EARLY ORDOVICIAN BRYOZOANS FROM NORTH-WESTERN RUSSIA

by VICTOR I. PUSHKIN *and* LEONID E. POPOV

ABSTRACT. A bryozoan assemblage from the Billingen Stage of north-western Russia (Ingria) is apparently the oldest known in the world. It consists of six species distributed among the trepostomate genera *Esthoniopora*, *Dianulites*, *Revalotrypa*, *Phragmophora* and *Hemiphragma*. Two species are new: *Phragmophora lavaense* Pushkin, sp. nov. and *Hemiphragma priscum* Pushkin, sp. nov. The bryozoans are characteristic of the medium diversity benthic fauna of uncertain origin which migrated into the Baltic Basin during Billingen time (late *Prioniodus elegans* – early *Oepikodus evae* zones). The Billingen bryozoans have a close similarity to the late Arenig bryozoan faunas of Baltoscandia that are also dominated by trepostomates, but differ significantly from the low diversity late Arenig bryozoan assemblages of North America, Ireland, North China, Vajgach and Novaja Zemlja.

BRYOZOANS from the early Arenig Billingen Stage of north-western Russia (Ingria) are some of the oldest known in the world (Pushkin 1987*a*, 1987*b*; Goryunova 1988). Arenig Bryozoa are also known from Poland (Dzik 1981), Ireland and Wales (Taylor and Curry 1985; Taylor and Cope 1987) and North America (McLeod 1978; Eilson *et al*. 1992). Early bryozoans have also been recorded from the upper Tremadoc and lower Arenig of South China (Hu and Spjeldnaes 1991).

The presence of bryozoans in the Billingen of the East Baltic was noted first by Modzalevskaya (1953) who recorded *Monticuliporella* (= *Esthoniopora*) *lessnikowae* Modzalevskaya and *Nicholsonella* (=*Revalotrypa*) *gibbosa* Bassler from the 'Glauconitic Sandstone' (BIâ) in a section on the eastern side of the Volkhov River near the old town of Ladoga. Later, Modzalevskaya (1986) illustrated several specimens referred to '*Dittopora annulata*' (von Eichwald) and '*D. clavaeformis*' Dybowski from the early Ordovician Mäeküla Beds from a section in the canyon of the Popovka River near Pavlovsk. In addition, *Revalotrypa eugeniae* was described by Goryunova (1988) from the Billingen of the Lava River section. Unfortunately, none of these publications contains information on the precise stratigraphical ranges of listed species, and their stratigraphical distribution within the Billingen is somewhat uncertain.

The new collection used for the present study includes 63 colonies of bryozoans, which are assigned to *Esthoniopora*? *lessnikowae* (Modzalevskaya), *Dianulites helenae* (Modzalevskaya), *Revalotrypa eugeniae* Goryunova, *R.*? *arborea* (Modzalevskaya), *Phragmophora lavaense* Pushkin, sp. nov. and *Hemiphragma priscum* Pushkin, sp. nov.

GEOLOGICAL SETTING

The early Ordovician strata in the vicinity of St Petersburg, Ingria, are exposed continuously for a distance about 250 km along the escarpment which is known in the local geological and geographical literature as Baltic–Ladoga Glint (= cliff). The Billingen Stage, corresponding to the upper *Prioniodus elegans* and *Oepikodus evae* conodont zones, represents a stratigraphical equivalent of the upper part of the Latorp Formation of Sweden and 'Latorp Horizont' of Kaljo (1987). The sections of the stage in Ingria comprise (in ascending order) the following lithostratigraphical units: (1) Mäeküla Beds, quartzose glauconitic sand, calcareous sandstone and clay *c.* 0·15–0·90 m thick; (2) Vassilkovo Beds, argillaceous glauconitic limestone with thin clay interlayers up to 0·5 m thick; and (3) Päite Beds, glauconitic limestone varying in lithology from clayey mudstone to bioclastic wackstone with numerous discontinuity surfaces, up to 0·70 m thick (Dronov *et al*. 1995, 1996). Underlying Hunnebergian strata are preserved only east of St Petersburg, between the Nazya river valley and the village of Kipuja, whereas in other sections exposed

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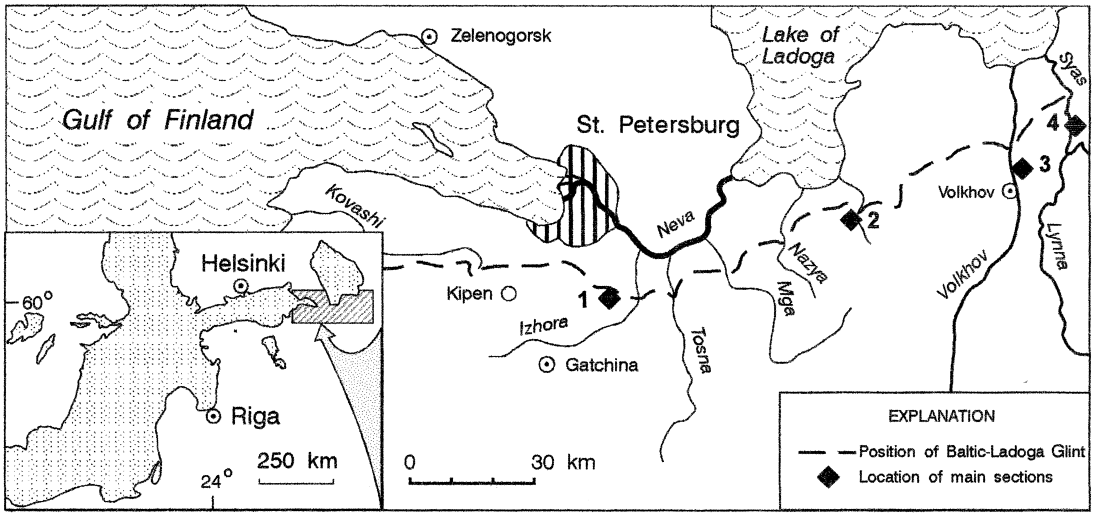


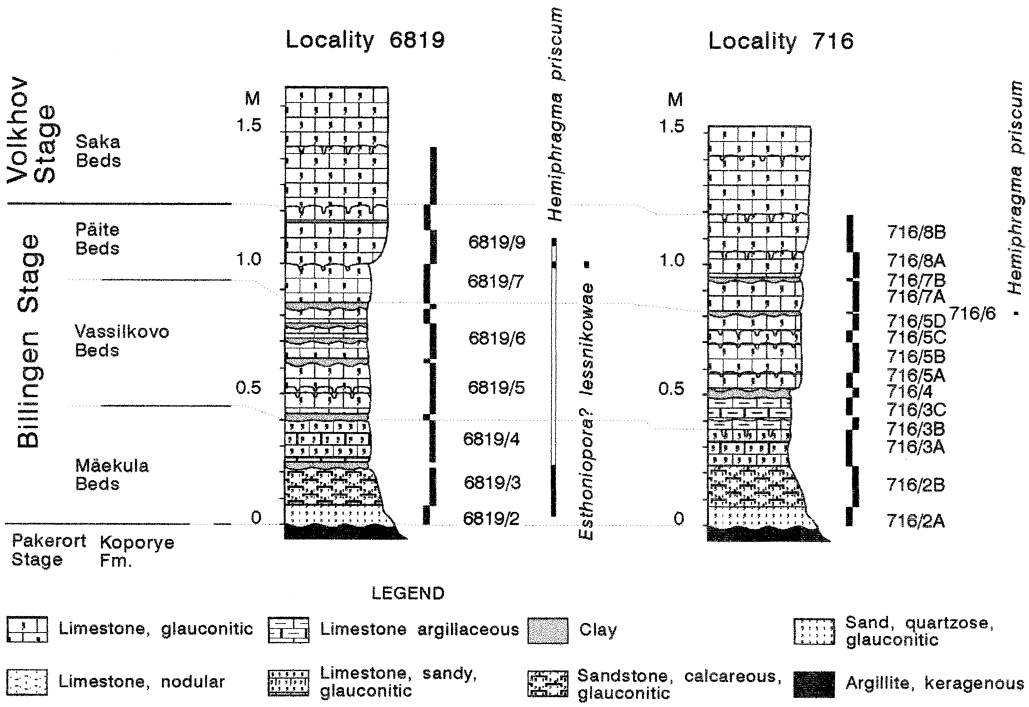
TEXT-FIG. 1. Map of St Petersburg district showing position of the Baltic-Ladoga Glint and major localities for Billingen bryozoans: 1, Popovka River near Pavlovsk; 2, Lava River canyon; 3, Volkhov River near the village of Obukhovo; 4, Syas River near the village of Chernetskaja.

along the Baltic–Ladoga Glint, the Mäeküla Beds rest discontinuously on the top of black argillite of the Koporye Formation. The lower boundary of the Billingen deposits in these sections represents a discontinuity with numerous traces of submarine erosion. The overlying beds are represented in the area by glauconitic limestone of the Saka Beds (Volkhov Formation), separated from the underlying Billingen deposits by a well defined non-sequence with a glauconitic veneer (Dronov *et al*. 1996).

