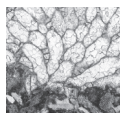


Bryozoan fauna from the Kunda Stage (Darriwilian, Middle Ordovician) of Estonia and NW Russia

ANDREJ ERNST



Bryozoan fauna from several outcrops of sediments of the Kunda Stage (Darriwilian, Middle Ordovician) of Estonia and NW Russia contains 18 species which belong to the palaeostomate orders Cystoporata, Esthonioporata, Trepstomata, and Cryptostomata. The studied material comes mainly from the collection of the Department of Geology, Tallinn University of Technology, as well as as specimens I have collected. One genus with one species and one more species are new: *Pakripora cavernosa* gen. et sp. nov. and *Dianulites pakriensis* sp. nov. Four bryozoans are identified to genus level only. One cryptostome bryozoan shows unique morphology unknown in any similar genera. In general, the studied fauna shows close relations to other localities within the Baltic region, with some few relations to the Ordovician of China. The bryozoans developed massive and erect colonies, showing adaptation to the shallow to moderately deep environment with moderate water energy and relatively high level of sedimentation. • Key words: Ordovician; Darriwilian; Bryozoa; systematics; palaeogeography; palaeoecology.

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Ordovician Bryozoa were one of many marine groups which evolved rapidly during the Great Ordovician Biodiversification Event (GOBI). According to the recent compilation (Ernst 2018) bryozoans experienced significant diversification in the period from the Tremadocian (Lower Ordovician) to the late Sandbian (Upper Ordovician). Bryozoan faunas of Baltoscandia played an important role in this diversification; however, the detailed knowledge of those faunas is patchy. Since the monumental work of Bassler (1911) no comprehensive restudy of this diverse and widely distributed group in the Baltoscandian region has been attempted. Separate bryozoan taxa were treated in various publications (e.g. Modzalevskaya 1953, 1986; Lavrentjeva 1975, 1985; Gorjunova & Lavrentjeva 1993; Fedorov *et al.* 2017; Koromyslova & Fedorov 2021).

The only exception is the unpublished dissertation made by Ralf Männil (1959) in which he summarized an immense overview of the Ordovician bryozoans of Estonia. Unfortunately, only a few of his species were subsequently published by him or others (Männil 1958; Pushkin 1987, 1990; Gorjunova & Lavrentjeva 1993). Therefore, the majority of taxa established by Männil (1959) are invalid and still await their re-evaluation.

This paper is devoted to the study of bryozoans from several outcrops of sediments of the Kunda Stage

(Darriwilian, Middle Ordovician) of Estonian and NW Russia. Middle Ordovician bryozoans are known from various localities in Baltoscandia (e.g. Bassler 1911; Gorjunova 2005, 2009; Koromyslova 2004, 2007, 2011). Bryozoans are relatively rare fossils in the rocks of this age, therefore, the available material which has been mainly studied using oriented thin sections represents significant interest. The majority of bryozoan samples for this study derive from the collection of the Department of Geology of Tallinn University of Technology. I collected additional material in Estonia (Harku quarry) and in NW Russia (Putilovo quarry) (Fig. 1).

Stratigraphy and environmental setting

The Ordovician succession of the East Baltic is now subdivided into 18 regional stages (e.g. Kaljo & Nestor 1990; Meidla 1997; Nölvak *et al.* 2006). The Kunda regional stage represents the lower part of the Darriwilian (Middle Ordovician) overlaying the Volkhov regional stage and followed by Aseri regional stage (Fig. 2). The outcrops of the Kunda stage are quite uniform in their sedimentological characteristic and contain mainly glauconite-rich limestones (bioclastic packstones to wackestones, with varying amounts of terrigenous



Figure 1. Map of the Baltic region showing position of studied localities (asterisks).

particles) which often contain ferruginous oolites. The fauna is scarce and represented by rare bryozoans, brachiopods, crinoids, and trilobites. The depositional environment corresponds to the cool-water to temperate conditions accompanied by sea-level lowstands (*e.g.* Cocks & Torsvik 2005; Dronov & Rozhnov 2007; Hansen *et al.* 2011; Torsvik & Cocks 2016).

Series	Stage	Regional stage
Middle Ordovician	Dariwilian	Uhaku
		Lasnamägi
		Aseri
		Kunda
	Dapingian	Volkhov

Figure 2. Stratigraphy of the Middle Ordovician in the Baltic region (modified after Hints *et al.* 2008).

Material and methods

I collected material for this study and borrowed additional samples from the collection of the Department of Geology, Tallinn University of Technology. The studied samples derive from following localities (Fig. 1): Paldiski, Estonia (59° 23' 15" N, 24° 02' 10" E); Väike-Pakri island, Estonia (59° 21' 28" N, 23° 58' 44" E); Aseri, Estonia (59° 26' 50" N, 26° 51' 48" E); Harku Quarry, Estonia (59° 23' 48" N, 24° 33' 46" E); Putilovo Quarry, Russia (59° 51' 30" N, 31° 24' 30" E).

Normal/transverse, longitudinal, and tangential sections were prepared from the studied material. This resulted in 134 thin sections were made (24 × 48 mm and 50 × 50 mm). Samples and thin sections are housed in the collection of the Department of Geology, Tallinn University of Technology (index GIT). Bryozoans were investigated in thin sections using a binocular microscope in transmitted light. Morphologic character terminology is partly adopted from Anstey & Perry (1970) and Hageman (1993).

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Superorder Palaeostomata Ma *et al.*, 2014
Order Cystoporata Astrova, 1964
Suborder Ceramoporina Bassler, 1913
Family Ceramoporidae Ulrich, 1882

Genus *Ceramopora* Hall, 1851 in Silliman *et al.* (1851)

Type species. – *C. imbricata* Hall, 1852. Niagaran Group (middle Silurian); Lockport, New York, USA.

Diagnosis. – Colonies thin discoidal expansions; encrusting, free, or in a combination. Autozooezia large, commonly rhombically arranged cavity ovate or rhomboidal in cross section, budding from the epitheca. Communication pores abundant, most commonly just distal to ends of the lunaria. Lunaria small in the inner exozone, large on the colony surface. Diaphragms absent. Exilazooecia few to abundant in intermonticulate areas, generally small and subcircular in cross section, lacking diaphragms. Monticulae with depressed centres, exilazooecia of central cluster more angular than intermonticulate exilazooecia.

Remarks. – The genus *Ceramopora* Hall, 1851 in Silliman *et al.* (1851) differs from the genus *Ceramoporella* Ulrich, 1882 by the absence of diaphragms and having more common communication pores, from the genus *Acanthoceramoporella* Utgaard, 1968 – by the absence of acanthostyles.

Occurrence. – Upper Ordovician–middle Silurian; North America, Europe, Siberia.

***Ceramopora* cf. *magnicellularis* Männil & Pushkin, 1990 in Pushkin (1990)**

Figure 3A–E; Table 1

1990 *Ceramopora magnicellularis* Männil & Pushkin, 1990; Pushkin, p. 7, pl. 1, fig. 1.

Material. – Single specimen GIT 155-2041a–d (four thin sections).

Table 1. Descriptive statistics of *Ceramopora* cf. *magnicellularis* Männil & Pushkin, 1990 in Pushkin (1990) (one colony measured). Abbreviations: N – number of measurements; \bar{x} – mean; MIN – minimal value; MAX – maximal value; SD – sample standard deviation; CV – coefficient of variation.

	N	MIN	MAX	\bar{x}	SD	CV
Aperture width, mm	25	0.30	0.58	0.43	0.063	14.53
Aperture spacing, mm	25	0.40	0.60	0.48	0.056	11.53
Lunarium width, mm	25	0.17	0.30	0.22	0.032	14.35
Lunarium length, mm	25	0.07	0.19	0.12	0.033	27.91
Lunarium thickness, mm	25	0.05	0.11	0.08	0.018	24.32
Diaphragm spacing, mm	20	0.25	0.65	0.44	0.097	22.15
Exilazooecia width, mm	25	0.06	0.19	0.12	0.034	29.28

Description. – Massive colony consisting of three subcolonies, 22 mm thick in its central part and 32 mm wide at its base. Subcolonies 5–20 mm in height, produced by encrusting layers. Autozooezia growing from thin epitheca, bending in the early exozone to the colony

surface. Epitheca 0.010–0.015 mm thick. Basal diaphragms abundant, straight or inclined, thin. Autozooezial apertures rounded to subpolygonal, 4.0–4.4 spaced per 1 mm². Lunaria well-developed, rounded to slightly triangular, consisting of granular material; ends of lunaria indenting autozooezia. Exilazooecia small to large, irregularly shaped in transverse section, common to abundant, not completely separating autozooezia, arranged in 1–2 rows between apertures, 1–6 surrounding each autozooezial aperture and 4.1–4.6 spaced per 1 mm² of colony surface, with rounded to flat roofs, rounded-polygonal in tangential section. Autozooezial walls granular prismatic, 0.010–0.015 mm thick in endozone and 0.04–0.05 mm thick in exozone. Maculae not observed.

Remarks. – The species *Ceramopora magnicellularis* Männil & Pushkin, 1990 in Pushkin (1990) was established on the base of a single holotype (GIT 537-1635) from the Aseri Stage of Ojaküla, Estonia. This sample is missing from the collection of Tallinn University of Technology (Ursula Toom, personal communication 2021). The present material has similar shape and size of autozooezial apertures with well-developed lunaria (aperture width 0.30–0.58 mm vs. 0.44–0.63 mm in the sample GIT 537-1635). The present material has also more abundant diaphragms and exilazooecia than the holotype. Generic concept of *Ceramopora* (see Utgaard, 1983, pp. 358, 359) includes absence of diaphragms which are present in the genus *Ceramoporella* Ulrich, 1882. Pushkin (1990) mentioned diaphragms spaced 0.5–1.0 mm in autozooezia of *Ceramopora magnicellularis*. In the studied material diaphragms are spaced more closely: 0.25–0.65 mm.

The present material differs from *Ceramopora explicata* Pushkin, 1976 from the Ordovician of Belarus in having larger autozooezial apertures (aperture width 0.30–0.58 mm vs. 0.40–0.50 mm in *C. explicata*) and in having smaller exilazooecia which can exceed the size of regular autozooezia in *C. explicata*.

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Väike-Pakri cliff, Estonia.

Order Esthonioporata Astrova, 1978
Family Dianulitidae Vinassa de Regny, 1921

Genus *Dianulites* Eichwald, 1829

Type species. – *D. detritus* [= *D. fastigiatus*] Eichwald, 1829. Lower to Middle Ordovician; Russia, Estonia.

Diagnosis. – Colony turbinate, cone or horn-shaped, sometimes compound, occasionally with a conical central cavity, in some species massive hemispherical; zooecia opening on upper, distal surface of colony; colony sides

comprising exterior wall; not differentiated into endozone and exozone; maculae variably developed, some moniticulate. Zooecia long polygonal tubes, monomorphic or obscurely polymorphic; walls thin, indistinct, granular, inclusion-rich; styles lacking; diaphragms moderately abundant, microstructural fabric strongly radial (modified after Taylor & Wilson 1999).

Remarks. – *Dianulites* Eichwald, 1829 belongs to the family of its own: Dianulitidae Vinassa de Regny, 1921. It shows similarities to the unplaced genus *Nicholsonella* Ulrich, 1890. These genera possess re-crystallized walls which suggest a diagenetically unstable aragonitic (McKinney 1971) or high Mg calcite composition (Taylor & Wilson 1999, Smith *et al.* 2006). *Nicholsonella* differs from *Dianulites* in having abundant mesozooecia and acanthostyles.

Occurrence. – Lower to Upper Ordovician; Europe, North and South America, Asia.

***Dianulites collucatus* Pushkin, 2001
in Pushkin & Popov (2001)**

Figure 3F, G; 4A–D; Table 2

2001 *Dianulites collucatus* Pushkin; Pushkin & Popov, pp. 26, 27, pl. 3, figs 1–6; p. 4, figs 1–6, text-figs 3.5–3.8.

Material. – GIT 155-1527a–e, GIT 852-1a–g, GIT 852-6a–d, GIT 852-21a–c, GIT 852-23a–c, GIT 852-24a–d, GIT 852-25a–d, GIT 852-26a–d (thirty-four thin sections).

Table 2. Descriptive statistics of *Dianulites collucatus* Pushkin, 2001 in Pushkin & Popov (2001) (seven colonies measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	150	0.30	0.51	0.42	0.046	10.98
Aperture spacing, mm	150	0.35	0.60	0.45	0.044	9.76
Macrozoecia width, mm	30	0.52	0.60	0.55	0.021	3.87
Macrozoecia spacing, mm	30	0.53	0.63	0.57	0.032	5.66
Lunarium thickness, mm	25	0.05	0.11	0.08	0.018	24.32
Diaphragm spacing, mm	20	0.25	0.65	0.44	0.097	22.15
Exilazooecia width, mm	25	0.06	0.19	0.12	0.034	29.28

Description. – Colonies usually massive hemispherical, discoidal, sometimes irregular massive, multilayered and composed of several subcolonies. Hemispherical colonies 6–30 mm thick in its central part and 17–45 mm wide at their bases. Massive multilayered colonies up to 45 × 45 mm in size. Secondary overgrowth 6.9–16.0 mm thick. Exozone indistinct. Autozoecia long, prismatic, growing from epitheca. Epitheca 0.01–0.02 mm thick.

Autozoecial apertures polygonal, 4.4–5.8 spaced per 1 mm². Diaphragms straight, rare to common, widely spaced, locally abundant. Heterozooecia *sensu stricto* not observed; immature zooids of smaller diameter locally present. Acanthostyles absent. Autozoecial walls indistinctly granular, irregularly thickened, 0.01–0.03 mm thick. Maculae indistinct, composed of macrozoecia.

Remarks. – *Dianulites collucatus* Pushkin, 2001 in Pushkin & Popov (2001) differs from *D. petropolitanus* (Dybowski, 1877) in having smaller autozoecial apertures (aperture width 0.30–0.51 mm vs. 0.58–0.70 mm in *D. petropolitanus*). *Dianulites collucatus* differs from *D. janischevskyi* Modzalevskaya, 1953 in having slightly larger autozoecia (aperture width 0.30–0.51 mm vs. 0.25–0.40 mm in *D. janischevskyi*) and in having indistinct maculae composed of macrozoecia vs. maculae composed of smaller zooecia in *D. janischevskyi*.

Occurrence. – Obukhovo Fm., Kunda Stage, Darriwilian, Middle Ordovician; Putilovo quarry, Russia. Kunda Stage, Darriwilian, Middle Ordovician; Aseri quarry, Harku quarry, Estonia.

***Dianulites pakriensis* sp. nov.**

Figure 4E–H, 5A–C; Table 3

Holotype. – GIT 537-1294a–d (four thin sections) originally assigned to *Dianulites robustus* Männil, 1959 (unpublished).

Table 3. Descriptive statistics of *Dianulites pakriensis* sp. nov. (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.32	0.55	0.40	0.049	12.41
Aperture spacing, mm	20	0.46	0.70	0.54	0.057	10.65
Mesozooecia width, mm	20	0.07	0.17	0.12	0.028	23.21
Mesozooecia per aperture	20	2.00	6.00	4.00	1.124	28.10
Lunarium thickness, mm	25	0.05	0.11	0.08	0.018	24.32
Diaphragm spacing, mm	20	0.25	0.65	0.44	0.097	22.15
Exilazooecia width, mm	25	0.06	0.19	0.12	0.034	29.28

Paratypes. – GIT 537-1295 and GIT 537-2004.

Type horizon and locality. – Kunda Stage, Darriwilian, Middle Ordovician; Väike-Pakri island, Estonia.

Material. – Types only.

Etymology. – The species is named after finding near Pakri, Estonia.

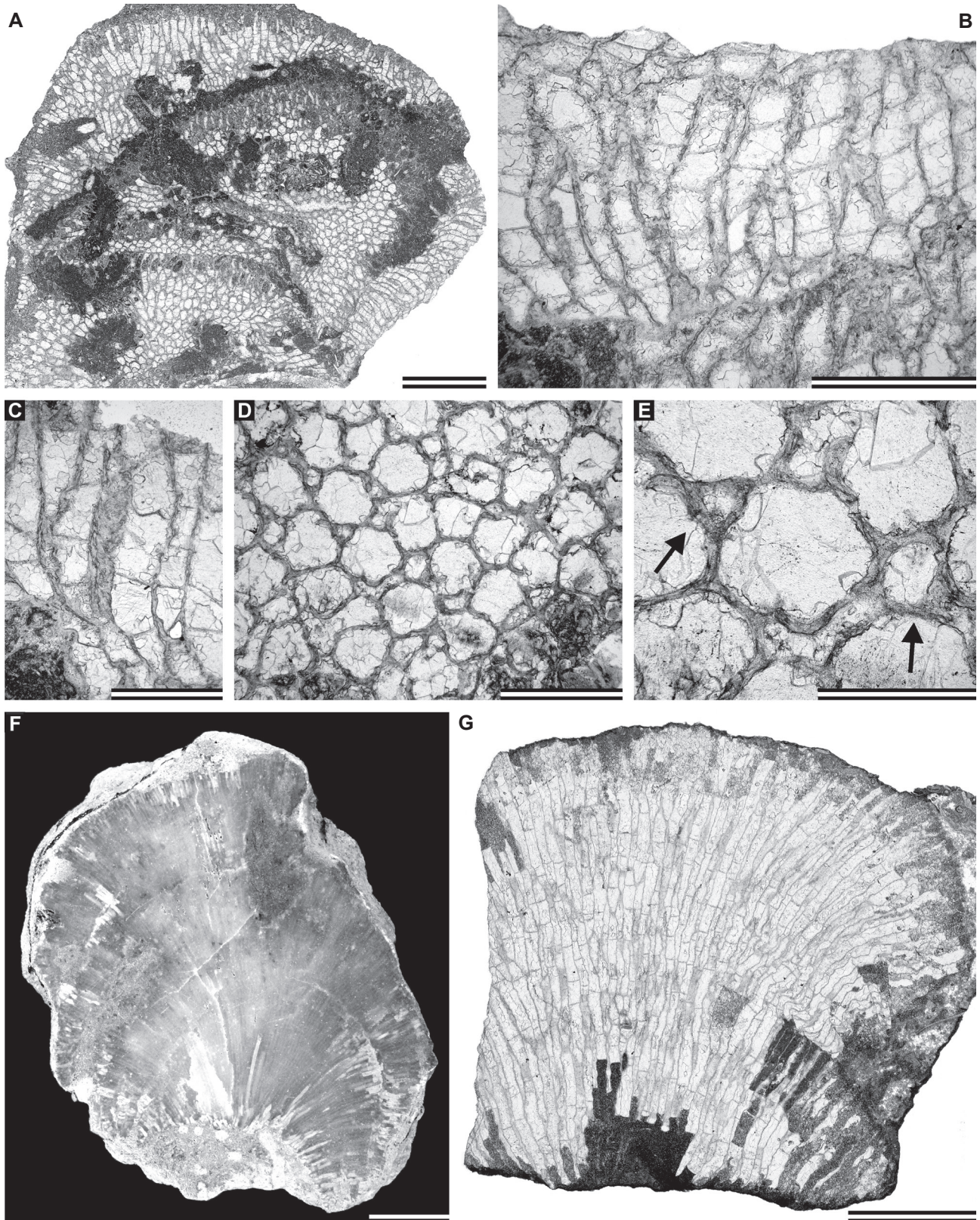


Figure 3. A–E – *Ceramopora magnicellularis* Männil & Pushkin, 1990 in Pushkin (1990); A – longitudinal section through the multilayered colony, GIT 155-2041b; B, C – longitudinal section of separate sheets, GIT 155-2041b; D, E – tangential section showing autozooeical apertures and exilazoecia (arrows), GIT 155-2041d. • F, G – *Dianulites collucatus* Pushkin, 2001 in Pushkin & Popov (2001); F – fragment of the colony cut in the middle, GIT 852-24; G – thin section through the middle part of the colony, GIT 852-26a. Scale bars: 19 mm (F), 5 mm (A, G), 1 mm (B–D), 0.5 mm (E).

