Bryozoans from the lower Silurian (Wenlock) Steinsfjorden Formation of Ringerike, southern Norway

ANDREJ ERNST & HANS ARNE NAKREM

A stenolaemate bryozoan fauna from the lower Silurian (Wenlock) Steinsfjorden Formation of the Ringerike district, southern Norway contains 10 species (2 cystoporates, 6 trepostomes, and 2 cryptostomes). Six species are new: *Heterotrypa ringerikensis* sp. nov., *Trematopora maculata* sp. nov., *Amplexopora crassiparietum* sp. nov., *A. evae* sp. nov., *Orthopora worsleyi* sp. nov., and *Mediaporina kiaeri* sp. nov. One species is described in open nomenclature: *Eridotrypella* sp. Trepostome bryozoans dominate this assemblage, both by diversity and abundance. The bryozoans occur in carbonates associated with evaporite minerals and sedimentary structures indicating very shallow depositional settings. *Key words:* lower Silurian, Bryozoa, Norway, taxonomy.


Andrej Ernst, Institut für Geologie, Universität Hamburg, Bundesstr. 55, D-20146 Hamburg, Germany; Andrej.Ernst@uni-hamburg.de • Hans Arne Nakrem, Natural History Museum (Geology), University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway; h.a.nakrem@nhm.uio.no

The purpose of this study is to describe the bryozoan fauna of the lower Wenlock Brattstad Member, Steinsfjorden Formation of the Ringerike district, Oslo Region, Norway (Fig. 1). The bryozoans present in these beds have been known since the work by Kiær (1908), but they have not until now been given a systematic treatment. The number of previously known species is low, and their distribution in Ringerike can add very little to the already established biostratigraphy of the area.

The Brattstad Member (upper “Etage” 9e and 9f of Kiær 1908) is 30 m thick in the studied areas of Nes bus stop, Ødegårdsviken and Åsa (Fig. 2). The lithology consists of medium to thickly bedded limestones with interbedded marls and dolomitic limestones. The limestones contain a relatively rich and varied fauna with thick massive favositid and oncolitic biostromes (the “Favosites Limestone” of Kiær 1908) near the top of the member from which the bryozoan material derives. Kiær (1908, p. 113) lists fossils from these beds (“Etage 9F”) in various localities in the Ringerike district, but only one bryozoan taxon, “Monticuliporen [*Amplexopora*(?) sp.]”, is mentioned. Whitaker (1977, pp. 24–26) also refers to the bryozoan-rich beds as “polyzoan (*Amplexopora*)” beds. Spjeldnes (1982) describes the bryozoan occurrences in these beds as “colonies ranging from only a few cm in diameter to small bioherms with three-dimensional frameworks”. Bryozoans are even found in the lowermost levels of the overlying red beds of the Ringerike Group (late Wenlock to Ludlow age). The age of the bryozoan beds are Sheinwoodian to Homarian as based on occurrences of ostracodes and brachiopods as well as agnathans and thelonots (on directly overlying beds) (Worsley et al. 1983, 2011). Geochemical analyses of interbedded bentonites (Hetherington et al. 2011) support these datings.

**Depositional environment**

Alternations of marls, red argillaceous dolomites, dolomitic limestones, and limestones, with occurrence of oosparite, oncilites, algal laminated dolomitic limestones with mud cracks, stromatolites as well as evaporitic minerals (Fig. 3B) indicate developments of shallow subtidal to supratidal environments (Olaussen 1981). The fossil components are characterized by many individuals belonging to few taxa, notably gastropods, ostracods, brachiopods and rare trilobites (Kiær 1908, Olaussen 1981). Tabulate corals (Fig. 3C) and echinoderms are locally present.

The common microfacies are represented by floatstones with abundant bryozoans (mainly trepostomes (Fig. 3A, F), locally poorly washed rudstones (Fig. 3E), and bryozoan and algal bindstones (Fig. 3B–D). The matrix is usually micrite-rich, containing various skeletal grains (Fig. 3G). Calcimicrobes are common on some localities,
represented by various *Girvanella* and *Rothpletzella* species. Microbial crusts are common, often forming oncoids (Fig. 3C).

The faunal composition and microfacies characteristics are reduced due to stressed conditions in an environment with fluctuating salinities.

**Material and methods**

Bryozoan samples were collected from the localities Nes bus stop, Ødegårsviken and Åsa (see Fig. 1). The investigated bryozoans were studied from thin sections using a transmitted light binocular microscope. 107 oriented and non-oriented thin sections were used. The material is housed at the Natural History Museum (Geology), Oslo, under numbers PMO 221.750–221.841.

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 (Fig. 4): Branch Width, Branch Thickness, Exo-(Endo-) zone Width, Autozooecial Aperture Width, Autozooecial Aperture Spacing (Along Branch/diagonally for cryptostomes), Acanthostyle Diameter, Lunarium Width/Length/Thickness, Vesicle Diameter/Spacing/Number per Aperture, Wall Thickness in Exozone, and Macular Diameter (Spacing), Autozooecial Diaphragm Spacing, Meso- (Exila-, Hetero-) zooecia Width, Mesozoecial 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.
Results and discussion

The bryozoan colonies are generally well preserved and show little signs of abrasion. Large, thin branches up to 5 mm in diameter are often not broken, the whole fauna has only been transported a short distance, and they may represent time intervals of more normal marine conditions. However, they are not considered preserved in situ. The bryozoans are therefore interpreted as typical for the depositional environment in which the sediments were formed. The three bryozoans species previously known have a Wenlock or Ludlow stratigraphic distribution elsewhere. The new species described herein have many similarities with species known from time equivalent strata in Europe and the USA, but only further research may reveal their biostratigraphic as well as biogeographic value.

