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The Upper Ordovician Katian Stage Bryozoans from the Dzheromo Formation of the Moyerokan River Section (Northern Siberian Platform) and Their Paleogeographical Significance

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Abstract—In the upper part of the Dzheromo Formation (Dolborian Regional Stage, Katian Stage, Upper Ordovician) along the Moyerokan River (Northern Siberian Platform), seventeen bryozoan species were revealed, seven from which, owing to the poor preservation of the colonies, were identified in an open nomenclature. The bryozoans belong to ten genera from four orders: Cystoporata (*Constellaria vesiculosa* (Modzalevskaya in Modzalevskaya et Nekhoroshev), *Lunaferamita*? sp.), Trepostomata (*Calloporella* sp. 1, *Calloporella* sp. 2, *Stigmatella* sp., *S. convestens* Astrova in Ivanova et al., *Batostoma varians* (James), *Orbignyella moyerokanensis* sp. nov., *Leptotrypa* sp.), Fenestrata (*Parachasmatopora* sp.), and Cryptostomata (*Phaenopora plebeia* Nekhoroshev in Modzalevskaya et Nekhoroshev, *P. pennata* Nekhoroshev, *P. erecta* Nekhoroshev in Modzalevskaya et Nekhoroshev, *P. carinata* Nekhoroshev, *P. viluensis* Nekhoroshev in Modzalevskaya et Nekhoroshev, *Phaenoporella* sp., and *Ph. multipora* Nekhoroshev). The genera *Lunaferamita*, *Orbignyella*, and *Parachasmatopora* were first found in the Ordovician of the Siberian Platform, and the genus *Calloporella* was found in the Dolborian Regional Stage. The species *O. moyerokanensis* sp. nov. is endemic to Northern Siberia, while the majority of the species have a wide geographic distribution. The studied bryozoan complex demonstrates some connection with bryozoan assemblages from the Taimyr Peninsula, Kotelny Island, the Sette-Daban Ridge, and Mongolia at the species level. At the generic level, it is close to the bryozoan assemblages from Laurentia, Baltica, the Argentine Precordillera, and China.

Keywords: bryozoans, Upper Ordovician, Dolborian Regional Stage, taxonomy, paleogeography

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INTRODUCTION

The first description of bryozoans from Ordovician and Silurian deposits of Siberia was published by Sheinman (1927). However, bryozoans of the Siberian Platform were studied intensively only since the middle of the 20th century. They were described from many Middle–Upper Ordovician and Silurian localities by G.G. Astrova (Astrova, 1951, 1965; Ivanova et al., 1955), E.A. Modzalevskaya and V.P. Nekhoroshev (Modzalevskaya and Nekhoroshev, 1955; Modzalevskaya, 1961; Nekhoroshev, 1961), and A.M. Yaroshinskaya and K.N. Volkova (Yaroshinskaya, 1978; Volkova, 1982; Lopushinskaya et al., 1983; Volkova and Yaroshinskaya, 1984).

The bryozoan assemblage from the upper part of the Dzheromo Formation (Dolborian Regional Stage, Katian Stage, Upper Ordovician) in the Moyerokan River section, a right tributary of the Moyero River, is characterized for the first time. Some information on the taxonomic composition of bryozoans of the Baksian (Sandbian and Katian stages, Upper Ordovician) and Dolborian regional stages from the Moyero and Moyerokan river sections was previously presented by Rozman et al. (1979) on the basis of the definitions made by G.G. Astrova. In addition, bryozoans from the Middle and Upper Ordovician and Silurian of the Moyero River section were described by E.A. Modzalevskaya and V.P. Nekhoroshev (Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961), and data on their distribution are presented by Myagkova et al. (1963).

The present paper aims at characterizing the taxonomic composition of the bryozoan assemblage from the upper part of the Dzheromo Formation in the Moyerokan River section, estimating its stratigraphic significance, and expanding our knowledge of the paleobiogeography of Late Ordovician bryozoans.

GEOLOGICAL SETTING, STRATIGRAPHY AND SEDIMENTARY ENVIRONMENTS

Ordovician deposits are widespread in the Siberian Platform. At least two sedimentary basins, the Irkutsk and Tungus basins, also known as the Irkutsk amphitheater and the Tungus syneclise, respectively, are distinguished by the nature of sedimentation evolution (Fig. 1a). Bryozoans described in this paper were collected in two outcrops of the upper part of the Dzheromo Formation near the Moyerokan River mouth, the right tributary of the Moyero River (Fig. 1b). A general section of deposits that crop out here is given in Fig. 2. The Ordovician section in the Moyero River is located the in northeast of the Tungus Basin (Fig. 1a). This section is one of the best and most completed reference sections of the Ordovician on the Siberian Platform. Its systematic study began in the early 1950s and has continued to this day (Nikiforova, 1955; Myagkova et al., 1963, 1977; Dronov et al., 2014, 2021; Pokrovsky et al., 2018).

Ordovician deposits in the Moyero River section, including those which crop out along its tributary, the Moyerokan River, belong to the Moyero structural-facies zone (Kanygin et al., 2007, 2010a). Upper Ordovician deposits are represented here by the Dzheromo Formation, including the Chertovskian, Baksian, and Dolborian regional stages (Kanygin et al., 2017). Despite the fact that the Siberian paleocontinent was located at low, near-equatorial latitudes during Ordovician (Cocks and Torsvik, 2007; Pavlov et al., 2021), Upper Ordovician deposits of the Tungus epicontinental basin (Mangazea, Dolbor, and Dzheromo formations and their analogs) are represented by a series of cold-water carbonates (Kanygin et al., 2010b; Dronov and Zaitsev, 2011; Dronov, 2013). It is these sediments that contain numerous diverse bryozoans and mollusks, forming a bryomol or bryozoan-mollusk association characteristic of temperate carbonates (James, 1997; Dronov, 2001; Pedley and Carannante, 2006).

It should be noted that a similar situation was recorded on the North American Platform, which was also located in the near-equatorial belt during the entire Ordovician. Similarly, this platform was characterized by warm-water carbonate sedimentation in the Early and Middle Ordovician, which was replaced by cold-water sedimentation in the Late Ordovician (Brookfield, 1988; Holland and Patzkowsky, 1996). In both case, this is explained by upwelling that occurred during a strong transgression following a major regression and tectonic rearrangement associated with the onset of the Taconic orogeny (Holland and Patzkowsky, 1996; Ettensohn, 2010). The same processes caused by the Caledonian (Taconic) orogeny were also noted on the Siberian Platform (Dronov, 2009, 2012, 2020).

The section of the upper part of the Dzheromo Formation (Dolborian Regional Stage, Katian Stage, Upper Ordovician; Kanygin et al., 2017) in outcrops nos. 101A and 101B along the Moyerokan River (Fig. 1b) consists of layers of bioclastic limestones varying in thickness from 1.5–3.0 to 5.0–12.0 cm, which alternate with layers of greenish gray or cherry red siltstones (Fig. 2). Layers of bioclastic limestones are composed of storm deposits (tempestites), while siltstone layers represent background sediments. Both of these deposits were accumulated in the distal part of the cold-water ramp at depths between a fair weather wave base and storm wave base (Dronov, 2013, 2017).

Most of the described bryozoans were collected from the upper bedding surfaces of the bioclastic limestone layers in outcrop no. 101B (Fig. 1b). This outcrop is located 1.5 km upstream from the main outcrop no. 101A, described in the monograph by Myagkova et al. (1977) (Fig. 2). The outcrop 101A has a more complete section of the upper part of the Dzheromo Formation, but most of it is covered by scree. In outcrop 101B, only a small fragment of this section crops out along the boundary of the lower, predominantly green, and middle, predominantly red, parts of the formation (Fig. 2). This fragment represents a steep anticlinal fold complicated by a fault and is located at the very river water line. Therefore, the bedding surfaces of the bioclastic limestone beds with numerous bryozoans and remains of other fossil organisms are well washed by rainfall and the river and easily accessible for collection and study.

MATERIALS AND METHODS

The studied collection of bryozoans no. 5846 collected by the team of the Geological Institute, Russian Academy of Sciences (Moscow), is stored in the Laboratory of Higher Invertebrates, Borissiak Paleontological Institute, Russian Academy of Sciences (PIN RAS, Moscow).

Bryozoans were found on the surface of five plates of bioclastic limestone. However, the studied plates are different in a number of colonies on their surface, as well as in the identified taxonomic composition of bryozoans.

Along with the study of bryozoan colonies in oriented thin sections, scanning electron microscopy (SEM) and X-ray computed microtomography (μCT) were applied to study. Paleozoic bryozoans are usually studied in thin sections, because their systematics is based on the features of intracolonial structures. However, SEM data on external morphological features of bryozoans are also important for more comprehensive identification. Microtomography has been widely used in recent years to identify internal and external structures of both fossil and modern bryozoans (see literature review in Key and Wyse Jackson, 2022). Using microtomography, new data on some Ordovician bryozoans have been obtained (Fedorov et al., 2017; Fedorov and Koromyslova, 2019; Koromyslova and Fedorov, 2021; Koromyslova et al., 2021). Therefore, we have considered it appropriate to use this method to study very small and thin bryozoan colonies

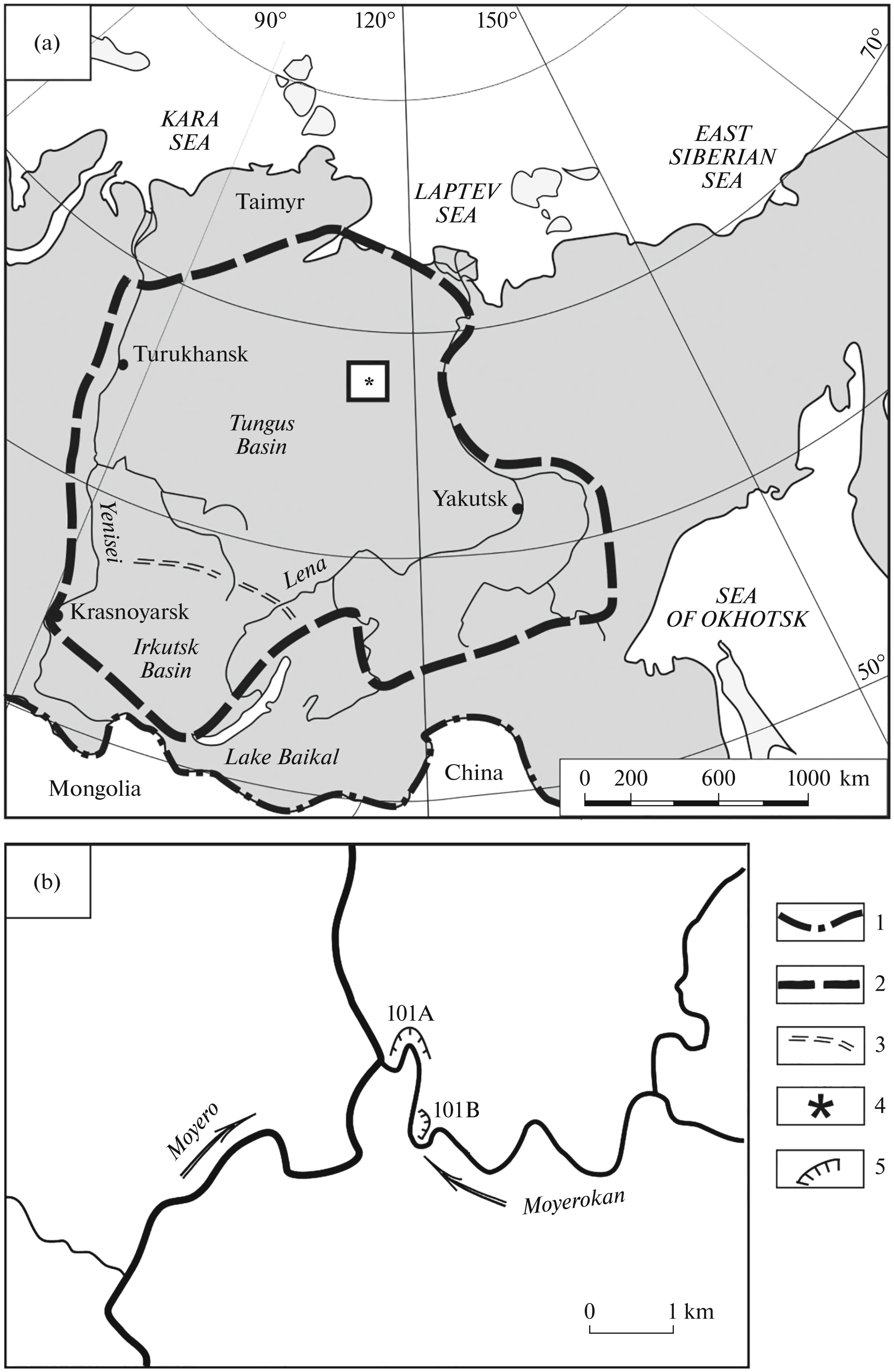


Fig. 1. Scheme of location of the studied Ordovician outcrops and the study area. (a) Location of the study area; (b) location of the studied outcrops: (1) boundaries of the Russian Federation; (2) boundaries of the Siberian Platform; (3) conventional boundaries of the Tungus and Irkutsk sedimentary basins; (4) location of the study area; (5) studied outcrops (outcrop 101A, N 67°22′10″, E 104°05′21″).