Diagnosis. – Large ramose colonies with indistinct exozones; secondary overgrowth occurring; autozooeal diaphragms absent; 3.5–4.5 autozooeal apertures per 1 mm²; heterozoecia (immature zooecia?) abundant, 2–5 surrounding each autozooeal aperture; acanthostyles absent; maculae composed of immature zooecia (zooecia smaller in size but identical to normal autozoecia in shape and budding pattern).

Description. – Large ramose colonies with indistinct exozones. Branches 19–28 mm in diameter. Secondary overgrowth 1.6–2.4 mm in thickness. Autozoecia long, prismatic, growing parallel to branch axis and bending at low angles in exozones. Diaphragms absent. Autozooeal apertures polygonal, 3.5–4.5 spaced per 1 mm². Tubes of smaller diameter (immature zooecia?) between autozoecia abundant, 2–5 surrounding each autozooeal aperture, rounded-polygonal, restricted to the outer exozone. Acanthostyles absent. Autozooeal walls indistinctly granular, irregularly thickened, 0.015–0.030 mm thick. Maculae composed of immature zooecia present, 1.15–1.25 mm in diameter.

Remarks. – According to the rules of the Zoological Nomenclature, the species *Dianulites robustus* of Männil in his dissertation (1959) is not valid. Therefore, his material has been used to establish a new species. *Dianulites pakriensis* sp. nov. differs from *D. petropolitanus* (Dybowski, 1877) in having smaller autozooeal apertures (aperture width 0.32–0.55 mm vs. 0.58–0.70 mm in *D. petropolitanus*) and in absence of diaphragms. *Dianulites pakriensis* differs from *D. janischevskyi* Modzalevskaya, 1953 in having larger autozoecia (aperture width 0.32–0.55 mm vs. 0.25–0.40 mm in *D. janischevskyi*). *Dianulites pakriensis* differs from *D. collucatus* Pushkin, 2001 in Pushkin & Popov (2001) in colony shape (ramose vs. hemispheric massive), in absence of diaphragms and in presence of maculae composed of immature zooecia.

Genus *Esthoniopora* Bassler, 1911

Type species. – *E. communis* Bassler, 1911. Middle Ordovician, Darriwilian; Estonia.

Diagnosis. – Massive, usually hemispherical colonies. Autozoecia with polygonal apertures and thin straight walls. Diaphragms abundant, perforated, planar or sloped, sometimes like cystiphagms. Acanthostyles absent (modified after Astrova 1978).

Remarks. – *Esthoniopora* Bassler, 1911 differs from *Esthonioporella* Modzalevskaya, 1953 in absence of acanthostyles and in having thin autozooeal walls.

Occurrence. – Lower–Upper Ordovician; Estonia, NW Russia, Norway.

Esthoniopora communis Bassler, 1911

Figure 5D–G; Table 4

1911 *Esthoniopora communis* Bassler; pp. 260–263, text-figs 151–155.

1978 *Esthoniopora communis* Bassler, 1911. – Astrova, pl. 1, fig. 1.

2002 *Esthoniopora communis* Bassler, 1911. – Pushkin, p. 116, fig. 3h–j.

Material. – Single specimen GIT 155-2048a-d (four thin sections).

Table 4. Descriptive statistics of *Esthoniopora communis* Bassler, 1911 (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.33	0.52	0.39	0.047	12.10
Aperture spacing, mm	20	0.35	0.56	0.43	0.049	11.21
Mesozoecia width, mm	11	0.06	0.14	0.10	0.030	29.40
Hemiphragm spacing, mm	20	0.20	0.41	0.27	0.047	17.53

Description. – Massive hemispheric colony, 22 mm wide at its base and 16 mm high in its central part. Secondary overgrowth occurring, 1.4–1.9 mm thick. Exozone indistinct. Autozoecia long, prismatic, growing from epitheca. Epitheca 0.005–0.010 mm thick. Autozooeal apertures polygonal, 5.1–5.6 spaced per 1 mm². Mesozoecia *sensu stricto* absent, immature zooecia smaller than autozoecia common, 0.06–0.14 mm in diameter. Hemiphragms abundant, restricting more than half of the autozooeal chamber space, curved proximally, tapering to their ends. Autozooeal walls amalgamated, 0.020–0.025 mm thick in endozone and 0.03–0.05 mm thick in exozone. Maculae not observed.

Remarks. – *Esthoniopora communis* Bassler, 1911 differs from *E. subsphaerica* (Bassler, 1911) in having larger autozoecia (average aperture width 0.39 mm vs. 0.25 mm in *E. subsphaerica*; measurements for *E. subsphaerica* from Ernst & Nakrem 2011).

Occurrence. – The studied material comes from the Kunda Stage (Darriwilian, Middle Ordovician) of Aseri cliff, Estonia. *Esthoniopora communis* Bassler, 1911 is a common species in the Lower to Middle Ordovician of Estonia and Belarus, as well as Norway (unpublished).

Family Revalotrypidae Gorjunova, 1988

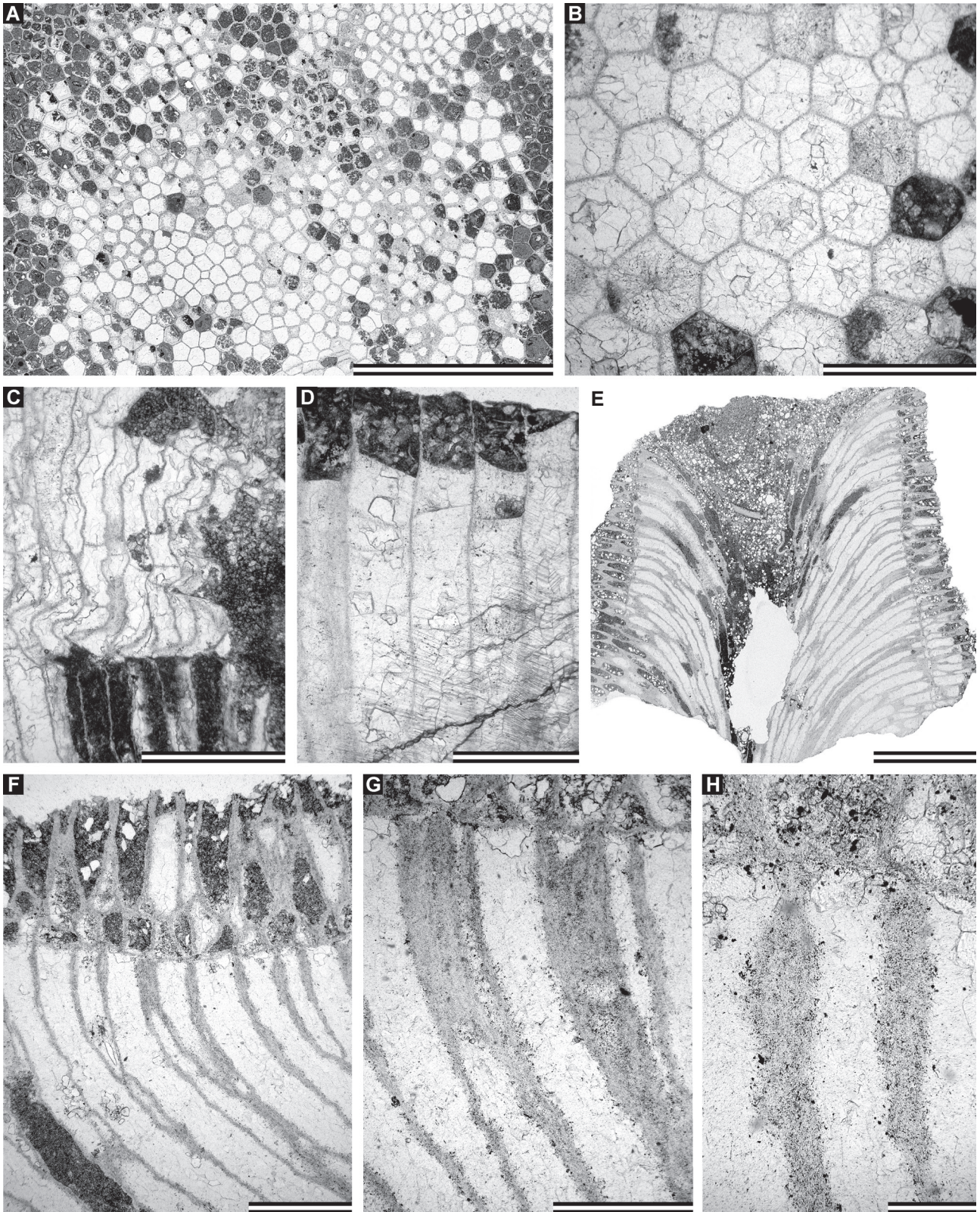


Figure 4. A–D – *Dianulites collucatus* Pushkin, 2001 in Pushkin & Popov (2001); A – tangential section, GIT 852-1d; B – tangential section, GIT 852-24d; C – longitudinal section, GIT 852-26a; D – longitudinal section, GIT 852-24a. • E–H – *Dianulites pakriensis* sp. nov. Holotype GIT 537-1294b, longitudinal thin section showing autozoecial chambers and secondary overgrowths. Scale bars: 5 mm (A, E), 2 mm (C), 1 mm (B, D, F, G), 0.5 mm (H).

Genus *Revalotrypa* Bassler, 1952

Type species. – *Nicholsonella gibbosa* Bassler, 1911. Ordovician; Estonia.

Diagnosis. – Colonies encrusting laminate (unilaminate and multilaminate), massive discoidal, hemispherical, mushroomlike, nodular, rodlike, and branched ramose. Endozones poorly defined. Autozooecia tubular, growing from thick epitheca. Diaphragms widely spaced, straight or concave. Autozooecial apertures circular to oval. Neozooecia arranged around autozooecia, occasionally forming accumulations. Apertures of exilazooecia circular, oval, or irregularly triangular or tetragonal, varying in size. Acanthostyles absent. Autozooecial walls granular, straight to strongly crenulated.

Remarks. – *Revalotrypa* Bassler, 1952 is unique because of its granular (re-crystallized) walls which this genus shares with *Nicholsonella* Ulrich, 1890 or *Dianulites* Eichwald, 1829. Such a wall structure suggests a diagenetically unstable aragonitic (McKinney 1971) or high-magnesium calcite composition (Taylor & Wilson 1999). However, *Dianulites* hardly possesses any heteromorphs (obscure mesozooecia), whereas *Nicholsonella* has common to abundant mesozooecia with frequent diaphragms as well as acanthostyles.

Occurrence. – Lower to Middle Ordovician of Russia and China, Upper Ordovician (Katian) of Morocco, Upper Ordovician (Hirnantian) of Canada.

***Revalotrypa gibbosa* (Bassler, 1911)**

Figure 6A–F; Table 5

1911 *Nicholsonella gibbosa* Bassler; p. 224, pl. 2, figs 1–6.

1988 *Revalotrypa gibbosa* (Basler, 1911). – Gorjunova, p. 35, pl. 3, figs 2, 3.

2011 *Revalotrypa gibbosa* (Basler, 1911). – Koromyslova, p. 917, pl. 3, figs 1–3, pl. 4, figs 1, 2.

Material. – Fourteen colonies GIT 381–21a, GIT 155–2056a–c, GIT 852–3a, GIT 852–5a–c, GIT 852–9a–b, GIT 852–10a, GIT 852–11a–b, GIT 852–12a–b, GIT 852–13a–b, GIT 852–14a–c, GIT 852–15a–b, GIT 852–16a–c, GIT 852–17a, GIT 852–19 (twenty-six thin sections).

Description. – Colonies mainly mushroomlike, consisting of several encrusting subcolonies growing in series. Subcolonies 0.4–3.3 mm thick in their central parts. Autozooecia tubular, growing from 0.010–0.020 mm thick epitheca. Autozooecial apertures rounded to slightly polygonal, 4.9–7.2 spaced per 1 mm². Autozooecial diaphragms uncommon. Neozooecia abundant, 8–17 sur-

rounding each autozooecial aperture and 28–45 spaced per 1 mm², large, with polygonal apertures. Autozooecial walls granular, straight but locally strongly crenulated, 0.05–0.015 mm thick. Indistinct maculae consisting of slightly larger zooecia.

Table 5. Descriptive statistics of *Revalotrypa gibbosa* (Bassler, 1911) (seven colonies measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	86	0.22	0.43	0.31	0.040	12.88
Aperture spacing, mm	81	0.28	0.55	0.41	0.050	12.40
Mesozooecia width, mm	86	0.04	0.19	0.08	0.028	33.99
Mesozooecia per aperture	49	8.0	17.0	11.8	2.294	19.38

Remarks. – *Revalotrypa gibbosa* (Bassler, 1911) differs from *R. eugeniae* Gorjunova, 1988 in having larger autozooecial apertures (aperture width 0.22–0.43 mm vs. 0.25–0.27 mm in *R. eugeniae*). *Revalotrypa gibbosa* differs from *R. papillaris* (Modzalevskaya, 1953) in its colony form (mushroomlike vs. rod-shaped in *R. papillaris*) and in having larger autozooecial apertures (aperture width 0.22–0.43 mm vs. 0.22–0.27 mm in *R. papillaris*). *Revalotrypa gibbosa* differs from *R. krestensis* Koromyslova, 2008 in Gorjunova & Koromyslova (2008) in having larger autozooecial apertures (aperture width 0.22–0.43 mm vs. 0.20–0.34 mm in *R. krestensis*).

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Väike-Pakri island, Harku quarry, Estonia. Obukhovo Fm., Kunda Stage, Darriwilian, Middle Ordovician; Putilovo quarry, Russia.

***Revalotrypa papillaris* (Modzalevskaya, 1953)**

Figure 6G, H; 7A, B

1953 *Nicholsonella papillaris* Modzalevskaya; p. 127, pl. 5, figs 1–3, text-fig. 12.

1953 *Nicholsonella rotundicellularis* Modzalevskaya; p. 128, pl. 5, figs 4, 5, text-fig. 13.

2011 *Revalotrypa papillaris* (Modzalevskaya, 1953). – Koromyslova, pp. 917–919, pl. 5, fig. 1.

Material. – GIT 852–7a (one thin section), GIT 852–20.

Description. – Colonies rod- or club-shaped, with flat bases, 2.60–2.85 mm in diameter. Autozooecia tubular, growing directly from the base. Autozooecial apertures rounded to slightly polygonal, 0.18–0.27 mm wide. Autozooecial diaphragms uncommon. Neozooecia abundant, 0.04–0.07 mm in diameter. Autozooecial walls granular, straight but locally strongly crenulated, 0.010–0.018 mm thick. Maculae not observed.

