# Late Carboniferous bryozoans from La Hermida, Spain

ANDREJ ERNST and ELKE MINWEGEN

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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. *Streblotrypa* (*Streblascopora*) *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, Cystoporida, Fenestellida, Carboniferous, Picos de Europa Formation, Spain.

*Andrej Ernst [ae@gpi.uni-kiel.de], Institut für Geowissenschaften, Christian-Albrechts-Universität zu Kiel, Ludewig-Meyn-Str. 10, D-24118 Kiel, Germany;*
*Elke Minwegen [minwegene@hotmail.com], Theodor-Fliedner-Str. 1a, D-51371 Leverkusen, Germany.*

## 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, Forschunginstitut 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

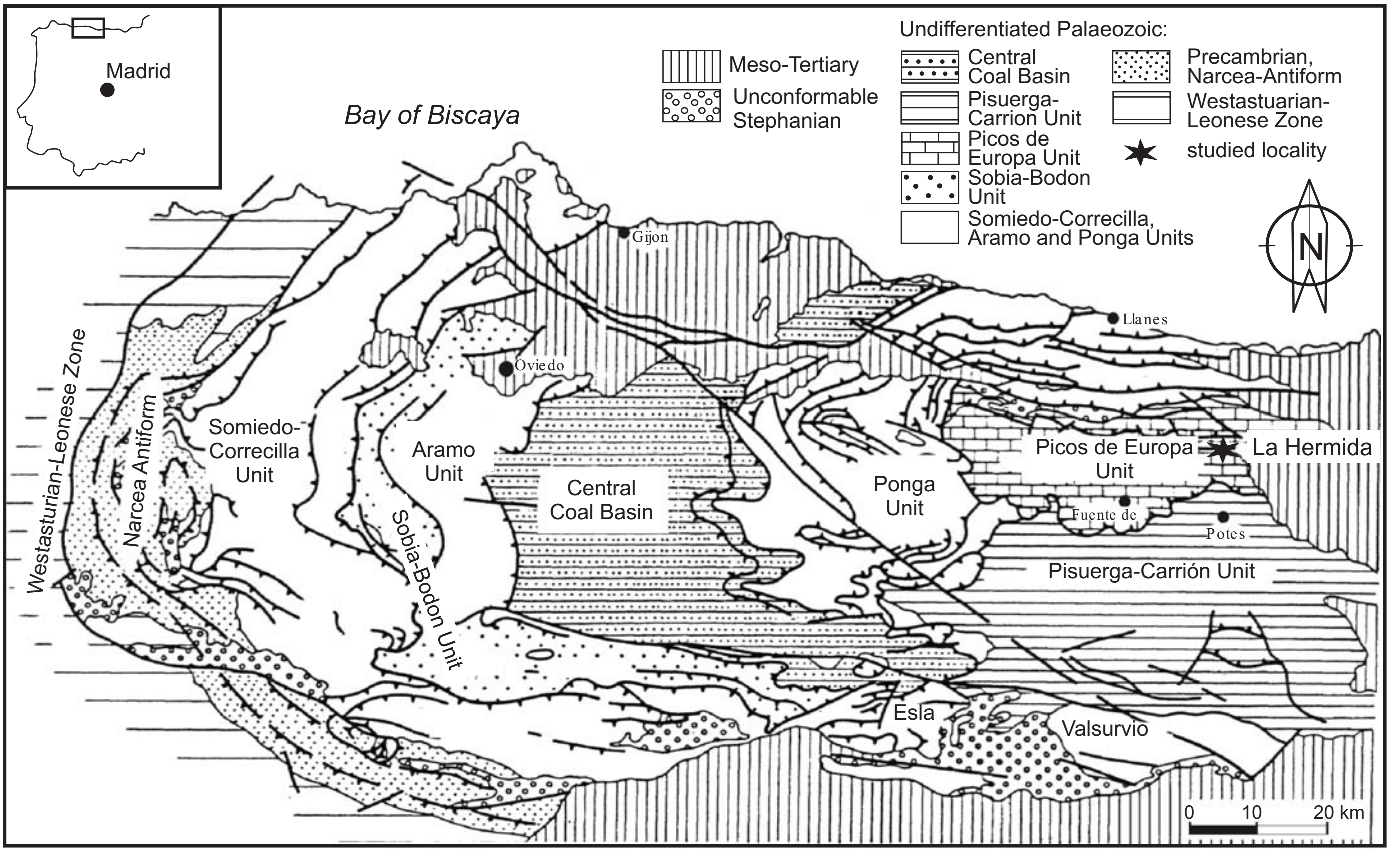



Fig. 1. Geographical position of the at locality La Hermida, Spain.

## 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.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 14 | 0.35 | 0.043 | 12.498 | 0.27 | 0.42 |
| lunaria length | 4 | 0.15 | 0.055 | 36.515 | 0.09 | 0.21 |
| lunaria width | 4 | 0.26 | 0.024 | 9.127 | 0.24 | 0.29 |
| vesicular diameter | 20 | 0.09 | 0.026 | 27.801 | 0.05 | 0.13 |
| number of vesicles per 1 mm vertically | 6 | 13.38 | 1.139 | 8.512 | 12 | 15 |
| number of apertures per 2 mm | 6 | 3.42 | 0.539 | 15.754 | 2.5 | 4.0 |

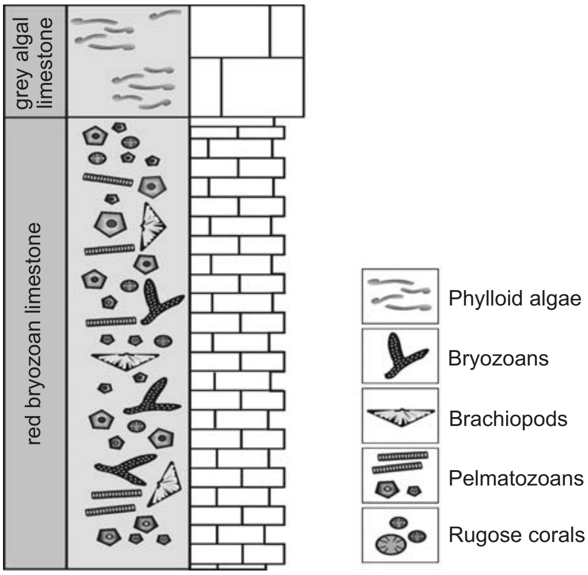



Fig. 2. Lithofacies of the investigated profile at La Hermida, Spain.

*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 flattened 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 most similar genus *Hexagonella* Waagen and Wentzel, 1886 in having smaller and less abundant vesicles and also in and fewer vesicle-built ridges on the colony surface.

