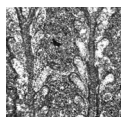


# Fenestrate Bryozoa of the Moniello Formation (Lower–Middle Devonian, NW Spain)

JUAN LUIS SUÁREZ ANDRÉS & PATRICK N. WYSE JACKSON



Lower–Middle Devonian non-fenestellid fenestrate bryozoans of NW Spain are reported, from two coastal sections of the upper Emsian–lower Eifelian Moniello Formation, the type locality at Moniello Inlet and at Arnao. Eighteen species of non-Fenestellidae fenestrates belonging to thirteen genera and six families have been identified; nine species are new: *Bashkirella arnaoense*, *Utopora parva*, *Bigeyina cantabrica*, *B. spinosa*, *Fenestrapora elegans*, *Paraseptopora geometrica*, *P. irregularis*, *Kalvariella antiqua* and *Filites robustus*. Fenestrates described herein, together with earlier reported taxa of the Family Fenestellidae from the Moniello Formation show palaeobiogeographic affinities with those of neighbouring Gondwanan regions, especially with Bohemia, but also with Middle Devonian assemblages from Eastern North America. The fenestrate fauna from NW Spain comprises seven species common with the Lower Devonian of the Prague Basin (Bohemia, Czech Republic) and genera with relatively limited geographic distributions, such as *Utopora* and *Filites*. A remarkable feature of the studied fauna is the presence of several species that represent the earliest and westernmost reported occurrence of their genera, *Bashkirella*, *Paraseptopora* and *Kalvariella*, as well as previously reported *Cavernella asturica*. The occurrence of these species together with the stratigraphic and geographic position of previously reported ones indicate the existence of large gaps in the distribution of these Lazarus genera. • Key words: Fenestrates, Emsian, Eifelian, taxonomy, diversity, palaeobiogeography, Lazarus taxa.

SUÁREZ ANDRÉS, J.L. & WYSE JACKSON, P.N. 2017. Fenestrate Bryozoa of the Moniello Formation (Lower–Middle Devonian, NW Spain). *Bulletin of Geosciences* 92(2), 153–183 (9 figures, 16 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received March 9, 2017; accepted in revised form April 25, 2017; published online June 23, 2017; issued June 30, 2017.

Juan Luis Suárez Andrés, SONINGEO, S.L. Parque Científico y Tecnológico de Cantabria, C/ Isabel Torres, 9 – 39011, Santander, Spain; [juanl\\_suarez@yahoo.es](mailto:juanl_suarez@yahoo.es) • Patrick N. Wyse Jackson, Department of Geology, Trinity College, Dublin 2, Ireland; [wysjcknp@tcd.ie](mailto:wysjcknp@tcd.ie)

Bryozoans are common among benthic faunas throughout most of the Palaeozoic. Their associations tend to be dominated by members of the orders Trepostomata and Cystoporata during the Early Palaeozoic, while those of the orders Fenestrata and Cryptostomata are usually predominant in the Late Palaeozoic (Ernst 2013). The studies devoted to the Devonian bryozoan fauna of NW Spain during the last number of years reveal a well-represented, highly diverse group providing important palaeobiogeographic and palaeobiologic data (Ernst 2010, 2011, 2012; Suárez Andrés & McKinney 2010; Ernst *et al.* 2011; Ernst & Buttler 2012; Suárez Andrés & Wyse Jackson 2014; Suárez Andrés *et al.* 2014; Suárez Andrés & Ernst 2015). The Lower–Middle Devonian succession of NW Spain provides a rich record of episodes of reefal development, an outstanding evidence of high biodiversity that has received close attention for decades (Méndez-Bedia 1976, Méndez-Bedia *et al.* 1994, Soto *et al.* 1994, Fernández *et al.* 2006, Fernández-Martínez *et al.* 2006, among others). Bryozoans are locally very abundant and fenestrates gene-

rally constitute the most conspicuous group, but their composition has only been studied in detail in recent studies.

This paper is a contribution to the knowledge of the Devonian fenestrate fauna from NW Spain with a focus on the systematic composition and the palaeobiogeographic relationships of the representatives of the order Fenestrata from the upper Emsian–lower Eifelian Moniello Formation. Eighteen species and thirteen genera belonging to six families are reported herein from the Moniello Formation (Asturias, northern slope of the Cantabrian Mountains); nine of these species are new. These data, along with those reported in previous works, are used to assess the palaeobiogeographic affinities of the Lower–Middle Devonian Spanish fenestrates.

## Geological setting

The bryozoan fauna described herein belongs to the Moniello Formation, a calcareous unit within the Cantabrian

Zone of the Iberian Massif (Fig. 1), which represents the external zone of the Variscan Orogen (Alonso *et al.* 2009). The Cantabrian Zone constitutes a part of the provinces of Asturias and León, (NW Spain), with a thick Palaeozoic succession affected by thin-skinned tectonics (Pérez-Estaún *et al.* 1988). The Moniello Formation is a 200–300 m thick unit composed of limestones and marls, outcropping at the northern slope of the Cantabrian Mountains. The age of this unit is late Emsian–early Eifelian (Lower–Middle Devonian), between the *Polygnathus serotinus* and the *P. costatus partitus* zones (García-López & Sanz-López 2002, García-López *et al.* 2002). Its lateral equivalent at the southern slope is the Santa Lucía Formation (Comte 1936). Méndez-Bedia (1976) described the bio- and lithofacies present in the Moniello Formation and reported transition from coastal to platform and reefal environments from the eastern sections of the unit towards the west. Arbizu *et al.* (1979) formally described the Moniello Formation and its biostratigraphy. The reefal facies have been studied by the Research Group on Devonian Reefs of the University of Oviedo (Méndez-Bedia *et al.* 1994, Soto *et al.* 1994, Fernández *et al.* 2006, Fernández-Martínez *et al.* 2006).

Two outcrops located on the central coast of Asturias and corresponding to the outermost carbonate platform, reefal and peri-reefal facies (Méndez-Bedia 1976) have been sampled for this study. The first is the type section, exposed immediately westward of the Moniello Inlet. The second one is a discontinuous outcrop between the localities of Salinas and Arnao, which is the westernmost and thus the most distal section of the Moniello Formation along the coast of Asturias (Fig. 1). The Arnao section shows incomplete outcrops of this unit strongly affected by tectonics, covered by overlying disconformable deposits. This section has been documented for decades due to the development of reefal facies including a well-preserved bioherm (Méndez-Bedia 1976; Sánchez de la Torre & Manjón 1976; Méndez-Bedia & Soto 1984; Soto & Méndez-Bedia 1985; Arbizu *et al.* 1991; Arbizu & Méndez-Bedia 2006a, b).

## Material and methods

The Moniello and Arnao outcrops of the Moniello Formation were sampled for fenestrate bryozoans. Most of the specimens are preserved in calcite, though partial silicification is relatively common. Specimens were sectioned and acetate peels were prepared of three standard oriented sections, whenever possible. At least two tangential sections at different depths were prepared to observe morphological details; this procedure is generally advisable for fenestrates, but especially relevant for appreciation of characteristics of the superstructures developed above the

obverse surfaces of zoaria in the Semicosciniidae. Samples were observed under optical microscope and digital imaging was carried out; morphometric characters were measured on digital images by means of the software Image J.

In contrast with other fenestrate families, the Semicosciniidae frequently show very distinct variations in chamber size and morphology depending on the position of autozoecia relative to fenestrules and dissepiments. These morphological variations are documented in the description of species, and separate morphometric measurements are given for chambers developed adjacent to fenestrules and to dissepiments and for those not affected by these interactions. Characters, such as the maximal chamber width or chamber length are specifically documented (see the corresponding tables). In species with sinuous branches (*i.e.* *Bigeyina victrola* and *Fenestrapora elegans* sp. nov.), measurements of branch spacing have been treated in two separate groups, those adjacent to fenestrules and adjacent to dissepiments, to reflect bimodality. In pinnate species (families Septoporidae and Acanthocladiidae), zoarial and zooecial characters were measured on main branches and pinnae and tabulated separately. One hundred forty specimens were studied for the systematic treatment presented herein. One hundred thirty of them were adequately described and figured, while the rest (all three specimens of *Prolixicella* sp. and ten specimens assigned to *Anastomopora* sp.) have been identified to the genus level only, due to their poor state of preservation and/or the small number of specimens obtained, and have been briefly described but not figured. Most species have been identified in both outcrops, except for *Eosemicoscium* aff. *burultobense*, found only in Moniello Inlet, and *Paraseptopora geometrica*, *Penniretepora bohémica* and *Bashkirella arnaoense*, in Arnao.

All specimens are deposited at the Department of Geology of the University of Oviedo. Accession numbers (DGO) for the species described in this paper are indicated within the systematic description.

## Systematic Palaeontology

Phylum Bryozoa Ehrenberg, 1831  
Class Stenolaemata Borg, 1926  
Order Fenestrata Elias & Condra, 1957  
Suborder Phylloporinina Lavrentjeva, 1979  
Family Phylloporinidae Ulrich, 1890

### Genus *Prolixicella* Ernst & Schroeder, 2007

*Type species.* – *Prolixicella bifurcata* Ernst & Schroeder, 2007; Givetian, Germany.

