Stenolaemate bryozoans from the Mjøsa Formation (Late Ordovician, Katian) of Helgøya (Mjøsa), southern Norway

Andrej Ernst & Hans Arne Nakrem

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A stenolaemate bryozoan fauna from the Late Ordovician (Katian) Mjøsa Formation of Bergevika (Helgøya, Mjøsa), southern Norway contains nine species. Seven species belong to the Order Trepostomata: *Esthoniopora subsphaerica* (Bassler, 1911), *Hallopora gracilens* Bassler, 1927, *Diazipora parva* (Bassler, 1911), *Hemiphragma batheri* Bassler, 1911, *Eridotrypa suecica* Brood, 1978, *Trematopora brutoni* sp. nov. and *Anaphragma latviense* Pushkin, 1976. Two species belong to the Suborder Ptilodictyina of the Order Cryptostomata: *Trigonodictya cyclostomoides* (Eichwald, 1855) and *Astrovidictya sparsa* Lavrentjeva *in* Gorjunova & Lavrentjeva, 1993. The bryozoan faunal association is similar to that found in equivalent Baltoscandian units elsewhere, but rather different from Laurentian units. Their known biostratigraphic range is generally Late Ordovician.

Andrej Ernst, Institut für Geowissenschaften der Christian-Albrechts-Universität zu Kiel, Ludewig-Meyn-Str. 10, D-24118 Kiel, Germany. E-mail: ae@gpi.uni-kiel.de. Hans Arne Nakrem, Natural History Museum (Geology), University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway. E-mail: h.a.nakrem@nhm.uio.no

Introduction

The Mjøsa Formation is widely distributed in the Toten-Nes-Hamar districts in the northern part of the Oslo Region (Fig. 1). Its base is not seen in the Ringsaker-Helgøya area but elsewhere it displays an abrupt change to bioclastic limestone from the underlying shales and limestones of the Furuberget Formation (Owen et al. 1990). The Mjøsa Formation is subdivided into five members (see Fig. 1) and the bryozoans described here come from the Bergevika Member of Katian age (Bergström et al. 2010) from the northern part of the Bergevika locality at the island Helgøya in the lake Mjøsa (Fig. 1).

The fauna of the shallow water limestones of the Bergevika Member includes in addition to bryozoans, brachiopods, trilobites, corals, as well as stromatoporoids, algae and microfossils. Stromatoporoids and corals dominate the fauna in general, whereas bryozoans are abundant only in certain beds. Locally, *Solenopora*-stromatoporiod bioherms are developed indicating a rather shallow depositional environment.

The age of the Mjøsa Formation has recently been refined by Bergström *et al.* (2010) to span the late Sandbian-Katian stages of the Late Ordovician based on $\delta^{13}C$ chemostratigraphy. Their conodont faunas can be correlated with coeval units of the North American Mid-continent, especially the Lexington Limestone, but differ markedly from those known from Baltoscandian units.

Significance of the Mjøsa Formation bryozoans

The bryozoans described herein comprise a fauna of eight previously known species and one new: *Trematopora brutoni* sp.nov. The species belong to nine genera previously known from other Baltoscandian occurrences of Katian age. One species, *Hallopora gracilens*, is also known from the Upper Ordovician of Anticosti Island (Bassler 1927), *Astrovidictya sparsa* is additionally known from the Upper Ordovician of southern France (Ernst & Key 2007) whereas the remaining species are only known from Upper Ordovician Baltoscandian units. The temporal distribution of the identified bryozoan species in the Mjøsa Formation is similar to their distribution elsewhere, especially in other Baltoscandian units. Most species are long ranging with a general Late Ordovician range and their biostratigraphical value seems rather limited.

At the generic level, *Esthoniopora* and *Diazipora* have a restricted Baltoscandian distribution, *Astrovidictya* is, in addition, also known from south France (Gondwanan biogeographic province) whereas the remaining five genera have a general global distribution.

The biogeography of Late Ordovician bryozoans has been discussed in Ross (1985), Tuckey (1990), Anstey *et al.* (2003) and Jiménez-Sánchez & Villas (2010). Tuckey

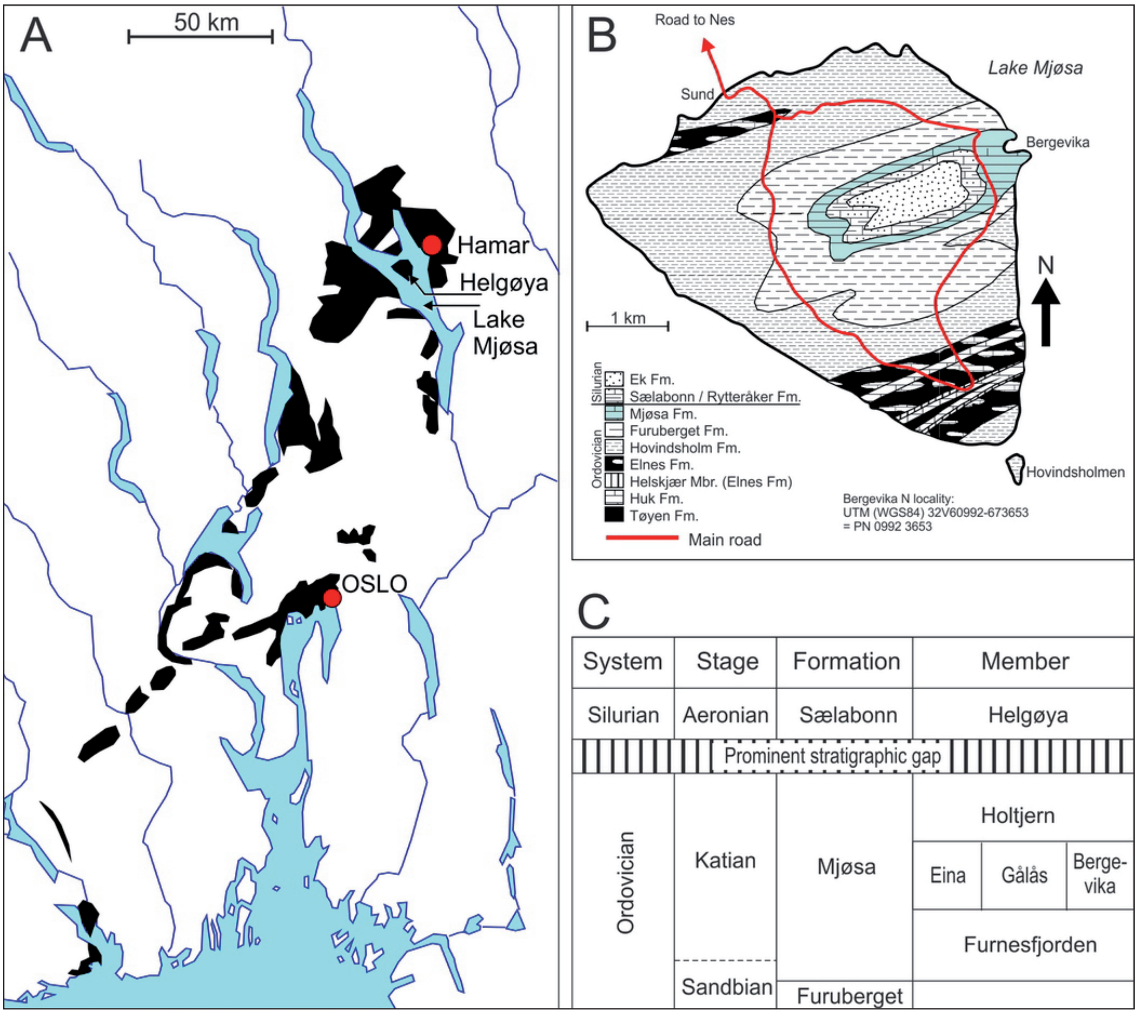

Figure 1. A: Map showing the distribution of Ordovician rocks in the Oslo Region (based on Owen et al. *1990)*
B: Geological map of Helgøya (based on Skjeseth 1963)
C: Stratigraphy of the Upper Ordovician in the Mjøsa area (based on Bergström et al. *2010)*

(1990) prepared an on-line database of bryozoan occurrences *(http://www.geology.iupui.edu/Research/Paleolab/Ord_Sil_NEXUS_datafile.htm)* which has subsequently been used in e.g. Anstey *et al.* (2003) and Jiménez-Sánchez & Villas (2010). The database includes occurrences of Ordovician bryozoans from the Oslo Region, but unfortunately no references are given. Until now the only reference to Ordovician bryozoans from the Oslo Region is Brood (1980) although Spjeldnæs (1982) refers to undocumented occurrences. The data obtained from our analysis of the Mjøsa Formation bryozoans have been added to the abovementioned database in the current investigation, but the resulting DCA and PCO analysis using PAST (Hammer *et al.* 2001) do not differ much from the plots presented by Jiménez-Sánchez & Villas (2010: figs. 2 and 3). However, the Baltoscandian units group slightly better when the data include the Mjøsa Formation bryozoans (Fig. 2).

Bergström *et al.* (2010), in their work on chemostratigraphy and conodonts of the Mjøsa Formation, concluded that the conodont fauna differs strikingly from that present in most coeval Baltoscandic deposits but shows a remarkably similarity to that in some formations of the North American Midcontinent, such as the Lexington Limestone. This distribution and possible migration pattern is different from what is concluded from the bryozoans in the present work. This might be due to larval dispersal and the ability of adult conodonts to migrate over larger distances. Spjeldnæs (1981) and Bergström *et al.* (2010) attribute faunal distribution patterns to climatic parameters and the closing of the Iapetus Ocean by the Late Ordovician.