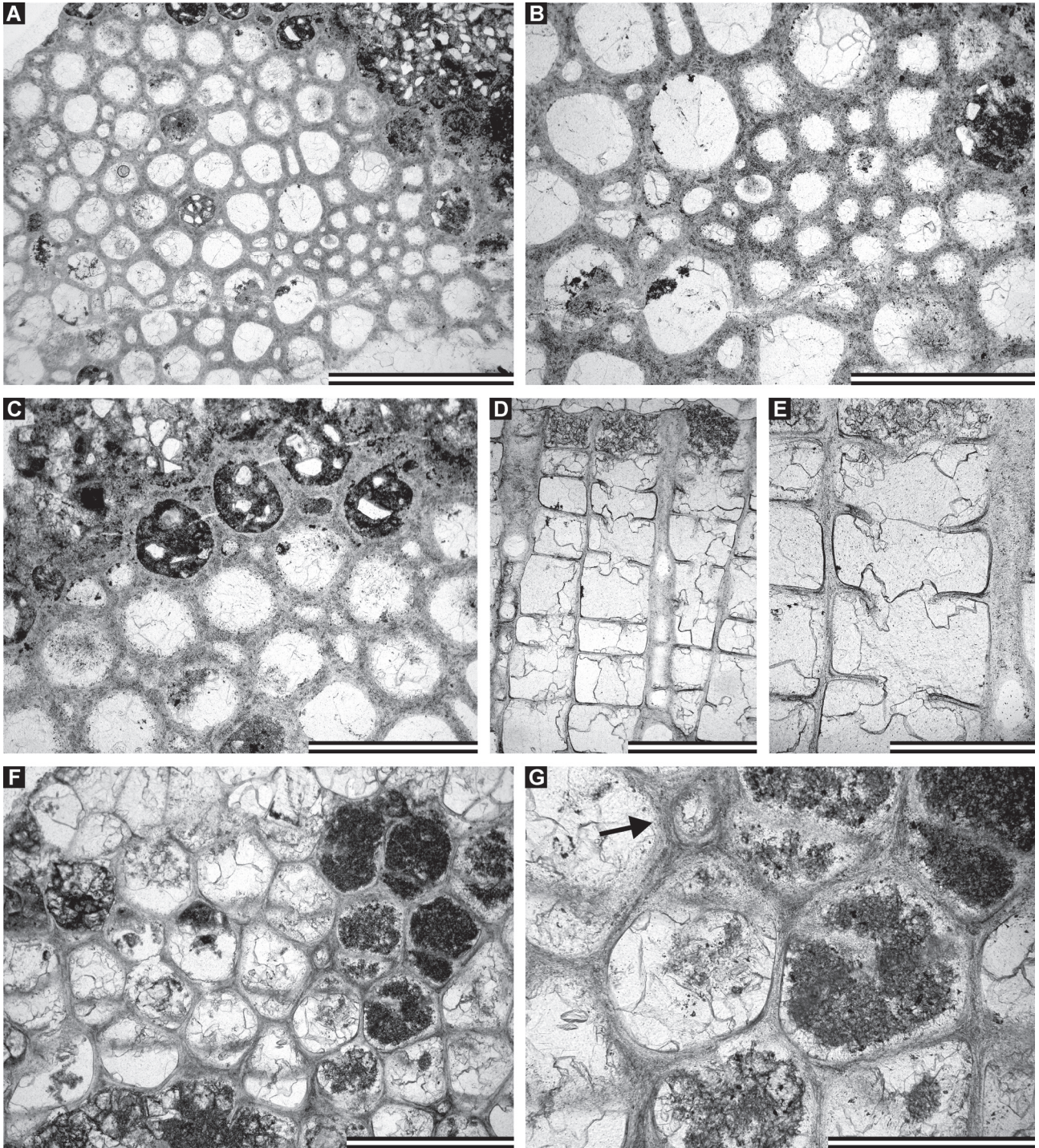


Figure 5. A–C – *Dianulites pakriensis* sp. nov. Holotype GIT 537-1294d, tangential section showing autozooeal apertures, heterozooecia (immature zooecia?), and a macula, composed of heterozooecia. • D–G – *Esthoniopora communis* Bassler, 1911; D, E – longitudinal section showing autozooeal chambers with hemiphragms, GIT 155-2048b; F, G – tangential section showing autozooeal apertures and immature zooecia (arrow), GIT 155-2048d. Scale bars: 2 mm (A), 1 mm (B–D, F), 0.5 (E, G).

Remarks. – *Revalotrypa papillaris* (Modzalevskaya, 1953) differs from all species of the genus in its rod-shaped colony and abundant small neozooecia. *Revalotrypa papillaris* differs from *R. eugeniae* Gorjunova, 1988 in having rod-

shaped colony vs. laminar encrusting one in the latter genus. *Revalotrypa papillaris* differs from *R. krestensis* Koromyslova, 2008 in Gorjunova & Koromyslova (2008) in its rod-shaped colony instead of massive one in the latter species.

Occurrence. – Studied material comes from the Obukhovo Fm. (Kunda Stage, Darriwilian, Middle Ordovician) of the Putilovo quarry, Russia.

Genus *Orbipora* Eichwald, 1856

Type species. – *Orbitulites distinctus* Eichwald, 1829. Middle Ordovician of Estonia and Sweden.

Diagnosis. – Massive colonies. Autozooeceia large with irregular polygonal apertures and amalgamated structureless walls, indistinctly thickened. Diaphragms rare to absent, locally numerous. Abundant acanthostyles of different shape and size, typically with wide hyaline cores and narrow laminated sheaths. Heterozooeceia absent (after Astrova 1978).

Remarks. – The genus *Orbipora* Eichwald, 1856 differs from the genus *Nekhorosheviella* Modzalevskaya, 1953 in shape and sizes of acanthostyles, such as in usually rare diaphragms. The single known species of the latter genus, *Nekhorosheviella cribrosa* Modzalevskaya, 1953 has two distinct types of acanthostyles – large with wide calcitic cores, and small ones, positioned in middle parts of walls. Furthermore, it has indistinctly lamellar walls and abundant diaphragms in autozooeceia.

Occurrence. – Lower–Middle Ordovician of the Baltoscandian region; Middle Ordovician of the Northern America.

Orbipora indenta Bassler, 1911

Figure 7C–F; Table 6

1911 *Orbipora indenta* Bassler; pp. 257, 258, text-fig. 150a–d.

non 1996 *Orbipora indenta* Bassler, 1911. – Buttler & Massa, fig. 4b.

non 2007 *Orbipora indenta* Bassler, 1911. – Buttler, Cherns & Massa, pp. 484, 485, pl. 1, figs 1–3.

Material. – Single specimen GIT 155-2043a–c (three thin sections).

Description. – Massive hemispheric colony, ca. 14 mm wide at its base and 9 mm high in its central part. Secondary overgrowth not observed. Exozone indistinct. Autozooeceia long, prismatic. Epithecium not seen in this sample. Autozooeceial apertures polygonal, 6.4–6.9 spaced per 1 mm². Autozooeceial diaphragms few, straight. Acanthostyles large, deeply indenting into the autozooeceial cavity, 4–7 surrounding each autozooeceial aperture. Autozooeceial walls amalgamated, 0.025–0.030 mm thick. Maculae not observed.

Table 6. Descriptive statistics of *Orbipora indenta* Bassler, 1911 (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.25	0.40	0.32	0.044	13.82
Aperture spacing, mm	20	0.30	0.48	0.39	0.053	13.69
Acanthostyle diameter, mm	20	0.06	0.10	0.08	0.013	16.15
Acanthostyles per aperture	20	4.0	7.0	4.85	1.040	21.44

Remarks. – *Orbipora indenta* Bassler, 1911 differs from other species of *Orbipora* by large acanthostyles deeply indenting into the autozooeceial cavity. It differs from *Orbipora acanthophora* Bassler, 1911 in having smaller autozooeceial apertures and less abundant acanthostyles (see below).

The species described as *Orbipora indenta* Bassler, 1911 by Buttler & Massa (1996) and Buttler *et al.* (2007) from the Upper Ordovician (Katian) of Libya, does not belong to this species. It has different wall structure and morphology of acanthostyles with wide dark laminated sheaths and narrow hyaline cores.

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Väike-Pakri cliff, Estonia (present material). Bassler (1911) reported his material from the lower *Asaphus* Limestone (Kunda Stage) at Hälludden, island of Öland, Sweden.

Orbipora acanthophora Bassler, 1911

Figure 7G, 8A–E; Table 7

1911 *Orbipora acanthophora* Bassler; pp. 255–257, text-fig. 149a–d.

2007 *Orbipora acanthophora* Bassler, 1911. – Koromyslova, pp. 139–143, pl. 4, figs 1–2.

Material. – Two colonies GIT 155-2051a–h and GIT 155-2053a–c (eleven thin sections).

Table 7. Descriptive statistics of *Orbipora acanthophora* Bassler, 1911 (two colonies measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	50	0.35	0.57	0.44	0.050	11.26
Aperture spacing, mm	50	0.40	0.68	0.52	0.064	12.31
Acanthostyle diameter, mm	50	0.03	0.17	0.09	0.030	34.02
Acanthostyles per aperture	20	6.0	11.0	7.7	1.694	22.15
Mesozooeceia width, mm	26	0.08	0.27	0.16	0.050	31.07

Description. – Massive multilayered, irregularly shaped colonies of maximum size by 20 × 30 mm. Secondary overgrowths 1.9–5.8 mm in thickness. Exozone in-

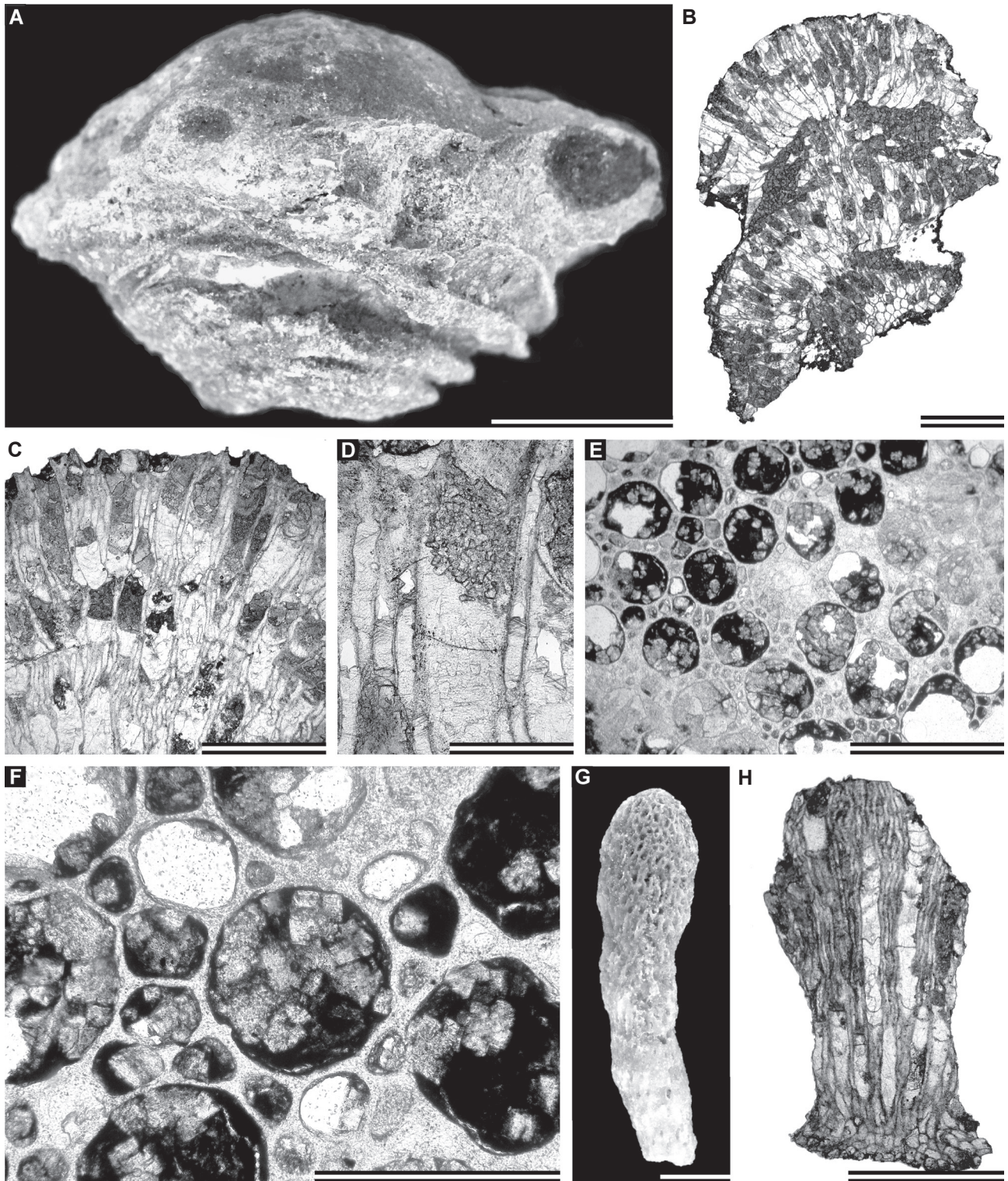


Figure 6. A–F – *Revalotrypa gibbosa* (Bassler, 1911); A – separate hemispheric multilayered colony, GIT 852-19; B – thin section through the hemispheric multilayered colony, GIT 852-16b; C, D – longitudinal section showing autozooeical chambers and neozoecia, GIT 852-13a; E, F – tangential section showing autozooeical apertures and neozoecia, GIT 852-13b. • G, H – *Revalotrypa papillaris* (Modzalevskaya, 1953); G – fragment of a colony, GIT 852-20; H – longitudinal section showing autozooeical chambers and neozoecia, GIT 852-7a. Scale bars: 5 mm (A), 2 mm (B, C, G, H), 1 mm (E), 0.5 mm (D, F),

distinct. Autozooecia long, prismatic growing from 0.005–0.010 mm thick epitheca. Autozooecial apertures polygonal, 2–5 spaced per 1 mm². Autozooecial diaphragms few, straight. Acanthostyles large, slightly indenting into the autozooecial cavity, 6–11 surrounding each autozooecial aperture and 7–12 spaced per 1 mm². Autozooecial walls amalgamated, 0.035–0.060 mm thick. Maculae not observed.

Remarks. – *Orbipora acanthophora* Bassler, 1911 is similar to *O. distincta* (Eichwald, 1829) but differs from it in having less abundant acanthostyles (6–11 per aperture vs. 15–20 in *O. distincta*). *Orbipora acanthophora* differs from *O. indenta* Bassler, 1911 in having larger autozooecial apertures (average aperture width 0.44 mm vs. 0.32 mm in *O. indenta*) and more abundant acanthostyles (6–11 acanthostyles per aperture vs. 4–7 in *O. indenta*).

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Harku quarry, Estonia (present material). Bassler (1911) reported his material from the lower *Asaphus* Limestone (Kunda Stage) at Hälludden, island of Öland, Sweden. Koromyslova (2007, p. 139) gives the range of *O. acanthophora* from the Kunda Stage of Sweden and NW Russia to the Uhaku Stage of Estonia.

***Orbipora* aff. *distincta* (Eichwald, 1829)**

Figure 8F–H; 9A, B; Table 8

Material. – Single colony GIT 852-2a–d (four thin sections).

Table 8. Descriptive statistics of *Orbipora* aff. *distincta* (Eichwald, 1829) (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.20	0.40	0.31	0.054	17.52
Aperture spacing, mm	20	0.30	0.47	0.38	0.046	12.16
Acanthostyle diameter, mm	20	0.030	0.055	0.042	0.008	18.27
Acanthostyles per aperture	8	11	20	17	2.976	17.51

Description. – Massive hemispheric colony encrusting a cephalopod shell, 8.1 mm wide at its base and 4.5 mm high in its central part. Secondary overgrowth not observed. Exozone indistinct. Autozooecia long, prismatic.

Epitheca not seen in this sample. Autozooecial apertures polygonal, 9–10 spaced per 1 mm². Autozooecial diaphragms few, straight. Acanthostyles moderate in size, not exceeding the wall thickness and not indenting into the autozooecial cavity, 11–20 arranged in one row around each autozooecial aperture and 55–71 spaced per 1 mm². Autozooecial walls amalgamated, 0.035–0.055 mm thick. Maculae indistinct, consisting of slightly larger autozooecia.

Remarks. – The present material is most similar to the species *Orbipora distincta* (Eichwald, 1829) in the number, size, and arrangement of acanthostyles. However, it differs from the material described by Bassler (1911, p. 253) and Koromyslova (2007, p. 144) in having smaller autozooecial apertures. Bassler (1911) measured aperture size as 0.8–1.0 mm, whereas Koromyslova (2007) gave aperture diameters 0.32–0.524 mm. The present material has average aperture diameter of 0.31 mm (range 0.20–0.40 mm).

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Harku quarry, Estonia.

Order Trepostomata Ulrich, 1882

Family Dittoporidae Vinassa de Regny, 1921

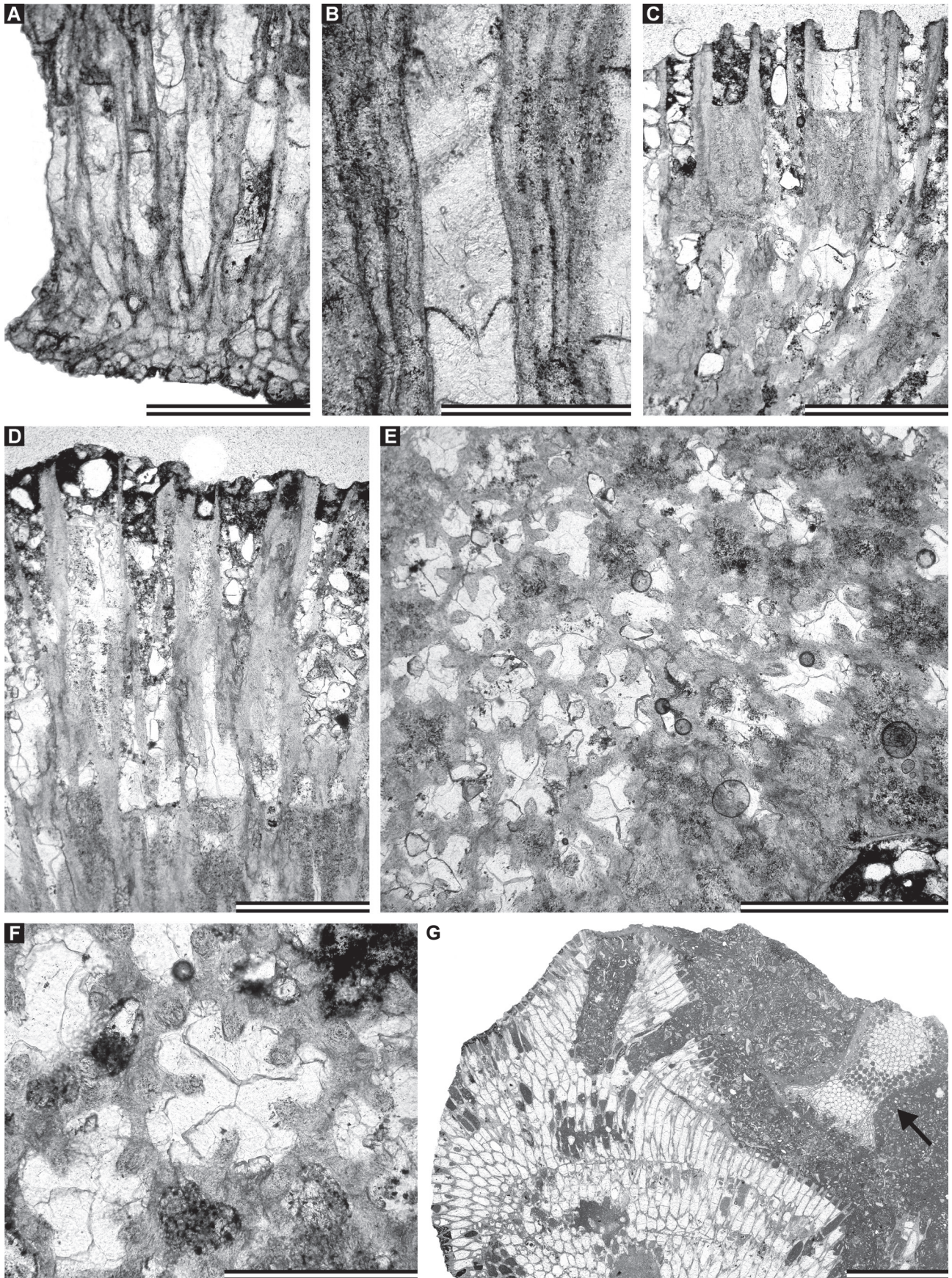
Genus *Dittopora* Dybowski, 1877

Type species. – *Dittopora clavaeformis* Dybowski, 1877. Lower Ordovician, Arenigian; Estonia, Russia.