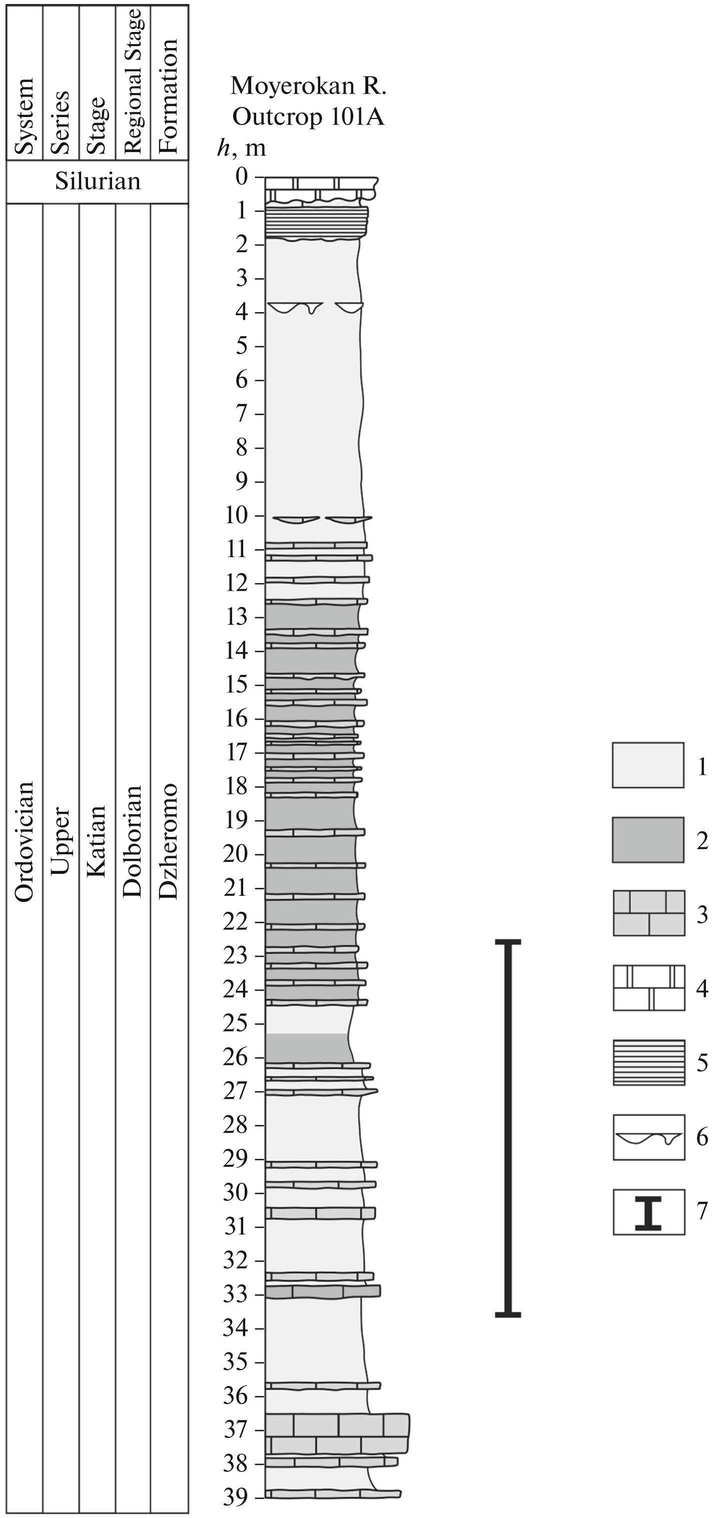


Fig. 2. The structure of the section of the upper part of the Dzheromo Formation (Dolborian Regional Stage, Katian Stage, Upper Ordovician) in studied outcrops along the Moyerokan River. (1) Greenish gray siltstone; (2) cherry red siltstone; (3) bioclastic limestone (packstone); (4) gray thick laminated limestone (mudstone and/or wackestone); (5) yellowish gray, laminar-bedded dolomite; (6) cone-shaped and/or bulbous accumulations of detritus in the stratum of greenish gray siltstone; (7) interval of the section (outcrop 101B) from which bryozoans were sampled.

from the upper part of the Dzheromo Formation along the Moyerokan River. Satisfactory results were obtained for three specimens recognized as *Calloporella* sp. 2, *Leptotrypa* sp., and *P. erecta* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955. The internal structure was studied by microtomography in the first two bryozoans, and the external morphology of the latter was clarified.

The study of bryozoan colonies on Tescan Vega 2 and Tescan Vega 3 scanning electron microscopes and on a NeoScan N80 (Belgium) X-ray scanner and also the preparation of thin sections and their study on a Leica M165C stereoscopic microscope (SM) were carried out at PIN RAS. The samples (coated with Au-Pd alloy and uncoated) were studied using a backscattered electron detector (BSE) operating in a low-vacuum environment (10 Pa) at accelerating voltage of 20 or 30 kV. X-ray computed microtomography of samples was performed without filter at 50 kV and 80 μA; samples were rotated 180° at 0.2° step; exposure was 79 ms/frame; and pixel resolution ranged from 1.0 to 1.2 μm.

The elements of bryozoan colonies were measured from SEM and CM images and also as a result of microtomographic data processed in the CTVox software. The dimensions of bryozoans in the text are given in microns in the following sequence: observed range, arithmetic mean ± standard deviation (in brackets), number of specimens (*N*), and total number of measurements (*n*).

TAXONOMIC COMPOSITION OF THE BRYOZOAN ASSEMBLAGE

The studied bryozoans from deposits of the Dolborian Regional Stage along the Moyerokan River belong to ten genera from four orders: Cystoporata, Trepostomata, Fenestrata, and Cryptostomata. Ten specimens were identified to the species level, while the remaining taxa are defined in open nomenclature because of poor preservation of colonies. Taxonomic identification and distributuin of the studied bryozoans are explained and summarized below.

Bryozoans of order **Cystoporata** are represented by genera *Constellaria* Dana, 1846 and, presumably, *Lunaferamita* Utgaard, 1981 (suborder Fistuliporina Astrova, 1964, family Constellariidae Ulrich, 1896). The species *C. vesiculosa* (Modzalevskaya in Modzalevskaya et Nekhoroshev, 1955) belongs to the first genus, whereas *Lunaferamita*? sp. belongs to the second genus. Initially, the species *C. vesiculosa* was considered as part of the genus *Stellipora* Hall, 1847. At present, despite the objections of Astrova (1965), this genus is considered a junior synonym of the genus *Constellaria* (Ross, 1963; Utgaard, 1981; Goryunova, 1996).

Constellaria vesiculosa (Plate I, figs. 1–7; specimen PIN, nos. 5846/1, 5846/2; sizes of colony elements were determined on the basis of thin section images). This species is characterized by encrusting colonies with stellate spots—monticles developed on their surface. The lower parts of monticles, namely, the central part and 9–10 rays diverging from it, are composed of vesicular tissue (Plate I, figs. 3, 5). Radial rows, consisting of 2–3 rows of autozooecia apertures, are elevated between these rays. Autozooecial apertures are rounded or oval, 130–140 μm across (132 ± 5 μm; $N = 1$, $n = 8$); there are four apertures per 1 mm along each radial row. Vesicles, polygonal in tangential section, 70–90 μm in size, may also be located between autozooecia (Plate I, fig. 6). Autozooecial diaphragms are absent. The presence of acanthostyles is unclear.

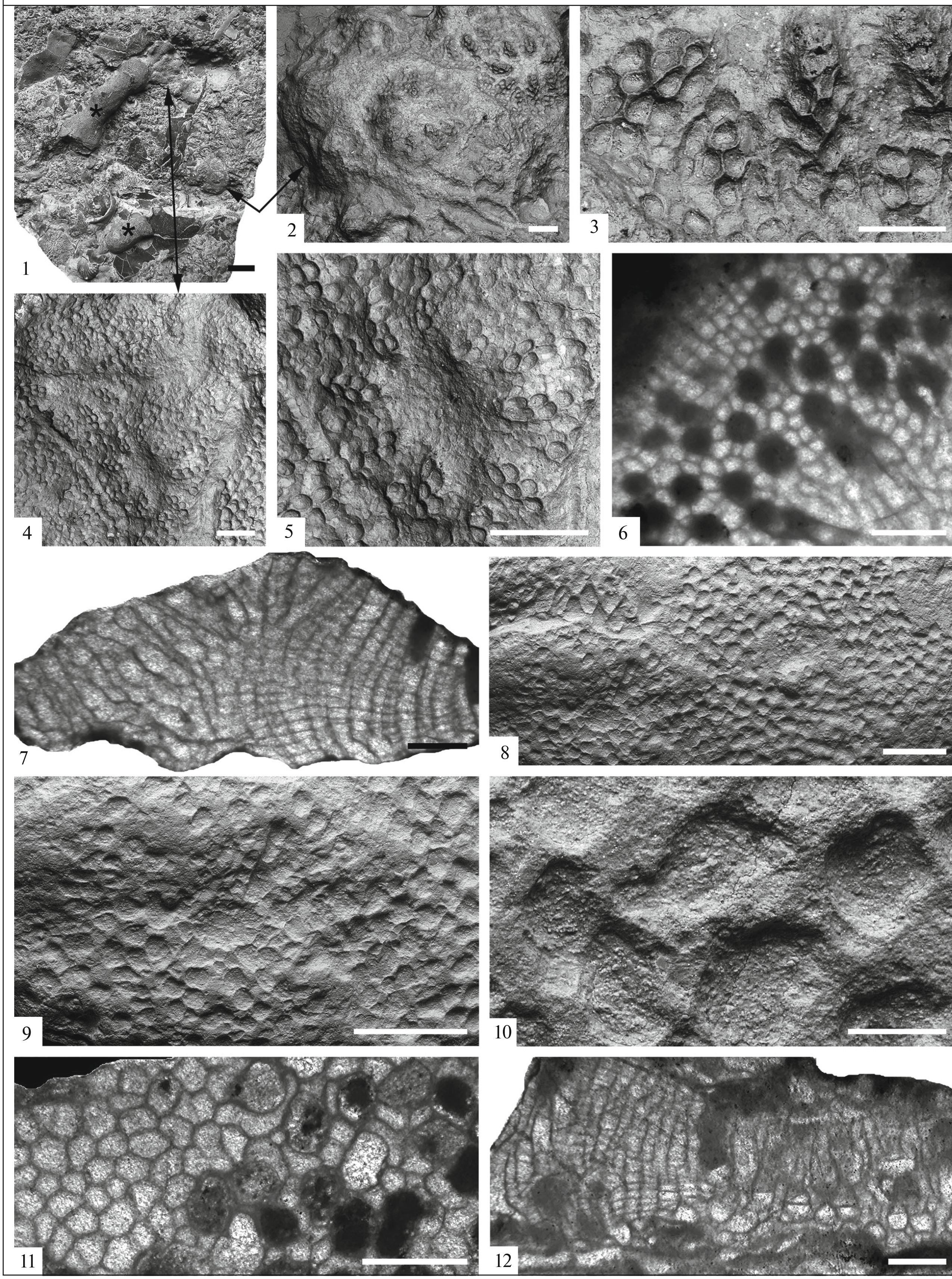
According to previously published data, *C. vesiculosa* has the following distribution: Middle Ordovician on Vaigach Island (Astrova, 1965); Middle–Upper Ordovician of the Siberian Platform (Modzalevskaya and Nekhoroshev, 1955; Astrova, 1965; Rozman et al., 1979; Volkova, 1982; Volkova and Yaroshinskaya, 1984): Chertovskian Regional Stage in the Moyero River, Baksian Regional Stage in the Kulyumbe River basin, Dolborian Regional Stage in the Podkamennaya Tunguska, Chunka, and Rybokupchaya river basins; Upper Ordovician of Gorny Altai and Gornaya Shoriya (Yaroshinskaya, 1960); Upper Ordovician of Poland (Kiepura, 1962); Upper Ordovician of the Jiangxi Province, China (Hu, 1986).

***Lunaferamita*? sp.** (Plate I, figs. 8–12; specimen PIN, no. 5846/3; sizes of colony elements were determined on the basis of thin section images). One colony encrusting a brachiopod shell is attributed to this species. The stellate monticles on the colony surface are indistinct. Autozooecial apertures are irregularly shaped or subrounded, 190–220 μm across (205 ± 11 μm; $N = 1$, $n = 12$); there are 4–6 apertures per 1 mm oriented in different directions; lunarium-like structures are observed in the apertures (Plate I, fig. 10). Vesicular tissue is located between autozooecia or forms accumulations. Vesicles are polygonal in tangential section, 70–150 μm across (108 ± 22 μm; $N = 1$, $n = 12$). The presence of acanthostyles is uncertain.

Lunaferamita? sp. is similar to species *Stellipora complicata* Astrova, 1965 described from the Upper Ordovician (Dolborian Regional Stage, Podkamennaya Tunguska River) of the Siberian Platform in formless monticles and the size of autozooecial aper-

Plate I. Bryozoans of order Cystoporata (suborder Fistuliporina) from the upper part of the Dzheromo Formation; SEM (figs. 2–5, 8–10) and thin sections (figs. 6, 7, 11, 12). (1) Plate of bioclastic limestones with studied bryozoans; two colonies of *Orbignyella moyerokanensis* sp. nov. are shown by asterisks; *Constellaria vesiculosa* (Modzalevskaya in Modzalevskaya et Nekhoroshev), by arrows; (2–7) *C. vesiculosa*: (2, 3) specimen PIN, no. 5846/1; (4–7) specimen PIN, no. 5846/2; (8–12) *Lunaferamita*? sp., specimen PIN, no. 5846/3. Scale bar 1 cm for fig. 1; 1 mm for figs. 2, 4, 5, 8, 9; 500 μm for figs. 3, 6, 7, 11, 12; 200 μm for fig. 10.

Plate I



tures (Astrova, 1965). However, the studied bryozoans colony was presumably assigned to the genus *Lunaferamita*, because lunarium-like structures are observed in autozooecial apertures.

