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The position of *Urnatella gracilis* Leidy, 1852 on the molecular phylogenetic tree changes the view on the systematics of colonial Entoprocta

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ABSTRACT: In currently accepted system, the colonial Entoprocta are represented by three families: Barentsiidae, Loxokalypodidae, and Pedicellinidae. The two only known freshwater species, *Urnatella gracilis* Leidy, 1852 and *Loxosomatoides sirindhornae* Wood, 2005, are included in two different families, Barentsiidae and Pedicellinidae respectively. Although the available molecular data on colonial entoprocts are poor, they show that the current taxonomical system needs to be revised. The main aim of this study is to elucidate the phylogenetic position of the freshwater species *Urnatella gracilis* using molecular data that were obtained for this species for the first time. The material was collected in the Don River (Russia). The study is based on the molecular analyses of partial fragments of two genetic markers: 28S rRNA and 18S rRNA. According to the results of study, *Urnatella gracilis* forms a monophyletic clade with *Barentsia benedeni* (Foettinger, 1887) and *Loxosomatoides sirindhornae*. The close relationship of two freshwater species means that the colonization of fresh waters could have occurred within one family of Entoprocta but not independently in two families, Barentsiidae and Pedicellinidae, as it was suggested earlier. The type of organization of the colony of both *Loxosomatoides* and *Urnatella* may have evolved from the colonial ancestor similar to *B. benedeni*. Based on the results of phylogenetic analysis, we propose to exclude *B. benedeni* from the genus *Barentsia* and to assign it to the reinstalled genus *Arthropodaria*. We also propose to restore the family Urnatellidae with genera *Arthropodaria*, *Loxosomatoides*, and *Urnatella*.
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KEY WORDS: Kamptozoa, taxonomy, phylogeny, 28S, 18S, colonization of fresh waters.

Положение *Urnatella gracilis* Leidy, 1852 на молекулярно-филогенетическом древе меняет представления о систематике колониальных внутрипорошицевых

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РЕЗЮМЕ: В существующей на сегодняшний день системе колониальные Entoprocta

представлены тремя семействами: Barentsiidae, Loxokalypodidae и Pedicellinidae. Известно всего два пресноводных вида, *Urnatella gracilis* Leidy, 1852 и *Loxosomatoides sirindhornae* Wood, 2005, которые относятся к двум разным семействам, Barentsiidae и Pedicellinidae, соответственно. Молекулярно-генетические данные по колониальным внутрипорошицевым малочисленны, но они свидетельствуют о том, что существующая таксономическая система нуждается в пересмотре. Основной целью данного исследования стало выяснение филогенетического положения пресноводного вида *Urnatella gracilis* с использованием молекулярных данных, ранее для этого вида отсутствовавших. Материал был собран в реке Дон (Россия). Исследование основано на молекулярно-генетическом анализе частичных фрагментов двух генетических маркеров: 28S рРНК и 18S рРНК. Согласно результатам исследования, *Urnatella gracilis* образует монофилетическую кладу с *Barentsia benedeni* (Foettinger, 1887) и *Loxosomatoides sirindhornae*. Близкое родство двух пресноводных видов означает, что колонизация пресных вод могла произойти в пределах одного семейства Entoprocta, а не двух, как предполагали ранее. Оба типа организации колоний пресноводных представителей (типа *Loxosomatoides* и типа *Urnatella*) могли эволюционировать от организации колоний предка, сходного по строению с *B. benedeni*. Исходя из полученных результатов, мы предлагаем исключить *B. benedeni* из рода *Barentsia* и отнести его к восстановленному роду *Arthropodaria*. Предлагается также восстановить семейство Urnatellidae с родами *Arthropodaria*, *Loxosomatoides* и *Urnatella*.
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КЛЮЧЕВЫЕ СЛОВА: Kamptozoa, таксономия, филогения, 28S, 18S, колонизация пресноводных местообитаний.