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Cystoporata Astrova, 1964
Family Fistuliporidae Ulrich, 1882
Genus Fistulipora M’Coy, 1849
Type species. – Fistulipora minor M’Coy, 1849. Carboniferous; England.

Diagnosis. – Massive, encrusting or ramose colonies. Cylindrical autozooecia with thin walls and complete diaaphragms. Apertures rounded, possessing horse-shoe shaped lunaria. Autozooecia separated by the extrazooecial vesicular skeleton.

Comparison. – Fistulipora M’Coy, 1849 differs from Eridopora Ulrich, 1882 in having rounded, horseshoe-shaped lunaria instead of triangular ones. Furthermore, Eridopora develops persistently encrusting colonies, whereas Fistulipora may also develop massive and branched colonies.

Occurrence. – Ordovician to Permian; worldwide.

Fistulipora nummulina Nicholson & Foord, 1885
Figure 5A–E, Table 1

Table 1. Measurements of Fistulipora nummulina Nicholson & Foord, 1885. Abbreviations: N – number of measurements; X – mean; SD – standard deviation; CV – coefficient of variation; MIN – minimal value; MAX – maximal value.

<table>
<thead>
<tr>
<th>Character</th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture width, mm</td>
<td>33</td>
<td>0.16</td>
<td>0.027</td>
<td>16.46</td>
<td>0.12</td>
<td>0.22</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>31</td>
<td>0.24</td>
<td>0.035</td>
<td>14.41</td>
<td>0.17</td>
<td>0.32</td>
</tr>
<tr>
<td>Vesicle width, mm</td>
<td>23</td>
<td>0.10</td>
<td>0.031</td>
<td>32.55</td>
<td>0.03</td>
<td>0.15</td>
</tr>
<tr>
<td>Vesicle spacing, mm</td>
<td>25</td>
<td>0.10</td>
<td>0.028</td>
<td>28.98</td>
<td>0.06</td>
<td>0.15</td>
</tr>
<tr>
<td>Vesicles per aperture</td>
<td>8</td>
<td>6.0</td>
<td>1.414</td>
<td>23.57</td>
<td>4.0</td>
<td>8.0</td>
</tr>
</tbody>
</table>

Material. – PMO 221.756, PMO 221.758, PMO 221.790, PMO 221.764, PMO 221.817, PMO 221.820, PMO 221.822, PMO 221.824, PMO 221.827, PMO 221.829.

Description. – Encrusting colonies, 0.25–0.85 mm in thickness. Autozooecia growing from 0.002–0.008 m thick epitheca, bending sharply at their bases towards colony surface. Autozooecial apertures circular to oval. Basal dia-phragms rare to absent. Lunaria well developed, horseshoe shaped to slightly triangular, 0.06–0.08 mm wide, 0.03–0.04 mm long and 0.03–0.04 mm thick. Vesicles abundant, 4–8 surrounding each autozooecial aperture, irregularly shaped, medium in size, often large at the base, polygonal in tangential section, box-like to hemispheric, with plane or concave roofs in exozone. Autozooecial walls granular, 0.003–0.005 mm thick. Extensive extrazooecial material in exozone developed. Maculae not observed.

Remarks. – Fistulipora nummulina Nicholson & Foord, 1885 is similar to F. parva Hennig, 1908 from the Wenlock of Gotland, but differs by smaller autozooecial apertures (aperture width 0.12–0.22 mm vs 0.22–0.25 mm in F. parva). Fistulipora nummulina differs from F. ternavensis Astrova, 1965 from the lower Silurian (Wenlock) of Moldova in smaller and closer spaced autozooecial apertures (aperture width 0.12–0.22 mm vs 0.18–0.23 mm in F. ternavensis).


Fistulipora crustula Bassler, 1906
Figures 5F–J, 6A, B, Table 2

1906 Fistulipora crustula Bassler, p. 24, pl. 7, figs 7–10, pl. 8, figs 16, 17, pl. 23, fig. 15.

Material. – PMO 221.775–221.776.
Description. – Encrusting colonies, 0.65–1.38 mm in thickness. Autozooecia growing from 0.015–0.030 m thick epitheca, bending sharply at their bases towards colony surface. Autozooecial apertures circular to oval. Basal diaphragms rare to common, thin, deflected proximally. Lunaria well developed, horseshoe shaped. Vesicles irregularly shaped, medium in size, polygonal in tangential section, box-like to hemispheric, with concave roofs in exozone, 5–11 surrounding each autozooecial aperture. Autozooecial walls granular, 0.003–0.005 mm thick. Maculae consisting of vesicular skeleton common, 0.30–0.40 mm in diameter. Macrozoecia locally occurring.

Remarks. – Fistulipora crustula Bassler, 1906 is similar to F. crustuliformis Astrova, 1959 from the upper Silurian (Ludlow) of Tuva (Russia), but differs from the latter in smaller autozoecia (aperture width 0.18–0.25 mm vs 0.22–0.26 mm in F. crustuliformis).

Occurrence. – Rochester Shale, Wenlock, lower Silurian; USA. Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian; Ødegårdsviken, Ringerike, Norway.

Order Trepostomata Ulrich, 1882
Suborder Halloporina Astrova, 1965
Family Heterotrypidae Ulrich, 1890
Genus Heterotrypa Nicholson, 1879
Type species. – Monticulipora frondosa d’Orbigny, 1850. Upper Ordovician (Cincinnatian); North America.