*Stratigraphic and geographic range*.—Upper Carboniferous to Lower Permian; Russia, Spain.

## *Coscinium hermidensis* sp. nov.

Fig. 3D–F; Table 2.

*Derivation of the name*: After the type locality.

*Type material*: Holotype (SMF 1729) and two paratypes (SMF 1775 and SMF 1736).

*Type locality*: La Hermida, Spain.

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

*Other material*.—SMF 1725, 1746, 1752, 1761, 1771, 1796, and 21 additional fragments.

Table 2. Measurements of *Coscinium hermidensis* sp. nov. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 20 | 0.16 | 0.012 | 7.749 | 0.14 | 0.19 |
| branch width | 4 | 3.19 | 0.598 | 18.751 | 2.63 | 4.00 |
| branch thickness | 5 | 1.95 | 0.372 | 19.095 | 1.63 | 2.40 |

*Diagnosis*.—*Coscinium hermidensis* sp. nov. differs from the most similar species *C. cyclops* Keyserling, 1846 in having smaller apertures (0.14–0.19 *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 fenestrules, 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. $3F_1$). 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.

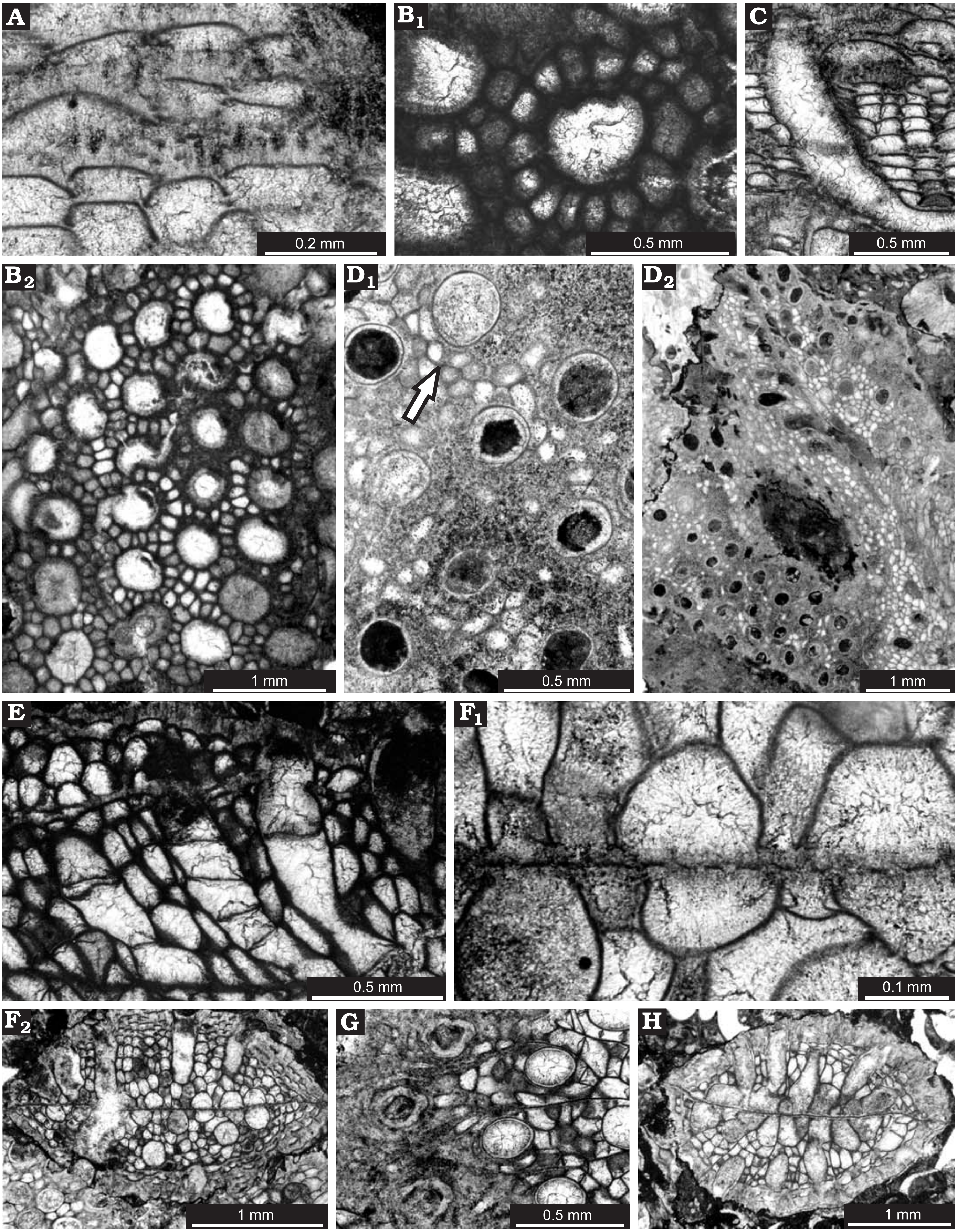
## Family Cystodictyonidae Ulrich, 1884

## 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 hemisepta at zooecial bend, indenting zooecial 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 hemisepta but absence of diaphragms.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*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 *pustulae* (= 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. Autozooecia short, budding parallel to the mesotheca for a distance of about three zooecial 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 autozooecium below the superior hemiseptum. Terminal diaphragms 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 autozooecia in 3–4 rows.

*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.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 20 | 0.15 | 0.015 | 9.992 | 0.13 | 0.18 |
| branch width | 20 | 2.32 | 0.556 | 23.967 | 1.30 | 3.74 |
| branch thickness | 20 | 1.59 | 0.316 | 19.835 | 1.14 | 2.34 |

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

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 11 | 0.18 | 0.014 | 7.952 | 0.16 | 0.20 |
| branch width | 5 | 1.40 | 0.389 | 27.808 | 1.00 | 2.00 |

## Family Goniocladiidae Nikiforova, 1938

## Genus *Cystocladia* nov.

*Derivation of the name*: The name derives from a combination of the Greek words *cystos* (= vesicle) and *clados* (= branch), signifying the presence of vesicles and the branching colony shape.

*Type species*: *Cystocladia hispanica* sp. nov.

*Diagnosis*.—The new genus is defined by ramose branched colonies, long autozooecia 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 autozooecia 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.

