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New findings of the genus *Revalotrypa*, the oldest bryozoan genus of Baltoscandia, in north-western Russia

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Abstract: New findings of esthonioporate bryozoans of the species *Revalotrypa* cf. *inopinata*, representing one of the oldest bryozoans of Baltoscandia, are described from an outcrop located in Leningrad Oblast' (north-western Russia). The colonies of this species are very small and were extracted from limestone-cemented nodules found in glauconitic sandstones of the lower part of the Joa Member (*Paroistodus proteus* conodont zone, lowermost Floian, Lower Ordovician). Combined X-ray microtomography and the examination of traditional thin sections under a stereomicroscope and a light microscope were used to study the morphology of this species.

Key-words:

- Bryozoa;
- Ordovician;
- Floian;
- Baltoscandia;
- micro-CT

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Résumé : *Nouvelles découvertes du genre* **Revalotrypa**, *le plus vieux genre bryozoaire de Baltoscandia, au nord-ouest de la Russie.-* Les nouvelles découvertes de bryozoaires esthonioporates de l'espèce *Revalotrypa* cf. *inopinata*, représentant l'un des plus anciens bryozoaires de Baltoscandie, sont décrites dans un affleurement situé dans l'oblast de Léningrad (nord-ouest de la Russie). Les colonies de cette espèce sont très petites et furent extraites de nodules calcaires cimentés trouvés dans les grès glauconitiques de la partie inférieure du Membre Joa (zone de condonte *Paroistodus proteus*, Floïen basal, Ordovicien inférieur). La microtomographie à rayons X combinée et l'examen de coupes minces traditionnelles au stéréomicroscope et au microscope optique sont utilisés pour étudier la morphologie de cette espèce.

Mots-clefs :

- Bryozoaires ;
- Ordovicien ;
- Floïen ;
- Baltoscandie ;
- microtomographie

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Introduction

There are not any unequivocal Cambrian bryozoans, including a 'cryptostomate bryozoan' Pywackia baileyi LANDING in LANDING et al., 2010, described from the Upper Cambrian (Tinũ Formation) of Mexico (LANDING et al., 2010, 2015), which has been reinterpreted as an octocoral with a 'pennatulacean-like morphology' (TAYLOR et al., 2013). Tremadocian to early Floian (Early Ordovician) bryozoans are poorly represented in the geological record (Fig. 1), while late Floian bryozoans are comparatively common, especially in north-western Russia (MODZALEVSKAYA, 1953; PUSHKIN & POPOV, 1999; GORJUNOVA, 2009; KORO-MYSLOVA, 2011). The oldest known unequivocal bryozoans in the world are cryptostomate and esthonioporate bryozoans from the Tremadocian of central China (Hu & SPJELDNÆS, 1991; XIA et al., 2007; ZHANG et al., 2009; MA et al., 2014b, 2015). The esthonioporate bryozoan species Revalotrypa inopinata FEDOROV et al., 2017, and R. yugaensis FEDOROV et al., 2017, from the lowermost Floian (Lower Ordovician) of the Leningrad Oblast', Russian Federation, are the oldest known unequivocal bryozoans of Baltoscandia, and most likely, the oldest of the entire Baltica paleocontinent. The esthonioporate species Orbipora sp., described by TAYLOR & COPE (1987) from the Ogof Hen Formation (lower Floian) of South Wales,

United Kingdom, is younger than R. yugaensis and R. inopinata, since FORTEY & RUSHTON (2000) correlated the Ogof Hen Formation with the upper part of the T. phyllograptoides graptolite zone (Fig. 1). There are two further candidates for the oldest bryozoan species, including the cystoporate bryozoan Ceramopora? unapensis Ross, 1966, from the uppermost Tremadocian or lowermost Floian deposits of Oklahoma, USA, and esthonioporate bryozoan Dianulites borealis ASTROVA, 1965, from Early Ordovician deposits of Arctic Russia (ASTROVA, 1965; ERNST et al., 2014). However, the classification of Ceramopora? unapensis as a bryozoan was subsequently questioned by TAYLOR (1993), whereas the precise age of D. borealis is uncertain. According to ERNST et al. (2014), D. borealis is found in uppermost Tremadocian deposits, whilst NEKHOROSHEVA (2015) suggested that *D. borealis* is not older than the Floian stage.