Diagnosis. – Frondose, ramose or less commonly encrusting colonies. Autozooecial walls variably thick. Zoocelial boundaries form a conspicuous dark line in inner exozones and in a broad zone of abutting laminae or are completely obscured in outer exozones. Walls generally amalgamated. Diaphragms are generally few in endozones, but are moderately abundant in some species. In exozones, autozooecial diaphragms are closely and regularly spaced, thin, planar and perpendicular to
the zooecial walls. Intermonticular mesozooecia range from abundant and regularly arranged to scattered or absent. Mesozooecia commonly develop moniliform chambers at proximal ends and tend to become smaller or are terminated distally within exozones. Diaphragms in mesozooecia noticeably thicker and more closely spaced than autozooecial diaphragms. Acanthostyles common, small to moderately large, occurring both in endozone and exozone. Monticules generally have a central cluster of a few mesozooecia.

Remarks. – Heterotrypa differs from the most similar genus Dekayia Milne-Edwards & Haime, 1851 by having fewer and smaller acanthostyles as well as more abundant mesozooecia.

Occurrence. – Ordovician to Devonian; worldwide.

Heterotrypa ringerikense sp. nov.

Figures 6C–F, 7A–E, Table 3

Etymology. – The species has its name after Ringerike, an area SW of the Oslo Region, which is famous for its rich Silurian bryozoan-bearing rocks.

Holotype. – PMO 202.721B.


Type locality. – Ødegårdsviken, Ringerike, Norway.

Type stratum. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian.

Diagnosis. – Ramose branched colonies; secondary overgrowth common; autozooecial diaphragms rare to common, thin; mesozooecia rare to common; acanthostyles moderately large, 2–7 surrounding each autozooecial aperture; macroacanthostyles present; maculae consisting of macrozooecia.

Description. – Ramose branched colonies, branch diameter 2.4–5.0 mm. Exozone distinct, 0.45–1.25 mm wide, endozone 1.30–2.88 mm wide. Secondary overgrowth common, 0.65–1.00 mm in thickness. Autozooecial long, polygonal in cross section in endozone, bending sharply in exozone. Autozooecial apertures polygonal. Autozooecial diaphragms rare to common, thin, concentrated mainly in the transition between exo- and endozones. Mesozooecia rare to common, originating at base of exozone, beaded in places of development of diaphragms. Diaphragms in mesozooecia straight. Acanthostyles moderately large, prominent, having distinct hyaline cores, 2–7 surrounding each autozooecial aperture. Macroacanthostyles locally present. Autozooecial walls 0.005–0.010 mm thick, granular-prismatic in endozone; showing reversal V-shaped lamination, integrated with locally visible serrated dark border between zooecia, locally weakly monilae-shaped thickened, 0.013–0.050 mm thick in exozone. Maculae consisting of macrozooecia.

Remarks. – Heterotrypa ringerikense sp. nov. differs from H. enormis Astrova, 1959 from the upper Silurian (Ludlow) of western Tuva (Russia) by larger and more abundant acanthostyles (acanthostyle diameter 0.025–0.065 mm vs 0.03 mm in H. enormis; 2–7 acanthostyles around each aperture vs 3–4 in H. enormis). Heterotrypa ringerikense sp. nov. differs from H. ovata Astrova, 1957 from the upper Silurian (Ludlow) of western Tuva (Russia) by less abundant mesozooecia and by larger and more abundant acanthostyles (2–7 acanthostyles around each aperture vs 1–2 in H. ovata).

Occurrence. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian; Ødegårdsviken, Ringerike, Norway.

Genus Asperopora Owen, 1969

Type species. – Callopora aspera Hall, 1852. Silurian (Wenlock); USA (New York), England.
Table 3. Measurements of Heterotrypa ringerikense sp. nov. Abbreviations as in 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>6</td>
<td>3.50</td>
<td>1.172</td>
<td>33.51</td>
<td>2.40</td>
<td>5.00</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>6</td>
<td>0.74</td>
<td>0.312</td>
<td>42.08</td>
<td>0.45</td>
<td>1.25</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>6</td>
<td>2.01</td>
<td>0.612</td>
<td>30.40</td>
<td>1.30</td>
<td>2.88</td>
</tr>
<tr>
<td>Aperture width, mm</td>
<td>55</td>
<td>0.17</td>
<td>0.025</td>
<td>15.13</td>
<td>0.11</td>
<td>0.22</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>55</td>
<td>0.20</td>
<td>0.031</td>
<td>14.94</td>
<td>0.15</td>
<td>0.29</td>
</tr>
<tr>
<td>Aperture width, mm (macular)</td>
<td>20</td>
<td>0.24</td>
<td>0.025</td>
<td>10.47</td>
<td>0.2</td>
<td>0.28</td>
</tr>
<tr>
<td>Aperture spacing, mm (macular)</td>
<td>20</td>
<td>0.30</td>
<td>0.044</td>
<td>14.63</td>
<td>0.24</td>
<td>0.42</td>
</tr>
<tr>
<td>Mesozooecia width, mm</td>
<td>50</td>
<td>0.06</td>
<td>0.021</td>
<td>37.98</td>
<td>0.03</td>
<td>0.10</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>45</td>
<td>0.044</td>
<td>0.009</td>
<td>20.22</td>
<td>0.025</td>
<td>0.065</td>
</tr>
<tr>
<td>Macracanthostyle diameter, mm</td>
<td>20</td>
<td>0.067</td>
<td>0.012</td>
<td>17.22</td>
<td>0.043</td>
<td>0.088</td>
</tr>
<tr>
<td>Exozonal wall thickness, mm</td>
<td>45</td>
<td>0.030</td>
<td>0.010</td>
<td>31.96</td>
<td>0.013</td>
<td>0.050</td>
</tr>
<tr>
<td>Acanthostyles per aperture</td>
<td>45</td>
<td>3.7</td>
<td>1.424</td>
<td>38.38</td>
<td>2.0</td>
<td>7.0</td>
</tr>
<tr>
<td>Mesozooecial diaphragms spacing, mm</td>
<td>10</td>
<td>0.10</td>
<td>0.025</td>
<td>25.40</td>
<td>0.05</td>
<td>0.14</td>
</tr>
</tbody>
</table>

