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ORIGINAL ARTICLE

Description and phylogenetic position of the first sand-dwelling entoproct from the western coast of North America: *Loxosomella vancouverensis* sp. nov.

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Abstract

The Entoprocta is a poorly known lineage of suspension-feeding animals, with 180 described species, most of which are colonial or commensal. A small number of interstitial entoprocts are known, and these are from very few localities in Europe and the eastern coast of North America. We found the solitary entoproct reported here while undertaking a meiofaunal biodiversity survey off the western coast of Vancouver Island in British Columbia, Canada. This species, *Loxosomella vancouverensis* sp. nov., is the first putatively meiofaunal entoproct described from the western coast of North America.

Key words: eastern North Pacific Ocean, Vancouver Island, Entoprocta, Loxosomatidae, meiofauna biodiversity

Introduction

Marine sediment is a frontier for micro-metazoan species discovery (Giere 2009). It is also home to some of the most poorly understood metazoan lineages on Earth, including the Entoprocta, of which only 180 species are known (Iseto et al. 2008). According to some molecular phylogenetic evidence, entoprocts may be closely related to cyclophorans (Hejnlø et al. 2009) and to ectoprocts (Hausdorf et al. 2007, 2010; Helmkamp et al. 2008; Bleidorn et al. 2009; Hejnlø et al. 2009; Nesnidal et al. 2010). Entoprocts can be colonial or solitary, and the latter comprise the Loxosomatidae (118 species) (Nielsen 1995, 2010; Iseto et al. 2008). Loxosomatids are generally commensalistic and attach themselves, e.g. to the inner sides of polychaete tubes or the surface of larger invertebrates, which may provide shelter or water currents to supplement the entoprocts' own ciliary feeding currents (Iseto et al. 2008; Table I). Loxosomatids reproduce sexually or asexually by budding. Although a number of species have larvae with a long planktonic stage, many species produce a small number of creeping–swimming type

larvae, which have a very short free-swimming existence, suggesting that loxosomatids might have low rates of dispersal (Nielsen 1964). Only one loxosomatid has been described as free-living interstitial, although several undescribed meiofaunal entoprocts exist, and more are likely to be discovered (Giere 2009, p. 229). Nielsen (2010) noted that new entoproct species are discovered whenever a new locality is searched, indicating that our knowledge of loxosomatids is very fragmentary.

Meiofauna, as defined here, are microscopic eukaryotes (i.e. not fully visible with the naked eye) ranging from approximately 60 μm to 2 mm in body size: some of these species are interstitial, i.e. live in the spaces between grains of sand, rather than burrowing through the sediment, as infaunal invertebrates do (Giere 2009, p. 1). Among metazoan representatives, interstitial mode of life requires firm adhesion and subsequent release from frequently shifting sand grains, and the presence of an adhesive foot at the end of a stalk in interstitial entoprocts is well suited to these demands. One interstitial entoproct has been described, namely *Loxosoma isolata*, from the Adriatic Sea (Salvini-Plawen

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Table I. Summary of representative loxosomatid species. *Loxosomella harmeri*, *L. varians*, *L. murmanica*, *Loxomitra mizugamaensis* and *Loxomitra tetraorganon* are most closely related to *L. vancouverensis* sp. nov. as inferred from Figure 2. *Loxosoma isolata* is a meiofaunal species. The remaining species listed are *Loxosomella* species, most of which are commensals; these are listed alphabetically, beginning with *Loxosomella almugnecarensis*. Species for which no DNA sequence data are currently available are indicated with an asterisk. All measurements are in micrometers (μm).