In this article, findings of esthonioporate bryozoans of the genus *Revalotrypa* are described from a new location. Specimens of *Revalotrypa* cf. *inopinata* were extracted from a thin layer of dense sandstone nodules cemented by limestone, occurring within glauconitic sandstones of the lower part of the Leetse Formation. The nodulebearing layer has been correlated with the base of the Floian Stage (Lower Ordovician).

				SOUTH CHINA (YANGTZE)					S. WALES	NW RUSSIA (BALTOSCANDIA)							
Series	Stage	Time Slice	Formation	Graptolite biozone	Co bio	nodont ozone)7 1., 2007				Conodont biozone	Graptolite biozone	ition	Stage	Slice	ge	es
				<u>Wu</u> et al., 2010; <u>Zhang</u> et al., 2019; <u>Wang</u> et al., 2019			a et al., 200		<u>Fortey</u> & <u>Rushton,</u> 2000		<u>Bergström</u> <u>Suyarkova</u> & <u>Ogg</u> et	<i>et al.,</i> 2004; <u>Koren</u> ' 2009; <i>al.</i> , 2012	Forma	Regional	Time S	Stag	Seri
Ť	Floian +	FI1 → unghuayuan →		Tetragraptus approximatus	Se gri div	errato- nathus versus	Ma <i>et al.</i> , 2015 <i>prisca</i> Xia in Xia <i>a nodulifera</i> Xia		bipora sp. 🗕 🗕 🗕) 7 = 17 = 17 =	↑ Prioniodus elegans	Tetragraptus phyllo- graptoides	tse 🔸	≜ Bi	+ F⊡	Floian +	+
Lower Ordovician		Tr3	⁻ enhsiang [H	Hunne- graptus copiosus Araneograp- tus murray Aorograptus victoriae	Paltodus 'deltifer'	Triangu- lodus bifidus Paroisto- dus proteus	lodictya simplex - Prophyllodictya - Nekhorosheviel	2007 ——— ia <i>et al.</i> , 2007 –	004	itopinata Fedorov et al., 20 itopinata Fedorov et al., 20 ugaensis Fedorov et al., 20	Paroistodus proteus	Hunne- graptus copiosus Araneo- graptus murray) Lee	J Hunneber	Tr3		vician
	an	Tr2	-	Adelograpt- hus tenellus	Cola quad	ptoconus Iraplicatus	lkuldo.	et al., a in Xi	<		Paltodus deltifer	Kiaero- graptus supremus	Vazya	arangi	Tr2	an	Ordo
	Tremadoci	Tr1	Nantsinkuan	R. flabelli- formis anglica Aniso- graptus matanensis	Rossodus manitouensis Chosonodina herfurthi Cordylodus angulatus		 Pi uus normalis Xia in Xia amus ovalis Xia in Xia Orbiramus minus Xii 			Revalotrypa ii Revalotrypa cf. ii Revalotrypa y	Cordylodus angulatus	Ádelo- graptus hunneber- gensis d d s s s o o o	Koporye	(erort	Tr1	Tremadoci	Lower
				R. flabelli- formis parabola ?	la gr fluc	apeto- nathus ctivagus	, in the second s	Orbir			Cordylodus lindstromi	Rhabdino	+ Tosna	+ Pa			

Figure 1: Geographic and stratigraphic distribution of Tremadocian to early Floian bryozoans.



The aims of this study are: (1) to describe the new outcrop yielding the oldest bryozoans of Baltoscandia, and (2) to describe the morphological characteristics of new specimens of the esthonioporate bryozoan genus *Revalotrypa* from Baltoscandia.

