zoobank.
org:pub:C7694617-7ECE-42E9-ABCF-C5E5DEF433CD.

Type material

The examined specimens are registered and deposited in the collection of the Museum für Naturkunde Berlin, Germany (MfN) previously Zoologisches Museum Berlin (ZMB), collection "Vermes", catalogue "Freilebende Würmer" (Free-living Worms). All specimens were collected with a multicorer in the northwestern Weddell Sea, Southern Ocean (Table 1). Information on sampling location indicate "Expedition, coordinates, water depth, station-deployment-core number, sediment horizon". Morphometrics of each individual are given in Table 3.

Holotype, ZMB 12934 (with embryos, 1 slide): RV *Polarstern* PS118, 63° 57.882' S, 55° 54.469' W, 415 m, 8-7-3, 4–5 cm.

of tentacles, number of larvae or buds observed at each individual, and length and width measurements are given (for terminology of body parts see Fig. 2)

Individual	tentacles	larvae L /	Length				Width	
	no	buds B no	total [µm]	calyx [µm]	peduncle [μm]	foot [µm]	lophophore [µm]	calyx [µm]
Holotype	12	4 L	773	512	55	206	294	285
Paratype 1	12	4 L	534	336	48	150	213	214
Paratype 2	10	4 B	399	270	27	102	150	159
Paratype 3	10	1 B	354	231	27	96	162	141
Paratype 4	12	1 L	525	324	36	165	183	156
Paratype 5	10	_	379	227	48	103	136	94
Paratype 6	10	4 B ^{a)}	573	370	30	173	167	124
Paratype 7	12	3 L	576	345	36	194	197	112
Paratype 8	12	8 L	715	506	94	115	209	191
Paratype 9	10	_b)	524	324	52	148	124	103

a) one of which broken off but preserved in same slide; b) gonads with early-stage larvae inside calyx (Fig. 4b)

Paratype 1, ZMB 12935 (with embryos, 1 slide): RV *Polarstern* PS118, 63° 58.264' S, 55° 54.322' W, 413 m, 8-5-6, 3-4 cm.

Paratype 2, ZMB 12936 (with buds, 1 slide): RV *Polarst-ern* PS118, 63° 58.264' S, 55° 54.322' W, 413 m, 8-5-6, 3–4 cm.

Paratype 3, ZMB 12937 (with buds, 1 slide): RV *Polarst-ern* PS118, 63° 58.264' S, 55° 54.322' W, 413 m, 8-5-6, 3–4 cm.

Paratype 4, ZMB 12938 (with embryo, 1 slide): RV *Polarster*n PS118, 63° 58.264' S, 55° 54.322' W, 413 m, 8-5-6, 3-4 cm.

Paratype 5, ZMB 12939 (1 slide): RV *Polarstern* PS118, 63° 57.882' S, 55° 54.469' W, 415 m, 8-7-3, 1–2 cm.

Paratype 6, ZMB 12940 (with buds, 1 slide): RV *Polarstern* PS118, 63° 57.882' S, 55° 54.469' W, 415 m, 8-7-3, 1–2 cm.

Paratype 7, ZMB 12941 (with embryos, 1 slide): RV *Polarstern* PS118, 63° 57.882' S, 55° 54.469' W, 415 m, 8-7-3, 2–3 cm.

Paratype 8, ZMB 12942 (with embryos, 1 slide): RV *Polarstern* PS118, 63° 57.882' S, 55° 54.469' W, 415 m, 8-7-3, 3–4 cm.

Paratype 9, ZMB 12943 (1 slide): RV *Polarstern* PS118, 63° 57.882' S, 55° 54.469' W, 415 m, 8-7-3, 4–5 cm.

6 individuals, ZMB 12944 (1 vial): RV *Polarstern* PS118, 63° 58.264' S, 55° 54.322' W, 413 m, 8-5-6, 2–3 cm.

3 individuals, ZMB 12945 (1 vial): RV *Polarstern* PS118, 63° 58.264' S, 55° 54.322' W, 413 m, 8-5-6, 3–4 cm.

1 individual, ZMB 12946 (1 vial): RV *Polarstern* PS118, 63° 58.264' S, 55° 54.322' W, 413 m, 8-5-6, 4–5 cm.

3 individuals, ZMB 12947 (1 vial): RV *Polarstern* PS118, 63° 57.882' S, 55° 54.469' W, 415 m, 8-7-3, 0–1 cm.

