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, Eriodotrypa succeca Brood, 1978, Trematopora brutoni sp. nov. and Anaphragma latviense Pushkin, 1976. Two species belong to the Suborder Pitodictyina 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.

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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 (Bergstrøm 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-stromatoporoid bioherms are developed indicating a rather shallow depositional environment.

The age of the Mjøsa Formation has recently been refined by Bergstrøm et al. (2010) to span the late Sandbian-Katian stages of the Late Ordovician based on δ13C chemostратigraphy. Their conodont faunas can be correlated with coeval units of the North American Midcontinent, 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
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.

(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).
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:

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.


Comparison. *Esthoniopora* differs from *Esthonioporella* Modzalevskaya, 1953, in absence of acanthostyles and in having thin autozoecial 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. Autozoecia long, prismatic, growing from epitheca. Autozoecial apertures polygonal. Mesozooecia *sensu stricto* absent, immature zoecia smaller than autozoecia common. Hemiphragms abundant, restricting more than half of the autozoecial chamber space, curved proximally, tapering to their ends. Autozoecial walls amalgamated, 0.010-0.015 mm thick in endozone and 0.015-0.020 mm thick in exozone. Maculae consisting of larger autozoecia present, 1.95-2.34 mm in diameter.

Comparison. *Esthoniopora subsphaerica* (Bassler, 1911) differs from *E. communis* Bassler, 1911 in having smaller autozoecia (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 autozoecia in cross section, usually smaller autozoecia 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.


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.

<table>
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<tr>
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<th>N</th>
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<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
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<tbody>
<tr>
<td>Autozoecial Aperture Width, mm</td>
<td>20</td>
<td>0.25</td>
<td>0.036</td>
<td>14.27</td>
<td>0.19</td>
<td>0.31</td>
</tr>
<tr>
<td>Aperture Spacing, mm</td>
<td>20</td>
<td>0.29</td>
<td>0.031</td>
<td>10.99</td>
<td>0.24</td>
<td>0.36</td>
</tr>
<tr>
<td>Aperture Width, mm, macular</td>
<td>20</td>
<td>0.37</td>
<td>0.065</td>
<td>16.25</td>
<td>0.29</td>
<td>0.54</td>
</tr>
<tr>
<td>Aperture Spacing, mm, macular</td>
<td>20</td>
<td>0.45</td>
<td>0.071</td>
<td>15.87</td>
<td>0.36</td>
<td>0.54</td>
</tr>
<tr>
<td>Immature Zooecia Width, mm.</td>
<td>20</td>
<td>0.087</td>
<td>0.016</td>
<td>18.19</td>
<td>0.070</td>
<td>0.125</td>
</tr>
</tbody>
</table>
Family Mesotrypidae Astrowa, 1965
Genus Diazipora Vinassa de Regny, 1921

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


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. 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. Autozoococial apertures rounded to oval. Autozoococial 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 autozoecia completely from each other. Mesozooecial diaphragms planar, densely spaced. Autozoococial walls indistinctly laminated, 0.005-0.010 mm thick in endozone; displaying distinct reverse V-shaped structure with dark autozoococial border, having well developed wall cortex continued in diaphragms, 0.025-0.075 mm thick in exozone. Maculae indistinct, consisting of larger autozoecia.

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. elegantula), 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, Helgoya, Norway.

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

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

Family Mesotrypidae Astrowa, 1965
Genus Diazipora Vinassa de Regny, 1921

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


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. Autozoecia tubular, growing from epitheca. Autozoecial apertures rounded to slightly angular. Autozoecial diaphragms common, mainly inclined or cystoidal. Mesozooecia abundant, 8-9 surrounding each autozoecial aperture, completely isolating autozoecia, originating in endozone. Mesozooecial diaphragms densely spaced. Autozoecial 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 autozoecia and mesozooecia. PMO 214.883; B, transverse section, PMO 214.887; E-D, tangential section showing autozoecial apertures and mesozooecia, PMO 214.879. E-H. *Diazipora parva* (Bassler, 1911), PMO 214.889. E-F, longitudinal section showing autozoecia and mesozooecia (arrow – cystiphragmoid diaphragm); G-H, tangential section showing autozoecial apertures and mesozooecia.
**Table 3. Descriptive statistics of **Diazipora parva** (Bassler, 1911). Abbreviations as for Table 1.**