Material and methods

The investigated bryozoans were studied from thin sections using a transmitted light binocular microscope. Thirty-six oriented and non-oriented thin sections were used. The material is housed at the Natural History Museum (Geology), Oslo, under numbers PMO 214.875-214.910.

Morphological character terminology is adopted from Anstey & Perry (1970) for trepostomes, and Hageman (1993) for cryptostomes. The following morphologic characters were measured for statistical use:
Branch Width, Branch Thickness, Exo- (Endo-) zone Width, Autozooecial Aperture Width, Autozooecial Aperture Spacing (Along / Across Branch), Acanthostyle Diameter, Wall Thickness in Exozone, and Macular Diameter (Spacing), Autozooecial 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 autozooecial aperture. Statistics were summarized using arithmetic mean, sample standard deviation, coefficient of variation, and minimum and maximum values.

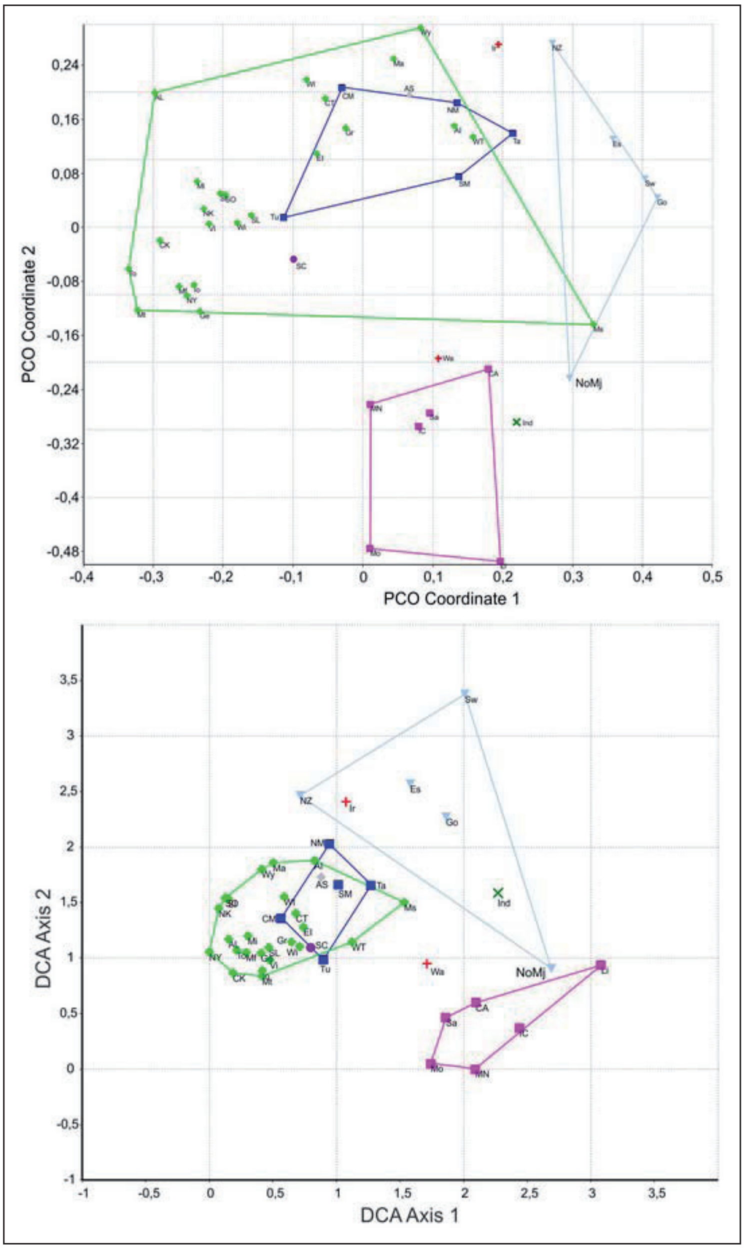

Figure 2. Detrended correspondence analysis (DCA) and principal coordinates analysis (PCO) of the Late Ordovician bryozoan occurrences compared with the Mjøsa Formation bryozoans using PAST (Hammer et al. 2001).
Red: Avalonia; blue: Siberia; dark green: India; green: Laurentia; purple: South China; pink: Mediterranean Area; grey: Altai Sayan; sky blue: Baltica.
Abbreviations used:
AI: Anticosti Island, AL: Alabama, AS: Altai Sayan, AV: Avalonia, Bo: Bohemia, CA: Carnic Alps, CK: Central Kentucky, CM: Central Mongolia, CT: Central Tennessee, EI: Northeast Illinois, Es: Estonia, Ge: Georgia, Go: Gotland, Gr: Greenland, IC: Iberian Chains, Ind: India, Io: Iowa, Ir: Ireland, Li: Libya, Ma: Manitoba, Mf: Meaford, Mi: Michigan, MN: Montagne Noire, Mo: Morocco, Ms: Missouri, Mt: Manitoulin Island, NK: North Kentucky, NM: Northwest Mongolia, NoMj: Norway, Mjøsa Fm., NZ: Novaya Zemlya, NY: New York, PC: Precordillera Argentina, Sa: Sardinia, SC: South China, SI: South Indiana, SL: Saint Lawrence River Valley, SM: South Mongolia, SO: South Ohio, Sw: Sweden, Ta: Taimyr, To: Toronto, Tu: Tuva, Vi: Virginia, Wa: Wales, WI: Northwest Illinois, Wi: Wisconsin, WT: West Texas, Wy: Wyoming.
In order to ease comparison we have used the same abbreviations and color codes as those used in Jiménez-Sánchez & Villas (2010).

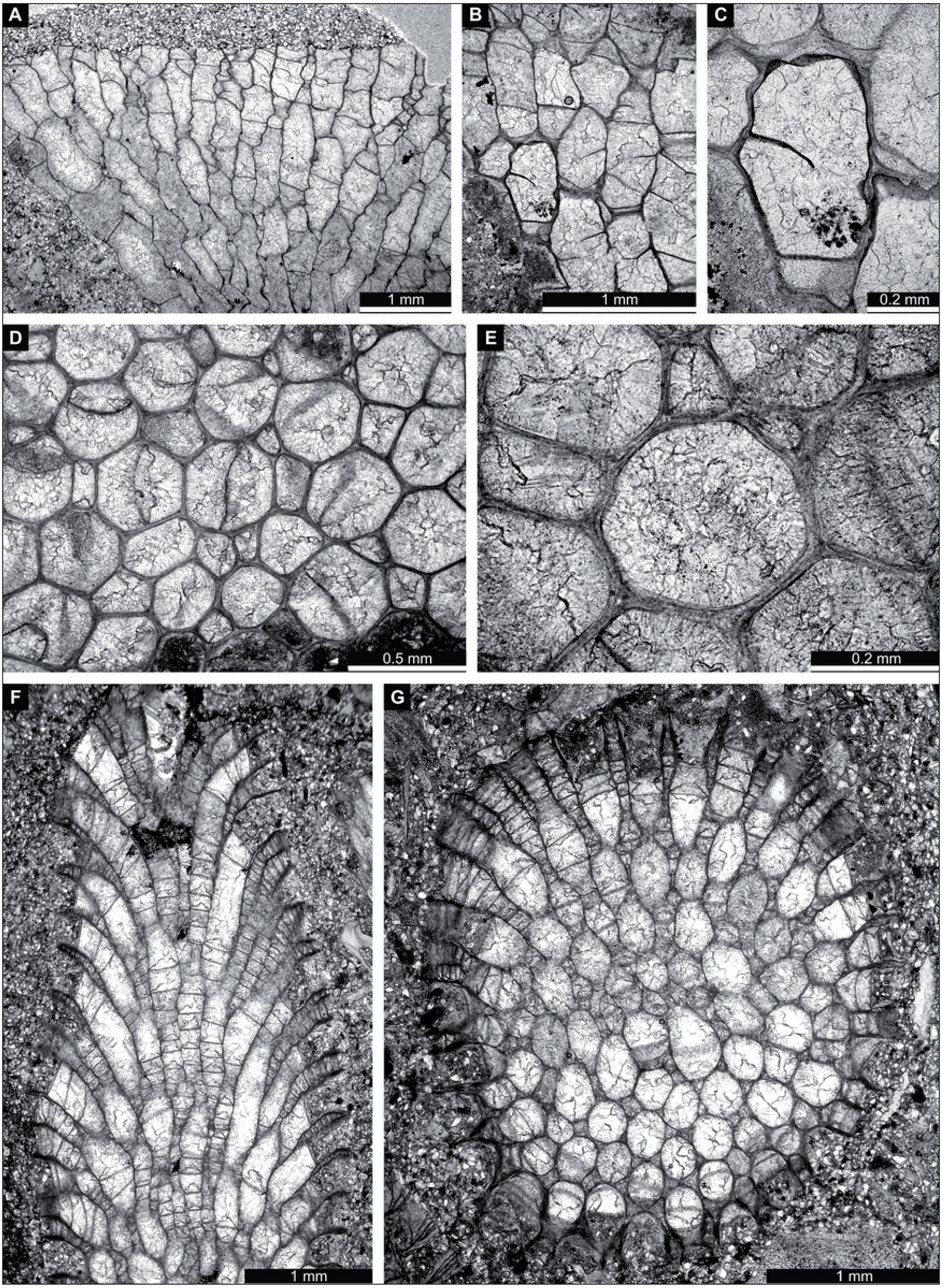

Figure 3. A-E. Esthoniopora subsphaerica *(Bassler, 1911). A, longitudinal section showing autozooecia and hemiphragms, PMO 214.904; B-C, longitudinal section showing hemiphragms in autozooecia, PMO 214.897, D-E, tangential section showing autozooecial apertures, PMO 214.904. F-G.* Hallopora gracilens *Bassler, 1927. F, longitudinal section, PMO 214.883; G, transverse section, PMO 214.887.*

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Trepostomata Ulrich, 1882
Suborder Esthonioporina Astrova, 1978
Genus *Esthoniopora* Bassler, 1911

Type species. *E. communis* Bassler, 1911. Lower-Middle Ordovician (Llanvirn-Caradoc); Estonia.

