Late Carboniferous bryozoans from La Hermida, Spain

ANDREJ ERNST and ELKE MINWEGEN


Fifteen bryozoan species belonging to thirteen genera have been identified from an outcrop of the Picos de Europa Formation (Moscovian, Upper Carboniferous) at La Hermida in northern Spain. Three species and one genus are new—Coscinium hermidensis sp. nov., Cystodictya pustulosa sp. nov., and Cystocladia hispanica gen. et sp. nov. Rhabdomesid bryozoans are the most diverse order with seven species, followed by cystoporids (four species), fenestellids (three species) and trepostomids (one species). Bryozoans with erect branched or reticulate colonies dominate in the studied assemblage; only two species possess encrusting colonies. Together with associated crinoids, the bryozoan assemblage indicates a subtidal environment below the zone of vigorous water movement. The La Hermida bryozoan fauna confirms the Upper Carboniferous age of the Picos de Europa Formation and allows various biogeographical interpretations. All previously known species of the genus Coscinium were reported from the Lower Permian of Russia. Clausotrypa monticola is known from the Lower Permian of Russia and Arctic as well as from the Upper Carboniferous of Carnic Alps (Austria). Rhabdomeson cf. propatulissimum and Penniretepora pseudotrilineata are known from the same level of Italian Carnic Alps. Strebhorytropsa (Strebhascopora) nikiforovae and Rhombocladia punctata are known from the Upper Carboniferous (Moscovian) of Ukraine. Fistulipora petaloida is known from Kasimovian Stage of Russian Plate. Several other species show connections with North America.

Key words: Bryozoa, Cystoporoida, Fenestellida, Carboniferous, Picos de Europa Formation, Spain.

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Introduction

Carboniferous bryozoans are commonly abundant and diverse. However, our knowledge about them is very uneven. Whereas Carboniferous rocks of North America, certain parts of Australia, the British Isles and the European part of Russia and Ukraine contain well studied bryozoan faunas, they are scarcely investigated in other regions such as Asia, Africa and Antarctica. Except for the British Isles, Carboniferous bryozoans in western Europe are poorly known. Existing publications give only a superficial impression of the Carboniferous faunas of Spain, France, Hungary, and Austria (Kodsi 1967; Ceretti 1963, 1964, 1967; Delvolvé and McKinney 1983; Zágoršek 1993; Ernst 2003, 2005; Ernst et al. 2005). Revision of many of the taxa is necessary. Carboniferous rocks of Cantabria, northern Spain, contain locally abundant bryozoans (González and Suaréz Andréz 1999; Elias Samankassou, personal communication 2005). However, our knowledge of them is very limited and needs to be expanded (Ernst et al. 2005).

The material used for the present study comes from La Hermida in the Rio Deva valley, northern Spain (Minwegen 2001; Fig. 1). The locality is situated along national road N621 from Panes to Potes, on the eastern flank of the Picos de Europa Massif (GPS-position: 31 629 552 E, 4 789 900 N). The unit containing a bryozoan-pelmatozoan assemblage comprises the basal four metres of a reef mound (Fig. 2). It is overlain by 2 metres of grey, strongly cemented algal limestones representing phylloid algae-cement-boundstone (Minwegen 2001). The bryozoan-pelmatozoan unit consists of reddish limestones and marls with abundant skeletal fragments, mostly large crinoids, bryozoans and brachiopods. The microfacies are ruditic pelmatozoan packstones in the core of the mound, which change to bryozoan boundstones at the flanks and bryozoan-rubble limestones at the margins. The rocks at La Hermida belong to the Picos de Europa Formation (Moscovian = Westphalian B to ?D).

Studied material comprises a single hand-sized block, 0.1 m in diameter, from which 50 standard thin sections were prepared. Investigation of the bryozoans was performed from thin sections and acetate peels using a binocular microscope.

Institutional abbreviation.—SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany. Collection numbers: SMF 1723–1798, 2110, and 2154.

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1931
Class Stenolaemata Borg, 1926
Order Cystoporida Astrova, 1964
Suborder Fistuliporina Astrova, 1964
Family Fistuliporidae Ulrich, 1882
Genus Fistulipora M‘Coy, 1849

Type species: Fistulipora minor M‘Coy, 1850, by original designation; Carboniferous, England.

Diagnosis.—Massive, encrusting or ramose colonies. Cylindrical autozooecia with thin walls and complete diaphragms. Apertures rounded, possessing distinct horseshoe shaped lunaria. Autozooecia separated by extrazooidal vesicular skeleton (after Utgaard 1983).

Remarks.—The similar genus Eridopora Ulrich, 1882 differs from Fistulipora M‘Coy, 1849 in having persistently encrusting colonies and triangular lunaria.

Stratigraphic and geographic range.—Ordovician to Permian; worldwide.

Fistulipora petaloida Schulga-Nesterenko, 1955

Fig. 3A–C; Table 1.

1955 Fistulipora petaloida sp. nov; Schulga-Nesterenko 1955: 70–71, pl. 7: 2, text-fig. 3e.

Material.—Two fragments SMF 1737, 1759.

Description.—Encrusting colony, commonly multilayered. Single sheets reaching 0.63 to 1.13 mm in thickness. Autozooecial apertures rounded to oval, spaced 2.5–4.0 in 2 mm on the colony surface in growth direction, separated usually by 1–2 rows of vesicles. Lunaria prominent, 0.21–0.29 mm wide and 0.09–0.21 mm long. Basal diaphragms thin, horizontal or slightly inclined, usually 1–2 in each autozooecium. Vesicles polygonal in cross-section, having rounded roofs in longitudinal section, spaced 9–10 in 1 mm colony thickness. Outer granular skeleton well developed, bearing small abundant styles.

Discussion.—This species is similar to Dybowskiella (=?Fistulipora) lebedevi Nikiforova, 1933 from the Lower Carboniferous of the Donetsk Basin, Ukraine. However, the latter species has distinctly smaller lunaria—0.075–0.100 versus 0.090–0.210 mm long and 0.210–0.290 mm wide in Fistulipora petaloida.