Species	Author and year	Total length	Calyx length	Calyx width	Stalk length	Foot length	Number of tentacles	Locality and habitat
<i>Loxosomella vancouverensis</i> sp. nov.	Present paper	440	140	150	135	130	12	Vancouver Island; marine sand
<i>Loxosomella harmeri</i>	Schultz 1895	500–1500				250–750	12	White Sea (Russia), Denmark; on polychaetes
<i>Loxosomella varians</i>	Nielsen 1964	438–750	350	210	88		8	Denmark, Swedish W. coast; on/in polychaetes
<i>Loxosomella murmanica</i>	Nilus 1909	512	352	336		160		Kola Fjord (Russia), English Channel, W. coast of France, Denmark; on sipunculan
<i>Loxomitra mizugamensis</i>	Iseto 2002	≤ 1114			$3 \times$ calyx length		9	Okinawa Island (Japan); glass slides
<i>Loxomitra tetraorganon</i>	Iseto 2002	≤ 1200					9	Ryukyu Islands (Japan); glass slides
<i>Loxosoma isolata</i> *	Salvini-Plawen 1968	650	320	200	330		16	Punta Croce (Italy); medium coarse marine sand
<i>Loxosomella almugnecarensis</i> *	Tierno de Figueroa & Sanchez-Tocino 2009	400	250	200	150	152	10	Granada (Spain); on sponges
<i>Loxosomella ameliae</i> *	Sanchez-Tocino & Tierno de Figueroa 2009	820	460	190	360	260	10–12	Granada (Spain); on sponges
<i>Loxosomella atkinsae</i> *	Bobin & Prenant, 1953a (data from Nielsen 1964)	700–1100					10–12	Roscoff (France), Denmark; sipunculan tubes
<i>Loxosomella compressa</i> *	Franzén 1973 (data from Nielsen 1964)	445–700	178	78	267		8	Bergensfjord (W. Norway), Skagerrak-Kattegat (North Sea); on polychaetes
<i>Loxosomella discopoda</i> *	Nielsen & Ryland 1961 (data from Nielsen 1964)	180–200	156	91		86	6	Denmark, Bergensfjord; on ophiuroids
<i>Loxosomella elegans</i> *	Nielsen 1964	575–670				283	10–13	Denmark; polychaete tubes
<i>Loxosomella fauveli</i> *	Bobin & Prenant 1953b (data from Nielsen 1964)	530–800	305	179	225		8–13	Plymouth, Roscoff, Kattegat; on polychaetes
<i>Loxosomella glandulifera</i> *	Franzén 1962 (data from Nielsen 1964)	1600–3000	300	170	1300		8	Gullmarfjord (W. coast Sweden), Denmark; polychaete tubes
<i>Loxosomella macginitieorum</i> *	Soule & Soule 1965	1000–1600					22–34	Southern California; on/in stomatopod crustaceans
<i>Loxosomella marsypos</i> *	Nielsen & Ryland 1961 (data from Nielsen 1964)	≤ 350	135				8–12	Denmark, Bergensfjord; polychaete tubes
<i>Loxosomella nordgaardii</i> *	Ryland 1961 (data from Nielsen 1964)	402–475	313		88		8	Denmark, Bergensfjord; in bryozoan orifices
<i>Loxosomella ornata</i> *	Nielsen 1964	418–435	360		59		10–14	Between Denmark and Sweden; polychaete tubes

Table 1 (Continued)

Species	Author and year	Total length	Calyx length	Calyx width	Stalk length	Foot length	Number of tentacles	Locality and habitat
<i>Loxosomella phascosomatium</i> *	(Vogt 1876) (data from Nielsen 1964)	500	230	180	270		10–18	Arctic, NW Atlantic; on small mussels and sipunculans
<i>Loxosomella plakorticola</i> *	Iseto et al. 2008	1200	245–461		0.83–1.76 × calyx length	160	14–18	Okinawa Island (Japan); on sponges
<i>Loxosomella polita</i> *	Nielsen 1964	367–420		145	177		6–10, usually 8	Between Denmark and Sweden; on polychaetes and in polychaete tubes
<i>Loxosomella prenaniti</i> *	Soule & Soule 1965	800–1100					12	Southern California; on/in stomatopod crustaceans
<i>Loxosomella scaura</i> *	Nielsen 1964	≤ 900					10–14	Denmark; on polychaetes
<i>Loxosomella simiis</i> *	Nielsen 1964	323–415				141	10–11	Denmark, Bergensfjord; polychaete tubes

1968), but undescribed species have been reported off the coasts of North Carolina and Florida (USA) and Roscoff (France) (i.e. mostly undescribed species; Giere 2009). Here, we describe the first putative interstitial entoproct species from the western coast of North America, suggesting that increased exploration of marine sediments worldwide will yield additional entoproct species adapted to interstitial lifestyles.