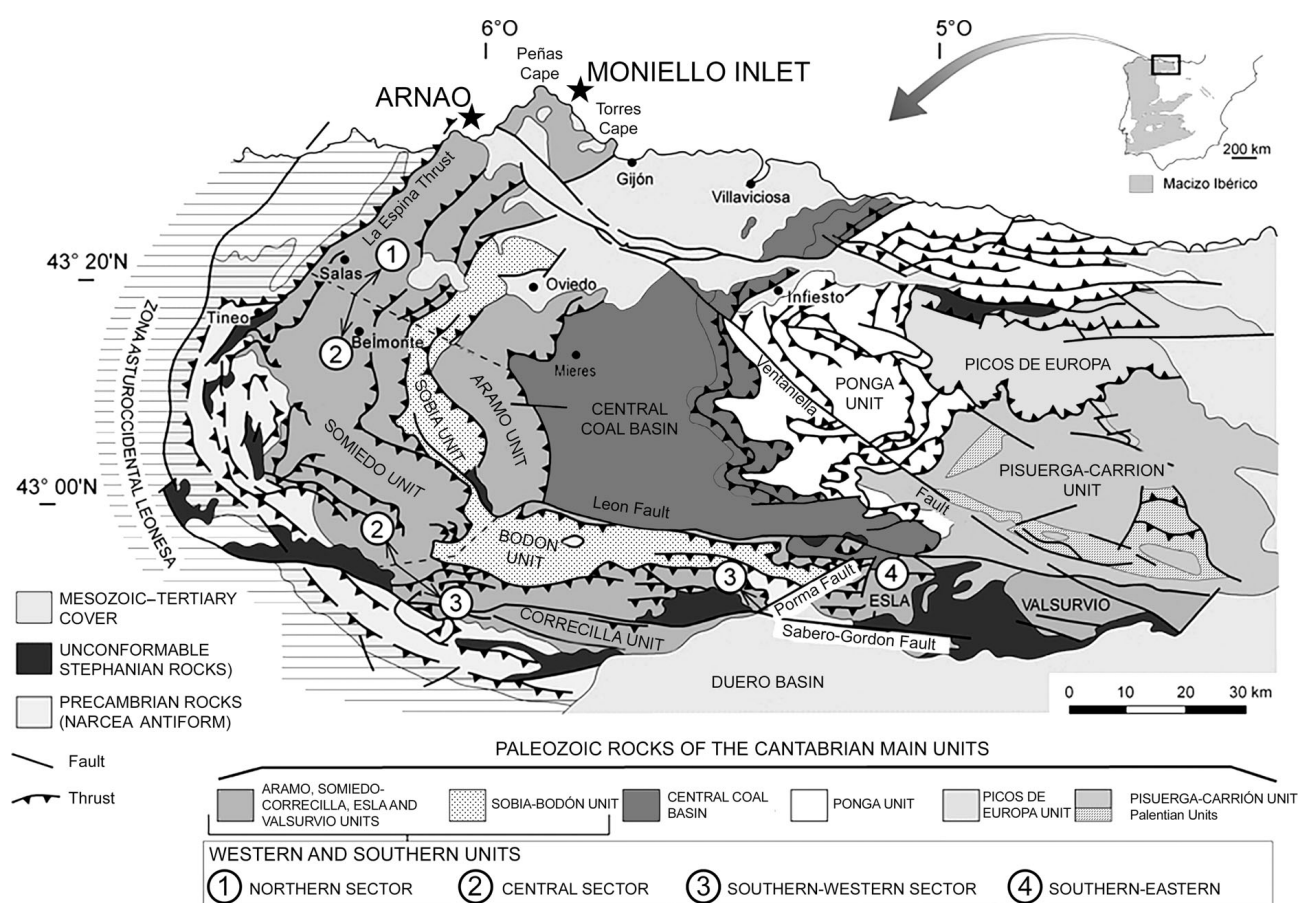


Figure 1. Geological map of the Cantabrian Zone after Pérez Estaún *et al.* (2004) showing the location of the Arnao and Moniello outcrops, Asturias, NW Spain.

### *Prolixicella* sp.

**Material.** – Three small specimens, DGO 13032–13034; one sectioned, recrystallized.

**Description.** – Exterior: Zoarium dendroid; multiserial branches straight to gently curved, bifurcating, anastomoses absent. Branch width 0.30–0.64 mm, average 0.46 mm.

**Interior:** Autozooeal chambers tubular, very long. Hemisepta and heterozooecia not observed. Macrostyles present on the reverse surface of branches.

**Remarks.** – Only one of the three small specimens collected has been sectioned, and internal features cannot be clearly appreciated due to recrystallization. Good quality images illustrating zooecial characters could not be obtained, so the species is not figured herein. The number, size and preservation of specimens allow for assignment to *Prolixicella* but prevent unequivocal species identification of the Spanish material; thus this material is kept in open nomenclature. Ernst & Schroeder (2007) provided the diagnosis of *Prolixicella*, reporting the absence of heterozooecia according to

observations on its type species, *P. bifurcata*, from the Givetian of Germany. Ernst (2012) described two new species, *P. iberica* and *P. parva*, from the Emsian of NW Spain and emended the original diagnosis to reflect the presence of apparent reproductive heterozooecia in *P. parva*. *Prolixicella* sp. has narrower branches than *P. iberica* and *P. parva*. The species defined by Ernst (2012) represent the earliest record of this genus and the only one from the Early Devonian.

**Occurrence.** – Lower Eifelian. Arnao, Cantabrian Zone, NW Spain.

Family Chasmatoporidae Shulga-Nesterenko, 1955

### Genus *Bashkirella* Nikiforova, 1939

**Type species.** – *Bashkirella ornata* Nikiforova, 1939; Lower Permian, Urals, Russia.

### *Bashkirella arnaoense* sp. nov.

Figure 2A–E, Table 1

**Holotype.** – DGO 13025.

**Table 1.** Measurements of *Bashkirella arnaoense* sp. nov. X: mean; SD: standard deviation; CV: coefficient of variation; Max: maximal value; Min: minimal value; N: number of measurements.

	X	SD	CV	MAX	MIN	N
Branch width (mm)	0.75	0.155	0.0240	1.02	0.42	23
Fenestrule length (mm)	2.83	0.265	0.0702	3.07	2.34	8
Fenestrule width (mm)	1.77	0.312	0.0976	2.38	1.57	6
Aperture spacing across branch (mm)	0.43	0.014	0.0002	0.42	0.44	2
Aperture width (mm)	0.12	0.007	0.0001	0.13	0.11	4
Aperture length (mm)	0.21	0.005	0.0001	0.21	0.20	4
Maximal chamber width (mm)	0.19	0.034	0.0011	0.25	0.13	17

*Paratypes.* – DGO 13026, 13029.

*Type horizon and locality.* – Lower Eifelian, Moniello Formation. Arnao.

*Material.* – Seven specimens, DGO 13025–13031; four sectioned.

*Etymology.* – From the Asturian village of Arnao, the type locality. Gender neuter.

*Diagnosis.* – *Bashkirella* with wide branches and largely spaced, oval apertures. Fenestrules large, highly variable in size.

*Description.* – Exterior: Zoarium irregularly reticulate, branches anastomosed. Fenestrules medium to large, irregular in shape and size. Apertures oval, arranged in 3–5 rows.

Interior: Autozooeical chambers elongate, sack-shaped to tubular, arranged in 3–5 rows around a weakly defined axis. Moderately short vestibule. Hemisepta absent; terminal diaphragms may occur. Prominent styles between zooeical apertures and on the reverse of branches. Laminar skeleton moderately thickened on the reverse of branches. Modified irregular zooecia, with larger and shorter chambers than those of regular autozooeica, may occur at anastomoses.

*Remarks.* – *Bashkirella arnaoense* is the earliest reported species of this genus. Two other Devonian species had

been previously described, *B. devonica* (Dessilly, 1967) from the upper Eifelian of Belgium and Germany (Ernst & Schroeder 2007) and *B. bifurcata* (Gorjunova, 1966) from the upper Eifelian of Armenia. Both species have thinner branches and closer autozooeical aperture spacing than *B. arnaoense*. Fenestrules of *B. arnaoense* are larger than those of the other Eifelian species. Fenestrules in *Bashkirella* are too irregular in shape and size to consider mean values statistically significant for species description and comparison; minimal and maximal values might be used instead to provide some sense of morphological variation, but these should not be considered as a critic character for species discrimination.

*Occurrence.* – Lower Eifelian. Arnao, Cantabrian Zone, NW Spain.

Suborder Fenestrina Astrova & Morozova, 1956  
Family Semicosciniidae Morozova, 1987

### Genus *Utropora* Pošta, 1894

*Type species.* – *Fenestella (Utropora) nobilis* Barrande, 1894 in Pošta (1894); Lower Devonian, Prague Basin (Czech Republic).