Bryozoans of order **Trepostomata** are represented by suborders Halloporina Astrova, 1965 and Amplexoporina Astrova, 1965. The first suborder includes the following genera: *Calloporella* Ulrich, 1883 with species *Calloporella* sp. 1 and *Calloporella* sp. 2 (family Halloporidae Bassler, 1911), *Stigmatella* Ulrich et Bassler, 1904 with species *Stigmatella* sp. and *S. convestens* Astrova in Ivanova et al., 1955 (family Heterotrypidae Ulrich, 1890), and *Batostoma* Ulrich, 1882 with species *B. varians* (James, 1878) (family Trematoporidae Miller, 1889). The second suborder includes the following genera: *Orbignyella* Ulrich et Bassler, 1904 with species *O. moyerokanensis* sp. nov. and *Leptotrypa* Ulrich, 1883 with species *Leptotrypa* sp. (both genera from family Atactotoechidae Duncan, 1939).

***Calloporella* sp. 1** (Plate II, figs. 1–4; specimen PIN, no. 5846/4; the colony sizes were determined on the basis of the colony surface images). A fragment of a small platy colony was assigned to this species. Autozooecial apertures are rounded or oval, 170–330 μm across (247 ± 43 μm; $N = 1$, $n = 16$); there are 7–9 apertures per 2 mm. Diaphragms in autozooecia are irregularly arranged. Mezozooecia are numerous, not completely separating autozooecial apertures from each other. Mezozooecial apertures are rounded-triangular 50–110 μm across (73 ± 22 μm; $N = 1$, $n = 9$). Mezozooecial diaphragms are numerous. Near the colony surface, thickenings resembling acanthostyles are observed in zooecial walls (Plate II, figs. 2, 4).

***Calloporella* sp. 2** (Plate II, figs. 5–10; specimen PIN, no. 5846/5; the sizes were determined on the basis of the colony surface images). A large platy colony was assigned to this species. Autozooecial apertures are rounded or oval, 150–280 μm across (199 ± 30 μm; $N = 1$, $n = 24$); 7 apertures per 2 mm. The diaphragms in autozooecia are unclear. Mezozooecia are numerous, almost completely surrounding autozooecia. Mezozooecial apertures are rounded, 60–100 μm across (75 ± 13 μm; $N = 1$, $n = 12$). Mezozooecial diaphragms are sparse. The presence of acanthostyles is unclear. *Calloporella* sp. 2 was studied only from the outer surface, as the colony is very thin. This did not allow it to be separated from the limestone plate for making thin sections. One very small fragment (about 2 mm in size) was studied with μCT (Plate II, figs. 8–10). However, the internal structure of the colony could not be reliably established.

Only one species of the genus *Calloporella*, *C. lamellaris* (Modzalevskaya in Modzalevskaya et Nekhoroshev, 1955), was previously described from the Ordovician of the Siberian Platform, originating from the Krivolutskian Regional Stage (corresponding to the Mukteian, Volginian, and Kirensk-Kudrinian Regional Stages of the Darriwilian Stage of the Middle Ordovician; see Kanygin et al., 2017) along the Lena, Moyero, and Nyuya rivers (Modzalevskaya and Nekhoroshev, 1955; Astrova, 1965, 1978). *Calloporella* sp. 1 differs from *Calloporella* sp. 2 in larger autozooecial apertures. According to the external morphology of the colony and the size of zooecia, *C. lamellaris* is the most similar to *Calloporella* sp. 2, while in inner morphology it the most similar to *Calloporella* sp. 1.

Stigmatella convestens (Pate III, figs. 1–5; specimen PIN, no. 5846/6). A large lamellar colony, approximately 30 mm in diameter and 5 mm thick, was assigned to this species. Maculae, which are a cluster of large autozooecia, 2.5–2.5 mm in size, are not elevated above the colony surface. Autozooecial apertures are rounded-polygonal, 510–570 μm (548 ± 20 μm; $N = 1$, $n = 6$) in maculae, 330–480 μm (394 ± 42 μm; $N = 1$, $n = 18$) between maculae. The sizes were determined on the basis of the colony surface images. There are 3–4 apertures per 2 mm of space in maculae and 5 apertures between maculae. Diaphragms are abundant, mostly straight; the distance between them is 160–450 μm (302 ± 73 μm; $N = 1$, $n = 18$). Mezozooecia partially separate autozooecial apertures from each other, beaded in longitudinal sections. Mezozooecial apertures quadrangular, 60–110 μm across (95 ± 21 μm; $N = 1$, $n = 6$) (sizes were determined on the basis of thin section images). Diaphragms are very frequent, straight, spaced 60–80 μm apart. The presence of acanthostyles is unclear.

This species was described by Astrova on the basis of a single specimen from the Dolborian Regional Stage in the Podkamennaya Tunguska River section (Ivanova et al., 1955; Astrova, 1965). The species *S. convestens* is also known from the Upper Ordovician of southwestern Tuva (Upper Karginian Subformation) (Modzalevskaya, 1977) and southwestern Altai (Upper Kabinskian Subformation) (Avrov and Modzalevskaya, 1982). The studied specimen is different from the specimen described by Astrova in the presence of maculae, larger autozooecial apertures in the space between maculae (330–480 μm vs. 280–460 μm), and irregularly developed autozooecial diaphragms. Acanthostyles in specimens from Tuva are more distinct. *S. convestens* is also most similar to the species *Diplotrypa sincera* Astrova, 1965 described from Middle Ordovician of Vaigach Island (Astrova, 1965), which obviously requires additional study of representatives of these species.

***Stigmatella* sp.** (Plate III, figs. 6–8; specimen PIN, no. 5846/7; sizes of colony elements were determined on the basis of thin section images). A flattened ramose colony is assigned to this species. The exozone is narrow; the endozone is broad. Autozooecial apertures rounded or petaloid, 220–370 μm across (298 ± 48 μm; $N = 1$, $n = 12$). There are 5–6 apertures per 2 mm. Autozooecial diaphragms are rare. Mezozooecia are numerous, almost completely surrounding the autozooecia. Mezozooecial apertures are rounded, 80–100 μm in size. Mezozooecial diaphragms are frequent,

Plate II

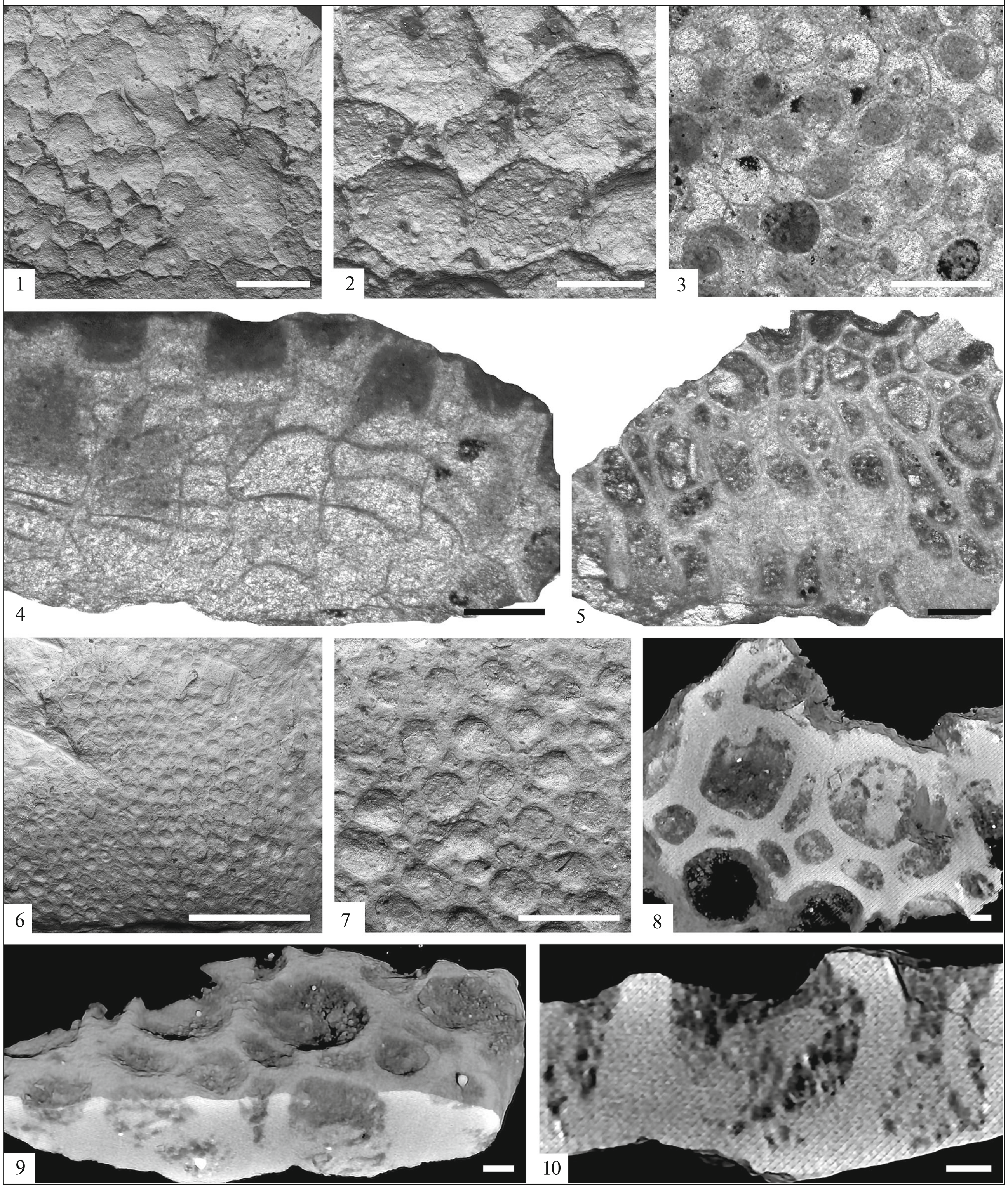


Plate II. Bryozoans of order Trepostomata (suborder Halloporina) from the upper part of the Dzheromo Formation; SEM (figs. 1, 2, 6, 7), thin sections (figs. 3–5), and μCT (figs. 8–10). (1–4) *Calloporella* sp. 1, specimen PIN, no. 5846/4; (5–10) *Calloporella* sp. 2, specimen PIN, no. 5846/5. Scale bar 2 mm for fig. 6; 500 μm for figs. 1, 3, 7; 250 μm for figs. 4, 5; 200 μm for fig. 2; 50 μm for figs. 8–10.

developed within the mature region. The presence of acanthostyles is unclear.

The studied bryozoan colony is similar to the specimens of *Stigmatella tungusensis* Astrova in Ivanova et al., 1955 assigned by Astrova (Ivanova et al., 1955) to group "r." However, this species was previously described only from the Krivolutskian Regional Stage along Podkamennaya Tunguska and Kulyumbe rivers (Ivanova et al., 1955; Volkova, 1982). In addition, *Stigmatella* sp. differs from *S. tungusensis* (group "r") in larger autozooecial apertures (5–6 apertures instead of 7–8 per 2 mm).

Batostoma varians (Plate III, figs. 9–11; specimen PIN, no. 5846/8; sizes of colony elements were determined on the basis of thin section images). This species is characterized by large branching colonies, divided into endo- and exozones. The exozone is rather wide. Autozooecial apertures are rounded to oval, 250–460 μm across (360 ± 60 μm; $N = 1$, $n = 12$). In the endozone, autozooecial diaphragms are irregularly arranged; the distance between them is 760–900 μm; their number in the exozone increases, the distance between them is 150–380 μm. Mezozooecia are rare, beaded in transverse section. Mezozooecial diaphragms are numerous; the distance between them is about 100 μm. Acanthostyles are small, numerous, developed near the colony surface.

According to previously published data, *B. varians* has the following distribution: Middle–Upper Ordovician of the Siberian Platform (Ivanova et al., 1955; Astrova, 1978; Yaroshinskaya, 1978; Rozman et al., 1979; Volkova, 1982; Volkova and Yaroshinskaya, 1984): Baksian Regional Stage in the Kulyumbe River section, Chertovskian, Baksian and Dolborian regional stages in the Podkamennaya Tunguska and Bolshaya Nirunda river sections, Ketian Regional Stage, Nirundian Regional Stage along Bolshaya Nirunda River; Middle Ordovician: Lower Karginian Subformation in southwestern Tuva (Modzalevskaya, 1977); Upper Ordovician: Kulonian Formation, the Sette-Daban Ridge (Modzalevskaya, 1970), Tolmachevskian Regional Stage of Taimyr Peninsula (Nekhorosheva, 1965, 1966b, 2018), Malodiring-Ayan Formation of Kotelny Island (Nekhorosheva, 2018), and the Richmond Formation of North America (Cumings and Calloway, 1912).

***Orbignyella moyerokanensis* sp. nov.** (Plate IV, figs. 1–12; specimen PIN, nos. 5846/9, 5846/10). The representatives of the genus *Orbignyella* were first found in Ordovician deposits of the Siberian Platform. The description of the new species is given below.

***Leptotrypa* sp.** (Plate V, figs. 1–5; specimen PIN, no. 5846/11; the sizes of structural elements were determined on the basis of colony surface images). A fragment of one small lamellar colony 1 mm long and 1.4 mm wide was assigned to this species. Autozooecial apertures are rounded-polygonal or petaloid, 170–270 μm in diameter (226 ± 30 μm; $N = 1$, $n = 8$). There are no autozooecial diaphragms. Exilazooecia are rare, 110–130 μm across. Acanthostyles are large, 30–40 μm across, 3–5 near each aperture, sometimes embedded in the aperture cavity.

