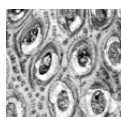


Late Ordovician (Sandbian) bryozoans and their depositional environment, Furuberget Formation, Mjøsa District, Oslo Region, Norway

ANDREJ ERNST & HANS ARNE NAKREM



A stenolaemate bryozoan fauna from the Late Ordovician (Sandbian) Furuberget Formation of the Mjøsa district, southern Norway contains 10 species. One species belongs to the Order Cyclostomata: *Corynotrypa delicatula* (James, 1878). Five species belong to the Order Trepostomata: *Parvohallopora ramosa* (d'Orbigny, 1850), *Mesotrypa orientalis* Bassler, 1911, *Mesotrypa egena* Bassler, 1911, *Dekayia sugarensis* Ross, 1969, and *Eridotrypa aedilis* (Eichwald, 1855). Four species belong to the Suborder Ptilodictyina of the Order Cryptostomata: *Graptodictya perelegans* (Ulrich, 1878), *Oanduellina leuchtenbergi* Pushkin, 1977, *Phaenopora similis* Nekhoroshev, 1961, and *Ptilodictya capillaris* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993). The bryozoan faunal association is similar to that found in time-equivalent Baltoscandian and Laurentian units elsewhere. Their known biostratigraphic range is generally Late Ordovician (Sandbian–Katian). • Key words: Late Ordovician, Bryozoa, Norway, taxonomy, palaeobiogeography.

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The Furuberget Formation is widely distributed in the Mjøsa district in the northern part of the Oslo Region (Fig. 1A). Here the base of the Furuberget Formation is in a gradational sequence from the grey shales of the underlying Hovinsholm Formation to green/grey shales with limestones and calcareous siltstones. The age of the unit, as based on brachiopods and trilobites has recently been refined as Sandbian by Bergström *et al.* (2011) based on $\delta^{13}\text{C}$ chemostratigraphy of the overlying Mjøsa Formation (Fig. 1B). The fauna of the Furuberget Formation is, in addition to bryozoans, characterized by brachiopods, trilobites and various algae, *e.g.* *Coelosphaeridium* (Owen *et al.* 1990).

Depositional environment

The bryozoan samples investigated herein are fossiliferous and represent organic rich peloidal floatstone to rudstone with significant siliciclastic components (Fig. 2A). Abundant bryozoans, trilobites, brachiopods, gastropods, echinoderms (pelmatozoans) and calcareous algae (*Coelosphaeridium* sp.) are common in investigated thin sections.

Skeletal remains of some bryozoans, brachiopods and trilobites are locally silicified (Fig. 2C). Trilobites, probably of the genus *Chasmops* are represented by large forms, often having large schizochroal eyes (Fig. 2B–D).

The matrix consists of different components, among them the most important are calcite (sparite), quartz and fecal peloids. Sparitic calcite occurs between other components and in former voids (*e.g.* bryozoan chambers). Quartz grains are irregularly polygonal, 0.02–0.08 mm in diameter. The peloids are represented by rounded to oval micritic grains, 0.03–0.06 mm in diameter (Fig. 4B–F). The grains show mainly homogenous internal structure.

Based on the faunal components and sedimentary information the depositional environment of the investigated part of the Furuberget Formation can be interpreted as a slightly deepened basin within the photic zone (algae and trilobites with large eyes), and below the storm wave base. The high portion of siliciclastic components infers a placement of this basin not far away from land or a delta system. Bryozoans, brachiopods and pelmatozoans are suspension feeders which in turn indicates that the environment in which the fauna derives from was nutrition rich, mesotrophic, or even eutrophic. The source of the fecal

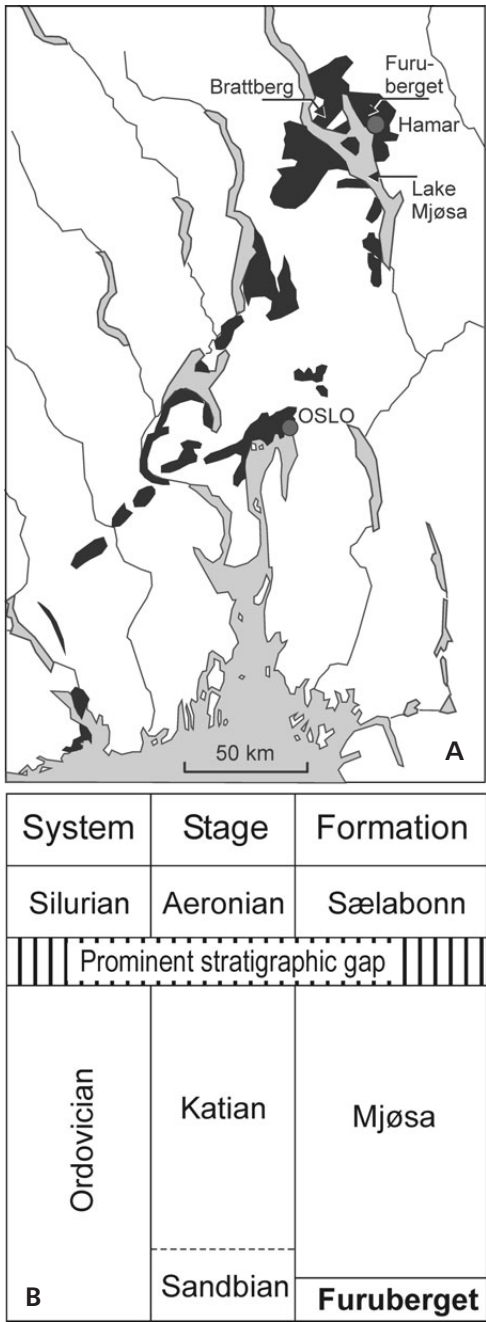


Figure 1. Locality map (A) and stratigraphy (B).

peloids is not fully understood. According to their size, their producers can be brachiopods or pelmatozoans, because they appear to be too large for bryozoans and too small for trilobites. Gastropods are not present in large

numbers and it seems unlikely that they could produce such amount of fecal peloids.

Material and methods

All bryozoan samples come from the Furuberg locality (UTM WGS84 32V 610 6743), except for the *Corynotrypa delicatula* specimen which is from Brattstad (UTM WGS84 32V 598 6746). The investigated bryozoans were studied from thin sections using a transmitted light binocular microscope. Sixty six oriented and non-oriented thin sections were used. The *Corynotrypa delicatula* specimen was identified from in imprint in a gastropod steinkern. The material is housed at the Natural History Museum (Geology), Oslo, under numbers PMO 221.294 to 221.370.

Morphological character terminology is adopted from Anstey & Perry (1970) for trepostomes, Hageman (1993) for cryptostomes and Taylor & Wilson (1994) for *Corynotrypa delicatula*. The following morphologic characters were measured for statistical use:

Branch width, branch thickness, exo- (endo-) zone width, autozooeal aperture width, autozooeal aperture spacing (along/across branch), acanthostyle diameter, wall thickness in exozone, and macular diameter (spacing), autozooeal diaphragm spacing, meso- (exila-) zooecia width, meso- (exila-) zooecial diaphragm spacing.

The spacing of structures was measured as the distance between centres. Additional quantitative characters include the number of mesozooecia, exilazooecia and acanthostyles surrounding each autozooeal aperture. Statistics were summarized using arithmetic mean, sample standard deviation, coefficient of variation, and minimum and maximum values.

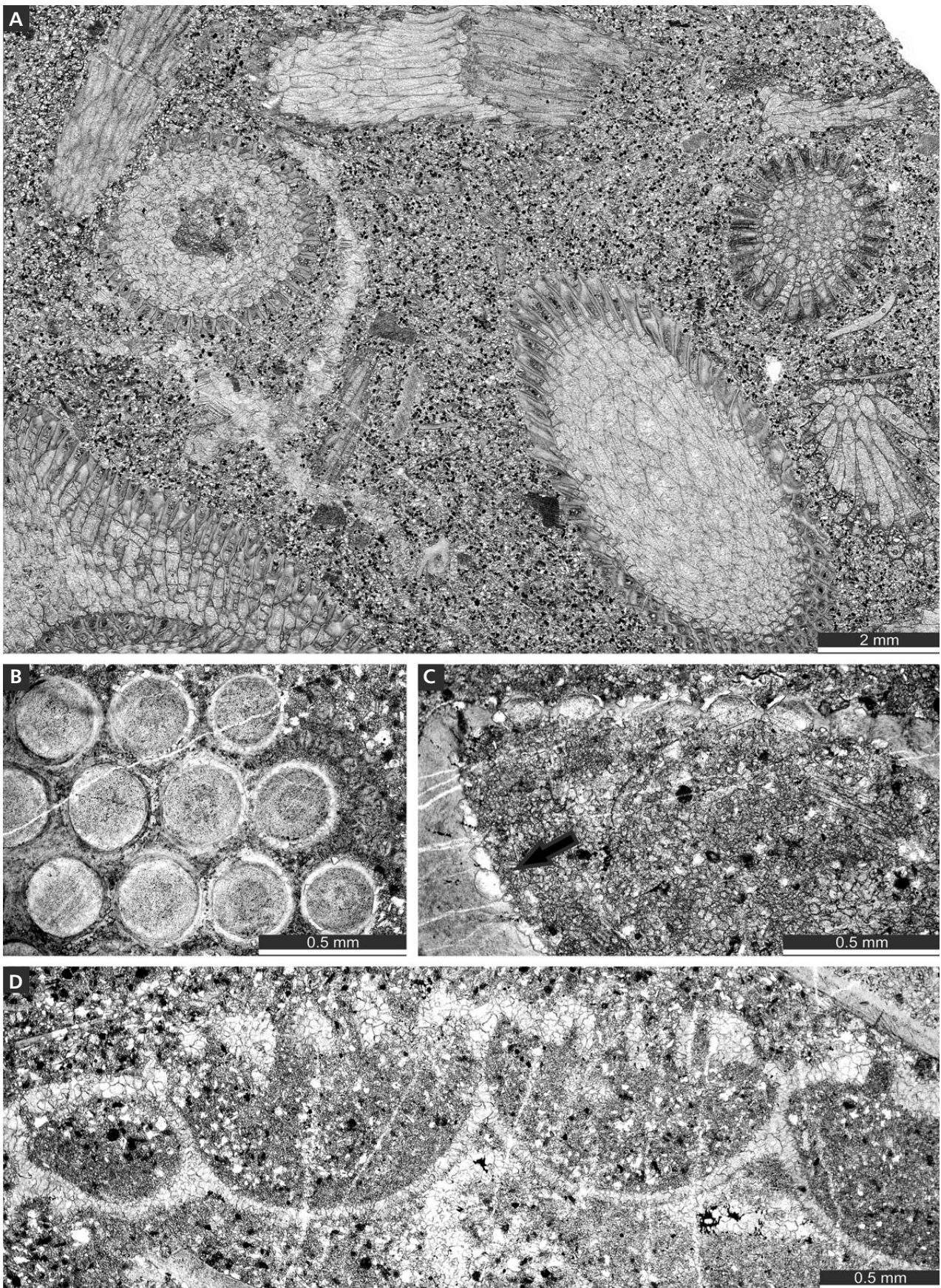
Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Cyclostomata Busk, 1852
Suborder Paleotubuliporina Brood, 1973
Family Corynotrypidae Dzik, 1981

Genus *Corynotrypa* Bassler, 1911

Type species. – *Hippothoa delicatula* James, 1878. Upper Ordovician; North America.