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

Comparison. *Esthoniopora* differs from *Esthonioporella* Modzalevskaya, 1953, in absence of acanthostyles and in having thin autozooecial walls.

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

Esthoniopora subsphaerica (Bassler, 1911)
Figure 3A-E; Table 1

1911 *Hemiphragma subsphaericum* Bassler, 1911: 292-294, pl. 10, fig. 2, text-figs 178-179.

Material. Two thin sections of a single colony PMO 214.897, PMO 214.904.

Description. Massive colony, 5 mm thick in its central part. Exozone indistinct. Autozooecia long, prismatic, growing from epitheca. Autozooecial apertures polygonal. Mesozooecia *sensu stricto* absent, immature zooecia smaller than autozooecia common. Hemiphragms abundant, restricting more than half of the autozooecial chamber space, curved proximally, tapering to their ends. Autozooecial walls amalgamated, 0.010-0.015 mm thick in endozone and 0.015-0.020 mm thick in exozone. Maculae consisting of larger autozooecia present, 1.95-2.34 mm in diameter.

Comparison. *Esthoniopora subsphaerica* (Bassler, 1911) differs from *E. communis* Bassler, 1911 in having smaller autozooecia (0.19-0.31 mm vs. 0.30-0.60 mm in *E. communis*).

Occurrence. Kukruse – Rakvere stages (Upper Ordovician, Caradoc); Estonia. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway.

Suborder Halloporina Astrova, 1965
Family Halloporidae Bassler, 1911
Genus *Hallopora* Bassler, 1911

Type species. *Callopora elegantula* Hall, 1852, Lower Silurian (Niagaran); USA.

Diagnosis. Ramose cylindrical colonies with distinct exozones. Apertures polygonal or rounded-polygonal, with perforated covers in some species. Walls in exozone weakly, sometimes significantly thickened, displaying diagonally laminated microstructure. Diaphragms thin, planar and sloping, especially abundant in distal part of exozone. Mesozooecia variable in number, with frequent diaphragms. Mural spines and cup-like apparati may occur. Styles absent.

Comparison. *Hallopora* Bassler, 1911 differs from *Diplotrypa* Nicholson, 1879 by its ramose colony form, arrangement of diaphragms and wall microstructure. *Parvohallopora* Singh, 1979 differs from *Hallopora* by the angular to subcircular shape of autozooecia in cross section, usually smaller autozooecia and mesozooecia, as well as rare cystoidal diaphragms.

Occurrence. Lower Ordovician to Upper Silurian, North America, Europe, Siberia, Australia.

Hallopora gracilens Bassler, 1927
Figure 3F-G, 4A-D; Table 2

1927 *Hallopora gracilens* Bassler: 154-155, pl. 8, figs 10-11, pl. 10, figs 6-8.
1987 *Hallopora gracilens* Bassler, 1927 – Pushkin in Ropot & Pushkin: 148, pl. fig. 5, pl. 6. fig. 1.
2007 *Hallopora gracilens* Bassler, 1927 – Ernst & Key: 385, pl. 8, figs 5-7.

Material. PMO 214.875, PMO 214.879, PMO 214.880, PMO 214.881, PMO 214.882, PMO 214.883, PMO 214.887, PMO 214.888, PMO 214.897.

Table 1. Descriptive statistics of *Esthoniopora subsphaerica* (Bassler, 1911). Abbreviations: N = number of measurements, X = mean, SD = sample standard deviation, CV = coefficient of variation, MIN = minimal value, MAX = maximal value.

	N	X	SD	CV	MIN	MAX
Autozooecial Aperture Width, mm	20	0.25	0.036	14.27	0.19	0.31
Aperture Spacing, mm	20	0.29	0.031	10.99	0.24	0.36
Aperture Width, mm, macular	20	0.37	0.060	16.25	0.29	0.54
Aperture Spacing, mm, macular	20	0.45	0.071	15.87	0.36	0.54
Immature Zooecia Width, mm.	20	0.087	0.016	18.19	0.070	0.125

Table 2. Descriptive statistics of *Hallopora gracilens* Bassler, 1927. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch Width, mm	5	2.9	0.464	15.90	2.4	3.5
Exozone Width, mm	5	0.4	0.073	18.52	0.3	0.5
Autozooecial Aperture Width, mm	20	0.19	0.022	11.75	0.16	0.24
Aperture Spacing, mm	20	0.29	0.033	11.33	0.23	0.34
Aperture Width, mm, macular	7	0.27	0.022	8.11	0.25	0.31
Aperture Spacing, mm, macular	7	0.42	0.067	16.19	0.34	0.49
Mesozooecia Width, mm	25	0.07	0.018	27.39	0.04	0.10
Mesozooecia per Aperture	15	5.9	1.302	22.19	4.0	9.0
Autozooecial Diaphragms Spacing, mm	25	0.13	0.039	31.22	0.05	0.22
Mesozooecial Diaphragms Spacing, mm	25	0.07	0.014	20.67	0.04	0.10
Exozonal Wall Thickness, mm	25	0.038	0.014	37.58	0.025	0.075

Description. Ramose colonies, branch diameter 2.4-3.5 mm. Exozone distinct, 0.3-0.5 mm wide, endozone 1.8-2.5 mm wide. Secondary overgrowths occurring, 0.4 mm thick. Autozooecia long, growing parallel to branch axis for a long distance in endozone, in exozone bending sharply and intersecting branch surface at angles of 80-90°, having rounded-polygonal shape in cross section in endozone. Autozooecial apertures rounded to oval. Autozooecial diaphragms thin, planar, rare to common in endozone; becoming common in exozone, planar, rarely inclined, developed as extension of wall cortex. Cap-like apparati and mural spines absent. Mesozooecia arising in endozone, polygonal in cross section, often separating autozooecia completely from each other. Mesozooecial diaphragms planar, densely spaced. Autozooecial walls indistinctly laminated, 0.005-0.010 mm thick in endozone; displaying distinct reverse V-shaped structure with dark autozooecial border, having well developed wall cortex continued in diaphragms, 0.025-0.075 mm thick in exozone. Maculae indistinct, consisting of larger autozooecia.

Comparison. *Hallopora gracilens* Bassler, 1927 differs from the species *H. elegantula* (Hall, 1852) in having smaller apertures (average apertures widths 0.19 mm vs. 0.31 mm in *H. elegentula*), more slender colonies and lacking mural spines and cup-like apparati.

Occurrence. Upper Ordovician, Ashgill; Anticosti Island, Canada. Upper Ordovician, Nabala, Vormsi and Pirgu stages (Caradoc-Ashgill); Estonia and Belarus. Upper Ordovician, Upper Caradoc; Grange du Pin, Montagne Noire, southern France. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway.

Family Mesotrypidae Astrova, 1965
Genus *Diazipora* Vinassa de Regny, 1921

Type species. *Mesotrypa milleporacea* Bassler, 1911; Middle Ordovician of Estonia.

Diagnosis. Lamellar encrusting colonies, with epitheca or free-lying. Autozooecial apertures irregularly rounded, walls thin, longitudinal-fibrous. Diaphragms abundant, curved and intersecting. Mesozooecia numerous, very small. Acanthostyles absent.

Comparison. This genus is distinguished from the genus *Mesotrypa* by abundant, exceptionally small mesozooecia.

Occurrence. Two species of the genus are known: *D. milleporacea* (Bassler, 1911) from the Upper Ordovician (Caradoc) of Estonia, Sweden and Siberia (Pai Khoi), and *D. parva* (Bassler, 1911) from the Upper Ordovician (Caradoc) of Estonia and Norway.

Diazipora parva (Bassler, 1911)
Figure 4E-H; Table 3

1911 *Mesotrypa milleporacea parva* Bassler: 203-204, text-fig. 110.

Material. Two colonies PMO 214.888 (tangential section) and PMO 214.889 (tangential and longitudinal sections).

Description. Lamellar encrusting colonies, 1.1 mm in thickness. Autozooecia tubular, growing from epitheca. Autozooecial apertures rounded to slightly angular. Autozooecial diaphragms common, mainly inclined or cystoidal. Mesozooecia abundant, 8-9 surrounding each autozooecial aperture, completely isolating autozooecia, originating in endozone. Mesozooecial diaphragms densely spaced. Autozooecial walls 0.02-0.03 mm thick through the colony, indistinctly laminated, amalgamated. Cingulum developed, 0.010-0.015 mm thick.