Table 1. Measurements of Fistulipora petaloida Schulga-Nesterenko, 1955. Abbreviations: N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

<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</td>
<td>14</td>
<td>0.35</td>
<td>0.043</td>
<td>12.498</td>
<td>0.27</td>
<td>0.42</td>
</tr>
<tr>
<td>lunaria length</td>
<td>4</td>
<td>0.15</td>
<td>0.055</td>
<td>36.515</td>
<td>0.09</td>
<td>0.21</td>
</tr>
<tr>
<td>lunaria width</td>
<td>4</td>
<td>0.26</td>
<td>0.024</td>
<td>9.127</td>
<td>0.24</td>
<td>0.29</td>
</tr>
<tr>
<td>vesicular diameter</td>
<td>20</td>
<td>0.09</td>
<td>0.026</td>
<td>27.801</td>
<td>0.05</td>
<td>0.13</td>
</tr>
<tr>
<td>number of vesicles per 1 mm vertically</td>
<td>6</td>
<td>13.38</td>
<td>1.139</td>
<td>8.512</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>number of apertures per 2 mm</td>
<td>6</td>
<td>3.42</td>
<td>0.539</td>
<td>15.754</td>
<td>2.5</td>
<td>4.0</td>
</tr>
</tbody>
</table>
Stratigraphic and geographic range.—Moscow River, Russian Plate; Kasimovian Stage, Upper Carboniferous. Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

Family Hexagonellidae Crockford, 1947
Genus Coscinium Keyserling, 1846
Type species: C. cyclops Keyserling, 1846, by subsequent designation of Nikiforova 1938; Lower Permian, Timan, Russia.

Diagnosis.—Reticulate colonies built by anastomosing flat-tened bifoliate branches. Mesotheca trilayered, with longitudinal ridges. Autozooecial chambers tubular, hemispherical in cross section adjacent to mesotheca, indented ovoid to circular distal to mesotheca. Autozooecial apertures rounded, with distinct peristomes and lunaria. Diaphragms sparse. Vesicular skeleton consisting of small flat vesicles (after Utgaard 1983).

Remarks.—Coscinium Keyserling, 1846 differs from the similar species C. cyclops Keyserling, 1846 in having smaller apertures (0.14–0.19 mm versus 0.25 mm in C. cyclops) and in more closely spaced apertures (12–13 versus average 8 per 5 mm longitudinally). The new species differs from C. keyserlingi Stuckenberg, 1895 in having smaller apertures and poorly developed lunaria.

Description.—Bifoliate frondescent colony. Branches lens-shaped in cross-section, 2.63–4.00 mm wide and 0.68–1.05 mm thick, occasionally anastomosing to give oval fenestrales, 0.9 mm wide and 2.0 mm long. Mesotheca straight, three-layered, consisting of dark medial layer and two outer pale layers, 0.04–0.05 mm thick, containing abundant hyaline rods. Rods 0.01 mm in diameter, spaced densely (Fig. 3F). Indistinct longitudinal crests present on mesotheca. Autozooecia short, budding parallel to the mesotheca for a distance of about three zooecial diameters, semicircular in basal cross section, completely separated by vesicular skeleton, arranged in 8–10 rows on branches. Apertures oval, spaced 9–10 longitudinally and 12–13 diagonally in 5 mm distance. Lunaria weakly developed. Autozooecia surrounded by a thick layer of granular skeleton. Autozooecial diaphragms rare to common, thin, planar. Skeletal vesicles relatively large, with rounded roofs, covered at the colony surface by a thick layer of dense calcitic material, arranged in 2–3 rows between autozooecia.

Family Cystodictyonidae Ulrich, 1884
Genus Cystodictya Ulrich, 1882
Type species: C. ocellata Ulrich, 1882, by original designation; Lower Mississippian, Kentucky, USA.

Diagnosis.—Bifoliate colony, branching in plane of mesotheca. Ridges between autozooecial rows lacking. Mesotheca thin to moderately thick, with low ridges parallel to ranges of autozooecia. Autozooecia with peristomes and lunaria, basally teardrop-shaped, quadrate in cross-section; partly isolated by vesicles; recumbent portion short; blunt proximolateral hemisepa at zoecial bend, indenting zoecial cavity and producing slight hook-shaped appearance of autozooecia in the deep tangential section. Diaphragms lacking. Walls laminated; boundary serrated. Vesicles small, boxlike (after Utgaard 1983).

Remarks.—Cystodictya Ulrich, 1882 differs from the similar Sulcoretepora d’Orbigny, 1849 in the presence of hemisepas but absence of diaphragms.
Stratigraphic and geographic range.—Middle Devonian to Lower Permian; worldwide.

Cystodictya pustulosa sp. nov.

Figs. 3G, H, 4A, B; Table 3.

Derivation of the name: The name derives from Latin *pustulæ* (= vesicle) and refers to the presence of abundant vesicles.

Type material: Holotype (SMF 1776) and two paratypes (SMF 1743 and 1751).

Type locality: La Hermida, Spain.

Type horizon: Picos de Europa Formation, Moscovian, Upper Carboniferous

Other material.—SMF 1738, 1778, 1769, and 14 additional fragments.

Diagnosis.—Cystodictya pustulosa sp. nov. differs from the most similar species *C. zigzag* Ulrich, 1888 in having more closely spaced apertures (12–13 versus 10 per mm longitudinally in *C. zigzag*). The new species differs from other *Cystodictya* species in having abundant skeletal vesicles.

Description.—Bifoliate frondescent colony. Branches lens-shaped in cross-section, 1.30–3.74 mm wide and 1.14–2.34 mm thick. Mesotheca 0.03–0.04 mm thick, three-layered, consisting of a medial dark layer and two pale outer layers. Autozoecia short, budding parallel to the mesotheca for a distance of about three zoecial diameters, semicircular or trapezoid in basal cross section, not separated by vesicles at mesotheca; completely separated by vesicular skeleton in the exozone, arranged in 5–8 rows on branches. Apertures rounded to oval, spaced 12–13 longitudinally and 7–8 diagonally per 5 mm. Lunaria distinct, shallow, occupying half of the apertural space, containing 3–4 styles. Both inferior and superior hemisepta present, long, curved proximally; superior hemisepta located at transition from endozone to exozone; inferior hemiseptum hook-shaped, located at the floor of the autozoocoeum below the superior hemiseptum. Terminal diafragms occasionally present, planar or curved distally. Skeletal vesicles abundant, box-shaped, large and high at their bases becoming smaller and flatter in the exozone, with rounded roofs, polygonal in tangential section, covered at the colony surface by thick layer (0.12–0.23 mm) of dense skeleton, arranged in interspaces between autozoecia in 3–4 rows.

Cystodictya pustulosa sp. nov.

Diagnosis: The name derives from Latin *pustulæ* (= vesicle) and *clados* (= branch), signifying the presence of vesicles and the branching colony shape.

Type species: *Cystodictya hispanica* sp. nov.

Stratigraphic and geographic range.—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

Table 3. Measurements of *Cystodictya pustulosa* sp. nov. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimal value; MAX, maximal value.

<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</td>
<td>20</td>
<td>0.15</td>
<td>0.015</td>
<td>9.992</td>
<td>0.13</td>
<td>0.18</td>
</tr>
<tr>
<td>branch width</td>
<td>20</td>
<td>2.32</td>
<td>0.556</td>
<td>23.967</td>
<td>1.30</td>
<td>3.74</td>
</tr>
<tr>
<td>branch thickness</td>
<td>20</td>
<td>1.59</td>
<td>0.316</td>
<td>19.835</td>
<td>1.14</td>
<td>2.34</td>
</tr>
</tbody>
</table>

Table 4. Measurements of *Cystocladia hispanica* sp. nov. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimal value; MAX, maximal value.