Type locality

Northwestern Weddell Sea (Southern Ocean), 63° 57.882' S, 55° 54.469' W, sediment sample collected during RV *Polarstern* cruise PS118, station-deployment-core no. 8-7-3, 415 m, 4–5 cm sediment depth (Fig. 1).

Etymology

This species is dedicated to Sigrid Corus, grandmother of Finn Corus, who always supports him and has a great love for nature.

Description

Holotype (Figs. 2, 3; Table 3). A medium-sized species. Total body length of adult 773 µm (including foot). Length of calyx 512 µm. Width of lophophore 294 µm. Body (calyx) widest at median part (285 µm). From there, body tapers gradually towards the foot forming a short, stout peduncle (length 55 µm). Foot length is 206 µm. Lophophore carrying twelve contracted tentacles. Food groove not closed on apical side of lophophore. Conspicuous Y-shaped row of cells on aboral side of calyx: two rows of single cells reach from the outer edge of the lophophore just anterior to the position of the stomach where they join a third cell row which ends shortly before the foot gland. Foot gland conspicuous (Figs. 2, 3). Foot groove accompanied by 11 paired accessory gland cells with pairing visible in most of them. Gland cells on the same side clearly separated by distinct spaces. Tip of the foot armed with a pair of thin adhesive papillae.

Adult variation (Table 3). Adults do not have larvae and buds at the same time. Adults with larvae carry 12 tentacles. Individuals with buds usually have 10 tentacles. In the type material, both stages are represented by 5 individuals, each.

Sexually reproducing adults carry larvae in atrium (Holotype, Paratypes 1, 4, 7, 8; Fig. 4a, c, d; Table 3). Number of observed larvae between 1 and 8. Adults with larvae usually with 12 tentacles. Total body length of these adults $525-773~\mu m$ (including foot), width of calyx (body) $112-285~\mu m$. Width of lophophore $183-294~\mu m$. Foot length varied between $115~and~206~\mu m$. Number of observed paired accessory glands up to 13.

Bud-carrying individuals (Paratypes 2, 3, 6; Fig. 5; Table 3) usually smaller than larvae-bearing adults with a total body length 354–573 μm. Number of tentacles usually 10. Maximum of two buds on each side of the calyx observed. Younger buds situated anteriorly of older ones. Maximum length of buds measured 168 μm.

Larvae (Figs. 2–4) of different stages are located in the atrium and calyx of the adult animals. The calyx can be deformed due to the presence of the larvae. The large size of the larvae suggests lecithotrophy.

Systematic discussion

Current status of the genus Loxosomella and differentiation from Loxosoma

Based on morphological characters, Nielsen (2010) recommended that the genus *Loxosomella* should be used in a wider sense. He therefore included *Loxocorone* Iseto, 2002, *Loxomitra* Nielsen, 1964 and *Loxomespilon* Bobin & Prenant, 1953 as subgenera of *Loxosomella* sensu stricto.



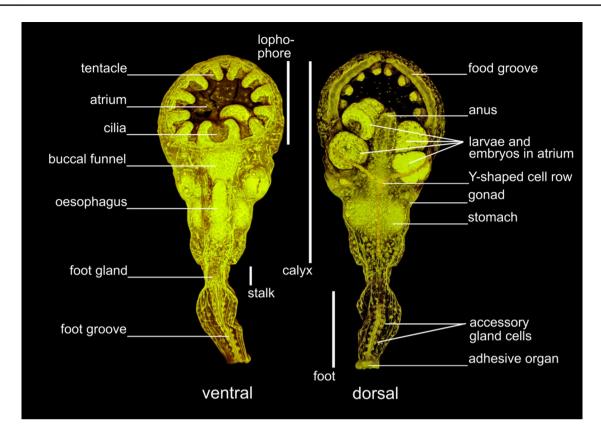


Fig. 2 Loxosomella sigridae sp. n., Holotype, collected in the northwestern Weddell Sea during the 2019 RV *Polarstern* expedition PS118 (st. 8): confocal laser-scanning images with morphological terms used in the description (length of calyx 512 μm, peduncle 55 μm, foot 206 μm)

This taxonomical move made it possible to assign new species to the genus even when the diagnostic details of decisive characteristics were undescribed. At the same time, genetic findings suggested that the genus *Loxosomella* may be paraphyletic (Fuchs et al. 2010). Recent molecular phylogenetic analyses using two genetic markers have further suggested that the entire family Loxosomatidae may need to be revised (Borisanova and Schepetov 2023). This situation highlights the need to combine both, molecular and morphological analyses in order to arrive at a sound phylogenetic conclusion.