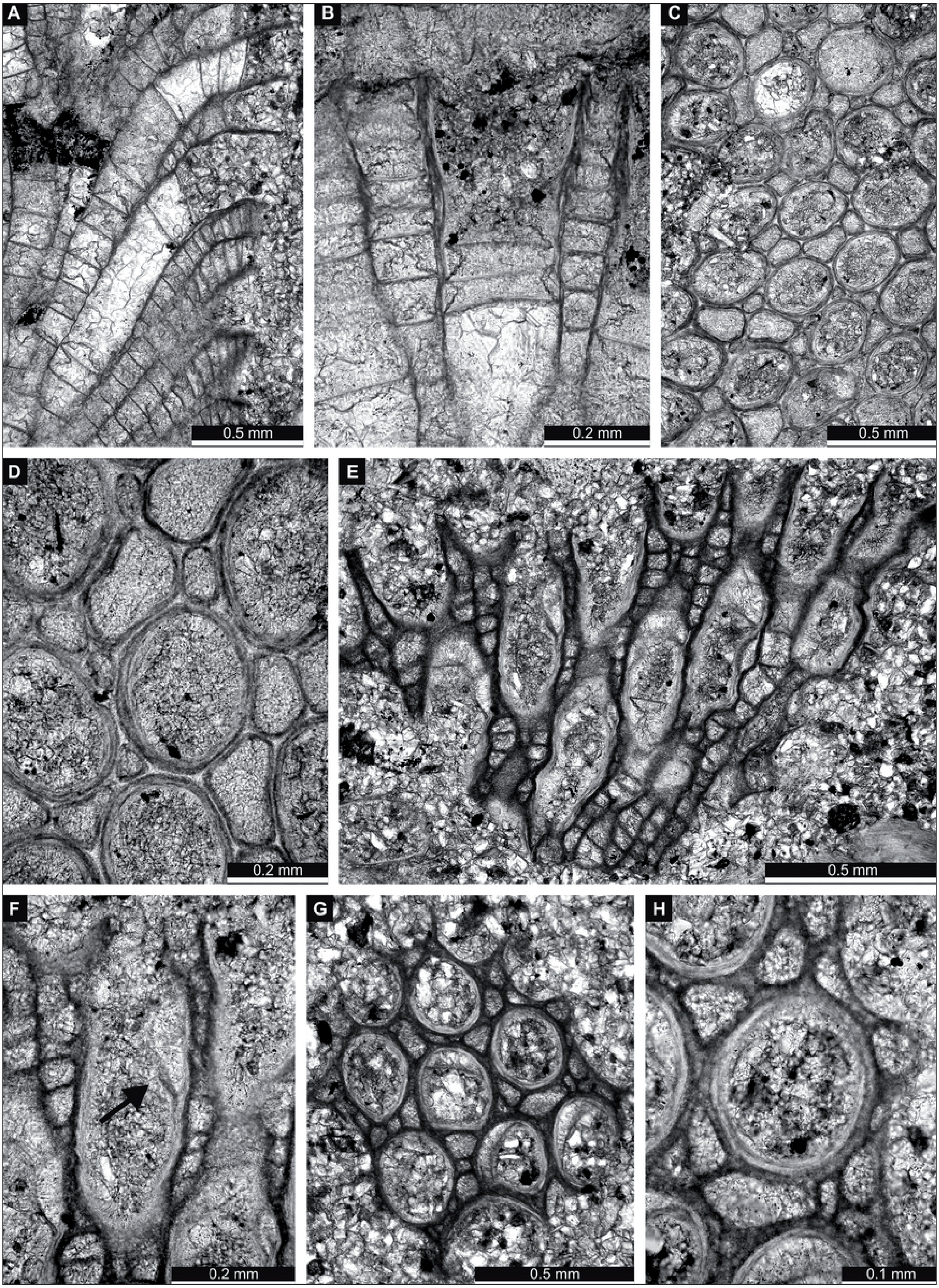

Figure 4. A-D. Hallopora gracilens *Bassler, 1927. A, longitudinal section showing autozooecia and mesozooecia, PMO 214.883; B, transverse section, PMO 214.887; E-D, tangential section showing autozooecial apertures and mesozooecia, PMO 214.879. E-H.* Diazipora parva *(Bassler, 1911), PMO 214.889. E-F, longitudinal section showing autozooecia and mesozooecia (arrow – cystiphragmoid diaphragm); G-H, tangential section showing autozooecial apertures and mesozooecia.*

Table 3. Descriptive statistics of *Diazipora parva* (Bassler, 1911). Abbreviations as for Table 1

	N	X	SD	CV	MIN	MAX
Autozooecial Aperture Width, mm	20	0.14	0.017	12.11	0.12	0.18
Aperture Spacing, mm	20	0.21	0.025	11.70	0.18	0.28
Mesozooecia Width, mm	20	0.04	0.013	31.30	0.02	0.07
Mesozooecial Diaphragms Spacing, mm	10	0.055	0.008	13.98	0.045	0.065

Comparison. Diazipora parva (Bassler, 1911) differs from *D. milleporacea* (Bassler, 1911) in having smaller colonies and smaller autozooecial diaphragms (autozooecial aperture width 0.12-0.18 vs. 0.30-0.40 mm in D. milleporacea).

Occurrence. Upper Ordovician (Caradoc, Kukruse stage); Estonia. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway.

Family Heterotrypidae Ulrich, 1890
Genus *Hemiphragma* Ulrich, 1893

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

Diagnosis. Colonies massive and ramose. Autozooecia with polygonal and polygonal-rounded apertures. Complete and perforated diaphragms abundant in exozone. Autozooecial 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.

Comparison. *Hemiphragma Ulrich*, 1893 is most similar to *Phragmopora* Vinassa de Regny, 1921, differing in the presence of acanthostyles and smaller mesozooecia.

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

Hemiphragma batheri Bassler, 1911
Figure 5A-F; Table 4

1911 *Hemiphragma batheri* Bassler: 296-297, text-fig. 182.

Material. PMO 214.905, PMO 214.909, PMO 214.910.

Description. Ramose colonies, branch diameter 5.0-5.2 mm. Endozone 3.2-3.4 mm wide; exozone 0.8-1.0 mm wide. Autozooecia polygonal in cross section in endozone, becoming rounded-polygonal in exozone, bending at high angles in exozone, bearing moderately thick hemiphragms. Hemiphragms most abundant in outermost parts of autozooecia, long and curved to proximal end on their inner edge. Basal diaphragms common, Mesozooecia rare, small, restricted to exozone, containing densely spaced diaphragms. Acanthostyles common, up to 5 surrounding each autozooecial aperture, having distinct hyaline cores and wide laminated sheaths. Walls straight, displaying hyaline microstructure, 0.010-0.015 mm thick in endozone; laminated, integrated, with distinct median lining, thick in exozone. Maculae consisting of larger autozooecia present, 1.3-1.6 mm in diameter.

Comparison. *Hemiphragma batheri* Bassler, 1911 differs from *H. subtile* Conti, 1990 in having smaller autozooecia (average autozooecial aperture width 0.20 mm vs. 0.26 mm in *H. subtile*).

Occurrence. Öland, Sweden. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway.

Table 4. Descriptive statistics of *Hemiphragma batheri* Bassler, 1911. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooecial Aperture Width, mm	25	0.20	0.042	20.37	0.12	0.26
Aperture Spacing, mm	25	0.31	0.041	13.22	0.23	0.40
Aperture Width, mm, macular	7	0.31	0.014	4.56	0.28	0.32
Aperture Spacing, mm, macular	7	0.45	0.037	8.18	0.40	0.50
Mesozooecia Width, mm	6	0.051	0.010	20.31	0.038	0.063
Acanthostyle Diameter, mm	20	0.037	0.008	21.06	0.025	0.050
Exozonal Wall Thickness, mm	20	0.089	0.017	19.25	0.055	0.125