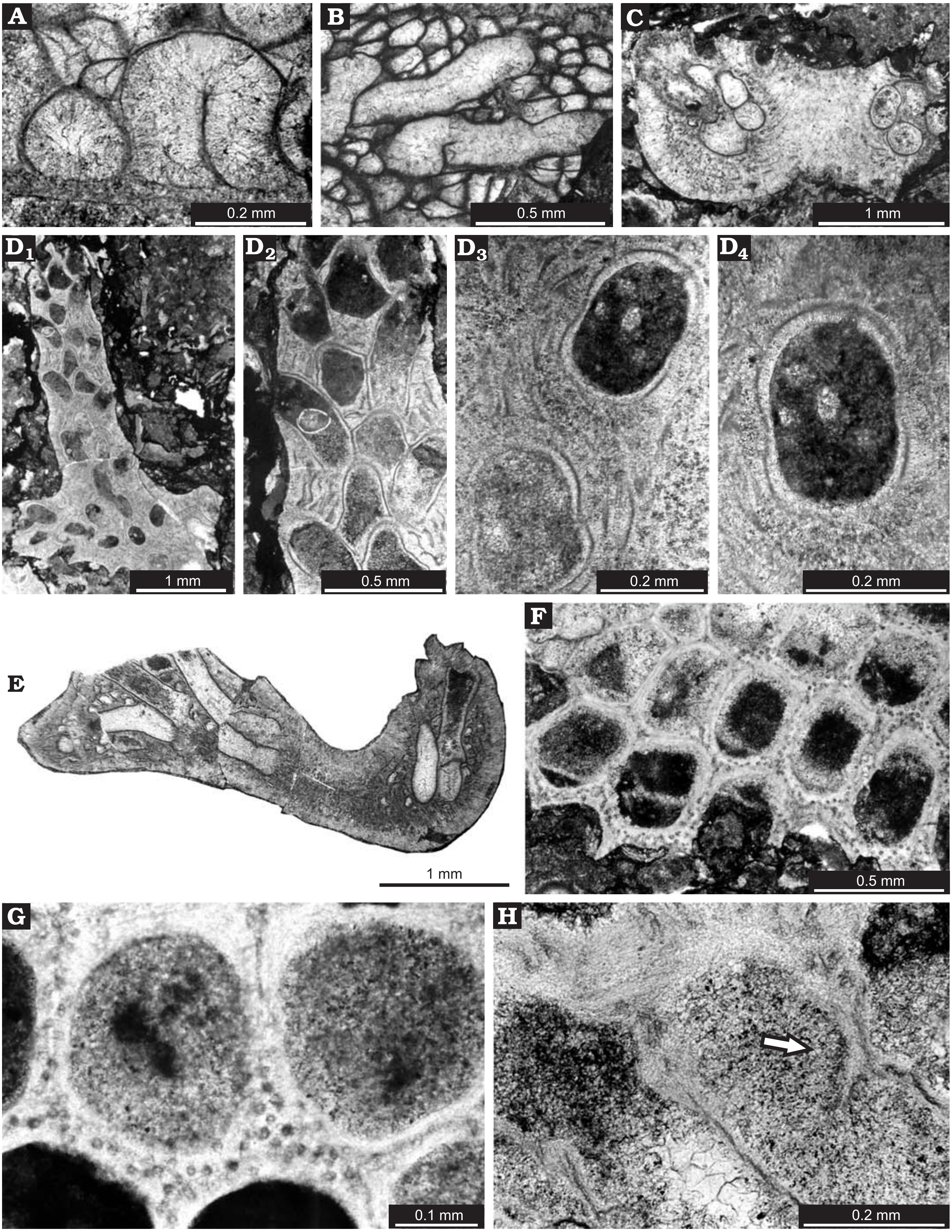
*Derivation of the name*: After Spain.

*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.

← Fig. 3. Cystoporid bryozoans *Fistulipora*, *Coscinium*, and *Cystodictya* from the La Hermida locality, Spain, Late Carboniferous (Moscovian). **A**–**C**. *Fistulipora petaloida* Schulga-Nesterenko, 1955. **A**. SMF 1737, longitudinal section displaying styles in outer granular skeleton and skeletal vesicles. **B**. SMF 1759, tangential section of the colony surface: close view of a single aperture ($B_1$) and view of several apertures ($B_2$). **C**. SMF 1737, longitudinal section of autozooecial chamber showing diaphragm and vesicular skeleton. **D**–**F**. *Coscinium hermidensis* sp. nov. **D**. Holotype SMF 1729, tangential section of the colony surface displaying apertures ($D_1$, arrow—lunarium) and fused branches ($D_2$). **E**. SMF 1736, longitudinal section displaying autozooecial chambers with diaphragms and vesicular skeleton. **F**. Paratype SMF 1775, cross section of the branch displaying mesotheca with rods ($F_1$), autozooecial chambers and vesicular skeleton ($F_2$). **G**, **H**. *Cystodyctia pustulosa* sp. nov. **G**. Holotype SMF 1776, tangential section of the colony displaying apertures. **H**. Paratype SMF 1743, cross section of the branch.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*Other material*.—SMF 1744, 1753, 1798, 1799, 2110.

*Diagnosis*.—As for genus.

*Description*.—Ramose 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 autozooecial 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 autozooecia. Hemisepta absent, diaphragms not observed. Colony surface covered by granular calcitic material.

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

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

*Diagnosis*.—Encrusting, rarely ramose colonies. Autozooecia possessing rounded-polygonal and oval apertures. Walls moniliform. Hemiphragms short, positioned on one side of autozooecia. Exilazooecia rare. Acanthostyles both large and small, rarely only small or only large (translated after Astrova 1978).

*Discussion*.—*Stenophragmidium* Bassler, 1952 differs from *Tabulipora* Young, 1883 by the presence of hemiphragms instead of ring septa.

*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.

2005 *Stenophragmidium isospinosum* sp. nov.; Ernst et al. 2005: 306, pl. 2: 4–5.

*Material*.—SMF 1730, 1731, 1745.

*Description*.—Encrusting colony of thin lamellar expansions, 0.6 mm thick. Autozooecial apertures rounded-polygonal, 6–7 spaced in 2 mm distance and 10 in 1 square mm of the colony surface. Diaphragms absent in autozooecia. Hemiphragms common, positioned on proximal side of autozooecial chamber. Exilazooecia not observed. Macroacanthostyles absent. Abundant microacanthostyles protruding from walls in the exozone, positioned perpendicular to the skeletal lamination, arranged irregularly, 0.01–0.02 mm in diameter. Zooecial walls finely laminated, 0.015–0.020 mm thick in the endozone; displaying reversed U-shaped lamination and dark, serrated median wall lining, 0.08–0.10 mm thick in the exozone.