Only one species for the genus *Leptotrypa*, *L. jadrenkinae* Jaroshinskaya in Volkova et Jaroshinskaya, 1984, was described from the Ordovician of the Siberian Platform, from the Dolborian Regional Stage in the Nizhnyaya Chunku section (Volkova and Yaroshinskaya, 1984). *Leptotrypa* sp. is similar to *L. jadrenkinae* in external colony structure. However, *Leptotrypa* sp. differs from *L. jadrenkinae* in smaller autozooecial apertures (170–270 vs. 230–350 μm) and the presence of autozooecial diaphragms.

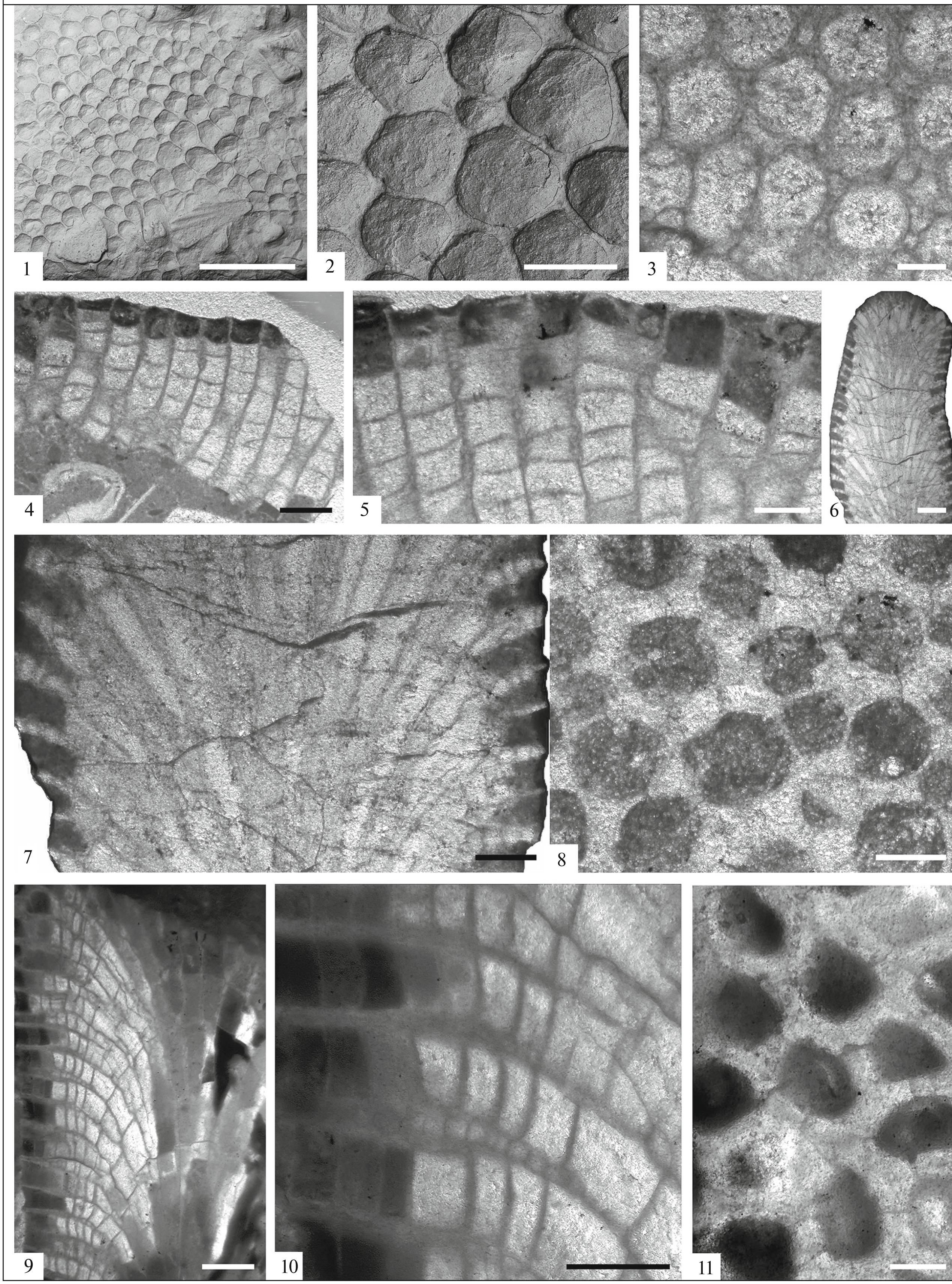
Bryozoans of order **Fenestrata** are represented by genus *Parachasmatopora* Morozova et Lavrentjeva, 1981 with species *Parachasmatopora* sp. (family Chasmatoporidae Schulga-Nesterenko, 1955, suborder Phylloporinina Lavrentjeva, 1979). This genus differs from the most similar genus *Chasmatopora* Eichwald, 1890 in the presence of two to three rows of autozooecia on branches instead of four rows in *Chasmatopora*.

***Parachasmatopora* sp.** (Plate V, figs. 6–14; specimen PIN, nos. 5846/12, 5846/13, 5846/14; the sizes of structural elements were determined on the basis of the colony surface images). The reticulate colonies with wavy-curved, anastomosing branches are assigned to this species. Autozooecia on the branches are arranged in two to three rows, less commonly in four rows (Plate V, figs. 9–11). Autozooecial apertures are rounded to oval, 100–140 μm in maximum diameter (114 ± 12 μm; $N = 3$, $n = 24$). There are 8–9 apertures per 2 mm along the branch. Zooecial walls are penetrated by capillaries (Plate V, fig. 14). The surface of the reverse side of the colony is longitudinally wavy, with numerous microstyles (Plate V, fig. 12) and, presumably, capillaries located at the border of zooecia (Plate V, fig. 13).

Parachasmatopora sp. is the most similar to *P. maennili* Morozova et Lavrentjeva, 1981 in aperture size (100–140 vs. 100–120 μm in *P. maennili*) (Morozova and Lavrentieva, 1981; Lavrentieva, 1985). However, only the external morphology has been studied in *Parachasmatopora* sp. because the colonies of this species are very thin and brittle, which did not allow them to be separated from the limestone plate for making thin sections. One very small fragment (about 1 mm in size) was studied by means of μCT. Nevertheless, this did not

Plate III. Bryozoans of order Trepostomata (suborder Halloporina) from the upper part of the Dzheromo Formation; SEM (figs. 1, 2) and thin sections (figs. 3–11). (1–5) *Stigmatella convestens* Astrova in Ivanova et al., specimen PIN, no. 5846/6; (6–8) *Stigmatella* sp., specimen PIN, no. 5846/7; (9–11) *Batostoma varians* (James), specimen PIN, no. 5846/8. Scale bar 1 mm for figs. 1, 6, 9; 750 for fig. 4; 500 μm for figs. 2, 5, 7, 10; 250 μm for figs. 3, 8, 11.

Plate III



reveal the internal structure of autozooecia, since their internal cavities appeared to be filled with mycrite.

The bryozoans of the genus *Parachasmatopora* were first described in the Ordovician of the Siberian Platform. Bryozoans of genus *Chasmatopora*, *C.* cf. *moyeroensis* Nekhoroshev, 1955 (Moyero River) and *C. pusilla* Astrova, 1965 (Podkamennaya Tunguska), of order Fenestrata were previously described from deposits of the Dolborian Regional Stage. However, both of these species are currently assigned to the genus *Moorephylloporina* Bassler, 1952, which is included in the suborder Fenestellina Astrova et Morozova, 1956 (see Morozova, 2001).

Bryozoans of order **Cryptostomata** are represented by abundant fragments of bryozoan colonies belonging to genera *Phaenopora* Hall, 1851 and *Phaenoporella* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955 (family Ptilodictyidae Zittel, 1880, suborder Ptilodictyina Astrova et Morozova, 1956). The composition of the first genus includes 58 species; the composition of the second genus includes 12 species (Goryunova and Lavrentieva, 1993). We studied only the most complete colonies, since almost all *Phaenopora* and *Phaenoporella* systematics is based on external morphological characters. To determine the species of these genera, it is necessary to know the shape of the colony, as well as the number of rows of autozooecial apertures on the colony surface, which varies in different parts of the colony. The inner structure of bryozoans of *Phaenopora* and *Phaenoporella* are of the same type and the systematic significance of some characters has not been established yet.

The studied bryozoans of genus *Phaenopora* are represented by the following species: *P. plebeia* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955, *P. pennata* Nekhoroshev, 1961, *P. erecta* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955, *P. carinata* Nekhoroshev, 1961, and *P. viluensis* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955; bryozoans of genus *Phaenoporella* are represented by *Phaenoporella* sp. and *P. multipora* Nekhoroshev, 1961. According to (Astrova, 1965), some species of genus *Phaenopora* should be included in the composition of genera *Fimbriapora* Astrova, 1965 and *Ensipora* Astrova, 1965, but Nekhoroshev (1977) proved the unreasonableness of separating these genera (see also Nekhorosheva, 1966a; Goryunova and Lavrentieva, 1993; Goryunova, 1996).

Phaenopora* [=*Fimbriapora*] *plebeia (Plate VI, figs. 1–9; specimen PIN, nos. 5846/15, 5846/16, 5846/17; the sizes were determined on the basis of the colony surface images). A few fragments of thinly branched bilateral colonies 1.5–2.5 mm wide are attributed to this species. Autozooecial apertures oval-rectangular, in marginal rows 150–220 μm long (177 ± 21 μm; $N = 3$, $n = 14$) and 90–130 μm wide (108 ± 14 μm; $N = 3$, $n = 14$). There are 7–8 apertures per 2 mm of colony. The apertures are arranged almost in chessboard order in 6–11 rows on the colony surface (Plate VI, figs. 1, 8) and separated by wide ridges of about 60–70 μm wide. In transverse sections are a few rows with oblique autozooecial apertures (Plate VI, fig. 6). Metazooecia are arranged in pairs near each aperture (Plate VI, figs. 2, 9). Metazooecial apertures irregularly rounded, 30–60 μm in maximum diameter (46 ± 12 μm; $N = 2$, $n = 6$). There are no tubercles between metazooecia. The mesotheca is almost straight (Plate VI, fig. 7).

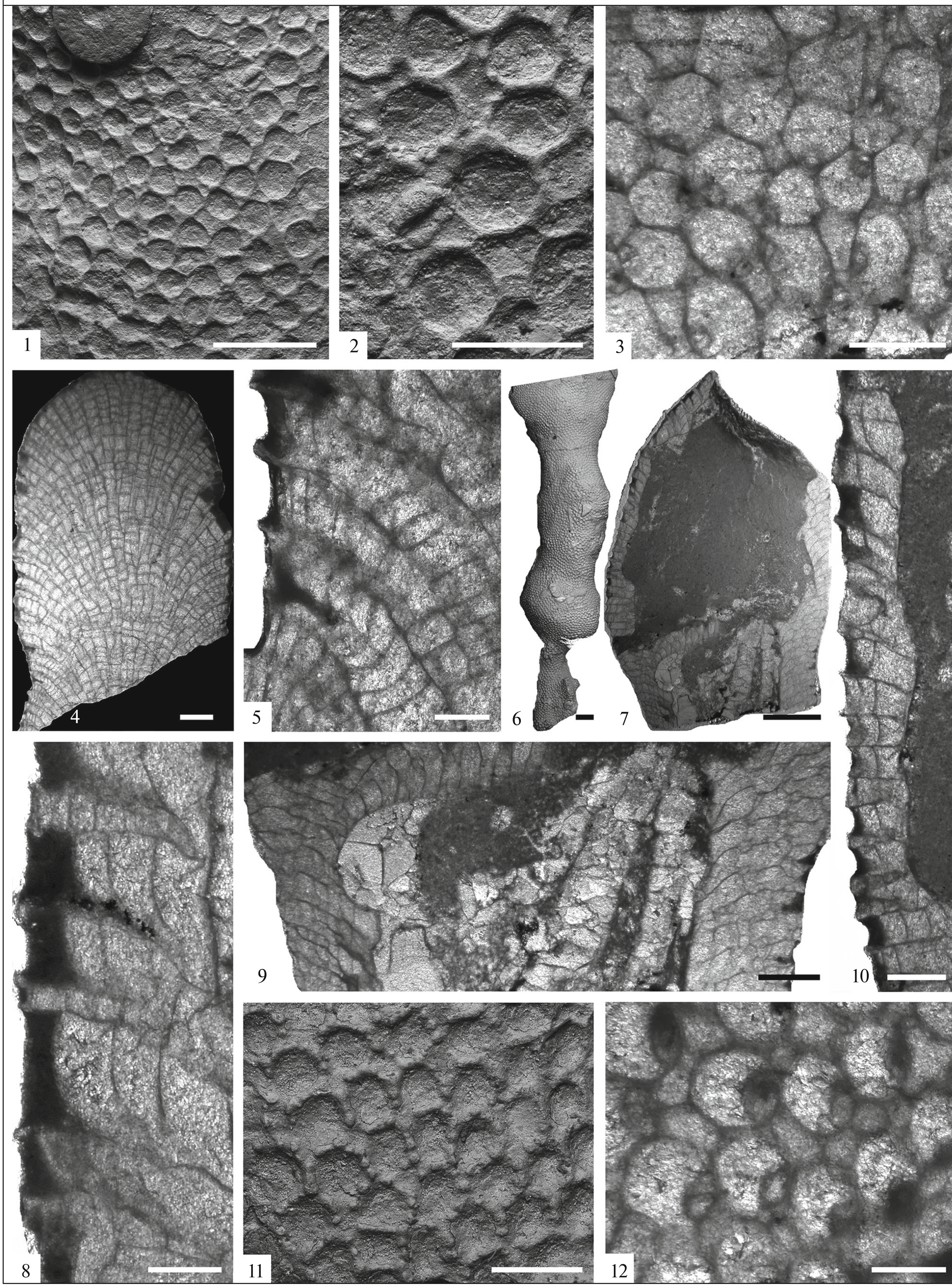
In one of the studied specimens, the lower hemiseptum is long, oblique downward; the upper hemiseptum is long, straight and vertical (Plate VI, fig. 3). In another specimen, the upper hemiseptum is short; the character of the lower hemiseptum is unclear (Plate VI, fig. 5). A visible difference between the morphological features of hemisepta in these two colonies may be due to their different degree of preservation. In addition, the development of hemisepta was not considered either in the first description of the species or later in (Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961). According to Astrova (1965, p. 261), however, in this species, "the upper hemiseptum occurs in the form of a slight protrusion; the lower one is short, strongly thickened, and oblique."