Until the systematic situation of the family is clarified, new loxosomatid species will continue to be assigned to one of the two genera on the basis of the morphological characteristics of the attachment organ of the specimens. In buds of *Loxosomella* species, the peduncle terminates in an attachment organ with a foot gland and a foot groove with accessory gland cells (Mortensen 1911; Nielsen 1964). In adult individuals of *Loxosomella*, this foot may be either retained or reduced. In the latter case, the species show a variety of different morphological attachment structures (Borisanova 2018). Until recently, it was assumed that, in contrast to *Loxosomella*, both adult and

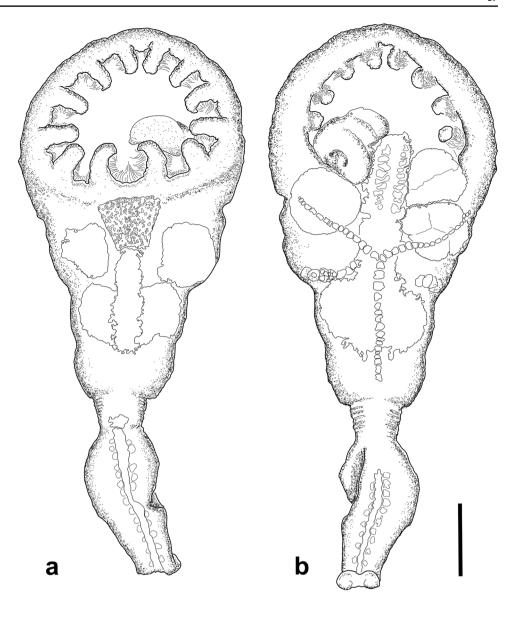
bud stages of members of the genus *Loxosoma* invariably possess a distinctive muscular disc, which enables them to adhere to the substrate (Bobin and Prenant 1953; Nielsen 1964; Emschermann 1993; Borisanova and Chernyshev 2019). However, Borisanova and Schepetov (2023) found that the muscular disc, being present in buds of one *Loxosoma* species, can be lost in the adult. Therefore, species may be erroneously placed in the genus *Loxosomella* if only the adult stage is known. However, this problem does not affect the placement of the new species presented here in the genus *Loxosomella* (see below).

Placement of *L. sigridae* sp. nov. in the genus *Loxosomella* and differentiation from congeners

Our material was fixed in formaldehyde and not suitable for genetic analyses. Therefore, the taxonomic placement is based on morphological characters. The new species is placed in the genus *Loxosomella* Mortensen, 1911, because it shows the complex elongated foot organ with a foot gland and a foot groove with accessory gland cells in bud-carrying stages and sexually reproducing adults (Figs. 2–5). Further, the conspicuous Y-shaped row of cells on the aboral side of



Fig. 3 Loxosomella sigridae sp. n., Holotype, collected in the northwestern Weddell Sea during the 2019 RV Polarstern expedition PS118 (station-deployment-core 8-7-3, sediment horizon 4–5 cm): Habitus of sexually reproducing adult with 12 tentacles and 4 larvae in the atrium. a Drawing of ventral view. b Aboral view. Scale bar: 100 µm



the body has only been described in a few other species of this particular genus (Nielsen 1964). Like the vast majority of previously described members of the genus *Loxosomella*, *L. sigridae* sp. nov. is a solitary species. The only to date known exception is the recently described colonial species *Loxosomella coronata* Borisanova 2021 (Borisanova 2021).

Members of the genus *Loxosomella* show a wide range of morphological variations for example in the number of tentacles, location of buds or shape of the foot (Nielsen 2017). Adults that retain the complex foot organ with foot groove and accessory gland cells as observed in *L. sigridae* sp. nov. were also described for e.g. *Loxosomella teissieri* (Bobin & Prenant, 1953), *Loxosomella elegans* Nielsen, 1964, *Loxosomella polita* Nielsen, 1964, *Loxosomella similis* Nielsen, 1964, *L. vancouverensis* Rundell & Leander, 2012 and *Loxosomella decorata* Nielsen, 2017. The foot groove of *L.*