Materials and methods

Collection of material

Shell hash, mixed with marl and silt, was collected by dredge at 15–20 m depth near Wizard Islet, Trevor Channel, Barkley Sound, on the western coast of Vancouver Island, British Columbia (BC), Canada (125°09.659' W; 48°51.580' N) on 20 September 2009. Wet sediment was kept in plastic containers on ice and immediately transported to the lab at Bamfield Marine Sciences Centre (Bamfield, BC) for sieving. Organisms were sieved into a large plastic Petri dish using the Uhlig seawater ice method and 230 µm Nitex plankton mesh (Uhlig 1964; Giere 2009, p. 75). Individual entoprocts (three individuals: one for LM, one for DNA, and one for the holotype) were captured by glass pipette under a dissecting microscope. Behaviour was observed under a Leica MZ6 stereomicroscope. Sediment from repeated dredges of this and nearby localities on 20 September 2009, and on 19 April 2010 yielded no additional specimens. Isolated entoproct specimens were kept in filtered seawater pending light microscopy (LM) and DNA extraction. Live entoprocts were relaxed in isotonic MgCl₂ solution and photographed under LM or photographed in situ under the dissecting microscope without relaxation.

DNA extraction, PCR amplification and sequencing

Entoprocts were dissolved in MasterPure kit buffer plus proteinase K solution at 55°C for > 24 h and DNA was subsequently extracted according to the kit protocol (MasterPure Complete DNA and RNA Purification Kit, Epicentre Biotechnologies). 18S rDNA was PCR amplified using illustra PuReTaq Ready-to-Go PCR beads (GE Healthcare), 22 µl dH₂O, 1 µl genomic DNA and the following primer pairs (1 µl of 10 µM concentration each): 1F, 5R; 3F, 9R (Giribet et al. 1996). PCR products were purified with ExoSAP-IT enzyme (USB, Affymetrix, Inc.) and sequenced using an ABI 3730 DNA Analyser and Big Dye chemistry (Applied Biosystems). A new sequence derived from the entoproct

described here was deposited into GenBank (accession number JF692209).

Alignment and phylogenetic analyses

The new sequence was edited in Sequencher (Gene Codes) and aligned with available entoproct sequences from GenBank (accession numbers AY218100, FJ196109, FJ196111, GU125745–GU125757, AJ001734, U36272) using ClustalX (Thompson et al., 1997). The alignment was improved by eye using MacClade 4 (Maddison & Maddison 2001).

Maximum parsimony (MP) and maximum likelihood (ML) analyses were conducted using *Symbion americanus* (Cycliophora; EF142081 (Baker & Giribet 2007)) as the outgroup, based on previous studies demonstrating a possible close relationship between cycliophorans and entoprocts (Funch & Kristensen 1995; Hejnol et al. 2009; Fuchs et al. 2010). MP analyses were conducted using heuristic searches, the tree-bisection-reconnection branch-swapping algorithm and 1000 random stepwise addition replicates. All characters were unordered and equally weighted. Bootstrap support (Felsenstein 1985) was assessed in PAUP* v. 4.0.b10 (Swofford 2002) based on 1000 pseudoreplicates. For maximum likelihood (ML) analyses, jModelTest v.01.1 (Guindon & Gascuel 2003; Posada 2008) was run using the Akaike information criterion model evaluation approach. The general time-reversible model with gamma distribution and number of invariant sites (GTR + G + I) was the best fit for the data. Ten likelihood replicates and non-parametric bootstrap analyses (100 pseudoreplicates) were performed in GARLI v. 0.95 (Zwickl 2006) under the GTR (6-rate) model and using default settings and rate matrix specified by jModelTest output.

Taxonomy

***Loxosomella vancouverensis* sp. nov.**

DNA sequence

Voucher 18S rDNA sequence is deposited on GenBank (GenBank accession number JF692209).

Holotype

Specimen collected by dredge from sandy bottom (i.e. shell hash, mixed with marl and silt). Depth: 15–20 m. Locality: (marine), Wizard Islet, Trevor Channel, Barkley Sound, on the western coast of Vancouver Island, British Columbia (BC), Canada (125°09.659' W; 48°51.580' N). Specimen fixed and

stored in 8% glutaraldehyde within an airtight tube. Deposited in the Beaty Biodiversity Museum (Marine Invertebrate Collection) at the University of British Columbia, Vancouver, Canada (catalogue number BBMMI4013).