Table 5. Measurements of *Stenophragmidium isospinosum* Ernst, Schäfer, and Reijmer, 2005. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimal value; MAX, maximal value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 20 | 0.24 | 0.018 | 7.580 | 0.20 | 0.28 |

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

*Stratigraphic and geographic range*.—San Emiliano Formation, Upper Carboniferous (Westphalian B/C); Valverdín, Cantabrian Mountains, northern Spain. Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

## Order Rhabdomesida Astrova and Morozova, 1956
## Suborder Rhabdomesina Astrova and Morozova, 1956
## Family Rhabdomesidae Vine, 1885
## Genus *Rhabdomeson* Young and Young, 1874

= *Coeloconus* Ulrich, 1889

*Type species*: *Rhabdomeson progracile* Wyse Jackson and Bancroft, 1995b, by subsequent designation of Wyse Jackson and Bancroft (1995b) (ICZN Opinion 1874); Lower Carboniferous, England.

*Diagnosis*.—Rhabdomesid with delicate dendroid colony having irregularly dichotomising branches. Autozooecia regularly budding around central axial cylinder in annual or spiral pattern. Hemisepta common. Autozooecial apertures elliptical, pyriform or rhombic, closely spaced, arranged in quincunx 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. *propatulissimum* Ceretti, 1963

Fig. 5A–D; Table 6.

?1963 *Rhabdomeson propatulissimum* sp. nov.; Ceretti 1963: 315–316, pl. 25: 13.

← Fig. 4. Cystoporid bryozoans *Cystodictya*, *Cystocladia*, and trepostomid bryozoan *Stenophragmidium* from the La Hermida locality, Spain, Late Carboniferous (Moscovian). **A**, **B**. *Cystodictya pustulosa* sp. nov. **A**. SMF 1738, cross section of the branch displaying mesotheca and autozooecial chamber with inferior hemiseptum. **B**. SMF 1778, deep tangential section displaying autozooecial chambers and hook-shaped hemiseptum. **C**–**E**. *Cystocladia hispanica* gen. et sp. nov. **C**. Paratype SMF 1777, cross section of the dichotomising branch. **D**. Holotype SMF 1774, tangential section of the colony: arrangement of autozooecial chambers and vesicular skeleton ($D_1$, $D_2$), and shape of autozooecial apertures ($D_3$, $D_4$). **E**. SMF 1753, cross section of the dichotomising branch. **F**–**H**. *Stenophragmidium isospinosum* Ernst, 2005. **F**. SMF 1730, tangential section close to the colony surface. **G**. SMF 1731, tangential section displaying microacanthostyles in skeleton. **H**. SMF 1745, longitudinal section showing hemiphragm (arrow).

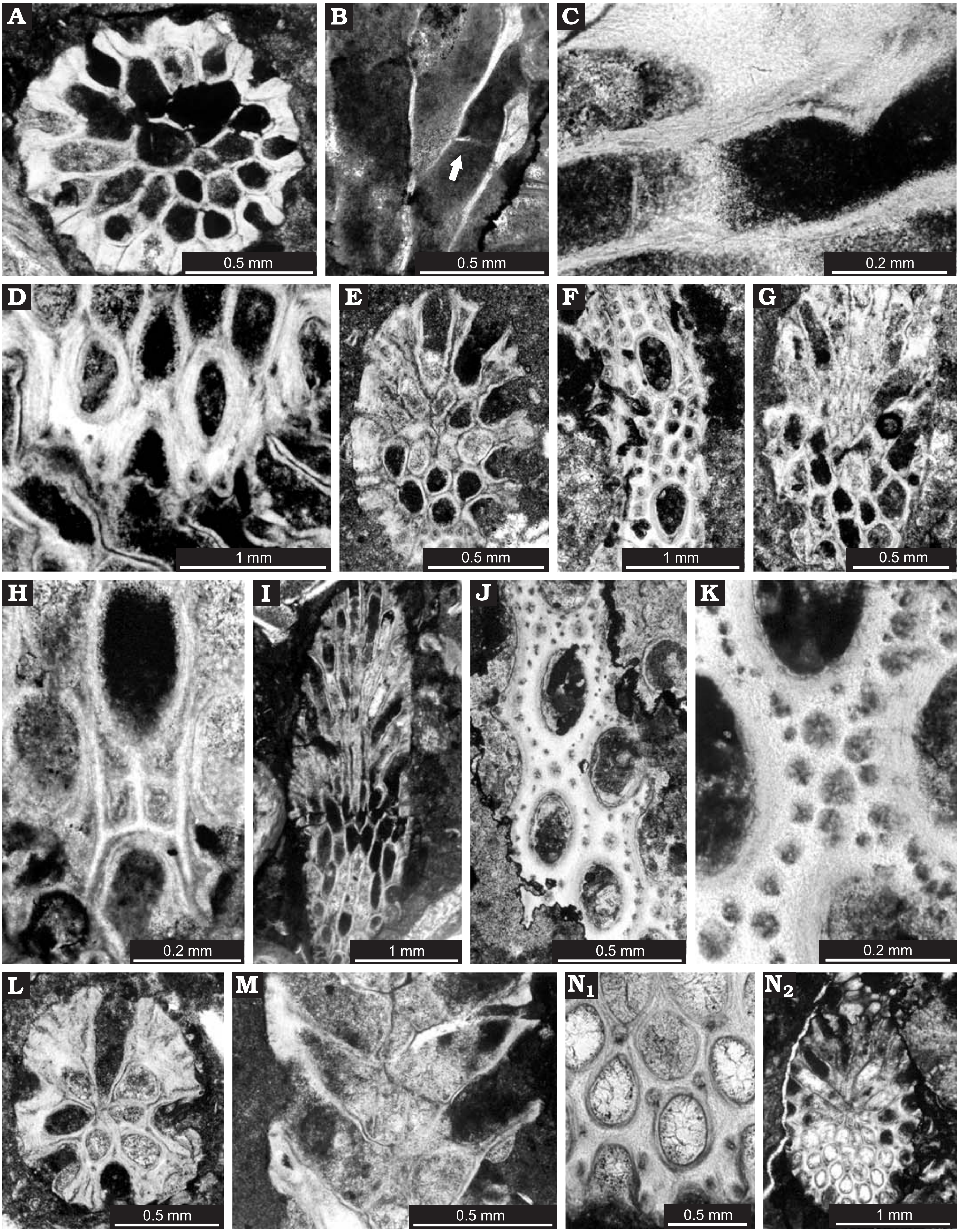
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Table 6. Measurements of *Rhabdomeson* cf. *propatulissimum* Ceretti, 1963. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 4 | 0.08 | 0.008 | 9.563 | 0.07 | 0.09 |
| macroacanthostyle diameter | 4 | 0.06 | 0.009 | 14.142 | 0.05 | 0.07 |
| branch width | 7 | 1.32 | 0.216 | 16.334 | 1.05 | 1.68 |
| axial tube diameter | 7 | 0.27 | 0.099 | 36.140 | 0.17 | 0.45 |

*Material*.—SMF 1758, 1763, 1764, 1766, 1770, 1779.