Figure 2. A – floatstone with branched colonies of trepostome bryozoans [*Parvohallopora ramosa* (d'Orbigny, 1850), *Eridotrypa aedilis* (Eichwald, 1855)], PMO 221.304. • B – tangential section of schizochroal trilobite eye, PMO 221.362. • C – longitudinal section of the trilobite carapace with schizochroal eye (arrow – partial silicification), PMO 221.340. • D – longitudinal section of calcareous alga *Coelosphaeridium* sp., PMO 221.348.



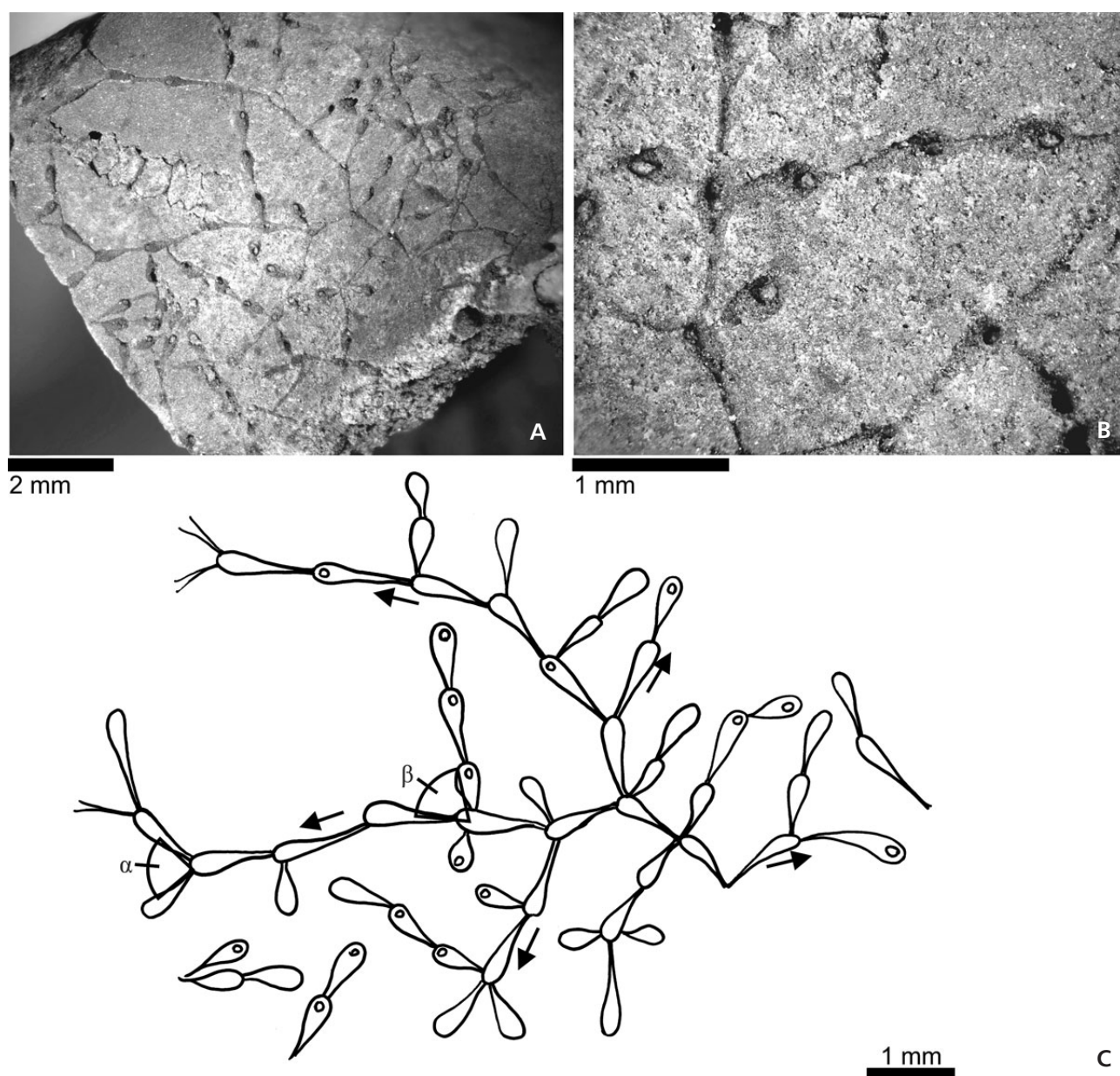


Figure 3. *Corynotrypa delicatula* (James, 1878), PMO 221.354. • A, B – imprints (natural casts) of *Corynotrypa delicatula* in a silt steinkern. • C – drawing of part of a *Corynotrypa delicatula* colony. Arrows indicate colony growth directions. α – bifurcation angle, β – lateral ramification angle.

Diagnosis. – See Taylor & Wilson, 1994.

Occurrence. – Ordovician–Permian; worldwide.

***Corynotrypa delicatula* (James, 1878)**

Figure 3A–C, Table 1

Material. – PMO 221.354. Single colony preserved as cast in a steinkern of an unknown gastropod.

Description. – Colony encrusting uniserial, runner-like

colony. Autozooecia monomorphic but astogenetically variable moderately long and slender, with relatively short and narrow proximal portion. Observed range of length 0.60 to 1.15 mm, width 0.20–0.26 mm. Exterior wall not observed (dissolved). Branches divide at intervals by bifurcation, and by lateral ramifications of little variation in angles, averaging 75 to 78°. Apertures rounded, 0.06–0.10 mm in diameter. Ancestrula not observed.

Comparison. – *Corynotrypa delicatula* is distinguished from *C. inflata* (James, 1878) and other species of *Cory-*

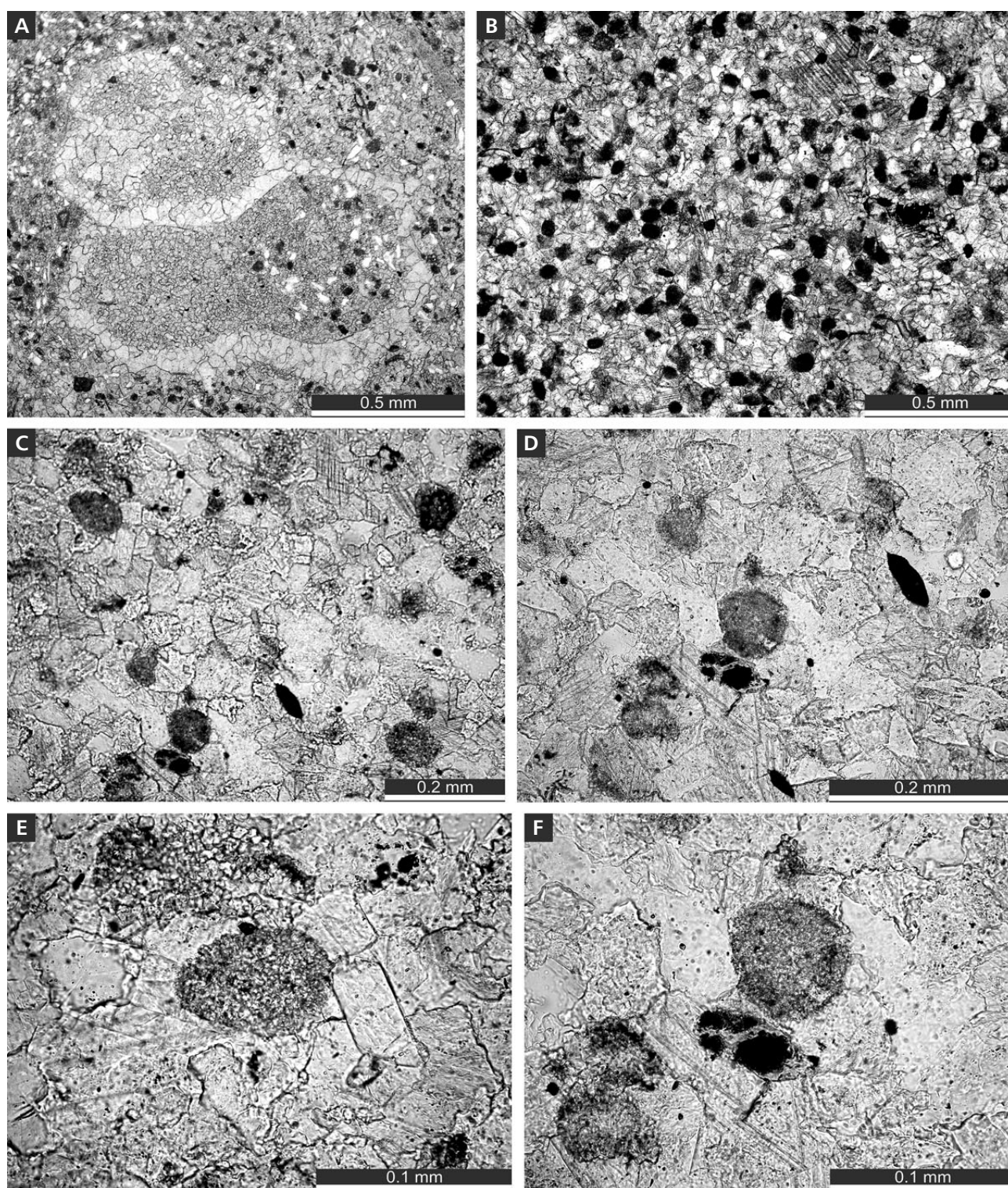


Figure 4. A – gastropod shell, PMO 221.346. • B, C – matrix containing quartz grains, fecal pellets and sparite calcite, PMO 221.304. • D–F – fecal pellets, PMO 221.298.

notrypa by the presence of very long, slender zooids and by the development of secondary zones of astogenetic change (Fig. 5).

Occurrence. – Sandbian–Katian, Upper Ordovician; USA. Sandbian; Estonia. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

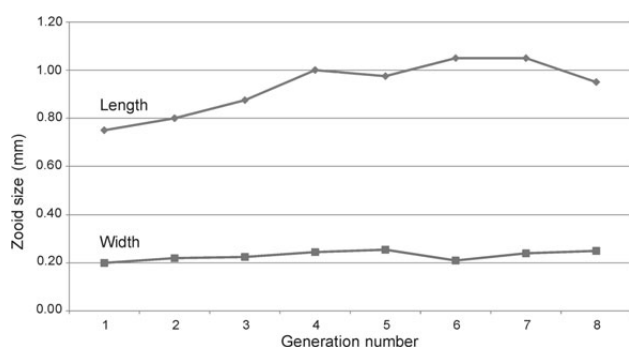


Figure 5. Plot showing changes in zooid length and zooid width along lateral branches of *Corynotrypa delicatula*. The secondary zone of astogenetic change for zooid length is significantly increasing whereas zooidal width shows little change.

Table 1. Measurements of *Corynotrypa delicatula* (James, 1878). Abbreviations: N – number of measurements; X – mean; SD – standard deviation; CV – coefficient of variation; MIN – minimal value; MAX – maximal value.

	N	X	SD	CV	MIN	MAX
Zooid length, mm	24	0.85	0.161	18.82	0.60	1.15
Zooid width, mm	24	0.23	0.021	9.02	0.20	0.26
Aperture diameter	16	0.09	0.013	15.28	0.06	0.10
Bifurcation angle	8	75.6	6.286	8.31	67.0	83.9
Lateral ramification angle	10	77.6	10.463	13.48	57.0	88.2

Order Trepostomata Ulrich, 1882
Suborder Halloporina Astrova, 1965
Family Halloporidae Bassler, 1911

Genus *Parvohallopora* Singh, 1979

Type species. – *Monticulipora ramosa* d'Orbigny, 1850.
Upper Ordovician; North America.