**Material.** – PMO 221786–221.787, PMO 221.793, PMO 221.798, PMO 221.800.

**Description.** – Encrusting colonies, 0.7–1.0 mm thick. Autozoecia budding from a thin epitheca, growing a short distance parallel to the substrate, then bending sharply to the colony surface. Autozoecial apertures rounded-polygonal. Autozoecial diaphragms common, straight, thin. Acanthostyles abundant, 1–3 surrounding each aperture, originating at the base of exozone, having distinct calcite cores and dark, laminated sheaths, deeply indenting into autozoecial space. Mesozooecia abundant, 6–11 surrounding each autozoecial aperture, rounded-polygonal in transverse section, originating at the base of exozone. Autozoecial walls laminated, merged, 0.020–0.050 mm thick. Maculae not observed.

**Occurrence.** – Upper Ordovician to upper Silurian; Europe, USA.

**Asperopora bellum** (Pushkin, 1976)

Figure 7F–I, Table 4

1976 *Lioclema bellum* Pushkin, pp. 30–31, text-fig. 13, pl. 11, fig. 3.
peripheral parts of exozone displaying obliquely laminated microstructure.

Remarks. – *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.

*Trematopora maculata* sp. nov.

Figure 8A–H, Table 5

Etymology. – The species is named after presence of maculae of macrozooecia.

Holotype. – PMO 221.816.

Paratypes. – PMO 221.783–PMO 221.784, PMO 221.786–PMO 221.787, PMO 221.791, PMO 221.799, PMO 221.815, PMO 221.817–221.841.

Type locality. – Ødegårdsviken, Ringerike, Norway.

Type stratum. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian.

Diagnosis. – Branched colonies with distinct exozones; secondary overgrowth common; autozooecial diaphragms rare to common; mesozooecia common to abundant in exozone, beaded, 2–4 surrounding each autozooecial aperture; acanthostyles moderately large, 1–4 surrounding each autozooecial aperture; autozooecial walls laminated with locally visible zooecial border, locally monilae-shaped thickened, maculae of few macrozooecia.

Description. – Ramose branched colonies, branch diameter 2.7–4.6 mm. Exozone distinct, 0.4–1.1 mm wide, endozone 1.4–2.6 mm wide. Secondary overgrowth common. Autozooecia long, polygonal in cross section in endozone, bending sharply in exozone. Autozooecial apertures rounded to slightly angular. Autozooecial diaphragms rare to common, thin, concentrated mainly in the transition between exo- and endozones. Mesozooecia common to abundant, originating at base of exozone, beaded in places of development of diaphragms, 2–4 surrounding each autozooecial aperture. Diaphragms in mesozooecia straight, abundant. Acanthostyles moderately large, prominent, having distinct hyaline cores, 1–4 surrounding each autozooecial aperture. Acanthostyles highly thickened, granular-prismatic in endozone; showing reversal V-shaped lamination, integrated with locally visible dark border between zooecia, locally monilae-shaped thickened, 0.02–0.06 mm thick in exozone. Maculae formed by few macrozooecia.
Remarks. – *Trematopora maculata* sp. nov. is similar to *T. beikhemensis* Astrova, 1959 from the Wenlock of western Tuva (Russia), but differs by presence of macrozooecia, broader exozozone, and thicker walls. *Trematopora maculata* sp. nov. differs from *T. cristata* Kopaevich, 1984 from the Wenlock of Mongolia by presence of macrozooecia and less elongated apertures.

Occurrence. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian; Ødegårdsviken, Ringerike, Norway.

Suborder Amplexoporina Astrova, 1965
Family Amplexoporidae Miller, 1889

**Genus Amplexopora** Ulrich, 1882

*Type species.* – *Atactopora septosa* Ulrich, 1879. Upper Ordovician; USA.

*Diagnosis.* – Ramose, frondescent, incrusting or massive colonies. Monticules generally well developed. Wall structure commonly appearing integrate in the exozozone, sometimes amalgamate. Laminae from adjacent zooecia intersect a sharply defined zoecial boundary at angles of less than 90° to form a V-shaped pattern pointing distally. Distinct zoecial linings present in several species. Diaphragms are extremely variable in thickness, curvature, parallelism and spacing, with compound and cystoidal diaphragms and cystiphragms common in many species. Mesozooecia lacking or few; early chambers are beaded and later diaphragms regularly and closely spaced. Acanthostyles usually abundant and of two types: those that are concentrated generally in zoecial and extend throughout the width of the exozozone, occurring in all species; and additional acanthostyles that are concentrated between zoecial corners and extend through a part of the exozozone width occurring in some species. These additional acanthostyles cause inflections of zoecial walls.

Remarks. – *Amplexopora* differs from *Monotrypa* by abundant diaphragms and wall microstructure with sharply defined zoecial boundary.

Boardman (1960) revised the genus *Amplexopora* and designated *Atactopora septosa* Ulrich, 1879 as the type species. According to the emended diagnosis of Boardman (1960) (followed here), *Amplexopora* possesses mesozooecia with abundant diaphragms. On the contrary, Astrova (1978, p. 105) mentioned exilazooecia in *Amplexopora*, tube-like heterozoecia without or with few diaphragms. Based on this character she defined the suborder Amplexoporina, which comprises trepostome bryozoans with exilazooecia. Furthermore, Astrova (1978) re-designated *Amplexopora cingulata* Ulrich, 1882 as the type species of *Amplexopora*. According to Boardman (1960, p. 17) this species was never described or figured (except in Astrova 1978, pl. 17, fig. 2).