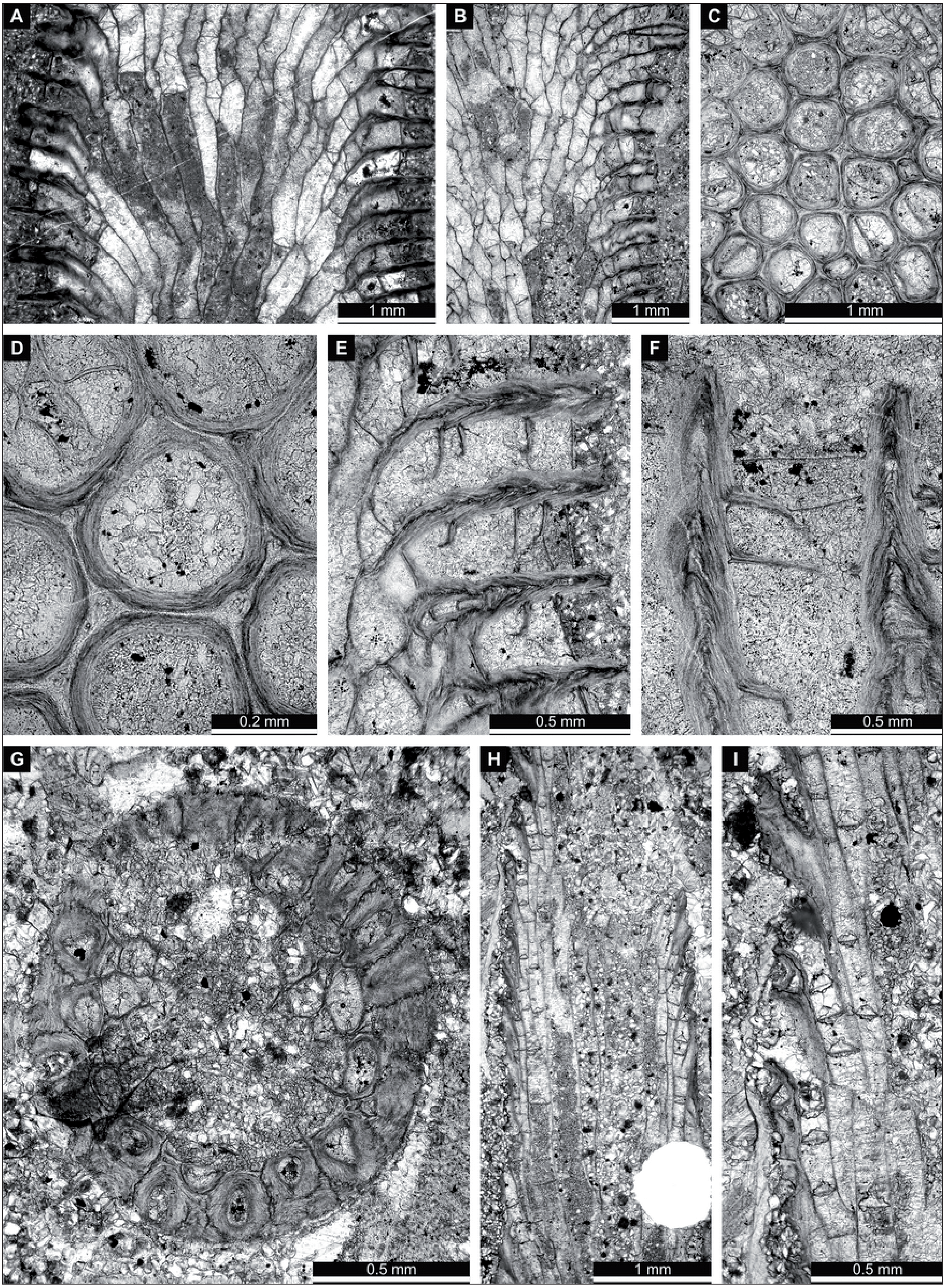

Figure 5. A-F. Hemiphragma batheri *Bassler, 1911. A, longitudinal section, PMO 214.909; B, longitudinal section, PMO 214.910; C-D, tangential section, PMO 214.905; E-F, longitudinal section of exozone showing hemiphragms and wall structure, PMO 214.910. G-I.* Eridotrypa suecica *Brood, 1978. G, branch transverse section, PMO 214.901; H-I, branch longitudinal section, PMO 214.906.*

Family Trematoporidae Miller, 1889
Genus *Eridotrypa* Ulrich, 1893

Type species. *Cladopora aedilis* Eichwald, 1855 [= *Eridotrypa mutabilis* Ulrich, 1893]. Middle Ordovician, Estonia.

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, sometimes closed by calcitic skeleton. Acanthostyles rare to common, small and short, sometimes absent. Small, needle-like structures in zooecial walls may occur.

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

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

Eridotrypa suecica Brood, 1978
Figure 5G-I, 6A-C; Table 5

1978 *Eridotrypa suecica* Brood: 58, pl. 5, figs 1-3.

Material. PMO 214.883, PMO 214.884, PMO 214.888, PMO 214.890, PMO 214.895, PMO 214.896, PMO 214.897, PMO 214.899, PMO 214.901, PMO 214.906, PMO 214.907.

Description. Ramose colonies, branch diameter 1.05-2.50 mm, with 0.20-0.48 mm wide exozones and 0.65-1.54 mm wide endozones. Autozooecia long, oriented for long distance parallel to branch axis, bending slightly in exozone, polygonal and having larger diameter in endozone, oval to rounded-polygonal in exozone. Autozooecial diaphragms spaced widely in endozone, more densely in inner exozone, and usually absent in outermost parts of zooecia. Mesozooecia rare, small, short, polygonal in cross section, spaced usually at junctions between autozooecia, bearing closely spaced diaphragms. Acanthostyles common, 3-4 surrounding each aperture, small, having narrow hyaline cores, restricted to exozone. Autozooecial walls in endozone having indistinct lamination, 0.005-0.010 mm thick, becoming continually thicker in the inner exozone. Autozooecial walls in exozone displaying serrated dark border between autozooecia and distinct reverse V-shaped lamination.

Comparison. *Eridotrypa suecica* Brood, 1978 differs from *E. obliqua* Conti, 1990 in having smaller autozooecial apertures (average autozooecial aperture width 0.10 mm vs. 0.16 mm in *E. obliqua*).

Occurrence. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway. Dalmanitina beds (Upper Ordovician, Hirnantian); Sweden.

Genus *Trematopora* Hall, 1852

Type species. *T. tuberculosa* Hall, 1852; Lower Silurian (Niagaran); North America.

Diagnosis. Ramose colonies, often beginning from encrusting base. Autozooecial apertures oval to rounded with peristomes. Diaphragms usually rare, often absent in endozone. Abundant mesozooecia with abundant diaphragms, thin-walled and beaded in initial parts of exozone, near colony surface becoming thick-walled. Mesozooecial apertures completely covered by laminated skeleton. Acanthostyles abundant, often arranged near outer peristome range or in mesozooecial walls. Walls thin in endozone, thickened in peripheral parts of exozone displaying obliquely laminated microstructure.

Comparison. *Trematopora* Hall, 1852 differs from *Batostoma* Ulrich, 1882 by having oval to rounded autozooecial apertures and abundant mesozooecia covered with skeletal material, from *Eridotrypa* Ulrich, 1893 by having autozooecia that bend sharply in exozone, possess rounded apertures and are arranged irregularly on the colony surface, as well as by abundant acanthostyles.

Occurrence. Ordovician to Silurian, worldwide.

Table 5. Descriptive statistics of *Eridotrypa suecica* Brood, 1978. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch Width, mm	13	1.61	0.484	30.08	1.05	2.50
Exozone Width, mm	13	0.32	0.093	29.41	0.20	0.48
Autozooecial Aperture Width, mm	20	0.10	0.017	17.40	0.07	0.12
Aperture Spacing, mm	20	0.20	0.023	11.63	0.16	0.24
Acanthostyle Diameter, mm	5	0.03	0.007	19.17	0.03	0.04
Exozonal Wall Thickness, mm	11	0.08	0.030	39.37	0.05	0.15
Axial Zooecia Width, mm	10	0.22	0.031	14.19	0.18	0.25