Bryozoans make their first appearance in the glauconitic clay and calcareous glauconitic sandstone of the Mäeküla Beds (*Prioniodus elegans* Zone) in the sections exposed along the Popovka River valley, south of St Petersburg. All other studied specimens were recovered from argillaceous glauconitic limestone and clay of the Vassilkovo and Päite beds (*Oepikodus evae* Zone) in four localities south and east of St Petersburg (Text-figs 1–3).

Locality 6819 is situated in the south-western outskirts of a town of Pavlovsk on the northern side of the Popovka River canyon about 50 m upstream of a bridge across the river in the village of Popovo and just opposite the old German cemetery situated on the high, far side of the river (Text-figs 1–2). This locality has yielded the earliest bryozoans known within East Baltic region. The bryozoan fauna is represented exclusively by *Hemiphragma priscum* sp. nov. which was recovered from the lower Mäeküla Beds (interval of 0·04–0·023 m above the top of the Koporye Formation, samples 6819/2 and 6819/3) in association with conodonts of the upper *Prioniodus elegans* Zone and a diverse assemblage of brachiopods including *Panderina abscissa* (Pander), *Paurorthis resima* (Rubel), *Angusticardinia recta* (Pander), *Porambonites latus* Pander, *Plectella uncinata* (Pander), ostracods and trilobites. The bryozoans *Hemiphragma priscum* sp. nov. and *Esthoniopora*? *lessnikowae* (Modzalevskaya) also occur occasionally in thin interlayers of clay and argillaceous limestone associated with surfaces of non-deposition separating beds of hard glauconitic limestone in the upper part of the Päite Beds (sample 6819/9, intervals 0·98–1·02 m and 1·08–1·10 m above the top of the Koporye Formation). Samples from Päte Beds also contain the brachiopods *Panderina lata* (Pander), *Ranorthis*? *trivia* Rubel and the trilobite *Megistaspis estonica rossica* (Balashova).

Locality 716 is *c.* 0·5 km upstream of locality 6819 on the south side of the Popovka River (Text-fig. 2; sample 716/6). *Hemiphragma priscum* sp. nov. occurs here in a thin layer of greyish brown clay in the base of Päite Beds, in association with the brachiopods *Panderina lata* (Pander), *Ranorthis*? *trivia* Rubel and *Paurorthis resima* (Rubel).

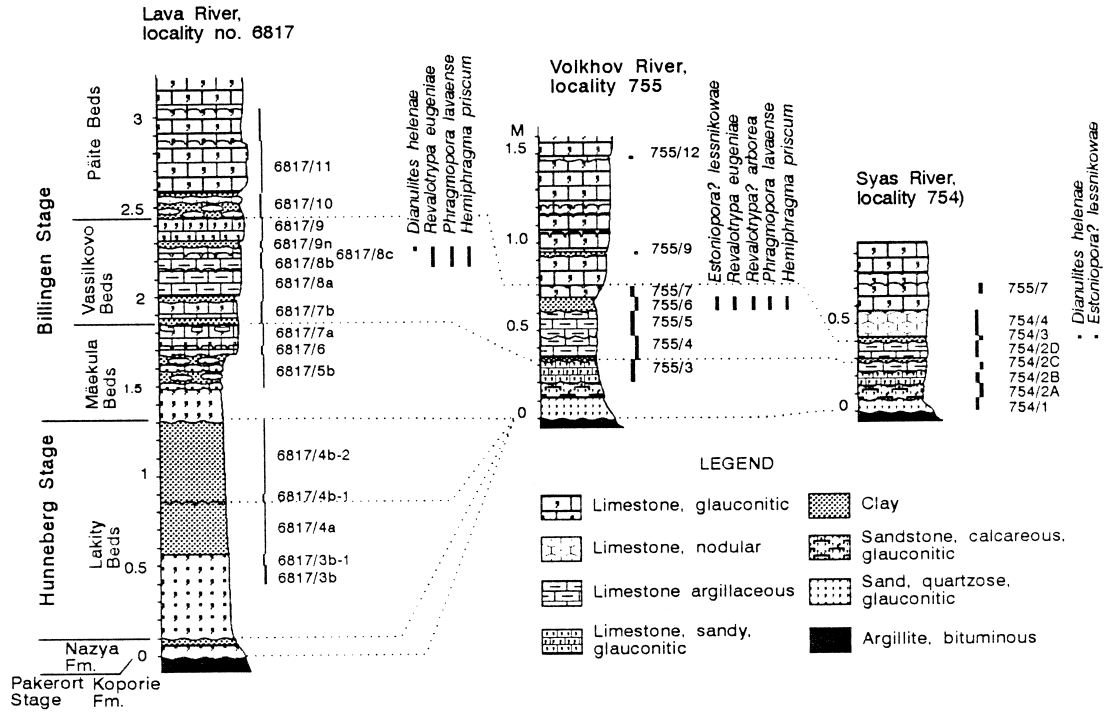


TEXT-FIG. 2. Range chart showing stratigraphical subdivisions and distribution of bryozoans in two sections of Billingen deposits in the Popovka River canyon near the town of Pavlovsk, south of St Petersburg.

Locality 6817 lies on the west side of the Lava River *c.* 600 m north of the village of Vassilkovo. This locality was described and illustrated first by Raymond (1916). Detailed data on the stratigraphy as well as faunal logs for the Hunneberg and Billingen deposits exposed in this section were provided recently by Mägi *et al*. (1989) and Dronov *et al*. (1995, fig. 2). All the bryozoans were sampled from an argillaceous glauconitic limestone in the upper part of the Vassilkovo Beds (samples 6817/8b, 6817/8c). The bryozoan assemblage includes *Esthoniopora*? *lessnikowae*, *Dianulites helenae*, *Revalotrypa eugenae* Goryunova, *Revalotrypa*? *arborea*, *Phragmopora lavaense* sp. nov. and *Hemiphragma priscum* sp. nov. The associated fauna includes trilobites, brachiopods and pelmatozoans, and conodonts diagnostic of the *Oepikodus evae* Zone (see Mägi *et al*. 1989 and Dronov *et al*. 1995 for detailed information).

Locality 755 is situated on the cliff along the eastern side of the Volkhov River in the southern outskirts of the village of Obukhovo (Text-figs 1–2). The bryozoans *Esthoniopora*? *lessnikowae*, *Dianulites helenae*, *Revalotrypa eugenae*, *Revalotrypa*? *arborea*, *Phragmopora lavaense* sp. nov. and *Hemiphragma priscum* sp. nov. occur in this section in a layer of glauconitic clay up to 70 mm thick at the top of the Vassilkovo Beds (sample 755/6). The associated brachiopod assemblage is dominated by *Panderina tetragona* and *Paurorthis resima*. Other brachiopod species are: *Antigonambonites excavatus*, *Neumania erecta* (Pander) and *Plectella crassa* (Pander). All of these brachiopods are widespread in the Billingen of the East Baltic (Rubel 1961; Rubel and Popov 1994; Dronov *et al*. 1995).

Locality 754 is a natural exposure along the ravine on the eastern side of the Syas River in northern outskirts of the village of Chernetskaja. It was first mentioned and briefly described by Lamansky (1905, p. 85). The bryozoans *Esthoniopora*? *lessnikowae* and *Dianulites helenae* were recovered in this section from a calcareous clay *c.* 30–50 mm thick at the base of Päite Beds. The associated assemblage includes the brachiopods *Orthidium* sp. nov., *Ranorthis*? *trivia* Rubel, *Panderina tetragona* (Pander) and *Paurorthis resima*, *Antigonambonites excavatus*, *Tetralobula* sp. nov., *Idiostrophia*? *acuminata* (Pander), *Plectella* aff. *crassa*, and a new genus and species of Leptellinae, as well as ostracods, trilobites



TEXT-FIG. 3. Range chart showing stratigraphical subdivisions and distribution of bryozoans in three sections of Billingen deposits exposed along the Lava, Volkhov and Syas river valleys east of St Petersburg.

and echinoderms. These brachiopod species are characteristic of the uppermost Billingen in the East Baltic (Dronov *et al.* 1995).