Introduction

Phylum Entoprocta includes about 200 species of solitary and colonial animals. Until 1972, three families were distinguished within the phylum: Loxosomatidae Hincks, 1880, Urnatellidae Annandale, 1915, and Pedicellinidae Johnston, 1847 (Hyman, 1951; Brien, 1959). Loxosomatidae included all solitary species; Urnatellidae comprised the only freshwater colonial species known at the time, *Urnatella gracilis* Leidy, 1852; Pedicellinidae included all other colonial species. The taxon Urnatellidae was first mentioned by Allman (1856) a few years after the description of the species *U. gracilis* by Leidy (1852). Annandale (1915) presented a diagnosis of Urnatellidae and included two genera in the family: freshwater *Urnatella* Leidy, 1852 and brackish-water *Loxosomatoides* Annandale, 1908. Annandale (1915) indicated the following features of the family: brackish-water or freshwater habitat, formation of resting buds, and some details of the calyx morphology. However, the structure of the stalk and the organization of the colonies of these two genera are different. Based on these morphological features, the genus *Loxosomatoides* was later transferred to the family Pedicellinidae (Marcus, 1939; Toriumi, 1951). The family Urnatellidae was recognized as monotypic (Hyman, 1951; Brien, 1959).

Emschermann (1972) proposed a new classification of Entoprocta. He distinguished two orders within the phylum: Solitaria and Coloniales. Order Coloniales was subdivided into two suborders. Suborder Astolonata included the new family Loxokalypodidae Emschermann, 1972 with the only known at the time species *Loxokalypus socialis* Emschermann, 1972. The remaining colonial entoprocts were united in the suborder Stolonata. Emschermann (1972) proposed to exclude from the family Pedicellinidae species, which have stalk differentiated into muscular nodes and nonmuscular rods and proposed a new family Barentsiidae Emschermann, 1972 for them. The family Pedicellinidae was restricted to representatives with muscular

Table 1. Amplification primers and conditions.

Marker	Primers	PCR conditions	Reference
28S rRNA	**28SC1** ACC CGC TGA ATT TAA GCA T **28SC2** TGA ACT CTC TCT TCA AAG TTC TTT TC	5 min — 94 °C, 35×[15 s — 94 °C, 30 s — 50 °C, 45 s — 72 °C], 7 min — 72 °C	Le *et al*., 1993
18S rRNA	**1F** TAC CTG GTT GAT CCT GCC AGT AG **5R** CTT GGC AAA TGC TTT CGC	5 min — 94 °C, 35×[30 s — 94 °C, 30 s — 49 °C, 1 min — 72 °C], 7 min — 72 °C	Giribet *et al*., 1996; Whiting *et al*., 1997

stalk for entire length. The family Urnatellidae was abolished, and the genus *Urnatella* was included in the family Barentsiidae.

In 2010, the first molecular phylogenetic study of phylum Entoprocta was conducted (Fuchs *et al*., 2010). This analysis showed that the second freshwater entoproct species, *Loxosomatoides sirindhornae* Wood, 2005 (now belonging to the family Pedicellinidae), forms a sister clade to a clade joining species of the genus *Barentsia* Hincks, 1880 (now belonging to the family Barentsiidae) and the genus *Pedicellina* Sars, 1835 (now belonging to the family Pedicellinidae). These data showed that the currently accepted classification of Entoprocta needs a revision.

In our study, an updated molecular-phylogenetic tree of phylum Entoprocta based on partial sequences of the nuclear genes 28S rDNA and 18S rDNA, is presented, including for the first time the data on *Urnatella gracilis*.

Material and methods

Specimens of *Urnatella gracilis* were collected on the 7–9th of August 2024 in the Don River near Serafimovich town (49.492385° N, 42.766220° E) from a depth of 0.5–1 m from stones and shells of Viviparidae and Unionidae. Samples were fixed in 96% ethanol.