<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</td>
<td>11</td>
<td>0.18</td>
<td>0.014</td>
<td>7.952</td>
<td>0.16</td>
<td>0.20</td>
</tr>
<tr>
<td>branch width</td>
<td>5</td>
<td>1.40</td>
<td>0.389</td>
<td>27.808</td>
<td>1.00</td>
<td>2.00</td>
</tr>
</tbody>
</table>

Family Goniocardiidae Nikiforova, 1938

Genus *Cystocladia* nov.

Diagnosis: The new genus is defined by ramose branched colonies, long autozoecia budding in bundle in endozone and opening on one side of branches, large lunaria, well-developed vesicular skeleton, and lacking diaphragms, hemiphragms or hemisepta. *Cystocladia* gen. nov. differs from other goniocladiids in absence of a median lamina which divides the branch into two symmetrical halves.

Discussion.—The fistuliporid genus *Cheilotrypa* Ulrich, 1884 is similar to *Cystocladia* gen. nov., differing in having a radial arrangement of autozoecia on the branch. Another similar fistuliporid genus *Fistulocladia* Bassler, 1929 differs in having a bundle of vesicles in the axial part of the branch.

Stratigraphic and geographic range.—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

Cystocladia hispanica sp. nov.

Fig. 4C–E; Table 4.

Derivation of the name: After Spain.

Type material: Holotype (SMF 1774) and two paratypes (SMF 1777 and 1747).

Type locality: La Hermida, Spain.

Type horizon: Picos de Europa Formation, Moscovian, Upper Carboniferous

Stratigraphic and geographic range.—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

Table 4. Measurements of *Cystocladia hispanica* sp. nov. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimal value; MAX, maximal value.
Other material.—SMF 1744, 1753, 1798, 1799, 2110.

Diagnosis.—As for genus.

Description.—Ramous branched colonies. Branches rounded to slightly flattened, frequently ramifying dichotomously. Autozooecia relatively long, arranged as a bundle in the endozone, opening on one side of branches, circular to oval in cross section, isolated by vesicular skeleton. Apertures oval, arranged in a quincuncial pattern, spaced 4 per 2 mm longitudinally. Lunaria large, occupying more than half of the autozoecial diameter, consisting of moderately thick calcitic skeleton. Vesicles relatively small, polygonal in tangential section, high in the endozone but becoming flat in the exozone, in 1–2 rows separating autozoecia. Hemisepta absent, diaphragms not observed. Colony surface covered by granular calcitic material.

Order Trepostomida Ulrich, 1882
Suborder Amplexoporina Astrov, 1965
Family Anisotrypidae Dunaeva and Morozova, 1967
Genus Stenophragmidium Bassler, 1952

Type species: Stenophragma lobatum Munro, 1912, by original description; Lower Carboniferous (Viséan) of England.


Stratigraphic and geographic range.—Lower to Upper Carboniferous; Europe, North America, China, and Russia.

Stenophragmidium isospinosum Ernst, Schäfer, and Reijmer, 2005

Fig. 4F–H; Table 5.


Material.—SMF 1730, 1731, 1745.

Description.—Encrusting colony of thin lamellar expansions, 0.6 mm thick. Autozoecial apertures rounded-polygonal, 6–7 spaced in 2 mm distance and 10 in 1 square mm of the colony surface. Diaphragms absent in autozoecia. Hemiphragms common, positioned on proximal side of autozoecial chamber. Exilazooecia not observed. Macroacanthostyles absent.

Table 5. Measurements of Stenophragmidium isospinosum Ernst, Schäfer, and Reijmer, 2005.

<table>
<thead>
<tr>
<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</td>
<td>20</td>
<td>0.24</td>
<td>0.018</td>
<td>7.580</td>
<td>0.20</td>
</tr>
</tbody>
</table>

Abundant microacanthostyles protruding from walls in the exozone, positioned perpendicular to the skeletal laminations, arranged irregularly, 0.01–0.02 mm in diameter. Zoocellular walls finely laminated, 0.015–0.020 mm thick in the endozone; displaying reversed U-shaped laminations and dark, serrated median wall lining, 0.08–0.10 mm thick in the exozone.

Discussion.—The La Hermida material corresponds exactly with Stenophragmidium isospinosum Ernst, Schäfer, and Reijmer, 2005 described from the Valverdin section of the San Emiliano Formation in the Upper Carboniferous (Westphalian B/C) of the Cantabrian Mountains.

Order Rhabdomesida Astrova and Morozova, 1956
Suborder Rhabdomesina Astrova and Morozova, 1956
Family Rhabdomesidae Vine, 1885

Genus Rhabdomeson Young and Young, 1874

= Coelococus Ulrich, 1889


Diagnosis.—Rhabdomesid with delicate dendroid colony having irregularly dichotomising branches. Autozoecia regularly budding around central axial cylinder in annual or spiral pattern. Hemisepta common. Autozoecial apertures elliptical, pyriform or rhombic, closely spaced, arranged in quincuncx on colonial surface; of constant or variable dimensions around branch. Stylets abundant and structurally diverse (after Wyse Jackson and Bancroft 1995a).

Stratigraphic and geographic range.—Middle Devonian to Upper Permian; worldwide.

Rhabdomeson cf. progracile Ceretti, 1963

Fig. 5A–D; Table 6.


http://app.pan.pl/acta51/app51-569.pdf
Material.—SMF 1758, 1763, 1764, 1766, 1770, 1779.

Description.—Ramoso colony with small axial cylinder and distinct exozone, 1.05–1.68 mm in diameter. Axial cylinder 0.17–0.45 mm in diameter. Autozooecia budding in spiral pattern around axial cylinder, rhomboidal in cross-section. Autozooecial apertures oval, arranged in regular diagonal rows, 5 longitudinally and 7–8 diagonally. Macroacanthostyles large, arranged biserially in interspaces between apertures. Microacanthostyles small, arranged in one row between macroacanthostyles. Superior hemiseptum blunt, obscure, positioned far distally; inferior hemiseptum long, straight or curved slightly to distal, restricting about the third of the autozooecial lumen, positioned roughly in the middle of the autozooecium.