Occurrence. – Lower Ordovician–lower Silurian; North America, Australia, Siberia, Europe.

*Amplexopora crassiparietum* sp. nov.

*Figure* 9A–F, *Table* 6

*Etymology.* – The species is named after its thick walls (from Latin "crassus" = thick, and "parietis" = wall).

*Holotype.* – PMO 221.770.

*Paratypes.* – PMO 221.750–221.755, PMO 221.757, PMO 221.760, PMO 221.761–221.762, PMO 221.765–221.769, PMO 221.765, PMO 221.807–221.808, PMO 221.810, PMO 221.811, PMO 221.814.

*Type locality.* – Nes bus stop, Ringerike, Norway.

*Type stratum.* – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian.

*Diagnosis.* – Branched colonies with distinct wide exozozone; autozooecial apertures polygonal; mesozooecia rare; acanthostyles common, spaced 1 to 5 around autozooecial apertures, moderate in size, locally absent; maculae consisting of macrozooecia.

*Description.* – Branched colonies, branch diameter 2.75–5.20 mm. Exozozone distinct, 0.40–1.40 mm wide, endozozone 1.55–2.90 mm wide. Secondary overgrowths absent. Autozooecia long, growing parallel to branch axis for a long distance in endozozone, in exozozone bending, having polygonal shape in transverse section in endozozone. Autozooecial apertures polygonal. Diaphragms in endozozone rare, planar, thin; in exozozone abundant, straight or slightly curved. Mesozooecia rare, small, polygonal in cross section, restricted to exozozone. Acanthostyles common, spaced 1 to 5 around autozooecial apertures, moderate in size, having distinct hyaline cores and wide,
**Remarks.** – *Amplexopora crassiparietum* sp. nov. differs from *A. silurica* Astrova, 1970 from the lower Silurian (Llandovery) of Ukraine (Podolia) in smaller autozoecial apertures (aperture width 0.08–0.14 mm vs 0.17–0.20 mm in *A. silurica*), and in less abundant acanthostyles (1–5 vs 4–7 per autozoecial aperture in *A. silurica*).

**Occurrence.** – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian; Nes bus stop and Åsa, Ringerike, Norway.

*Amplexopora evae* sp. nov.  
Figures 10A–F, 11A, B, Table 7

**Etymology.** – The species is named for the junior author’s wife to honour her participation in bryozoan fieldwork.

**Holotype.** – PMO 170.890.

**Paratypes.** – PMO 170.886, PMO 170.882, PMO 170.887–170.888, PMO 221.773–221.777, PMO 221.780, PMO 221.804–221.805.

**Type locality.** – Ødegårdsviken, Ringerike, Norway.

**Type stratum.** – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian.

**Diagnosis.** – Branched and encrusting colonies; branches with distinct wide exozones; autozoecial apertures polygonal; mesozooecia rare; acanthostyles common, spaced 1 to 5 around autozoecial apertures, moderate in size, locally absent; maculae consisting of macrozooecia.

**Description.** – Branched colonies, branch diameter 2.55–3.40 mm. Exozone distinct, 0.35–1.00 mm wide, endozone 1.10–2.18 mm wide. Secondary overgrowths common, 0.65–2.50 mm thick. Encrusting colonies 1.5–2.5 mm thick. In branched colonies, autozoecia long, growing parallel to branch axis for a long distance in endozone, in exozone bending, having polygonal shape in transverse section in endozone. In encrusting colonies autozoecia arise directly from the epitheca with narrow endozonal part. Acanthostyles common, spaced 1 to 5 around autozoecial apertures, moderate in size, having distinct hyaline cores and wide, dark sheaths, situated in the dark median lining of autozoecial walls, originating from base of exozone; locally acanthostyles absent. Autozoecial walls in endozone 0.005–0.010 mm thick, granular; in exozone 0.030 to 0.135 mm thick, displaying reverse V-shaped lamination with dark, serrated median lining. Maculae indistinct, 0.8–1.3 mm in diameter, consisting of macrozooecia.

**Table 6.** Measurements of *Amplexopora crassiparietum* sp. nov. Abbreviations as in 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>10</td>
<td>3.91</td>
<td>0.916</td>
<td>23.43</td>
<td>2.75</td>
<td>5.20</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>10</td>
<td>0.90</td>
<td>0.312</td>
<td>34.64</td>
<td>0.40</td>
<td>1.40</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>10</td>
<td>2.11</td>
<td>0.439</td>
<td>20.80</td>
<td>1.55</td>
<td>2.90</td>
</tr>
<tr>
<td>Aperture width, mm</td>
<td>40</td>
<td>0.11</td>
<td>0.017</td>
<td>15.93</td>
<td>0.08</td>
<td>0.14</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>40</td>
<td>0.20</td>
<td>0.023</td>
<td>11.33</td>
<td>0.15</td>
<td>0.26</td>
</tr>
<tr>
<td>Aperture width, mm (macular)</td>
<td>16</td>
<td>0.19</td>
<td>0.030</td>
<td>15.72</td>
<td>0.15</td>
<td>0.25</td>
</tr>
<tr>
<td>Aperture spacing, mm (macular)</td>
<td>16</td>
<td>0.26</td>
<td>0.023</td>
<td>9.14</td>
<td>0.22</td>
<td>0.30</td>
</tr>
<tr>
<td>Mesozooecia width, mm</td>
<td>30</td>
<td>0.048</td>
<td>0.013</td>
<td>26.91</td>
<td>0.025</td>
<td>0.078</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>30</td>
<td>0.034</td>
<td>0.006</td>
<td>17.36</td>
<td>0.025</td>
<td>0.050</td>
</tr>
<tr>
<td>Acanthostyles per aperture</td>
<td>40</td>
<td>3.1</td>
<td>0.888</td>
<td>28.89</td>
<td>1.0</td>
<td>5.0</td>
</tr>
<tr>
<td>Autozoecial diaphragms spacing, mm</td>
<td>40</td>
<td>0.15</td>
<td>0.044</td>
<td>29.09</td>
<td>0.07</td>
<td>0.24</td>
</tr>
<tr>
<td>Exozonal wall thickness, mm</td>
<td>40</td>
<td>0.079</td>
<td>0.023</td>
<td>29.50</td>
<td>0.030</td>
<td>0.135</td>
</tr>
</tbody>
</table>