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted and purified from all whole samples preserved in 96% EtOH following the invertebrate protocol of the Canadian Center for DNA Barcoding (Ivanova *et al*., 2006). Recovered DNA was used as a template for amplification of partial 28S rRNA (~308bp) and partial 18S rRNA (~854bp) genetic markers. Polymerase chain reaction (PCR) conditions and primers are available in Table 1. PCRs were performed with an "HS Taq" kit (Eurogen Lab, Russia), following the manufacturer's protocol. For sequencing, 2 µL of amplicons were purified by EtOH + Ammonium acetate precipitation (Osterburg *et al*., 1975) and used as a template for the sequencing reactions (same primers as the original PCR) with a NovaDye Terminator v3.1 sequencing kit by GeneQuest (Russia). After additional purification, sequencing reactions were denaturated with Formamide HiDi (Thermo FS, USA) and analyzed using Locus 1616 Genetic Analyzer (Helicon, Russia). All novel sequences were submitted to NCBI GenBank (accession numbers PV082255; PV082259).

Molecular Data Analysis

A total list of samples used for the phylogenetic analysis can be found in Table 2. Raw reads for each gene were assembled and checked for ambiguities and low-quality data in Geneious R10 (Biomatters, Auckland, New Zealand). Edited sequences were verified for contamination using the BLAST-n algorithm run over the GenBank nr/nt database (Altschul *et al*., 1990). Original data and publicly available sequences of the 28S and 18S markers were aligned with the MUSCLE (Edgar, 2004) algorithm in MEGA7.0.26. Final alignments for each marker comprised 300 bp for 28S and 1788 bp for 18S. Phylogenetic reconstructions were conducted for the concatenated multi-gene dataset. The best-fit nucleotide evolution models were tested in the MEGA7 toolkit based on the Bayesian Information Criterion (BIC), the K2 + G model was chosen for both partitions. The analyses were performed by applying evolutionary models separately to partitions representing single markers. The Bayesian phylogenetic analyses and estimation of posterior probabilities were performed in MrBayes 3.2.7 (Ronquist, Huelsenbeck, 2003). Two independent analyses were carried out, they were initiated with a random starting tree with 20% of trees discarded as burn-in and ran for 5x10^6 generations. The Markov chains were sampled at intervals of 500 generations. The analysis was converged and terminated when the

Table 2. List of samples used for molecular phylogenetic analysis.

Species	Voucher	Locality	28s	18s	References
Urnatella gracilis	Ur1	The Don River	PV082259	PV082255	Our data
Barentsia benedeni		Laboratory culture		U36272	Mackey *et al.*, 1996
Barentsia discreta	GNM Entoprocta 11	Shimoda, Shizuoka, Japan	GU125742	GU125757	Fuchs *et al.*, 2010
Barentsia gracilis	GB	Sweden	FJ196138	FJ196109	Fuchs *et al.*, 2009
Barentsia hildegardae				AJ001734	Littlewood *et al.*, 1998
Pedicellina cernua	GB			FJ196111	Fuchs *et al.*, 2009
Loxosomatoides sirindhornae	GNM Entoprocta 10	Mae Klong River, Thailand	GU125741	GU125756	Fuchs *et al.*, 2010
Loxomitra mizugamaensis	GNM Entoprocta 9	Mizugama, Okinawa, Japan	GU125739	GU125754	Fuchs *et al.*, 2010
Loxomitra tetraorganon		Mizugama, Okinawa, Japan	GU125740	GU125755	Fuchs *et al.*, 2010
Loxosoma aripes	uk-31a	White Sea	OP846520	OP846517	Borisanova, Schepetov, 2023
Loxosoma axisadversum	La04	Hokkaido, Oshiro Bay, Japan	LC005491	LC005493	Kajihara *et al.*, 2015
Loxosoma pectinaricola		Tjärnö, Sweden	GU125733	GU125748	Fuchs *et al.*, 2010
Loxosomella aeropsis	E5	Sea of Okhotsk	MG021198	MG028643	Borisanova *et al.*, 2018
Loxosomella harmeri	GNM Entoprocta 4	Sweden, löpnr.318	GU125734	GU125749	Fuchs *et al.*, 2010
Loxosomella malakhovi	P4	Sea of Okhotsk	MG021201	MG028645	Borisanova *et al.*, 2018
Loxosomella murmanica	GB		DQ279950	AY218100	Giribet *et al.*, 2004, Giribet *et al.*, 2006
Loxosomella parguerensis	GNM Entoprocta 2	Belize	GU125731	GU125746	Fuchs *et al.*, 2010
Loxosomella plakorticola	GNM Entoprocta 7	Manza, Okinawa, Japan	GU125737	GU125752	Fuchs *et al.*, 2010
Loxosomella profundorum	GB	North-Western Pacific, near Kuril Islands		KM192152	Borisanova *et al.*, 2015
Loxosomella stomatophora	GNM Entoprocta 8	Manza, Okinawa, Japan	GU125738	GU125753	Fuchs *et al.*, 2010
Loxosomella vancouverensis	GB	Vancouver Island, British Columbia		JF692209	Rundell, Leander, 2012
Loxosomella varians	GNM Entoprocta 3	Tjärnö, Sweden	GU125732	GU125747	Fuchs *et al.*, 2010
Loxosomella vivipara	GNM Entoprocta 1	Belize	GU125730	GU125745	Fuchs *et al.*, 2010
Symbion pandora			AY218133	AY218106	Giribet *et al.*, 2004