*Description*.—Ramose 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. binodosum* 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 "l", Upper Carboniferous (Gzhelian); Italy, Carnic Alps.

## Family Hyphasmoporidae Vine, 1885
## Genus *Streblotrypa* Vine, 1885
## Subgenus *Streblotrypa* (*Streblotrypa*) Vine, 1885

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

*Diagnosis*.—Ramose 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.

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

### *Streblotrypa* (*Streblotrypa*) sp.

Fig. 5E, F.

*Material*.—SMF 1780, 1732.

*Description*.—Ramose 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 fasciculata* Bassler 1929, by original designation; Upper Permian, Indonesia.

*Diagnosis*.—Ramose colonies. Clearly defined bundle of axial zooecia in the endozone. Diaphragms rare. Hemisepta rare or absent. Metazooecia present between the autozooecial apertures (translated after Gorjunova 1985).

← 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. *propatulissimum* 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 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 ($H_1$), and oblique section of the branch displaying axial tube and autozooecial chambers ($H_2$). **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 ($N_1$) and arrangement of autozooecia ($N_2$).

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.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| branch width | 6 | 1.80 | 0.485 | 26.985 | 1.00 | 2.25 |
| aperture width | 46 | 0.15 | 0.015 | 10.267 | 0.12 | 0.18 |
| acanthostyle diameter | 36 | 0.06 | 0.009 | 15.492 | 0.04 | 0.08 |
| number of acanthostyles per aperture | 28 | 4.50 | 0.509 | 11.315 | 4 | 5 |
| number of apertures per 2 mm longitudinally | 7 | 3.15 | 0.569 | 18.055 | 2.5 | 4.0 |
| number of apertures per 2 mm diagonally | 6 | 5.57 | 0.524 | 9.415 | 5.0 | 6.5 |
| aperture spacing along branch | 20 | 0.53 | 0.060 | 11.342 | 0.44 | 0.63 |
| aperture spacing across branch | 19 | 0.40 | 0.052 | 13.171 | 0.31 | 0.48 |

*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.

1955 *Streblotrypa nikiforovae* sp. nov.; Morozova 1955: 62–63, pl. 9: 2.

*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 Gonzáles 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.

1938 *Clausotrypa monticola* (Eichwald, 1860); Nikiforova 1939: 181, pl. 14: 4–7, pl. 15: 7–10.

1941 *Clausotrypa monticola* (Eichwald, 1860); Schulga-Nesterenko 1941: 219, pl. 13: 3–6.

1981 *Clausotrypa monticola* (Eichwald, 1860); Morozova and Krutchinina 1981: 67, pl. 20: 3, 4.

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 8. Measurements of *Rhombopora lepidodendroides* Meek, 1872. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 25 | 0.12 | 0.017 | 13.770 | 0.10 | 0.15 |
| macroacanthostyle diameter | 10 | 0.07 | 0.010 | 15.380 | 0.05 | 0.08 |
| microacanthostyle diameter | 20 | 0.02 | 0.005 | 26.251 | 0.01 | 0.03 |
| branch width | 4 | 1.18 | 0.222 | 18.881 | 0.90 | 1.43 |

Table 9. Measurements of *Rhombopora corticata* Moore, 1929. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 10 | 0.18 | 0.015 | 8.664 | 0.14 | 0.20 |
| macroacanthostyle diameter | 10 | 0.07 | 0.007 | 10.497 | 0.06 | 0.08 |
| microacanthostyle diameter | 10 | 0.04 | 0.007 | 16.696 | 0.03 | 0.05 |
| branch width | 5 | 1.65 | 0.242 | 14.601 | 1.41 | 2.03 |

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*.—Ramose 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 *Klaucena* 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*.—Devonian to Permian; worldwide.

### *Rhombopora lepidodendroides* Meek, 1872

Fig. 5J–M; Table 8.

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

*Description*.—Ramose 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, (Westphalian B/C) of Valverdín, Cantabrian Mountains (Ernst et al. 2005).

### *Rhombopora corticata* Moore, 1929

Fig. 6B, C; Table 9.

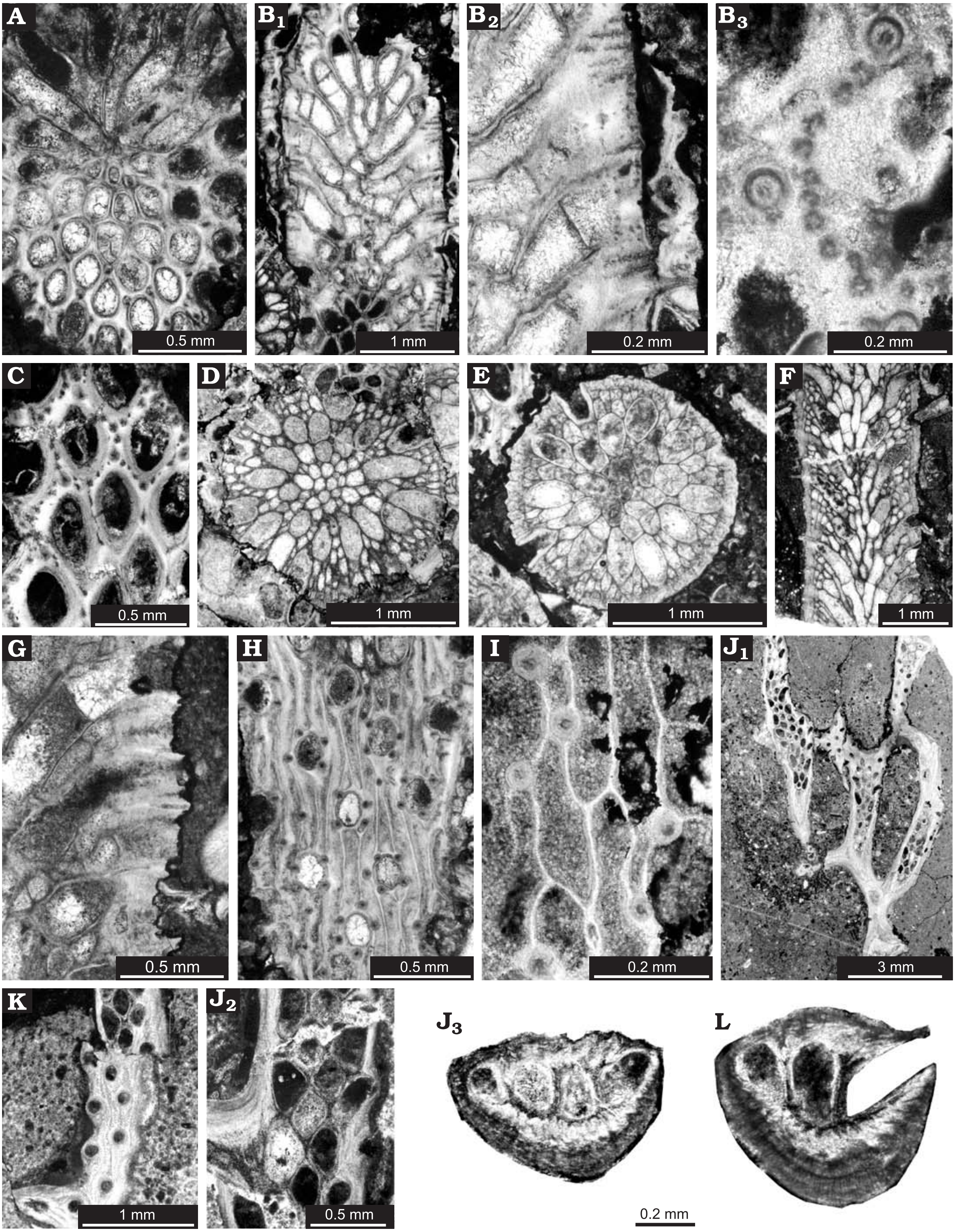
1929 *Rhombopora corticata* sp. nov.; Moore 1929: 137, pl. 17: 3, 4; text-fig. 4i, j.