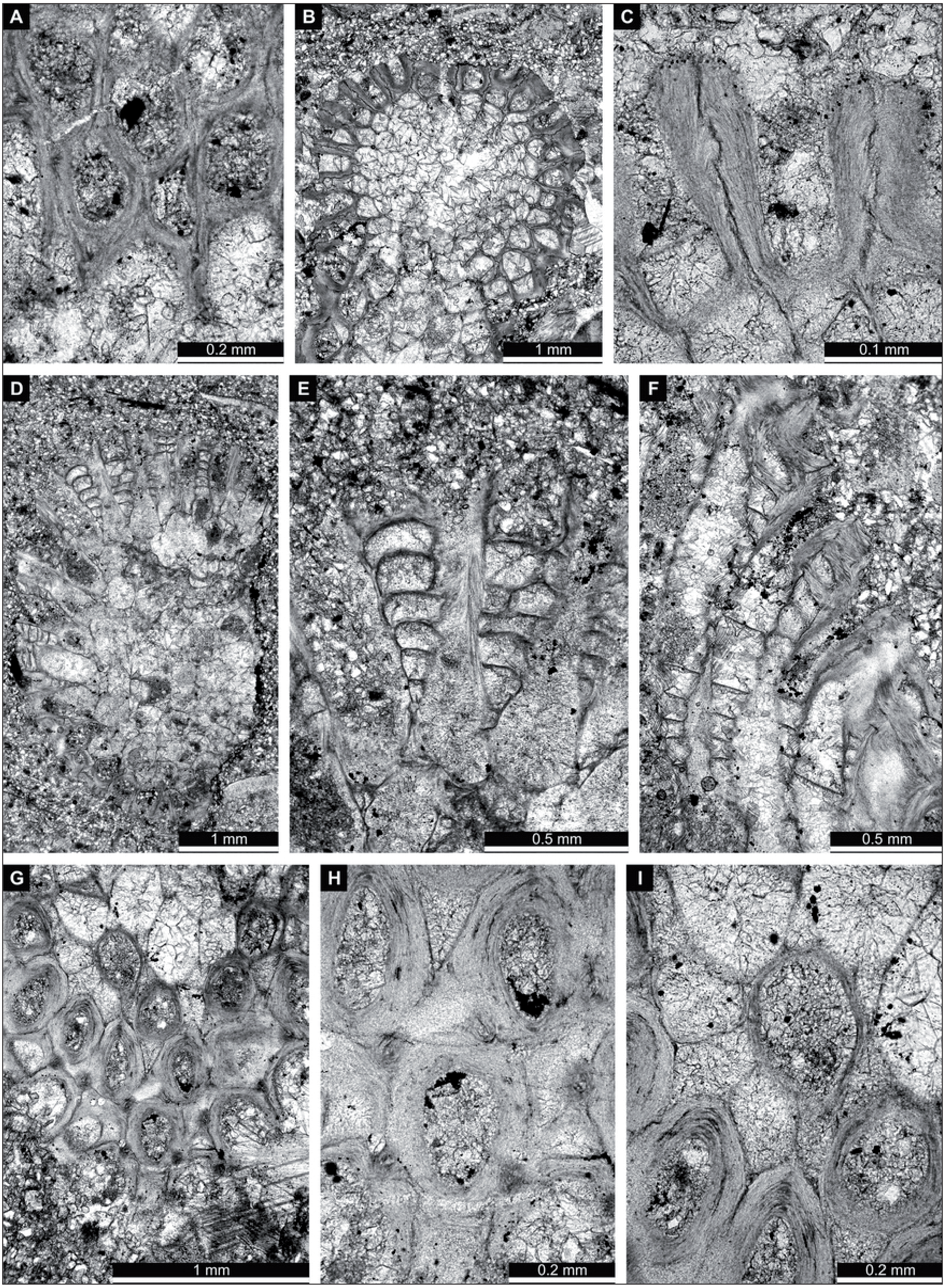

Figure 6. A-C. Eridotrypa suecica Brood, 1978. A, tangential section, PMO 214.896; B-C, branch transverse section, PMO 214.906. D-I. Trematopora brutoni sp. nov. D-E, branch transverse section, paratype PMO 214.887; F, longitudinal section of exozone showing autozooecia and mesozooecia, paratype PMO 214.893; G-I, tangential section showing autozooecia, mesozooecia and acanthostyles, holotype PMO 214.901.

Trematopora brutoni sp. nov.
Figure 6D-I; Table 6

Etymology. The new species is named in honour of David L. Bruton, who has contributed extensively to the study of the Lower Palaeozoic of the Oslo Region.

Holotype. PMO 214.901.

Paratypes. PMO 214.876, PMO 214.877, PMO 214.879, PMO 214.884, PMO 214.887, PMO 214.890, PMO 214.893, PMO 214.896, PMO 214.900, PMO 214.903, PMO 214.906, PMO 214.907.

Type locality. Bergevika, Helgøya (UTM WGS84 32V60992-673653), Norway.

Type horizon. Mjøsa Formation (Upper Ordovician, Katian).

Diagnosis. Ramose colonies with distinct narrow exozone; autozooecia polygonal in exozone, rounded to angular in endozone; basal diaphragms rare; 4-8 mesozooecia surrounding each aperture; 3-4 acanthostyles surrounding each aperture.

Description. Ramose colonies, branch diameter 2.6-5.2 mm. Exozone distinct, 0.3-0.9 mm wide, endozone 2.0-3.4 mm wide. Autozooecia long, polygonal in cross section in endozone, bending sharply in exozone. Autozooecial apertures rounded to slightly angular. Autozooecial diaphragms rare, thin. Mesozooecia abundant, originating at base of exozone, beaded in places of development of diaphragms, 4-8 surrounding each aperture. Diaphragms in mesozooecia straight, 5-6 spaced per 1 mm of mesozooecial length. Acanthostyles large, prominent, having distinct hyaline cores, 3-4 surrounding each aperture. Autozooecial walls 0.005-0.010 mm thick, granular-prismatic in endozone; laminated, 0.06-0.12 mm thick in exozone.

Comparison. *Trematopora brutoni* sp. nov. differs from *T. sardoa* (Vinassa de Regny, 1910) from the Upper Ordovician of Italy and France in having larger autozooecial apertures (average autozooecial aperture width 0.16 mm vs. 0.09 mm in *T. sardoa*).

Suborder Amplexoporina Astrova, 1965
Family Amplexoporidae Miller, 1889
Genus *Anaphragma* Ulrich & Bassler, 1904

Type species. *Anaphragma mirabile* Ulrich & Bassler, 1904. Upper Ordovician (Richmondian); USA (Illinois).

Diagnosis. Ramose colonies. Walls in endozone range from straight to crenulated, laminated and generally displaying dark zooecial boundaries; in exozone laminae forming U-shaped pattern in longitudinal section, but a V-shaped pattern common in walls of early exozones occurring throughout the length of zooecia in some colonies; in tangential section amalgamate. Thin, complete diaphragms are sparsely distributed, one to several in a very few zooecia; most zooecia completely lacking diaphragms. Laminated acanthostyles common, extremely variable in their dimensions within the species. Exilazooecia common to rare, having walls comparable in thickness with zooecia (modified after Boardman 1960).

Comparison. *Anaphragma* Ulrich & Bassler, 1904 differs from *Amplexopora* Ulrich, 1882 in absence of diaphragms and in strongly crenulated endozonal walls.

Occurrence. Lower to Upper Ordovician of Europe and North America.

Anaphragma latviense Pushkin, 1976
Figure 7A-G; Table 7

1976 A*naphragma latviense* Pushkin: 295-296, pl. 3, fig. 3, pl. 4, fig. 1.

Material. PMO 214.890, PMO 214.892, PMO 214.893, PMO 214.894, PMO 214.900, PMO 214.902.

Description. Ramose colonies, branch diameter 5.0-5.5 mm. Exozone distinct, 0.7-0.9 mm wide, endozone 3.6-3.7 mm wide. Autozooecia long, polygonal in cross section in endozone, bending sharply in exozone. Autozooecial apertures angular with rounded corners. Autozooecial diaphragms absent. Exilazooecia rare, originating at base of exozone. Acanthostyles moderately large, having indistinct hyaline cores and laminated sheaths, generally rare

Table 6. Descriptive statistics of *Trematopora brutoni* sp. nov. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch Width, mm	7	3.5	0.921	26.06	2.6	5.2
Exozone Width, mm	7	0.6	0.198	32.66	0.3	0.9
Autozooecial Aperture Width, mm	25	0.16	0.031	18.66	0.12	0.22
Aperture Spacing, mm	25	0.34	0.037	10.84	0.28	0.42
Mesozooecia Width, mm	25	0.14	0.045	31.22	0.07	0.24
Acanthostyle Diameter, mm	25	0.06	0.010	17.04	0.04	0.09
Mesozooecial Diaphragms Spacing, mm	25	0.11	0.033	29.60	0.05	0.16

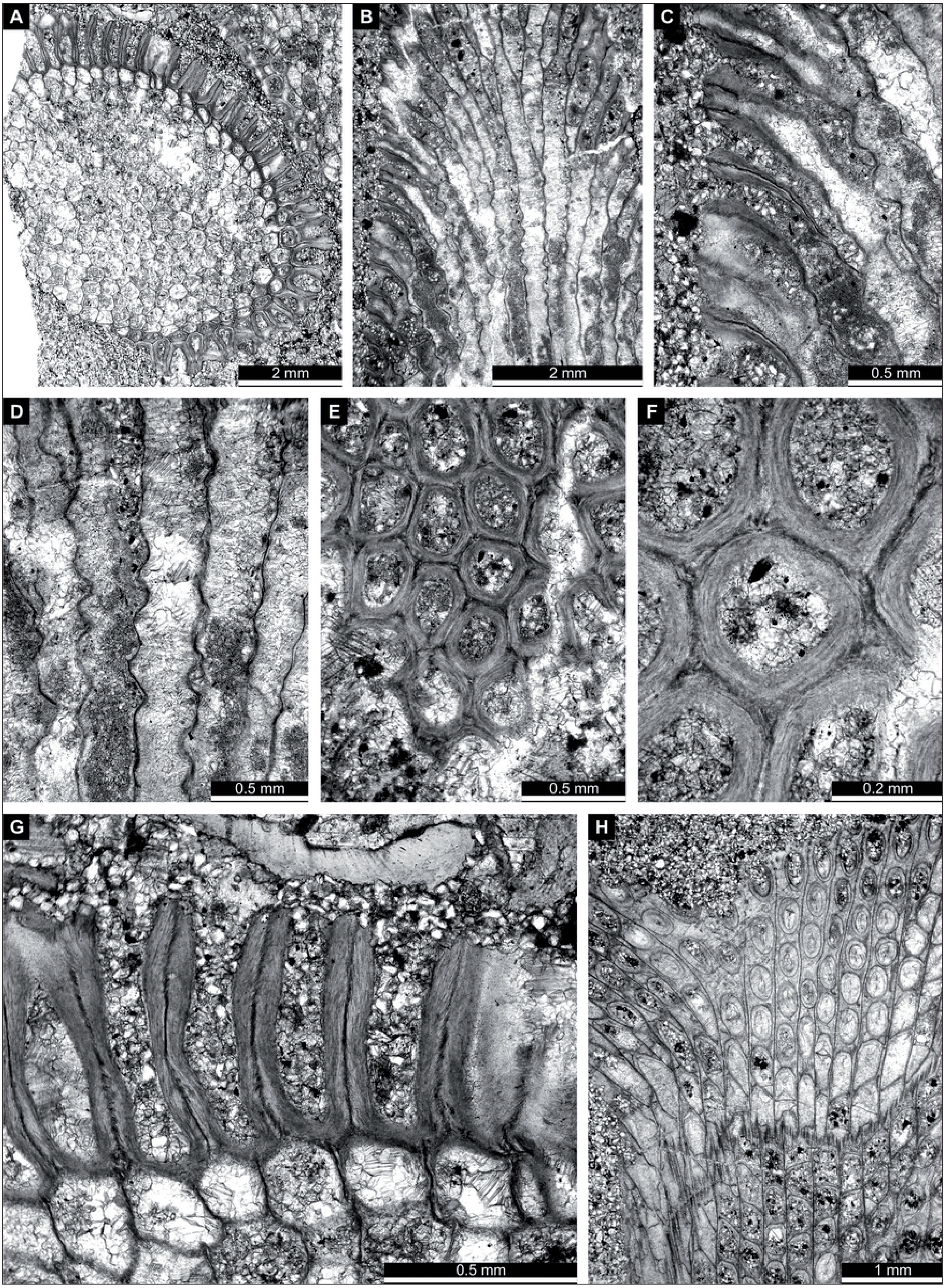

Figure 7. A-G. Anaphragma latviense *Pushkin, 1976. A, branch transverse section, PMO 214.900; B-D, longitudinal section showing autozooecial walls in endozone and exozone, PMO 214.890; E-F, tangential section, PMO 214.890; G, transverse section showing autozooecia in exozone, PMO 214.900. H,* Trigonodictya cyclostomoides *(Eichwald, 1855), branch oblique section, PMO 214.882.*