Discussion.—The present material is very similar to *Rhabdomeson protalissimum* Ceretti, 1963 from the Upper Carboniferous of the Italian Carnic Alps. This species, which has been described and depicted only superficially from a single example, possesses two macroacanthostyles between the apertures, branches measuring 0.80–1.10 mm in diameter, an axial tube 0.11–0.15 mm in diameter, and apertures 0.07–0.09 mm wide. Other aspects of the internal structure are unknown. *R. binothorum* McKinney, 1972 from the Bangor Formation (Chester, Lower Carboniferous) of the USA has the same arrangement of macro- and microacanthostyles, 0.6–0.9 mm branch diameter, and long superior and inferior hemisepta.

Stratigraphic and geographic range.—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain. Probably also Auernig Formation, bed “I”, Upper Carboniferous (Gzhelian); Italy, Carnic Alps.

### Table 6. Measurements of *Rhabdomeson cf. protalissimum* Ceretti, 1963. N. number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
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<tr>
<td>aperture width</td>
<td>4</td>
<td>0.08</td>
<td>0.008</td>
<td>9.563</td>
<td>0.07</td>
<td>0.09</td>
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<tr>
<td>macroacanthostyle diameter</td>
<td>4</td>
<td>0.06</td>
<td>0.009</td>
<td>14.142</td>
<td>0.05</td>
<td>0.07</td>
</tr>
<tr>
<td>branch width</td>
<td>7</td>
<td>1.32</td>
<td>0.216</td>
<td>16.334</td>
<td>1.05</td>
<td>1.68</td>
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<tr>
<td>axial tube diameter</td>
<td>7</td>
<td>0.27</td>
<td>0.099</td>
<td>36.140</td>
<td>0.17</td>
<td>0.45</td>
</tr>
</tbody>
</table>

Family *Hyphasmoporidae* Vine, 1885

Genus *Streblotrypa* Vine, 1885

Subgenus *Streblotrypa* (*Streblotrypa*) Vine, 1885

*Type species:* *Streblotrypa nichkis* Vine, 1885, by original designation; Middle Carboniferous, England.

Diagnosis.—Ramoso colonies. Indistinct bundle of about 10 or fewer axial zooecia in the endozone. Diaphragms rare. Hemisepta usually present. Metazooecia usually restricted to rows between the autozooecial apertures; styles usually lacking (translated after Gorjunova 1985).

Remarks.—*Streblotrypa* (*Streblotrypa*) Vine, 1885 differs from *S. (Streblascopora)* Bassler, 1929 by having an indistinctly defined axial bundle and well-developed hemisepta.

*Streblotrypa* (*Streblotrypa*) sp.

Fig. 5E, F.

Material.—SMF 1780, 1732.

Description.—Ramoso colony, 0.68–0.78 mm in diameter. Axial bundle not clearly defined. Median axis indistinct. Autozooecial apertures oval, 0.09–0.10 mm in width, spaced 4 per 2 mm of the branch length and 6 diagonally in the same distance. Metazooecia rounded, arranged in 3–4 longitudinal rows between autozooecia, 0.02–0.03 mm in diameter, 16–24 spaced on the interapertural area. Diaphragms and hemisepta absent.

Remark.—*Streblotrypa* (*Streblotrypa*) angulatum Karklins, 1986 from the Late Mississippian of Utah, USA is very similar to the present material. However, this American species has thicker branches (0.82–1.02 versus 0.68–0.78 mm) and fewer metazooecia between the apertures (8–16 versus 16–24).

Stratigraphic and geographic range.—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

Subgenus *Streblotrypa* (*Streblascopora*) Bassler, 1929

*Type species:* *Streblotrypa fasiculata* Bassler 1929, by original designation; Upper Permian, Indonesia.


—Fig. 5. Rhabdomesid bryozoans *Rhabdomeson*, *Streblotrypa* (*Streblotrypa*), *Streblotrypa* (*Streblascopora*), *Rhombopora*, and *Saffordotaxis* from the La Hermida locality, Spain. Late Carboniferous (Moscovian). A–D. *Rhabdomeson* cf. *protalissimum* Ceretti, 1963. A. SMF 1763, cross section of the branch. B. SMF 1764, longitudinal section displaying axial tube and inferior hemiseptum, the arrow points to the inferior hemiseptum. C. SMF 1779, longitudinal section displaying long inferior and blunt superior hemisepta. D. SMF 1770, tangential section displaying autozooecial apertures, macroacanthostyles and paurostyles. E, F. *Streblotrypa* (*Streblotrypa*) sp. E. SMF 1780, cross section of the branch. F. SMF 1732, tangential section displaying autozooecial apertures and metazooecia. G–I. *Streblotrypa* (*Streblascopora*) nikiforovae (Morozova, 1955). G. SMF 1781, cross section of the branch. H. SMF 1762, tangential section displaying autozooecial apertures and metazooecia (H₂), and oblique section of the branch displaying axial tube and autozooecial chambers (H₂). J–M. *Rhombopora lepidodendroides* Meek, 1872. J. SMF 1767, tangential section displaying autozooecial apertures, macroacanthostyles and paurostyles. K. SMF 1782, tangential section showing macroacanthostyles and paurostyles. L. SMF 1783, cross section of the branch. M. SMF 1784, longitudinal section of the branch. N. *Saffordotaxis* cf. *yanagidae* Sakagami, 1964, SMF 1740, oblique section of the branch displaying autozooecial apertures and acanthostyles (N₁) and arrangement of autozooecia (N₂).

http://app.pan.pl/acta51/app51-569.pdf
Discussion.—The subgenus Streblotrypa (Streblascopora) Bassler, 1929 differs from the subgenus S. (Streblotrypa) Vine, 1885 by having a distinct axial bundle with usually more than 10 axial zooids, and rare and poorly developed hemisepta.

Stratigraphic and geographic range.—Carboniferous to Permian; worldwide.

Streblotrypa (Streblascopora) nikiforovae (Morozova, 1955) Fig. 5G–I.


Material.—SMF 1762, 1781 (and three additional fragments).

Description.—Ramose branched colonies, 0.75–1.15 mm in diameter. Axial bundle 0.21–0.22 mm in diameter, containing 9–13 axial zooecia, arranged in 3–4 rows in longitudinal section. Autozooecial apertures oval, 0.09–0.11 mm in width, spaced 4.5 per 2 mm of the branch length. Metazooecia rounded, arranged in 2–3 longitudinal rows between autozooecia, 0.03–0.04 mm in diameter, 6–10 spaced in the interapertural area. Diaphragms and hemisepta absent.

Discussion.—Streblotrypa (Streblascopora) nikiforovae (Morozova, 1955) is very similar to S. (S.) prisca (Gabb and Horn, 1862) from the Stephanian of the USA (Hageman 1993). The latter species differs in the larger number of metazooecia (4–19 versus 6–10 in present material), and in having superior and inferior hemisepta. The species described as Streblotrypa sp. by González and Suárez Andréz (1999) is very similar superficially. However, the internal structure is unknown in this species.