sigridae sp. nov. is accompanied by 9 to 13 mostly paired accessory gland cells. Nielsen (1964) shows drawings of *L. elegans* with 16 to 22 (his Fig. 10), *L. similis* with 14 to 17 (his Fig. 12) and *L. polita* with 14 or 15 pairs of accessory gland cells (his Fig. 13). *L. vancouverensis* has approx. 12 (Fig. 1 in Rundell and Leander 2012), *L. decorata* between 9 and 10 (Fig. 2 in Nielsen 2017) and *L. teissieri* 19 to 23 paired gland cells (Fig. 33 in Nielsen, 1989). Contrary to these species, the accessory gland cells of *L. sigridae* sp. nov. are clearly separated by distinct spaces between the cells of the same side.

The tip of the foot of *L. sigridae* sp. nov. is armed with a pair of adhesive papillae. Such adhesive organs were also described for e.g. *L. elegans*, *L. vancouverensis* and *L. decorata* (Nielsen 1964, 2017; Rundell & Leander 2012). However, in *L. decorata*, these organs show characteristic



scalloped latero-posterior edges while the edges of the adhesive papillae of *L. sigridae* sp. nov., *L. elegans* and *L. van-couverensis* are smooth.

The characteristic Y-shaped cell row on the aboral body side of *L. sigridae* sp. nov. was previously only described for *L. elegans*, *L. polita*, *L. similis* and *Loxosomella kindai* Krylova, 1985. The original description of the latter was unavailable to us. However, in all other species including *L. sigridae* sp. nov., the Y-shaped cell row nearly reaches the sensory papillae. These papillae are not as pronounced in *L. sigridae* sp. nov. as in *L. elegans* (Nielsen 1964). In this group, *L. sigridae* sp. nov. is the largest species with up to 773 μm and 10 or 12 tentacles (Table 3). *L. elegans* is reported to measure up to 670 μm (10–13 tentacles), *L. polita* reaches 420 μm (6–10 but mostly 8 tentacles) and *L. similis* measures up to 415 μm with 10–11 tentacles (Nielsen 1964).

Only seven species of Loxosomella were previously reported from the Antarctic (Franzén 1973; Emschermann 1993): L. antarctica Franzén, 1973, Loxosomella antedonis Mortensen, 1911, Loxosomella brochobola Emschermann, 1993, L. compressa Nielsen & Ryland, 1961 subsp. antarctica Franzén, Loxosomella seiryoini Emschermann, 1993, Loxosomella tonsoria Emschermann, 1993 and Loxosomella varians Nielsen, 1964. Neither of these species is morphologically similar to the new species L. sigridae sp. nov. because they all lack the typical elongated foot with accessory gland cells and adhesive papillae at the tip and the characteristic Y-shaped cell row.

Reproductive cycle

Nielsen (1964, 1971) describes how most of the solitary Loxosomatidae grow and reproduce. In many species, adults release lecithotrophic larvae. These larvae go through a short planktonic phase before they settle and transform to a stage that asexually produces buds. Buds are released and develop into sexually reproducing adults.

In the new species *L. sigridae* sp. nov., we observed a tendency towards a smaller body size in bud-carrying individuals compared to larvae-bearing ones. Additionally, we found that all bud-carrying specimens of *L. sigridae* sp. nov. had 10 tentacles, while the larvae-bearing adults had 12 tentacles (Table 3). The only exception (Paratype 9, Fig. 4b) may represent a transitional stage towards sexually reproducing adult: while this individual held 10 tentacles, early-stage larvae were visible inside the calyx but not in the atrium. These findings may indicate that in *L. sigridae* sp. nov., the life stage that produces buds precedes the sexually reproducing stage.

Environment and ecology

Water-column and sediment characteristics

Environmental parameters were determined for the three stations 6, 8 and 38 sampled during RV *Polarstern* expedition PS118 (Witte et al. 2019; Fig. 1, Table 1) and are presented in Table 4. Biotic sediment data are presented by Weith et al. (2023). Abiotic water-column measurements were obtained from Janout et al. (2020). Additional information on biotic parameters of the water column can be obtained from Weith et al. (2024b).