**Table 7.** Measurements of *Amplexopora evae* sp. nov. Abbreviations as in 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>6</td>
<td>3.10</td>
<td>0.334</td>
<td>10.78</td>
<td>2.55</td>
<td>3.40</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>6</td>
<td>0.74</td>
<td>0.309</td>
<td>41.65</td>
<td>0.35</td>
<td>1.00</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>6</td>
<td>1.62</td>
<td>0.386</td>
<td>23.82</td>
<td>1.10</td>
<td>2.18</td>
</tr>
<tr>
<td>Aperture width, mm</td>
<td>85</td>
<td>0.15</td>
<td>0.026</td>
<td>17.02</td>
<td>0.10</td>
<td>0.21</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>85</td>
<td>0.19</td>
<td>0.031</td>
<td>15.82</td>
<td>0.12</td>
<td>0.30</td>
</tr>
<tr>
<td>Aperture width, mm (macular)</td>
<td>16</td>
<td>0.20</td>
<td>0.015</td>
<td>7.35</td>
<td>0.18</td>
<td>0.23</td>
</tr>
<tr>
<td>Aperture spacing, mm (macular)</td>
<td>16</td>
<td>0.27</td>
<td>0.039</td>
<td>14.57</td>
<td>0.20</td>
<td>0.33</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>61</td>
<td>0.049</td>
<td>0.013</td>
<td>26.40</td>
<td>0.025</td>
<td>0.080</td>
</tr>
<tr>
<td>Acanthostyles per aperture</td>
<td>75</td>
<td>2.7</td>
<td>1.075</td>
<td>39.72</td>
<td>1.0</td>
<td>5.0</td>
</tr>
<tr>
<td>Mesozooecia width, mm</td>
<td>60</td>
<td>0.05</td>
<td>0.018</td>
<td>36.31</td>
<td>0.02</td>
<td>0.09</td>
</tr>
<tr>
<td>Mesozooecial diaphragms spacing, mm</td>
<td>20</td>
<td>0.12</td>
<td>0.036</td>
<td>30.16</td>
<td>0.07</td>
<td>0.20</td>
</tr>
<tr>
<td>Autozoecial diaphragms spacing, mm</td>
<td>49</td>
<td>0.19</td>
<td>0.061</td>
<td>31.70</td>
<td>0.09</td>
<td>0.35</td>
</tr>
<tr>
<td>Exozonal wall thickness, mm</td>
<td>40</td>
<td>0.046</td>
<td>0.013</td>
<td>29.05</td>
<td>0.025</td>
<td>0.075</td>
</tr>
</tbody>
</table>

**Figure 9.** *Amplexopora crassiparietum* sp. nov. • A – longitudinal section, holotype PMO 221.770. • B, C – transverse section, holotype PMO 221.770. • D – longitudinal section, holotype PMO 221.770. • E – tangential section, holotype PMO 221.770. • F – tangential section, paratype PMO 221.760.
sheaths, situated in the dark median lining of autozooecial walls, originating from base of exozone; locally acanthostyles absent. Autozooecial walls in endozone 0.005–0.010 mm thick, granular; in exozone 0.025–0.075 mm thick, displaying reverse V-shaped lamination with dark, serrated median lining. Maculae indistinct, consisting of macrozooecia, 0.70–1.35 mm in diameter.

Remarks. – Amplexopora evae sp. nov. differs from A. crassiparietum sp. nov. in thinner autozooecial walls and larger autozooecial apertures.

Occurrence. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian; Ødegårdsviken, Ringerike, Norway.

Family Eridotrypellidae Morozova, 1961

Genus Eridotrypella Duncan, 1939

Type species. – Batostomella obliqua Ulrich, 1890. Middle Devonian; Michigan (USA).

Diagnosis. – Branched colonies. Autozooecial apertures irregularly polygonal. Autozooecial walls laminated, without distinct zooecial boundaries, irregularly thickened, containing spherulites. Diaphragms complete, varying in number. Exilazooecia rare. Acanthostyles varying in size and number.

Comparison. – Eridotrypella Duncan, 1939 differs from Eostenopora Duncan, 1939 in colony form (ramose branched vs encrusting or massive colonies).

Occurrence. – Silurian–?Carboniferous; worldwide.

Eridotrypella sp. A

Figure 11C–H, Table 8

Material. – PMO 221.789, PMO 221.782, PMO 221.796.