### *Utropora parva* sp. nov.

Figure 2F–J, Table 2

*Holotype.* – DGO 12961.

*Paratypes.* – DGO 12962–12965.

*Type horizon and locality.* – Upper Emsian, Moniello Formation. Moniello Inlet.

*Material.* – Six specimens, DGO 12961–12966.

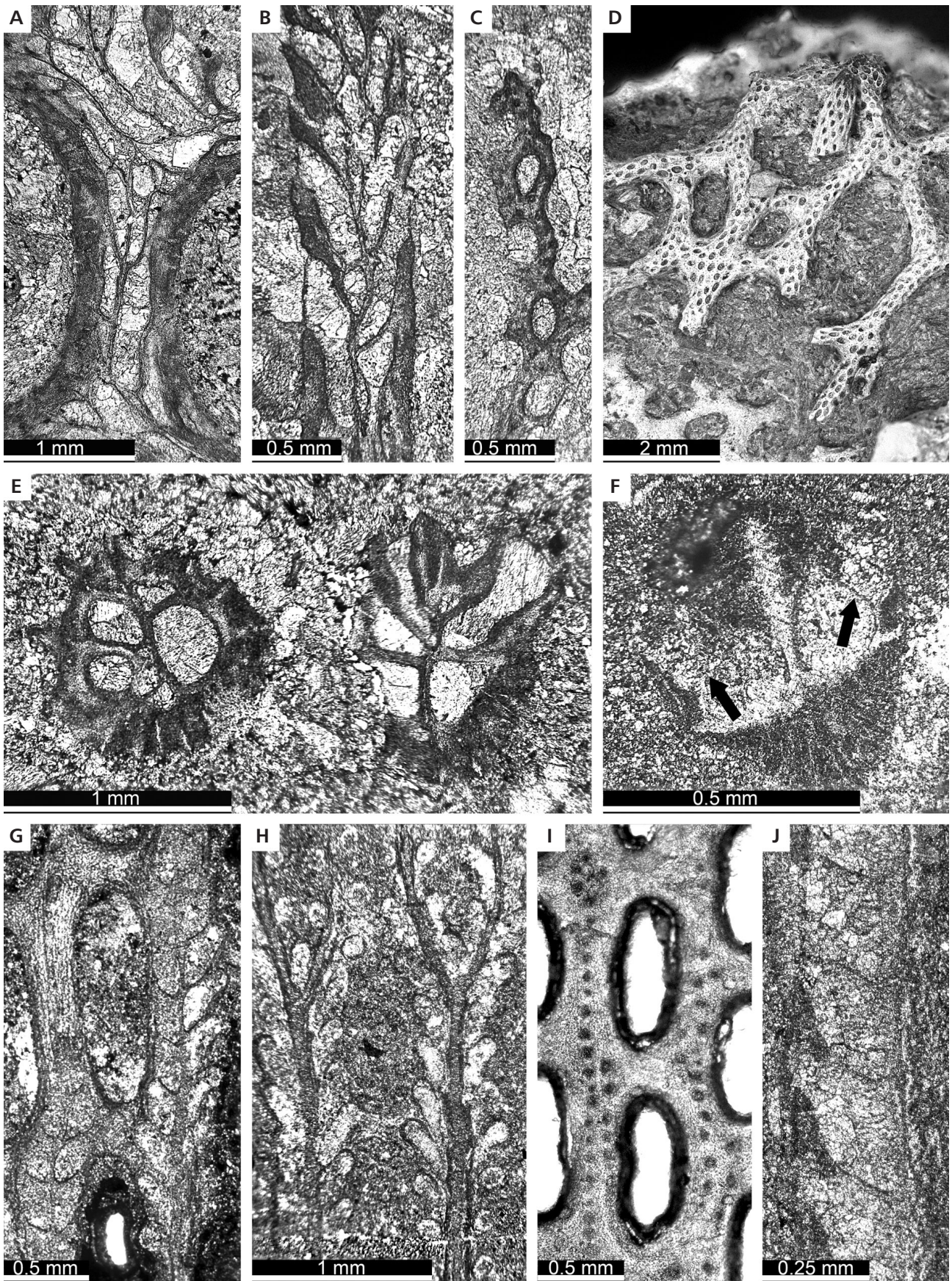
*Etymology.* – From Latin *parva*, small, referring to chamber length. Gender feminine.

*Diagnosis.* – *Utropora* with wide branches, relatively small fenestrules and short and wide zooeical chambers.

*Description.* – Exterior: Zoarium reticulate, fan-shaped. Branches slightly sinuous, dissepiments wide. Keel wide

**Figure 2.** A–E – *Bashkirella arnaoense* sp. nov. Moniello Formation. • A – tangential section; enlarged zooecia can be observed at anastomoses, DGO 13026. • B, C – tangential sections, DGO 13025, holotype; B – arrangement of autozooeica and terminal diaphragms sealing apertures (left); C – zooeical apertures and styles. • D – fragmentary specimen showing anastomosed meshwork, DGO 13031. • E – transverse section of two branches, DGO 13029. • F–J – *Utropora parva* sp. nov. Moniello Formation. • F – transverse section of a branch cutting distal tubes, (arrows). Holotype, DGO 12961. • G – oblique tangential section, DGO 12962. • H – shallow tangential section; the position of the distal tube can be observed. Holotype, DGO 12961. • I – tangential section through the reverse of branches, DGO 12964. • J – longitudinal section, DGO 12964.







**Table 2.** Measurements of *Utropora parva* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.51	0.077	0.0060	0.68	0.44	17
Branch width (mm)	0.39	0.043	0.0019	0.49	0.32	22
Fenestrule length (mm)	0.90	0.133	0.0176	1.25	0.71	25
Fenestrule width (mm)	0.35	0.069	0.0048	0.46	0.20	23
Dissepiment width (mm)	0.33	0.053	0.0028	0.45	0.25	37
Distance between branch centres (mm)	0.67	0.095	0.0090	0.88	0.51	24
Aperture spacing across branch (mm)	0.32	0.037	0.0014	0.39	0.25	26
Aperture spacing along branch (mm)	0.28	0.030	0.0009	0.37	0.22	52
Aperture width (mm)	0.13	0.010	0.0001	0.16	0.11	53
Maximal chamber width aside fenestrules (mm)	0.13	0.015	0.0002	0.16	0.11	29
Chamber length aside fenestrules (mm)	0.26	0.027	0.0007	0.31	0.22	29
Maximal chamber width aside dissepiments (mm)	0.18	0.016	0.0003	0.21	0.16	29
Chamber length aside dissepiments (mm)	0.26	0.031	0.0009	0.35	0.21	29
Chamber depth (mm)	0.18	0.020	0.0004	0.23	0.14	15
Angle transverse wall-basal plate (degrees)	62.88	8.11	65.76	74.17	50.64	11

and low, blunt, nodes lacking. Two rows of autozooecia per branch, apertures lobulated with a thick peristome. Fenestrules moderately large, elliptical to rectangular, irregular in size.

**Interior:** Autozooecial chambers flask-shaped, long vestibule in lateral position. Axial wall straight, locally sinuous. Hemisepta lacking. Basal plate almost flat, granular skeleton thick in the keel. Microstyles abundant, macrostyles on the reverse of branches. Heterozooecia not observed.

**Remarks.** – *U. parva* sp. nov. differs from *U. nobilis*, the type species, in its more delicate meshwork and shorter zooecial chambers; from *U. parallela* [Barrande, 1894 in Pořta (1894)], from the Lower Devonian of Prague Basin,

in having wider branches with a longer spacing and shorter chambers. *U. parva* sp. nov. resembles *U. vera* Morozova & Lavrentjeva, 1998, from the Emsian–Eifelian of Transcaucasia, but it has thinner branches and shorter chambers than the latter. *U. aff. nobilis* Bigey, 1972a from the Emsian of the Armorican Massif (France) is similar to *U. parva* sp. nov. in its branch width, but its branch spacing is wider and fenestrules are larger.

**Occurrence.** – Emsian–lower Eifelian. Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

### Genus *Semicoscinium* Prout, 1859

**Type species.** – *Semicoscinium rhomboideum* Prout, 1859; Hamilton, Eifelian (Middle Devonian), Falls of the Ohio, Indiana, USA.