While salinity did not differ between the three stations, station 8 showed an intermediate water temperature close to the seafloor ($_{bottom}$ T=-1.53 °C). Station 8 had more than ten times higher $_{sed}$ Chl a values in the sediment (0–5 cm) than station 6, while its $_{sed}$ Phaeo values were nearly as high as those of station 38. Little to no difference was found between stations 6 and 8 for $_{sed}$ C/N $_{molar}$. This indicator of freshness of organic material in the sediment showed that the available food at these two stations (both $_{sed}$ C/N $_{molar}$ \sim 8) was not as degraded as at station 38 with a $_{sed}$ C/N $_{molar}$ of 10.8. Station 8 was the location with the highest sand content (20%) and consequently held the lowest content of silt&clay (79% vs 94% and 84% at stations 6 and 38, respectively). Additionally, the sediment at station 8 contained a low amount of coarse sand which was negligible at the other two stations.

Abundance and distribution of *Loxosomella sigridae* sp. nov. and other groups of the meiofaunal size class

Benthic meiofauna was analysed from three stations 6, 8 and 38 of the RV *Polarstern* expedition PS118 (Fig. 1). *L. sigridae* sp. nov. was only present in sediment cores from station 8 (Table 1). In total, 26 individuals were found distributed over three cores from two different MUC-deployments (Table 2). In core 8-7-3, the individuals were spread over all sediment layers. In core 8-5-6, *L. sigridae* sp. nov. was not present in the first two sediment horizons, and in core 8-7-7, it was only found in the 3-4-cm layer.

Individuals of *L. sigridae* sp. nov. were very rare in the investigated sediment samples (maximum of 3.6 ind. 10 cm^{-2} ; Table 1). To highlight the extreme differences in individual numbers, values for Nematoda and Copepoda are given. As usual for meiofauna, Nematoda were the most abundant group (with a maximum of nearly 4600 ind. 10 cm^{-2} at station 38) followed by Copepoda. These crustaceans showed low numbers of individuals at station 6 (max. $138 \text{ ind. } 10 \text{ cm}^{-2}$), were slightly more abundant at station 8 (max. $277 \text{ ind. } 10 \text{ cm}^{-2}$) and were represented by extremely high numbers at station $38 \text{ (max. } 940 \text{ ind. } 10 \text{ cm}^{-2}$).







<Fig. 4 Loxosomella sigridae sp. n., confocal laser-scanning images of Paratypes collected in the northwestern Weddell Sea during the 2019 RV Polarstern expedition PS118. **a** Paratype 7, individual with 12 tentacles and 3 larvae (station-deployment-core 8-7-3, sediment horizon 2–3 cm). **b** Paratype 9, with 10 tentacles and gonads with early-stage larvae inside calyx (8-7-3, 4–5 cm). **c** Paratype 1, with 12 tentacles and 4 larvae (8-5-6, 3–4 cm). **d** Paratype 4, with 12 tentacles and 1 larva (8-5-6, 3–4 cm). Scale bar: 100 μm

Families of co-occurring Polychaeta

Data on polychaete families found during PS118 are presented by Weith et al. (2024a). Members of only two families of Polychaeta were present in all 9 sediment layers where Entoprocta were found. Cirratulidae and Paraonidae showed respective maximum numbers of 9 and 7 individuals per sediment layer within a core (Table 5). Members of these two families had a maximum body length of 1.5 cm. The highest numbers of individuals in a single sediment layer were found for Hesionidae (22 ind.) and Opheliidae (15 ind.), both in the 0–1 cm layer of core 8-7-3. Lumbrineridae, Onuphidae, Orbiniidae and Sphaerodoridae were rarely found (max. 4 ind. per family in the total of the 9 sediment layers that held entoprocts; Table 5). Sorting of macrofauna was carried out after fixation and sieving processes. None of the polychaetes examined had Entoprocta on them.

Ecological discussion

Entoprocta and the environment

For the Southern Ocean, solitary Entoprocta have previously been described from locations west and north of the Antarctic Peninsula and from the Weddell Sea. To date, only two records are known from the northwestern Weddell Sea (Franzén 1973; Emschermann 1993). *Loxosomella antarctica* Franzén, 1973 was discovered north of Joinville Island on gravel mixed with clay and stones and *L. compressa antarctica* was found in sand and gravel south of Seymour Island (Fig. 1, 64°20'S, 56°38' W, 150 m depth). The site south of Seymour Island is close to the type locality of the new species *L. sigridae* sp. nov. (station 8). However, station 8 is situated at 413–415 m depth.

Thus, knowledge of the relationship between environmental factors and Entoprocta within this region is limited. We therefore aimed to describe the habitat of *L. sigridae* sp. nov. in as much detail as possible (see above: *Water-column and sediment characteristics*).