According to previously published data, *P. plebeia* has the following distribution: Middle–Upper Ordovician and Lower Silurian of the Siberian Platform (Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961; Astrova, 1965; Rozman et al., 1979; Volkova, 1982; Volkova and Yaroshinskaya, 1984): Baksian Regional Stage in the Kulyumbe River section, Dolborian Regional Stage along the Moyero and Podkamennaya Tunguska river sections, the upper Upper Ordovician in the Morkoka River section, Llandoverian Stage in the Vilyui, Markha, Morkoka, Oldondo, Moyero, and Podkamennaya Tunguska river sections; Upper Ordovician: Korotkinskian Regional Stage of Central Taimyr (Nekhorosheva, 1966a, 1966b, 1997a), Kulonian Formation, the Sette-Daban Ridge (Modzalevskaya, 1970), Sairin assemblage of the Katian Stage, Gobi-Altai zone of Southern Mongolia (Ariunchimeg, 2009), and the Anisin and Teryutekh formations of Kotelny Island (Nekhorosheva, 2018).

Phaenopora* [=*Ensipora*] *pennata (Plate VI, figs. 10–12; specimen PIN, no. 5846/18; the sizes were determined on the basis of the colony surface

Plate IV. Bryozoans of order Trepostomata (suborder Amplexoporina) from the upper part of the Dzheromo Formation; SEM (figs. 1, 2, 6, 11) and thin sections (figs. 3–5, 7–10, 12). (1–12) *Orbignyella moyerokanensis* sp. nov.: (1–5) holotype PIN, no. 5846/9; (6–12) paratype PIN, no. 5846/10. Scale bar 2 mm for figs. 6, 7; 1 mm for figs. 1, 4; 750 μm for fig. 9; 500 μm for figs. 2, 3, 10, 11; 250 μm for figs. 5, 8, 12.

Plate IV



images). A fragment of direct, presumably nonbranching ribbon-shaped bilateral colony about 3.0 mm wide is attributed to this species. Autozooecial apertures are oval-rectangular: in marginal rows 230–280 μm long (244 ± 22 μm; *N* = 1, *n* = 5) and 90–120 μm wide (114 ± 15 μm; *N* = 1, *n* = 5); in middle rows 170–210 μm long (190 ± 14 μm; *N* = 1, *n* = 6) and 80–110 μm wide (95 ± 14 μm; *N* = 1, *n* = 6). There are 7.5 apertures (in the center) and 6 (at the edges) per 2 mm of colony length. Apertures are located almost in chessboard order in 14–16 rows on the surface of the colony (Plate VI, fig. 10), separated by narrow ridges. Up to four marginal pinnate rows with oblique autozooecial apertures are observed in longitudinal sections. Metazooecia are located in pairs near each aperture. There are no tubercles between metazooecia. The lower and upper hemisepta straight and short. The nature of the mesotheca is unknown.

The species *P. pennata* was first discovered in the Ordovician of the Siberian Platform. According to the previously published data, *P. pennata* has the following distribution: Upper Ordovician, Kulonian Formation, the Sette-Daban Ridge (Modzalevskaya, 1970); Sairin assemblage of the Katian Stage, Gobi–Altai zone of Southern Mongolia (Ariunchimeg, 2009); Lower Silurian, Llandoverian Stage of the Siberian Platform in the Vilyui, Markha, Maimecha, and Podkamennaya Tunguska river basins (Nekhoroshev, 1961; Astrova, 1965) and Central Taimyr (Nekhorosheva, 1997b).

Phaenopora* [=*Ensipora*] *erecta (Plate VI, figs. 13–16; specimen PIN, no. 5846/19; the sizes were determined on the basis of the colony surface images). A fragment of direct ribbon-shaped, nonbranching bilateral colony about 2.0 mm wide belongs to this species. Autozooecial apertures are oval-rectangular: in marginal rows 240–310 μm long (278 ± 24 μm; *N* = 1, *n* = 8) and 100–120 μm wide (111 ± 7 μm; *N* = 1, *n* = 8); in middle rows 190–210 μm long (202 ± 8 μm; *N* = 1, *n* = 12) and 90–110 μm wide (100 ± 5 μm; *N* = 1, *n* = 12). There are 7.5 apertures per 2 mm of colony length in the center and 6–7 at the edges. Apertures are located almost in chessboard order in 11–12 rows on the surface of the colony, being separated by ridges of about 20 μm wide. Pinnate rows are absent; however, in two marginal rows, apertures are large and oblique. Metazooecia are arranged in pairs near each aperture (Plate VI, fig. 13). Metazooecial apertures are irregularly rounded, 20–35 μm in maximum diameter (30 ± 6 μm; *N* = 1, *n* = 10). There are tubercles between metazooecia (Plate VI, fig. 14). The lower hemiseptum is long, subhorizontal, curved upwards (Plate VI, fig. 15). The character of the upper hemiseptum is unclear, but according to Astrova (1965), it should be long and upwardly directed.

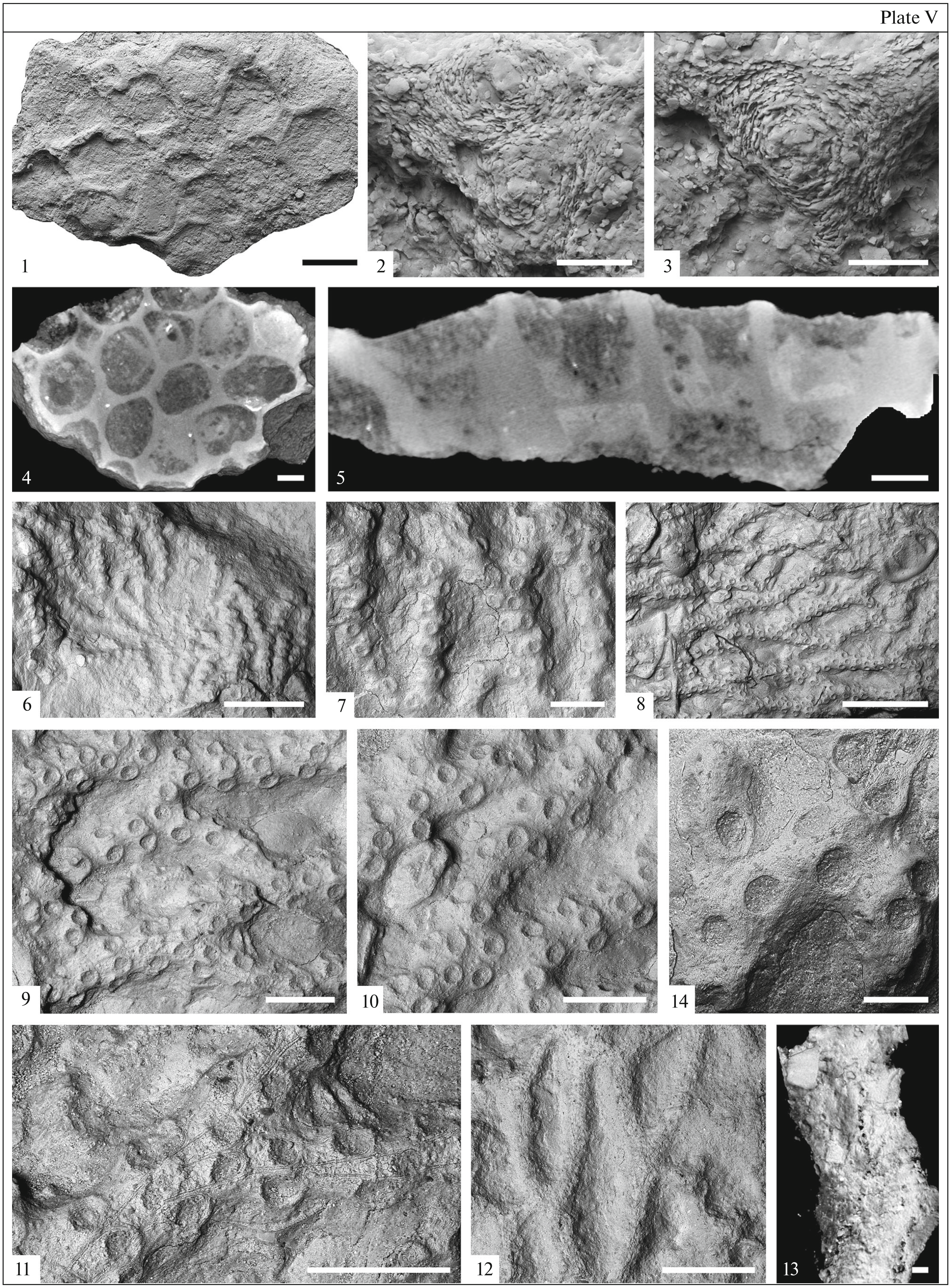
According to previously published data, *P. erecta* has the following distribution: Middle–Upper Ordovician of the Siberian Platform (Astrova, 1965): Mangazea Formation (corresponding to the Chertovskian and Baksian regional stages) and Dolborian Regional Stage in the Podkamennaya Tunguska River section; Upper Ordovician: Kulonian Formation, the Sette-Daban Ridge (Modzalevskaya, 1970); Sairin assemblage of the Katian Stage, the Gobi-Altai zone of Southern Mongolia (Ariunchimeg, 2009); Korotkinskian Regional Stage of Central Taimyr (Nekhorosheva, 1997a); Anisin and Teryutekh formations of Kotelny Island (Nekhorosheva, 2018); Lower Silurian: Llandoverian Stage in the Vilyui, Markha, and Moyero river sections in the Siberian Platform (Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961); Khutsinbulak Beds in northwestern Mongolia and Dashtygoyskian Regional Stage in Central Tuva (Nekhorosheva, 2018).

Phaenopora* [=*Ensipora*] *carinata (Plate VII, figs. 1–8; specimen PIN, nos. 5846/20, 5846/21; the sizes were determined on the basis of the colony surface images). This species is characterized by straight, ribbon-shaped, nonbranched, bilateral colonies up to 2.5 mm wide. Autozooecial apertures are oval-rectangular: in marginal rows 190–240 μm long (203 ± 14 μm; *N* = 1, *n* = 12) and 80–120 μm wide (99 ± 14 μm; *N* = 1, *n* = 12); in middle rows 140–170 μm long (158 ± 11 μm; *N* = 1, *n* = 12) and 60–85 μm wide (71 ± 8 μm; *N* = 1, *n* = 12). There are 10 apertures per 2 mm of colony length in the center and 7–8 at the edges. Apertures are located almost in chessboard order in 10–11 straight rows on the colony surface, separated by wide ridges about 80 μm wide (Plate VII, figs. 2, 4, 7). Pinnate rows are absent; however, in the transverse sections, apertures of one or two marginal rows may be oblique. Metazooecia are very small, observed in longitudinal sections (Plate VII, figs. 5, 8) and occasionally on the colony surface. They are arranged presumably in pairs near each aperture (Plate VII, fig. 4). There are tubercles between metazooecia (Plate VII, fig. 3). The upper hemiseptum is short (Plate VII, figs. 5, 8). The character of the lower hemiseptum and mesotheca is unknown.

According to previously published data, the species *P. carinata* has the following distribution: Middle Ordovician of the Siberian Platform (Nekhoroshev, 1961): Mangazea Formation (corresponding to the Chertovskian and Baksian regional stages) in the Chunya River section; Upper Ordovician: Upper Bar-

Plate V. Bryozoans of orders Trepostomata (suborder Amplexoporina) (figs. 1–5) and Fenestrata (suborder Phylloporinina) (figs. 6–14) from the upper part of the Dzheromo Formation; SEM (figs. 1–3, 6–12, 14) and μCT (figs. 4, 5, 13). (1–5) *Leptotrypa* sp., specimen PIN, no. 5846/11; (6–14) *Parachasmatopora* sp.: (6, 7) specimen PIN, no. 5846/13; (8–13) specimen PIN, no. 5846/12; (14) specimen PIN, no. 5846/14. Scale bar 2 mm for figs. 6, 8; 1 mm for fig. 12; 500 μm for figs. 7, 9–11; 200 μm for figs. 1, 14; 100 μm for figs. 4, 5; 50 μm for fig. 13; 20 μm for figs. 2, 3.

Plate V



aninskian Regional Stage of the Southern Verkhoyansk Region, Baraniy Stream (Volkova et al., 1978).