### *Semicoscinium discretum* (Prantl, 1932)

Figure 3A–G, Table 3

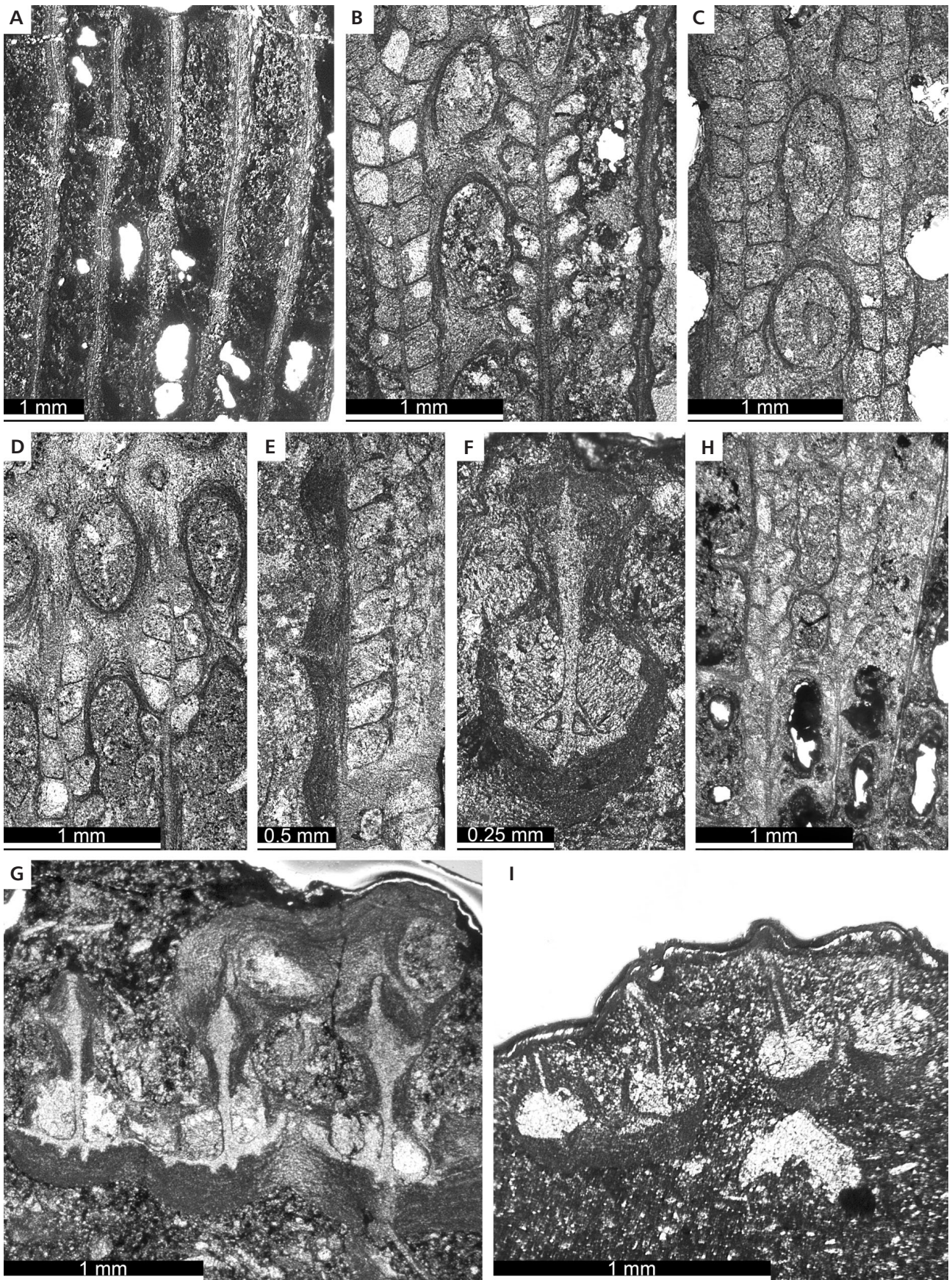
- 1932 *Isotrypa discreta*; Prantl; p. 25, pl. 4, fig. 11 (*non* 10), pl. 5, fig. 18.  
 1932 *Fenestella capillosa* Pořta (*pars*). – Prantl, pl. 1, fig. 11 (*non* pl. 2, fig. 5).  
 1932 *Fenestella pannosa* Pořta (*pars*). – Prantl, pl. 2, fig. 9 (*non* pl. 1, fig. 4, pl. 2, fig. 8).  
 1932 *Semicoscinium sacculus sacculus* (Barrande) (*pars*). – Prantl, pl. 2, fig. 18 (*non* pl. 2, fig. 17, pl. 3, figs 6–7).  
 1986 *Semicoscinium discreta* (Prantl, 1932). – McKinney & Kříž, pp. 38–39, fig. 21.  
 1998 *Semicoscinium cf. discretum* (Prantl, 1932) (*pars*). – Suárez Andrés, pp. 194–195, pl. 1, fig. 8, pl. 2, figs 1–4.  
 2011 *Quadrisemicoscinium discretum* (Prantl, 1932). – Ernst *et al.*, pp. 325–326, figs 10g–h, 11a–c, 12a–c.

**Material.** – Six specimens, DGO 12831–12836.

**Description.** – Exterior: Reticulate zoarium; branches straight or slightly sinuous, connected by broad, oval dissepiments. Keel high, separating two rows of autozooecia. Circular apertures rimmed by a peristome. Fenestrules oval, not too long. Superstructure consisting of apical widening of keel with scalloped flanks. The ichnogenus *Caupokeras* McKinney, 2009 may occur on the superstructure.

**Figure 3.** A–G – *Semicoscinium discretum* (Prantl, 1932). Moniello Formation. • A – tangential section cutting festooned keel tops, DGO 12834. • B – oblique tangential section from chamber bases to lower part of keels, DGO 12835. • C – deep tangential section showing morphological variability of chambers, DGO 12836. • D–F – DGO 12835; D – deep tangential section through chamber base, basal plate and reverse macrostyles; E – longitudinal section; F – transverse section of a branch showing the superstructure. • G – transverse section of a colony with tubes of *Caupokeras* developed on the upper part of keels, DGO 12831. • H, I – *Eosemicoscinium aff. burultobense* Plamenskaya, 1991. Moniello Formation, DGO 12887; H – oblique tangential section; I – transverse section of branches showing thin keels.







**Table 3.** Measurements of *Semicoscinium discretum* (Prantl, 1932). Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.88	0.125	0.0156	1.16	0.70	30
Branch width (mm)	0.49	0.057	0.0032	0.62	0.40	26
Fenestrule length (mm)	0.72	0.101	0.0102	0.93	0.56	28
Fenestrule width (mm)	0.39	0.067	0.0045	0.61	0.26	29
Dissepiment width (mm)	0.40	0.116	0.0135	0.69	0.24	33
Distance between branch centres (mm)	0.71	0.135	0.0182	0.92	0.38	56
Aperture spacing across branch (mm)	0.30	0.049	0.0024	0.41	0.23	22
Aperture spacing along branch (mm)	0.27	0.029	0.0008	0.33	0.21	39
Aperture width (mm)	0.13	0.026	0.0007	0.19	0.09	19
Maximal chamber width aside fenestrules (mm)	0.16	0.021	0.0005	0.21	0.10	48
Chamber length aside fenestrules (mm)	0.26	0.027	0.0007	0.34	0.21	48
Chamber depth	0.28	0.044	0.0019	0.36	0.21	40
Maximal chamber width aside dissepiments (mm)	0.23	0.033	0.0011	0.29	0.16	48
Chamber length aside dissepiments (mm)	0.27	0.031	0.0010	0.34	0.22	48
Angle transverse wall-basal plate (degrees)	70.15	4.64	21.51	79.88	59.68	40

Interior: Autozooecial chambers box-shaped, higher than long, with a short vestibule. Deep tangential section approximately square, chambers larger aside dissepiments. Axial wall straight, locally slightly sinuous. Hemisepta absent. Basal plate thick, faintly concave, with 3–5 robust longitudinal reverse ridges. Granular skeleton widened on the upper region of the keel, with a trident-shaped end. Coarse macrostyles commonly present on the reverse surface of branches; minute microstyles common. Laminar skeleton thickened on the reverse of branches, preferentially alongside dissepiments. Possible brood chambers occupy zooecial positions aside dissepiments.

**Remarks.** – *Semicoscinium discretum* differs from *S. fungi-forme* (Plamenskaya, 1991), from the Emsian of Kazakhstan, in having wider branches and larger fenestrules.

**Occurrence.** – Zlíčov Limestone, Emsian, Prague Basin, Czech Republic; Santa Lucía and Moniello Formations, upper Emsian–lower Eifelian, Cantabrian Zone, NW Spain.

### Genus *Eosemicoscinium* Morozova, 1987

**Type species.** – *Semicoscinium pyramidatum* Kopajevich, 1975; Lower Silurian, Estonia.

**Table 4.** Measurements of *Eosemicoscinium* aff. *burultobense* Plamenskaya, 1991. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.64	0.013	0.0002	0.65	0.62	3
Branch width (mm)	0.30	0.036	0.0013	0.35	0.28	3
Fenestrule length (mm)	0.61	0.081	0.0065	0.70	0.55	3
Fenestrule width (mm)	0.19	0.037	0.0014	0.23	0.16	3
Dissepiment width (mm)	0.08	0.008	0.0001	0.09	0.07	4
Distance between branch centres (mm)	0.44	0.047	0.0022	0.52	0.40	7
Aperture spacing across branch (mm)	0.23	0.030	0.0009	0.28	0.18	16
Aperture spacing along branch (mm)	0.28	0.030	0.0009	0.33	0.24	11
Aperture width (mm)	0.10	0.007	0.0001	0.11	0.09	11
Maximal chamber width aside fenestrules (mm)	0.10	0.016	0.0003	0.11	0.09	2
Chamber length aside fenestrules (mm)	0.23	0.032	0.0011	0.25	0.20	2

### *Eosemicoscinium* aff. *burultobense* Plamenskaya, 1991

Figure 3H–I, Table 4

aff. 1991 *Eosemicoscinium burultobense*; Plamenskaya, pp. 103–104, pl. 20, figs 6–7.