Diagnosis. – Ramose colonies. Axial bundle composed of zooecia with diaphragms. Autozooecia and mesozooecia budding from the axial bundle. Autozooecial apertures oval and petaloid. Diaphragms abundant in endozone. Hemiphragms present, usually concentrated in exozone. Mesozooecia abundant, large, usually sealed with calcitic material near colony surface, containing abundant diaphragms. Acanthostyles abundant, often indenting autozooecial apertures. Autozooecial walls hyaline in endozones; indistinctly laminated in exozones. Maculae formed by heterozooecia and acanthostyles present.

Remarks. – *Dittopora* Dybowski, 1877 differs from *Hemiphragma* Ulrich, 1893 in the distribution of hemiphragms mainly in the transition between endozone and

Figure 7. A–B – *Revalotrypa papillaris* (Modzilevskaya, 1953), longitudinal section showing autozooecial chambers and neozooecia, GIT 852-7a. • C–F – *Orbipora indenta* Bassler, 1911; C, D – longitudinal section, GIT 155-2043b; E – tangential section showing autozooecial apertures and acanthostyles, GIT 155-2043a; F – tangential section showing autozooecial apertures and acanthostyles, GIT 155-2043c. • G – longitudinal thin section containing *Orbipora acanthophora* Bassler, 1911 and *Sonninopora* sp. (top right, arrow), GIT 155-2051b. Scale bars: 10 mm (G), 1 mm (A, C–E), 0.5 mm (B, F).



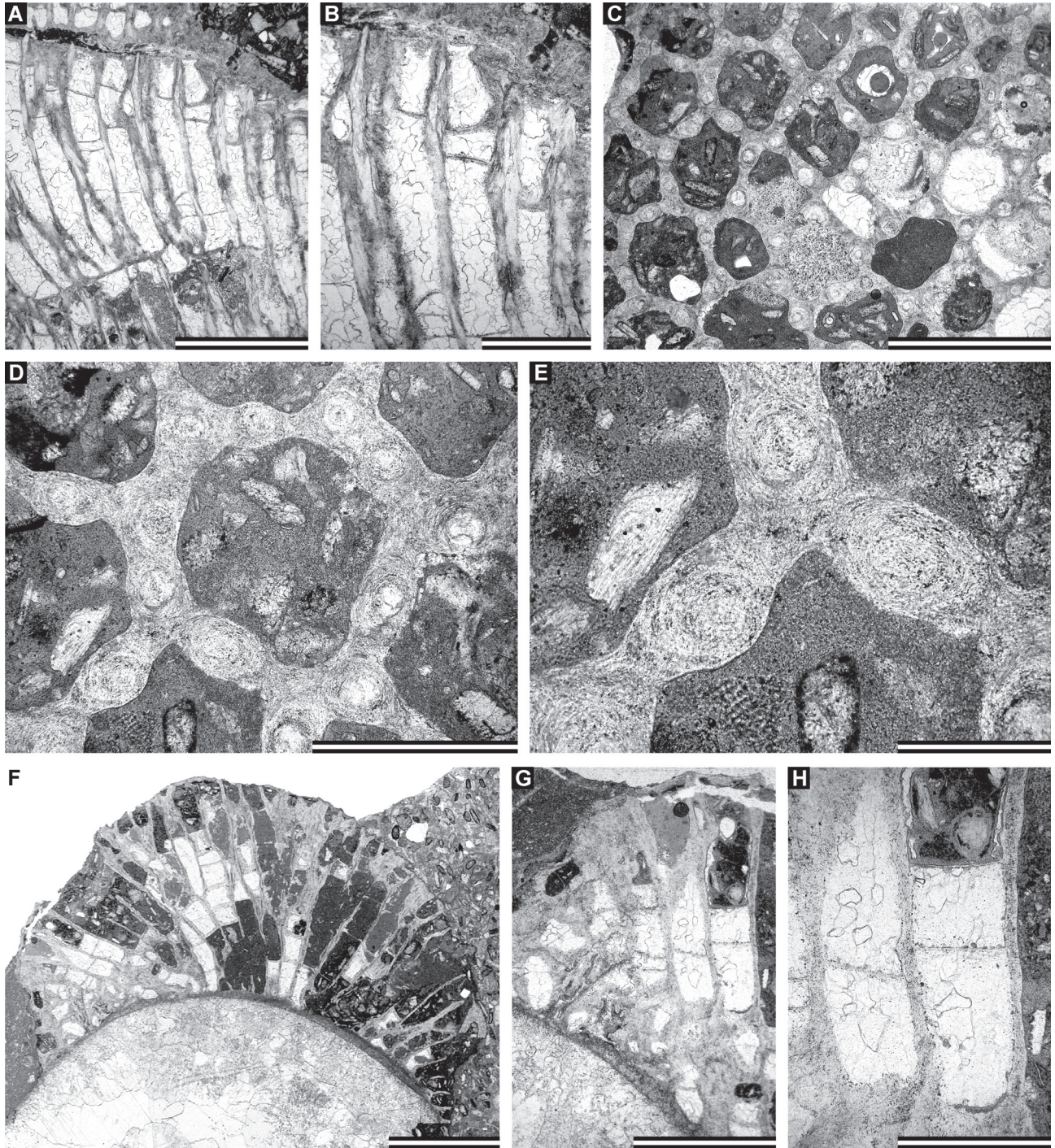
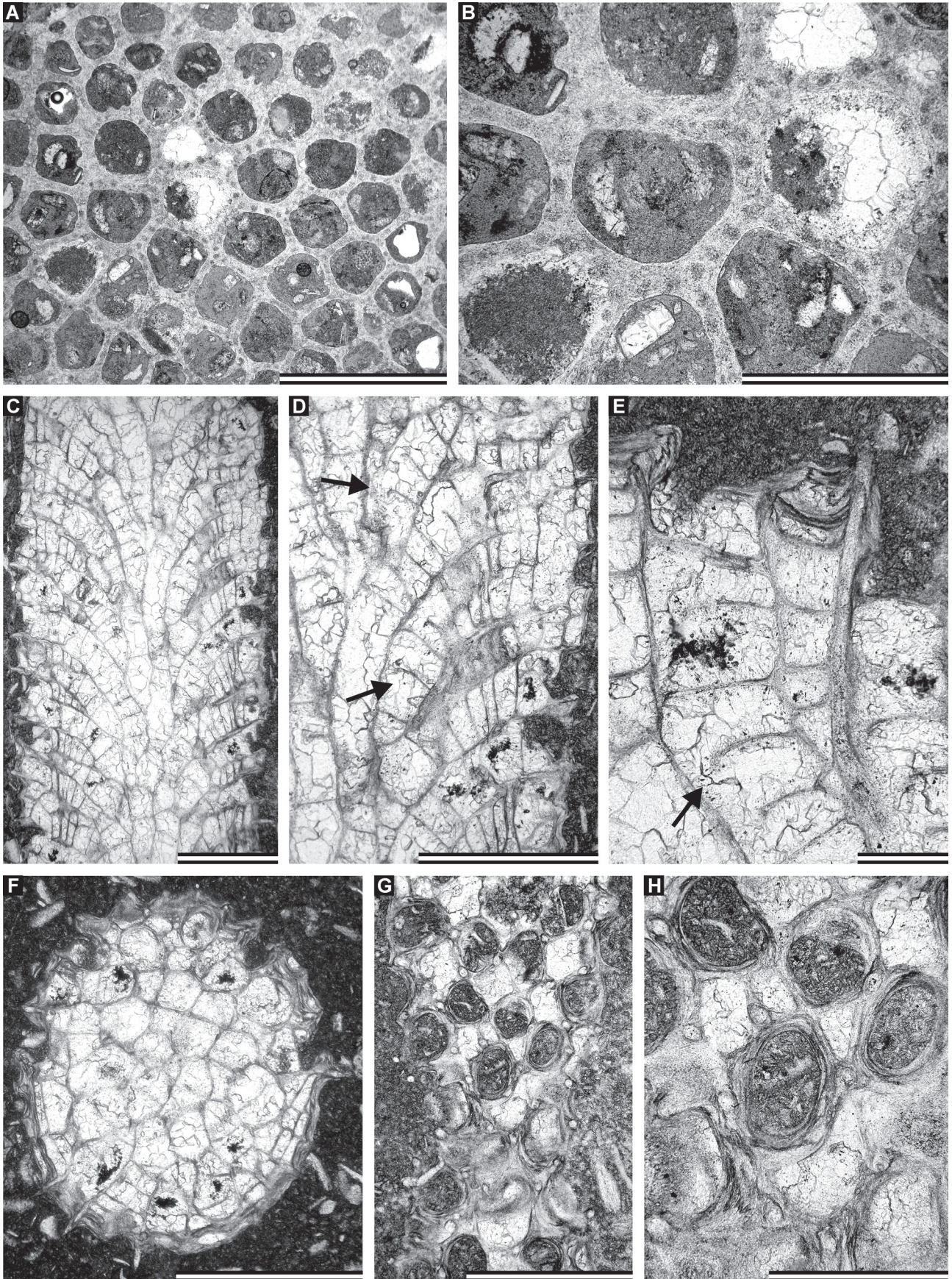


Figure 8. A–E – *Orbipora acanthophora* Bassler, 1911; A, B – longitudinal section showing autozooeal chambers and acanthostyles, GIT 155-2051b; C–E – tangential section showing autozooeal apertures and acanthostyles, GIT 155-2051g. • F–H – *Orbipora* aff. *distincta* (Eichwald, 1829); F – longitudinal section of hemispheric colony on a cephalopod shell, GIT 852-2a; G, H – longitudinal section showing autozooeal chambers with rare diaphragms, GIT 852-2a. Scale bars: 2 mm (A, F), 1 mm (B, C, G), 0.5 mm (D, H), 0.2 mm (E).

Figure 9. A, B – *Orbipora* aff. *distincta* (Eichwald, 1829), tangential section showing autozooeal apertures and acanthostyles, GIT 852-2d. • C–H – *Dittopora sokolovi* Modzalevskaya, 1953; C–E – branch longitudinal sections showing autozooeal chambers with hemiphragms (arrows), mesozooeia and acanthostyles, GIT 852-22b; F – branch transverse section, GIT 852-22g; G, H – tangential section showing autozooeal apertures, mesozooeia and acanthostyles, GIT 852-22h. Scale bars: 1 mm (A, C, D, G), 0.5 (B, F, H), 0.2 mm (E)



exozone, and in presence of smaller styles in addition to the normal acanthostyles.

Pushkin (1987) established the genus *Dybowskites* in which he placed the majority of species of *Dittopora*. He distinguished *Dybowskites* from *Dittopora* and *Hemiphragma* by the presence of the axial bundle of zoecia. However, the type species of *Dybowskites*, *Lioclemella clava* Bassler, 1911 does not have hemiphragms and axial bundle of zoecia.

Gorjunova (2005) erected the Family Ralfimartitidae Gorjunova, 2005, in which she placed the genus *Dybowskites* and restricted this genus to forms without axial bundle. The whole concept of the Family Ralfimartitidae is based on the presence of “aulozooecia”, which are described as heterozooecia in form of large hollow spines. However, those are acanthostyles with wide hyaline cores and narrow laminated sheaths (which are interpreted by Gorjunova (2005) as walls of “aulozooecia”). Neither images in Gorjunova (2005) nor own thin sections of bryozoans placed in this family show any signs of hollow spaces in these structures. They must be regarded as unusually large acanthostyles. The genera belonging in the Family Ralfimartitidae Gorjunova, 2005 need critical re-evaluation.

The generic diagnosis of *Dittopora* Dybowski, 1877 is accepted here after Astrova (1978).

Occurrence. – Lower Ordovician–lower Silurian; Europe (Baltic Region, Belarus, Great Britain).

***Dittopora sokolovi* Modzalevskaya, 1953**

Figure 9C–H; Table 9

1953 *Dittopora sokolovi* Modzalevskaya; pp. 161, 162, pl. 13, figs 1–4, text-fig. 30.

1977 *Dittopora* sp. Pushkin, p. 103, pl. 1, fig. 1.

1987 *Dybowskites sokolovi* (Modzalevskaya, 1953). – Pushkin, p. 162, pl. 12, figs 1, 2.

Material. – Eight thin sections containing five colonies (GIT 852-22a–i).

Description. – Ramose colonies, frequently dichotomizing. Branches 1.95–2.55 mm in diameter, with 1.10–1.71 mm wide endozones and 0.37–0.60 mm wide exozones. Autozoecia long in endozones forming an indistinct axial bundle, bending abruptly in exozones, having polygonal shape in transverse section of endozones.

Autozoecial apertures rounded to slightly polygonal or petaloid, 5–8.6 spaced per 1 mm². Basal diaphragms few to absent. Hemiphragms abundant, concentrated in the transition between endozone and exozone. Mesozooecia large, abundant, 3–6 surrounding each autozoecial aperture and 9–16 spaced per 1 mm². Acanthostyles abundant, 2–6 surrounding each autozoecial aperture and 14–21 spaced per 1 mm², originating in endozones, having distinct hyaline cores and wide laminated sheaths, indenting both autozoecia and mesozooecia. Smaller styles sporadically present between acanthostyles, 0.025–0.030 mm in diameter. Walls straight, displaying hyaline microstructure, 0.005–0.010 mm thick in endozone; laminated, integrated, 0.04–0.12 mm thick in exozone. Maculae not observed in the present material.

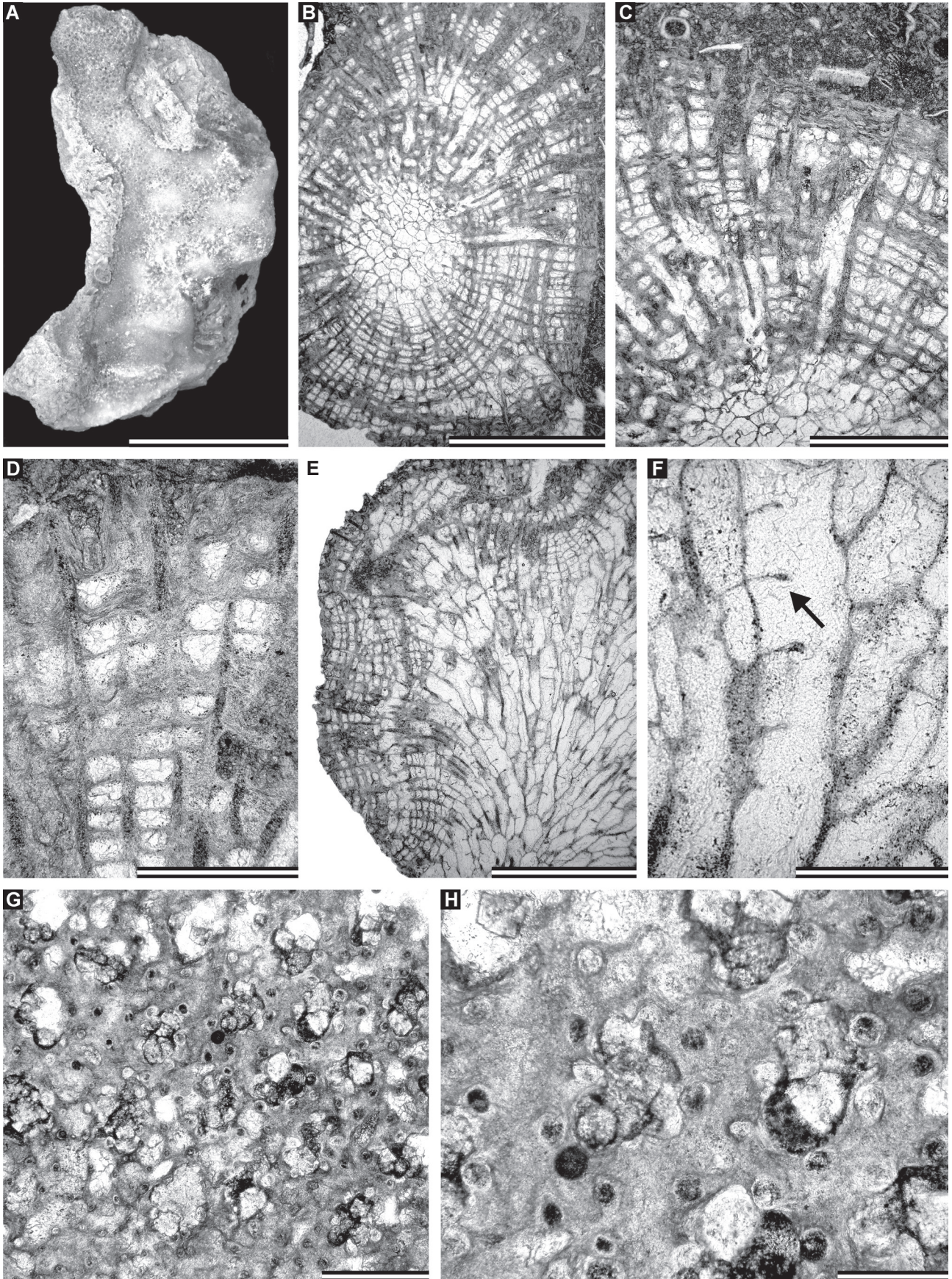
Table 9. Descriptive statistics of *Dittopora sokolovi* Modzalevskaya, 1953 (six colonies measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Branch diameter, mm	16	1.95	2.55	2.28	0.199	8.72
Exozone width, mm	16	0.37	0.60	0.46	0.065	14.22
Endozone width, mm	16	1.10	1.71	1.37	0.167	12.20
Aperture width, mm	25	0.14	0.25	0.19	0.029	14.90
Aperture spacing, mm	25	0.25	0.45	0.35	0.047	13.63
Acanthostyle diameter, mm	25	0.04	0.08	0.06	0.009	15.08
Acanthostyles per aperture	20	2.0	6.0	3.6	0.995	27.63
Mesozooecia width, mm	25	0.08	0.22	0.13	0.041	30.55
Mesozooecia per aperture	20	3.0	6.0	4.5	0.827	18.38
Mesozooecial diaphragm spacing, mm	20	0.02	0.18	0.11	0.045	41.02
Hemiphragm spacing, mm	20	0.11	0.25	0.17	0.039	22.28

Remarks. – *Dittopora sokolovi* Modzalevskaya, 1953 differs from *D. claevisformis* Dybowski, 1877 in having of branching colony instead of rod-like in the latter species, as well as in having smaller autozoecial apertures (aperture width 0.14–0.25 mm vs. 0.24–0.28 mm in *D. claevisformis*; measurements for *D. claevisformis* are from Koromyslova 2011, p. 943).