Diagnosis. – Ramose colonies. Colonial surface smooth or with regularly spaced monticules. Exozone well developed. Autozooeceia intersecting colonial surface at sharp angles, polygonal in transverse section in endozone, becoming polygonal or circular to subcircular in exozone. Autozooeceal diaphragms planar to curved, rarely cystoidal, usually present in endozone, sometimes absent in exozone. Mesozooecia abundant between most autozooeceia, rounded to subrounded or rarely polygonal in transverse section, having diameters less than a half of autozooeceia. Mesozoeceal diaphragms planar to curved.

Comparison. – *Parvohallopora* Singh, 1979 differs from *Hallopora* Bassler, 1911 by its absence of mural spines, smaller and more abundant mesozooecia, polygonal shape of autozooeceal transverse section in endozones, rare cystoidal diaphragms, and wall microstructure with U to V shaped laminae.

Occurrence. – Middle to Upper Ordovician, North America and Europe.

Parvohallopora ramosa (d'Orbigny, 1850)

Figures 6A–H, 7A, Table 2

Material. – PMO 221.304, 221.320, 221.330–332, 221.335–336, 221.338–339, 221.341, 221.345–350.

Description. – Ramose colonies, branch diameter 2.9 to 6.2 mm. Exozone 0.38–1.64 mm wide, endozone 2.14 to 2.92 mm wide. Autozooeceia long, polygonal in transverse section in endozone, growing for a long distance in endozone, then bending gently and intersecting colonial surface at angles of 80–90°. Autozooeceal apertures oval to polygonal. Basal diaphragms thin, straight, rare to common in endozones; thick, straight to curved, rarely cystoidal, common to abundant in exozones. Mural spines absent. Mesozooecia abundant, 3–10 surrounding each autozooeceal aperture, moderately large to large, polygonal to rounded, originating in the outer endozone, usually closed by skeleton, possessing numerous diaphragms. Mesozoeceal diaphragms straight, thin in proximal parts becoming thick near colony surface. Styles absent. Autozooeceal walls straight, 0.005 to 0.010 mm thick in endozone; 0.025–0.100 mm thick, with distinct reversed U to V shaped structure in exozone.

Comparison. – *Parvohallopora ramosa* (d'Orbigny, 1850) differs from *P. onealli* (James, 1878) in having thicker branches [branch diameter in studied material 2.9–6.2 mm, 3.3–9.2 mm in type material (Singh 1979, p. 231) vs. 1.2–2.4 mm (Karklins 1984, p. 73) and 2.28–2.80 mm (Ernst & Key 2007, p. 386) in *P. onealli*]. Furthermore, autozooeceia in *Parvohallopora ramosa* are oriented at higher angle than those in *P. onealli* (80–90° vs. 25–35°). *Parvohallopora ramosa* is also similar to *P. nodulosa* (Nicholson, 1874) from the Upper Ordovician of USA, but differs from it in having abundant diaphragms.

Occurrence. – Upper Ordovician; USA (see Singh 1979,

Figure 6. *Parvohallopora ramosa* (d'Orbigny, 1850). • A – branch transverse section, short detail, PMO 221.348. • B – branch transverse section, short detail, PMO 221.304. • C – longitudinal section, short detail, PMO 221.329. • D – longitudinal section, short detail, PMO 221.327. • E, F – longitudinal section, short detail, PMO 221.329. • G – branch transverse section showing mesozooecium, PMO 221.348. • H – tangential section, short detail, PMO 221.328.

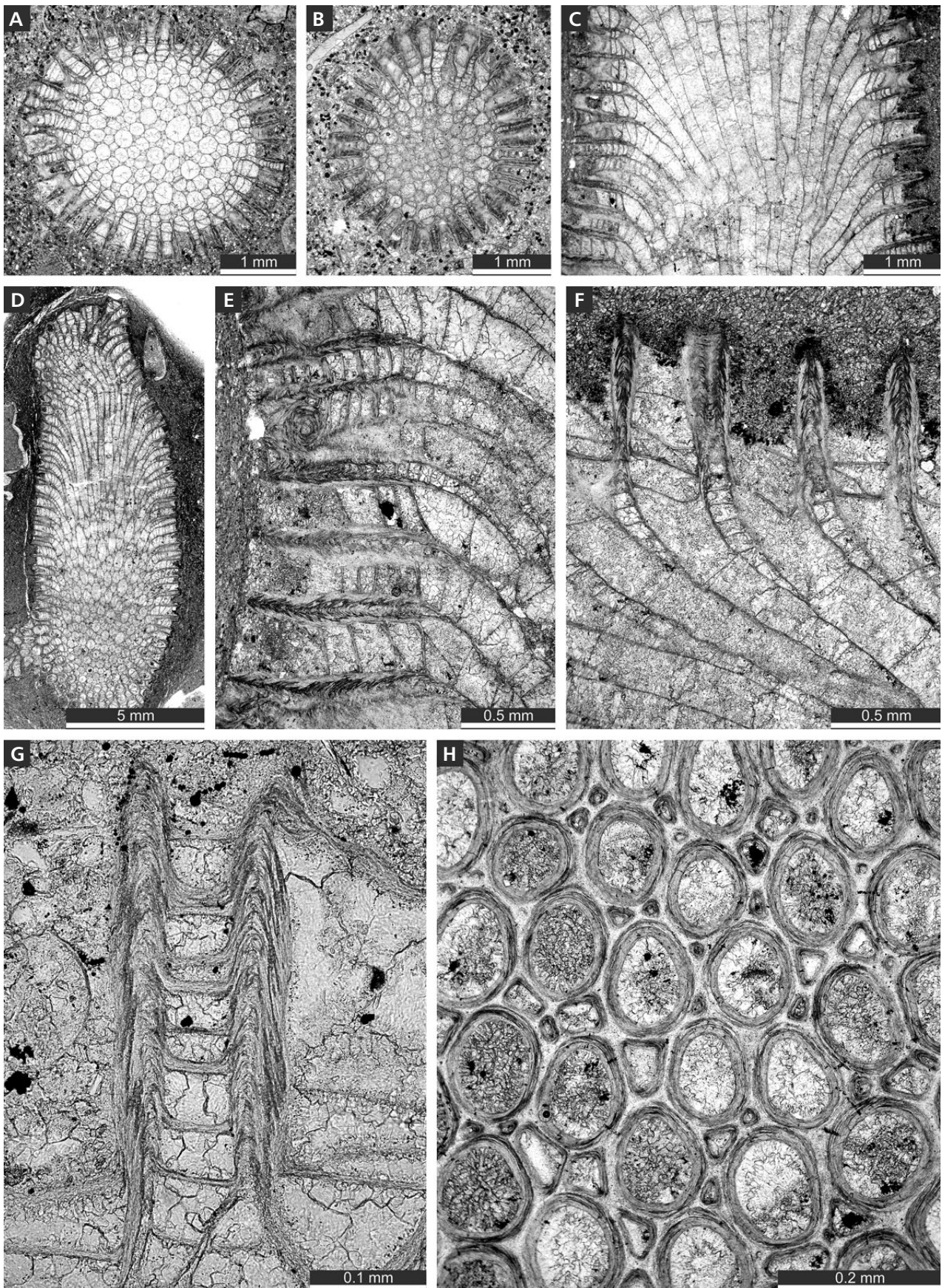


Table 2. Measurements of *Parvohallopora ramosa* (d'Orbigny, 1850). Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	11	4.35	1.146	26.37	2.90	6.20
Exozone width, mm	11	0.77	0.328	42.58	0.38	1.64
Aperture width, mm	35	0.20	0.026	13.03	0.14	0.24
Aperture spacing, mm	35	0.29	0.025	8.46	0.25	0.35
Aperture width, mm (macular)	12	0.29	0.024	8.26	0.26	0.34
Aperture spacing, mm (macular)	12	0.42	0.037	8.79	0.36	0.50
Mesozoecia width, mm	35	0.079	0.025	30.98	0.035	0.13
Mesozoecia per aperture	35	6.6	1.646	24.84	3.0	10.0
Autozoecial diaphragms spacing, mm	35	0.14	0.044	31.79	0.08	0.29
Mesozoecial diaphragms spacing, mm	35	0.06	0.016	28.46	0.03	0.10
Exozonal wall thickness, mm	35	0.055	0.020	36.76	0.025	0.10

Table 3. Measurements of *Mesotrypa orientalis* Bassler, 1911. Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	45	0.26	0.022	8.60	0.20	0.31
Aperture spacing, mm	45	0.29	0.030	10.34	0.25	0.39
Mesozoecia width, mm	45	0.071	0.021	29.29	0.025	0.130
Mesozoecia per aperture	45	5.2	0.894	17.20	2.0	6.0
Mesozoecial diaphragms spacing, mm	45	0.048	0.010	21.39	0.023	0.068
Exozonal wall thickness, mm	20	0.021	0.007	33.96	0.010	0.035

pp. 228, 229, for complete synonymy). Furuberget Formation, Upper Ordovician (Sandbian); Norway.

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. Autozoecial apertures polygonal or rounded. Walls thin, longitudinally laminated, indistinctly separated. Diaphragms planar, sloped, curved, and funnel-shaped. Mesozoecia abundant, budding from base of

colony. Acanthostyles may be large, growing from the base of colony, or small, visible at colony surface.

Comparison. – *Mesotrypa* Ulrich, 1893 differs from the most similar genus *Diazipora* Vinassa de Regny, 1921 by having acanthostyles and larger mesozoecia.

Occurrence. – Middle Ordovician to Lower Silurian; world-wide.

Mesotrypa orientalis Bassler, 1911

Figures 7B–I, 8A, B, Table 3

1911 *Mesotrypa discoidea orientalis* Bassler, pp. 196–198, text-fig. 106.

Material. – PMO 221.315, 221.317, 221.333, 221.334, 221.335, 221.337, 221.339–221.340, 221.341–221.343, 221.345, 221.350, 221.351, 221.353, 221.355–221.358, 221.360–221.362, 221.365, 221.367, 221.369.

Description. – Discoidal colonies with short endozones, 0.8–3.5 mm thick. Secondary overgrowths not observed. Autozoecia bending gently from epitheca, radiating from colony centre to periphery. Autozoecial apertures polygonal. Autozoecial diaphragms abundant, thin, planar or curved, often cystoidal, rare to absent in the outermost parts of autozoecia. Mesozoecia common, 2–6 surrounding each autozoecial aperture, polygonal in transverse section, originating at the base of colony, beaded, bearing straight closely spaced diaphragms. In deeper sections six mesozoecia are arranged in regular hexagonal pattern around autozoecia. Autozoecial walls finely laminated, 0.005 to 0.010 mm thick in endozone, 0.010–0.035 mm thick in exozone. Secondary cingulum commonly developed, 0.005–0.010 mm thick, with lamination parallel to autozoecial wall surface. Mural spines common, originating in cingulum, curved proximally. Acanthostyles indistinct, spine-like, positioned in junctions between apertures. Distinct cluster of larger autozoecia in centre of the colony present, 1.05–1.26 mm in diameter.

Comparison. – *Mesotrypa orientalis* Bassler, 1911 is similar to *M. raritabulata* Modzalevskaya, 1953, from the Upper Ordovician (Sandbian) of NW Russia, but differs in having less abundant mesozoecia (2–6 vs. 6–8 in *M. raritabulata*).

Figure 7. A – *Parvohallopora ramosa* (d'Orbigny, 1850), tangential section, short detail, PMO 221.328. • B–I – *Mesotrypa orientalis* Bassler, 1911. • B, C – transverse section of the colony, short detail, PMO 221.345. • D – transverse section of the colony, short detail, PMO 221.356. • E, F – tangential section showing central cluster of zooecia, PMO 221.341. • G, H – tangential section showing autozoecial apertures and mesozoecia, PMO 221.315. • I – tangential section showing autozoecial apertures, mesozoecia and acanthostyles, PMO 221.339.