<table>
<thead>
<tr>
<th></th>
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<tr>
<td>Autozooecial Aperture Width, mm</td>
<td>20</td>
<td>0.14</td>
<td>0.017</td>
<td>12.11</td>
<td>0.12</td>
<td>0.18</td>
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<td>Aperture Spacing, mm</td>
<td>20</td>
<td>0.21</td>
<td>0.025</td>
<td>11.70</td>
<td>0.18</td>
<td>0.28</td>
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<tr>
<td>Mesozooecia Width, mm</td>
<td>20</td>
<td>0.04</td>
<td>0.013</td>
<td>31.30</td>
<td>0.02</td>
<td>0.07</td>
</tr>
<tr>
<td>Mesozooecial Diaphragms Spacing, mm</td>
<td>10</td>
<td>0.055</td>
<td>0.008</td>
<td>13.98</td>
<td>0.045</td>
<td>0.065</td>
</tr>
</tbody>
</table>

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, Helgoya, Norway.

**Family Heterotrypidae Ulrich, 1890**

**Genus Hemiphragma** Ulrich, 1893

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


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.

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

<table>
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<tr>
<th></th>
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<tbody>
<tr>
<td>Autozooecial Aperture Width, mm</td>
<td>25</td>
<td>0.20</td>
<td>0.042</td>
<td>20.37</td>
<td>0.12</td>
<td>0.26</td>
</tr>
<tr>
<td>Aperture Spacing, mm</td>
<td>25</td>
<td>0.31</td>
<td>0.041</td>
<td>13.22</td>
<td>0.23</td>
<td>0.40</td>
</tr>
<tr>
<td>Aperture Width, mm, macular</td>
<td>7</td>
<td>0.31</td>
<td>0.014</td>
<td>4.56</td>
<td>0.28</td>
<td>0.32</td>
</tr>
<tr>
<td>Aperture Spacing, mm, macular</td>
<td>7</td>
<td>0.45</td>
<td>0.037</td>
<td>8.18</td>
<td>0.40</td>
<td>0.50</td>
</tr>
<tr>
<td>Mesozooecia Width, mm</td>
<td>6</td>
<td>0.051</td>
<td>0.010</td>
<td>20.31</td>
<td>0.038</td>
<td>0.063</td>
</tr>
<tr>
<td>Acanthostyle Diameter, mm</td>
<td>20</td>
<td>0.037</td>
<td>0.008</td>
<td>21.06</td>
<td>0.025</td>
<td>0.050</td>
</tr>
<tr>
<td>Exozonal Wall Thickness, mm</td>
<td>20</td>
<td>0.089</td>
<td>0.017</td>
<td>19.25</td>
<td>0.055</td>
<td>0.125</td>
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</table>

**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, Helgoya, Norway.

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

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


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


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.

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


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*).

<table>
<thead>
<tr>
<th>Table 6. Descriptive statistics of <em>Trematopora brutoni</em> sp. nov. Abbreviations as for Table 1.</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
</tr>
<tr>
<td>-----------------</td>
</tr>
<tr>
<td>Branch Width, mm</td>
</tr>
<tr>
<td>Exozone Width, mm</td>
</tr>
<tr>
<td>Autozooecial Aperture Width, mm</td>
</tr>
<tr>
<td>Aperture Spacing, mm</td>
</tr>
<tr>
<td>Mesozooecia Width, mm</td>
</tr>
<tr>
<td>Acanthostyle Diameter, mm</td>
</tr>
<tr>
<td>Mesozooecial Diaphragms Spacing, mm</td>
</tr>
</tbody>
</table>
Figure 7. A-G. Anaphragma latviense Pushkin, 1976. A, branch transverse section, PMO 214.900; B-D, longitudinal section showing autozoecial walls in endozoone and exozone, PMO 214.890; E-F, tangential section, PMO 214.890; G, transverse section showing autozoecia in exozone, PMO 214.900. H, Trigonodictya cyclostomoides (Eichwald, 1855), branch oblique section, PMO 214.882.
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 lamellar 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. *Anaphragma 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