Loxosomella sigridae sp. nov. may not be free-living meiofauna

To date, free-living meiofaunal Entoprocta have only been described from shallow-water coarse sediments that allow a constant water current and provide enough space between the sand grains (Nielsen 2020). Salvini-Plawen (1968) and Rundell and Leander (2012) reported *Loxosoma isolata* and *Loxosomella vancouverensis* from coarse sand and shell hash with marl and silt, respectively. The only station where we found *Loxosomella sigridae* sp. nov. (station 8) was characterized by the highest sand content detected during our study (20.3%, grain size fraction 63–500 μm). However, this sediment cannot be described as "coarse sand" (>500 μm) but rather as "sandy mud" because it contained 79.3% silt&clay (<63 μm). Silt and clay particles clog the already small interstices between the sand grains and prevent sufficient water flow which is necessary for suspension feeding.

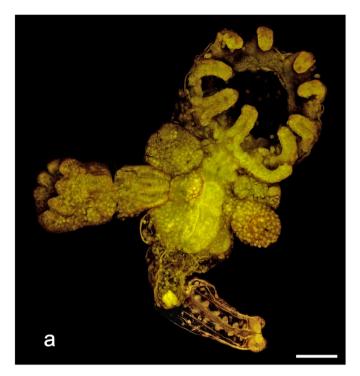
Furthermore, the free-living meiofaunal species *L. van-couverensis* has a body size of only 440 µm (Rundell and Leander 2012), while adult *L. sigridae* sp. nov. measure 525–773 µm. With this large body size, a truly interstital life style is not possible in finer sediments such as at station 8. Further, no Entoprocta were found during a large-scale meiofauna study in sediments from the NW WS and Bransfield Strait that contained 19.6% and 29% sand, respectively (pers. observation; Veit-Köhler et al. 2018). Based on the animal size and the grain-size composition of the sediment, we suggest that *L. sigridae* sp. nov. is not free-living meiofauna.

Loxosomatidae and their connection to polychaete hosts

Most of the solitary Entoprocta are symbionts and most are related to polychaetes. Because of a strong host specificity, the distribution of host species directly influences the distribution of entoprocts (Nielsen 1964). This host specificity, at least at the family level, has been described for several Antarctic species. *Loxosomella antarctica* lives on the aphroditid polychaete *Laetmonice producta* (and the ophiuroid *Ophiurolepis gelida*), *Loxosomella compressa antarctica* on the polynoid scale worm *Harmothoë spinosa* and *Loxosomella varians* on *Nephtys* (*Aglaophamus*) *foliosus* (Franzén 1973; Emschermann 1993).

Loxosomatidae may live on the polychaete host itself or in its burrows or tubes. In both cases, they use the water currents produced by the host to filter for food and take up oxygen (Nielsen 1989; Borisanova 2018). When living directly on the host, Loxosomatidae are found on all kinds of appendages such as chaeta, cirri, gills, notopodia, parapodia, the ventral side of elytra or the prostomium (Nielsen 1964; Emschermann 1993; Borisanova 2018). Additionally, the polychaete host may live in a tube and create a water current





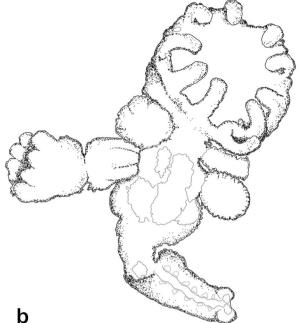


Fig. 5 Loxosomella sigridae sp. n., Paratype 2, collected in the northwestern Weddell Sea during the 2019 RV *Polarstern* expedition PS118 (station-deployment-core 8–5-6, sediment horizon 3–4 cm):

Specimen with 10 tentacles and 4 buds (two on right and two on left side of body), ventral view. **a** Image taken with confocal laser–scanning microscope. **b** Line drawing. Scale bar: 50 µm

from which the small energy symbionts profit. Further, loxosomatids may live on polychaetes that co-inhabit the tubes of other polychaetes. Truly tube-living Loxosomatidae are