Occurrence. – Lower to Middle Ordovician of Estonia, Belarus, and Russia. Obukhovo Fm., Kunda Stage, Darriwilian, Middle Ordovician; Putilovo quarry, Russia (studied material).

Figure 10. A–H – *Dittopora annulata* (Eichwald, 1860); A – external view of the branched colony, GIT 852-18; B–D – branch transverse section showing autozoecial chambers, mesozooecia and acanthostyles, GIT 852-18b; E – branch longitudinal section showing autozoecial chambers, mesozooecia and acanthostyles, GIT 852-18d; F – branch longitudinal section showing hemiphragms in autozoecial chambers of early exozone (arrow), GIT 852-18d; G, H – tangential section showing autozoecial apertures, mesozooecia and acanthostyles, GIT 852-18c. Scale bars: 10 mm (A), 2 mm (B, E), 1 mm (C), 0.5 mm (D, F, G), 0.2 mm (H).



***Dittopora annulata* (Eichwald, 1860)**

Figure 10A–H; Table 10

- 1860 *Chaetetes annulatus* Eichwald; p. 480, pl. 28, figs 2a–c, 3a–d.
1877 *Dittopora anulata* (Eichwald, 1860). – Dybowski, p. 86, pl. 2, fig. 5 [incorrect subsequent spelling].
1911 *Dittopora annulata* (Eichwald, 1860). – Bassler, pp. 304, 305, pl. 3, fig. 5, pl. 11, figs 16, 17, text-figs 186, 187.
1986 *Dittopora annulata* (Eichwald, 1860). – Modzalevskaya, p. 78, pl. 1, figs 8–13.
2011 *Dittopora annulata* (Eichwald, 1860). – Koromyslova, p. 945, pl. 19, figs 1, 2, pl. 20, figs 1–3, pl. 21, figs 1–3.

Material. – Single colony GIT 852-18a–d (four thin sections).

Table 10. Descriptive statistics of *Dittopora annulata* (Eichwald, 1860) (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.13	0.26	0.20	0.036	17.48
Aperture spacing, mm	20	0.30	0.50	0.37	0.049	13.29
Acanthostyle diameter, mm	20	0.035	0.060	0.044	0.007	16.25
Acanthostyles per aperture	10	4.0	8.0	5.9	1.287	21.81
Mesozoecia width, mm	20	0.06	0.16	0.11	0.030	27.10
Mesozoecia per aperture	10	6.0	9.0	7.6	1.265	16.64
Mesozoecial diaphragm spacing, mm	20	0.08	0.14	0.11	0.020	17.75
Mesozoecia width, mm	25	0.08	0.22	0.13	0.041	30.55
Mesozoecia per aperture	20	3.0	6.0	4.5	0.827	18.38
Mesozoecial diaphragm spacing, mm	20	0.02	0.18	0.11	0.045	41.02

Description. – Ramose bifurcating colony. Branch diameter 2.7–4.9 mm, with 1.34–2.70 mm wide endozones and with 0.68–1.51 mm wide exozones. Secondary overgrowths common, 0.5–1.5 mm in thickness. Autozoecia long, having polygonal to slightly rounded cross sections in inner endozone, growing at first parallel to branch axis in endozone, and then bending gently towards exozone, increasing in diameter; bending sharply in basal exozone and decreasing in diameter; from base of exozone growing nearly perpendicular to colony surface. Autozoecial apertures oval, usually strongly petaloid due

to indenting acanthostyles, opening in annulated pattern on colony surface, 13.5–16.0 spaced in 1 mm². Thin, straight basal diaphragms abundant in endozones; rare to absent in exozones. Hemiphragms common to abundant, concentrated in the transition between endozone and exozone. Mesozoecia abundant, polygonal in cross section, originating in endozone, bearing abundant diaphragms, 6–9 surrounding each autozoecial aperture, covered on colony surface by laminated calcitic skeleton. Acanthostyles large, prominent, abundant, possessing wide hyaline cores and thin laminated sheaths, originating at the base of exozone, deeply inflecting autozoecial living chambers, 4–8 surrounding each aperture, 59.0–60.0 spaced in 1 mm² of branch surface. Smaller styles sporadically present between acanthostyles, 0.020–0.025 mm in diameter. Autozoecial walls granular-prismatic, 0.005–0.010 mm thick in endozone; finely laminated, 0.05–0.11 mm thick in exozone. Maculae transversally annular, depressed, composed of mesozoecia and acanthostyles, 1.2–2.1 mm wide and spaced 2.3–3.0 mm from centre to centre longitudinally.

Remarks. – Pushkin (1987) placed *Dittopora annulata* (Eichwald, 1860) in the genus *Dybowskites*, whereas Gorjunova (2005) assigned it to her genus *Rozhnovites*. However, the type species of *Rozhnovites*, *R. limatus* Gorjunova, 2005 possesses no hemiphragms. *Dittopora annulata* corresponds to the diagnosis of the genus *Dittopora*, therefore, it is retained within this genus. It differs from *Dittopora sokolovi* Modzalevskaya, 1953 in having more abundant mesozoecia and acanthostyles (6–9 mesozoecia per aperture vs. 3–6 in *D. sokolovi*; 4–8 acanthostyles per aperture vs. 2–6 in *D. sokolovi*).

Occurrence. – Latorp–Kunda horizons, Floian–Darriwilian, Lower–Middle Ordovician; NW Russia. Obukhovo Fm., Kunda Stage, Darriwilian, Middle Ordovician; Putilovo quarry, Russia (studied material).

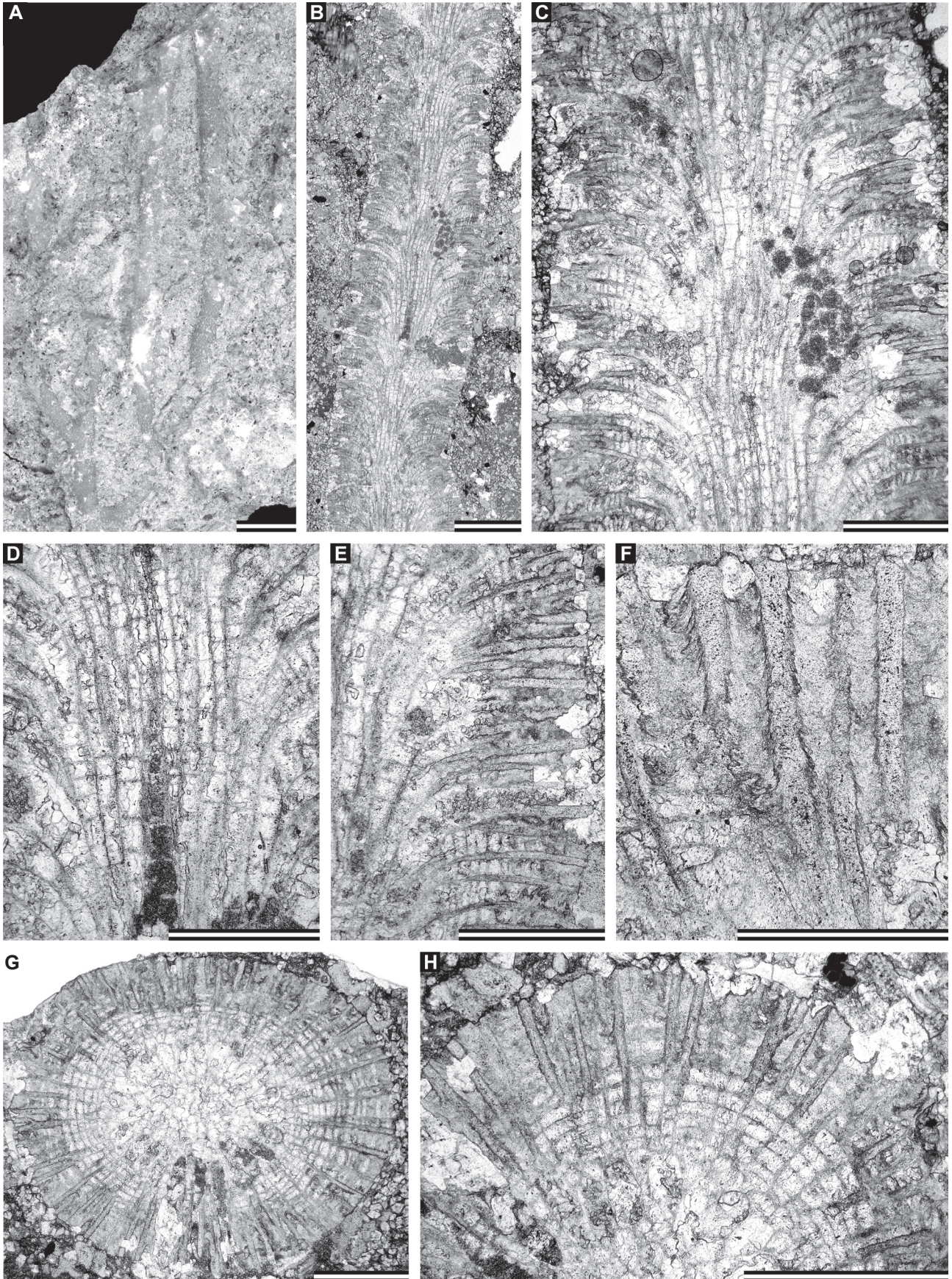
***Dittopora* aff. *annulata* (Eichwald, 1860)**

Figure 11A–H, 12A–E; Table 11

Material. – Single specimen GIT 155-2045a–j (ten thin sections).

Description. – Ramose colonies with rare bifurcations. Branch diameters 3.25–4.00 mm, with, 1.37–1.74 mm wide endozones and 0.81–1.13 mm wide exozones. Secondary overgrowths unknown. Autozoecia long,

Figure 11. A–H – *Dittopora* aff. *annulata* (Eichwald, 1860); A – branched colony imbedded in the rock, GIT 155-2045; B–F – longitudinal section, showing autozoecial chambers, mesozoecia and acanthostyles, GIT 155-2045g; G, H – transverse section showing autozoecial chambers, mesozoecia and acanthostyles, GIT 155-2045h. Scale bars: 10 mm (A), 2 mm (B), 1 mm (C, D, E, G, H), 0.5 mm (F).



having polygonal to slightly rounded cross sections in inner endozone, growing at first parallel to branch axis in endozone, and then bending gently towards exozone, increasing in diameter; bending sharply in basal exozone and decreasing in diameter; from base of exozone growing nearly perpendicular to colony surface. Autozooeal apertures oval, usually strongly petaloid due to indenting acanthostyles, opening in annulated pattern on colony surface, 7–11 spaced in 1 mm². Thin, straight basal diaphragms abundant in endozones; rare to absent in exozones. Hemiphragms common to abundant, concentrated in the transition between endozone and exozone. Mesozooecia abundant, polygonal in cross section, originating deeply in endozone, bearing abundant diaphragms, 8–9 surrounding each autozooeal aperture, covered on colony surface by laminated calcitic skeleton. Acanthostyles large, prominent, abundant, possessing wide hyaline cores and thin laminated sheaths, originating at the base of exozone, deeply inflecting autozooeal living chambers, 5–11 surrounding each aperture, spaced 44–61 in 1 mm² of branch surface. Autozooeal walls granular-prismatic, 0.005–0.010 mm thick in endozone; finely laminated, 0.018–0.036 mm thick in exozone. Smaller styles sporadically present between acanthostyles, concentrated mainly around mesozooecia, 0.025–0.035 mm in diameter. Maculae transversally annular, depressed, composed of mesozooecia and acanthostyles, 0.29–0.54 mm wide and spaced 2.1–2.3 mm from centre to centre longitudinally.

Table 11. Descriptive statistics of *Dittopora* aff. *annulata* (Eichwald, 1860) (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.13	0.26	0.20	0.036	17.48
Aperture spacing, mm	20	0.30	0.50	0.37	0.049	13.29
Acanthostyle diameter, mm	20	0.035	0.060	0.044	0.007	16.25
Acanthostyles per aperture	10	4.0	8.0	5.9	1.287	21.81
Mesozooecia width, mm	20	0.06	0.16	0.11	0.030	27.10
Mesozooecia per aperture	10	6.0	9.0	7.6	1.265	16.64
Mesozooecial diaphragm spacing, mm	20	0.08	0.14	0.11	0.020	17.75

Remarks. – The present material is superficially similar to *Dittopora annulata* (Eichwald, 1860) (see above). However, it has smaller autozooea (aperture width 0.13 mm vs. 0.20 mm in *D. annulata*), as well as more abundant and larger acanthostyles (7–11 acanthostyles per aperture vs. 4–8 in *D. annulata*; average acanthostyle diameter 0.070 mm vs. 0.044 mm in *D. annulata*). As far as only one colony is available, this species is described in the open nomenclature.

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Väike-Pakri cliff, Estonia.

Genus *Hemiphragma* Ulrich, 1893

Type species. – *Batostoma irrasum* Ulrich, 1886. Middle Ordovician (Trenton); North America.

Diagnosis. – Colonies massive and ramose. Autozooea with polygonal and polygonal-rounded apertures. Autozooeal diaphragms present. Hemiphragms occurring throughout autozooeal chambers. Autozooeal walls in exozone strongly thickened, partly integrated, displaying sloped and longitudinally lamellar microstructure. Mesozooecia usually rare, but sometimes abundant. Acanthostyles usually small and rare, but sometimes abundant.

Remarks. – *Hemiphragma* Ulrich, 1893 is most similar to *Phragmopora* Vinassa de Regny, 1921, differing in having acanthostyles and smaller mesozooecia.

Occurrence. – Lower to Middle Ordovician; North America, Europe, Siberia.

Hemiphragma rotundatum Bassler, 1911

Figure 12F–H, 13A–C; Table 12

1911 *Hemiphragma rotundatum* Bassler, pp. 294, 295, text-fig. 180.

1986 *Hemiphragma rotundatum* Bassler, 1911. – Modzalevskaya, pp. 82, 83, pl. 2, figs 4, 5.

Material. – Single specimen GIT 155-287a-d (four thin sections).

Table 12. Descriptive statistics of *Hemiphragma rotundatum* Bassler, 1911 (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.25	0.32	0.28	0.019	6.79
Aperture spacing, mm	20	0.30	0.50	0.37	0.056	15.19
Acanthostyle diameter, mm	20	0.030	0.065	0.047	0.009	18.86
Acanthostyles per aperture	10	6.0	10.0	8.0	1.155	14.43
Mesozooecia width, mm	20	0.05	0.12	0.09	0.021	22.80
Mesozooecia per aperture	10	3.0	7.0	4.7	1.252	26.63
Mesozooecial diaphragm spacing, mm	20	0.07	0.15	0.10	0.020	19.74
Hemiphragm spacing, mm	20	0.12	0.22	0.15	0.029	18.65

Description. – Globular multilayered colony in size of 14 × 18 mm. Separate layers 1.7–4.7 mm in thickness.