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

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


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

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

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


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

<table>
<thead>
<tr>
<th></th>
<th>N</th>
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<tr>
<td>Branch Width, mm</td>
<td>4</td>
<td>3.06</td>
<td>0.575</td>
<td>18.80</td>
<td>2.65</td>
<td>3.90</td>
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<tr>
<td>Branch Thickness, mm</td>
<td>7</td>
<td>0.69</td>
<td>0.082</td>
<td>11.81</td>
<td>0.60</td>
<td>0.84</td>
</tr>
<tr>
<td>Autozooecial Aperture Width, mm</td>
<td>35</td>
<td>0.11</td>
<td>0.019</td>
<td>16.83</td>
<td>0.08</td>
<td>0.15</td>
</tr>
<tr>
<td>Aperture Spacing Along Branch, mm</td>
<td>35</td>
<td>0.41</td>
<td>0.054</td>
<td>13.28</td>
<td>0.30</td>
<td>0.52</td>
</tr>
<tr>
<td>Aperture Spacing Across Branch, mm</td>
<td>35</td>
<td>0.31</td>
<td>0.042</td>
<td>13.59</td>
<td>0.25</td>
<td>0.42</td>
</tr>
<tr>
<td>Maximal Chamber Width, mm</td>
<td>25</td>
<td>0.20</td>
<td>0.025</td>
<td>12.10</td>
<td>0.15</td>
<td>0.26</td>
</tr>
<tr>
<td>Median Rods Spacing, mm</td>
<td>20</td>
<td>0.07</td>
<td>0.014</td>
<td>20.89</td>
<td>0.05</td>
<td>0.10</td>
</tr>
</tbody>
</table>
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 autozoecia and extrazoecial deposits consisting of laminar and vesicular portions, PMO 214.885; F, longitudinal section showing autozoecial chambers and vesicles (arrow), PMO 214.885.

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. Autozoocural 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. Trigonodictya 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 & Lavrentjeva, 1993
Family Stictoporellidae Nickles & Bassler, 1900
Genus Astrovidictya Gorjunova & Lavrentjeva, 1993


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


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. 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. Autozoocural 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. Trigonodictya 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


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


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. 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. Autozoocural 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. Trigonodictya 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.

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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.

Abbreviations as for Table 1.

<table>
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<tr>
<th></th>
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<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooecial Aperture Width, mm</td>
<td>25</td>
<td>0.10</td>
<td>0.016</td>
<td>16.37</td>
<td>0.08</td>
<td>0.13</td>
</tr>
<tr>
<td>Aperture Spacing Along Branch, mm</td>
<td>15</td>
<td>0.40</td>
<td>0.069</td>
<td>17.41</td>
<td>0.31</td>
<td>0.56</td>
</tr>
<tr>
<td>Aperture Spacing Across Branch, mm</td>
<td>15</td>
<td>0.24</td>
<td>0.028</td>
<td>11.81</td>
<td>0.20</td>
<td>0.30</td>
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<tr>
<td>Metazooecia Width, mm</td>
<td>20</td>
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<td>0.009</td>
<td>29.39</td>
<td>0.02</td>
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Estonia, Lithuania. Upper Ordovician (Upper Caradoc to Lower Ashgill); Montagne Noire, southern France. Mjøsa Formation (Upper Ordovician, Katian); Bergevika, Helgøya, Norway.

Acknowledgements – We are grateful to Magne Høyberget and Bjørn Funke for their help on our field trip to the studied locality. The Deutsche Akademische Austauschdienst (DAAD) supported Andrej Ernst’s study visit to the Natural History Museum, University of Oslo, with a one-year fellowship 2001-2002 (grant D/02/00949). Thanks to journal referees Catherine M. Reid and June R.P. Ross for their valuable comments improving the manuscript.

References

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