Geological background

In north-western Russia, Ordovician sedimentary rocks comprise an east-west trending elongated plateau, bounded in the north by the Baltic-Ladoga Klint (Fig. 2). Ordovician strata are composed mainly of limestone (SELIVANOVA & KOF-MAN, 1971) with the exception of the lower part, which is represented by non-carbonate sequences. These include the lower Tremadocian Obolus Sandstone and the Dictyonema Shale (the Tosna and Koporye formations, respectively), glauconite-bearing guartz sandstone of the middle Tremadocian Nazya Formation, and glauconitic sandstone of the upper Tremadocian to lower Floian Leetse Formation (POPOV et al., 1989). Sedimentary disconformities are described from the base of both the Nazya Formation and the Leetse Formation. The Leetse Formation is conformably overlain by a medium-bedded glauconitic limestone of the Päite Member, informally known as the 'Lower Dikary Member' (upper Floian). The Päite Member forms part of the Volkhov Formation, which comprises the base of the Ordovician carbonate sequence.

Lower Ordovician rocks were deposited in the epeiric Baltoscandian paleobasin, which covered a significant portion of the East European Craton during the Ediacaran - Early Paleozoic (e.g., NIKI-SHIN et al., 1996; SLIAUPA et al., 2006). Facies equivalents of the Leetse Formation include gray and reddish bioclastic limestones in central Sweden and graptolite shale in the Oslo region of Norway (Pärnaste & Bergström, 2013), however, bryozoans are absent from the coeval Scandinavian deposits (e.g., LINDSKOG et al., 2018). Furthermore, no bryozoans have been discovered in deposits of the Hunneberg and Billingen regional stages in Estonia and Belarus, which belong to the same facies zone as the Leningrad Oblast' (MÄNNIL, 1959; PUSHKIN, 1987).

The Leetse Formation is divided into four members in the Russian part of the Baltic-Ladoga Klint (anonymous, 1987). In the west, it includes only 2 members: the Joa and the Mäeküla members (Fig. 3). The Joa Member consists of weaklycemented quartz-glauconitic and glauconitic sandstone, with layers of quartz or glauconiticquartz sandstone at the base, and locally, intercalated layers of clay. The Mäeküla Member comprises more tightly cemented calcareous glauconitic sandstone and sandy limestone. In the east, pale gray clay with interlayers of purplish-gray clay of the Lakity Member wedge into the Joa Member, and the dark-green rocks of the Mäeküla Member are replaced by variegated limestone with interlayers of clay, comprising the Vassilkovo Member (see FEDOROV *et al.*, 2017, for details).

In general, the thickness of the Leetse Formation in the vicinity of Saint-Petersburg varies from about 0.5 to 2.7 m, progressively decreasing in a south to south-easterly direction (FEDOROV & ERSHOVA, 2012), whilst the age of the basal layers of the Leetse Formation also decreases in the same direction (ERSHOVA, 2008).

The Leetse Formation comprises three North Atlantic conodont zones (Fig. 3): *Paroistodus proteus*, *Prioniodus elegans*, and *Oepikodus evae* (ToLMACHEVA, 2001; ERSHOVA, 2008). LÖFGREN (1993) subdivided the *P. proteus* conodont zone into 4 subzones, however, ToLMACHEVA (2001) and ToLMACHEVA *et al.* (2001) recognized only the upper subzone (*Oelandodus elongates - Acodus deltatus deltatus*) at the base of the most complete sections of north-western Russia. In the Diabasbrottet stratotype section, the base of this subzone is just below the base of the *Tetragraptus approximatus* graptolite zone, *i.e.*, the base of the Floian stage (BERGSTRÖM *et al.*, 2004).