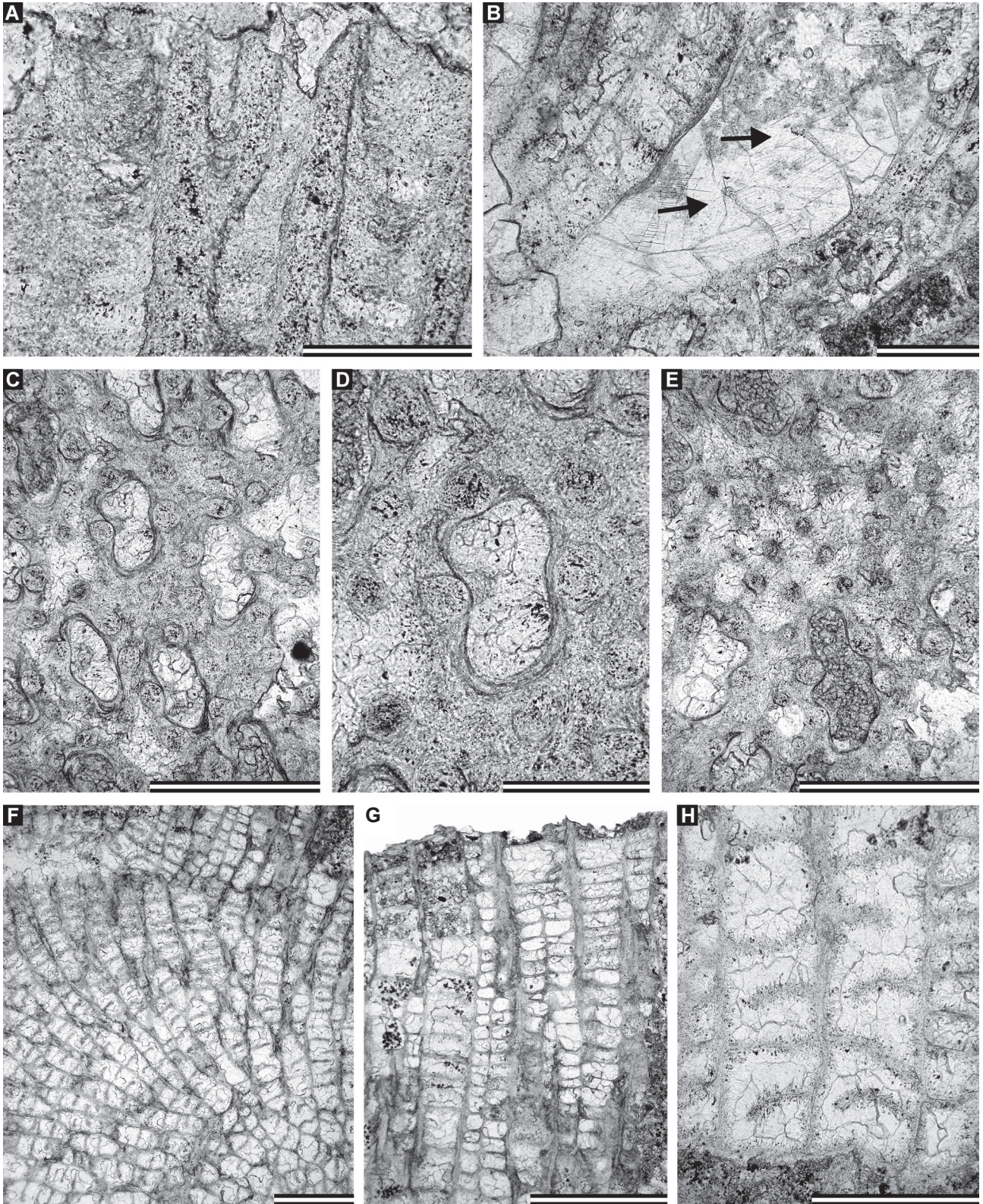


Figure 12. A–E – *Dittopora* aff. *annulata* (Eichwald, 1860); A – transverse section showing autozooeal chambers, mesozooeia and acanthostyles, GIT 155-2045h; B – longitudinal section, showing autozooeal chambers with hemiphragms (arrows), GIT 155-2045d; C–E – tangential section showing autozooeal apertures, mesozooeia and acanthostyles (E – macula composed of mesozooeia and acanthostyles), GIT 155-2045i. • F–H – *Hemiphragma rotundatum* Bassler, 1911, longitudinal section showing autozooeal chambers with hemiphragms and mesozooeia, GIT 155-287b. Scale bars: 1 mm (F, G), 0.5 mm (C, E, H), 0.2 mm (A, B, D).

Exozones indistinct. Autozooeceia long, prismatic, budding from a thin epitheca. autozooeceial apertures rounded-polygonal to petaloid, 7–9 spaced per 1 mm². Hemiphragms most abundant throughout the colony, long and thick, curved to proximal end on their inner edge. Basal diaphragms few to absent. Mesozooecia large, abundant, 3–7 surrounding each autozooeceial aperture and 10–14 spaced per 1 mm². Acanthostyles abundant, 6–10 surrounding each autozooeceial aperture and 22–32 spaced per 1 mm², having distinct hyaline cores and wide laminated sheaths. Walls straight, displaying hyaline microstructure, 0.005–0.010 mm thick in endozone; laminated, integrated, 0.03–0.05 mm thick in exozone. Indistinct maculae consisting of larger autozooeceia present.

Remarks. – *Hemiphragma rotundatum* Bassler, 1911 differs from *H. pygmeum* Bassler, 1911 from the Upper Ordovician of Estonia and Sweden in larger autozooeceia (aperture width 0.25–0.32 mm vs. 0.15–0.25 mm in *H. pygmeum*). *Hemiphragma rotundatum* differs from *H. insolitum* Koromyslova & Fedorov, 2021 from the Middle Ordovician (Dapingian) of Russia in its globular colony instead of encrusting one and in having smaller mesozooecia (average mesozooecial width 0.09 mm vs. 0.15 mm in *H. insolitum*).

Occurrence. – Lower–Middle Ordovician of Estonia and NW Russia. Kunda Stage, Darriwilian, Middle Ordovician; Väike-Pakri cliff, Estonia (present material).

Family Mesotrypidae Astrova, 1965

Genus *Mesotrypa* Ulrich, 1893

Type species. – *Diplotrypa infida* Ulrich, 1886. Middle Ordovician, North America.

Diagnosis. – Massive, hemispheric, conical or discoidal colonies. Autozooeceial apertures polygonal or rounded. Walls thin, longitudinally laminated, indistinctly separated. Diaphragms planar, sloped, curved, and funnel-shaped. Mesozooecia abundant, budding from base of colony. Acanthostyles may be large, growing from the base of colony, or small, visible at colony surface.

Remarks. – *Mesotrypa* Ulrich, 1893 differs from *Diazipora* Vinassa de Regny, 1921 by having acanthostyles and larger mesozooecia.

Occurrence. – Middle Ordovician to lower Silurian, worldwide.

***Mesotrypa bystrowi* Modzalevskaya, 1953**
Figure 13D–G; Table 13

For full synonymy see Pushkin (2002, p. 428).

Material. – Single colony GIT 155-2055a–c (three thin sections).

Table 13. Descriptive statistics of *Mesotrypa bystrowi* Modzalevskaya, 1953 (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.23	0.31	0.27	0.023	8.54
Aperture spacing, mm	20	0.28	0.40	0.33	0.032	9.49
Mesozooecia width, mm	20	0.05	0.18	0.11	0.040	35.43
Mesozooecia per aperture	10	5.0	7.0	6.1	0.876	14.35
Mesozooecial diaphragm spacing, mm	20	0.03	0.09	0.06	0.016	27.57
Zooecial diaphragm spacing, mm	20	0.15	0.48	0.28	0.100	35.45

Description. – Discoidal hemispheric colony with short endozones, 16 mm wide at its base and 10 mm high in its central part. Secondary overgrowths not observed. Autozooeceia bending gently from epitheca, radiating from colony centre to periphery. Autozooeceial apertures polygonal, 7.6–9.5 spaced per 1 mm². Autozooeceial diaphragms abundant, thin, planar or curved. Mesozooecia large, abundant, 5–7 surrounding each autozooeceial aperture and 22–31.5 spaced per 1 mm², polygonal in cross section, originating at the base of colony, bearing straight closely spaced diaphragms. Autozooeceial walls finely laminated, 0.003–0.008 mm thick. Acanthostyles indistinct, spine-like, 0.025–0.035 mm in diameter, positioned in junctions between apertures. Maculae not observed.

Remarks. – *Mesotrypa bystrowi* Modzalevskaya, 1953 differs from *M. egena* Bassler, 1911 from the Upper Ordovician of Estonia and Norway in having smaller autozooeceial apertures (average aperture width 0.27 mm vs. 0.30 mm in *M. egena*; measurements from Ernst & Nakrem 2012) and more abundant mesozooecia (5–7 per aperture vs. 2–6 in *M. egena*).

Occurrence. – Middle to Upper Ordovician of Estonia and NW Russia (Pushkin 2002, p. 430). Kunda Stage, Darriwilian, Middle Ordovician; Harku Quarry, Estonia (present material).

Family Bimuroporidae Key, 1990

Genus *Sonninopora* Vinassa de Regny, 1921

Type species. – *Hallopora tenuispinosa* Bassler, 1911. Ordovician (Sandbian–Katian); Estonia.

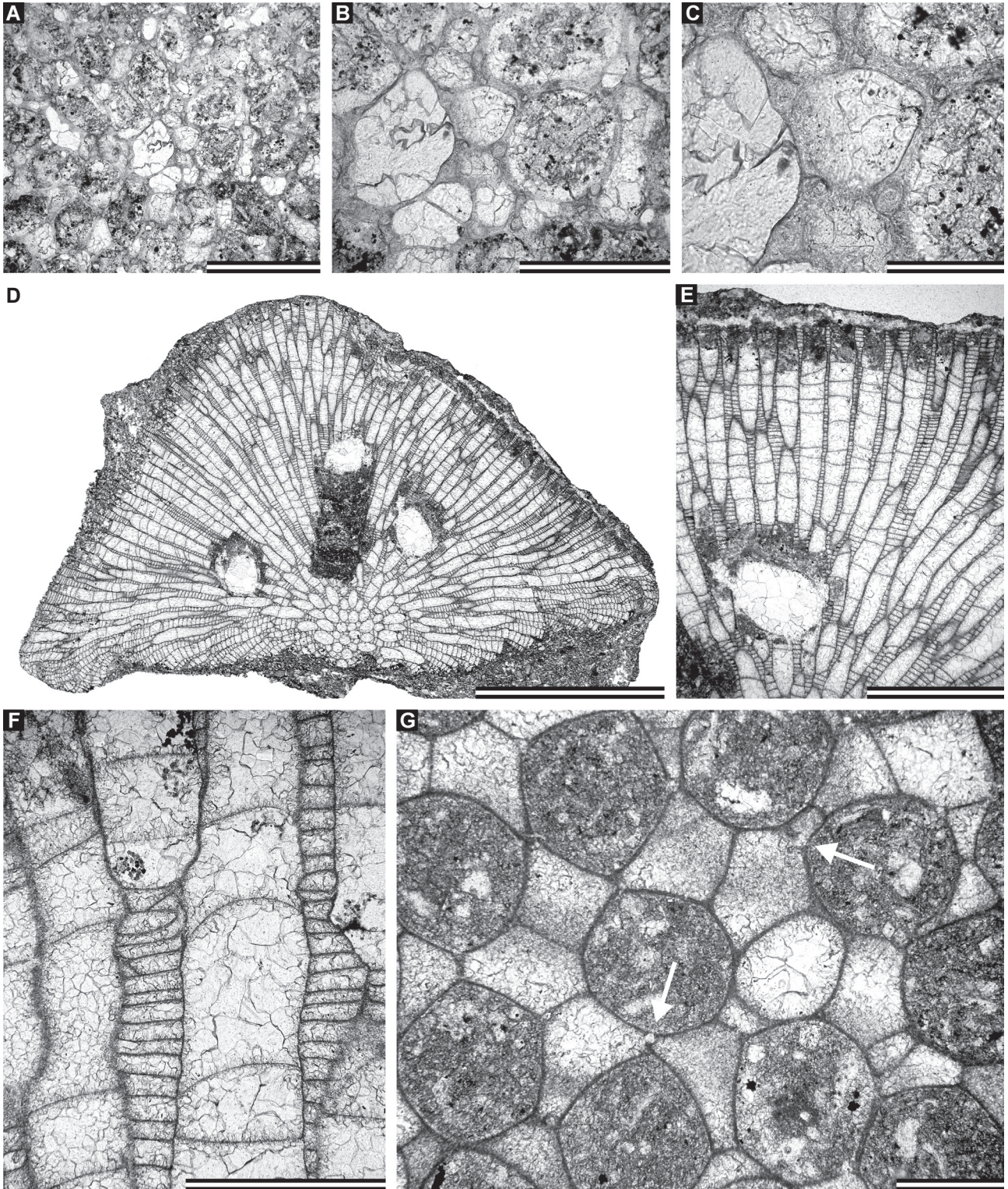


Figure 13. A–C – *Hemiphragma rotundatum* Bassler, 1911, tangential section showing autozooeal apertures, acanthostyles, and mesozooecia, GIT 155-287c. • D–G – *Mesotrypa bystrowi* Modzalevskaya, 1953; D – longitudinal section of a hemispheric colony with borings, GIT 155-2055b; E, F – longitudinal section showing autozooeal chambers with diaphragms and mesozooecia, GIT 155-2055b; G – tangential section tangential section showing autozooeal apertures, acanthostyles, and mesozooecia, GIT 155-2055c. Scale bars: 5 mm (D), 2 mm (E), 1 mm (A), 0.5 mm (B, F), 0.2 mm (C, G).

Diagnosis. – Colonies ramose or encrusting. Branches circular in transverse section. Zooecial budding disordered when almost all zooecia beginning their ontogeny as mesozooecia and expand into autozooecia. Autozooecial walls in endozone straight, autozooecial walls thin and integrate in exozone, boundary irregular; mesozooecial walls in endozone fluted, mesozooecia common in exozone, almost completely surrounding autozooecia; exozonal acanthostyles with cores of clear calcite. Mural spines, cap-like apparatus (*sensu* Conti & Serpagli 1987) absent. Maculae composed of macrozooecia and mesozooecia (modified after Key 1990).

Remarks. – *Sonninopora* Vinassa de Regny, 1921 differs from *Bimuropora* Key, 1990 in having thinner exozonal walls and more abundant mesozooecia. *Sonninopora* differs from *Champlainopora* Ross, 1970 in having an unordered zooecial arrangement without long, large axial zooecia, and more abundant mesozooecia.

Occurrence. – Ordovician (Darriwilian–Katian); Estonia, Canada.

Sonninopora sp.

Figure 14A–F; Table 14

Material. – Single specimen GIT 155-2051b, c, e, f (four thin sections).

Table 14. Descriptive statistics of *Sonninopora* sp. (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.18	0.32	0.26	0.038	14.71
Aperture spacing, mm	20	0.23	0.42	0.32	0.062	19.52
Acanthostyle diameter, mm	20	0.025	0.040	0.032	0.003	10.18
Acanthostyles per aperture	9	4.0	7.0	5.3	1.000	18.75
Mesozooecia width, mm	20	0.05	0.15	0.09	0.029	31.37
Mesozooecia per aperture	10	4.0	8.0	6.5	1.581	24.33
Mesozooecial diaphragm spacing, mm	20	0.06	0.11	0.09	0.015	16.91
Hemiphragm spacing, mm	20	0.12	0.22	0.15	0.029	18.65

Description. – Subramose colony (incomplete), ca 7.4 mm wide, with indistinct exozone. Basal diaphragms uncommon, 1–2 in each autozooecium. Autozooecia long, originating mostly from mesozooecia. Autozooecial apertures rounded-polygonal, 12–13 spaced per 1 mm². Mesozooecia moderate in size, abundant, 4–8 surrounding each autozooecial aperture and 22–28 spaced per 1 mm², slightly beaded, bearing abundant straight and rarely inclined diaphragms. Acanthostyles abundant, 4–7

surrounding each autozooecial aperture, having distinct hyaline cores and wide laminated sheaths. Walls straight, displaying hyaline microstructure, 0.005–0.008 mm thick in endozone; laminated, integrated, 0.018–0.036 mm thick in exozone. Maculae not observed in the studied material. Vesicular skeleton at the base of the colony present.

Remarks. – The present material is similar to *Sonninopora tenuispinosa* (Bassler, 1911) from the Upper Ordovician (Sandbian–Katian) of Estonia. It has eventually smaller autozooecial apertures. Bassler (1911) and Key & Judd (1994) did not provide measurements of apertures of the type material of *Hallopora tenuispinosa* Bassler, 1911. Measured aperture widths from the text-fig. 213 of Bassler (1911) gave values of 0.30–0.40 mm vs. 0.18–0.32 mm in present material. Key & Judd (1994, p. 236) gave the number of mesozooecia per 1 mm² as 7.3–14.4 vs. 22–28 in the present material.

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Harku quarry, Estonia.

Family uncertain

Genus *Pakripora* gen. nov.

Type species. – *Pakripora cavernosa* sp. nov.

Etymology. – The new genus is named after finding it at Pakri, Estonia.

Diagnosis. – Ramose colonies with distinct exozones and secondary overgrowths; autozooecia polygonal in exozone, containing abundant diaphragms; short and blunt mural spines in autozooecial walls of chambers in exozone; mesozooecia abundant; acanthostyles abundant, with distinct wide hyaline cores and narrow laminated sheaths; maculae common, slightly depressed, composed of mesozooecia and acanthostyles.

Remarks. – The new genus is characterized by abundant acanthostyles and mesozooecia, as well as by the presence of mural spines in autozooecia. Männil (1959, pp. 317–319) established the species *Leioclema? pakrianum*. The genus *Leioclema* Ulrich, 1882 differs from the new genus in having rare to absent diaphragms in autozooecia as well as in absence of mural spines in autozooecia. Moreover, acanthostyles in *Leioclema* possess distinct narrow hyaline cores and wide laminated sheaths (Tavener-Smith 1969).