SYSTEMATIC PALAEONTOLOGY

Most of the material described here was collected by L. E. Popov during the course of investigation into the early Ordovician faunas of the East Baltic. Type specimens of new species (of which the authorship is Pushkin) and figured specimens are housed in the Belorussian Geological Prospecting Research Institute, Minsk (BELNIGRI).

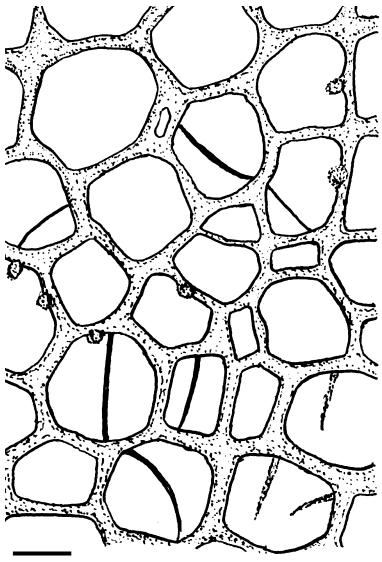
Order TREPOSTOMATA Ulrich, 1882
Suborder ESTHONIOPORINA Astrova, 1978
Family ESTHONIOPORIDAE Vinassa de Regny, 1920

Genus ESTHONIOPORA Bassler, 1911

Esthoniopora? *lessnikowae* (Modzalevskaya, 1953)

Plate 1, figures 1–2; Text-figure 4

1911 *Esthoniopora communis* Bassler (*pars*), p. 260, text-fig. 153 (*non* text-figs 152, 154–155).
1953 *Monticuliporella lessnikowae* Modzalevskaya, p. 108, pl. 1, figs 3–5, text-fig. 2.
1961 *Esthoniopora lessnikowae* (Modzalevskaya); Männil, p. 131, pl. 8, fig. 5.



TEXT-FIG. 4. *Esthoniopora*? *lessnikowae* (Modzalevskaya, 1953); lower Ordovician, Billingen Stage, Päite Beds, Popovka River near Pavlovsk; sample 6819/9; *Camera lucida* drawing of specimen BELNIGRI 12/70-24; tangential section showing general arrangement of polygonal zooecial openings and structure of walls. Scale bar represents 0·25 mm.

Holotype. No. 408, Department of Historical Geology, Geological Faculty of the University of St Petersburg; Mäeküla Beds, Billingen Stage, eastern side of the River Volkhov near the old town of Ladoga.

Figured material. BELNIGRI 12/70-24, 12/71-3. Total of six colonies.

Revised diagnosis. *Esthoniopora* with disc-shaped, hemispherical or nodular colonies; style-like structures rare, true styles absent; diaphragms and hemiphragms numerous, curved; hemiphragms occupy more than half of zooecial diameter, cystiphragm-like in appearance.

Description. Colonies small, disc-shaped, hemispherical with base flat and concentrically wrinkled, or nodular. The base in some colonies is covered by small 'mesopore-like' (exilazooecia-like) zooecia. External surface smooth or with prominent macules in the well-developed colonies. Diameter of the base *c.* 5·0–8·5 mm; height of colonies varying between 1·5 mm and 4·5 mm. Budding parallel. Zooecial openings polygonal, usually five- or six-sided. Zooecial openings always larger in maculae (Pl. 1), but the same shape. Size of maculae *c.* 0·7–1·0 mm, and the distance between maculae *c.* 1·5–2·0 mm. Ordinary intermacular zooecia usually *c.* 0·4–0·5 mm in diameter and macular zooecia on average *c.* 0·6 mm across. Walls homogenous, slightly thickened, *c.* 0·04–0·07 mm wide, sometimes with indistinctly granular structure and occasionally with granular style-like projections (Text-fig. 4). Diaphragms and hemidiaphragms numerous, usually curved. The length of hemiphragms usually about one-half to two-thirds of zooecial diameter. Hemiphragms often cystiphragm-like in appearance. Thickness of diaphragms and hemiphragms *c.* 0·02–0·04 mm. Exilazooeccia-like cells are usually developed near the peripheral parts of the base, forming a 'cellular base' (after Männil 1961, pp. 119–135). Diameter of exilazooecia-like polymorphs *c.* 0·15–0·23 mm. Styles absent.

Remarks. Study of the specimens in our collection shows that style-like structures are only occasionally developed, whereas true cystiphragms are absent. Therefore this species may be assigned with some doubts to *Esthoniopora*. *E*.? *lessnikowae* can be distinguished from *E. communis* Bassler, 1911 in having more frequent diaphragms and hemiphagms as well as in the cystiphragm-like appearance of the hemiphragms. This species was assigned originally to *Monticuliporella* (Modzalevskaya 1953). However, it is assigned here tentatively to *Esthoniopora*, because true cystiphragms are absent and style-like structures are only occasionally present.

Occurrence. Lower Ordovician, Billingen Regional Stage, Vassilkovo Beds, east side of the Volkhov River near the village of Obukhovo, sample 755/6; Päite Beds, Popovka River near Pavlovsk, sample 6819/9; east side of River Syas near the village of Chernetskaja, sample 754/3.

Family DIANULITIDAE Vinassa de Regny, 1920

Genus DIANULITES von Eichwald, 1829

Dianulites helenae (Modzalevskaya, 1953)

Plate 1, figures 2–4

1953 *Monotrypa helenae* Modzalevskaya, p. 163, pl. 14, figs 6–7, text-fig. 32.

Holotype. No. 10, Department of Historical Geology, Geological Faculty of the University of St Petersburg; Kunda Stage, Obukhovo Formation, River Volkhov.

Figured material. BELNIGRI 12/70-2, 12/71-2.

Revised diagnosis. *Dianulites* with nodular or hemispherical colonies; base flat, concentrically wrinkled; external surface smooth; budding radial; zooecial openings polygonal, five- or six-sided; maculae indiscernible; zooecia *c*. 0·50-0·55 mm in diameter; small, juvenile zooecia (?exilazooecia), three- or five-sided, in cross section, originating everywhere along with adult zooecia; walls of zooecia variably granulated, gently undulating in longitudinal section, slightly thickened with thickness *c*. 0·02-0·04 mm; diaphragms rarely developed or absent; styles absent.

Remarks. *Dianulites helenae* is somewhat similar to *D. maculatus* Modzalevskaya (1953) from the Aseri Stage of the East Baltic, but may be distinguished in having hemispherical colonies with a smooth external surface and the undulating walls of the zooecia.

Occurrence. Lower Ordovician, Billingen Stage, Vassilkovo Beds, western side of River Lava near the village of Vassilkovo, sample 6817/8C; Päite Beds, east side of Syas River near the village of Chernetskaja, sample 754/3.