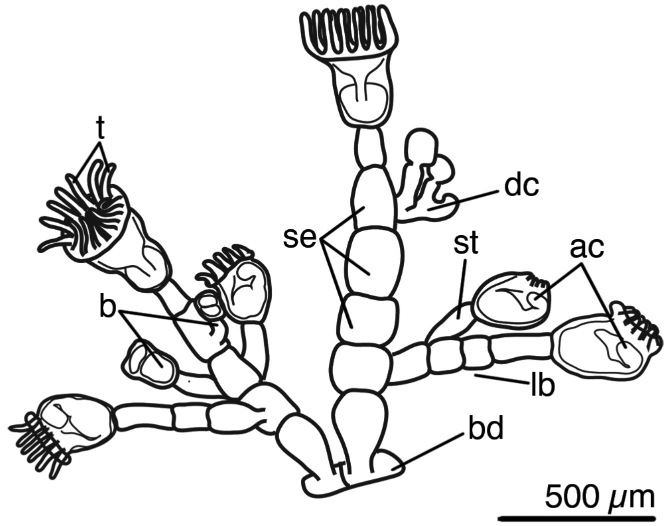

Fig. 1. Drawing of the colony of *Urnatella gracilis* from the Don River.
Abbreviations: ac — anal cone, b — bud, bd — basal disc, dc — daughter colony, lb — lateral branch, se — segments of the stalk, st — muscular stalk of young zooid, t — tentacle.

standard deviation of split frequencies reached <0.01. The Maximum likelihood analysis was conducted in raxmlGUI 2.0 (Edler *et al*., 2021) with automatically estimated pseudo-replicate number defined by the autoMRE algorithm (Pattengale *et al*., 2010) under the GTRCAT approximation, applied to each partition individually. Final phylogenetic tree images were rendered in FigTree 1.4.0.

Results

Brief morphological description

The colony consists of 1–2 stalks arisen from a common septate basal disc (Fig. 1). A stalk usually consists of 5–7 segments (up to 9 segments). The segments are swollen in the middle part, smooth and not bearing any spines. The first (lower) segment of the stalk is usually 1.5–2 times longer than the others. The last segment, which bears the calyx, is narrower than the others, cylindrical in shape and transparent. The calyx is separated from the stalk by a septum and a star-cell complex. The calyx bears 12–13 tentacles (young calyxes have 10 tentacles). The anal cone is small, rounded, lying horizontally in the calyx. The lateral branches of the colony develop on the stalk by budding. In young lateral zooids the stalk is unbranched, fully muscular; segments appear with age. From one zooid of the first generation 2–3 zooids of the second generation may develop. Zooids of the second generation may in turn develop buds of the third generation. Daughter colonies, consisting of two-three young zooids, may bud on stalk segments. They detach from the stalk of the maternal zooid and attach to the substrate.

The size of zooids depends on the number of stalk segments and varies from 500 μm in young specimens with not yet segmented stalks to 2.5 mm in zooids with a large number of segments. Calyxes are usually 350–430 μm long, in young buds — about 200 μm.