**Material.** – A single fragmentary specimen, DGO 12887.

**Description.** – Exterior: Zoarium reticulate, branches straight and thin, connected by delicate round dissepiments, somewhat irregularly spaced. Keel very high, thin, apex spear-shaped, nodes lacking. Autozooecia arranged in two rows separated by the keel, zooecial apertures circular, alternating, almost orthogonal to the meshwork plane, with a thin, short peristome. Fenestrules rectangular, elongate, some not much longer than wide, exceptionally wider than long due to abnormally short dissepiment spacing.

Interior: Autozooecial chambers parallelogram-shaped in deep tangential section, chamber length larger than width. Kidney-shaped chamber morphology in shallower tangential sections, cutting vestibule and chamber vault. Short, distal tube with very low divergence from branch axial plane. Zooecial transversal walls forming sharp angles with axial wall, lateral walls generally straight. Hemisepta lacking. Basal plate concave, sometimes almost flat; reverse longitudinal reverse ridges few and minute or absent. Microstyles relatively coarse, arranged in irregular rows on the reverse of branches. Laminar skeleton thin on the obverse, slightly thickened on the reverse of branches. Heterozooecia not observed.

**Remarks.** – The specimen can be assigned with certainty to *Eosemicoscinium*; the meshwork is more delicate than



those of known Devonian species, including *E. serratum* Ernst, 2012, identified in the Emsian La Vid Group (León, Spain), from which it differs in the absence of scalloped laminar skeleton on the keel. The morphology of the studied specimen resembles that of *E. burultobense* Plamenskaya, 1991, from the Emsian of Kazakhstan, in the spacing of apertures in a single row. Nevertheless, branch width and spacing are slightly smaller in the Spanish specimen, so it has been kept in open nomenclature.

**Occurrence.** – Upper Emsian–Eifelian. Moniello Inlet, Cantabrian Zone, NW Spain.

### Genus *Bigeyina* Suárez Andrés & McKinney, 2010

**Type species.** – *Cyclopelta winteri* Bornemann, 1884; Eifelian (Middle Devonian), Germany.

### *Bigeyina ibera* Ernst, 2012

Figure 4A–E, Table 5

2012 *Bigeyina ibera*; Ernst, p. 235, fig. 19a–g.

**Material.** – Nine specimens, DGO 12934–12940, 13035–13036.

**Description.** – Exterior: Zoarium reticulate, narrow conical, occasionally tubular, individual or composite. Obverse on the outer surface. Branches straight or slightly sinuous, dissepiments robust, forming rings on the reverse surface, with wing-shaped cross section. Keel high, supporting superstructure and separating two rows of autozoecia; apertures lobulated, with a short, thin peristome. Fenestrules oval, medium sized. Superstructure an asymmetric “Y”-shaped expansion of the upper region of the keel, with regularly spaced bridges between adjacent keels.

Interior: Autozoecial chambers rounded polygonal aside dissepiments, pentagonal-rectangular aside fenestrules. Axial wall zigzag. Hemisepta absent. Basal plate concave, flattened at dissepiment junctions, without reverse ridges. Asymmetric bifurcation of granular skeleton in the superstructure. Laminar skeleton thickening on the top concave surface of keel laths may form convex deposits during astogeny. Vesicular tissue abundant. Microstyles very thin, common; macrostyles absent. Heterozoecia not observed.

**Remarks.** – *B. ibera* can be distinguished from other species present in the Moniello Formation by its colony shape and the presence of bridges between keels. Furthermore, it differs from *B. cantabrica* in having narrower branches and smaller fenestrules; from *B. victrola* in the straight morphology of branches, and from *B. spinosa* in having

**Table 5.** Measurements of *Bigeyina ibera* Ernst, 2012. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.62	0.172	0.0295	0.94	0.23	25
Branch width (mm)	0.29	0.088	0.0077	0.50	0.20	21
Fenestrule length (mm)	0.53	0.057	0.0033	0.65	0.48	9
Fenestrule width (mm)	0.27	0.045	0.0021	0.33	0.19	11
Dissepiment width (mm)	0.32	0.076	0.0057	0.41	0.23	7
Distance between branch centres (mm)	0.58	0.137	0.0189	0.88	0.37	37
Aperture spacing across branch (mm)	0.30	0.049	0.0024	0.38	0.23	14
Aperture spacing along branch (mm)	0.32	0.056	0.0032	0.42	0.25	28
Aperture width (mm)	0.13	0.025	0.0006	0.17	0.08	32
Maximal chamber width aside fenestrules (mm)	0.16	0.041	0.0017	0.24	0.10	30
Chamber length aside fenestrules (mm)	0.24	0.024	0.0006	0.29	0.20	28
Maximal chamber width aside dissepiments (mm)	0.21	0.026	0.0007	0.25	0.17	20
Chamber length aside dissepiments (mm)	0.25	0.024	0.0006	0.28	0.17	20
Angle transverse wall-basal plate (degrees)	71.90	–	–	71.90	71.90	1

more elongate chambers and in the absence of spines on the reverse surface of dissepiments. Some colonies of *B. ibera* developed complex tubular morphologies by bifurcation, as described by Suárez Andrés & McKinney (2010), an extremely rare growth habit among fenestrates, which in this genus has only been observed in the Devonian of Spain.

**Occurrence.** – Emsian–lower Eifelian. Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

### *Bigeyina victrola* (McKinney & Kříž, 1986)

Figure 4F–I, Table 6

1986 *Cyclopelta victrola*; McKinney & Kříž, p. 46, figs 25, 26a.

**Material.** – Five specimens, DGO 12956–12960.

**Description.** – Exterior: Zoarium reticulate, conical. Branches sinuous, dissepiments very short and wide. Keel high, sinuous, separating two rows of autozoecia. Apertures circular, faintly lobulated, with a thin peristome. Fenestrules oval, arranged in a rhombic pattern, superstructure an expansion of the uppermost region of the keel.

Interior: Autozoecial chambers polygonal, rounded and larger close to dissepiments. Axial wall zigzag. Hemisepta

**Table 6.** Measurements of *Bigeyina victrola* (McKinney & Kříž, 1986). Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.83	0.074	0.0055	0.99	0.73	15
Branch width (mm)	0.44	0.063	0.0040	0.55	0.33	20
Fenestrule length (mm)	0.63	0.094	0.0088	0.84	0.46	42
Fenestrule width (mm)	0.34	0.060	0.0036	0.51	0.24	38
Dissepiment width (mm)	0.47	0.085	0.0072	0.73	0.33	40
Aperture spacing across branch (mm)	0.29	0.042	0.0017	0.41	0.22	36
Aperture spacing along branch (mm)	0.23	0.022	0.0005	0.27	0.18	42
Aperture width (mm)	0.10	0.009	0.0001	0.12	0.08	45
Maximal chamber width aside fenestrules (mm)	0.14	0.018	0.0003	0.18	0.10	51
Chamber length aside fenestrules (mm)	0.21	0.020	0.0004	0.27	0.17	51
Maximal chamber width aside dissepiments (mm)	0.22	0.031	0.0009	0.29	0.16	54
Chamber length aside dissepiments (mm)	0.22	0.023	0.0006	0.27	0.17	54
Chamber depth (mm)	0.23	0.027	0.0007	0.27	0.20	12
Angle transverse wall-basal plate (degrees)	7.34	6.25	39.04	8.46	6.23	12
Distance between branch centres aside fenestrules (mm)	0.68	0.066	0.0044	0.83	0.54	40
Distance between branch centres aside dissepiments (mm)	0.49	0.074	0.0055	0.74	0.37	38

absent. Basal plate slightly concave, flattened at dissepiment junctions. Symmetric bifurcation of granular core of superstructure, laminar skeleton thickened on top of the keel laths and reverse surface of branches. Microstyles and macrostyles present on reverse surface. Heterozoecia not observed.

**Remarks.** – *B. victrola* differs from all other known species of *Bigeyina* in its branch sinuosity, which in turn affects the arrangement of fenestrules and of dissepiments. The characteristic annular processes on the reverse surface of the colony corresponding with dissepiments as developed in *B. spinosa* are lacking in this species.