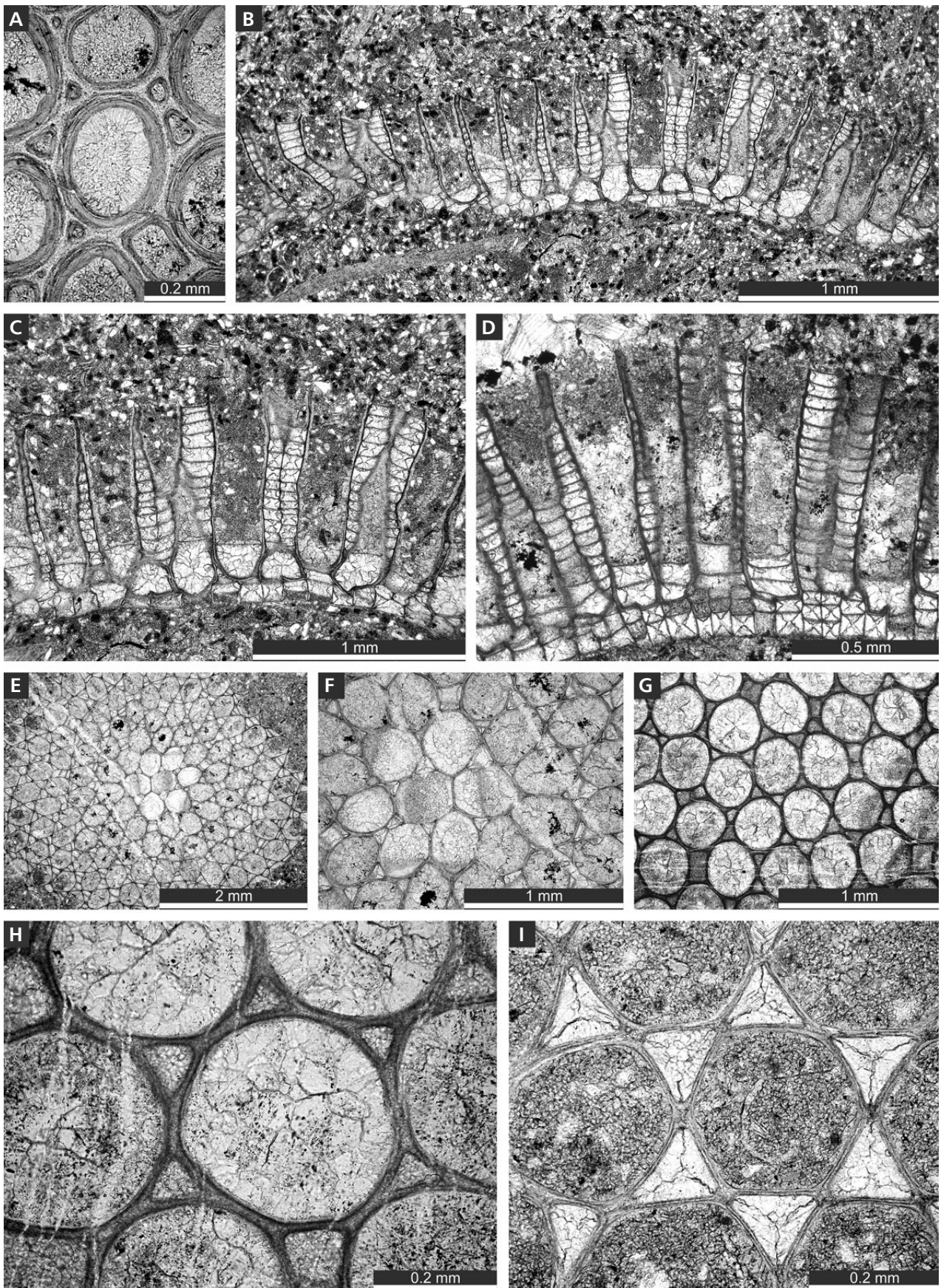


Table 4. Measurements of *Mesotrypa egena* Bassler, 1911. Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	40	0.30	0.022	7.17	0.25	0.36
Aperture spacing, mm	40	0.35	0.028	7.96	0.30	0.41
Mesozooecia width, mm	40	0.07	0.019	26.87	0.04	0.14
Mesozooecia per aperture	40	4.2	1.107	26.51	2.0	6.0
Mesozooecial diaphragms spacing, mm	40	0.040	0.012	31.24	0.015	0.065
Exozonal wall thickness, mm	40	0.03	0.007	21.95	0.02	0.05
Autozoecial diaphragms spacing, mm	40	0.12	0.060	49.43	0.05	0.31

Occurrence. – Jövi Stage, Upper Ordovician (Sandbian); Estonia. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

Mesotrypa egena Bassler, 1911

Figure 8C–I, Table 4

1911 *Mesotrypa egena* Bassler, pp. 198, 199, text-fig. 10.

Material. – PMO 221.314, 221.333, 221.339, 221.340, 221.345, 221.346, 221.348–221.349, 221.352, 221.353, 221.358, 221.366.

Description. – Discoidal colonies with short endozones, 2.8–5.2 mm thick. Secondary overgrowths common, 0.75–1.90 mm thick. Autozoecia bending gently from epitheca, radiating from colony centre to periphery. Autozoecial apertures polygonal. Autozoecial diaphragms abundant, thin, planar or curved, often cystoidal, rare to absent in the outermost parts of autozoecia. Mesozooecia common, 2–6 surrounding each autozoecial aperture, polygonal in transverse section, originating at the base of colony, beaded, bearing straight closely spaced diaphragms. Autozoecial walls finely laminated, 0.02 to 0.05 mm thick. Secondary cingulum often developed, 0.005 to 0.015 mm thick, with lamination parallel to autozoecial wall surface. Mural spines common, originating in cingulum, curved proximally. Acanthostyles indistinct, spine-like, positioned in junctions between apertures. Maculae not observed.

Comparison. – *Mesotrypa egena* Bassler, 1911 is similar to *M. echinata* Ulrich & Bassler, 1904 from the Upper

Ordovician (Trentonian) of USA, but differs in having indistinct acanthostyles instead of large ones in *M. echinata*. *Mesotrypa egena* is also similar to *M. infida* (Ulrich, 1886) from the Upper Ordovician (Trentonian) of USA but differs from it in having indistinct acanthostyles. *Mesotrypa egena* Bassler, 1911 differs from *M. orientalis* Bassler, 1911 (present paper) in having larger and wider spaced autozoecial apertures (average aperture width 0.30 mm vs. 0.26 mm in *M. orientalis*; average aperture spacing 0.35 mm vs. 0.29 mm in *M. orientalis*).

Occurrence. – Keila Stage, Upper Ordovician (Sandbian); Estonia. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

Family Heterotrypidae Ulrich, 1890

Genus *Dekayia* Milne-Edwards & Haime, 1851

Type species. – *Dekayia aspera* Milne-Edwards & Haime, 1851. Upper Ordovician (Cincinnatian); North America.

Diagnosis. – Ramose, encrusting or massive colonies. Maculae generally low or flush with the colonial surface and can have megazooecia, slightly larger acanthostyles, and a central cluster of mesozooecia, which is subsolid in some species. Autozoecia are generally angular or subangular in transverse section. Autozoecial walls are characteristically undulatory to crenulated. In exozones individual zooecial walls irregular and thick. Diaphragms commonly absent in inner endozone and either distantly and irregularly spaced or lacking in the outer endozone and the exozone. Mesozooecia rare in intermonticular areas and commonly absent. They consist of series of beaded chambers, visible in some longitudinal and transverse sections. Tubular diaphragms do occur in mesozooecia but are extremely rare. Acanthostyles occur in all species, can originate throughout endozone and inner exozone and some terminate below colony surface.

Comparison. – *Dekayia* Milne-Edwards & Haime, 1851 differs from *Heterotrypa* Nicholson, 1879 by having fewer mesozooecia and usually larger acanthostyles.

Occurrence. – Middle to Upper Ordovician; North America, Europe, India, China.

Figure 8. A, B – *Mesotrypa orientalis* Bassler, 1911, tangential section showing autozoecial apertures, mesozooecia and mural spines (arrows), PMO 221.333. • C–I – *Mesotrypa egena* Bassler, 1911. • C – longitudinal section, short detail PMO 221.346; D – longitudinal section, short detail, PMO 221.315. • E–G – longitudinal section showing autozoecial chambers with diaphragms, cingulum and mural spines, PMO 221.346. • H–I – tangential section showing autozoecial apertures and mesozooecia, PMO 221.358.

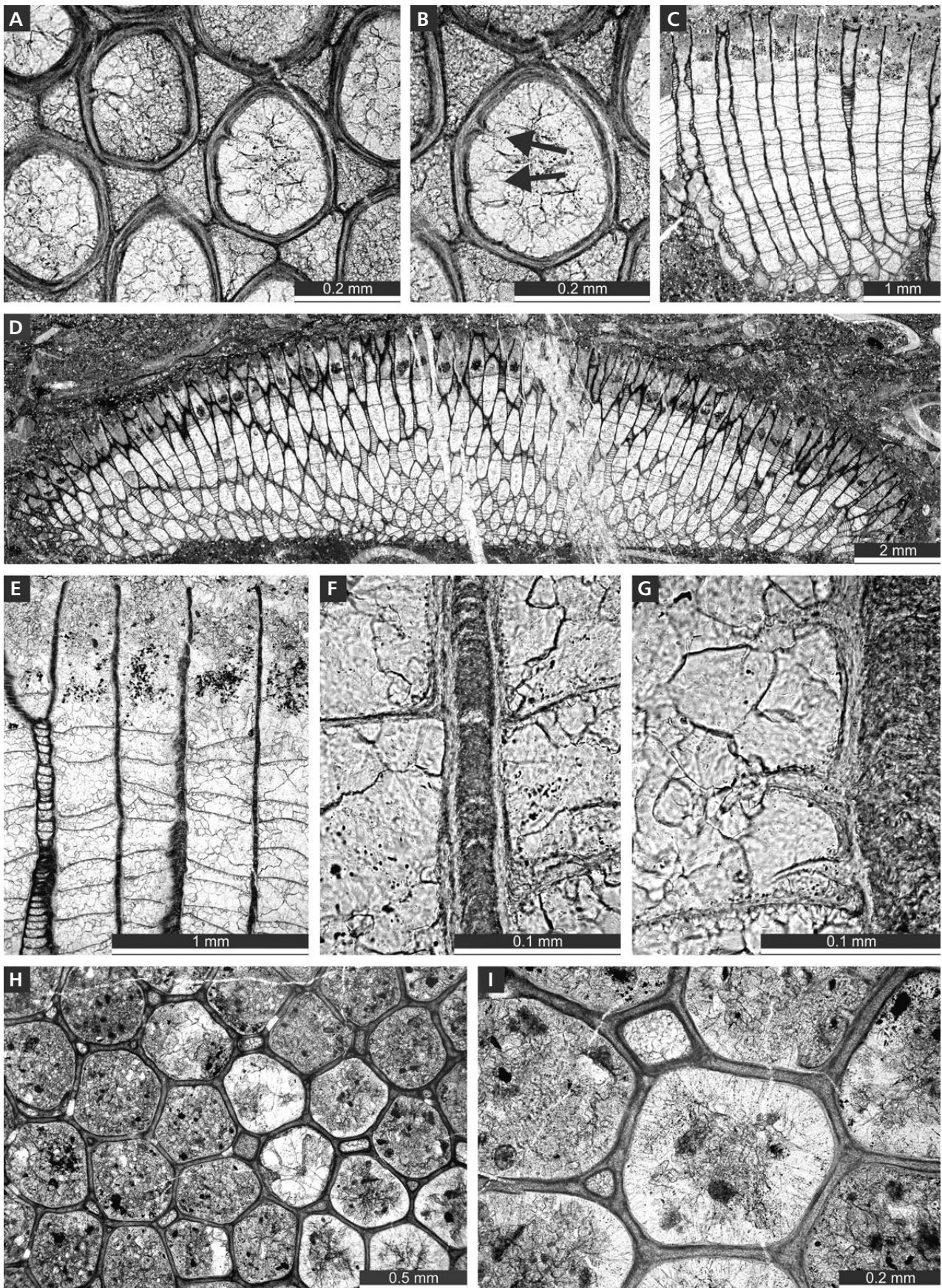


Table 5. Measurements of *Dekayia sugarensis* Ross, 1969. Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.21	0.025	11.92	0.17	0.26
Aperture spacing, mm	25	0.24	0.031	12.74	0.18	0.30
Aperture width, mm (macular)	6	0.29	0.017	5.97	0.26	0.31
Aperture spacing, mm (macular)	6	0.32	0.027	8.44	0.29	0.36
Mesozooecia width, mm	25	0.068	0.022	32.44	0.040	0.115
Acanthostyle diameter, mm	25	0.053	0.011	20.38	0.035	0.075
Acanthostyles per aperture	25	3	0.889	29.24	2	5