1995 *Rhombopora corticata* Moore, 1929; Sakagami 1995: 262, figs. 1: 7, 8; 2: 1, 2.

2005 *Rhombopora corticata* Moore, 1929; Ernst et al. 2005: 307–309, pl. 2: 2, pl. 3: 6.

*Material*.—SMF 1741, 1756 (and three additional fragments).

*Description*.—Ramose branched colonies, 1.41–2.03 mm in diameter. Autozooecial apertures oval, arranged in regular diagonal rows, spaced 3 in 2 mm distance longitudinally and 6 in the same distance diagonally. Paurostyles 0.030–0.054 mm in


A
0.5 mm
B1
1 mm
B2
0.2 mm
B3
0.2 mm
C
0.5 mm
D
1 mm
E
1 mm
F
1 mm
G
0.5 mm
H
0.5 mm
I
0.2 mm
J1
3 mm
K
1 mm
J2
0.5 mm
J3
L
0.2 mm

diameter, arranged in a single row between autozooecia 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*.—*Rhombopora 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*: *Rhombopora incrassata* Ulrich, 1890, by original designation; Lower Mississippian, Kentucky (USA).

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

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

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

## *Saffordotaxis* cf. *yanagidae* Sakagami, 1964

Figs. 5N, 6A; Table 10.

cf. 1964 *Saffordotaxis yanagidae* sp. nov.; Sakagami 1964: 299–301, pl. 45: 1–4.

*Material*.—SMF 1740, 2154.

*Description*.—Ramose branched colonies, 1.05–1.20 mm in diameter. Autozooecia 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. Heterozooecia absent. Actinotostylets 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 *Saffordotaxis yanagidae* Sakagami, 1964 from the *Millerella yowarensis* 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 10. Measurements of *Saffordotaxis* cf. *yanagidae* Sakagami, 1964. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 9 | 0.09 | 0.010 | 11.164 | 0.07 | 0.10 |
| acanthostyle diameter | 9 | 0.04 | 0.005 | 12.122 | 0.03 | 0.05 |
| number of acanthostyles per aperture | 5 | 5.40 | 0.894 | 16.564 | 4 | 6 |

*Stratigraphic and geographic range*.—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain. ?*Millerella yowarensis* Zone of the Akiyoshi Limestone (top Serpukhovian), Upper Carboniferous; Japan.

## Order Fenestellida Astrova 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 autozooecia. Autozooecia arranged in four alternating rows on branches, 5–6 rows before and 2–3 after bifurcation. Autozooecial chambers tubular, short, having weakly developed inferior hemisepta and short vestibule, regularly hexagonal in mid tangential section. Autozooecial apertures rounded. Keels between longitudinal rows of autozooecia weakly developed or absent. Microacanthostyles and nodes usually present on obverse surface (translated after Morozova 2001).

*Discussion*.—*Polypora* M'Coy, 1844 is similar to *Paucipora* Termier and Termier, 1971 but the latter has strongly developed hemisepta and shorter autozooecia.

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

← Fig. 6. Rhabdomesid bryozoans *Saffordotaxis*, *Rhombopora*, *Clausotrypa*, and fenestellid bryozoan *Polypora* from the La Hermida locality, Spain, Late Carboniferous (Moscovian). **A**. *Saffordotaxis* cf. *yanagidae* Sakagami, 1964, SMF 1740, oblique section of the branch showing budding pattern of autozooecia. **B**, **C**. *Rhombopora corticata* Moore, 1929. **B**. SMF 1741, longitudinal section of the branch displaying autozooecial chambers, diaphragms ($B_1$), macroacanthostyles and paurostyles ($B_2$), and tangential section displaying macroacanthostyles and paurostyles ($B_3$). **C**. SMF 1756, tangential section of the branch. **D–I**. *Clausotrypa monticola* (Eichwald, 1860). **D**. SMF 1785. **E**. SMF 1786, cross sections of branches displaying well developed axial bundle (D) and lacking one (E). **F**. SMF 1787, longitudinal section of the branch. **G**. SMF 1733, longitudinal section of the branch showing acanthostyles, exilazooecia and diaphragms. **H–I**. SMF 1788 (**H**) and SMF 1739 (**I**), tangential sections showing autozooecial apertures, acanthostyles and ribs on the colony surface. **J–L**. *Polypora* cf. *remota* Condra, 1902. **J**. SMF 1765, tangential section of the colony fragment ($J_1$), deeper view displaying autozooecial chambers ($J_2$), and cross section of the branch ($J_3$). **K**. SMF 1789, tangential section of the branch. **L**. SMF 1790, cross section of the branch.

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.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 10 | 0.09 | 0.006 | 6.924 | 0.08 | 0.10 |
| aperture spacing along branch | 10 | 0.35 | 0.038 | 10.665 | 0.31 | 0.44 |
| aperture spacing across branch | 10 | 0.29 | 0.028 | 9.775 | 0.25 | 0.34 |
| maximal chamber width | 10 | 0.16 | 0.019 | 11.973 | 0.13 | 0.19 |

## *Polypora* cf. *remota* Condra, 1902

Fig. 6J–L; Table 11.