Table 7. Descriptive statistics of *Anaphragma latviense* Pushkin, 1976. Abbreviations as for Table 1

	N	X	SD	CV	MIN	MAX
Branch Width, mm	5	5.2	0.232	4.43	5.0	5.5
Exozone Width, mm	5	0.8	0.091	10.91	0.7	0.9
Autozooecial Aperture Width, mm	35	0.20	0.038	18.62	0.16	0.31
Aperture Spacing, mm	35	0.32	0.044	13.45	0.26	0.48
Exilazooecia Width, mm	20	0.07	0.023	33.43	0.03	0.11
Exozonal Wall Thickness, mm	30	0.136	0.033	24.56	0.065	0.210

to common, but locally abundant, 3-6 surrounding each aperture. Autozooecial walls 0.005-0.010 mm thick, granular-prismatic, strongly crenulated in endozone; laminated, 0.066-0.210 mm thick in exozone.

Comparison. A*naphragma latviense* Pushkin, 1976 is similar to *A. mirabile* Ulrich & Bassler, 1904, but differs from the latter in having smaller autozooecial apertures (average autozooecial aperture width 0.20 mm vs. 0.27 mm in *A. mirabile*).

Occurrence. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway. Rakvere Stage (Caradoc, Upper Ordovician); Latvia.

Order Cryptostomata Vine, 1884
Suborder Ptilodictyina Astrova & Morozova, 1956
Family Rhinidictyidae Ulrich, 1893
Genus *Trigonodictya* Ulrich, 1893
[= *Astreptodictya* Karklins, 1969]

Type species. *Pachydictya conciliatrix* Ulrich, 1886. Middle Ordovician (Decorah Shale); USA (Minnesota).

Diagnosis. Irregularly branched colonies, sometimes with lateral ridge-like expansions. Mesotheca straight to sinuous in longitudinal section, locally zigzag in transverse section, containing median rods. Autozooecia arranged in straight ranges, subrectangular to subrhomboidal in transverse section of endozone, locally separated by extrazooecial vesicles in endozone, separated by extrazooecial stereom in exozone, rectangular in deep tangential section, becoming oval on the colony surface. Basal diaphragms straight to slightly curved. Extrazooecial skeletal deposits common, consisting of laminar and vesicular portions. Vesicular structures common in inner exozones, locally in endozones. Laminar stereom commonly with dark zones, longitudinally aligned, locally with indistinct mural spines. Autozooecial boundaries distinct, delineated laterally by continuous dark zones. Monticules absent.

Comparison. *Trigonodictya* Ulrich, 1893 differs from *Pachydictya* Ulrich, 1882 in regular arrangement of autozooecia in straight rows.

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

Trigonodictya cyclostomoides (Eichwald, 1855)
Figure 7H, 8A-F; Table 8

1855 *Micropora cyclostomoides* Eichwald: 459.
1859 *Micropora (Stictopora) cyclostomoides* Eichwald, 1855: 394, pl. 24, figs 16a-b.

Material. PMO 214.878, PMO 214.880, PMO 214.881, PMO 214.882, PMO 214.883, PMO 214.884, PMO 214.885, PMO

Table 8. Descriptive statistics of *Trigonodictya cyclostomoides* (Eichwald, 1855). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch Width, mm	4	3.06	0.575	18.80	2.65	3.90
Branch Thickness, mm	7	0.69	0.082	11.81	0.60	0.84
Autozooecial Aperture Width, mm	35	0.11	0.019	16.83	0.08	0.15
Aperture Spacing Along Branch, mm	35	0.41	0.054	13.28	0.30	0.52
Aperture Spacing Across Branch, mm	35	0.31	0.042	13.59	0.25	0.42
Maximal Chamber Width, mm	25	0.20	0.025	12.10	0.15	0.26
Median Rods Spacing, mm	20	0.07	0.014	20.89	0.05	0.10

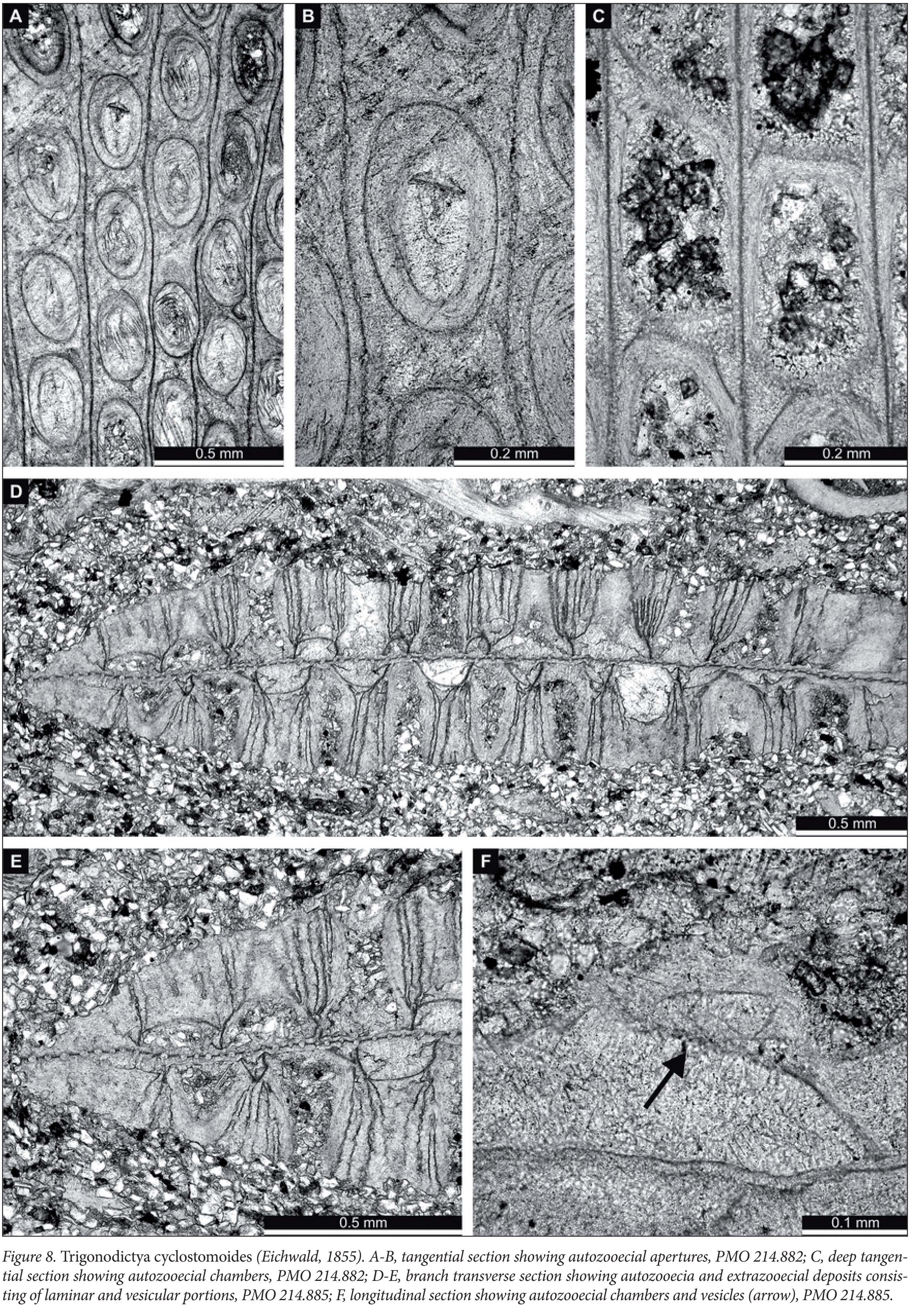

Figure 8. Trigonodictya cyclostomoides *(Eichwald, 1855). A-B, tangential section showing autozooecial apertures, PMO 214.882; C, deep tangential section showing autozooecial chambers, PMO 214.882; D-E, branch transverse section showing autozooecia and extrazooecial deposits consisting of laminar and vesicular portions, PMO 214.885; F, longitudinal section showing autozooecial chambers and vesicles (arrow), PMO 214.885.*

214.886, PMO 214.887, PMO 214.889, PMO 214.898, PMO 214.908.