**Occurrence.** – Pragian, Prague Basin, Czech Republic;

**Table 7.** Measurements of *Bigeyina cantabrica* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.74	0.185	0.0343	1.09	0.28	65
Branch width (mm)	0.38	0.092	0.0085	0.59	0.26	61
Fenestrule length (mm)	0.63	0.101	0.0102	0.94	0.39	66
Fenestrule width (mm)	0.32	0.076	0.0058	0.61	0.20	72
Dissepiment width (mm)	0.57	0.152	0.0231	1.07	0.27	71
Distance between branch centres (mm)	0.60	0.079	0.0063	0.83	0.34	106
Aperture spacing across branch (mm)	0.31	0.040	0.0016	0.39	0.22	104
Aperture spacing along branch (mm)	0.27	0.022	0.0005	0.32	0.21	122
Aperture width (mm)	0.11	0.011	0.0001	0.14	0.09	137
Maximal chamber width aside fenestrules (mm)	0.16	0.042	0.0018	0.29	0.08	125
Chamber length aside fenestrules (mm)	0.24	0.027	0.0007	0.31	0.16	125
Maximal chamber width aside dissepiments (mm)	0.24	0.033	0.0011	0.30	0.16	126
Chamber length aside dissepiments (mm)	0.25	0.024	0.0006	0.30	0.19	126
Chamber depth (mm)	0.23	0.033	0.0011	0.31	0.17	47
Angle transverse wall-basal plate (degrees)	76.95	8.78	77.13	89.10	59.38	47

Emsian–lower Eifelian, Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

***Bigeyina cantabrica* sp. nov.**

Figure 5A–D, Table 7

**Holotype.** – DGO 12860.

**Paratypes.** – DGO 12861–12867.

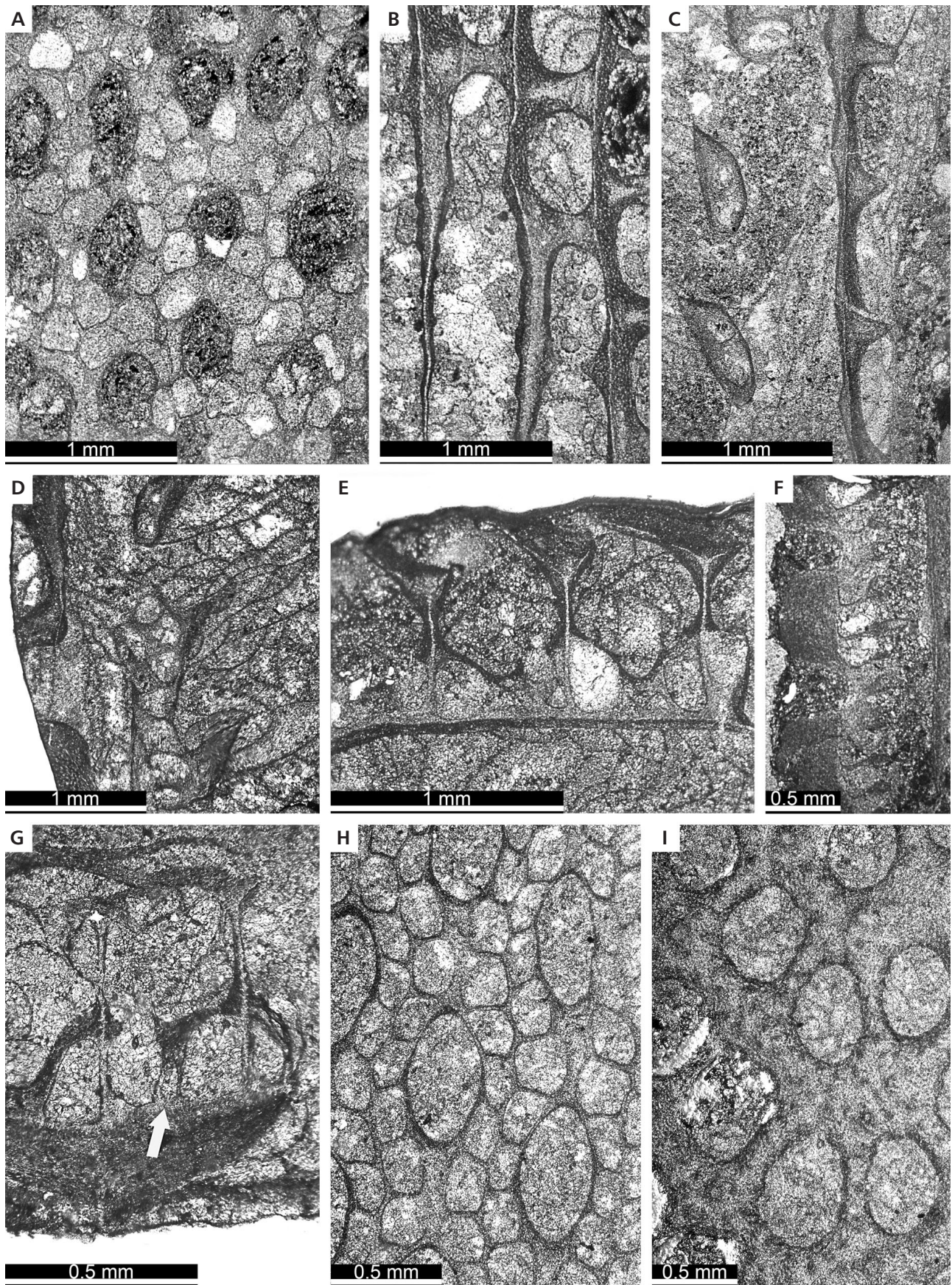
**Type horizon and locality.** – Upper Emsian, Moniello Formation. Arnao.

**Material.** – Twelve specimens, DGO 12860–12870, 12886.

**Etymology.** – From the Cantabrian Zone, the tectonostratigraphic unit in which the species has been identified. Gender feminine.

**Figure 4.** A–E – *Bigeyina ibera* Ernst, 2012. Moniello Formation. • A – deep tangential section showing chamber morphology, DGO 12935. • B – very shallow tangential section cutting bridged keels in uppermost superstructure, DGO 12937. • C – longitudinal section between two branches through dissepiments (left) and superstructure (right), DGO 12938. • D – longitudinal section of a branch, DGO 12937. • E – transverse section of several branches showing asymmetrical keel laths, DGO 12937. • F–I – *Bigeyina victrola* (McKinney & Kříž, 1986). Moniello Formation; F – longitudinal section of a branch, DGO 12960. • G – transverse section of branches with one kenozoecium (arrow), DGO 12958. • H, I – tangential sections, DGO 12957; H – deep tangential section; I – shallow tangential section cutting macrostylets on the reverse of branches.







**Table 8.** Measurements of *Bigeyina spinosa* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.92	0.114	0.0129	1.05	0.75	10
Branch width (mm)	0.43	0.090	0.0081	0.58	0.31	9
Fenestrule length (mm)	0.61	0.092	0.0084	0.85	0.45	29
Fenestrule width (mm)	0.31	0.044	0.0019	0.40	0.22	31
Dissepiment width (mm)	0.44	0.090	0.0081	0.58	0.25	23
Distance between branch centres (mm)	0.60	0.093	0.0086	0.88	0.41	29
Aperture spacing across branch (mm)	0.29	0.049	0.0024	0.40	0.21	28
Aperture spacing along branch (mm)	0.24	0.022	0.0005	0.30	0.19	40
Aperture width (mm)	0.10	0.010	0.0001	0.12	0.08	41
Maximal chamber width aside fenestrules (mm)	0.14	0.017	0.0003	0.18	0.11	30
Chamber length aside fenestrules (mm)	0.22	0.025	0.0006	0.30	0.18	30
Maximal chamber width aside dissepiments (mm)	0.23	0.022	0.0005	0.28	0.19	33
Chamber length aside dissepiments (mm)	0.22	0.038	0.0014	0.31	0.14	33
Chamber depth (mm)	0.23	0.023	0.0005	0.27	0.20	7
Angle transverse wall-basal plate (degrees)	70.26	6.39	40.83	79.30	60.60	7

**Diagnosis.** – *Bigeyina* with straight branches, symmetrically bifurcated keel and a single longitudinal ridge on the reverse surface of the basal plate.

**Description.** – Exterior: Zoarium reticulate, moderately open conical, obverse on the outer surface. Branches straight, dissepiments short and wide, transversely aligned, forming annular projections on the inner surface of the cone. Keel high, supporting the superstructure. Autozoecia arranged in two rows, apertures circular, possibly lobulated, peristome thin. Fenestrules oval, medium sized, regularly arranged. Superstructure an apical symmetrical expansion of the keel.

Interior: Autozoecial chambers bimodal; rounded pentagonal or hexagonal in dissepiment junctions, smaller and elongate aside fenestrules. Axial wall zigzag, occasionally almost straight. Hemisepta absent. Basal plate concave

with a single reverse ridge between dissepiments, almost flat and lacking ridges in dissepiment junctions. Granular skeleton bifurcated in the keel top. Astogenetic thickening of the laminar skeleton on the upper surface of the superstructure. Microstyles minute, very common; macrostyles absent. Heterozoecia not observed.

**Remarks.** – *B. cantabrica* sp. nov. differs from *B. ibera* in the colony shape and absence of keel bridges. From *B. spinosa* it differs in the absence of spines on the reverse surface of dissepiments and the presence of a single reverse ridge in the basal plate.