Phaenopora viluensis (Plate VII, figs. 9–12; specimen PIN, no. 5846/22). This species is characterized by large narrow leaf-shaped, nonbranching bilateral colonies with a thick median projection (Plate VII, fig. 9). The surface of the colony is covered by abundant, slightly elevated, regularly arranged maculae 2.5–2.7 mm in size; the distance between maculae is 1.1–1.5 μm (Plate VII, fig. 10). The maculae of this species are clusters of large autozooecia, with smaller autozooecia between them. Autozooecial apertures are rounded to oval; in maculae measuring 170–370 μm in maximum diameter (285 ± 72 μm; $N = 1$, $n = 12$), between maculae 190–230 μm (208 ± 9 μm; $N = 1$, $n = 12$) (the sizes were determined on the basis of the colony surface images). There are 7–8 apertures per 2 mm of space in maculae, and 8–9 apertures between them. Metazooecia are abundant, varying in number between autozooecial apertures (Plate VII, fig. 12). Metazooecial apertures irregularly rounded, 50–120 μm in maximum diameter (82 ± 20 μm; $N = 1$, $n = 12$; the sizes were determined on the basis of the thin section images).

According to previously published data, *P. viluensis* has the following distribution: Upper Ordovician: Korotkinskian Regional Stage of Central Taimyr (Nekhorosheva, 1997a); Upper Ordovician–Lower Silurian of the Siberian Platform: Dolborian Regional Stage in the Moyero River section, Upper Ordovician in the Morkoka River section, Llandoverian Stage in the Vilyui and Markha river sections (Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961).

***Phaenoporella* sp.** (Plate VII, figs. 13–15; specimen PIN, no. 5846/23; sizes of autozooecial apertures were determined on the basis of the thin section images). A fragment of a reticulate colony is attributed to this species. Autozooecial apertures are oval, 150–190 μm in maximum diameter (172 ± 15 μm; $N = 1$, $n = 5$). They are arranged in 9–10 rows on the branch (Plate VII, fig. 13), separated by ridges about 20 μm wide. There are 8–9 apertures per 2 mm of branch length and 10–12 apertures per 2 mm of width. Metazooecia are located in pairs near each aperture (Plate VII, fig. 15) and around fenestrules, forming a few concentrically arranged rows (Plate VII, fig. 14). Metazooecial apertures are oval, 70–90 μm in maximum diameter (80 ± 6 μm; $N = 1$, $n = 6$). No capillaries are observed.

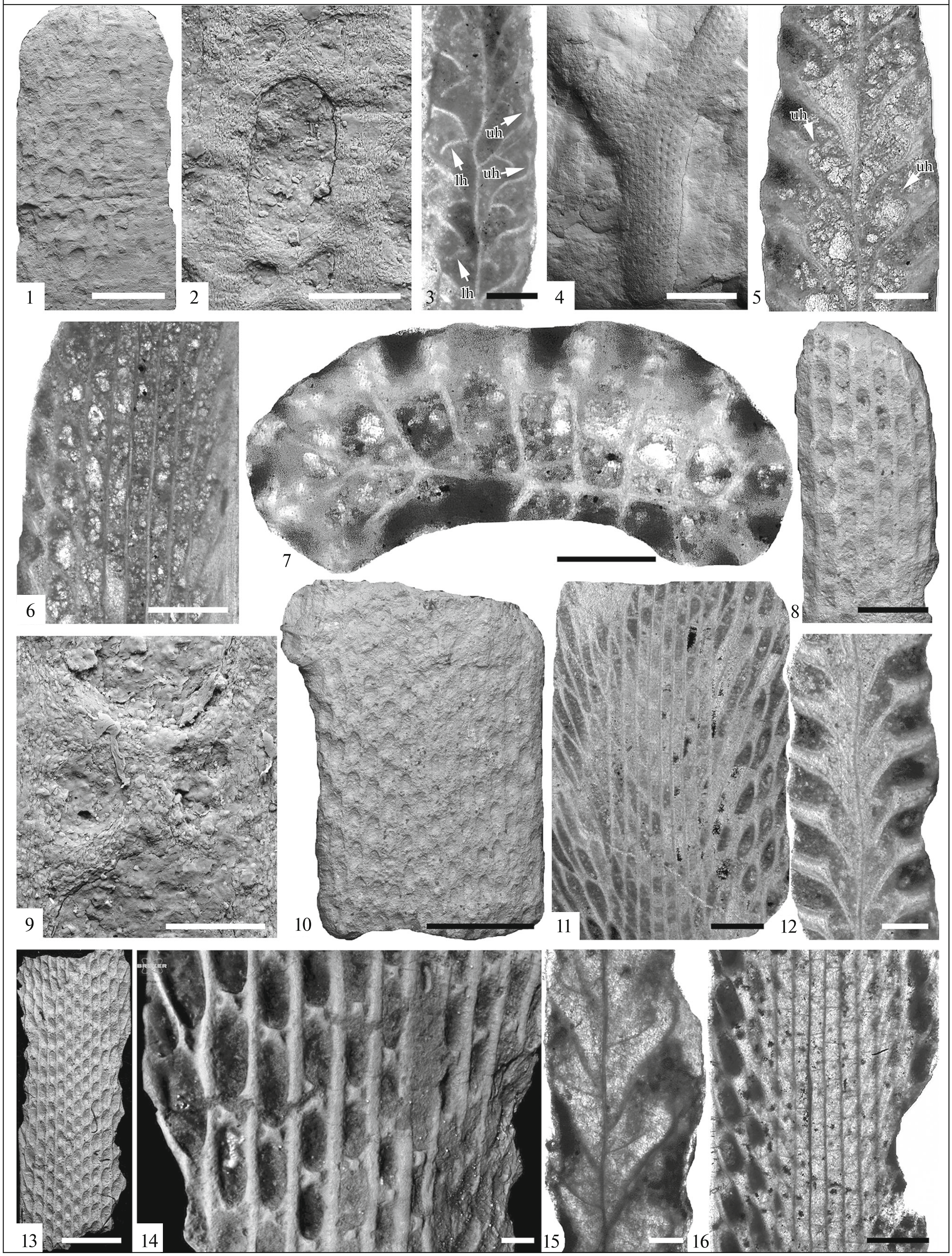
Phaenoporella sp. is similar to species *P. transenna-mesofenestralia* (Schoenmann, 1927) and *P. macrofenestralia* in the number of autozooecia on the rods and the size of the zooecia (Schoenmann, 1927). However, incompleteness of the studied sample does not allow a correct identification of the species. Both species are known from the Middle and Upper Ordovician of the Siberian Platform (Sheinmann, 1927; Nekhoroshev, 1961; Astrova, 1965; Yaroshinskaya, 1978), and *P. transenna-mesofenestralia* also occurs in the Upper Ordovician of the Southern Verkhoyansk Region (Volkova et al., 1978), the Sette-Daban Ridge (Modzalevskaya, 1970), and Gorny Altai (Yaroshinskaya, 1960).

Phaenoporella multipora (Plate VIII, figs. 1–8; specimen PIN, no. 5846/24; sizes of autozooecial apertures were determined on the basis of the thin section images). This species is characterized by large reticulate fan-shaped colonies with a narrow articular end. The latter in the studied colony looks like a thick rod of 380 μm wide in the middle part (Plate VIII, figs. 1–3). The meshwork is formed by the combination of anastomosing bilateral branches that are 150–210 μm wide (180 ± 18 μm; $N = 1$, $n = 12$). Fenestrules are rounded or oval, 110–190 μm in maximum diameter (153 ± 28 μm; $N = 1$, $n = 12$). Autozooecial apertures are oval, 110–150 μm in maximum diameter (126 ± 12 μm; $N = 1$, $n = 12$). They are arranged in 4–7 rows on the branch (Plate VIII, figs. 5–7), separated by ridges about 40 μm wide (Plate VIII, fig. 8). There are 8–9 apertures per 2 mm of branch length and 10–12 apertures per 2 mm of width. Metazooecia are abundant, chaotically arranged between autozooecial apertures (Plate VIII, figs. 7, 8) and around fenestrules, forming 5–6 concentric rows (Plate VIII, figs. 5, 6). Metazooecial apertures are irregularly rounded, 20–40 μm across (30 ± 5 μm; $N = 1$, $n = 12$). No capillaries are observed.

According to previously published data, *Ph. multipora* has the following distribution: Middle–Upper Ordovician of the Siberian Platform (Nekhoroshev, 1961; Astrova, 1965; Volkova and Yaroshinskaya, 1984): Mangazea Formation in the Chunya, Podkamennaya Tunguska, and Rybokupchaya river sections and Dolborian Regional Stage in the Markha and Nizhnyaya Chunku river sections; Upper Ordovician: the upper part of the Tolmachevskian Regional Stage (Nekhorosheva, 1966a, 1966b) and Korotkinskian Regional Stage (Nekhorosheva, 1997a) of the Taimyr Peninsula, the upper part of the Malodiring-Ayan Formation of Kotelny Island (Nekhorosheva, 2018).

Plate VI. Bryozoans of order Cryptostomata (suborder Ptilodictyina) from the upper part of the Dzheromo Formation; SEM (figs. 1, 2, 4, 8–10, 13), thin sections (figs. 3, 5–7, 11, 12, 15, 16), and μCT (fig. 14). (1–9) *Phaenopora plebeia* Nekhoroshev: (1–3) specimen PIN, no. 5846/15; (4–7) specimen PIN, no. 5846/16; (8, 9) specimen PIN, no. 5846/17; (10–12) *P. pennata* Nekhoroshev, specimen PIN, no. 5846/18; (13–16) *P. erecta* Nekhoroshev, specimen PIN, no. 5846/19. Designations: uh—upper hemiseptum, lh—lower hemiseptum. Scale bar 2 mm for fig. 4; 1 mm for figs. 10, 13; 500 μm for figs. 1, 6, 8, 11, 16; 250 μm for figs. 3, 5, 7, 12; 100 μm for figs. 2, 14, 15; 50 μm for fig. 9.

Plate VI



SYSTEMATIC DESCRIPTION

ORDER TREPOSTOMATA

SUBORDER AMPLEXOPORINA

FAMILY ATACTOTOECHIDAE DUNCAN, 1939

Genus *Orbignyella* Ulrich et Bassler, 1904

Orbignyella moyerokanensis Koromyslova et Dronov, sp. nov.

Plate I, fig. 1; Plate IV, figs. 1–12

Holotype. PIN, no. 5846/9; Northern Siberia, Moyerokan River (a right tributary of the Moyero River); Upper Ordovician, Katian Stage, Dolborian Regional Stage, Dzheromo Formation.

Description (the sizes were determined on the basis of the colony surface images). Colonies large, rod-shaped, massive (Plate IV, fig. 4) or encrusted with the formation of rod-like colonies (Plate IV, figs. 6–9), which is probably associated with overgrowing of a large cylindrical object. In the latter case, the autozooecia are apparently budded from the axial tubular basal plate. Fragments of a colony are up to 40 mm high, up to 10 mm thick. There is no division into endo- and exozones. Autozooecial walls are weakly wavy. Maculae are not observed. Apertures rounded, 210–370 μm across (262 ± 35 μm; $N = 2$, $n = 24$). There are 7–8 apertures per 2 mm. Diaphragms frequent, horizontal, sagging, curved, often cystiform near the colony surface. There are rare zooecia with irregularly tri- or quadrangular apertures (excilazooecia?), 110–240 μm across (159 ± 40 μm; $N = 2$, $n = 12$), not completely separating autozooecial apertures from each other. Acanthostyles large, up to 50 μm in size, abundant, densely encircling the zooecial apertures (up to 11–13 around each aperture); they are developed near the colony surface; no central cavity is observed in them.

Variability is manifested in the plasticity of colony shape.

Comparison. A new species is attributed to the genus *Orbignyella*, because some of the previously described species of this genus have the same variable colony shape. According to the variability in shape of the colony, *O. moyerokanensis* sp. nov. is similar to *Orbignyella settedabanica* Modzalevskaya, 1970 from the Middle Ordovician Labystakh Formation of the Sette-Daban Ridge and to *Orbignyella recondite* Astrova, 1965 from the Middle Ordovician of Vaigach Island. The new species differs from *O. settedabanica* in a smaller size of autozooecial apertures, larger mezozooecial apertures, and numerous acanthostyles; from *O. recondite*, it differs in larger autozooecial apertures and numerous acanthostyles. Representatives of the genus *Orbignyella* were first found in the Ordovician of the Siberian Platform.

Remarks. The new species is similar to *Batostoma varians*, which also occurs in the Dolborian Regional Stage of the Siberian Platform, in variability of colony shape and abundance of acanthostyles, However, unlike *B. varians*, *O. moyerokanensis* sp. nov. shows no division of the colony into endo- and exozones and no mesozooecia; acanthostyles are subsurface, and no central cavity is observed in them.

Distribution. Upper Ordovician, Katian Stage, Dolborian Regional Stage; Moyerokan River, Northern Siberia.

Material. Except holotype, one paratype from the same locality: PIN, no. 5846/10.

DISCUSSION

In the Siberian Platform, the most ancient bryozoans were found in Middle Ordovician deposits (Volginian Regional Stage, Darriwilian Stage) (Volkova, 1982; Volkova and Yaroshinskaya, 1984). However, in many other regions of the world, bryozoans are found in the Lower Ordovician (Pushkin and Popov, 1999; Taylor and Wilson, 1999; Xia et al., 2007; Ernst et al., 2014; Ma et al., 2015; Fedorov et al., 2017) and possibly in the Cambrian (Zhang et al., 2021). The bryozoan assemblage from Middle–Upper Ordovician of the Siberian Platform differs from other coeval assemblages in the absence of bryozoans of orders Esthonioporata and Cyclostomata. The only representative of Esthonioporata, *Dianulites petropolitanus* Dybowski, 1877, was described from the Volginian Regional Stage (Volkova, 1982; Volkova and Yaroshinskaya, 1984). At the same time, estonioporates and cyclostomes are known from different regions of the world (Modzalevskaya, 1953; Buttler, 1989; Taylor and Rozhov, 1996; Taylor and Wilson, 1996, 2016; Ernst and Key, 2007; Nekhorosheva, 1997a; Xia et al., 2007; Ernst and Munnecke, 2009; Jimenez-Sanchez, 2009; Ernst and Nakrem, 2011; Fedorov et al., 2017).