***Dekayia sugarensis* Ross, 1969**

Figure 9A–F, Table 5

1969 *Dekayia sugarensis* Ross, pp. 267–270, pl. 39, figs 2, 4–9, pl. 40, figs 1–8, pl. 41, figs 1–11, pl. 42, figs 1–9, table 6.

Material. – PMO 221.295, 221.296, 221.304–221.308, 221.310, 221.370.

Description. – Massive or subramose colonies with indistinct endozones, thickness of massive colonies 0.4 to 1.8 mm, diameter of subramose colonies 4.7–4.8 mm. Autozooecia bending gently from endozone, intersecting colony surface at right angles. Autozooecial apertures rounded to polygonal, often petaloid. Diaphragms in autozooecia rare to common, usually 1–5 in each autozooecium, thin, straight or slightly curved distally. Mesozooecia rare to common, more abundant in maculae, polygonal in transverse section, bearing thin, common diaphragms, strongly beaded, budding deeply in endozone. Acanthostyles abundant, large, varying in size, prominent, possessing wide hyaline core, 2–5 surrounding each autozooecial aperture. Autozooecial walls granular-prismatic, 0.005–0.010 mm thick in endozone; irregularly thickened, finely laminated, displaying reverse V-structure in longitudinal section, 0.015–0.025 mm thick in exozone. Maculae of megazooecia and mesozooecia indistinctly outlined.

Comparison. – *Dekayia sugarensis* Ross, 1969 differs from *D. minima* Conti, 1990 from the Upper Ordovician of Sardinia and southern France in having more abundant diaphragms and less abundant acanthostyles (2–5 vs. 2–7 per aperture in *D. minima*). *Dekayia sugarensis* differs also

from similar *D. stidhami* (Ulrich, 1890) from the Upper Ordovician of USA in having more abundant diaphragms and mesozooecia.

Occurrence. – Middle–Upper Ordovician (Trentonian); New York, USA. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

Family Trematoporidae Miller, 1889

Genus *Eridotrypa* Ulrich, 1893

Type species. – *Eridotrypa mutabilis* Ulrich, 1893, by original designation. Upper Ordovician; USA.

Diagnosis. – Ramose colonies, with narrow exozone. Autozooecia weakly bending towards branch surface, with oval and oval-rounded apertures, arranged in diagonal rows. Autozooecial walls in exozone thickened, having obliquely laminated microstructure. Diaphragms common throughout colony. Mesozooecia rare, short, differently closed at colony surface. Acanthostyles rare, small and short, sometimes absent. Small, needle-like structures in zooecial walls may occur.

Comparison. – *Eridotrypa* Ulrich, 1893 differs from the most similar genus *Batostoma* Ulrich, 1882 by its constant ramose colony form, weak bending of autozooecia to colony surface, short mesozooecia and small, rare acanthostyles and from *Bythopora* Miller & Dyer, 1878 by the constant presence of diaphragms in autozooecia and mesozooecia and in its wall microstructure.

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

***Eridotrypa aedilis* (Eichwald, 1855)**

Figures 9G–I, 10A–F, Table 6

1855 *Cladopora aedilis* Eichwald, p. 457.

1860 *Cladopora aedilis* Eichwald, 1855. – Eichwald, p. 404, pl. 24, figs 12, 13.

1877 *Monticulipora aedilis* (Eichwald, 1855). – Dybowski, p. 98, pl. 3, figs 5, 5a.

1911 *Eridotrypa aedilis* (Eichwald, 1855). – Bassler, pp. 242–244, pl. 4, figs 5, 5a, text-fig. 137, non fig. 138.

Figure 9. A–F – *Dekayia sugarensis* Ross, 1969. • A–C – longitudinal section showing autozooecia, mesozooecia and acanthostyles, PMO 221.295. • D–F – tangential section showing autozooecial apertures, acanthostyles and mesozooecia, PMO 221.304. • G–I – *Eridotrypa aedilis* (Eichwald, 1855). G – branch transverse section, short detail, PMO 221.308; H–I – branch transverse section, short detail, PMO 221.304.

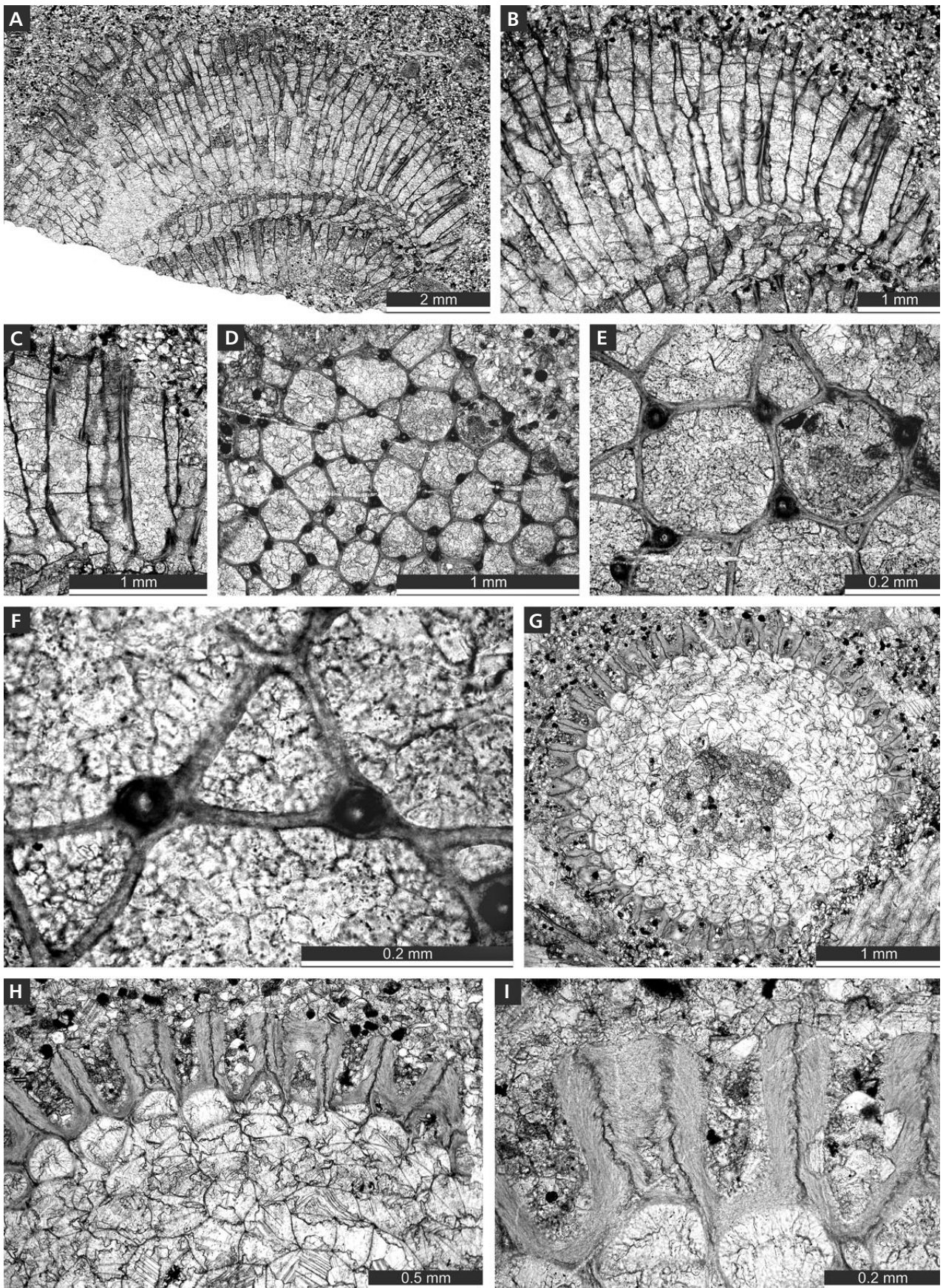


Table 6. Measurements of *Eridotrypa aedilis* (Eichwald, 1855). Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	15	3.82	0.579	15.17	3.10	5.10
Exozone width, mm	15	0.66	0.206	31.26	0.30	1.08
Endozone width, mm	15	2.50	0.557	22.26	1.74	3.84
Aperture width, mm	30	0.09	0.015	16.91	0.07	0.13
Aperture spacing, mm	30	0.24	0.033	14.01	0.18	0.30
Aperture width, mm (macular)	10	0.19	0.017	9.21	0.16	0.22
Aperture spacing, mm (macular)	10	0.31	0.035	11.17	0.26	0.36
Mesozooecia width, mm	20	0.05	0.013	28.58	0.03	0.08
Acanthostyle diameter, mm	20	0.03	0.008	22.68	0.02	0.05
Mesozooecial diaphragms spacing, mm	30	0.08	0.020	25.71	0.04	0.11
Autozoecial diaphragms spacing, mm	30	0.15	0.052	35.51	0.08	0.28
Exozonal wall thickness, mm	30	0.12	0.030	25.42	0.06	0.20
Axial zooecia width, mm	25	0.33	0.049	14.88	0.25	0.43

1984 *Eridotrypa aedilis* (Eichwald, 1855) – Karklins, pl. 25, figs 1, 2.

Material. – PMO 221.296, 221.297, 221.301, 221.302 to 221.305, 221.310–221.312, 221.361–221.362, 221.370.

Description. – Ramose colonies, branch diameter 3.10 to 5.10 mm, with 0.30–1.08 mm wide exozones and 1.74 to 3.84 mm wide endozones. Autozoecia long, oriented for long distance parallel to branch axis, then bending at angles of 24–30° in exozone and intersecting colonial surface at angles of 45–70°, polygonal and having larger diameter in endozone, oval to rounded-polygonal in exozone. Autozoecial diaphragms spaced widely in endozone, more densely in inner exozone, and usually absent in outermost parts of zooecia. Mesozooecia rare, small, short, polygonal in transverse section, spaced usually at junctions between autozoecia, bearing closely spaced diaphragms. Acanthostyles rare to common, small, having indistinct cores, restricted to the outermost exozone. Autozoecial walls in endozone having indistinct lamination, 0.005–0.010 mm thick, becoming continually thicker in the inner exozone and up to 0.06–0.20 mm in the outer exozone. Autozoecial walls in exozone displaying serrated dark border between autozoecia and distinct reverse V-shaped lamination.