Description. – Ramose branched colonies, 1.2 mm in diameter. Exozone 0.34 mm wide, endozone 0.52 mm wide. Exozones distinctly separated from endozones. Secondary overgrowth occurring, 0.28–0.66 mm thick. Autozooecia long in endozones, bending sharply in exozones. Autozooecial apertures polygonal with rounded corners. Autozooecial diaphragms absent to rare in endozones; common to abundant in transition between endozone and exozone, straight or inclined. Exilazooecia rare, short, polygonal in cross section. Acanthostyles rare, having distinct narrow cores and laminated sheaths, 0.030–0.035 mm in diameter. Autozooecial walls granular, locally weakly crenulated, 0.005–0.010 mm thick in endozones; serrated in the longitudinal view and merged in the tangential section, 0.04–0.06 mm thick in exozones. Maculae not observed.

Remarks. – Eridotrypella sp. differs from E. sepizensis Astrova, 1970 from the lower Silurian (Wenlock) of Estonia in less abundant acanthostyles and in larger apertures (aperture width 0.08–0.13 mm vs 0.13–0.20 mm in E. sepizensis). Eridotrypella sp. differs from E. duncanae Pushkin, 1976 from the upper Silurian (Ludlow) of Belarus in narrower branches (branch width 1.2 mm vs 2.5–5.0 mm in E. duncanae), and in smaller apertures (aperture width 0.08–0.13 mm vs 0.14–0.25 mm in E. duncanae).

Occurrence. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian; Ødegårdsviken, Ringerike, Norway.

Order Cryptostomata Vine, 1884
Suborder Rhabdomesina Astrova & Morozova, 1956

Family Rhabdomesidae Vine, 1884

Genus Orthopora Hall, 1886

Type species. – Trematopora regularis Hall, 1874. Lower Devonian; USA.

Diagnosis. – Branched colonies. Autozooecia short, budding from more or less distinct medial axis in spiral order. Autozooecial diaphragms rare to absent. Both superior and inferior hemisepta commonly present; sometimes double hemisepta occurring; rarely hemisepta absent. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls granular in the endozone; laminated in exozone. Paurostyles abundant, prominent. Acanthostyles present, less abundant than paurostyles. Heterozoecia absent.

Figure 10. Amplexopora evae sp. nov., holotype PMO 170.890. • A – general view of a branched colony. • B – transverse section. • C – longitudinal section. • D – longitudinal section of encrusting colony. • E – transverse section showing wall structure. • F – tangential section.
Remarks. – Orthopora Hall, 1886 differs from Trematella Hall, 1886 in absence of metazoecia and in presence of well-developed hemisepta.

Occurrence. – Silurian to Carboniferous of North America, Europe and China, Middle Permian of Oman.

Orthopora worsleyi sp. nov.
Figure 13A–H, Table 9

Etymology. – The species is named for David Worsley, who has been an inspiration to us in the study of Silurian rocks of the Oslo Region.

Holotype. – PMO 221.790.

Paratypes. – PMO 221.750–221.755, PMO 221.757, PMO 221.781–221.782, PMO 221.784–221.785, PMO 221.789, PMO 221.794, PMO 221.796.

Type locality. – Nes bus stop, Ringerike Norway.

Type stratum. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheepwoodian–Homerian.

Diagnosis. – Branched colonies; bifurcation common; both superior and inferior hemisepta well developed; acanthostyles abundant, arranged in single row between autozooecia, varying in size; paurostyles abundant.

Description. – Branched colonies arising from encrusting bases. Branches 0.42–0.77 mm in diameter, with 0.13–0.35 mm wide endozones and 0.10–0.25 mm wide exozones. Branch bifurcation common. Transverse sections of branches circular. Autozooecia medium in length, budding from indistinct medial axis in spiral order. Autozooecial diaphragms rare to absent. Superior hemisepta present, blunt, curved proximally, positioned near the bend of autozooecial chamber; inferior hemisepta long, positioned beneath superior hemisepta, curved distally. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls in the endozone granular, 0.003–0.005 mm thick; laminated in exozone. Acanthostyles abundant, arranged in longitudinal rows between apertures, varying in size, having narrow hyaline cores and wide laminated sheaths. Paurostyles abundant, arranged irregularly between acanthostyles, 0.008–0.016 mm in diameter. Heterozooecia absent.

Remarks. – Orthopora worsleyi sp. nov. differs from O. casualis Goryunova, 1985 from the lower Silurian Rochester Shale (Wenlock) of New York, USA in narrower branches (0.42–0.77 mm vs 0.80–1.20 mm in O. casualis), and in slightly smaller apertures (aperture width 0.04–0.08 mm vs 0.05–0.10 mm in O. casualis). Orthopora worsleyi sp. nov. differs from species described by Kopaevich (1975) as Orthopora rhombifera (Hall, 1874) from the upper Silurian (Přídolí) of Estonia in narrower branches (0.42–0.77 mm vs 0.76–1.17 mm in that species).

Occurrence. – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheepwoodian–Homerian; Ødegårdsviken, Ringerike, Norway.

Mediapora Pushkin in Pushkin et al., 1990

Type species. – Mediapora aspersa Kopaevich, 1975. Upper Silurian, Ludlow; Estonia.