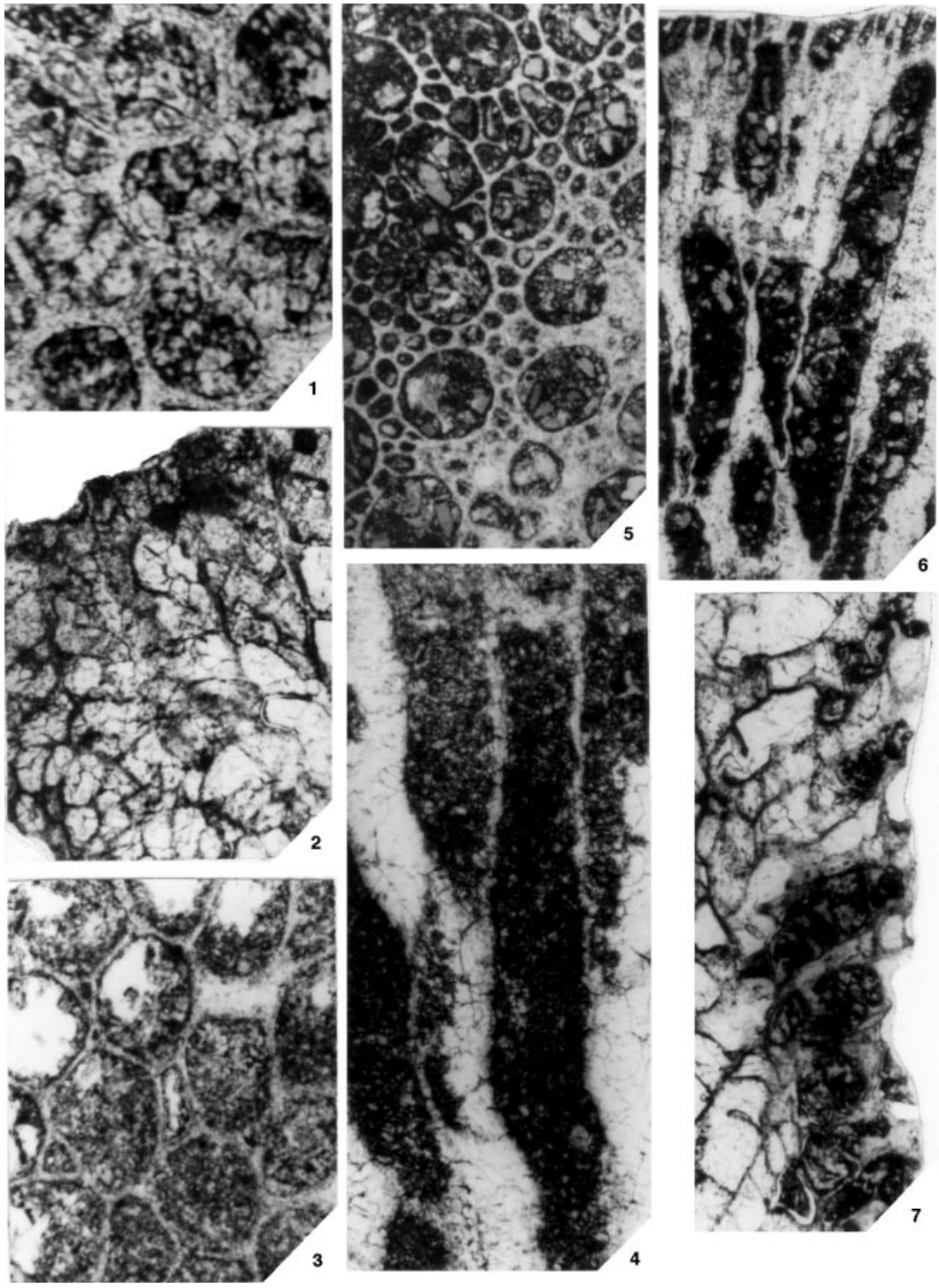
EXPLANATION OF PLATE 1

Figs 1–2. *Esthoniopora*? *lessnikowae* (Modzalevskaya, 1953). 1, BELNIGRI 12/70-24; lower Ordovician, Billingen Stage, Päite Beds, Popovka River near Pavlovsk, sample 6819/9; tangential section showing general arrangement of polygonal zooecial openings; ×40. 2, BELNIGRI 12/71-3; east side of River Volkhov near the village of Obukhovo, sample 755/6; longitudinal section across the subperipheral part of the colony showing inclined diaphragms and hemiphragms in the zooecial chambers and small exilazooecia-like cells in the basal part of the colony; ×30.

Figs 3–4. *Dianulites helenae* (Modzalevskaya, 1953). 3, BELNIGRI 12/71-2; east side of Syas River near the village of Chernetskaja, sample 754/3; tangential section showing general arrangement of polygonal adult and juvenile zooecial openings; ×40. 4, BELNIGRI 12/70-12; lower Ordovician, Billingen Stage, Vassilkovo Beds, River Lava near the village of Vassilkovo, sample 6817/8c; longitudinal section showing general structure of zooecial chambers lacking diaphragms; ×40.

Figs 5–6. *Revalotrypa eugeniae* Goryunova, 1988; BELNIGRI 12/70-4; lower Ordovician, Billingen Stage, Vassilkovo Beds, River Lava near the village of Vassilkovo; sample 6817/8c; 5, tangential section showing general arrangement of zooecial and exilazooecial openings; ×40. 6, longitudinal section showing general structure of zooecial and exilazooecial chambers lacking diaphragms; ×40.

Fig. 7. *Hemiphragma priscum* Pushkin, sp. nov.; BELNIGRI 12/12-45, holotype; lower Ordovician, Billingen Stage, Vassilkovo Beds, River Lava near the village of Vassilkovo; sample 6817/8c; longitudinal section showing general structure of zooecial chambers with hemiphragms and diaphragms, and mezozooecial chambers with diaphragms; ×30.



PUSHKIN and POPOV, Ordovician bryozoans

Suborder AMPLEXOPORINA Astrova, 1965
Family REVALOTRYPIDAE Goryunova, 1988

Revised diagnosis. Colonies massive, hemispherical, disc-like or nodular, not differentiated into endo- and exozone; zooecial openings circular or sub-polygonal in cross section, completely isolated from numerous small, homogeneous exilazooecial openings in peripheral parts of colonies; diaphragms in chambers of zooecia and exilazooecia occasionally developed or absent; walls of zooecia and exilazooecia homogenous or weakly granular, penetrated in peripheral parts of colonies by small style-like structures.

Remarks. Revalotrypidae was established by Goryunova (1988) and assigned to the order Cystoporata (=Cystoporida of Goryunova) mainly on the basis of having sub-circular zooecial openings. The genera *Revalotrypa* Bassler, 1936, *Favicella* Hall and Simpson, 1887, *Diazipora* Vinassa de Regny, 1920, *Haplotrypa* Bassler, 1936 and *Metelipora* Trizna, 1950 were originally referred to this family. Of these only *Haplotrypa* may be undoubtedly referred to the Cystoporata, because of the well-defined ceramoporoid wall microstructure (Bassler 1911, pp. 74–75), whereas *Diazipora* and *Revalotrypa* possess non-ceramoporoid wall microstructure and numerous polymorphs characteristic of the order Trepostomata. *Favicella* and *Metelipora* remain inadequately known and are both regarded here as *nomina dubia*. Therefore, the family Revalotrypidae in its original definition is extremely heterogeneous. *Revalotrypa* is re-assigned here to the order Trepostomata, and included in the monotypic family Revalotrypidae, because it is characterised by the development of numerous homogeneous, polymorphic zooecia, which were described by Dunaeva and Morozova (1967) as 'exilazooecia'. A similar morphology is unknown in other Ordovician taxa, but is recorded in the late Palaeozoic families Crustoporidae and Dyscritellidae. Revalotripidae may be distinguished from these two families by the absence of differentiation of the endo- and exozone in colonies, as well as in lacking a laminated microstructure of the walls and true styles.

Members of the Revalotrypidae differ from Amplexoporidae and Atactotoechidae in having homogenous or weakly granular zooecial walls and numerous polymorphic cells (exilazooecia) completely isolating the autozooecia.

Genus REVALOTRYPA Bassler, 1952

Type species. *Nicholsonella gibbosa* Bassler, 1911; Volkhov and Kunda stages of the East Baltic.

Revised diagnosis. Colonies massive (hemispherical, nodular, irregular), more rarely laminate, encrusting, bar-shaped and ramose; endozone and exozone not differentiated; zooecial openings circular or rounded polygonal in cross section; diaphragms in chambers of zooecia rare or lacking; walls of zooecia indistinctly granular or homogeneous, not thickened in the peripheral parts of colony; exilazooecia small, homogeneous, completely isolating zooecial openings in peripheral parts of colony; diaphragms in chambers of exilazooecia rare or lacking; walls of zooecia and exilazooecia penetrated by small, granular style-like structures.

Remarks. *Revalotrypa* may be distinguished from *Nicholsonella* Ulrich, 1890, which is the only similar genus, in having granular walls and development of numerous exilazooecia (small zooecia without diaphragms, after Dunaeva and Morozova 1967), whereas *Nicholsonella* is characterized by the presence of mesozoecia and true styles, which are absent in *Revalotrypa*.

Species included. *Nicholsonella gibbosa* Bassler, 1911 (= *N. papillaris* Modzalevskaya, 1953; = *N. rotundicellularis* Modzalevskaya, 1953) from the Volkhov, Kunda and Aseri stages (Arenig–Llanvirn) of Baltoscandia; *Revalotrypa eugeniae* Goryunova, 1988 from the Billingen Stage of Ingria, Russia; *Nicholsonella*? *arborea* Modzalevskaya, 1953 from the Billingen and Volkhov stages (Arenig) of Ingria, Russia; *Nicholsonella rotundicellularis* var. *duplex* (Modzalevskaya, 1953) from the Kunda Stage (upper Arenig–lower Llanvirn) of Ingria, Russia.