Phylogenetic analysis

The concatenated trees produced with Maximum Likelihood (ML) and Bayesian Inference (BI) analyses displayed similar topologies. All colonial species, including *Urnatella gracilis*, form a monophyletic group (posterior probability from BI (PP) = 1, bootstrap support from ML (BS) = 100) (Fig. 2). The monophyly of both families Barentsiidae and Pedicellinidae was compromised due to the position of *Pedicellina cernua* (Pallas, 1774) and *Barentsia benedeni* (Foettinger, 1887). The latter species forms a monophyletic group (PP = 1; BS = 100) with *Urnatella gracilis* (Barentsiidae) and *Loxosomatoides sirindhornae* (Pedicellinidae), however relationships between these three species are unresolved (PP = 0.85, BS = 58). *Pedicellina*

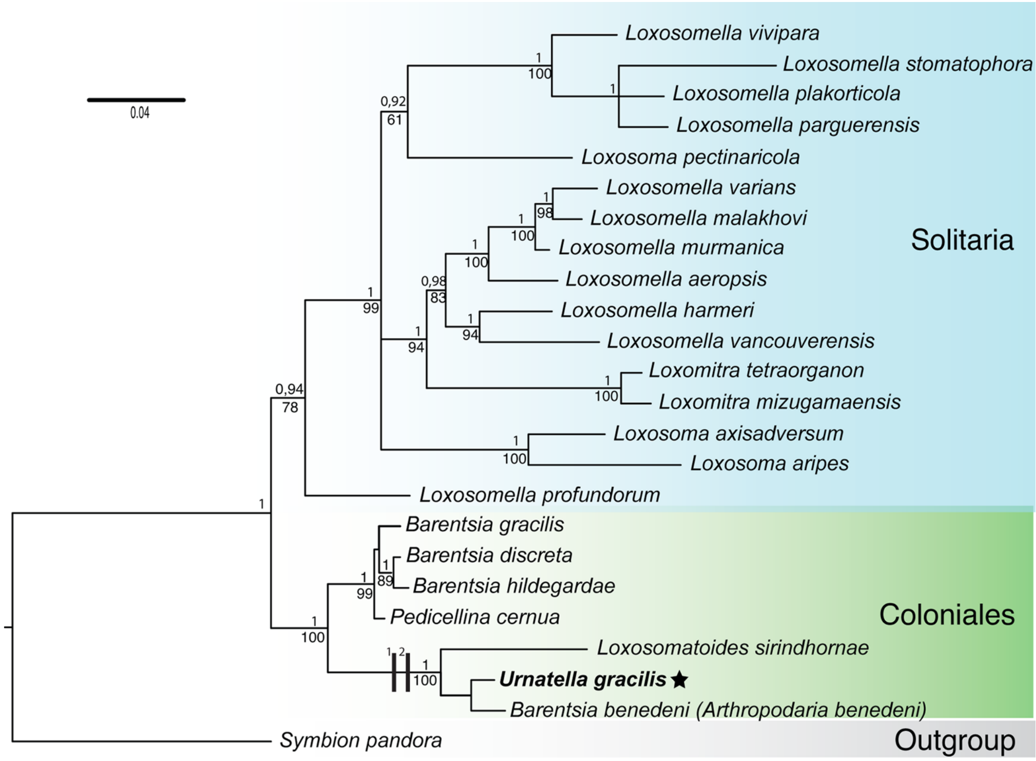

Fig. 2. Molecular phylogenetic tree based on Bayesian Inference, concatenated dataset of 28S rRNA and 18S rRNA partial gene sequences. Posterior probabilities are indicated above branches, bootstrap supports from Maximum Likelihood are indicated below branches. Asterisk indicates the position of *Urnatella gracilis*.

cernua (Pedicellinidae) forms a single clade with representatives of the genus *Barentsia* (with an exception of *B. benedeni*) (PP = 1; BS = 99), in this case the ingoup relationships were also unsupported (PP = 0.51, BS = 53) except sister relationships of *B. discreta* (Busk, 1886) and *B. hildegardae* Wasson, 1997 (PP = 1; BS = 89).