Stratigraphic and geographic range.—Upper Carboniferous (Moscovian); Ukraine. Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

Family Nematotrypidae Spjeldnaes, 1984

Genus Clausotrypa Bassler, 1929

Type species: C. separata Bassler, 1929, by original designation; Lower Permian, Timor, Indonesia.

Diagnosis.—Ramose cylindrical colonies. Autozooecia elongated-tubular with rare diaphragms; autozooecial apertures rounded or oval; exilazooecia common, irregularly shaped, closed by calcareous material near surface; acanthostyles common on the surface (translated after Gorjunova 1985).

Discussion.—Clausotrypa Bassler, 1929 is hard to compare with other rhabdomesid genera. Blake (1983) excluded this genus from the rhabdomesids. Gorjunova (1985) included it in the rhabdomesid family Nematotrypidae Gorjunova, 1985 because of the presence of a special type of heterozooecia which she called “tectitozooecia”. Wyse Jackson (1996) placed Clausotrypa with some reservations in the family Hyphasmoporidae Vine, 1885. This suggestion is followed in the present paper.

Stratigraphic and geographic range.—Lower Carboniferous to Upper Permian; Ireland, Russia, Oman, Indonesia, and Malaysia.

Clausotrypa monticola (Eichwald, 1860) Fig. 6D–I; Table 7.

1860 Myriolithes monticola sp. nov.; Eichwald 1860: 452, pl. 25: 6a, b.
2003 Clausotrypa monticola (Eichwald, 1860); Ernst 2003: 60, pl. 3: 2–5.

Material.—SMF 1723, 1733, 1739, S1748–1750, 1754, 1768, 1773, 1785–1788, 1797 (and about 30 additional fragments).

Description.—Cylindrical branches, 1.00–2.25 mm in diameter. Autozooecia long, cylindrical, budding parallel to the branch axis for a long distance, often building distinct axial bundle, turning gently to the colony surface. Autozooecial apertures oval, spaced 2.5–4 longitudinally and 5–6.5 diagonally in 2 mm. Diaphragms rare in autozooecia. Exilazooecia? (vesicles) numerous, restricted mostly to exozone, in 1–3 rows separating autozooecial apertures, having frequent diaphragms. Acanthostyles abundant, orig-

Table 7. Measurements of Clausotrypa monticola (Eichwald, 1860). N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

<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</td>
<td>6</td>
<td>1.80</td>
<td>0.485</td>
<td>26.985</td>
<td>1.00</td>
<td>2.25</td>
</tr>
<tr>
<td>aperture width</td>
<td>46</td>
<td>0.15</td>
<td>0.015</td>
<td>10.267</td>
<td>0.12</td>
<td>0.18</td>
</tr>
<tr>
<td>acanthostyle diameter</td>
<td>36</td>
<td>0.06</td>
<td>0.009</td>
<td>15.492</td>
<td>0.04</td>
<td>0.08</td>
</tr>
<tr>
<td>number of acanthostyles per aperture</td>
<td>28</td>
<td>4.50</td>
<td>0.509</td>
<td>11.315</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>number of apertures per 2 mm longitudinally</td>
<td>7</td>
<td>3.15</td>
<td>0.569</td>
<td>18.055</td>
<td>2.5</td>
<td>4.0</td>
</tr>
<tr>
<td>number of apertures per 2 mm diagonally</td>
<td>6</td>
<td>5.57</td>
<td>0.524</td>
<td>9.415</td>
<td>5.0</td>
<td>6.5</td>
</tr>
<tr>
<td>aperture spacing along branch</td>
<td>20</td>
<td>0.53</td>
<td>0.060</td>
<td>11.342</td>
<td>0.44</td>
<td>0.63</td>
</tr>
<tr>
<td>aperture spacing across branch</td>
<td>19</td>
<td>0.40</td>
<td>0.052</td>
<td>13.171</td>
<td>0.31</td>
<td>0.48</td>
</tr>
</tbody>
</table>
inating in the endozone, having clear calcite cores, 4–5 around each aperture.

**Discussion.**—*Clausotrypa monticola* (Eichwald, 1860) is similar to *C. conferta* Bassler, 1929 from the Lower Permian of Indonesia and Thailand. However, the latter species has smaller acanthostyles and larger autozooecial apertures (0.15–0.25 versus 0.12–0.18 mm in *Clausotrypa monticola*).

**Stratigraphic and geographic range.**—Upper Carboniferous to Lower Permian of Russia and Arctic. Carnic Alps (Austria); Upper Carboniferous, Lower *Pseudoschwagerina* Formation (Upper Gzhelian). Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

**Family Rhomboporidae Simpson, 1895**

**Genus Rhombopora Meek, 1872**

**Type species:** *Rhombopora lepidodendroides* Meek, 1872, by original designation; Upper Carboniferous, USA.

**Diagnosis.**—Ramoese colonies. Tubular autozooecia meet colony surface at low angles. Diaphragms can occur. Autozooecial apertures oval. One or two acanthostyles on the distal end of each aperture. Exozonal walls with abundant paurostyles arranged in a regular pattern around the apertures (translated after Gorjunova 1985).

**Discussion.**—*Rhombopora Meek, 1872 differs from *Klau−cena* Trizna, 1958 by the form of the autozooecia and by the absence of large acanthostyles, rare metazooecia. The rare metazooecia also distinguish it from *Megacanthopora* Moore, 1929.

**Stratigraphic and geographic range.**—The investigated material comes from the Picos de Europa Formation (Moscovian, Upper Carboniferous) of La Hermida, Northern Spain. This species apparently had a wide distribution (see Newton 1971 for synonymy list, and also Sakagami 1995). It has also been identified in the San Emiliano Formation, Upper Carboniferous−Permian (Ernst et al. 2005).

**Rhombopora corticata** Moore, 1929

**Description.**—Ramoese branched colonies, 0.9–1.4 mm in diameter. Autozooecial apertures oval, arranged in irregular diagonal rows, spaced 3–4 in 2 mm, and 6 diagonally in the same distance. Paurostyles 0.01–0.03 mm in diameter, arranged usually in a single, sometimes a double row between autozooecia. Large single megacanthostyles positioned in interspaces between apertures in angles of the hexagons of smaller paurostyles, having pale sheaths and dark cores, 0.05–0.078 mm in diameter.

**Discussion.**—*Rhombopora lepidodendroides* Meek, 1872 is similar *R. corticata* Moore, 1929, differing in its smaller diameter autozooecia and smaller colonies.