Table 4 Parameters describing the environment at stations 6, 8 and 38 of the RV *Polarstern* expedition PS118 (2019) to the northwestern Weddell Sea. Abbreviations used: Water-column parameters – bottom: measurement close to the seafloor; T: water temperature; Sal: salinity. Sediment parameters – sed: parameter measured from sediment samples; Chl a: content of chlorophyll a; Phaeo: content of phaeopigments; C/Nmolar: molar carbon:nitrogen ratio; silt&clay: grainsize fraction < 63 μm; sand: 63–500 μm; coarse sand: > 500 μm. All sediment parameters averaged from 0–5 cm sediment depth. Pigment and C/Nmolar measurements obtained from the same cores as animal counts (Table 1), grain-size measurements averaged from further environmental cores (preferably from the same deployments if available). Data are available from Janout et al. (2020) and Weith et al. (2023)

Environmental parameter	Station 6	Station 8	Station 38
bottomT [°C]	- 1.86	- 1.53	- 0.86
_{bottom} Sal	34.58	34.55	34.57
$_{sed}$ Chl $a [\mu g g^{-1}]$	0.28	3.47	4.06
sedPhaeo [μg g ⁻¹]	5.18	9.36	11.49
sedC/N _{molar}	7.98	8.1	10.83
silt&clay %	93.88	79.29	84.29
sand %	6.09	20.33	15.71
coarse sand %	0.03	0.38	0

found with their peduncle inserted in the wall of mud tubes. They may have population sizes of up to 150 individuals per tube (Nielsen 1964). In the existing literature about Antarctic solitary entoprocts (Franzén 1973; Emschermann 1993), no species were recorded that freely live in tubes of polychaetes.

Possible polychaete hosts of L. sigridae sp. nov.

Nielsen (1964) and Borisanova (2018) provide lists of polychaete families that have been reported to be hosts of Loxosomatidae. From the polychaete families found in our samples that contained L. sigridae sp. nov. (Table 5) Maldanidae, Onuphidae, Scalibregmatidae and Spionidae have so far been recorded as hosts of Loxosomatidae. While Scalibregmatidae construct galleries the members of the other three families build tubes of different styles (Rouse and Pleijel 2001). The polychaete families with the greatest number of individuals in the samples we analysed were Hesionidae and Opheliidae. These families were not previously associated with loxosomatid entoprocts. Both are among the six polychaete families observed in our samples that do not build tubes (Table 5). However, members of none of these families were found in all the sediment layers that contained L. sigridae sp. nov. in our study.



Table 5 Individual numbers of Polychaeta (family level) found in the same sediment horizons of station 8 as *Loxosomella sigridae* sp. n. (compare Table 2). Samples collected during RV *Polarstern* expedition PS118 (2019) to the northwestern Weddell Sea. Two polychaete families (marked by bold letters and numbers) were present in all samples that contained Enformacia. Polychaete.

	StaDeploymCore	8-5-6			8-7-3					8-7-7
	Sediment Depth [cm]	2–3	3,4	4-5	<u>1</u>	1–2	2–3	£ 4	4-5	34
Family	Life style	Indivi	dual nun	nbers per	Individual numbers per sediment horizon	t horizon	_			
Maldanidae	Tubes with membraneous lining or consolidated burrows	0	-	_	1	0	0	0	-	ы
Opheliidae	No tubes, burrowers	0	0	0	15	8	2	1	0	1
Orbiniidae	No tubes, burrowers	0	0	0	0	0	ъ	0	0	0
Paraonidae	Surface dwelling or burrowing, burrows often lined with mucus (temporary tubes)	w	7	1	7	4	7	1	4	_
Scalibregmatidae	No tubes, burrowing, construct galleries	0		1	0	_	1	0	1	0
Hesionidae	No tubes, in- or epifaunal	_	0	1	22	5	0	1	0	_
Sphaerodoridae	No tubes, in- or epifaunal	0	0	0	3	0	0	0	1	0
Dorvilleidae	No tubes, different feeding types	_	0	0	2	_	2	1	ж	0
Lumbrineridae	No tubes (only exception does not apply here), burrowing	0		0	2	_	0	0	0	0
Onuphidae	Mostly tubicolous	0	0	0	1	0	0	0	0	0
Cirratulidae	Most sediment dwelling, tube-building groups live on hard substrates	1	4	1	7	9	9	∞	e	6
Spionidae	Tubes with sediment/mucus lining (most groups), some bore into shells	0	0	0	5	0	0	0	-	0