Material and methods

Based on the findings of ERSHOVA (2008), we selected the thickest and most stratigraphically complete sections of the Leetse Formation in the Saint-Petersburg area (Leningrad Oblast') to study for bryozoan fauna in the lower part of the Joa Member. The thickest sections at the Lava River and Putilovo Quarry were not considered because their fauna has already been studied in detail (TOLMACHEVA et al., 2001). Three localities were chosen and sampled during this study: the Tolbovka River, Lamashka River, and Zolotoy Creek, which is the left-hand tributary of the Suma River (Fig. 2). Faunal remains comprising a carbonate skeleton were observed in deposits correlated to the upper part of conodont zone P. proteus (according to ERSHOVA, 2008) in two of the three localities, including on the left bank of the Tolbovka River, about 0.8 km south of Kotelskiy village, and on the right bank of the Lamashka River. The coeval nodule horizon was discovered in outcrops correlating to below the top of the P. proteus conodont zone on the right bank of the Zolotoy Creek, 0.9 km north-east of the Maloye Ruddilovo village, however fossilized carbonate skeletal remains were not observed at outcrop (Fig. 3).



Figure 2: Schematic geological map of Saint-Petersburg and the Leningrad Oblast' (modified after SOKOLOVA, 1971). Arrows 1-5 mark studied sections of the Leetse Formation; arrows 3, 4, 5 mark localities of the oldest bryozoans of Baltoscandia. The new occurrence at the Zolotoy Creek is shown by arrow 3 and marked with an asterisk on the insert map.

Thin intervals of glauconitic sandstone containing fossilized skeletal remains were sampled from the Tolbovka and Lamashka rivers. Approximately 5 kg of weakly-cemented, clayey, carbonate-bearing glauconitic sandstone was extracted from each outcrop. The samples were repeatedly washed with clean water to remove the mud component. After drying, the sandy residue was sieved into >1 mm and <1 mm size fractions. The >1 mm fraction was examined under an ordinary binocular microscope. As fossilized skeletal remains were not observed at outcrop, complete nodules were sampled from the Zolotov Creek section, along with the host clayey glauconitic sandstone. The total weight of the sample exceeded 15 kg. These samples were prepared in the same way as detailed above, with the surface

of the nodules and >1 mm fraction examined under a binocular microscope.

Only small valves of strongly dolomitized articulated brachiopods were found in samples from the Tolbovka River. The samples from Lamashka River contained only decalcified shells of articulated brachiopods, preserved as ferruginous internal/external molds in a weakly-consolidated clayey sand matrix. However, two very small bryozoans were obtained, together with numerous valves of small rhynchonelliform brachiopods and fragments of lingulids, from the host sandstone containing the nodular layer at Zolotoy Creek. A further attempt to obtain additional bryozoan samples from the nodules through repeated freezing and defrosting was unsuccessful.





Figure 3: Stratigraphic correlation of the Lower Ordovician sections yielding the oldest bryozoans of Baltoscandia, see text for details. Abbreviations: P., Pakerort; K., Koporye; N., Nazya; V., Varangu; P.d., *Paltodus deltifer*.

Since the two bryozoan colonies were very small, we firstly investigated the material using non-destructive methods, *i.e.*, scanning electron microscopy (SEM) and X-ray microtomography (micro-CT). The SEM analyses were performed at

the Center for Microscopy and Microanalysis of Research Park of Saint-Petersburg State University, Russian Federation, where a scanning electronic microscope Tabletop TM 3000 (Hitachi) was used. The colonies were then scanned with a



Skyscan 1172 (Bruker Corporation) at the Center for X-ray Diffraction Studies in the same institute. No filter was used and the voltage for analyses was 74 kV, while the current was 133 mA. Samples were rotated through 180° during examination and the rotation angle was 0.7°. The exposure was 1010 ms for each sample. The pixel resolution was slightly different for the two bryozoans. Sample 1 (PIN 5075/1013) was scanned with a resolution of 1.17 µm, while the pixel size was 1.17224 µm. Sample 2 (PIN 5075/1014) was scanned with a resolution of 1.24 µm, while the pixel size was 1.24132 µm. For each sample, 770 virtual sections were produced. Virtual three-dimensional (3D) models of the colony surfaces were created from the two-dimensional data. The raw micro-CT data were processed using the CTVox and DataViewer software.