Mural spines of similar morphology are present in the genus *Stenoporella* Bassler, 1936 from the Carboniferous of USA. However, *Stenoporella* belongs to the Suborder Amplexoporina Astrova, 1965 and develops exilazooecia

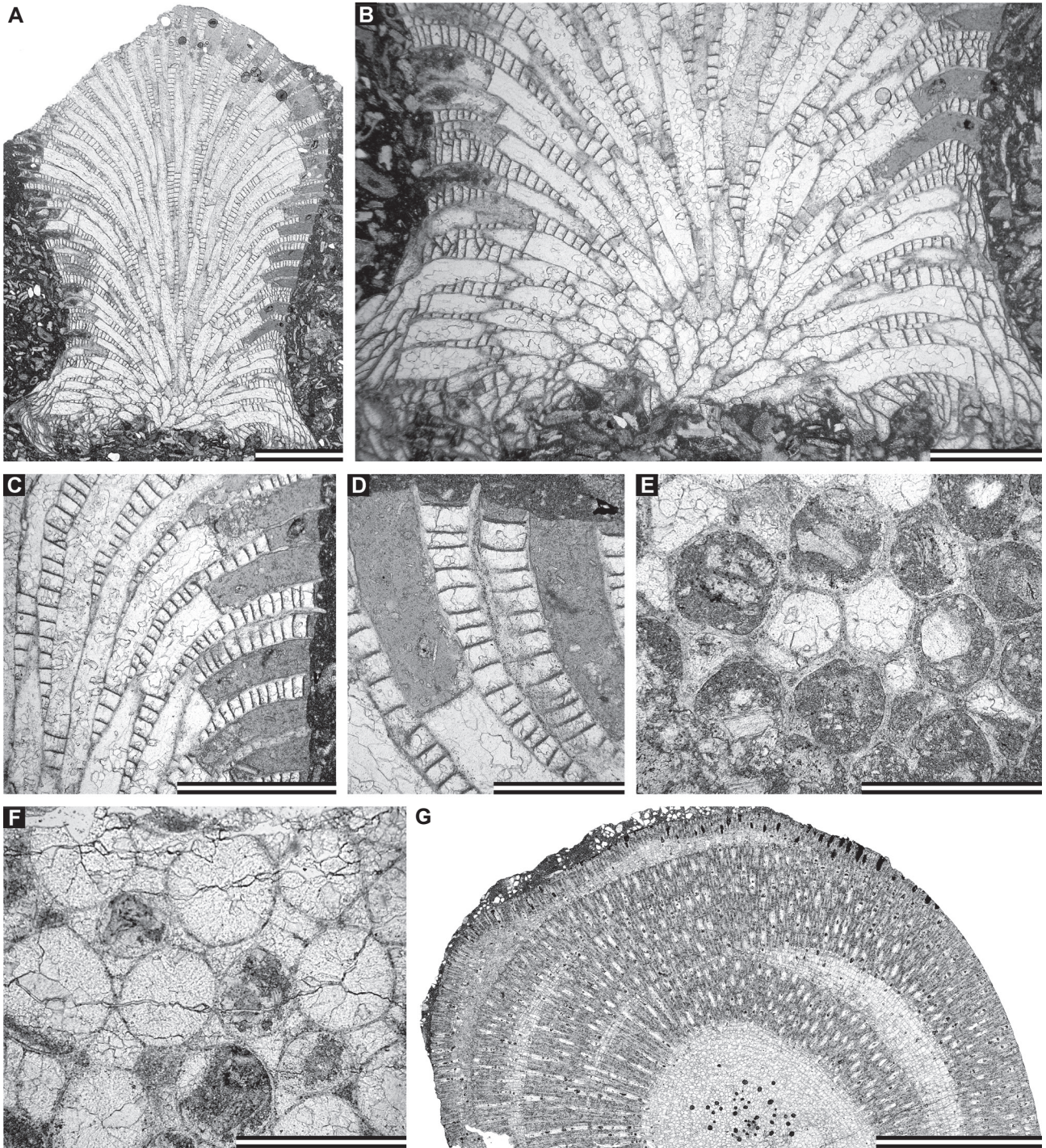


Figure 14. A–F – *Sonninopora* sp.; A–D – longitudinal section showing autozooeal chamber, mesozooea and acanthostyles, GIT 155-2051e; E, F – tangential section showing autozooeal apertures, acanthostyles and mesozooea, GIT 155-2051f. • G – *Pakripora cavernosa* gen. et sp. nov., transverse section showing endozone and exozone, holotype GIT 537-2265c. Scale bars: 5 mm (G), 2 mm (A), 1 mm (B, C), 0.5 mm (D–F).

instead of mesozooeia, and possesses typical acanthostyles known in the Family Stenoporidae, with distinct narrow hyaline cores and wide laminated sheaths.

Occurrence. – Kunda Stage, Darrivilian, Middle Ordovician; Väike-Pakri island, Paldiski, Estonia.

***Pakripora cavernosa* sp. nov.**

Figure 14G; 15A–H; 16A, B; Table 15

Holotype. – GIT 537-2265a–h (eight thin sections), originally assigned to *Leioclema pakrianum* Männil, 1959 (unpublished).

Table 15. Descriptive statistics of *Pakripora cavernosa* gen. et sp. nov. (two colonies measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.08	0.13	0.11	0.011	10.04
Aperture spacing, mm	20	0.24	0.35	0.28	0.026	9.29
Acanthostyle diameter, mm	20	0.04	0.06	0.05	0.006	12.32
Acanthostyles per aperture	20	4.0	7.0	4.8	0.768	16.00
Mesozoecia width, mm	20	0.040	0.075	0.060	0.009	16.57
Mesozoecia per aperture	20	7.0	9.0	8.0	0.686	8.63
Mesozoecial diaphragm spacing, mm	20	0.06	0.11	0.09	0.015	16.91
Hemiphragm spacing, mm	20	0.12	0.22	0.15	0.029	18.65

Paratypes. – GIT 155-2047a–b (two thin sections) from the Kunda Stage of the Väike-Pakri cliff. Unstudied material includes some more specimens deposited in the collection at the GIT. Specimens GIT 537-1227 and GIT 537-1308 come from the type locality Väike-Pakri island. The sample GIT 537-1227 consists of six large fragments which may represent remnants of two colonies (Ursula Toom, pers. comm. 2021). The specimen GIT 537-2266 comes from the Kunda Stage of Paldiski (locality opposite to the Väike-Pakri island). The holotype of Männil for *Leioclema pakrianum* Männil, 1959, GIT 537-1232 is missing from the collection (Ursula Toom, personal communication 2021), as well as the sample GIT 537-1242, which was assigned to this species. The specimen GIT 537-1301 was originally assigned by Männil (1959) to *Leioclema pakrianum*, but seems to represent another species.

Type horizon and locality. – Kunda Stage, Darriwilian, Middle Ordovician; Väike-Pakri island, Estonia.

Material. – Types only.

Etymology. – The species is named after presence of abundant mesozoecia (from the Latin “cavernosa” – pitted, porous).

Diagnosis. – Large ramose colonies with distinct exozones and secondary overgrowths; basal diaphragms straight, abundant; short and blunt mural spines in autozoecial walls of chambers in exozone; mesozoecia moderate in size, abundant, 7–9 surrounding each autozoecial aperture; mesozoecial diaphragms abundant, thickened

in exozones almost sealing mesozoecia; acanthostyles abundant, 4–7 surrounding each autozoecial aperture; macrozoecia few near maculae; maculae common, slightly depressed, composed of mesozoecia and acanthostyles.

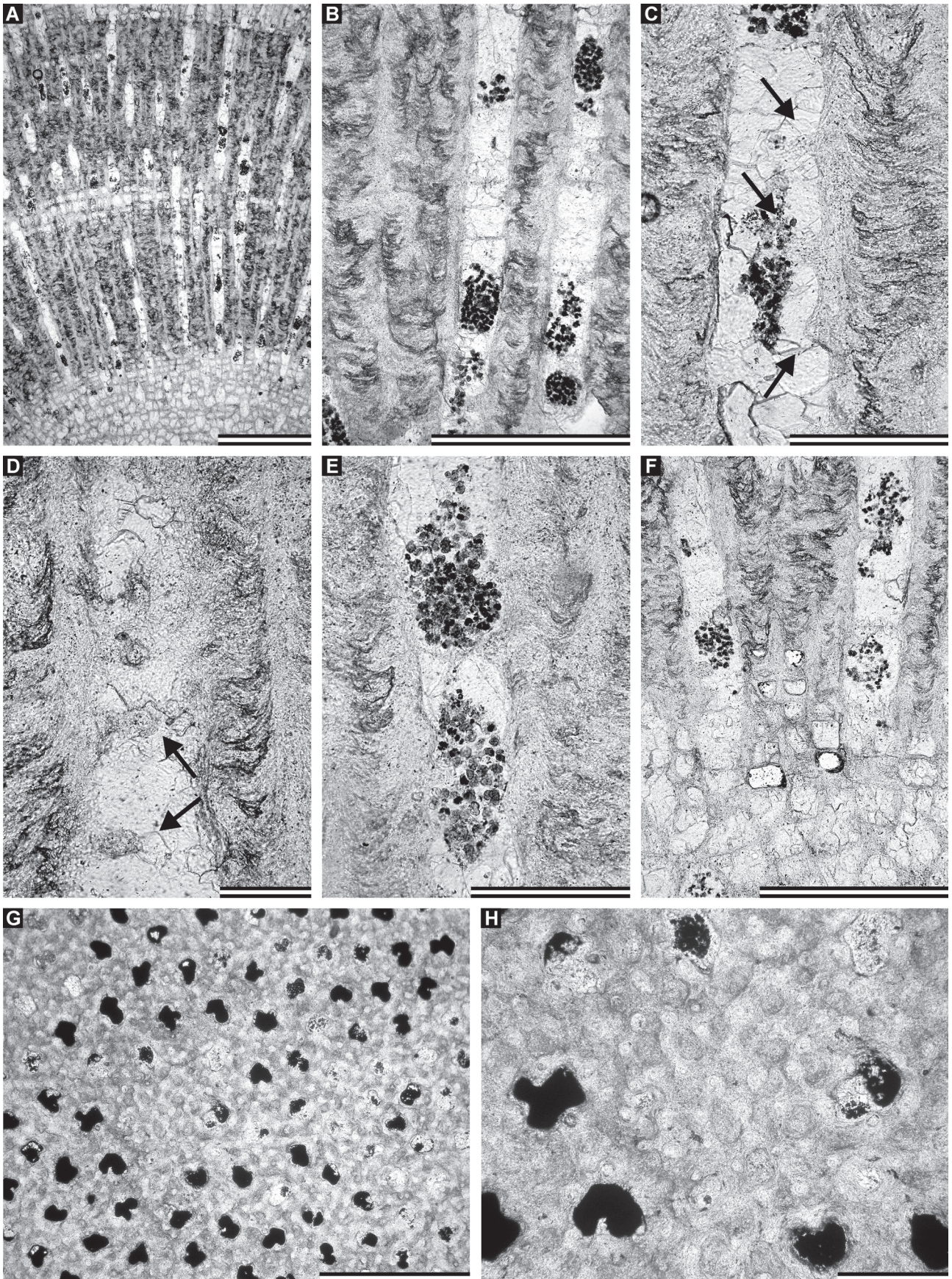
Description. – Ramose colonies, frequently dichotomizing. Branches 11–20 mm in diameter, with 5.1–7.6 mm wide endozones and 2.0–5.3 mm wide exozones. Secondary overgrowth common, 1.0–1.9 mm in thickness. Autozoecia long, polygonal in transverse section of endozones, bending abruptly in exozones. Basal diaphragms straight, abundant, concentrated in the transition between endozones and exozones. Mural spines in exozones, blunt, 0.025–0.050 mm in diameter and 0.030–0.055 mm long, spaced in alternating pattern (Fig. 15C–E). Autozoecial apertures rounded to petaloid, 11–15 spaced per 1 mm². Mesozoecia moderate in size, abundant, 7–9 surrounding each autozoecial aperture, originating deeply in endozones and containing abundant diaphragms in their endozonal parts and in the transition to exozones; in exozones mesozoecial diaphragms thickened almost sealing the mesozoecia. Acanthostyles abundant, 4–7 surrounding each autozoecial aperture, having distinct hyaline cores and wide laminated sheaths, originating at the base of exozones, indenting autozoecia and mesozoecia. Autozoecial walls straight, displaying hyaline microstructure, 0.005–0.010 mm thick in endozones; laminated, integrated, 0.04–0.12 mm thick in exozones. Mesozoecial walls 0.008–0.010 mm thick. Macrozoecia few, occurring near maculae, 0.16–0.21 mm in width. Maculae common, slightly depressed, composed of mesozoecia and acanthostyles, 0.55–0.85 mm in diameter, spaced 2.5–3.0 mm from centre to centre. Fossilized brown deposits abundant, representing accumulations of irregularly rounded brown to black particles, normally concealed between two neighbouring diaphragms (Fig. 15A–C, E, F). Particles in brown deposits 0.005–0.025 mm in diameter.

Remarks. – According to the rules of the Zoological Nomenclature, the species *Leioclema pakrianum* established by Männil in his dissertation (1959) is not valid. Therefore, his material has been used to erect a new species.

Order Cryptostomata Vine, 1884

Suborder Ptilodictyina Astrova & Morozova, 1956

Figure 15. A–H – *Pakripora cavernosa* gen. et sp. nov.; A – transverse section showing endozones and exozones, holotype GIT 537-2265c; B–E – transverse section showing zoecial chambers with brown deposits, diaphragms, and mural spines (arrows), holotype GIT 537-2265d; F – transverse section showing zoecial chambers showing zoecial chambers and mesozoecia at the base of exozones, holotype GIT 537-2265e; G, H – tangential section showing autozoecial apertures, acanthostyles, mesozoecia, and a macula composed of acanthostyles and mesozoecia (centred), holotype GIT 537-2265g. Scale bars: 1 mm (A, G), 0.5 mm (B, F), 0.2 mm (C, E, H), 0.1 mm (D).



**Genus *Prophyllodictya* Gorjunova, 1987
in Gorjunova & Lavrentjeva (1987)**

Type species. – *Prophyllodictya intermedia* Gorjunova, 1987 in Gorjunova & Lavrentjeva (1987). Ordovician, Floian (Volkhov horizon B_{IV}); Maardu, Estonia.

Diagnosis. – Colonies erect, lenticular, frondose or reticulate; branches oval or lens-shaped in transversal section; mesotheca straight, without hyaline rods; autozooecia long, tubular, bending in exozone; diaphragms rare or absent; hemisepta absent; autozooecial apertures oval, arranged in alternating rows on the colony surface; low ridges between apertures bearing paurostyles present; exozonal tubes present; maculae lacking autozooecia and bearing paurostyles and exozonal tubes occurring.

Remarks. – *Prophyllodictya* Gorjunova, 1987 in Gorjunova & Lavrentjeva (1987) differs from *Phyllodictya* Ulrich, 1882 in absence of hyaline rods in mesotheca and presence of exozonal tubes.

Occurrence. – Lower Ordovician (Tremadocian)–Upper Ordovician (Katian); China, Estonia, Russia, Spain.

***Prophyllodictya intermedia* Gorjunova, 1987
in Gorjunova & Lavrentjeva (1987)**

Figure 16C–F, 17A–C

1987 *Prophyllodictya intermedia* Gorjunova; Gorjunova & Lavrentjeva, p. 47, pl. 5, fig. 1, text-figs 1–3.

1993 *Prophyllodictya intermedia* Gorjunova, 1987. – Gorjunova & Lavrentjeva, p. 38, pl. 1, figs 1, 2.

1996 *Prophyllodictya intermedia* Gorjunova, 1987. – Gorjunova, pl. 35, fig. 1.

Material. – Two samples GIT 852-4a–b and GIT 852-8a (three thin sections).

Description. – Erect colony consisting of flat branches, 2.75 mm wide and 1.20–1.25 mm thick. Mesotheca straight, 0.015–0.020 mm in thickness. Long, tubular autozooecia, sharply bending in inner exozone. Autozooecial diaphragms rare. Autozooecial apertures oval, arranged in 13 alternating rows. Paurostyles between apertures in one row, 0.025–0.040 mm in diameter. Locally exozonal tubes present, 0.02–0.03 mm in diameter.

Remarks. – The citation of this genus and species used in the literature is actually incorrect: *Prophyllodictya intermedia* Gorjunova, 1987 (see Gorjunova & Lavrentjeva 1993; Gorjunova 1996). There is no publication Gorjunova (1987). The genus and species were published in the mutual paper of Gorjunova & Lavrentjeva (1987), even if authored by Gorjunova alone.

Prophyllodictya intermedia Gorjunova, 1987 in Gorjunova & Lavrentjeva (1987) is similar to *P. putilovensis* Lavrentjeva, 1993 in Gorjunova & Lavrentjeva (1993) but differs from the latter in having widely spaced autozooecial apertures (ca. 2 per 2 mm distance along the branch vs. 4–5 in *P. putilovensis*).

Occurrence. – Floian, Lower Ordovician of Russia and Estonia. Obukhovo Fm., Kunda Stage, Darriwilian, Middle Ordovician; Putilovo quarry, Russia (present material).

***Cryptostomata* sp. indet.**

Figure 17D–I, 18A–F; Table 16

Material. – Single specimen GIT 537-4098a (one thin section).

Table 16. Descriptive statistics of *Cryptostomata* sp. indet. (one colony measured). Abbreviations as for Table 1.

	N	MIN	MAX	X	SD	CV
Aperture width, mm	20	0.11	0.20	0.15	0.025	16.61
Aperture spacing along branch, mm	20	0.47	0.75	0.62	0.091	14.78
Aperture spacing diagonally, mm	20	0.28	0.45	0.38	0.054	14.29
Vesicle diameter, mm	10	0.05	0.11	0.07	0.017	23.14

Description. – Reticulate colony composed of flat bifoliate branches anastomosing at regular intervals. Branches 3.3–3.8 mm wide. Fenestrules circular to oval, 2.3–2.5 mm wide and 2.7–3.6 mm long. Autozooecia arranged in 8–10 alternating rows on branches, short, polygonal in mid tangential section. Long distally curved hemisepta dividing autozooecial chamber present (Fig. 18D–F). Autozooecial apertures circular to oval. Paurostyles in outer laminated skeleton, arranged in 1–2 rows on low crests around autozooecial apertures, forming polygonal pattern on colony surface, 0.02–0.03 mm in diameter (Fig. 17G–I). Autozooecial wall in endozone 0.005–0.010 mm thick. Polygonal vesicles at the base of exozone present, covered by laminated skeleton. Maculae not observed.