Comparison. – *Eridotrypa aedilis* (Eichwald, 1855) is similar to *E. mutabilis* Ulrich, 1893 from the Upper Ordovician of USA, but differs from it in having narrower branches (3.1–5.1 mm vs. 2.4–10.8 mm in *E. mutabilis*), and in smaller apertures (0.07–0.13 mm vs. 0.16–0.22 mm in *E. mutabilis*). *Eridotrypa aedilis* differs from *E. trentonensis* (Nicholson, 1881) from the Upper Ordovician of USA in having smaller apertures (0.07–0.13 mm vs. 0.10–0.16 mm in *E. trentonensis*).

Occurrence. – Jövi, Keila, Oandu and Rakvere Stages, Upper Ordovician (Sandbian–Katian); Estonia. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

Order Cryptostomata Vine, 1884

Suborder Ptilodictyina Astrova & Morozova, 1956

Family Escharoporidae Karklins, 1983

Genus *Graptodictya* Ulrich, 1882 [= *Arthropora* Ulrich, 1882]

Type species. – *Ptilodictya perelegans* Ulrich, 1878. Waynesville Shale (Upper Ordovician); Ohio, USA.

Diagnosis. – Branching colonies, irregularly anastomosing in some species. Mesotheca slightly sinuous in longitudinal section, may zigzag in transverse section. Autozoecia budding in exozone at angles 80–90° to mesotheca. Pustules abundant along autozoecial boundaries and throughout exozonal walls and extrazooecial skeleton. Living chambers elliptical to oval in transverse section. Superior hemisepta common, generally short and blunt, rarely thin and long, curving proximally. Exilazooecia absent to rare, generally subelliptical in transverse section, commonly closed by thickened walls. Monticules absent to rare. Extrazooecial stereom laminae commonly crinkled, forming abundant and longitudinally striae between autozoecia, and along colonial margins and proximal parts of colonies.

Comparison. – *Graptodictya* Ulrich, 1882 differs from *Proavella* Männil, 1958 in having branched rather than reticular colonies.

Occurrence. – Middle Ordovician to lower Silurian of Estonia, Sweden, North America.

Figure 10. A–F – *Eridotrypa aedilis* (Eichwald, 1855). • A – branch longitudinal section, PMO 221.312. • B – longitudinal section of exozone showing autozoecial chambers with diaphragms, PMO 221.294. • C – longitudinal section of exozone showing autozoecial walls, diaphragms and mesozooecium, PMO 221.370. • D – tangential section showing autozoecial apertures, mesozooecia and acanthostyles, PMO 221.294. • E – tangential section showing autozoecial apertures, mesozooecia and acanthostyles, PMO 221.294. • F – branch transverse section of endozone showing central cluster of axial zooecia, PMO 221.370. • G–I – *Graptodictya perelegans* (Ulrich, 1878). G, H – tangential section, short detail, PMO 221.337; I – tangential section, short detail, PMO 221.334.

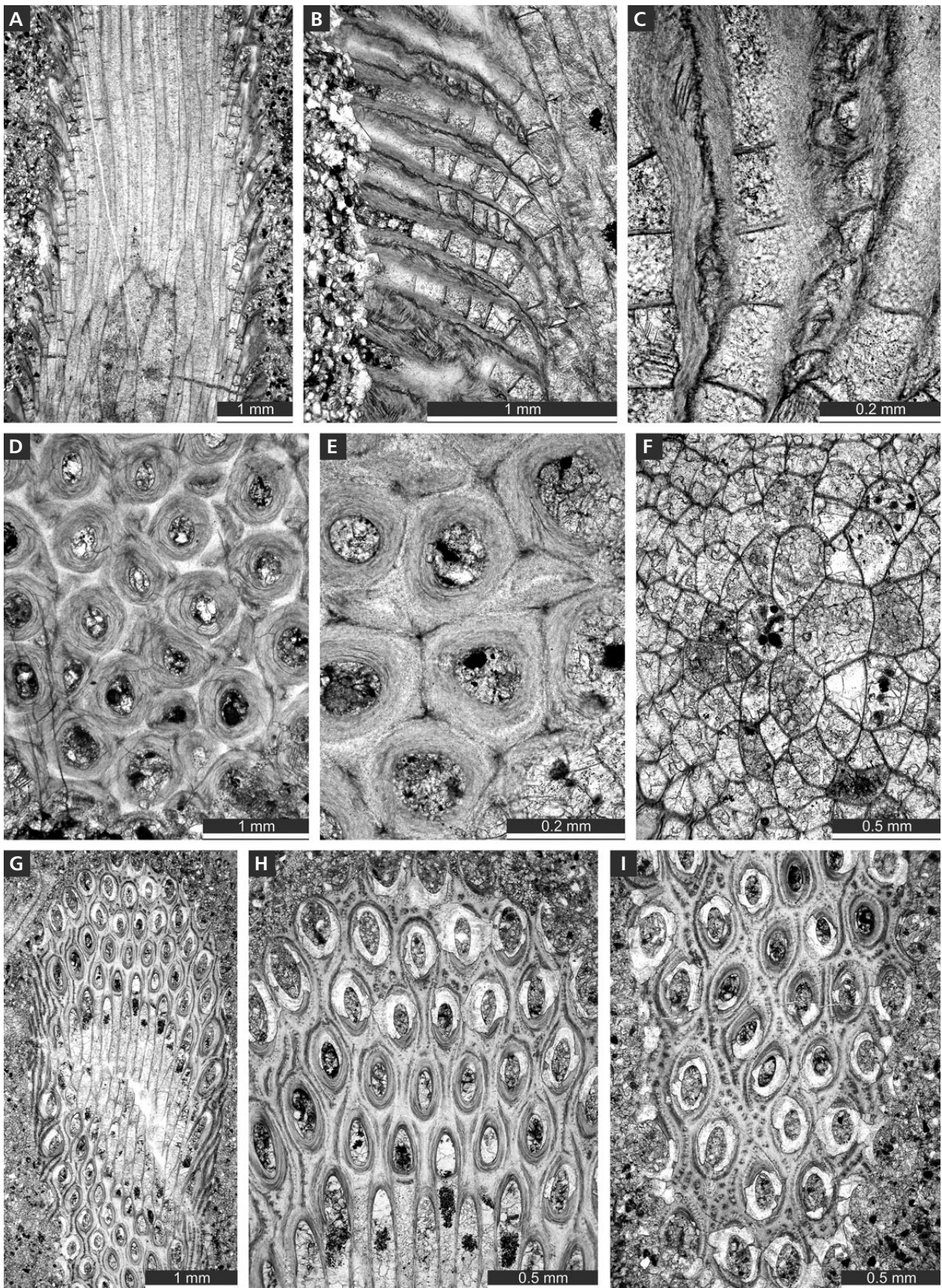


Table 7. Measurements of *Graptodictya perelegans* (Ulrich, 1878). Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	8	2.18	0.322	14.75	1.63	2.58
Branch thickness, mm	8	0.81	0.152	18.92	0.60	0.96
Aperture width, mm	55	0.08	0.015	18.69	0.06	0.11
Aperture spacing along branch, mm	55	0.55	0.055	9.91	0.39	0.72
Aperture spacing diagonally, mm	55	0.22	0.034	15.26	0.18	0.30
Autozooeal budding angle, endozone	7	29.6	4.276	14.46	23.0	35.0
Autozooeal budding angle, exozone	7	65.6	3.359	5.12	61.0	70.0

***Graptodictya perelegans* (Ulrich, 1878)**

Figures 10G–I, 11A–F, Table 7

- 1878 *Ptilodictya perelegans* Ulrich, p. 94, pl. 4, figs 16, 16a.
 1882 *Graptodictya perelegans* (Ulrich, 1878). – Ulrich, p. 165, pl. 7, figs 8, 8a.
 1900 *Graptodictya perelegans* (Ulrich, 1878). – Nickles & Bassler, p. 280.
 1908 *Graptodictya perelegans* (Ulrich, 1878). – Cumings, p. 836, pl. 29, fig. 8.
 1911 *Graptodictya perelegans* (Ulrich, 1878). – Bassler, p. 121, figs 47a–d.
 1953 *Graptodictya perelegans* (Ulrich, 1878). – Bassler, p. G137, fig. 98, 3a–c.
 1960 *Graptodictya perelegans* (Ulrich, 1878). – Phillips, pp. 19–21, pl. 7, figs 1–3, 6–7, pl. 8, fig. 4.
 1983 *Graptodictya perelegans* (Ulrich, 1878). – Karklins, p. 499, fig. 247, 1a–f.
 1984 *Graptodictya perelegans* (Ulrich, 1878). – Spjeldnaes, p. 30, pl. 4, figs 9–10, fig. 6E–G.
 1993 *Graptodictya perelegans* (Ulrich, 1878). – Gorjunova & Lavrentjeva, p. 75, pl. 13, fig. 4.

Material. – PMO 221.316, 221.317, 221.322, 221.329 to 221.330, 221.334, 221.337, 221.338–221.340, 221.353, 221.365.

Description. – Branching colonies, 1.63–2.58 mm wide, 0.60–0.96 mm thick. Autozooea quite long, budding in endozone at angles of 23–35° to the mesotheca, bending in exozone and intersecting branch surface at angles of

61–90°, oval to sub-polygonal in transverse section. Superior hemisepta short and blunt, curving proximally; inferior hemisepta absent. Autozooeal diaphragms occasionally present. Autozooeal apertures oval, arranged in 8–16 regular alternating rows. Heterozooea absent. Mesotheca straight, 0.005–0.007 mm thick. Extrazooeal skeletal laminae commonly crinkled, forming abundant longitudinal striae between autozooea, and along branch margins and proximal parts of colonies. Pustules common, 0.010 to 0.025 mm in diameter, arranged in loose rows between apertures. Small tubules in laminated skeleton occurring.

Comparison. – *Graptodictya perelegans* (Ulrich, 1878) is similar to *G. bonnemai* Bassler, 1911 from the Middle Ordovician of Estonia, but differs from it in presence of pustules and larger distances between autozooeal apertures along branch [0.39–0.72 mm vs. 0.31–0.38 mm in *G. bonnemai* (measured on own material from the Kukersite shale of Estonia)]. *Graptodictya perelegans* is also similar to *G. elegantula* (Hall, 1847) from the Middle Ordovician of USA, but differs from it in having smaller apertures (0.06–0.11 mm vs. 0.08–0.13 mm in *G. elegantula*).

Occurrence. – Upper Ordovician (Richmondian); USA. Upper Ordovician; Ojl Myr, Gotland, Sweden. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

Genus *Oanduellina* Pushkin, 1977

Type species. – *Oanduellina leuchtenbergi* Pushkin, 1977. Nabala Stage, Upper Ordovician (Katian); Latvia.

Diagnosis. – Colonies consisting of dichotomous branches, frond-shaped or anastomosed. Mesotheca straight or slightly undulating, without median rods. Autozooea short, with flattened proximal parts, rectangular with rounded roofs in transverse section, rectangular at their bases, having oval apertures. Autozooeal diaphragms rare to absent. Superior hemisepta weakly developed, commonly absent; inferior hemisepta absent. Abundant polygonal vesicles occurring in the transition between endozone and exozone, usually covered by extrazoidal material. Extrazoidal material containing paurostyles. Autozooeal walls coarsely laminated. Maculae lacking autozooea in some species present.