**Stratigraphic and geographic range.**—Devonian to Permian; worldwide.

**Rhombopora lepidodendroides** Meek, 1872

**Description.**—Ramoese branched colonies, 0.9–1.4 mm in diameter. Autozooecial apertures oval, arranged in irregular diagonal rows, spaced 3–4 in 2 mm, and 6 diagonally in the same distance. Paurostyles 0.01–0.03 mm in diameter, arranged usually in a single, sometimes a double row between autozooecia. Large single megacanthostyles positioned in interspaces between apertures in angles of the hexagons of smaller paurostyles, having pale sheaths and dark cores, 0.05–0.078 mm in diameter.

**Discussion.**—*Rhombopora lepidodendroides* Meek, 1872 is similar *R. corticata* Moore, 1929, differing in its smaller diameter autozooecia and smaller colonies.

**Stratigraphic and geographic range.**—The investigated material comes from the Picos de Europa Formation (Moscovian, Upper Carboniferous) of La Hermida, Northern Spain. This species apparently had a wide distribution (see Newton 1971 for synonymy list, and also Sakagami 1995). It has also been identified in the San Emiliano Formation, Upper Carboniferous−Permian (Ernst et al. 2005).

**Material.**—SMF 1728, 1734, 1767, 1782–1784.

**Table 8. Measurements of *Rhombopora lepidodendroides* Meek, 1872.**

<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</td>
<td>25</td>
<td>0.12</td>
<td>0.017</td>
<td>13.770</td>
<td>0.10</td>
<td>0.15</td>
</tr>
<tr>
<td>macroacanthostyle diameter</td>
<td>10</td>
<td>0.07</td>
<td>0.010</td>
<td>15.380</td>
<td>0.05</td>
<td>0.08</td>
</tr>
<tr>
<td>microacanthostyle diameter</td>
<td>20</td>
<td>0.02</td>
<td>0.005</td>
<td>26.251</td>
<td>0.01</td>
<td>0.03</td>
</tr>
<tr>
<td>branch width</td>
<td>4</td>
<td>1.18</td>
<td>0.222</td>
<td>18.881</td>
<td>0.90</td>
<td>1.43</td>
</tr>
</tbody>
</table>

**Table 9. Measurements of *Rhombopora corticata* Moore, 1929.**

<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</td>
<td>10</td>
<td>0.18</td>
<td>0.015</td>
<td>8.664</td>
<td>0.14</td>
<td>0.20</td>
</tr>
<tr>
<td>macroacanthostyle diameter</td>
<td>10</td>
<td>0.07</td>
<td>0.007</td>
<td>10.497</td>
<td>0.06</td>
<td>0.08</td>
</tr>
<tr>
<td>microacanthostyle diameter</td>
<td>10</td>
<td>0.04</td>
<td>0.007</td>
<td>16.696</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>branch width</td>
<td>5</td>
<td>1.65</td>
<td>0.242</td>
<td>14.601</td>
<td>1.41</td>
<td>2.03</td>
</tr>
</tbody>
</table>
diameter, arranged in a single row between autozoecia building a regular rhombic pattern. Single large acanthostyles positioned in interspaces between apertures at angles of hexagons of smaller paurostyles, having pale sheaths and dark cores, 0.06–0.08 mm in diameter.

**Discussion.**—*Rhabdopora corticata* Moore, 1929 is similar to *R. lepidondroides* Meek, 1872. It differs from the latter species in having larger colonies with a wider exozone as well as larger and more widely spaced apertures.

**Stratigraphic and geographic range.**—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain. San Emiliano Formation, Upper Carboniferous (Westphalian B/C); Spain. Upper Carboniferous Graham Formation (Pennsylvanian) of Texas, USA. *Pseudoschwagerina Zone* of Bolivia.

**Genus *Saffordotaxis*** Bassler, 1952

*Type species:* *Rhambopora incrassata* Ulrich, 1890, by original designation; Lower Mississippian, Kentucky (USA).

*Diagnosis.*—Ramose colonies with long and tube-like autozoecia budding in spiral pattern. Oval apertures arranged in regular diagonal rows. Diaphragms rare. Metazoecia absent; abundant actinotostyles in the exozonal walls, in single or multiple rows (translated after Gorjunova 1985).

**Discussion.**—*Saffordotaxis* Bassler, 1952 differs from the similar *Rhambopora* Meek, 1872 in having uniform styles.

**Stratigraphic and geographic range.**—Devonian to Permian; worldwide.

*Saffordotaxis cf. yanagidae* Sakagami, 1964

Figs. 5N, 6A; Table 10.


*Material.*—SMF 1740, 2154.

*Description.*—Ramose branched colonies, 1.05–1.20 mm in diameter. Autozoecia tubular, budding from the median axis in a spiral pattern. Apertures oval to petaloid due to indenting acanthostyles, arranged in regular diagonal rows, spaced 10 per 2 mm distance. Rare diaphragms present. Heterozoecia absent. Actinostyles common, spaced 4–6 around each aperture, having dark cores and laminated sheaths. Walls laminated, with dark median layer, 0.02 mm thick in endozone and 0.06–0.08 mm thick in exozone.

*Discussion.*—The present material is very similar to *Saffordo-

**Table 10. Measurements of *Saffordotaxis cf. yanagidae* Sakagami, 1964 from the *Millerella yowaresis Zone* of the Akiyoshi Limestone (top Serpukhovian) of Japan. The Japanese material differs slightly in having larger apertures (0.08–0.11 versus 0.07–0.10 mm in present material), and thinner colonies (0.80–1.10 versus 1.05–1.20 mm in present material).**

<table>
<thead>
<tr>
<th>aperture width</th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>0.09</td>
<td>0.010</td>
<td>11.164</td>
<td>0.07</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>acanthostyle diameter</td>
<td>9</td>
<td>0.04</td>
<td>0.005</td>
<td>12.122</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>number of acanthostyles per aperture</td>
<td>5</td>
<td>5.40</td>
<td>0.894</td>
<td>16.564</td>
<td>4</td>
<td>6</td>
</tr>
</tbody>
</table>

*Order Fenestellida* Astrov and Morozova, 1956

*Suborder Fenestellina* Astrova and Morozova, 1956

*Family Polyporidae* Vine, 1883

*Genus *Polypora* M’Coy, 1844*

*Type species:* *Polypora dendroides* M’Coy, 1844, by original designation; Lower Carboniferous, Ireland.

*Diagnosis.*—Reticular colonies of different shape built by straight or slightly undulating, bifurcating branches, joined at regular intervals by straight dissepiments without autozoecia. Autozoecia arranged in four alternating rows on branches, 5–6 rows before and 2–3 after bifurcation. Autozoecial chambers tubular, short, having weakly developed inferior hemisepta and short vestibule, regularly hexagonal in mid tangential section. Autozoecial apertures rounded. Keels between longitudinal rows of autozoecia weakly developed or absent. Microacanthostyles and nodes usually present on obverse surface (translated after Morozova 2001).