Description. Branched bifoliate, dichotomous colonies. Branches flattened, with sharp edges, 2.65-3.90 mm wide and 0.60-0.84 mm thick. Mesotheca three-layered, straight both in longitudinal and transverse sections, containing abundant median rods, 0.025-0.045 mm thick. Median rods densely spaced, 0.010-0.030 mm in diameter, continuous in dark zones separating longitudinal rows of autozooecia. Autozooecia regularly arranged in 9-12 alternating longitudinal rows, semicircular to trapezoid in transverse section in endozone, rectangular in deep tangential section, becoming oval on the colony surface. Autozooecial boundaries distinct, delineated laterally by continuous dark zones. Basal diaphragms rare or absent, straight. Extrazooecial skeletal deposits well developed, consisting of laminar and vesicular portions. Vesicular structures small, having flat to rounded roofs, rare to common in inner exozones. Laminar stereom with dark zones, longitudinally aligned, separating autozooecia in exozones. Monticules absent.

Comparison. T*rigonodictya cyclostomoides* (Eichwald, 1855) differs from *T. conciliatrix* (Ulrich, 1886) in having thinner colonies, rare diaphragms and weakly developed vesicular structures.

Occurrence. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway. Jövi – Keila stages (Upper Ordovician, Caradoc); Baltic region and NW Russia.

Suborder Stictoporellina Gorjunova *in* Gorjunova & Lavrentjeva, 1993
Family Stictoporellidae Nickles & Bassler, 1900
Genus *Astrovidictya* Gorjunova & Lavrentjeva, 1993

Type species. *A. sparsa* Lavrentjeva *in* Gorjunova & Lavrentjeva, 1993. Upper Ordovician, Caradoc, north-western Russia, Estonia, and Lithuania.

Diagnosis. Branching bifoliate colonies, branches oval or lens-shaped in cross-section. Mesotheca straight or crenulated, containing hyaline rods. Autozooecial diaphragms rare. Both superior and inferior hemisepta present, straight or hook-shaped, long. Apertures oval or elliptical. Single or doubled metazooecia between autozooecial apertures, becoming abundant at branch edges. Flat maculae lacking autozooecia may occur.

Remarks. *Astrovidictya* Gorjunova & Lavrentjeva, 1993 differs from *Oanduella* Männil, 1958 in having branched instead of reticulated anastomosing colonies as well as regular arrangement of metazooecia.

Occurrence. Upper Ordovician (Caradoc); NW Russia, Estonia, Lithuania. Upper Ordovician (Upper Caradoc to Lower Ashgill); Montagne Noire, southern France. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway.

Astrovidictya sparsa Lavrentjeva *in* Gorjunova & Lavrentjeva, 1993
Figure 9A-F; Table 9

1993 *Astrovidictya sparsa* Lavrentjeva: 86-87, pl. 16, fig. 4, pl. 17, fig. 1.
2007 *Astrovidictya sparsa* Lavrentjeva, 1993 – Ernst & Key: 410-413, pl. 19, figs 5-12, pl. 20, figs 1-3.

Material. Two thin sections of the same colony PMO 214.892, PMO 214.894.

Description. Bifoliate branching colony, ca 2.5 mm wide. Autozooecia short, bending sharply toward colony surface, rectangular at base, becoming oval at colony surface. Autozooecia arranged in 14 regular rows. Superior hemisepta long, thick, curved proximally; inferior hemisepta long, thin, straight. Metazooecia bottle-shaped, usually one, rarely two between autozooecia longitudinally, numerous along branch edges. Metazooecial apertures circular to oval, often sealed by skeletal material at colony surface, 0.02-0.05 mm in diameter. Zooecial walls granular, thin in endozone; thickened, coarsely laminated in exozone. Small granules (spherules) occurring at colony surface, few or none in deeper sections. Mesotheca could not be observed. Low longitudinal ridges developed on the colon surface.

Comparison. *Astrovidictya sparsa* Lavrentjeva *in* Gorjunova & Lavrentjeva, 1993 differs from *A. hamatilis* Lavrentjeva, 1993 in having larger apertures (0.08-0.13 mm vs. 0.05-0.10 mm in *A. hamatilis*), as well as an absence of diaphragms.

Occurrence. Upper Ordovician (Caradoc); NW Russia,

Table 9. Descriptive statistics of *Astrovidictya sparsa* Lavrentjeva *in* Gorjunova & Lavrentjeva, 1993. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Autozooecial Aperture Width, mm	25	0.10	0.016	16.37	0.08	0.13
Aperture Spacing Along Branch, mm	15	0.40	0.069	17.41	0.31	0.56
Aperture Spacing Across Branch, mm	15	0.24	0.028	11.81	0.20	0.30
Metazooecia Width, mm	20	0.03	0.009	29.39	0.02	0.05

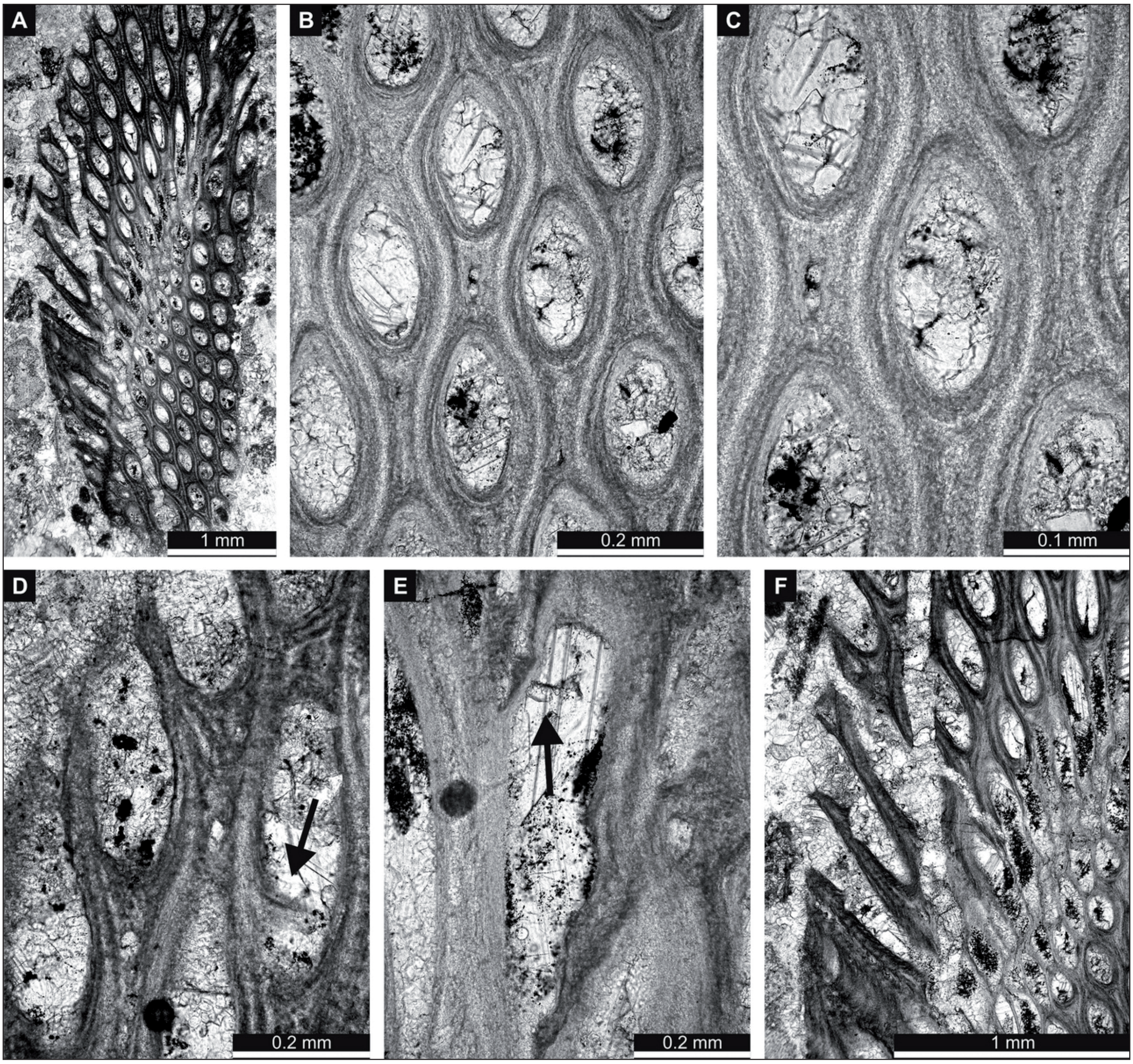

Figure 9. Astrovidictya sparsa *Lavrentjeva* in *Gorjunova & Lavrentjeva, 1993. A, oblique section of the branch, PMO 214.894; B-C, tangential section showing autozooecial apertures and metazooecia, PMO 214.894; D, shallow tangential section showing metazooecia, spherules in skeleton and superior hemiseptum (arrow); E, oblique section showing autozooecial chamber with thin inferior hemiseptum (arrow), PMO 214.892; F, oblique section of the colony, PMO 214.894.*

Estonia, Lithuania. Upper Ordovician (Upper Caradoc to Lower Ashgill); Montagne Noire, southern France. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway.

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