**Occurrence.** – Emsian–lower Eifelian. Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

***Bigeyina spinosa* sp. nov.**

Figure 5E–H, Table 8

**Holotype.** – DGO 12857.

**Paratypes.** – DGO 12967.

**Type horizon and locality.** – Upper Emsian, Moniello Formation, Arnao.

**Material.** – Five specimens, DGO 12857–12859, 12890, 12967.

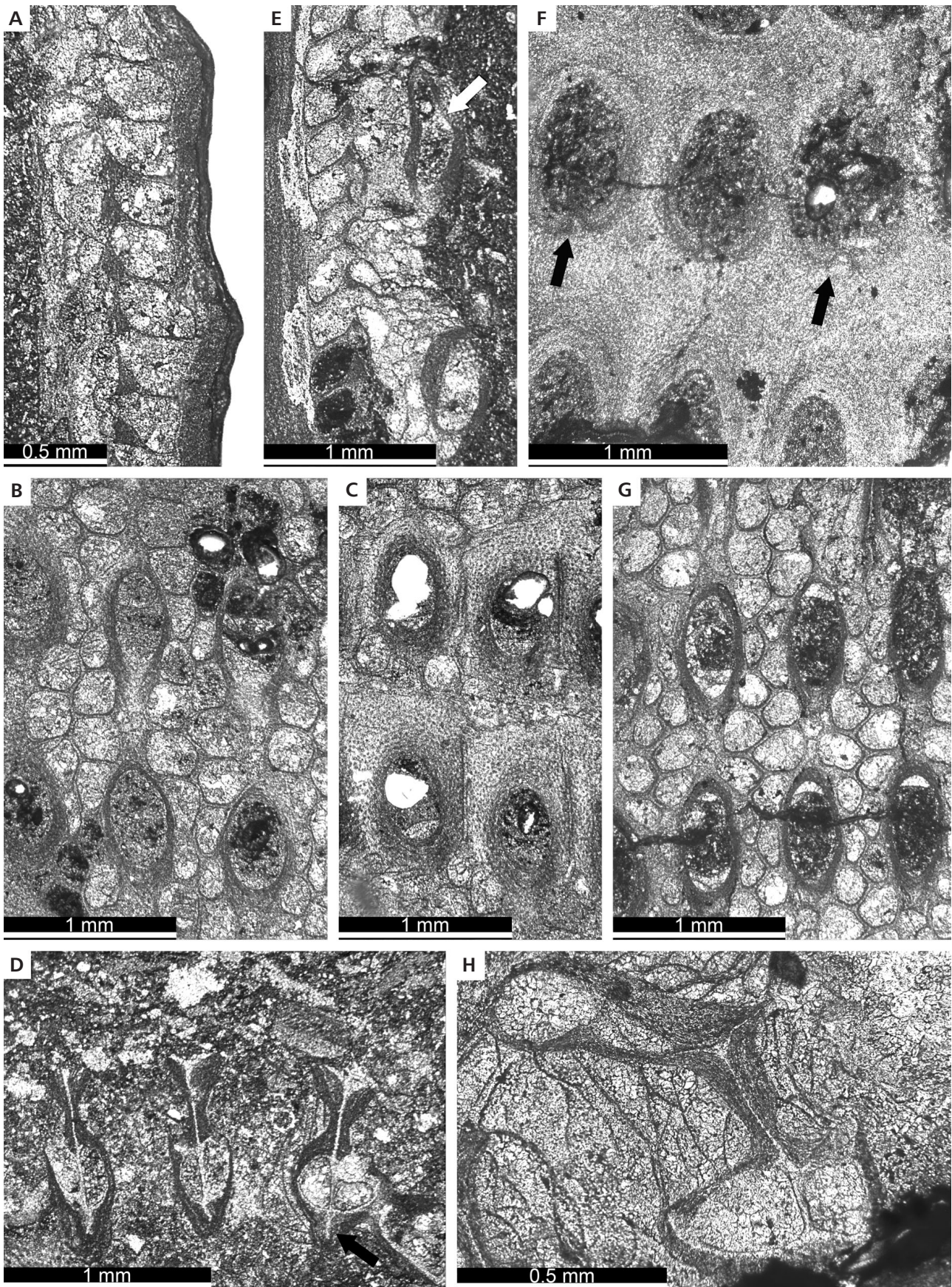
**Etymology.** – From Latin, *spinosa*, referring to the presence of spines on the distal edge of the reverse annular projections of dissepiments. Gender feminine.

**Diagnosis.** – *Bigeyina* with straight branches and spines on the reverse of the colony, placed on distal edges of annular dissepiments.

**Description.** – Exterior: Zoarium reticulate, conical, obverse on the outer surface. Branches straight, dissepiments short and wide, aligned transversely to branches and forming annular projections on the reverse of the colony. Small, robust spines on the reverse, placed on the distal edge of dissepiments and pointing distally. Keel high, separating two rows of autozoecia; zoecial apertures lobulated, peristome thin and short. Fenestrules oval, medium sized, regularly arranged. Superstructure a widened lath on

**Figure 5.** A–D – *Bigeyina cantabrica* sp. nov. Moniello Formation. • A – longitudinal section of a branch, DGO 12870. • B – deep tangential section, DGO 12863. • C – shallow tangential section of the reverse of branches, cutting the longitudinal ridge under the basal plate and abundant microstylets, DGO 12863. • D – transverse section of several branches between dissepiments showing the ridged basal plate (arrow), DGO 12870. • E–H – *Bigeyina spinosa* sp. nov. Moniello Formation. • E–G – holotype, DGO 12857; E – longitudinal section of a branch cutting zoecial chambers and *Caupokeras* (arrows); F – shallow tangential section of the reverse of the colony showing spines placed at distal edges of dissepiments over fenestrules (arrows); G – deep tangential section. • H – transverse section of a branch; microstructural details and *Caupokeras* can be observed, DGO 12890.







**Table 9.** Measurements of *Fenestrapora elegans* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	1.22	0.230	0.0530	1.53	0.95	13
Branch width (mm)	0.56	0.073	0.0053	0.66	0.43	14
Fenestrule length (mm)	1.09	0.140	0.0195	1.33	0.75	19
Fenestrule width (mm)	0.50	0.105	0.0111	0.69	0.30	19
Dissepiment width (mm)	0.65	0.123	0.0152	0.86	0.37	18
Distance between branch centres aside fenestrules (mm)	0.96	0.132	0.0174	1.24	0.74	15
Distance between branch centres aside dissepiments (mm)	0.74	0.109	0.0119	0.96	0.55	16
Aperture spacing across branch (mm)	0.31	0.041	0.0017	0.42	0.26	20
Aperture spacing along branch (mm)	0.28	0.022	0.0005	0.33	0.25	30
Aperture width (mm)	0.13	0.023	0.0005	0.20	0.11	19
Maximal chamber width aside fenestrules (mm)	0.16	0.013	0.0002	0.19	0.14	35
Chamber length aside fenestrules (mm)	0.25	0.024	0.0006	0.32	0.22	35
Maximal chamber width aside dissepiments (mm)	0.27	0.038	0.0014	0.31	0.19	22
Chamber length aside dissepiments (mm)	0.27	0.024	0.0006	0.32	0.22	22
Chamber depth (mm)	0.33	0.037	0.0013	0.38	0.24	16
Angle transverse wall-basal plate (degrees)	70.83	9.08	82.40	89.48	60.14	19

top of the keels. In some specimens the ichnogenus *Caupokeras* McKinney, 2009 is developed.

**Interior:** Autozooecial chambers large, equidimensional, pentagonal or hexagonal at dissepiment junctions; smaller and elongate pentagonal aside fenestrules. Axial wall zigzag, hemisepta absent. Basal plate concave, flattened at dissepiment junctions. Granular skeleton of the superstructure forming a very open, symmetrical bifurcation. Microstyles numerous, very thin. Heterozooecia not observed.

**Remarks.** – *B. spinosa* sp. nov. differs from all described *Bigeyina* species in having small spines on the reverse of

the colony, developed on the distal edge of annular projections of dissepiments.