*Discussion.*—*Polypora M’Coy, 1844 is similar to *Pauci-

*poria* Termier and Termier, 1971 but the latter has strongly developed hemisepta and shorter autozoecia.*

*Stratigraphic and geographic range.*—Lower Devonian to Upper Permian; worldwide.
Polypora cf. remota Condra, 1902

Fig. 6–L; Table 11.

Material.—SMF 1765, 1789, 1790.

Description.—Reticulate colony. Micrometric formula: 6.5 / 3 // 14–18. Branches frequently bifurcating, 0.70–0.75 mm wide, spaced 6.5 in 10 mm across the colony, joined by 0.27–0.39 mm wide dissepiments. Autozoocia arranged in 3–4 rows on branches. Autozoocia apertures rounded, 14–18 spaced in 5 mm of the branch length, 9–14 on each side of fenestrule. Autozoocia rhombic in mid tangential section. Both superior and inferior hemisepta absent. Fenestrules 2.58–3.63 mm long, 0.88–1.05 mm wide, 3 spaced per 10 mm distance. Outer laminated skeleton moderately developed, containing abundant microstylets. Nodes and keels absent on obverse surface; indistinct thickenings present on reverse surface.

Discussion.—This species is superficially similar to P. aestival Meek, 1872 from the Graham Formation of Texas. The latter species has 4–6 rows of autozoocia on branches, which are spaced 11–12 per 5 mm longitudinally. The species P. valida Moore, 1929 is also similar to P. remota but differs in its smaller fenestrule length. However, both species have been described superficially and no information is available about their internal morphology.

Stratigraphic and geographic range.—Pennsylvanian; worldwide.

Penniretepora pseudotrilineata Ceretti, 1963

Fig. 7A–C, I; Table 12.

Material.—SMF 1724, 1757, 1791, 1792.

Description.—Pinnate colony consisting of straight main branch with frequent secondary branches. Secondary branches diverging from main branch at 60–70°, spaced 4–6 on the main branch with secondary branch (A_2), apertures and apertural nodes (A_3). Fragment of the main branch with secondary branch (A_4), apertures and apertural nodes (A_5). 

Table 11. Measurements of Polypora cf. remota Condra, 1902. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimal value; MAX, maximal value.

<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</td>
<td>10</td>
<td>0.09</td>
<td>0.006</td>
<td>6.924</td>
<td>0.08</td>
<td>0.10</td>
</tr>
<tr>
<td>aperture spacing along branch</td>
<td>10</td>
<td>0.35</td>
<td>0.038</td>
<td>10.665</td>
<td>0.31</td>
<td>0.44</td>
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<tr>
<td>aperture spacing across branch</td>
<td>10</td>
<td>0.29</td>
<td>0.028</td>
<td>9.775</td>
<td>0.25</td>
<td>0.34</td>
</tr>
<tr>
<td>maximal chamber width</td>
<td>10</td>
<td>0.16</td>
<td>0.019</td>
<td>11.973</td>
<td>0.13</td>
<td>0.19</td>
</tr>
</tbody>
</table>

Type species: Retepora pluma Phillips, 1836, by original designation; Lower Carboniferous, Ireland.

Diagnosis.—Fine main branch and short, regularly arranged secondary branches without dissepiments. Two rows of autozoocia on the main branch and on the secondary branches (translated after Morozova 2001).

Discussion.—Penniretepora is a polyphyletic taxon which generally includes Palaeozoic bryozoans with pinnate colony form and two rows of apertures on both the main and secondary branches. The following genera were also established on the basis of a pinnate colony form: Acanthocladia King, 1849 (three or more autozoocia rows on branches); Kalvariella Morozova, 1970 (two rows on the main branch and 3–4 rows on secondary branches) and Diploporaria Nickles and Bassler, 1900 (like Penniretepora but with rare secondary branches). This distinction is considered to be very artificial. Acanthocladiida (sensu King 1849) has been revisited quite recently (Ernst 2001) and is apparently restricted to the Upper Permian Zechstein Basin. The monotypic genus Kalvariella is also known only from the Zechstein. Penniretepora and Diploporaria, as well as the remaining species assigned to Acanthocladiida need to be revised using characters of the autozoocia and the presence or absence of heteromorphs.

Acanthocladia King, 1849

Family Acanthocladidae Zittel, 1880

Genus Penniretepora d’Orbigny, 1849

=Acanthopora Young and Young, 1875; = Pinnatopora Vine, 1883
each side per 5 mm of main branch length. Apertures circular, arranged on both main and secondary branches in two rows; two-three apertures between two neighbouring secondary branches; spaced 13 per 5 mm along main branch length. Apertures 0.10–0.15 mm in diameter, surrounded by 12–15 nodes. Secondary laminated skeleton well developed, containing abundant microstylets; microstylets diverging from inner hyaline skeleton, regularly spaced across entire colony surface, 0.005–0.015 mm in diameter.

Discussion.—Although the internal morphology of *Penniretepora pseudotrilineata* Ceretti, 1963 is not described in the original description, this species is distinguished quite clearly from existing *Penniretepora* species. It combines characters such as triserial keel without nodes, rectangular to pentagonal autozooecial shape without hemisepta, and relatively strong main branches. Reverse side of colony roughly ribbed. Secondary laminated skeleton well developed, containing abundant microstylets; microstylets diverging from inner hyaline skeleton, regularly spaced across entire colony surface, 0.005–0.015 mm in diameter.

Suborder Phylloporinina Lavrentjeva, 1979

**Genus Rhombocladia** Rogers, 1900

*Type species:* *Rhombocladia delicata* Rogers, 1900, by original designation; lower part of the Upper Carboniferous (Upper Coal Measures); Kansas, USA.


**Discussion.**—*Rhombocladia* differs from *Chainodictyon* Foerste, 1887 in its branched instead of reticulate colony form and development of hemisepta, and from the genus *Kallodictyon* Morozova, 1981 in its colony form, thin dorsal wall and absence of leptozoecia on the dorsal surface of the colony.

**Stratigraphic and geographic range.**—Lower Carboniferous to Middle Permian; Russia, Australia, USA, Europe, and Thailand.

**Rhombocladia punctata** Dunaeva, 1961

*Fig. 7D–H; Table 13.*

1961 *Rhombocladia punctata* sp. nov.; Dunaeva 1961: 40–41, pl. 5: 5–7, text-figs. 4, 5.