Description

The pictured specimen (Figure 1) is 440 µm long at its greatest vertical dimension; calyx length (vertical): 140 µm; calyx width (at widest dimension): 150 µm. This species has 12 tentacles; each tentacle is approximately 55 µm long. The length taken from the base of the calyx to the tip of one of the attachment discs is 300 µm; stalk length (from base of calyx to the pedal gland): 135 µm; stalk width at widest point: 70 µm; stalk width at narrowest point: 30 µm. The length of the pedal gland is 40 µm; length of foot organ from the base of the pedal gland: 130 µm. No buds were present. Each tentacle possesses cilia. The digestive organs, mouth and anal cone lie within the calyx, below the tentacles, but are obscured in the LM and were not clearly visible in live specimens. The esophagus is visible below the calyx, and extends into the stalk. The hepatic cells of the stomach and gland cells of the stomach are visible above the oesophagus. There is a prominent grooved foot organ at the base of the stalk. There are two attachment discs at the base of the foot organ. The foot can strongly adhere to the substrate, remove itself, and re-attach. The external morphology of the foot organ may be diagnostic for this species, but until more interstitial entoproct species are captured, this is uncertain.

Etymology

This species is named after Vancouver Island and British Captain George Vancouver, who explored the Pacific Northwest region of North America in the 1790s.

Remarks on generic assignment

Our choice of genus for *Loxosomella vancouverensis* sp. nov. is based on its complex foot organ (as opposed to the suction-cup foot of *Loxosoma* Keferstein, 1862), and the presence of a differentiated pedal gland and pedal groove (Nielsen 1964).

Remarks on the new species

There is little information regarding the sister species for *L. vancouverensis* sp. nov., based on molecular evidence, as sampling for the phylogenetic

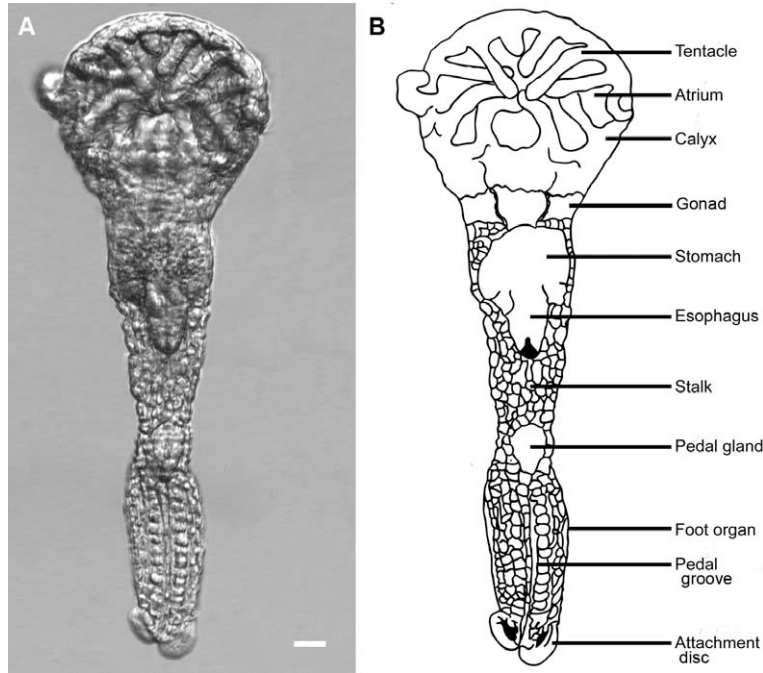


Figure 1. **A.** Light micrograph (LM) of an anesthetized live specimen of *Loxosomella vancouverensis* sp. nov., frontal view of full body (scale bar = 20 μ m). **B.** Line drawing based on Figure 1A, illustrating morphological features of *Loxosomella vancouverensis* sp. nov.

study is necessarily limited by the sequences available. On morphological grounds, species for comparison were not obvious because morphologically comparable species could not be identified in a review of loxosomatid species descriptions.

The foot organ in *Loxosomella vancouverensis* sp. nov., which is composed of a 130 μ m long structure with two adhesive structures at its terminus, differed from that of most other *Loxosomella* species, as well as the only described interstitial species *Loxosoma isolata* Salvini-Plawen, 1968, whose foot is composed of a simple, small suction cup at the end of the stalk (Salvini-Plawen 1968; Giere 2009, p. 230). The general external morphology of the foot organ of *L. vancouverensis* sp. nov. is most similar to the *Loxosomella elegans* specimen diagrammed by Nielsen & Jespersen (1997), although *L. elegans* is larger overall and has a longer foot (Nielsen 1964; see Table I).