Discussion

Geographical distribution of *Urnatella*

Urnatella gracilis is considered a cosmopolitan species. Originally described from North America (e.g., Leidy, 1852; Weise, 1961; Poirrier, Johnson, 1970), it was later found in Europe (e.g., Damas, 1939; Zambriborshch, 1958; Lüdemann, Kayser, 1961; Sklyarova, 1962; Lukacsovics, Pecsi, 1967; Pecsi, Erdelics, 1970; d'Hondt *et al.*, 2002), South America (e.g., Bonetto, Coridiola, 1963; Vieira, Migotto, 2011), Africa (Wiebach, 1965; Gugel, 1993) and Asia in rivers of southern India (Seshaiya, 1947; Chatterjee, 2021) and in Japan (Ikeda *et al.*, 1977; Oda, 1982). In addition to freshwater habitats, this species has also been observed in brackish waters, e.g., in coastal areas of the Black and Azov Seas in deltas and estuaries with salinity less than 5‰ (Zaitsev, Oztürk, 2001). Experiments show that *U. gracilis* can tolerate salinity increases up to 12‰ (Ishii *et al.*, 2024).

A morphological description of *U. gracilis* specimens collected in the Don River can be used in future for comparison with populations from other geographical locations when molecular genetic data are obtained for these populations. In the 20th century, two new species within the genus *Urnatella* were described — *U. dnjestriensis* Zambriborshch, 1958 from the Dniester River and *U. indica* Seshaiya, 1947 from southern India (Seshaiya, 1947; Zambriborshch, 1958). Later these species were synonymized with *U. gracilis* (Emschermann, 1965), despite some morphological differences: specimens from India have only 9–11 tentacles, and specimens from the

Dniester River are distinguished by the presence of spines on stalk segments. Colonies from the Don River have calyxes with 14 tentacles and no spines on the stalk, like most *Urnatella* from different geographical regions (Lukacsovics, Pecsi, 1967; Ikeda *et al*., 1977; King *et al*., 1988; Vranovsky, Sporka, 1998).

Urnatella **phylogenetic relationships and origin of freshwater entoprocts**

The molecular phylogenetic analysis confirms the monophyly of suborder Stolonata (order Coloniales) (according to Emschermann, 1972). At the same time, our results challenge the current taxonomical division within this suborder. Currently, two stolonate families, Pedicellinidae and Barentsiidae, are distinguished (Emschermann, 1972). The family Pedicellinidae includes the genera *Loxosomatoides*, *Myopedicellina* Shaw, Proctor et Borisanova, 2024, *Pedicellina*, and *Sangavella* du Bois-Reymond-Marcus, 1957; the family Barentsiidae includes the genera *Barentsia*, *Coriella* Kluge, 1946, *Pedicellinopsis* Hincks, 1884, *Pseudopedicellina* Toriumi, 1951, and *Urnatella* (Borisanova, 2018; Shaw *et al*., 2024). Our molecular phylogenetic analysis (Fig. 2) indicates that both Barentsiidae and Pedicellinidae are paraphyletic taxa. *Urnatella gracilis* (Barentsiidae) forms a single clade with *Barentsia benedeni* (Barentsiidae) and *Loxosomatoides sirindhornae* (Pedicellinidae). The second clade includes *Barentsia discreta*, *B. gracilis* (Sars, 1835), *B. hildegardae* (Barentsiidae), and *Pedicellina cernua* (Pedicellinidae).