Diagnosis. – Branched colonies. Autozooecia relatively

Table 9. Measurements of Orthopora worsleyi sp. nov. Abbreviations as in 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>21</td>
<td>0.59</td>
<td>0.098</td>
<td>16.57</td>
<td>0.42</td>
<td>0.77</td>
</tr>
<tr>
<td>Exozone width, mm</td>
<td>21</td>
<td>0.17</td>
<td>0.041</td>
<td>24.03</td>
<td>0.10</td>
<td>0.25</td>
</tr>
<tr>
<td>Endozone width, mm</td>
<td>21</td>
<td>0.25</td>
<td>0.064</td>
<td>25.33</td>
<td>0.13</td>
<td>0.35</td>
</tr>
<tr>
<td>Aperture width, mm</td>
<td>45</td>
<td>0.06</td>
<td>0.012</td>
<td>19.06</td>
<td>0.04</td>
<td>0.08</td>
</tr>
<tr>
<td>Aperture spacing along branch, mm</td>
<td>25</td>
<td>0.31</td>
<td>0.045</td>
<td>14.63</td>
<td>0.21</td>
<td>0.40</td>
</tr>
<tr>
<td>Aperture spacing diagonally, mm</td>
<td>25</td>
<td>0.15</td>
<td>0.019</td>
<td>12.57</td>
<td>0.12</td>
<td>0.20</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>30</td>
<td>0.031</td>
<td>0.006</td>
<td>18.38</td>
<td>0.025</td>
<td>0.045</td>
</tr>
</tbody>
</table>

Table 10. Measurements of Mediapora kiaeri sp. nov. Abbreviations as in 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>Aperture width, mm</td>
<td>19</td>
<td>0.08</td>
<td>0.014</td>
<td>17.79</td>
<td>0.06</td>
<td>0.10</td>
</tr>
<tr>
<td>Aperture spacing, mm</td>
<td>20</td>
<td>0.17</td>
<td>0.017</td>
<td>9.59</td>
<td>0.14</td>
<td>0.2</td>
</tr>
<tr>
<td>Heterozooecia width, mm</td>
<td>20</td>
<td>0.03</td>
<td>0.008</td>
<td>28.09</td>
<td>0.015</td>
<td>0.045</td>
</tr>
<tr>
<td>Acanthostyle diameter, mm</td>
<td>20</td>
<td>0.034</td>
<td>0.006</td>
<td>19.03</td>
<td>0.025</td>
<td>0.050</td>
</tr>
</tbody>
</table>

Remarks. – Orthopora Hall, 1886 differs from Trematella Hall, 1886 in absence of metazoecia and in presence of well-developed hemisepta.

Occurrence. – Silurian to Carboniferous of North America, Europe and China, Middle Permian of Oman.

Figure 13A–H, Table 9

Family Arthrostylidae Ulrich, 1882

Mediapora Pushkin in Pushkin et al., 1990

Type species. – Mediapora aspersa Kopaevich, 1975. Upper Silurian, Ludlow; Estonia.

Diagnosis. – Branched colonies. Autozooecia relatively

short, budding from more or less distinct medial axis in spiral order. Autozooecial diaphragms rare to common. Hemisepta absent. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls granular in the endozone; laminated in exozone. Paurostyles large, abundant, prominent. Acanthostyles absent. Heterozooecia tubular, common to abundant, restricted to exozone, bearing few diaphragms.

Remarks. – Mediaporina Pushkin in Pushkin et al., 1990 differs from Sceptropora Ulrich, 1888 in having branched colony instead of branched segments with expanded distal parts.

Occurrence. – Lower to upper Silurian of Europe (British Isles, Norway, Estonia, Belarus, Latvia).

Mediaporina kiaeri sp. nov.
Figure 12A–G, Table 10

Etymology. – The species name refers to Johan A. Kier

Figure 13. Orthopora worsleyi sp. nov. • A, B – oblique section, holotype PMO 221.790. • C, D – oblique section of the basal part of the colony, paratype PMO 221.798. • E – oblique section of dichotomous colony, PMO 221.783. • F, G – longitudinal section, PMO 221.784. • H – branch transverse section, paratype PMO 221.783.
who described the Silurian rocks of Ringerike in great detail in 1908.

**Holotype.** – PMO 221.754.

**Paratype.** – PMO 221.762.

**Type locality.** – Nes bus stop, Ringerike Norway.

**Type stratum.** – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian.

**Diagnosis.** – Branched colonies; autozooidal diaphragms rare to common; acanthostyles abundant, 7–9 surrounding each autozooidal aperture; heterozooecia abundant, 4–6 surrounding each autozooidal aperture.

**Description.** – Branches 1.05–1.20 mm in diameter, with 0.30–0.37 mm wide endozones and 0.34–0.45 mm wide exozones. Branch bifurcation not observed. Autozooidae moderately long, growing along the branch axis in endzone and bending sharply in exzone, polygonal in transverse section of endzone. Autozooidal diaphragms rare to common, 2–3 usually present in each autozooid. Hemisepta absent. Autozooidal apertures oval to slightly angular, arranged regularly in alternating rows on the colony surface. Walls in the endzone granular, 0.003–0.005 mm thick; indistinctly laminated in exzone. Acanthostyles abundant, 7–9 surrounding each autozooidal aperture, restricted to exzone, varying in size, having indistinct wide cores and narrow sheaths. Heterozooecia abundant, 4–6 surrounding each autozooidal aperture, originating at the base of exzone, rounded to oval at colony surface, containing thin diaphragms, often sealed by calcitic material at colony surface.

**Remarks.** – Mediaporina kiaeri sp. nov. differs from *M. aspersa* (Kopaevich, 1975) from the upper Silurian of Estonia by more abundant and smaller heterozooecia (heterozooecia vs *persa* (Kopaevich, 1975) from the upper Silurian of Estonia.

**Occurrence.** – Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian–Homerian; Nes bus stop, Ringerike, Norway.

**Acknowledgements**

The Deutsche Akademische Austauschdienst (DAAD) supported Andrej Ernst’s study visit to the Natural History Museum, University of Oslo, with a one-year fellowship 2002–2003 (grant D/02/00949). Patrick N. Wyse Jackson, Dublin, and Caroline Buttler, Cardiff, are thanked for their helpful reviews.

**References**


DOI 10.1080/03745485909494606


DOI 10.1080/00222938509459918


DOI 10.5962/bhl.title.62810