The zooecia of the studied bryozoan specimens were fully filled by micrite, which resulted in a low contrast between the sediment and the calcite colony walls on the micro-CT sections. For this reason, traditional thin sections were made at the A.A. Borissiak Palaeontological Institute of the Russian Academy of Sciences (PIN), Moscow, Russian Federation, to study the internal structure of the specimens. The thin sections were studied and imaged using a Leica M165C stereomicroscope (SM) and a Zeiss Axioplan 2 transmitted light microscope (TLM).

Dimensions are given in the text as the observed range, followed in parentheses by the arithmetic mean \pm standard deviation, number of colonies used (N), and total number of measurements made (n). All measurements were made using the micro-CT images.

The material forming the basis of this study is archived in the bryozoan collection of the Laboratory of Higher Invertebrates at the PIN, under number 5075.

Section of the Leetse Formation at the Zolotoy Creek

The following beds are exposed in order of decreasing stratigraphic age (*i.e.*, from the base to the top of the succession; Fig. 3):

Bed 1 has a thickness of 0.07 m and comprises sandstone, which is dark-green, quartz-glauconitic, fine-grained, muddy, completely bioturbated, and weakly-cemented. Bed 1 overlies the top of the *Dictyonema* Shale and the contact is represented by a disconformity.

Bed 2 has a thickness of 0.03 m and comprises clay, which is whitish, sandy, glauconite-bearing, and contains rare fragments of graptolite rhabdosomes.

Bed 3 has a thickness of 0.18 m and comprises sandstone, which is dark-green, quartz-glauconitic, clayey, fine-grained, weakly-cemented, and completely bioturbated.

Bed 4 has a thickness of 0.08 m and comprises sandstone, which is dark-green, glauconitic, very fine-grained to fine-grained, clayey, weaklycemented and completely bioturbated, with traces of deposit feeders infilled by a whitish clay. The sandstone includes disjointed nodules of dense sandstone cemented by limestone, ranging in size from a small coin to a fist. Two very small colonies of the bryozoan species *Revalotrypa* cf. *inopinata* FEDOROV *et. al.*, 2017 and numerous valves of small rhynchonelliform brachiopods and fragments of lingulids were found on the surface of the nodules and in the host sediments between them.

Bed 5 has a thickness of 0.89 m and comprises sandstone, which is dark-green, glauconitic, very fine-grained, clayey and muddy, weakly-cemented, and completely bioturbated, with numerous traces of deposit feeders infilled with whitish or violet-gray clay.

Bed 6 has a thickness of 0.14 m and comprises sandstone, which is dark-green, glauconitic, very fine-grained, densely cemented with limestone, and completely bioturbated.

Bed 7 has a thickness of 0.21 m and comprises sandy limestone, which is dark green, glauconitic, dolomitized, and completely bioturbated.

Bed 8 has a thickness of 0.42 m and comprises strongly dolomitized limestone, which is glauconitic and light-gray, with yellow bands of limonite impregnation along several hardground surfaces. The thickest band is located under the top of the bed, which is bored by numerous *Gastrochaenolites* ichno sp.

Systematic palaeontology

Phylum Bryozoa EHRENBERG, 1831

Class Stenolaemata Borg, 1926

Superorder Palaeostomata MA *et al.*, 2014a

Order Esthonioporata ASTROVA, 1978

Family Revalotrypidae GORJUNOVA, 1988

Genus Revalotrypa BASSLER, 1952

Revalotrypa cf. *inopinata* FEDOROV *et al.*, 2017

(Figs. 4 - 5)

Material: PIN 5075/1013 (Fig. 4), PIN 5075/ 1014 (Fig. 5).

Occurrence: Joa Member of the Leetse Formation (upper layers of the *Paroistodus proteus* conodont zone, Hunneberg Regional Stage, lowermost Floian), right bank of the Zolotoy Creek near Maloye Ruddilovo, Leningrad Oblast', Russian Federation.



Figure 4: *Revalotrypa* cf. *inopinata* FEDOROV *et al.*, 2017, PIN 5075/1013, early Floian. A-C. Micro-CT images. A. Surface model, front view of grain-shaped colony showing apertures of autozooecia (Az) and neozooecia (Nz), and area with constriction (C). B. Surface model, top view. C. Model of longitudinal section showing several zooecial apertures (Z). D-E. SEM images. D. General view of colony. E. Surface of colony. F-G. SM images. F. Longitudinal thin section through the central part of the colony showing almost radially located zooecia. G. Longitudinal thin section, zooecia (outline marked) filled by microspar.