Revalotrypa eugeniae Goryunova, 1988

Plate 1, figures 5–6; Text-figure 5

1988 *Revalotrypa eugeniae* Goryunova, p. 35, pl. 3, fig. 1.

Holotype. No. 3535/942, Palaeontological Institute, Moscow, lower Ordovician, Billingen Stage, Vassilkovo Beds, from the Lava River near the village of Vassilkovo.

Figured material. BELNIGRI 12/12-46, 12/70-4. Total of 17 colonies.

Revised diagnosis. *Revalotrypa* with nodular, rarely lamellar colonies; zooecial openings rounded, polygonal, sub-circular or sub-oval in outline, on average 0·25–0·30 mm in diameter; maculae absent; zooecial walls weakly granular, gently curved; exilazooecia budding from the base of colony, increasing in density and completely isolating zooecial apertures from each other in mature colonies; diaphragms usually absent, but may occur in some zooecia.

Remarks. A relatively large (0·25–0·45 mm) average diameter of the zooecia was given by Goryunova (1988) for *Revalotrypa eugeniae* Goryunova in her original description based on the single type specimen. Our observations, which also include the study of the new, more representative collection demonstrate that in *R. eugeniae* the range of the diameter of zooecia usually does not exceed 0·25–0·30 mm (with a maximum range of 0·21–0·38 mm), whereas in *R. gibbosa* (Bassler, 1911) the average sizes of zooecia are *c.* 0·30–0·35 mm (with a maximum range of 0·26–0·40 mm). The predominantly nodular shape of *R. eugeniae* colonies contrasts with the hemispherical colonies of *R. gibbosa*. The density of zooecia in *R. eugeniae* varies from 5–6 per 2 mm whereas in *R. gibbosa* it is not more than 4–5. Diaphragms usually occur in *R. gibbosa*, but are present only occasionally in *R. eugeniae*. Indistinctly granular, rounded structures *c.* 0·02 mm across occur sometimes in *R. eugeniae*. They may represent vestigial style-like structures.

The size of the largest specimen is *c.* $9 \times 1 \times 1$ mm, whereas the smallest one is *c.* $2 \times 2 \times 3$ mm. Lamellar colonies are usually smaller (3–5 mm across) than nodular colonies. The former commonly encrust surfaces of brachiopod shells or pelmatozoan columnals. Straight or curved diaphragms are occasionally present, but the majority of zooecia lack any kind of diaphragms.

Occurrence. Lower Ordovician, Billingen Stage, Vassilkovo Beds, west side of the Lava River near the village of Vassilkovo, samples 6817/8b, 6817/8c; east side of the River Volkhov south of the village of Obukhovo, sample 755/6.

Revalotrypa? *arborea* (Modzalevskaya, 1953)

Plate 2, figures 1–2; Text-figure 6

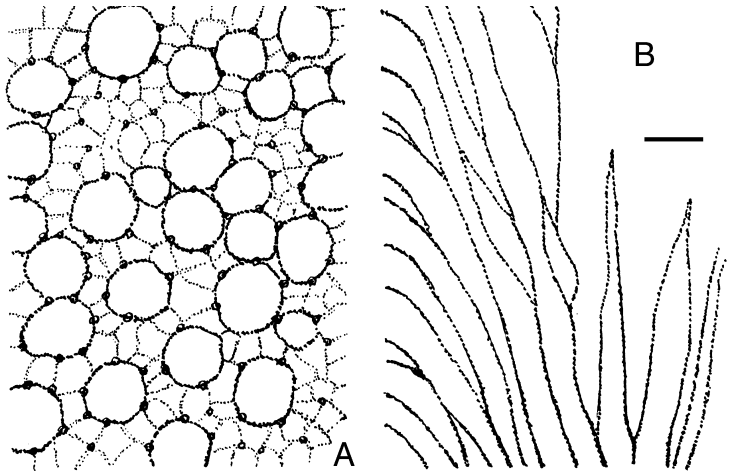
1953 *Nicholsonella arborea* Modzalevskaya, p. 131, pl. 6, figs 1–3; text-fig. 15.

Holotype. No. 35, Department of Historical Geology, Geological Faculty of the University of St Petersburg; Volkhov Regional Stage, River Volkhov.

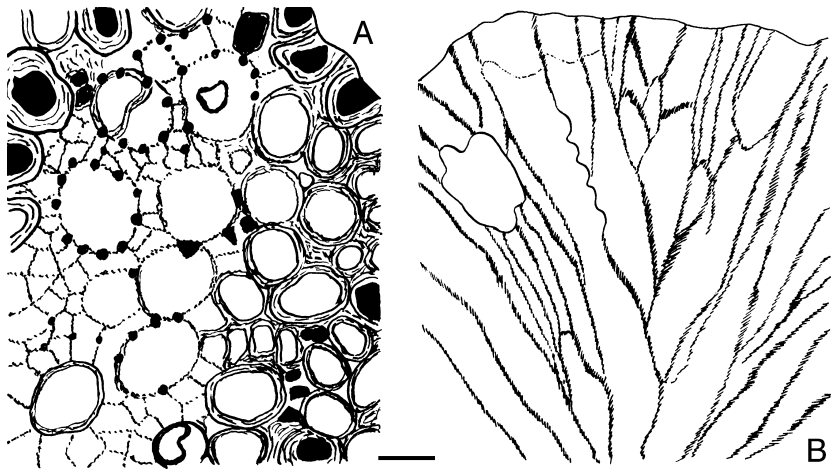
Figured material. BELNIGRI 12/72-1.

Diagnosis. See Modzalevskaya, 1953, p. 131.

Description of specimen from the Billingen Stage. Colony hemispherical with basal epitheca, *c.* 4·0–4·5 mm in diameter at the base and 2·5 mm high. Zooecial openings sub-circular, usually petaloid, *c.* 0·17–0·24 mm in diameter. Maculae absent. Peristomes usually 0·02–0·03 mm wide. Walls of zooecia simple, homogeneous. Diaphragms usually absent, occasionally developed in peripheral parts of the colony. Exilazooecia small, up to 0·07–0·10 mm across,



TEXT-FIG. 5. *Revalotrypa eugeniae* Goryunova, 1988; lower Ordovician, Billingen Stage, Vassilkovo Beds, Lava River near the village of Vassilkovo; sample 6817/8c; *Camera lucida* drawings of tangential (A) and longitudinal (B) sections showing general arrangement of zooecial and exillazooecial chambers based on specimen BELNIGRI 12/12-46. Scale bar represents 0·3 mm.



TEXT-FIG. 6. *Revalotrypa*? *arborea* (Modzalevskaya, 1953); lower Ordovician, Billingen Stage, Vassilkovo Beds, east side of the Volkhov River south of the village of Obukhovo; sample 755/6; *Camera lucida* drawings of tangential (A) and longitudinal (B) sections showing general arrangement of zooecial and exilazooecial openings, and style-like structures based on specimen BELNIGRI 12/72-1. Scale bar represents 0·25 mm.

lacking diaphragms, originating at colony base, peripherally forming continuous rows completely surrounding zooecial openings. Walls of exilazooecia possess numerous style-like structures *c.* 0·02–0·03 mm wide. Somewhat larger style-like structures, *c.* 0·07–0·11 mm wide, are also present near the zooecial openings, extending for a large distance into the zooecial chamber.

Remarks. The precise generic assignment of *Revalotrypa*? *arborea* (Modzalevskaya, 1953) remains uncertain, because it differs from all other known species of *Revalotrypa* in having the large style-like structures, up to 0·11 mm in diameter, in the walls of zooecia.

Occurrence. Lower Ordovician, Billingen Stage, Vassilkovo Beds, east side of the River Volkhov south of the village of Obukhovo, sample 755/6.

Suborder HALLOPORINA Astrova, 1965
Family PHRAGMOPORIDAE Pushkin, 1987*b*

Revised diagnosis. Colonies hemispherical, massive and ramose; zooecial openings of polygonal or rounded polygonal outline; numerous diaphragms and hemiphragms in the zooecial chambers; microstructure of zooecial walls indistinctly granular or lamellar; mesozooecia numerous; styles absent.

Remarks. Phragmoporidae can be distinguished from Dittoporidae by the complete absence of styles.