Table I outlines comparisons of body measurements and tentacle counts for *L. vancouverensis* sp. nov. with other described entoprocts, beginning with the species in the same clade as *L. vancouverensis* sp. nov. (Figure 2) and followed by meiofaunal species of *Loxosoma* and representative *Loxosomella* species that are commensals. Measurements in Table I follow those reported in Schultz (1895), Nilus (1909), Nielsen (1964), Salvini-Plawen (1968), Iseto (2002), Iseto et al. (2008), Sanchez-Tocino & Tierno de Figueroa (2009) and Tierno de Figueroa & Sanchez-Tocino (2009).

Only two entoproct species (*L. macginitieorum* and *L. prenanti*, Table I) are described from the western coast of North America (southern California, USA), but neither species is morphologically similar, or close in body length, to *L. vancouverensis* sp. nov. (Soule & Soule 1965). Furthermore, these two species are both commensal on the stomatopod crustacean *Pseudosquilla bigelowi*, a different life habit than *L. vancouverensis* sp. nov. (Soule & Soule 1965).

Ecology

Loxosomella vancouverensis sp. nov. was found living between sediment grains in shell hash mixed with marl and silt, at 15–20 m depth in northeastern Pacific coastal waters. Only three specimens were found in approximately 1 m³ of carefully examined sediment (a volume of sand that includes both 2009 and 2010 searches), suggesting that this species might be quite rare. Although we sieved some columns of sand twice, and spot-checked unsieved sand periodically under the dissecting scope, we cannot rule out the possibility that many entoprocts simply did not migrate through the columns into the Petri dish. Other invertebrates with a comparable locomotory mode as *L. vancouverensis* sp. nov. were rare within sand samples. We also cannot rule out the possibility that the specimens found were washed out of either a tubicolous polychaete or another invertebrate animal living in this environment. However, many polychaete tubes from the same

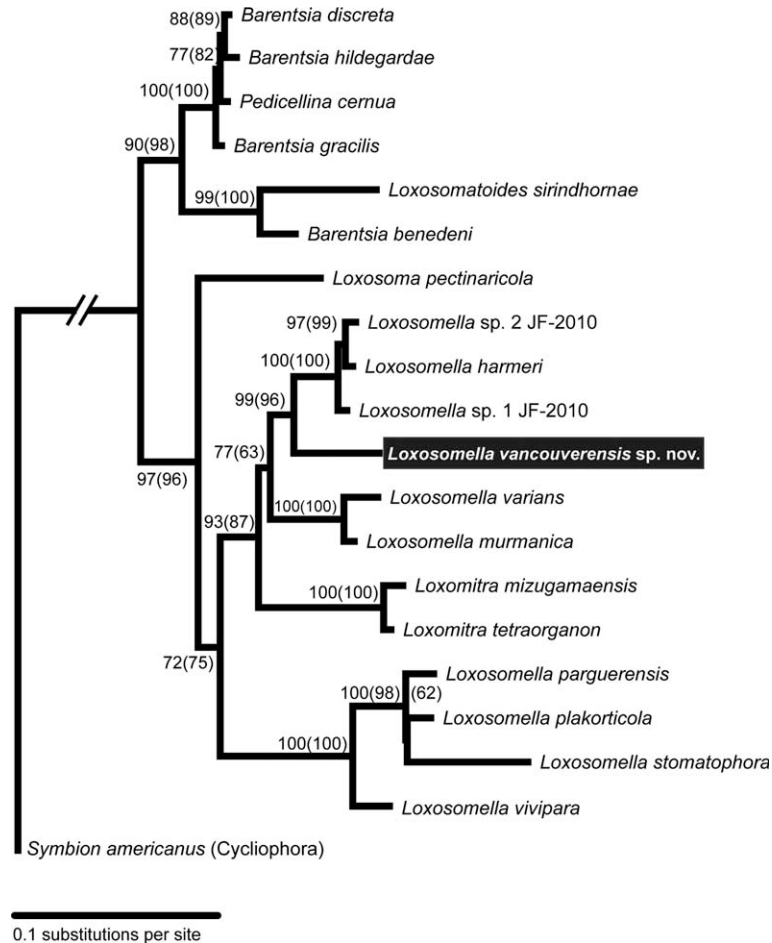


Figure 2. Phylogenetic position of *Loxosomella vancouverensis* sp. nov., relative to other entoprocts, based on 1781 bp of 18S rDNA. Maximum likelihood tree (GARLI; Zwickl 2006), $\ln L = -8062.08867$; bootstrap values greater than 50 indicated at nodes (MP bootstrap values in parentheses). Branch for outgroup *Symbion americanus* (Cycliophora) is scaled to 1/3.

dredge samples were examined and entoprocts were not present. This entoproct species was always found as a sand-dweller and had the tiny size and behaviour expected for interstitial animals (e.g. ability to attach, release, and then re-attach). Observations of the live animal feeding under the dissecting scope indicated strong ciliary currents combined with tentacular movement to capture microscopic food particles, as reported for other entoprocts (Riisgård et al. 2000).