1902 *Polypora remota* sp. nov.; Condra 1902: 353–354, pl. 24: 1, 2.
1999 *Polypora* sp. A; Gonzáles and Suárez Andréz 1999: 605, pl. 2: 4–6.

*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. Autozooecia arranged in 3–4 rows on branches. Autozooecial apertures rounded, 14–18 spaced in 5 mm of the branch length, 9–14 on each side of fenestrule. Autozooecia 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. aestacella* Meek, 1872 from the Graham Formation of Texas. The latter species has 4–6 rows of autozooecia 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; North America. Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain. Calizas del Cuera, Upper Moscovian (Podolski horizon), Upper Carboniferous; Playa de la Huelga, Spain.

## Family Acanthocladiidae Zittel, 1880

## Genus *Penniretepora* d'Orbigny, 1849

= *Acanthopora* Young and Young, 1875; = *Pinnatopora* Vine, 1883

*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 autozooecia 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 autozooecial 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. *Acanthocladia* (sensu King 1849) has been revised 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 *Acanthocladia* need to be revised using characters of the autozooecia and the presence or absence of heteromorphs.

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

## *Penniretepora pseudotrilineata* Ceretti, 1963

Fig. 7A–C, I; Table 12.

1963 *Penniretepora pseudotrilineata* sp. nov.; Ceretti 1963: 309–310, pl. 25: 4a, b, text-fig. 6.
?1999 *Penniretepora* sp. A.; Gonzáles and Suárez Andréz 1999: 607, pl. 2: 10, 11.

*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

Fig. 7. Fenestellid bryozoans *Penniretepora* and *Rhombocladia* from the La Hermida locality, Spain, Late Carboniferous (Moscovian). **A**–**C**, **I**. *Penniretepora pseudotrilineata* Ceretti, 1963. **A**. SMF 1724, tangential section of the branch: autozooecial chambers ($A_1$), triangular keel and apertures ($A_2$), fragment of the main branch with secondary branch ($A_3$), apertures and apertural nodes ($A_4$). **B**. SMF 1791, longitudinal section of the branch displaying autozooecial chamber, outer laminated skeleton and microstylets. **C**. SMF 1792, cross section of the branch. **I**. SMF 1724, reverse side of the colony. **D**–**H**. *Rhombocladia punctata* Dunaeva, 1961. **D**. SMF 1755, cross section of the branch. **E**–**F**. SMF 1793 (**E**) and SMF 1794 (**F**), longitudinal section of branches showing autozooecial chambers and superior hemisepta. **G**. SMF 1795, tangential section: close view of autozooecial apertures and microacanthostyles ($G_1$) and arrangement of apertures at the colony surface ($G_2$). **H**. SMF 1796, cross section of the branch displaying autozooecial walls with microacanthostyles. →

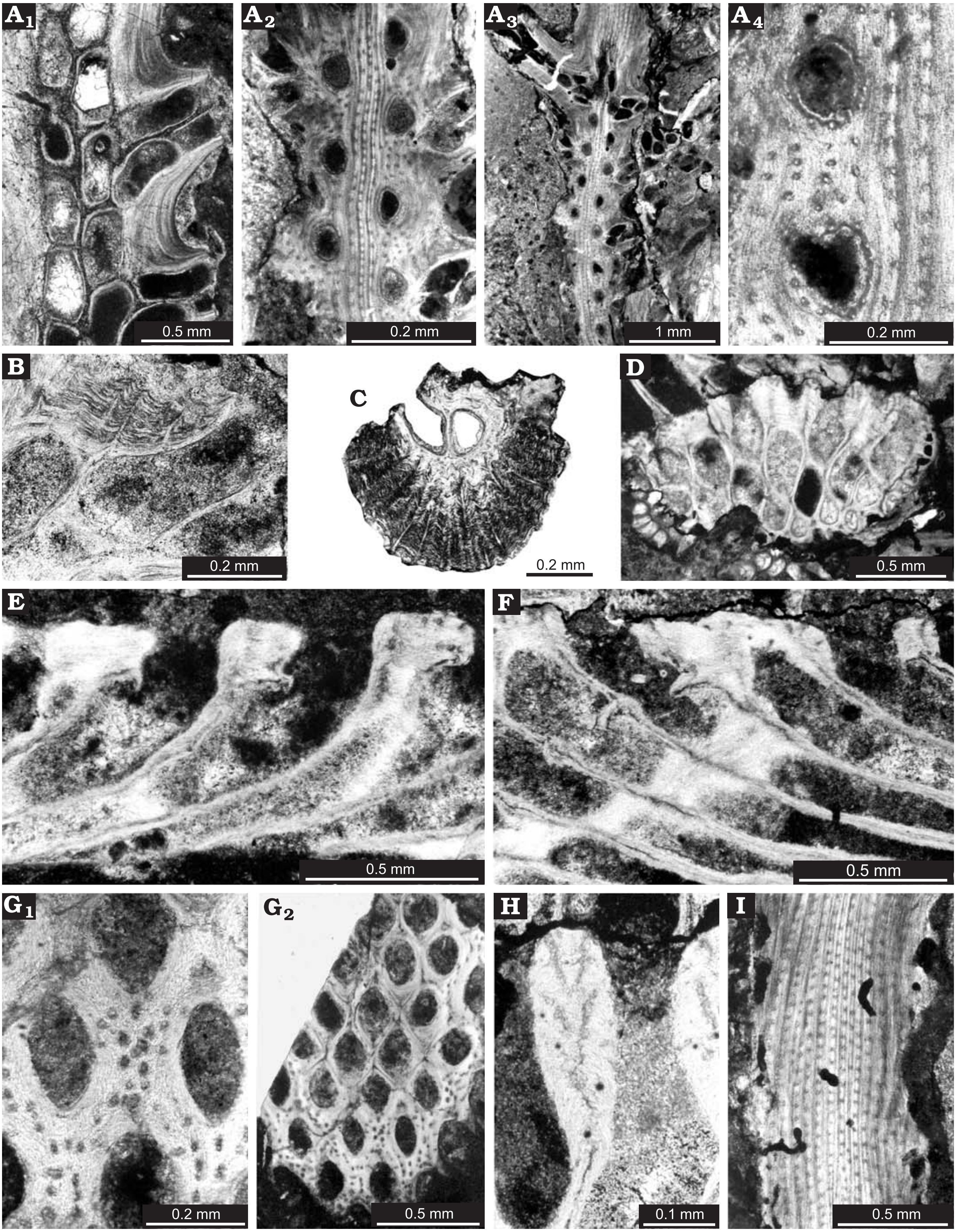

A1
0.5 mm
A2
0.2 mm
A3
1 mm
A4
0.2 mm
B
0.2 mm
C
0.2 mm
D
0.5 mm
E
0.5 mm
F
0.5 mm
G1
0.2 mm
G2
0.5 mm
H
0.1 mm
I
0.5 mm