It is noteworthy that *Urnatella* and *Barentsia benedeni* share a common morphological feature, which distinguishes them from other barentsiids — a segmented stalk. In other Barentsiidae species, including the type species of the genus, *B. bulbosa* Hincks, 1880, the stalk consists of a wide muscular base and a narrow, stiff peduncle, in some species with additional muscular nodes (Hincks, 1880; Emschermann, 1972; Borisanova, 2018). Molecular data for the type species of *Barentsia* are not available, but based on the morphology of the stalk we can assume that it is closer to *B. discreta*, *B. gracilis*, and *B. hildegardae* than to *B. benedeni*. Based on this assumption and the results of molecular phylogenetic analysis, we suggest that *B. benedeni* and *Urnatella* represents a separate phylogenetic lineage from Barentsiidae, and should be united in different family. *Barentsia benedeni* differs from *U. gracilis* by a presence of a creeping stolon (Foettinger, 1887). Ehlers (1890) proposed a genus *Arthropodaria* for colonial entoprocts with a segmented stalk and a developed stolon, and included only one species in it, *Arthropodaria benedeni* (Foettinger, 1887). Nasonov (1926) described another species, *A. kovalevskii* Nasonov, 1926, from brackish waters, but this species was later synonymized with *A. benedeni* (e.g. Zevina, Kuznetsova, 1956; Nielsen, 1989). We suggest to restore the genus *Arthropodaria* with a species *Arthropodaria benedeni*.

An important result of the molecular phylogenetic analysis is the revealed monophyly of *U. gracilis* and *L. sirindhornae*. These two species are the only known freshwater entoprocts. Although previous studies suggested an independent colonization of freshwater environments at least by two entoproct families, Barentsiidae and Pedicellinidae (Wood, 2005), the close phylogenetic affinity of *U. gracilis* and *L. sirindhornae* indicates that this colonization likely occurred within a single family of colonial Entoprocta. Despite the close relationship, *L. sirindhornae* and *U. gracilis* represent high morphological differences. In contrast to *U. gracilis*, in *L. sirindhornae* zooids depart from a thin creeping stolon rather than a basal disc; the stalk of zooids is fully muscular, not segmented; calyx is separated by a septum without a distinct star-cell complex whereas in *Urnatella* it is well-developed (Wood, 2005; Schwaha *et al*., 2010). These differences can be explained by considering the following hypothetical origin of freshwater entoprocts (Fig. 3). First, a marine ancestor of *Arthropodaria*-type with a stolon and a segmented stalk colonized brackish waters. Then, during the evolution of the branch leading to the *Urnatella*-type of organization, a basal disc developed from the creeping stolon by its extreme shortening. This hypothesis of the origin of the basal disc is supported by the presence of septa between the parts of the basal disc from which the zooids arise and the presence of a stolon-like base in daughter colonies that form on the stalk of zooids (Davenport, 1893; Emschermann, 1972). The segmented stalk is preserved in *Urnatella* from the ancestral form. The origin of the *Loxosomatoides*-type organization can be explained by the ability of *Arthropodaria* to form lateral colonies on the

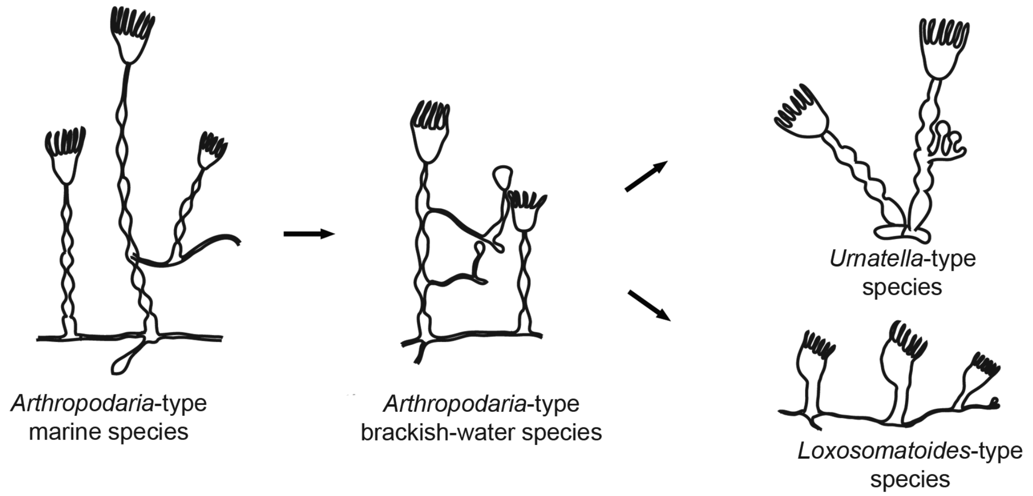

Fig. 3. Possible stages in the formation of the plan of the colony organization of *Urnatella* and *Loxosomatoides*.