Genera assigned. *Phragmopora* Vinassa de Regny, 1920; *Balticoporella* Vinassa de Regny, 1920.

Genus PHRAGMOPORA Vinassa de Regny, 1920

Type species. *Hemiphragma multiporatum* Bassler, 1911, from the middle Ordovician (Aseri–Kukruse stages) of the East Baltic.

Revised diagnosis. Phragmoporidae with hemispherical and slightly flattened massive colonies; mesozooecia numerous with closely spaced, straight diaphragms, usually forming small groups in maculae, diaphragms and hemiphragms numerous in zooecial chambers.

Remarks. *Phragmopora* can be distinguished easily from *Balticoporella* in having massive (not ramose) colonies, as well as in the hemiphragms and diaphragms which are developed in all parts of colony, and not only in the exozone as in *Balticoporella*.

Species assigned. *Hemiphragma multiporata* Bassler, 1911; *Archaeopora angulosa* von Eichwald, 1860; *Phragmopora lavaense* Pushkin, sp. nov.

Phragmopora lavaense Pushkin, sp. nov.

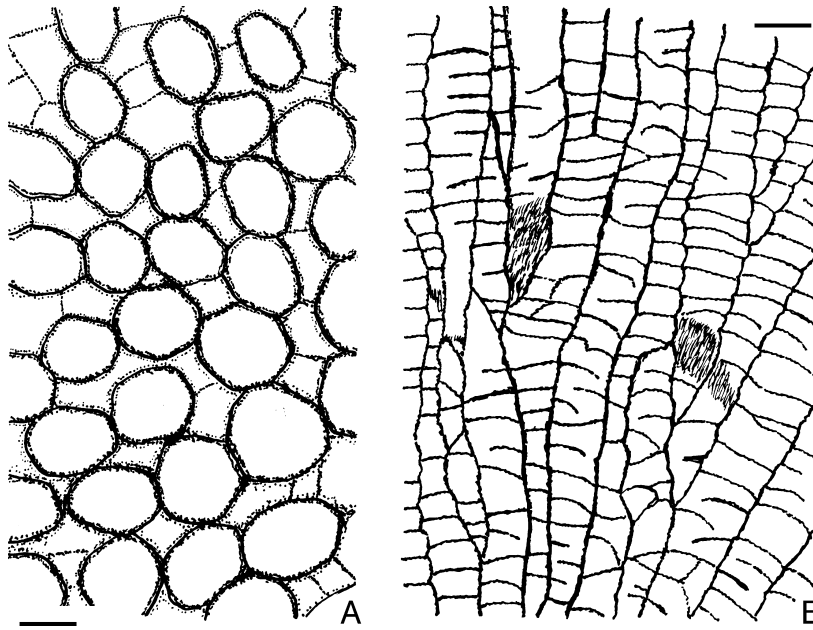
Plate 2, figures 3–4; Text-figure 7

Holotype. BELNIGRI 12/70-9, from the lower Ordovician, Billingen Stage, Vassilkovo Beds, River Lava near the village of Vassilkovo, sample 6817/8c.

Paratypes. BELNIGRI 12/70-1, 5-8a, 10, 13, 17, 19; 12/12-61, 62; 12/72-3, 10. Total of 15 colonies.

Diagnosis. *Phragmopora* with hemispherical or nodular colonies not differentiated into endozone and exozone; zooecial walls indistinctly granular, *c.* 0·03–0·06 mm thick; mesozooecia numerous, irregular, triangular or quadrangular in cross section, not completely isolating zooecial openings.

Description. Colonies hemispherical or nodular *c.* 3–10 mm across, not differentiated into endozone and exozone. Cellular base formed by mesozooecia developed occasionally at the periphery. Zooecial openings of about equal size over the entire colony, circular or rounded polygonal in outline (Text-fig. 7). Maculae absent. Walls of zooecia indistinctly granular, occasionally with lamellar structure, *c.* 0·03–0·06 mm thick. Diaphragms and hemiphragms numerous, regularly spaced, separated by intervals of *c.* 0·09–0·14 mm. Numerous mesozooecia usually present, but not completely isolating zooecial openings. Outline of mesozooecia irregular, usually triangular or quadrangular in cross section. Diaphragms in mesozooecia regularly spaced, separated by intervals of 0·10–0·15 mm and arranged nearly at right angles to the walls in cross section. Styles absent.



TEXT-FIG. 7. *Phragmopora lavaense* Pushkin, sp. nov.; lower Ordovician, Billingen Stage, Vassilkovo Beds, Lava River near the village of Vassilkovo; sample 6817/8c; *Camera lucida* drawings of tangential (A) and longitudinal (B) sections showing general arrangement of zooecial and mesozooecial openings, diaphragms and hemiphragms based on specimen BELNIGRI 12/70-9, holotype. Scale bars represent 0·25 mm (A) and 0·3 mm (B).

Remarks. *Phragmopora lavaense* Pushkin, sp. nov. differs from *P. multiporatum* (Bassler, 1911) in having thick, indistinctly granular zooecial walls and less abundant mesozooecia which do not completely separate zooecia from each other.

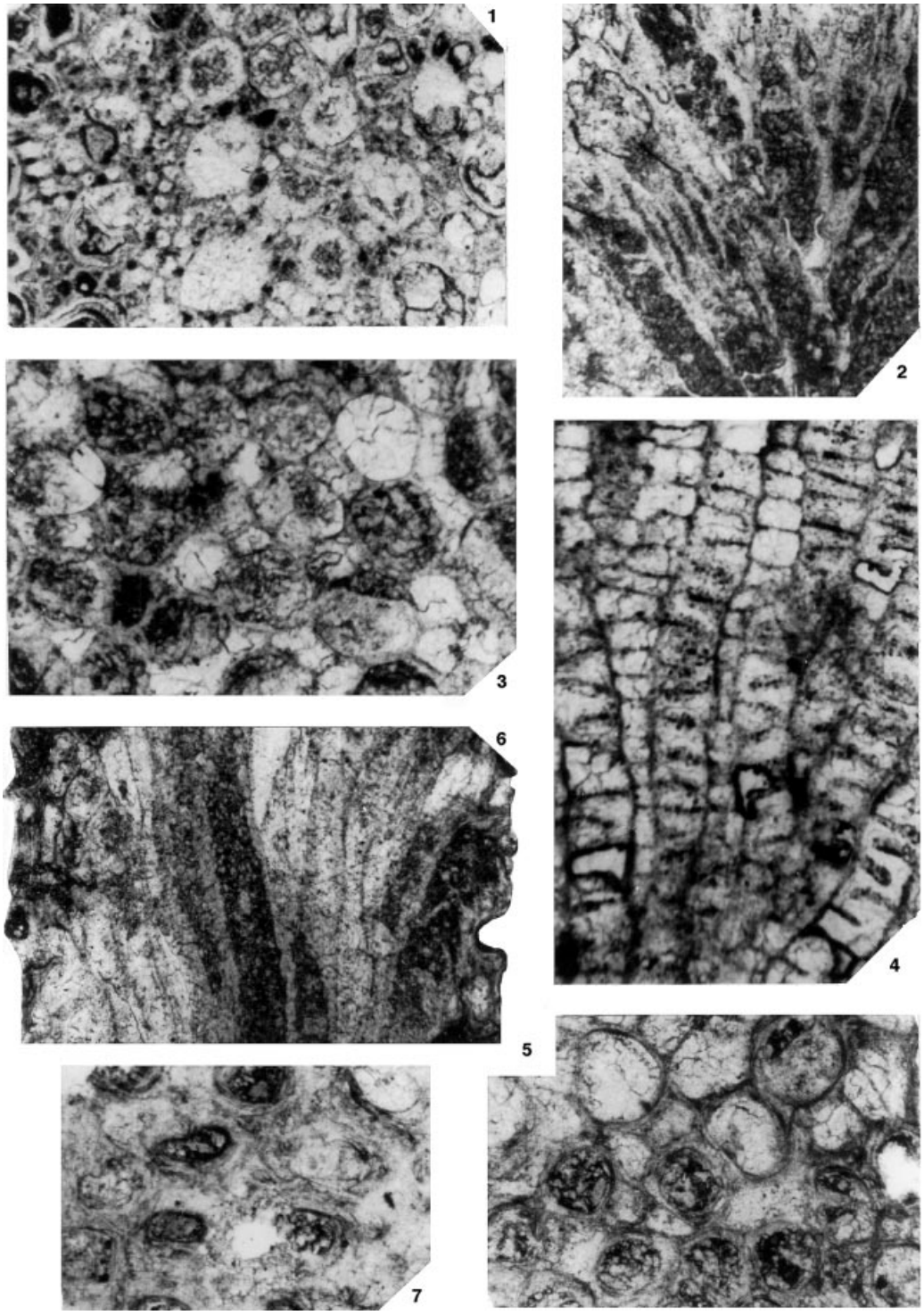
Occurrence. Lower Ordovician, Billingen Stage, Vassilkovo Beds, west side of the Lava River near the village of Vassilkovo, samples 6817/8b, 6817/8c; east side of the River Volkhov south of the village of Obukhovo, sample 755/6.