Comparison. – *Oanduellina* Pushkin, 1977 differs from *Sibiredictya* Nekhoroshev, 1961 in presence of superior

Figure 11. A–F – *Graptodictya perelegans* (Ulrich, 1878). • A – tangential section showing autozooeal apertures and pustules, PMO 221.334. • B – branch transverse section, short detail, PMO 221.342. • C, D – branch transverse section, short detail, PMO 221.340. • E, F – branch longitudinal section showing autozooeal chambers and hemisepta, PMO 221.353. • G, H – *Oanduellina leuchtenbergi* Pushkin, 1977, tangential sections, short detail, PMO 221.355.

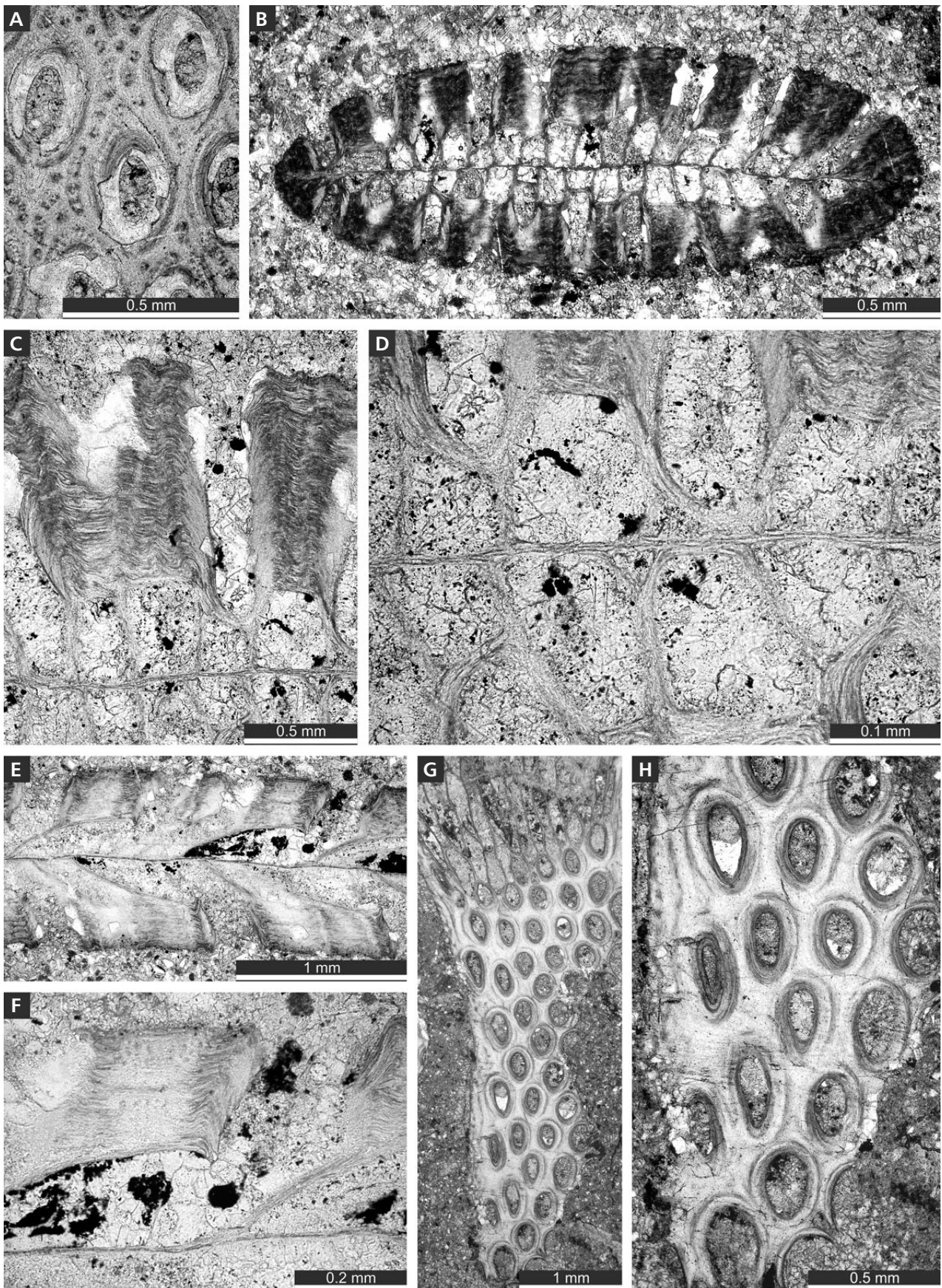


Table 8. Measurements of *Oanduellina leuchtenbergi* Pushkin, 1977. Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	5	2.49	0.274	11.03	2.13	2.75
Branch thickness, mm	6	0.74	0.119	16.15	0.58	0.83
Aperture width, mm	25	0.11	0.011	9.67	0.09	0.13
Aperture spacing along branch, mm	25	0.55	0.070	12.65	0.43	0.78
Aperture spacing diagonally, mm	25	0.27	0.030	11.24	0.22	0.34
Vesicle width, mm	25	0.06	0.015	26.06	0.04	0.10
Vesicle height, mm	10	0.059	0.012	20.82	0.038	0.075

hemisepta and maculae as well as in less regular arrangement of autozooeal apertures.

Occurrence. – Upper Ordovician (Sandbian–Katian); Estonia, Lithuania, NW Russia. Middle Ordovician; Arctic Russia. Upper Ordovician (Hirnantian); Mongolia, India. Lower Silurian (Llandovery); Estonia.

Oanduellina leuchtenbergi Pushkin, 1977

Figures 11G–H, 12A–H, Table 8

1911 *Pachydictya flabellum* Bassler, p. 140, pl. 8, figs 1, 2, text-figs 63, 64.

1977 *Oanduellina leuchtenbergi* Pushkin, p. 69, pl. 7, figs 1, 2, text-fig. 1.

1993 *Oanduellina leuchtenbergi* Pushkin, 1977. – Gorjunova & Lavrentjeva, p. 61, pl. 9, figs 1, 2.

Material. – PMO 221.314, 221.317, 221.324–221.326, 221.331, 221.338, 221.340, 221.341–221.343, 221.345, 221.347–221.350, 221.351, 221.352, 221.355, 221.357, 221.359, 221.361–221.362, 221.365–221.366, 221.368.

Description. – Bifoliate branched colonies, locally anastomosed, 2.13–2.75 mm wide, 0.58–0.83 mm thick. Mesotheca straight, 0.008–0.018 mm thick; median rods lacking. Autozooea short with flattened proximal parts, rectangular with rounded roofs in transverse section, rectangular at their bases, oval to slightly rhombic in deep tangential section. Autozooeal apertures oval, arranged in 14–18 irregular rows. Hemisepta absent. Autozooeal diaphragms absent. Abundant polygonal vesicles between apertures, moderate in size, commonly covered by extrazooeal

material, having flat rounded roofs. Extrazooeal material containing paurostyles, 0.02–0.03 mm in diameter. Autozooeal walls coarsely laminated. Maculae absent.

Comparison. – *Oanduellina leuchtenbergi* Pushkin, 1977 differs from *O. bella* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993) from the Upper Ordovician of Estonia in having branched colony shape instead of reticulate one and in smaller autozooeal apertures (aperture width 0.09 to 0.13 mm vs. 0.15–0.20 mm in *O. bella*). *Oanduellina leuchtenbergi* differs from *O. maculata* Pushkin, 1977 in having smaller apertures (aperture width 0.09 to 0.13 mm vs. 0.10–0.16 mm in *O. maculata*) and in absence of maculae.

Occurrence. – Upper Ordovician (Sandbian, Nabala Stage); Latvia. Upper Ordovician (Sandbian, Oandu Stage); Lithuania. Upper Ordovician (Sandbian, Rakvere Stage); Estonia. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

Family Ptilodictyidae Zittel, 1880

Genus *Phaenopora* Hall, 1851

[= *Fimbriopora* Astrova, 1965]

Type species. – *Phaenopora explanata* Hall, 1852. Silurian; Canada.

Diagnosis. – Bifoliate colonies, straight or branched. Mesotheca straight, thin. Autozooea almost straight. Diaphragms absent. Single superior or both superior and inferior hemisepta developed. Autozooeal apertures oval, rounded-rectangular. Ridges between autozooeal rows usually developed, sometimes absent at lateral parts of branches. Usually two metazooea between apertures. Monticules consisting of metazooea may present.

Comparison. – The genus *Phaenopora* Hall, 1851 differs from the genus *Phaenoporella* Nekhoroshev, 1956 by the branched colony shape instead of reticulated one, from the genus *Eichwaldictya* Lavrentjeva, 1990 – by absence of diaphragms and constant development of metazooea.

Occurrence. – Middle Ordovician–Middle Silurian; North America, Siberia, Mongolia, Europe.

Figure 12. A–H – *Oanduellina leuchtenbergi* Pushkin, 1977. • A – tangential section, short detail, PMO 221.355. • B – branch transverse section, short detail, PMO 221.345. • C, D – transverse section showing autozooeal chambers, vesicles and mesotheca, PMO 221.346. • E, F – longitudinal section, short details, PMO 221.341. • G, H – tangential section showing vesicles and paurostyles, PMO 221.357. • I – *Phaenopora similis* Nekhoroshev, 1961, branch transverse section, short detail, PMO 221.345.