The bryozoans from the Upper Ordovician deposits of the Dolborian Regional Stage of the Siberian Platform have been studied from many localities. In total, 58 species are known (Table 1). Along with bryozoans from other Regional Stages, they were described from Dolborian deposits in the Vilyui and Podkamennaya Tunguska river basins, as well as in the Moyero River section (Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961; Astrova, 1965; Rozman et al., 1979), along the Bolshaya Nirunda River (a tributary of the Podkamennaya Tunguska River) (Yaroshinskaya,

Plate VII. Bryozoans of order Cryptostomata (suborder Ptilodictyina) from the upper part of the Dzheromo Formation; SEM (figs. 2, 3, 6, 10, 11, 13, 14) and thin sections (figs. 4, 5, 7, 8, 12, 15). (1–8) *Phaenopora carinata* Nekhoroshev: (1–5) specimen PIN, no. 5846/20; (6–8) specimen PIN, no. 5846/21; (9–12) *P. viluensis* Nekhoroshev, specimen PIN, no. 5846/22; (13–15) *Phaenoporella* sp., specimen PIN, no. 5846/23. Scale bar 1 cm for fig. 9; 2 mm for figs. 1, 10, 13; 1 mm for figs. 2, 11; 500 μm for fig. 3; 250 μm for figs. 7, 12, 14, 15; 200 μm for fig. 6; 100 μm for figs. 4, 5, 8.

Plate VII

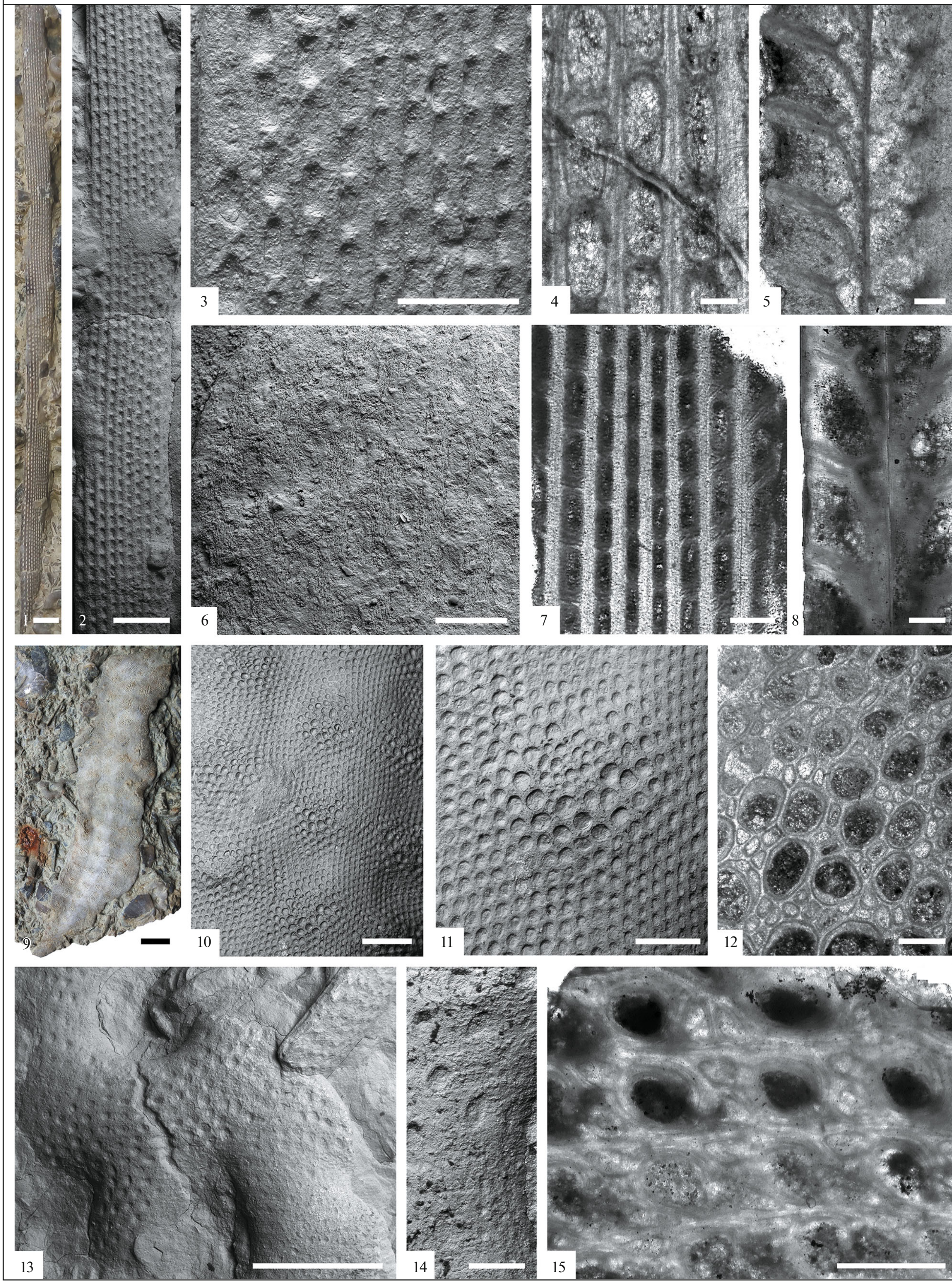


Plate VIII

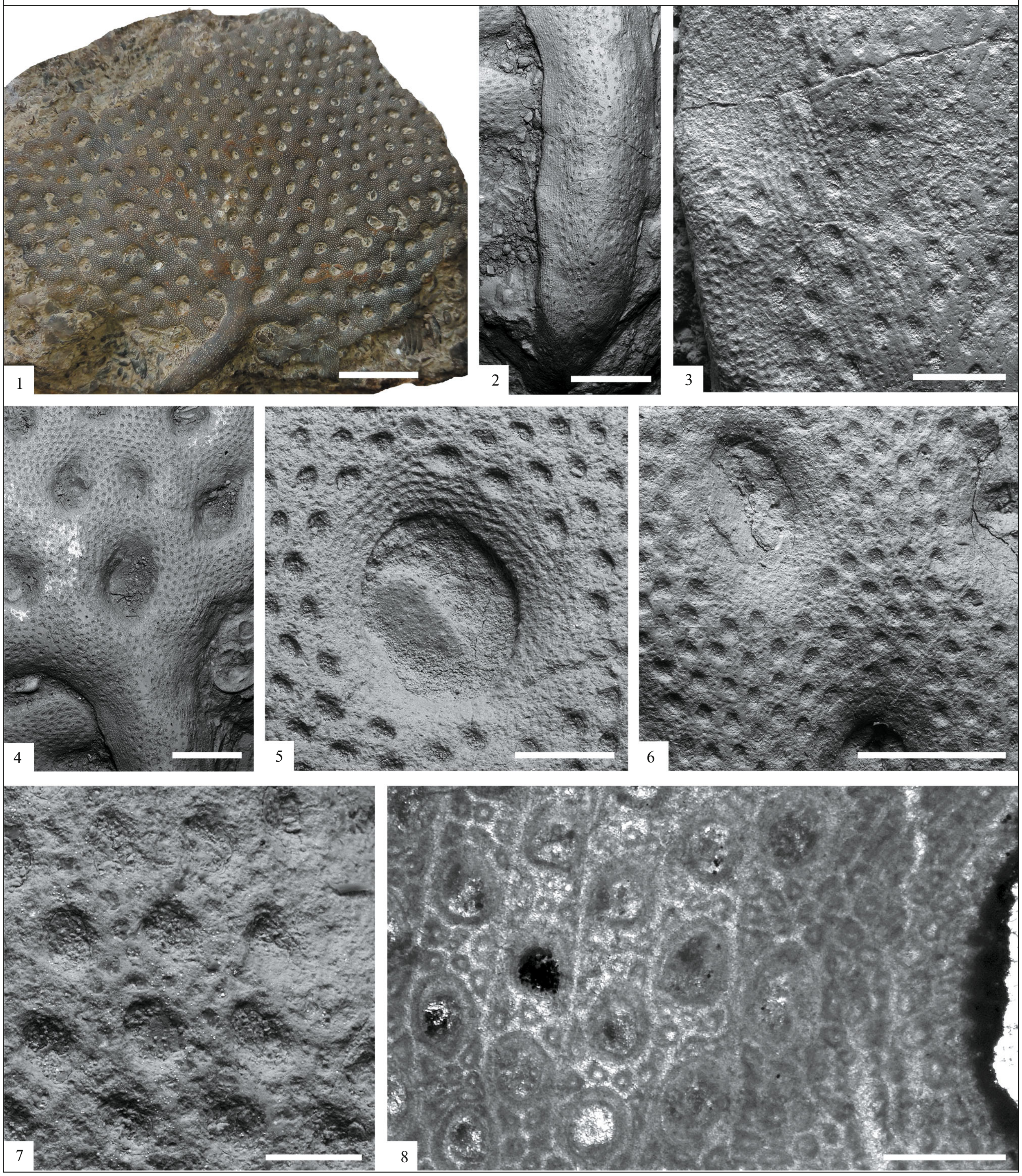


Plate VIII. Bryozoans of order Cryptostomata (suborder Ptilodictyina) from the upper part of the Dzheromo Formation; SEM (figs. 2–7) and thin sections (fig. 8). (1–8) *Phaenoporella multipora* Nekhoroshev, specimen PIN, no. 5846/24. Scale bar 1 cm for fig. 1; 2 mm for figs. 2, 4; 1 mm for fig. 6; 500 μm for figs. 3, 5; 250 μm for fig. 8; 200 μm for fig. 7.

Table 1. Bryozoans of the Dolborian Regional Stage of the Siberian Platform

Ser. no.	ORDER	TAXA	Bryozoans, previously described (after: Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961; Astrova, 1965, 1978; Yaroshinskaya, 1978; Rozman et al., 1979; Volkova, 1982; Volkova and Yaroshinskaya, 1984)							Bryozoans, described in the present paper
			Dolborian Regional Stage							
				Podkamennaya Tunguska River basin			Vilyui River basin	Kotui River basin		
									Moyerokan R.	
			Kulyumbe R. (Zagorminsk Formation)	Podkamennaya Tunguska River	Bol. Nirunda R.	Nizhnyaya Chunku R.	Vilyui, Morkoke, Markha rivers	Moyero R.	After Rozman et al., 1979	the upper part of the Dzheromo Formation
				species from Dolborian Formation (++), formation is not indicated for others						
	1	2	3	4	5	6	7	8	9	10
1	Cystoporata	*Amsassipora simplex* Jaroshinskaya, 1960				++				
2		*Constellaria vesiculosa* (Modzalevskaya in Modzalevskaya et Nekhoroshev, 1955)	+	+		++				+
3		*C. complicate* (Astrova, 1965)		+						
4		*Lunaferamita*? sp.								+
5	Trepostomata	*Calloporella* sp. 1								+
6		*Calloporella* sp. 2								+
7		*Stigmatella convestens* Astrova in Ivanova et al., 1955		+						+
8		*Stigmatella* sp.								+
9		*Nicholsonella mariae* Astrova, 1965			+				+	
10		*N. perculiara* Jaroshinskaya in Volkova et Jaroshinskaya, 1984				++				
11		*Trematoporina intercludens* (Astrova, 1965)	+		+	+				
12		*Batostoma varians* (James, 1878)	+	+	+					+
13		*B. nodosum* Astrova, 1965				++				
14		*B. arcticum* Astrova, 1965				+				
15		*B. polare* Astrova, 1965				+				
16		*B. implicatum* Nicholson, 1881		+					+	
17		*Trematopora propria* Jaroshinskaya, 1960				++				
18		*Eridotrypa granulosoformis* Jaroshinskaya, 1978			++					
19		*Mesotrypa echinata* Ulrich et Bassler, 1904		+		++				
20		*Homotrypa tumulosa* Astrova, 1955		+		+			+	
21		*H. mobilis* (Astrova, 1955)		+						

Table 1. (Contd.)

Ser. no.	ORDER	TAXA	Bryozoans, previously described (after: Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961; Astrova, 1965, 1978; Yaroshinskaya, 1978; Rozman et al., 1979; Volkova, 1982; Volkova and Yaroshinskaya, 1984)							Bryozoans, described in the present paper
			Dolborian Regional Stage							
				Podkamennaya Tunguska River basin			Vilyui River basin	Kotui River basin		
									Moyerokan R.	
			Kulyumbe R. (Zagorninsk Formation)	Podkamennaya Tunguska River	Bol. Nirunda R.	Nizhnyaya Chunku R.	Vilyui, Morkoke, Markha rivers	Moyero R.	After Rozman et al., 1979	the upper part of the Dzheromo Formation
				species from Dolborian Formation (++), formation is not indicated for others						
	1	2	3	4	5	6	7	8	9	10
22	Trepostomata	*H. aperta* (Astrova, 1955)	+		++	+				
23		*H. astricta* (Astrova, 1955)				++				
24		*H. rotunda* Jaroshinskaya, 1978				++				
25		*H. thuncuensis* Jaroshinskaya in Volkova et Jaroshinskaya, 1984				++				
26		*Monotrypella parvula* Jaroshinskaya, 1978			++					
27		*Orbignyella moyerokanensis* sp. nov.								+
28		*Leptotrypa jadrenkinae* Jaroshinskaya in Volkova et Jaroshinskaya, 1984				++				
29		*Leptotrypa* sp.								+
30	Fenestrata	*Chasmatopora pusilla* Astrova, 1965		+						
31		*C.* cf. *moyerensis* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955						+		
32		*Parachasmatopora* sp.								+
33	Cryptostomata	*Phaenopora angustobasis* Nekhoroshev, 1961		+						
34		*P. plebeia* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955		++			+	+		+
35		*P. pennata* Nekhoroshev, 1961								+
36		*P. viluensis* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955					+			+
37		*P. carinata* Nekhoroshev, 1961								+
38		*P. perelegans* Astrova, 1965		+						
39		*P. lata* Nekhoroshev, 1961		+						
40		*P. multifora* Nekhoroshev, 1961		+		+				
41		*P. limbata* Nekhoroshev, 1961		+						

Table 1. (Contd.)