EXPLANATION OF PLATE 2

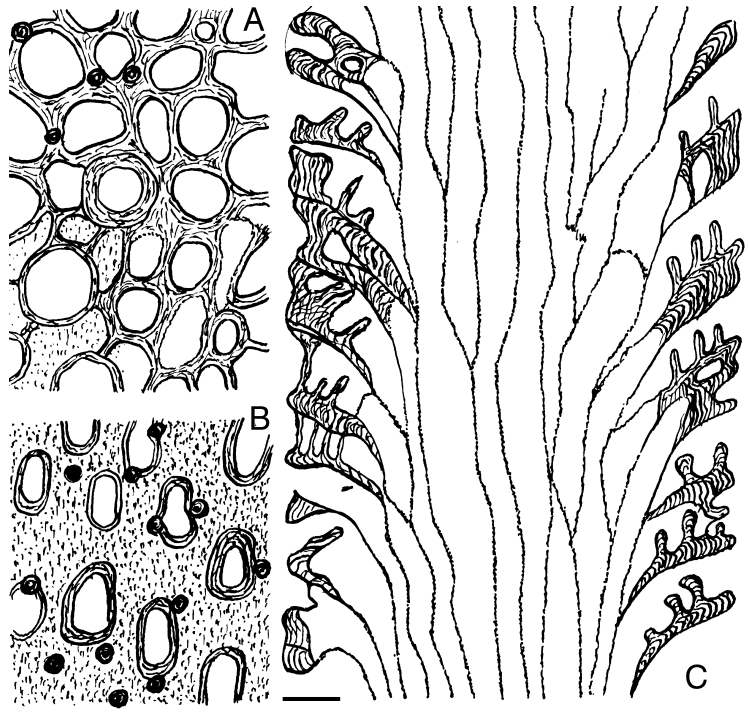
Figs 1–2. *Revalotrypa arborea* (Modzalevskaya, 1953); BELNIGRI 12/72-1; lower Ordovician, Billingen Stage, Vassilkovo Beds, east side of the Volkhov River south of the village of Obukhovo; sample 755/6. 1, tangential section showing general arrangement of zooecial, exilazooecial openings and style-like structures; ×40. 2, longitudinal section showing zooecial and exilazooecial chambers in the central part of colony; ×30.

Figs 3–4. *Phragmopora lavaense* Pushkin, sp. nov.; BELNIGRI 12/70-9, holotype; lower Ordovician, Billingen Stage, Vassilkovo Beds, Lava River near the village of Vassilkovo; sample 6817/8c. 3, tangential section showing general arrangement of rounded and polygonal zooecial openings and polygonal mesozooecial openings; ×40. 4, longitudinal section showing zooecial chambers with diaphragms and hemiphragms, and mesozooecial chambers with diaphragms; ×30.

Figs 5–7. *Hemiphragma priscum* sp. nov. 5–6, BELNIGRI 12/72-9; lower Ordovician, Billingen Stage, Vassilkovo Beds, east side of the Volkhov River south of the village of Obukhovo; sample 755/6. 5, tangential section showing arrangement of rounded zooecial openings, polygonal zooecial openings and rare styles; ×40. 6, longitudinal section of ramose colony *c.* 3 mm in diameter showing wide endozone and narrow exozone; ×30. 7, BELNIGRI 12/12-45, holotype; Lava River near the village of Vassilkovo; sample 6817/8c; tangential section showing oval zooecial openings separated by mesozooecial openings; ×40.



PUSHKIN and POPOV, Ordovician bryozoans



TEXT-FIG. 8. *Hemiphragma priscum* Pushkin, sp. nov.; lower Ordovician, Billingen Stage, Vassilkovo Beds; *Camera lucida* drawings. A, deepened tangential section, based on specimen BELNIGRI 12/72-9; east side of the Volkhov River south of the village of Obukhovo; sample 755/6. B, shallow tangential section showing zooecial openings separated by mesozooecial openings, based on specimen BELNIGRI 12/12-42; River Lava near the village of Vassilkovo; sample 6817/8c. C, longitudinal section based on specimen BELNIGRI 12/12-45, holotype; River Lava near the village of Vassilkovo; sample 6817/8c. Scale bar represents 0·25 mm.

Family DITTOPORIDAE Vinassa de Regny, 1920

Genus HEMIPHRAGMA Ulrich, 1893

Hemiphragma priscum Pushkin, sp. nov.

Plate 1, figure 7; Plate 2, figures 5–7; Text-figure 8

1986 *Dittopora annulata* (Eichwald); Modzalevskaya, pl. 1, figs 10–11.
1986 *Dittopora clavaeformis* Dybowski; Modzalevskaya, pl. 1, figs 3–5.

Holotype. BELNIGRI 12/12-45, from the lower Ordovician, Billingen Stage, Vassilkovo Beds, west side of the Lava River near the village of Vassilkovo, sample 6817-8C.

Figured paratypes. BELNIGRI 12/72-9, 12/12-42; other paratypes; 12/70-16, 18, 21–23, 25–29. Total of 13 colonies.

Diagnosis. *Hemiphragma* with ramose colonies; exozone narrow, not exceeding 18 per cent. of colony diameter; rare diaphragms and hemiphragms in zooecia developed only in exozone; mesozooecia rare, one or two per zooecium; zooecial apertures with up to six styles.

Description. Colonies ramose, *c.* 5–15 mm high and 1·5–3·5 mm in diameter with a smooth external surface. Exozone narrow, but well differentiated and about 10–18 per cent. as wide as the branch. Zooecial openings sub-oval, sometimes slightly irregular in outline. Maculae *c.* 0·5 mm across formed by relatively small groups of mesozooecia and surrounded by zooecia of normal size. Zooecial walls in endozone thin, straight, indistinctly granular. In exozone the thickness of zooecial walls increases to 0·03–0·08 mm and they acquire some traces of lamination. Hemiphragms present only in exozone, invariably situated on proximal zooecial walls and about one to three in number. Rare mesozooecia of one or two in number per each zooecia developed only within exozone of zooecia. Diameter of mesozooecia varies from 0·03 mm to 0·10 mm. About three to six styles usually present around the mouth of zooecia.

Remarks. *Hemiphragma priscum* sp. nov. can be distinguished from all other known species of *Hemiphragma* in having a narrow exozone not exceeding 18 per cent. of the diameter of the branch, indistinctly granular microstructure of its zooecial walls and a small number of diaphragms and hemiphragms in the zooecia which are developed only in the exozone.

Restudy of the specimens from the Mäeküla Beds of the Popovka River section referred by Modzalevskaya (1986) to '*Dittopora annulata*' (von Eichwald) and '*D. clavaeformis*' Dybowski, as well as new material obtained from the topotype locality suggests that they are conspecific with *Hemiphragma priscum*. Bryozoan specimens from the Mäeküla Beds are usually strongly recrystallized and their generic and specific identification remains provisional. However, colonies with a similar external morphology from the Vassilkovo and Päite beds invariably demonstrate characters of *Hemiphragma* in thin section and there is no record in our material of the presence of *Dittopora* in the Billingen Stage of the East Baltic.

Occurrence. Lower Ordovician, Billingen Stage, Mäeküla Beds, Popovka River near Pavlovsk, samples 6819/2 and 6819/3; Vassilkovo Beds, west side of the Lava River near the village of Vassilkovo, samples 6817/8b, 6817/8c; east side of the River Volkhov south of the village of Obukhovo, sample 755/6; Päite Beds, Popovka River near Pavlovsk, samples 6819/9 and 716/6.