Remarks. – The present specimen shows a unique morphology which does not allow any assignment: polygonal autozooecial chambers and rounded apertures, long curved hemisepta, vesicles and paurostyles. It resembles superficially the genus *Trepocryptopora* Yang, 1957 from the Lower Ordovician of China. However, the latter genus has no hemisepta and paurostyles, it possesses frondose colony instead of reticulate one in the present material. Furthermore, *Trepocryptopora* possesses open heterozooecia different to the vesicles of the present material, which are covered by laminated skeleton. The

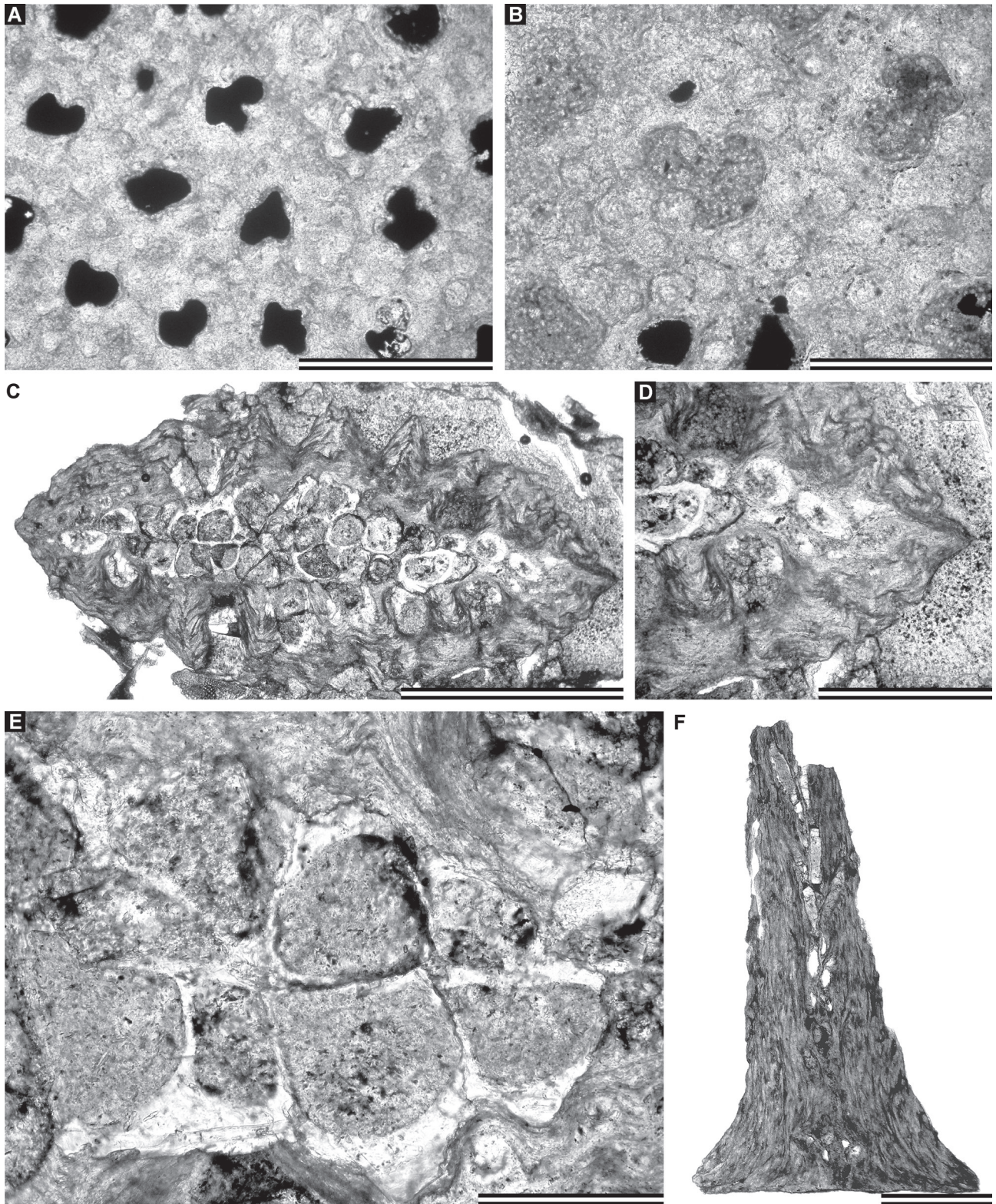
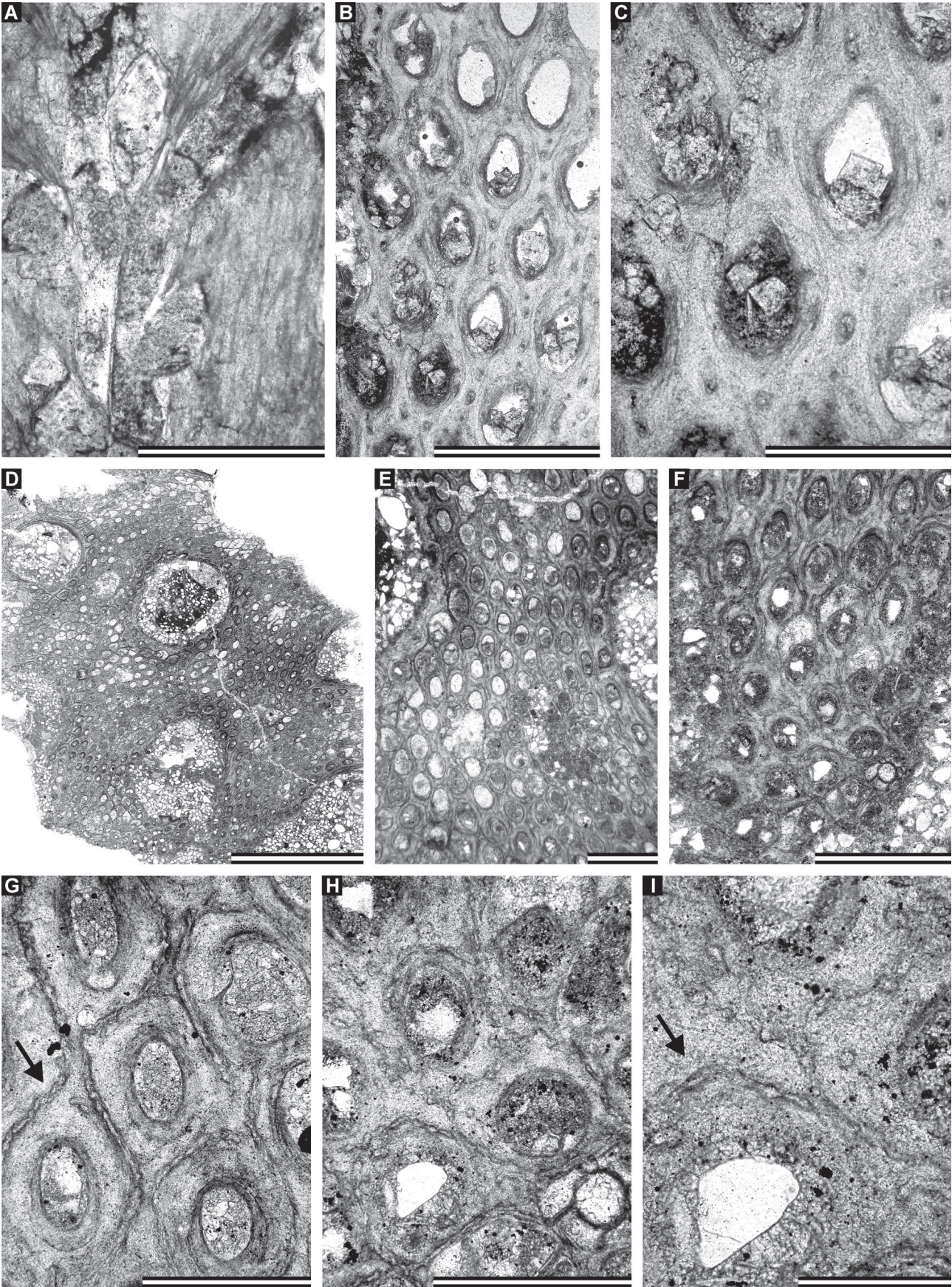


Figure 16. A–B – *Pakripora cavernosa* gen. et sp. nov., tangential section showing autozooeal apertures, acanthostyles, and mesozooeia in intermacular area, holotype GIT 537-2265g. • C–F – *Prophyllodictya intermedia* Gorjunova, 1987 in Gorjunova & Lavrentjeva (1987); C–E – branch transverse section, GIT 852-4a; F – longitudinal section through the basal part of the colony, GIT 852-8a. Scale bars: 1 mm (C, F), 0.5 mm (A, D), 0.2 mm (B, E).



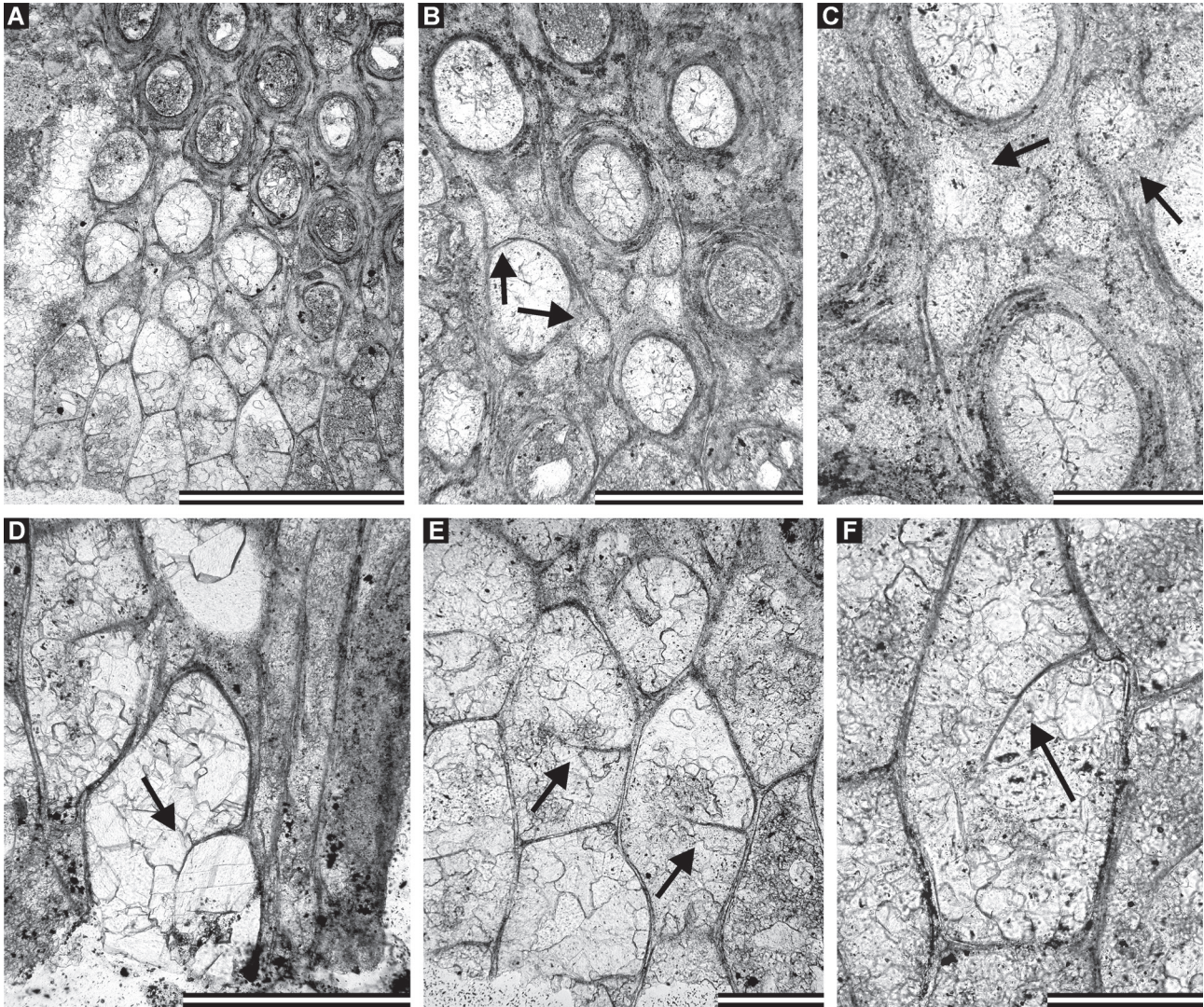


Figure 18. A–F – *Cryptostomata* sp. indet., GIT 537-4098a; A–C – tangential section showing autozooeceal apertures and vesicles (arrows); D–F – mid tangential section showing autozooeceal chambers with hemisepta (arrows). Scale bars: 1 mm (A), 0.5 mm (B, D), 0.2 mm (C, E, F).

present material shows some similarity to the genus *Phyllodictya* Ulrich, 1882 in presence and character of styles and in presence of vesicular skeleton. However, *Phyllodictya* has no long curved hemisepta and its autozooeceal chambers are oval in mid tangential section. The genus *Sibiredictya* Nekhoroshev, 1961 is similar in the colony shape, presence of styles and vesicular skeleton, but differs in absence of hemisepta.

Occurrence. – Kunda Stage, Darriwilian, Middle Ordovician; Paldiski, Estonia.

Discussion and conclusion

Described bryozoan fauna from the Kunda Stage (Darriwilian, Middle Ordovician) of Estonian and NW Russia contains 18 species which includes one cystoporate *Ceramopora* cf. *magnicellularis* Männil & Pushkin in Pushkin, 1990, eight esthonioporates *Dianulites collucatus* Pushkin, 2001 in Pushkin & Popov (2001), *D. pakriensis* sp. nov., *Esthoniopora communis* Bassler, 1911, *Revalotrypa gibbosa* (Bassler, 1911), *R. papillaris* (Modzalevskaya, 1953), *Orbipora indenta* Bassler, 1911,

Figure 17. A–C – *Prophyllodictya intermedia* Gorjunova, 1987 in Gorjunova & Lavrentjeva (1987), GIT 852-4b; A – longitudinal section; B, C – tangential section showing autozooeceal apertures and paurostyles. • D–I – *Cryptostomata* sp. indet., GIT 537-4098a; D – tangential section showing colony shape with oval fenestrules; E–I – tangential section showing autozooeceal apertures, paurostyles and crests around autozooeceal apertures (arrows). Scale bars: 5 mm (D), 1 mm (B, E, F), 0.5 mm (A, C, G, H), 0.2 mm (I).

O. acanthophora Bassler, 1911, and *O. aff. distincta* (Eichwald, 1829); six trepostomes *Dittopora sokolovi* Modzalevskaya, 1953, *D. annulata* (Eichwald, 1860), *D. aff. annulata* (Eichwald, 1860), *Hemiphragma rotundatum* Bassler, 1911, *Mesotrypa bystrovi* Modzalevskaya, 1953, *Sonninopora* sp., and *Pakripora cavernosa* gen. nov., sp. nov.; and two cryptostomes *Prophyllodictya intermedia* Gorjunova, 1987 in Gorjunova & Lavrentjeva (1987) and *Cryptostomata* sp. indet.

This species composition is quite endemic within the Baltic region. Genera *Esthoniopora* Bassler, 1911, *Orbipora* Eichwald, 1856 and *Dittopora* Dybowski, 1877 are mainly restricted to the Baltosandian region, whereas *Revalotrypa* Bassler, 1952 and *Prophyllodictya* Gorjunova, 1987 in Gorjunova & Lavrentjeva (1987) are also known from the Lower Ordovician of China (Yang 1957, Xia *et al.* 2007, Ma *et al.* 2015). Genera *Ceramopora* Hall, 1851 in Silliman, Silliman & Dana (1851), *Hemiphragma* Ulrich, 1893 and *Mesotrypa* Ulrich, 1893 show cosmopolitan distribution during the Middle Ordovician.

The studied fauna shows moderate diversity of colony forms: massive, branched ramose, rod-(club-) shaped, and lenticular (frondose and reticulate).

Massive colonies of various configuration are developed by nine species. They are mainly composed of subsequently overgrown encrusting sheets (*Ceramopora* cf. *magnicellularis*, *Dianulites collucatus*, *Esthoniopora communis*, *Revalotrypa gibbosa*, *Orbipora indenta*, *O. acanthophora*, *Hemiphragma rotundatum*). Forming of subcolonies is usual in *Ceramopora* cf. *magnicellularis*, *Dianulites collucatus*, and *Revalotrypa gibbosa* (Fig. 6B). *Mesotrypa bystrovi* is the only massive species which shows neither secondary overgrowths nor subcolonies (Fig. 13D). The species *O. aff. distincta* (Eichwald, 1829) is represented by small hemispheric colony which lacks any overgrowth, apparently due to its small size (Fig. 8F).

Revalotrypa papillaris has a unique colony which is rod- or club-shaped (Fig. 6G, H).

Dittopora species are all ramose, quite robust, with branch diameters ranging from 1.95 to 4.9 mm. The species *Dianulites pakriensis* and *Pakripora cavernosa* have both robust branched colonies (with branch diameters 19–28 mm in *Dianulites pakriensis* and 11.5–17.0 mm in *Pakripora cavernosa*). Secondary overgrowths are usual in the branched species.

The single specimen of *Sonninopora* sp. shows apparently branched colony as well. However, the true configuration of that colony is not clear in the present material (Fig. 14A).

Both cryptostomes (ptilodictyine) species are lenticular, with zooecia budding from the median lamina called mesotheca (Fig. 16C–E). Whereas *Prophyllodictya intermedia* possesses frondose colonies, the single

specimen of *Cryptostomata* sp. indet. represents reticulate colony with large oval fenestrules (Fig. 17D). Mesotheca is not seen in this specimen, however, as far as only tangential section is available.

Several species developed special structures called maculae. Those are areas on the colony surface differently composed as the rest of the colony. They are often composed of heterozooecia (e.g. *Dianulites pakriensis*, Fig. 5A, B), or heterozooecia and acanthostyles (e.g. *Dittopora* aff. *annulata*, Fig. 12E, or *Pakripora cavernosa*, Fig. 15G, H). Maculae can be positioned on the level of the colony surface, but usually they are either depressed or elevated. In the last case they are called monticulae. These structures serve mainly as sites of excurrent chimneys, with which the filtered water is expelled from the colony surface (e.g. Banta *et al.* 1974; Taylor 1975, 1979, 1999; Cook 1977; Winston 1978, 1979; Lidgard 1981). In *Dittopora annulata* and *D. aff. annulata* the maculae are transversally annular and depressed below the colony surface, whereas they are rounded and slightly elevated above the colony surface in *Pakripora cavernosa*. According to observations on modern bryozoans, large maculate species are able to determine their own water flow relatively independent from ambient conditions (e.g. Schopf *et al.* 1980). Development of maculae is regarded being an important adaption in bryozoan evolution (e.g. McKinney 1986, McKinney & Jackson 1989).

The dominance of massive (9) and erect (9) species as well as absence of encrusting bryozoans suggest rather middle shelf conditions, with moderate to low water energy and quite high sedimentation rates (e.g. Nelson *et al.* 1988, Hageman *et al.* 1997, Amini *et al.* 2004). Similar setting for the distribution of massive bryozoan colonies was observed in the Ordovician of Öland (Spjeldnaes 1996) or Silurian of Gotland (Brood 1984). Development of subcolonies and secondary overgrows point to the episodic sedimentation stops (e.g. Spjeldnaes 1996).

In addition, bryozoan colonies from the studied fauna often contain traces of bioerosion and bioclaustration. They mainly belong to *Trypanites* (Figs 3A; 13D, E), some others cannot be identified with certainty (Olev Vinn, personal communication 2021). Unknown bioclaustration is observed in the colony of *Orbipora acanthophora* (Fig. 7G).

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