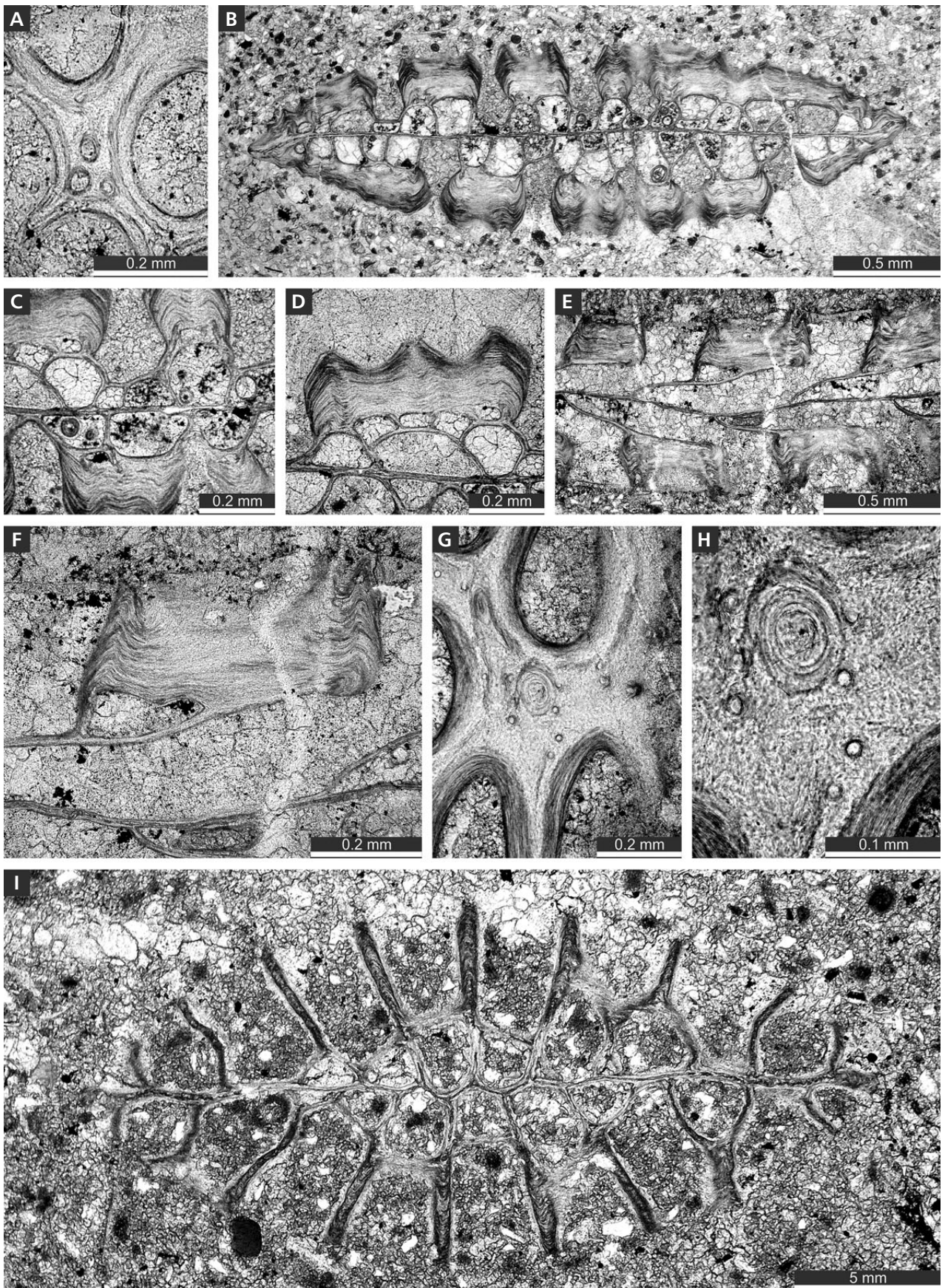


Table 9. Measurements of *Phaenopora similis* Nekhoroshev, 1961. Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	5	1.99	0.595	29.88	1.10	2.70
Branch thickness, mm	3	0.99	0.079	8.02	0.90	1.05
Aperture width, mm	30	0.11	0.007	6.04	0.10	0.12
Aperture spacing along branch, mm	30	0.28	0.033	11.98	0.20	0.34
Aperture spacing diagonally, mm	30	0.20	0.030	14.88	0.14	0.24
Metazooecia width, mm	15	0.02	0.008	32.83	0.02	0.05

Table 10. Measurements of *Ptilodictya capillaris* Lavrentjeva (in Lavrentjeva & Gorjunova, 1993). Abbreviations as in Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	20	0.09	0.016	19.15	0.07	0.12
Aperture spacing along branch, mm	20	0.31	0.014	4.44	0.28	0.34
Aperture spacing diagonally, mm	20	0.24	0.022	9.16	0.18	0.26

***Phaenopora similis* Nekhoroshev, 1961**

Figures 12I, 13A–C, Table 9

1961 *Phaenopora similis* Nekhoroshev, pp. 72, 73, pl. 5, figs 4–6.

Material. – PMO 221.297, 221.298, 221.301, 221.305 to 221.306, 221.310, 221.331, 221.343, 221.345–221.346, 221.348, 221.352, 221.356–221.357.

Description. – Broad and flattened bifoliate branches, 1.1–2.7 mm wide, 0.90–1.05 mm thick. Mesotheca zigzag folded in transverse section, three-layered, 0.015 to 0.020 mm thick. Autozooecia short, rectangular in deep tangential section. Autozooecial apertures oval to rectangular with rounded corners, arranged in 7–13 rows. Hemisepta not observed; occasional diaphragms occurring. Metazooecia small, shallow, having triangular apertures, arranged regularly in pairs between apertures. Autozooecial wall moderately thin, finely laminated.

Comparison. – *Phaenopora similis* Nekhoroshev, 1961 is similar to *P. plebeia* Nekhoroshev, 1961 from the Upper Ordovician–Lower Silurian of Siberia, but differs in having larger apertures (average aperture width 0.11 mm

vs. 0.07 mm in *P. plebeia*). *Phaenopora similis* is also similar to *P. oepiki* Toots, 1952 from the Upper Ordovician of Estonia, but differ from it in having smaller metazooecia and smaller distances between apertures (average distance between apertures 0.28 mm vs. 0.33 mm in *P. oepiki*).

Occurrence. – Middle–Upper Ordovician; Siberia. Furberget Formation, Upper Ordovician (Sandbian); Norway.

Genus *Ptilodictya* Lonsdale, 1839

Type species. – *Flustra lanceolata* Goldfuss, 1829. Lower Silurian (Wenlock); Great Britain.

Diagnosis. – Colonies lancet or belt form, rarely dichotomous ramose. Mesotheca straight, locally zigzag, sometimes thickened in exozone. Autozooecia straight, tubular, long; sub-rectangular to sub-hexagonal in endozone; commonly sub-rectangular in exozone, rarely oval. Apertures arranged in longitudinal rows, separated by straight ridges. Diaphragms absent. Hemisepta present: superior and sometimes inferior. Monticules irregularly distributed, flat to slightly raised.

Comparison. – *Ptilodictya* Lonsdale, 1839 differs from *Cladodictya* Lavrentjeva in Gorjunova & Lavrentjeva, 1993 in having longer autozooecia and presence of ridges.

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

***Ptilodictya capillaris* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993)**

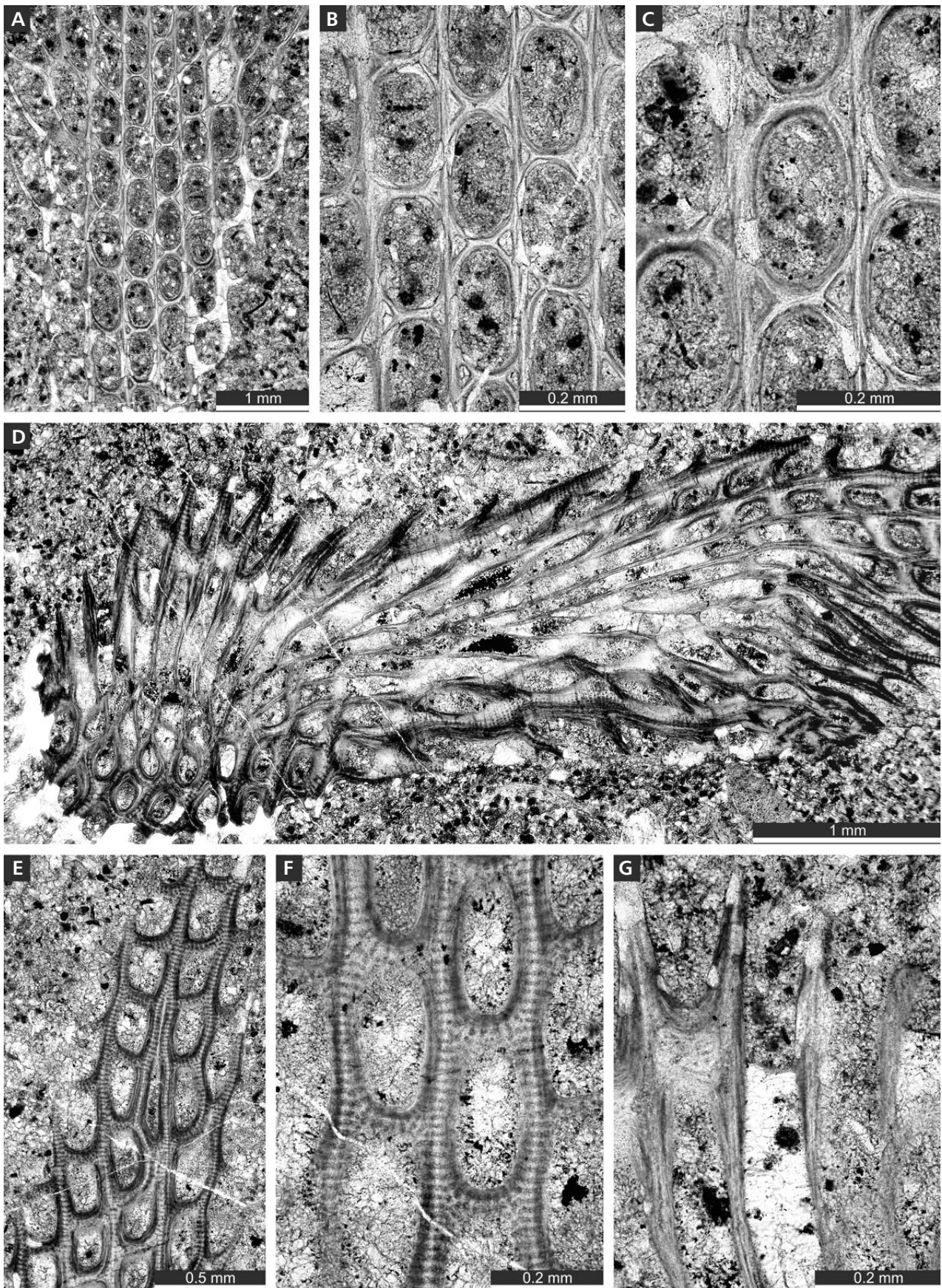
Figure 13D–G, Table 10

1993 *Ptilodictya capillaris* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993), pp. 66, 67, pl. 10, figs 5, 6.

Material. – Single colony PMO 221.356.

Description. – Bifoliate branched colony, 1.53 mm wide. Mesotheca zigzag folded, three-layered; median rods lacking. Autozooecia moderately long, rectangular in deep tangential section. Autozooecial apertures oval to rectangular with rounded corners, arranged in 7–8 rows.

Figure 13. A–C – *Phaenopora similis* Nekhoroshev, 1961, tangential section showing autozooecial apertures and metazooecia, PMO 221.357. • D–G – *Ptilodictya capillaris* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993), PMO 221.356. D – oblique section of the colony. short detail. • E, F – tangential section showing autozooecial apertures and spherules in autozooecial walls. • G – longitudinal section showing autozooecial chambers with diaphragms.



Superior hemisepta weakly developed; inferior hemisepta not observed. Occasional thin diaphragms occurring. Heterozooecia and styles absent. Autozooecial walls in endozone laminated with dark dividing layer, 0.015–0.025 mm thick; in exozone coarsely laminated, containing numerous spherules in autozooecia walls, regularly arranged in transverse bands. Spherules 0.005 to 0.010 mm in diameter.

Comparison. – *Ptilodictya capillaris* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993) is similar to *P. exilis* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993), but differs from it in having wider branches (1.53 mm vs. 0.7–1.0 mm in *P. exilis*).

Occurrence. – Middle Ordovician (Sandbian, Keila-Nabala Stages); Lithuania, Latvia. Furuberget Formation, Upper Ordovician (Sandbian); Norway.

Conclusions

The bryozoans described herein comprise a fauna of 10 previously known species. The species belong to nine genera previously known from other Baltoscandian as well as North American occurrences of Sandbian–Katian age. The Furuberget Formation faunas are completely different from those in the overlying unit (the Mjøsa Formation) and only one genus is shared (*Eridotrypa*) (Ernst & Nakrem, in press). The biogeography of Late Ordovician bryozoans has been discussed in Ross (1985), Tuckey (1990), Anstey *et al.* (2003), Jiménez-Sánchez (2009), Kácha & Šarič (2009), Jiménez-Sánchez & Villas (2010), Taylor & Sendino (2010) and briefly in Ernst & Nakrem (in press). On species level the Furuberget Formation bryozoan fauna resembles very much time equivalent units in the Baltic province, as well as North American (Laurentian) faunas. Slightly younger bryozoans from the Mjøsa Formation are rather different from Laurentian faunas indicating that there were more marine communication and less endemism in the Sandbian as compared with the Katian. All species are new additions for the Norwegian Ordovician to the bryozoan database used by *e.g.* Anstey *et al.* (2003) and Jiménez-Sánchez & Villas (2010).

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