Scale bars: A-C. 250 μm; D. 1 mm; E-F. 500 μm; G. 200 μm.



Figure 5: *Revalotrypa* cf. *inopinata* FEDOROV *et al.*, PIN 5075/1014, early Floian. A. SEM image of colony. B-D. Micro-CT images. B. Surface model of grain-shaped colony, front view. C. Model of longitudinal section showing a few zooecial tubes (arrowed). D. Model of tangential section, top view, showing two autozooecial apertures (Az). E-G. Longitudinal thin sections at different levels near the central part of the colony showing almost radially located zooecia (Z). E. TLM image. F. SM image. G. SM image showing the outline of the zooecia. Scale bars: A. 1 mm; B-D. 250 µm; E. 200 µm; F, G. 500 µm.

Description (measurements based on specimen PIN 5075/1013): Colonies grain-shaped, longitudinally elongated, presumably formed by encrusting around a small object (Figs. 4.A, .D, .F, 5.A-B, .G), and 2.5 mm long by 1.0 mm wide. Secondary overgrowths absent. Autozooecia tubular. Autozooecial apertures rounded to oval, 200-230 µm (215 ± 14 µm; N 1, n 6) long by 170-190 μm (180 \pm 9 $\mu m;$ N 1, n 6) wide, with five to six apertures per 2 mm distance. Autozooecial diaphragms not observed. Neozooecia abundant, separating autozooecia in one or two rows, with up to ten neozooecia surrounding each autozooecial aperture (Fig. 4.A-B, .E). Neozooecial apertures polygonal and 80-110 μ m (93 ± 14 µm; N 1, n 6) in diameter. One colony [PIN

5075/1013] exhibits an area with constriction, presumably consisting of small autozooecia and neozooecia (Fig. 4.A), 350 μ m wide.

Remarks: Two very small poorly preserved colonies of bryozoans were studied from the early Floian of Leningrad Oblast', Russian Federation, which presumably belong to the species *Revalotrypa* cf. *inopinata* based on a comparable colony form (FEDOROV *et al.*, 2017: Fig. 5). However, the preservation state of the studied material does not allow a definitive assignment. 3D models of the colony's surface of sample PIN 5075/1013 have been produced (Fig. 4.A-B), which facilitate a description of the external morphology of *Revalotrypa* cf. *inopinata* without using SEM images, which are of poor quality (Fig. 4.D-E).



However, the surface of the other specimen [PIN 5075/1014] is covered by glauconite grains (Fig. 5.A-B), precluding our ability to study its external morphology. The internal structures of these bryozoans are unclear, because their zooecia were filled by micrite and diagenetic recrystallization to microspar has affected their calcite walls. As a result, both the micro-CT sections (Figs. 4.C, 5.C-D) and the thin sections (Figs. 4.F-G, 5.E-G) have a low contrast between the sediment and the calcite walls.

Conclusions

Bryozoans *Revalotrypa* cf. *inopinata* FEDOROV *et al.*, 2017, are reported from a new location in the Leningrad Oblast', increasing the number of outcrops containing the oldest bryozoans in Baltoscandia to three. The oldest bryozoan fauna can be found here only in the upper part of the *P. proteus* conodont zone, near the base of the most complete sections of glauconitic sandstones, which contain nodular layers enriched with pure limestone that has not been subjected to secondary dolomitization.

Combined X-ray microtomography and the study of traditional thin sections under a stereomicroscope and a light microscope represent the most promising approaches for studying the morphology of these very small bryozoans. 3D modeling of a colony usually replaces 'traditional' thin-section study, because micro-CT allows sections through the whole colony providing information on the internal morphology, but in cases where zooecia are partly filled by microspar, resulting in a low contrast between the sediment and calcite colony walls in the micro-CT image, thin sections can be used.

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