Ser. no.	ORDER	TAXA	Bryozoans, previously described (after: Modzalevskaya and Nekhoroshev, 1955; Nekhoroshev, 1961; Astrova, 1965, 1978; Yaroshinskaya, 1978; Rozman et al., 1979; Volkova, 1982; Volkova and Yaroshinskaya, 1984)							Bryozoans, described in the present paper
			Dolborian Regional Stage							
				Podkamennaya Tunguska River basin			Vilyui River basin	Kotui River basin		
									Moyerokan R.	
			Kulyumbe R. (Zagorninsk Formation)	Podkamennaya Tunguska River	Bol. Nirunda R.	Nizhnyaya Chunku R.	Vilyui, Morkoke, Markha rivers	Moyero R.	After Rozman et al., 1979	the upper part of the Dzheromo Formation
				species from Dolborian Formation (++), formation is not indicated for others						
	1	2	3	4	5	6	7	8	9	10
42	Cryptostomata	*P. insignia* Nekhoroshev, 1961		++						
43		*P. erecta* Nekhoroshev in Modzalevskaya et Nekhoroshev, 1955		+	+			+	+	+
44		*P. praeerecta* Nekhoroshev, 1961			+			+		
45		*P.* aff. *lopatini* Nekhoroshev, 1961						+		
46		*P. mirabilis* Astrova, 1965		+						
47		*Phaenoporella transenna-mesofenestralia* (Schoenmann, 1927)		+	+	+		+	+	
48		*Ph. multipora* Nekhoroshev, 1961		+			++			+
49		*Ph. macrofenestralia* (Schoenmann, 1927)					+	+		
50		*Ph. anastomosa* Nekhoroshev, 1961				+		+		
51		*Ph. septoporoides* Nekhoroshev, 1961						+		
52		*Ph. sibirica* (Schoenmann, 1927)						+		
53		*Ph. ptiloporoides* Nekhoroshev, 1961				+		+		
54		*Ph. transformis* Nekhoroshev, 1961						+		
55		*Stictoporellina clausa* Nekhoroshev, 1961						+		
56		*Rhinidictya bifurcata* Nekhoroshev, 1961						+		
57		*Carinodictya carinata* (Astrova, 1955)						+		
58		*Sibiredictya usitata* Nekhoroshev, 1961						+		

1978; Rozman et al., 1979; Volkova and Yaroshinskaya, 1984), and along the Kulyumbe River (Volkova, 1982; Volkova and Yaroshinskaya, 1984). As seen in Table 1, the majority of bryozoans of the Dolborian Regional Stage were studied in the Podkamennaya Tunguska River basin. At the same time, bryozoans of the Dolborian Regional Stage from the Moyerokan River section are poorly studied. Astrova (Rozman et al., 1979) noted in the Dolborian deposits in the Moyerokan River section (without descriptions and images) the presence of five species of bryozoans from two orders: Trepostomata (*Nicholsonella mariae* Astrova, 1965, *Batostoma implicatum* Nicholson, 1881, *Homotrypa tumulosa* (Astrova, 1955)) and Cryptostomata (*Phaenopora* (=*Ensipora*) *erecta*, *Phaenoporella transenna-mesofenestralia*). In the Dolborian deposits in the Moyerokan River section, we identified bryozoans belonging to ten genera from four orders: Cystoporata (*Constellaria vesiculosa*, *Lunaferamita*? sp.), Trepostomata (*Calloporella* sp. 1, *Calloporella* sp. 2, *Stigmatella* sp., *S. convestens*, *Batostoma varians*, *Orbignyella moyerokanensis* sp. nov., *Leptotrypa* sp.), Fenestrata (*Parachasmatopora* sp.), and Cryptostomata (*Phaenopora plebeia*, *P. pennata*, *P. erecta*, *P. carinata*, *P. viluensis*, *Phaenoporella* sp., and *Ph. multipora*). Of these, seven species—*C. vesiculosa*, *S. convestens*, *B. varians*, *P. plebeia*, *P. viluensis*, *P. erecta*, and *Ph. multipora*—were previously found in the Dolborian deposits from the other areas of the Siberian Platform. Only one species—*P. erecta*—was noted by Astrova in this horizon in the Moyerokan River section (Table 1). Species *P. carinata* and *P. pennata* were found for the first time in the Dolborian Regional Stage of the Siberian Platform.

In addition, the genera *Lunaferamita*, *Orbignyella*, and *Parachasmatopora* were identified in the Ordovician of the Siberian Platform for the first time. The genus *Lunaferamita* was previously described from the Middle Ordovician of the United States (Utgaard, 1981) and the Upper Ordovician of northwestern China (Chang et al., 2011) and the Argentine Precordillera (Ernst and Carrera, 2022), whereas *Parachasmatopora* was described from the Upper Ordovician of Estonia, the United States, and the Argentine Precordillera (Lavrentieva, 1985; Ernst and Munnecke, 2009; Ernst and Carrera, 2022). Representatives of the genus *Orbignyella* are widely distributed in the Ordovician and Silurian throughout the world (Astrova, 1978). The genus *Calloporella* including *Calloporella* sp. 1 and *Calloporella* sp. 2 was first recognized in the Upper Ordovician of the Siberian Platform. Previously, only one species of this genus—*C. lamellaris*—was described from the Krivolutskian Regional Stage along the Lena, Moyero, and Nyuya rivers (Modzalevskaya and Nekhoroshev, 1955; Astrova, 1965, 1978). In modern terminology, this regional stage corresponds to the Mukteian, Volginian, and Kirensk-Kudrinian Regional Stages of the Darriwilian Stage of the Middle Ordovician (Kanygin et al., 2017).

The species *O. moyerokanensis* sp. nov. is endemic to the Siberian Platform. The other species have a wide geographical distribution (Table 2). Among them are *P. carinata*, *S. convestens*, *Ph. multipora*, *C. vesiculosa*, and *B. varians*, which apart from the Middle–Upper Ordovician of the Siberian Platform are known from other environments: *P. carinata*, from the Upper Ordovician of the Southern Verkhoyansk Region (Volkova et al., 1978); *S. convestens*, from the Upper Ordovician of southwestern Tuva (Modzalevskaya, 1977) and southwestern Altai (Avrov and Modzalevskaya, 1982); *Ph. multipora*, from the Upper Ordovician of the Taimyr Peninsula (Nekhorosheva, 1966b) and Kotelny Island (Nekhorosheva, 2018); *C. vesiculosa*, from the Middle Ordovician of Vaigach Island (Astrova, 1965) and Upper Ordovician of Gorny Altai and Gornaya Shoriya (Yaroshinskaya, 1960), Poland (Kiepura, 1962), and Jiangxi Province, China (Hu, 1986); *B. varians*, from the Middle Ordovician of southwestern Tuva (Modzalevskaya, 1977), Middle and Upper Ordovician of the United States (Cumings and Calloway, 1912; Astrova, 1955, 1965, 1978), and Upper Ordovician of the Sette-Daban Ridge (Modzalevskaya, 1970), Taimyr (Nekhorosheva, 1965, 1966b, 2018), and Kotelny Island (Nekhorosheva, 2018).

Apart from the Middle–Upper Ordovician and Lower Silurian of the Siberian Platform, species *P. viluensis*, *P. plebeia*, *P. pennata*, and *P. erecta* are known from other environments: *P. viluensis*, from the Upper Ordovician of Taimyr (Nekhorosheva, 1997a); *P. plebeian*, from the Upper Ordovician of the Sette-Daban Ridge (Modzalevskaya, 1970), Taimyr (Nekhorosheva, 1966a, 1966b, 1997a), Kotelny Island (Nekhorosheva, 2018), and Mongolia (Ariunchimeg, 2009); *P. pennata*, from the Upper Ordovician of the Sette-Daban Ridge (Modzalevskaya, 1970) and Mongolia (Ariunchimeg, 2009) and Lower Silurian of Taimyr (Nekhorosheva, 1997b); *P. erecta*, from the Upper Ordovician of the Sette-Daban Ridge (Modzalevskaya, 1970), Mongolia (Ariunchimeg, 2009), Taimyr (Nekhorosheva, 1997a), and Kotelny Island (Nekhorosheva, 2018) and Lower Silurian of northwestern Mongolia and Central Tuva (Nekhorosheva, 2018).

The studied bryozoans have little stratigraphic significance because the recognized taxa are distributed only in the Middle Ordovician and Lower Silurian. For paleogeographic constructions, the species *C. vesiculosa* and *B. varians*, as well as representatives of genera *Phaenopora* and *Phaenoporella*, may be of the greatest significance (Table 2). The first two species are characterized by a wide geographic distribution in the Middle–Late Ordovician, indicating biogeographic links between the Siberian, Paleo-Baltic, and North American basins at that time (see also the description of the biogeography of Late Ordovician bryozoans in Buttler et al., 2013). Species of the genera *Phaenopora* and *Phaenoporella* are abundant in Middle–Upper Ordovician deposits of the Siberian Platform and adjacent regions, as well as in the former Paleo-Baltic Basin and North America (see the distribution of species in Goryunova and Lavrentieva, 1993). Their well-preserved colonies are often easily identified at the species level on the basis of external characters. Previously, species of *Phaenopora* and *Phaenoporella*, along with other bryozoans, were used to correlate Ordovician deposits in some areas of the Altai Mountains with those of the Siberian Platform (Yaroshinskaya, 1960, 1970; Astrova, 1965), the Sette-Daban Ridge with the Siberian Platform and Taimyr Peninsula (Modzalevskaya, 1970), and Kotelny Island and the Taimyr Peninsula with the Siberian Platform (Nekhorosheva, 1997a, 2018).

The bryozoan assemblage from the upper part of the Dzheromo Formation identified in the Moyerokan River section is close at the generic level to those of Laurentia, Baltica, Argentine Precordillera, and China. At the species level, it shows some relationship

Table 2. Paleogeographic distribution of studied bryozoans

Ser. no.	Taxa	Siberian Platform	Taimyr Peninsula	Kotelny Island	Vaigach Island	Tuva	Gorny Altai and Gornaya Shoriya	Sette-Daban Ridge	Southern Verkhoyanssk Region	Poland	China	United States	Mongolia
	Lower Silurian												
1	*Constellaria vesiculosa*												
2	*Stigmatella convestens*												
3	*Batostoma varians*												
4	*Phaenopora plebeia*	+											
5	*Phaenopora viluensis*	+											
6	*Phaenopora carinata*												
7	*Phaenopora erecta*	+				+							+
8	*Phaenopora pennata*	+	+										
9	*Phaenoporella multipora*												
	Upper Ordovician												
1	*Constellaria vesiculosa*	+					+			+	+		
2	*Stigmatella convestens*	+				+	+						
3	*Batostoma varians*	+	+	+				+				+	
4	*Phaenopora plebeia*	+	+	+				+					+
5	*Phaenopora viluensis*	+	+										
6	*Phaenopora carinata*	+							+				
7	*Phaenopora erecta*	+	+	+				+					+
8	*Phaenopora pennata*	+						+					+
9	*Phaenoporella multipora*	+	+	+									
	Middle Ordovician												
1	*Constellaria vesiculosa*	+			+								
2	*Stigmatella convestens*												
3	*Batostoma varians*	+				+						+	
4	*Phaenopora plebeia*	+											
5	*Phaenopora viluensis*												
6	*Phaenopora carinata*	+											
7	*Phaenopora erecta*	+											
8	*Phaenopora pennata*												
9	*Phaenoporella multipora*	+											

to the Taimyr Peninsula, Kotelny Island, the Sette-Daban Ridge, and Mongolia, which confirms previous studies.

CONCLUSIONS

Our research has significantly increased our knowledge of the composition of the bryozoan assemblage from the upper part of the Upper Ordovician Dzheromo Formation of the Siberian Platform. In these deposits, ten bryozoan specimens were identified to the species level, while the remaining taxa were defined in open nomenclature. Bryozoans belong to ten genera from orders of Cystoporata, Trepostomata, Fenestrata, and Cryptostomata. The genera *Lunaferamita*, *Orbignyella*, and *Parachasmatopora* were first identified in the Ordovician of the Siberian Platform, and the genus *Calloporella* was identified in the Dolborian Regional Stage. The species *O. moyerokanensis* sp. nov. is endemic. The species *P. carinata*, *S. convestens*, *Ph. multipora*, *C. vesiculosa*, and *B. varians* were widespread in the Ordovician of the Siberian Platform and beyond, whereas *P. viluensis*, *P. plebeia*, *P. pennata*, and *P. erecta* are also known from the Lower Silurian of the Siberian Platform and other areas. The bryozoan assemblage recognized in the Moyerokan River section shows some relationship at the species level to bryozoan assemblages from the Taimyr Peninsula, Kotelny Island, the Sette-Daban Ridge, and Mongolia. At the generic level, it is close to bryozoan assemblages of Laurentia, Baltica, Argentine Precordillera, and China.

The data obtained can be further used in regional and interregional correlation and paleobiogeographic reconstructions.

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CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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