**Material.**—SMF 1755, 1760, 1793, 1794–1796 (and 17 additional fragments).

**Description.**—Dichotomously branching colonies. Branches 1.4–1.9 mm wide and 0.7–1.1 mm thick in their middle parts,
Table 14. Distribution of bryozoan species from the Picos de Europa Formation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Occurrence</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fistulipora petaloida Schulga-Nesterenko, 1955</td>
<td>Russian Plate</td>
<td>Kasimovian</td>
</tr>
<tr>
<td>Stenophragmidium isospinosum Ernst, Schafer, and Reijmer, 2005</td>
<td>Spain</td>
<td>Westphalian B/C</td>
</tr>
<tr>
<td>Streblotrypa (Streblascopora) nikiforovae Morozova, 1955</td>
<td>Ukraine</td>
<td>Moscovian</td>
</tr>
<tr>
<td>Rhambdocladia cf. propatulissimum Ceretti, 1963</td>
<td>? Carnic Alps, Italy</td>
<td>? Gzhelian</td>
</tr>
<tr>
<td>Clausotrypa monticola (Eichwald, 1860)</td>
<td>Russian Plate, Arctic</td>
<td>Upper Carboniferous – Early Permian</td>
</tr>
<tr>
<td>Rhombopora lepidodendroides Meek, 1872</td>
<td>N. America, Bolivia</td>
<td>Upper Carboniferous – Early Permian</td>
</tr>
<tr>
<td>Rhambopora corticata Moore, 1929</td>
<td>N. America, Bolivia</td>
<td>Pennsylvanian</td>
</tr>
<tr>
<td>Polyrea cf. remota Condra, 1902</td>
<td>N. America</td>
<td>Pennsylvanian</td>
</tr>
<tr>
<td>Penniretepora pseudotrilineata Ceretti, 1963</td>
<td>Carnic Alps, Italy</td>
<td>Gzhelian</td>
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<tr>
<td>Rhambocladia punctata Dunaeva, 1961</td>
<td>Ukraine</td>
<td>Kasimovian</td>
</tr>
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</table>

Discussion

Because of their relatively high diversification rates, Carboniferous bryozoans hold some potential for biostratigraphy (Bancroft 1987). Lower Carboniferous bryozoans have short stratigraphical ranges, but they tended to be endemic. In contrast, Late Carboniferous bryozoans had low origination rates, and many species had wide geographical and temporal distributions. Similar patterns are shown by other animal groups in the Carboniferous, such as fusulinids, corals and brachiopods (Ross and Ross 1985, 1987, 1996). Ross and Ross (1996) suggested that a fairly cool climate and rapid sea-level changes were responsible for a distinct decline in bryozoan faunas during the Moscovian.

During the Carboniferous bryozoan communities experienced significant changes in taxonomic composition, continuing a trend which had started in the Devonian. Cystoporid bryozoans played important roles in the Devonian and Lower Carboniferous, whereas the Upper Carboniferous bryozoan faunas became more “Permian” in their composition, with increasing dominance of fenestellid and rhabdomesid taxa.

The described bryozoan fauna represents the assemblage of a small shallow-water bioherm. Such a type of assemblage is typical for Upper Carboniferous shelf seas (Ross 1981). This fauna comes from the Picos de Europa Formation (Moscovian, Upper Carboniferous) at locality La Hermida, Northern Spain. The Moscovian Picos de Europa and Calizas del Cuera subunits, in which the fauna occurs, were parts of the northward retreating carbonate platform bounding the Cantabrian molasse basin to the north. In contrast, the San Emiliano Formation, in which some of the species also occur, was deposited in a fore-deep basin of the Cantabrian Zone (Reijmer et al. in press).

In the studied assemblage, rhabdomesids with 7 species are the most diverse and abundant group, followed by cystoporids with 4 species, fenestellids with 3 species, and one trepostomid species. This composition fits well with the global pattern described by Ross (1981). Except for Fistulipora petaloida and Stenophragmidium isospinosum which have encrusting colonies, all of the bryozoans possess erect colonies which are branching or reticulate. The La Hermida bryozoans are associated mostly with crinoids and less often with brachiopods, both of which are also suspension feeders. Benthic animals with erect growth-forms dominate here. Fragile stems of crinoids and bryozoans are mostly intact. Judging by the microfacies (crinoid packstone to bryozoan boundstone) and low breakage of erect, predominantly suspension-feeding benthic animals, a quiet subtidal environment is indicated, likely outer shelf or greater depth below normal wave base.

Most of the bryozoan genera from La Hermida have wide stratigraphical and geographical ranges. However, Coscinium is known only from northern regions (Arctic, northern Urals, Timan-Pechora, and Spitsbergen), while Cystodictya is typically a North American genus, known from the Middle Devonian to Pennsylvanian, with only one species reported from the Upper Carboniferous of the Russian Plate (C. absoluta Morozova and Lisitsyn, 2002).
The species composition of the bryozoan assemblage from La Hermida allows finer interpretations (Table 14). Two species—Rhombopora lepidodendroides Meek, 1872 and R. corticata Moore, 1929—originally described from the Pennsylvanian of North America, have wide distributions in the Upper Carboniferous. The occurrence of Polypora remota Condra, 1902 reinforces the North American connection of the La Hermida bryozoan assemblage. The species Fistulipora petaloida Schulga-Nesterenko, 1955 and Rhombocladia punctata Dunaeva, 1961 occur in the Kasimovian Stage of the Russian Plate and Ukraine. Another species, Streblotrypa (Streblasscopia) nikiforovae Morozova, 1955, was originally described from the Moscovian of Ukraine.

Gonzáles and Suárez Andréz (1999) described 9 species from the Moscovian of Calizas del Cuera. Three species from Calizas del Cuera are apparently present in the bryozoan assemblage from La Hermida—Streblotrypa sp. [= ?Streblotrypa (Streblasscopia) nikiforovae Morozova, 1955], Polypora sp. [= Polypora remota Condra, 1902], and Penniretpora sp. [= ?Penniretpora pseudotrilineata Ceretti, 1963]. Thamniscus sp. from this fauna seems to be an undescribed species of the family Carnocladiidae Ernst, 2001. So far, this family constitutes only one genus, Carnocladia Ernst, 2001, with two species from the Lower Permian (Asselian to Sakmarian) of the Carnic Alps, Austria.

Ernst et al. (2005) described 10 bryozoan species from the San Emiliano Formation of the San Emiliano and Valverdín sections in Cantabria. Based on the presence of Stenophragmium isospinosum Ernst, Schäfer, and Reijmer, 2005, Rhombopora lepidodendroides Meek, 1872 and R. corticata Moore, 1929, this fauna shows distinct connections to the La Hermida assemblage.

The bryozoans from La Hermida also show certain similarities to the Upper Carboniferous faunas of the Carnic Alps (Austria and Italy). The species Penniretpora pseudotrilineata Ceretti, 1963 was originally described from bed “I” of the Auernig Formation, Gzhelian. The species Clausotrypa monticola (Eichwald, 1860) also is present in the Lower Pseudoschwagerina Formation, Upper Gzhelian (Ernst 2003), and is apparently widely distributed in the Upper Carboniferous of Europe and the Arctic.

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References