Table 12. Measurements of *Penniretepora pseudotrilineata* Ceretti, 1963. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| main branch width | 4 | 0.80 | 0.066 | 8.321 | 0.70 | 0.85 |
| secondary branch width | 4 | 0.398 | 0.015 | 3.774 | 0.390 | 0.420 |
| secondary branch spacing | 9 | 0.85 | 0.129 | 15.217 | 0.66 | 1.05 |
| aperture width | 15 | 0.10 | 0.006 | 6.404 | 0.09 | 0.11 |
| aperture spacing along branch | 10 | 0.37 | 0.029 | 7.710 | 0.34 | 0.43 |
| aperture spacing across branch | 10 | 0.35 | 0.022 | 6.154 | 0.32 | 0.40 |
| maximal chamber width | 8 | 0.16 | 0.008 | 4.833 | 0.15 | 0.18 |

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. Autozooecia rectangular to pentagonal or kidney-shaped in mid tangential section on main and secondary branches. Hemisepta absent. Wide triserial keel on main branch. 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.

*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. The species *P. trilineata* Meek, 1872, as redescribed by Ceretti (1963) from the Upper Carboniferous of the Italian Carnic Alps, has thinner main branches (0.46 *versus* 0.7–0.85 mm in present material, and 0.81 mm given in the original description of *P. pseudotrilineata*), and more closely spaced apertures (17 per 5 mm *versus* 13 and 14 apertures in the present and Ceretti's material respectively). Moore (1929) gave similar measurements for the variety *Pinnatopora trilineata* var. *texana*—0.42– 0.55 mm main branch width and 15.5–16.0 apertures per 5 mm. Unfortunately, no internal morphology is known from the American material. The species *Penniretepora* sp. A, described by Gonzáles and Suárez Andréz (1999), is also very similar to *P. pseudotrilineata*. These authors mentioned the low, wide and undulose but not triserial keel. No illustrations of the keel of this species are available.

*Stratigraphic and geographic range*.—Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain. Auernig Formation, bed "l", Upper Carboniferous (Gzhelian); Italy, Carnic Alps. ? Calizas del Cuera, Upper Moscovian (Podolski horizon), Upper Carboniferous; Playa de la Huelga, Spain.

## 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.

*Diagnosis*.—Ramose dendroid colonies. Flattened branches carrying 4–12 zooecial rows. Vestibule weakly developed. Diaphragms rare. Superior hemisepta usually developed. Oval apertures arranged in a diagonal pattern. Microacanthostyles occur in zooecial walls, sometimes forming star-shaped accumulations. Rare heterozooecia (leptozooecia of Lavrentjeva 1985) occurring only on frontal surface, on lateral parts of branches. Dorsal wall very thin (translated after Lavrentjeva 1985).

*Disscusion*.—*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 leptozooecia 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 13. Measurements of *Rhombocladia punctata* Dunaeva, 1961. N, number of measurements; X, mean; SD, standard deviation; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

| | N | X | SD | CV | MIN | MAX |
|---|---|---|---|---|---|---|
| aperture width | 13 | 0.15 | 0.035 | 23.471 | 0.11 | 0.21 |
| branch width | 8 | 1.60 | 0.202 | 12.611 | 1.38 | 1.88 |
| branch thickness | 4 | 0.90 | 0.159 | 17.714 | 0.68 | 1.05 |

Table 14. Distribution of bryozoan species from the Picos de Europa Formation.

| Species | Occurrence | Age |
|---|---|---|
| *Fistulipora petaloida* Schulga-Nesterenko, 1955 | Russian Plate | Kasimovian |
| *Stenophragmidium isospinosum* Ernst, Schäfer, and Reijmer, 2005 | Spain | Westphalian B/C |
| *Streblotrypa* (*Streblascopora*) *nikiforovae* Morozova, 1955 | Ukraine | Moscovian |
| *Rhabdomeson* cf. *propatulissimum* Ceretti, 1963 | ? Carnic Alps, Italy | ? Gzhelian |
| *Clausotrypa monticola* (Eichwald, 1860) | Russian Plate, Arctic | Upper Carboniferous – Early Permian |
| *Rhombopora lepidodendroides* Meek, 1872 | N. America, Bolivia | Upper Carboniferous – Early Permian |
| *Rhombopora corticata* Moore, 1929 | N. America, Bolivia | Pennsylvanian |
| *Polypora* cf.*remota* Condra, 1902 | N. America | Pennsylvanian |
| *Penniretepora pseudotrilineata* Ceretti, 1963 | Carnic Alps, Italy | Gzhelian |
| *Rhombocladia punctata* Dunaeva, 1961 | Ukraine | Kasimovian |

lens-shaped in cross-section. Oval apertures arranged diagonally in 7 to 8 rows, 4.5 spaced in 2 mm of the branch length longitudinally and 7–8 diagonally. Autozooecial chambers long, bending gently to the colony surface, becoming rhombic in deeper tangential section, appearing rhombic to hexagonal in cross-section. Long superior hemisepta, curved proximally, positioned in distal parts of autozooecia; inferior hemisepta absent. Abundant microacanthostyles arranged irregularly between apertures, 0.02 mm in diameter. Walls 0.035–0.040 mm thick in the endozone, 0.13–0.16 mm thick in the exozone. Heterozooecia absent.

*Disscusion*.—This species is similar to *Rhombocladia multispinosa* McKinney, 1972 from the Bangor Limestone (Chesterian) of North America. The latter species differs in having large single macroacanthostyles between the apertures.

*Stratigraphic and geographic range*.—Kasimovian Stage, Upper Carboniferous; Donetsk Basin, Ukraine. Picos de Europa Formation, Moscovian, Upper Carboniferous; La Hermida, Spain.

# 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 stratigraphic 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* (*Streblascopora*) *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* (*Streblascopora*) *nikiforovae* Morozova, 1955], *Polypora* sp. [= *Polypora remota* Condra, 1902], and *Penniretepora* sp. [= ?*Penniretepora 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 Valverdin sections in Cantabria. Based on the presence of *Stenophragmidium 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 *Penniretepora pseudotrilineata* Ceretti, 1963 was originally described from bed "l" 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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