Discussion

Morphology

The body of the solitary entoproct is minute (440 μm in length) and consists of a cup-shaped calyx with 12 tentacles that contains internal organs atop a stalk and a foot organ consisting of a separate vertically grooved region with a distinct, medially located pedal groove. The visible internal organs include gonads, an oesophagus and a U-shaped

digestive tract. The side of the calyx bearing the tentacular crown is considered ventral (uppermost in Figure 1), while the stalk-side of the calyx is dorsal. The mouth and anus (anal cone) are positioned within the tentacular crown of the calyx. Entoprocts are known to have between 8 and 30 tentacles, which are extensions of the body wall (Barnes 1980), and bear a complex ciliary system (Riisgård et al. 2000). Tentacular cilia within the calyx are shown in Figure 1.

The foot organ terminates in two attachment discs (general entoproct body form described by Nielsen & Jespersen 1997). This foot organ provides the animal with the ability to fasten securely to the substrate, remove itself, and re-attach. In contrast, some loxosomatids, particularly commensal species, remain firmly attached once they settle (e.g. Nielsen & Jespersen 1997; Iseto et al. 2008), although others may remain free. Iseto (2002) notes that *Loxosomella* species cement themselves on a substratum throughout adulthood; this sometimes results in a dramatic reduction of the foot structure (Nielsen 1964). Other entoprocts are known to be able to attach the foot,

remove it, and re-adhere, but the secretions of the complex gland system that presumably allows for this activity have not been described (Nielsen & Jespersen 1997). Meiofaunal entoprocts are too poorly known to make generalizations regarding their degree of attachment, although presumably in the shifting, interstitial environment, permanent attachment organs would be selected against. Indeed, despite the fact that *Loxosomella vancouverensis* sp. nov. is most closely related to other *Loxosomella* species (Figure 2), individuals of this species were observed repeatedly attaching, releasing and re-attaching to non-living substrates (e.g. grains of sand and shell hash, and the Petri dish).

Molecular phylogenetic position

The topologies for MP and ML analyses are identical, and so only the ML topology is shown with bootstrap values from both analyses listed (Figure 2). The overall topology is similar to the results reported in Fuchs et al. (2010), which also resolved two main clades: one containing *Barentsia*, *Loxosomatoides* and *Pedicellina*, and the other clade containing *Loxomitra*, *Loxosoma* and *Loxosomella*. In our analyses, *Loxosomella vancouverensis* sp. nov. nested within a clade containing five commensal *Loxosomella* species and two *Loxomitra* species from non-living substrates (Figure 2) (Schultz 1895; Nilus 1909; Nielsen 1964; Iseto 2002, Fuchs et al. 2010). *L. vancouverensis* sp. nov. is sister to a clade consisting of *L. harmeri* and two undescribed species: *Loxosomella* sp. 1 (GU125750) and *Loxosomella* sp. 2 (GU125751). *Loxosomella* sp. 1 is commensal on a sipunculan and, like *L. vancouverensis* sp. nov., was collected in the Pacific northwest (Friday Harbor, USA).

The molecular phylogenetic position of *L. vancouverensis* sp. nov. and a reasonable assessment of recent studies (e.g. Fuchs et al. 2010; Nielsen 2010) support the placement of the species in *Loxosomella*. Although *Loxosomella* is currently paraphyletic (Fuchs et al. 2010; Nielsen 2010), molecular data places *L. vancouverensis* sp. nov. within a subclade of *Loxosomella* species. All of the species in this particular *Loxosomella* subclade (as shown in the phylogenetic tree; Figure 2) are commensal with marine invertebrates except *L. vancouverensis* sp. nov. A revision of *Loxosomella*, and potentially *Loxomitra*, will be necessary within the context of the emerging molecular phylogenetic framework for entoprocts and the inevitable discovery of additional marine meiofaunal species.

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