stalk. In *L. sirindhornae* the colonies are small and zooids are minute, with poorly developed star-cell complex (Wood, 2005). We suggest that these features may indicate a process of juvenilization that might have occurred during the evolution of the genus *Loxosomatoides* in brackish and freshwater environments. In *A. benedeni* a creeping stolon with several zooids can arise from the segment of the stalk of maternal zooid, reach the substrate and attach to it (Nasonov, 1926). Therefore, it can be assumed that *Loxosomatoides*-type organization evolved from young daughter colonies of *Arthropodaria*-type species with small zooids whose stalks are still undifferentiated and fully muscular.

Back to the family Urnatellidae?

The genus *Loxosomatoides* includes a freshwater species *L. sirindhornae* and several brackish-water species: *L. colonialis* Annandale, 1908, *L. laevis* Annandale, 1915 and possibly *L. athleticus* (Annandale, 1916) (Wasson *et al*., 2000, but see Schwaha *et al.*, 2010). Molecular data were obtained only for *L. sirindhornae*, but morphological features suggest that all these species are closely related. All species have similar organization of colonies; zooids with a calyx oriented obliquely to the stalk; an aboral shield on the calyx. In addition, all species are capable of forming hibernaculae, the resting buds in the form of short lateral stolons with expanded tip filled with cells. At the beginning of the 20th century Annandale (1915) proposed to unite *Loxosomatoides* and *Urnatella* into the family Urnatellidae based on their inhabitation in brackish and fresh waters and some morphological features. We suggest to restore the family Urnatellidae in the system of colonial Entoprocta with genera *Loxosomatoides*, *Urnatella,* and *Arthropodaria*. *Arthropodaria* inhabits both seas and brackish water (Nasonov, 1926; Nielsen, 1989; Wasson, 1997; Zaitsev, Oztürk, 2001), thus, colonization of brackish and fresh waters would be a common feature for representatives of the family Urnatellidae. Among morpho-physiological features it is possible to note the ability to form resting stages that represented by hibernaculae in *Arthropodaria* and *Loxosomatoides* and by segments of the stalk in *Urnatella*, which has lost the ability to form stolons and hence hibernaculae.

Taxonomical consequences

Family Urnatellidae Annandale, 1915

Marine, brackish-water and freshwater colonial species. Zooids depart from a creeping stolon or from a septate basal disc. Capable of forming resting stages (hibernaculae).

Genus *Arthropodaria* Ehlers, 1890

DIAGNOSIS: Zooids of the colony arise from the creeping stolon. Stalk of each zooid consists of many segments. Each segment includes narrow short stiff portion and expanded muscular part. Budding from segments possible. Hibernaculae formed on lateral stolons. Marine and brackish-water habitats.

TYPE SPECIES: *Arthropodaria benedeni* (Foettinger, 1887)

One described species.

Genus *Loxosomatoides* Annandale, 1908

DIAGNOSIS: Zooids arise from slender, branching, creeping stolon. Stalk of zooids with continuous longitudinal musculature. Calyx attached to stalk obliquely. Aboral side of calyx with dense thick cuticle forming an aboral shield. Hibernaculae formed when unfavorable conditions occur. Brackish-water and freshwater habitats.

TYPE SPECIES: *Loxosomatoides colonialis* Annandale, 1908

Four described species.

Genus *Urnatella* Leidy, 1852

DIAGNOSIS: Several zooids arise from a septate basal disc. Stalk of a zooid consists of a number of segments. Young colonies are formed on stalk segments of maternal zooid, and then separate. They consist of several zooids with still fully muscular, non-segmented stalks. Segments of stalk may function as resting stages. Hibernaculae absent. Freshwater habitats, but can occur in brackish waters.

TYPE SPECIES: *Urnatella gracilis* Leidy, 1852

One described species.

Conflict of interest

The authors have no competing interests to declare that are relevant to the content of this article.

Data availability

The data that support the findings of this study are available from the corresponding author, A.O. Borisanova, upon request.

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