DISCUSSION AND CONCLUSIONS

Hemiphragma priscum Pushkin, sp. nov. from the Mäeküla Beds of Popovka River section south of St Petersburg, which occurs together with conodonts of the upper *Prioniodus elegans* Zone, is the earliest known bryozoan. The bryozoan assemblage of the Vassilkovo Beds recovered from the sections east of St Petersburg is associated with conodonts diagnostic of the succeeding *Oepikodus evae* Zone and, therefore, is only slightly younger. It includes six species: *Esthoniopora*? *lessnikowae*, *Dianulites helenae*, *Revalotrypa eugenae*, *Revalotrypa*? *arborea*, *Phragmopora lavaense* Pushkin, sp. nov. and *Hemiphragma priscum* Pushkin, sp. nov., which belong to five different families of the Trepostomata and demonstrate a remarkable taxonomic and morphological variability. Since the cystoporate affinity of *Revalotrypa* and other Revalotrypidae proposed recently by Goryunova (1988) is not confirmed by our study, Billingen Bryozoa in the East Baltic are represented exclusively by the order Trepostomata.

The most recent discussions of the geographical distribution, taxonomic and morphological diversity of the earliest known Ordovician bryozoans were provided by Taylor and Curry (1985) and Taylor and Cope (1987). Early Ordovician bryozoan faunas of Baltoscandia are unique in their taxonomic diversity and in the predominance of trepostomates. In particular, the low diversity early Ordovician bryozoan assemblages of Vaigach and Novaja Zemlja on the opposite side of the Baltic Plate comprise taxa exclusively belonging to the order Cystoporata, whereas a bryozoan assemblage from the upper lower Ordovician of North China (Liangchiashan Limestone) include both cryptostomates and the trepostomate genus *Nicholsonella*, which is unknown within Billingen assemblages of the East Baltic, and makes its first appearance there only in the middle Volkhovian. The trepostomate genera *Dianulites* and *Nicholsonella* were reported from the Whiterockian Kanosh Shale of Utah (Wilson *et al.* 1992), which can be correlated with the Volkhov Stage of Baltoscandia. The record of the early Ordovician bryozoans from North America and Ireland (Tourmakeady Limestone) also includes genera of the orders Cystoporata (*Ceramopora*?) and Fenestrata (*Alwynopora*).

TABLE 1. Measurements of five specimens of *Esthoniopora*? *lessnikowae* (Modzalevskaya, 1953) (in mm).

No. of specimen	12/70-24	12/71-3	12/71-3a	12/72-4	12/72-4a
Diameter of zooecial openings in intermacular area	0·48–0·63	0·46–0·57	0·46–0·55	0·46–0·58	0·46–0·59
Diameter of zooecial openings in macular area (max.)	0·56–0·69	0·57–0·69	0·55–0·65	0·56–0·67	
Number of zooecia per 2 mm in intermacular area	3–3·5	3·5	3·5	3·5	
Number of zooecia per 2 mm in macular area	3	3			
Number of diaphragms and hemiphragms per 1 mm in zooecial chamber	3–4	3–4	4		2–4

TABLE 2. Measurements of three specimens of *Revalotrypa eugeniae* Goryunova, 1988 (in mm).

No. of specimen	12/70-4	12/12-43	12/12-46
Diameter of zooecial openings (max)	0·29–0·38	0·25–0·28	0·23–0·28
Number of zooecia per 2 mm	5–5·5	5·5–6	6
Diameter of exilazooecial openings (max.)	0·05–0·17 (ave. 0·07)	0·05–0·21	0·07–0·18
Number of exilazooecia around zooecial openings	14–15	9–12	10–12

TABLE 3. Measurements of five specimens of *Phragmopora lavaense* Pushkin, sp. nov. (in mm).

No. of specimen	12/70-9	12/71-5b	12/70-6	12/70-10	12/12-62
Diameter of zooecial openings (max.)	0·25–0·35	0·28–0·32	0·28–0·35	0·28–0·32	0·28–0·33
Number of zooecia per 2 mm	5·5	5·5	5–5·5	5·5	5–5·5
Number of diaphragms and hemiphragms per 1 mm in zooecial chamber	7–8	8–9	7	6–7	
Diameter of mesozooecial openings (max.)	0·14–0·35	0·14–0·21	0·10–0·24	0·10–0·24	0·14–0·21
Number of diaphragms per 1 mm in mesozooecial chamber	9–10	10		8	8

TABLE 4. Measurements of five specimens of *Hemiphragma priscum* Pushkin, sp. nov. (in mm).

No. of specimen	12/70-24	12/71-3	12/71-3a	12/72-4	12/72-4a
Diameter of colonies	1·7	4·0–5·2		2·1–2·5	1·4–1·5
Diameter of zooecial openings (max.)	0·21–0·28	0·22–0·35	0·22–0·31		0·21–0·35
Number of zooecia per 2 mm	5·5–6	5·5–6	5–6		6
Number of diaphragms and hemiphragms in zooecial chamber	3–5	3–11		2–3	2
Diameter of mesozooecial openings (max.)	0·09–0·21	0·07–0·24	0·07–0·14	0·07–0·13	0·07–0·24
Diameter of styles					0·02–0·04
Number of styles around zooecial opening	2–4	2–4	2–3		2–3

The first appearance of bryozoans in the East Baltic in Billingen (early Arenig) time coincides with significant environmental and faunal changes. During most of the Cambrian and Tremadoc the East Baltic was an area of deposition of mature quartzose cross-bedded sands and clays inhabited by a low diversity benthic fauna dominated by organophosphatic brachiopods, mostly obolids. These organophosphatic brachiopods became extinct before the end of *Cordylodus angulatus* Zone, possibly as a result of stagnation of the basin, suggested by the continuous deposition of '*Dictyonema*' Shale during the *Cordylodus angulatus*–early *Drepanoistodus deltifer* zones (Popov *et al*. 1989). The Tremadoc-Arenig boundary interval is characterized in the East Baltic by the deposition of condensed glauconitic sand and clay which started sometime during the late Tremadoc. At the beginning of the Hunneberg Stage a moderate taxonomic diversity *Thysanotos/Leptembolon* assemblage of organophosphatic brachiopods appeared in the East Baltic, possibly as a result of immigration (Popov and Holmer 1994). Billingen Stage (upper *Prioniodus elegans* and *Oepikodus evae* zones) has essentially different benthic faunal assemblages dominated by asaphid trilobites (*Megalaspides, Megistaspis* and *Proasaphus*), rhynchonelliformean (articulate) brachiopods and echinoderms. The bryozoans represent a distinctive component of these new faunal assemblages. The Billingen benthic fauna shows numerous similarities with succeeding assemblages of the Volkhov and Kunda stages, but has nothing in common with the older assemblages of organophosphatic brachiopods from the East Baltic, or with the low to medium diversity benthic assemblages dominated by olenid trilobites from the Upper Cambrian and lower Tremadoc of Scandinavia.

This pattern of faunal replacement suggests extinction followed by the immigration of a new benthic fauna. The Billingen benthic fauna of the East Baltic is characterized by an unusually high proportion of taxa new to the Baltic Basin and to Ordovician benthic faunas in general. The list of taxa includes not only the earliest known bryozoans, but also the earliest plectambonitoid strophomenide (*Plectella*), enteletoidean (*Paurorthis, Angusticardinia*) and clitambonitidine (*Oslogonites, Neumania*) brachiopods, encrinurid trilobites, as well as one of the earliest known ostracods (Mägi *et al.* 1989; Popov 1993). There is no evidence that this new fauna had evolved in the proximity of the Baltic Basin. In this context it is remarkable that ceratopygean trilobite assemblages, which appeared suddenly in the Baltic Basin sometime during the latest Tremadoc, demonstrate a close affinity and possibly an ancestry from the Late Cambrian trilobite assemblages of the South China Province of Shergold (1988). In the latest Cambrian similar trilobite faunas inhabited the Australian part of Gondwana and closely associated microplates (e.g. South China and south Kazakhstan) which were located presumably in temperate latitudes. This direction of migration of benthic faunas during the Tremadoc and early Arenig leads to the suggestion that the initial radiation of trepostomate bryozoans, as well as the origin of benthic faunal assemblages that invaded the Baltic Basin in the Billingen, took place on the shelf of one of peri-Gondwanan microplates or island arcs. The occurrence of trepostomate bryozoans in Wales (Taylor and Cope 1987), which was originally a part of the Avalonian microplate, rifted from the north African part of Gondwana sometime at the beginning of the Ordovician (Tornsvik *et al*. 1995), lends some more support to this suggestion.

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