The only two polychaete families that were found in all layers together with L. sigridae sp. nov. were Cirratulidae and Paraonidae. Species of these two families were to date not related to Loxosomatidae (Borisanova 2018; her Table 3 and references therein). Most species of Cirratulidae are free-living, sediment-dwelling surface and subsurface deposit feeders. The tube-building members of this family usually live on hard substrates, which were not found in our samples (Rouse and Pleijel 2001). Cirratulidae are tentaculate and have either two groups or a single pair of anteriorly attached palps (Fauchald and Jumars 1979; Jumars et al. 2015). Apart from the feeding palps, most of the examined Cirratulidae in our samples had additional tentacles originating from more posteriorly situated chaetigers. These tentacles facilitate deposit feeding (Jumars et al. 2015) and may present suitable and protected adhering points for Loxosomatidae even when the polychaete is burrowing in the sediment (compare Fig. 7a in Emschermann 1993).

The second family present in all sediment samples is the Paraonidae. Most species are non-selective deposit feeders which actively burrow in different sediment depths to feed. These species build elaborate, temporary, mucus-lined tubes that may prevent any attached symbionts from becoming detached, while the host moves. Paraonidae are equipped with a single median antenna on the prostomium but they have distinct branchia and post-chetal lobes to which entoprocts may adhere (Rouse and Pleijel 2001; Jumars et al. 2015).

While Cirratulidae have a greater number of structures to attach to but do not build tubes, Paraonidae build tubes but have fewer appendages. Adhering Entoprocta may be protected in both cases: by the appendages in the first family and by the tubes in the latter. Therefore, we aspect that members of either of these families may be hosts of the new Entoprocta species. Furthermore, we conclude from our findings that *L. sigridae* sp. nov. is an epizoic symbiont that uses polychaetes themselves as hosts rather than living freely in polychaete burrows, as these are only temporary in Paraonidae.

Sampling gear and collection of Entoprocta

A multicorer is usually used to sample soft sediments. It is suitable for investigations of meiofauna and small macroinfauna and the core liners perfectly fit for on-board incubation experiments (Witte et al. 2019; Säring et al. 2022). Its cores have a diameter of (approx.) 9.4 cm which results in samples with a much smaller surface area and volume compared to e.g. samples collected with a box corer. Thus, large vagile macrofauna (including Polychaeta) and sessile host organisms that need hard substrates to settle such as Sipunculidae, Bryozoa and Porifera are usually not sampled with

a multicorer. Samples taken during the *Meteor* and *Polarstern* expeditions on which the publication of Emschermann (1993) was based were collected using the Van Veen grab, Agassiz trawl, rectangular dredge and the epibenthic sledge. These gears are commonly used to sample megafauna, epibenthic macrofauna and macroinfauna (Mincks and Smith 2007; Glover et al. 2008; Gutt et al. 2016; Pineda-Metz and Gerdes 2018) and thus the chance of finding Entoprocta (attached to their hosts) is higher, especially when living material is immediately sorted on board (Emschermann 1993). The methods we use to preserve and quantitatively extract the fauna from the soft sediment (shaking during fixation, sieving, centrifuging) may have caused the entoprocts to detach, which made an exact assignment to the host impossible.

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Author Contributions All authors contributed to the study conception and design. FW and GV-K took the samples on board RV *Polarstern*, FC and FW analysed the fauna. FC and GV-K conducted taxonomic examinations on Entoprocta, FW determined Polychaeta. All authors wrote the original draft and read and approved the final manuscript.

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Data Availability The type material and syntypes are deposited in the Museum für Naturkunde Berlin, Germany (MfN; previously Zoologisches Museum Berlin, ZMB). The new species is listed in ZooBank: http://zoobank.org/urn:lsid:zoobank.org:act:E7624381-0061-402B-80EE-3CF097B2D57D. This article is registered in ZooBank: http://zoobank.org/urn:lsid:zoobank.org:pub:C7694617-7ECE-42E9-ABCF-C5E5DEF433CD. The datasets generated and/or analysed during the



current study are available in the PANGAEA repository: Polychaete data https://doi.pangaea.de/10.1594/PANGAEA.960304; biotic water-column and sediment data https://doi.org/10.1594/PANGAEA.960309, https://doi.org/10.1594/PANGAEA.960326; oceanographic water-column data https://doi.org/10.1594/PANGAEA.913182. All further data generated or analysed during this study are included in this published article.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical Approval No approval of research ethics committees was required to accomplish the goals of this study because work was conducted with unregulated invertebrate species. All necessary permits for sampling and observational field studies have been obtained from the competent authorities.

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