**Occurrence.** – Emsian–lower Eifelian, Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

### Genus *Fenestrapora* Hall, 1885

**Type species.** – *Fenestrapora biperforata* Hall, 1885; Middle Devonian, New York, USA.

### *Fenestrapora elegans* sp. nov.

Figure 6A–E, Table 9

**Holotype.** – DGO 12808.

**Paratypes.** – DGO 12809–12811.

**Type horizon and locality.** – Upper Emsian–lower Eifelian, Moniello Formation, Arnao.

**Material.** – Four specimens, DGO 12808–12811.

**Etymology.** – From Latin *elegans*, elegant. Gender feminine.

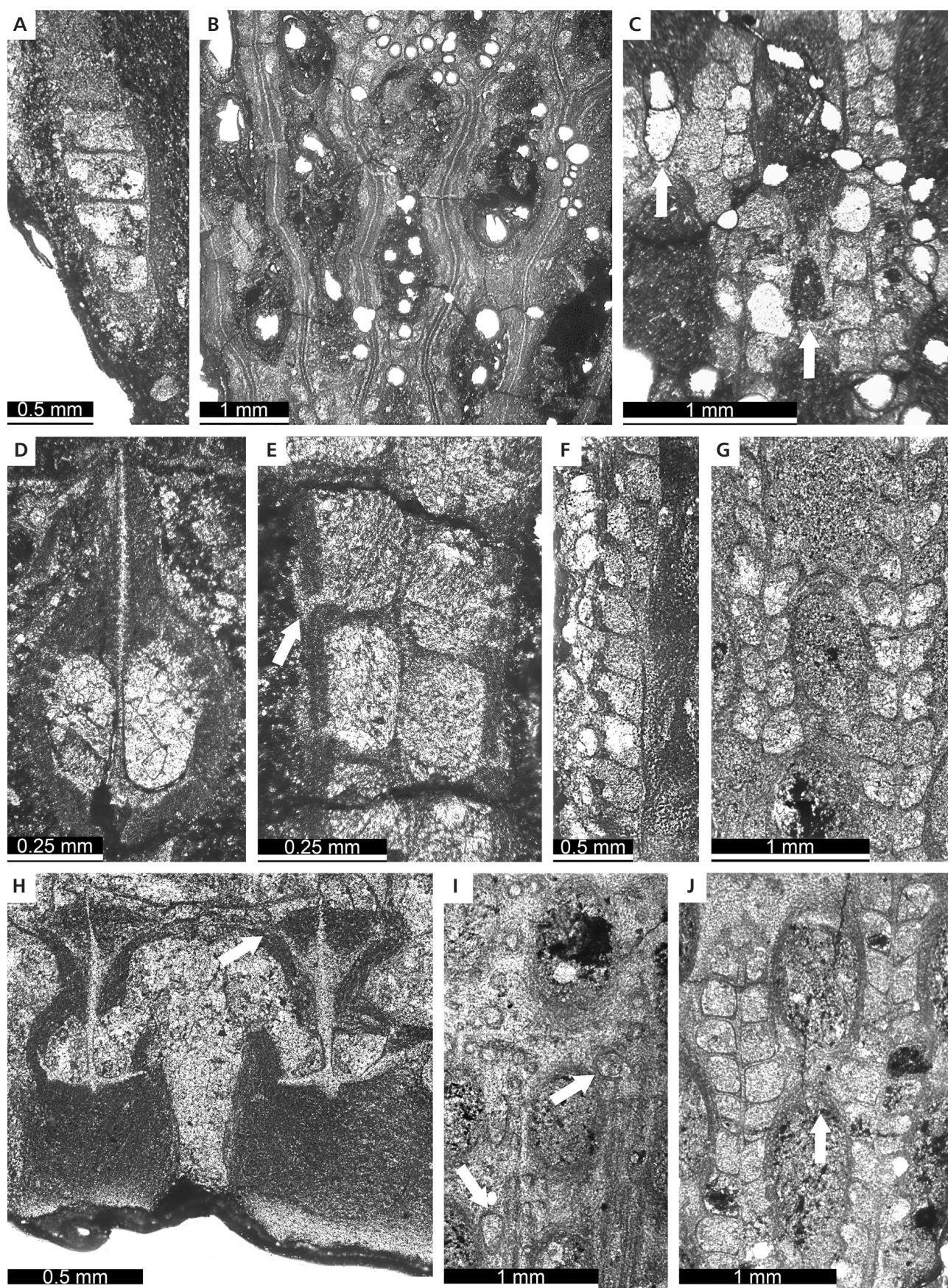
**Diagnosis.** – *Fenestrapora* with strongly sinuous branches, sharp spear-shaped keels, aviculomorphs on dissepiments.

**Description.** – Exterior: Zoarium reticulate, unknown if conical or fan-shaped. Branches sinuous, moderately wide, dissepiments short and wide. Keel high and thin, with a sharp edge. Two rows of autozooecia per branch, apertures rounded, with peristome. Fenestrules elliptical, moderately large, arranged in a rhombic pattern.

**Interior:** Autozooecial chambers rectangular, larger at dissepiment junctions, with a pore in the proximal region of the lateral wall connecting the chamber with the outer surface. Axial wall straight, occasionally sinuous. Hemisepta lacking. Basal plate concave, thick, laminar skeleton well developed, pierced by thin microstyles. Possible reproductive heterozooecia with enlarged chambers occupying positions aside dissepiments. Aviculomorphs present on the obverse of dissepiments, size roughly equal to autozooecia.

**Figure 6.** A–E – *Fenestrapora elegans* sp. nov. Moniello Formation. • A – longitudinal section, holotype, DGO 12808. • B–E – DGO 12809; B – shallow tangential section showing branch sinuosity; C – tangential section, aviculomorphs on dissepiments (arrows); D – transverse section of a branch showing microstructural details; E – tangential section; minute pores placed in the proximal region of autozooecial chambers (arrows). • F–J – *Fenestrapora occidentalis* Ulrich, 1890, Moniello Formation. • F – longitudinal section of a branch, DGO 12847. • G – oblique tangential section showing morphological differences in axial walls and chambers of neighbouring branches, DGO 12853. • H – transverse section of two branches with heavily thickened laminar skeleton; lateral nodes of scalloped superstructure can be observed (arrow), DGO 12842. • I – tangential section of the reverse cutting abundant styles and aviculomorphs (arrows). DGO 12846. • J – deep tangential section, DGO 12843.







**Table 10.** Measurements of *Fenestrapora occidentalis* Ulrich, 1890. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	1.00	0.201	0.0404	1.42	0.74	74
Branch width (mm)	0.47	0.076	0.0058	0.70	0.39	83
Fenestrule length (mm)	0.70	0.078	0.0061	0.83	0.56	102
Fenestrule width (mm)	0.38	0.068	0.0047	0.50	0.26	98
Dissepiment width (mm)	0.37	0.058	0.0033	0.47	0.29	128
Distance between branch centres (mm)	0.77	0.112	0.0125	0.95	0.54	140
Aperture spacing across branch (mm)	0.30	0.025	0.0006	0.35	0.27	26
Aperture spacing along branch (mm)	0.27	0.018	0.0003	0.30	0.25	54
Aperture width (mm)	0.12	0.014	0.0002	0.15	0.10	38
Maximal chamber width aside fenestrules (mm)	0.15	0.018	0.0003	0.19	0.13	209
Chamber length aside fenestrules (mm)	0.25	0.024	0.0006	0.30	0.22	209
Maximal chamber width aside dissepiments (mm)	0.23	0.018	0.0003	0.26	0.17	193
Chamber length aside dissepiments (mm)	0.26	0.031	0.0010	0.32	0.21	193
Chamber depth (mm)	0.26	0.031	0.0009	0.31	0.22	50
Angle transverse wall-basal plate (degrees)	69.32	5.85	34.21	77.64	61.53	44

**Remarks.** – *F. elegans* sp. nov. differs from all known species of *Fenestrapora* in the shape of branches and keels, as well as the presence of pores in zooecial chambers. This character, present in some Semicoscinidae, has been previously observed also in *Septatopora* Engel, 1975, *Polypora stenostoma* Tavener-Smith, 1971, *Dissotrypa* Ernst & Königshof, 2010 and *Adlatipora* Gautier *et al.*, 2013, though pores in these taxa are placed on the frontal wall instead of the lateral ones.

**Occurrence.** – Upper Emsian–lower Eifelian, Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

### ***Fenestrapora occidentalis* Ulrich, 1890**

Figure 6F–J, Table 10

1890 *Fenestrapora occidentalis*; Ulrich, pp. 558–559, pl. 44, figs 2, 2a, pl. 54, figs 7–7e.

1998 *Semicoscinium* cf. *discretum* (Prantl, 1932). – Suárez Andrés, *partim* (non pl. 1, fig. 8, p. 191, non pl. 2, figs 1–4, p. 193).

2012 *Fenestrapora occidentalis* Ulrich, 1890. – Ernst, p. 229, figs 15f–h, 16a–e.

**Material.** – Nineteen specimens, DGO 12837–12855.

**Description.** – Exterior: Zoarium reticulate, conical, ob-

verse on the outer surface. Branches sinuous, occasionally straight; dissepiments short and wide. Keel high, separating two rows of autozooecia; apertures rounded, peristome incomplete. Fenestrules elliptical to oval, medium sized. Superstructure a terminal expansion of the keel, with scalloped flanks.

**Interior:** Autozooecial chambers rectangular, rhombic or polygonal, short and high, larger and rounded at dissepiment junctions. Axial wall straight or slightly zigzag. Hemisepta lacking. Basal plate concave, with few longitudinal reverse ridges, commonly one beneath the axial wall. Granular core of superstructure forming a sharp ridge on top of the keel; regularly spaced microstyles on both flanks. Laminar skeleton well developed, pierced by abundant micro- and macrostyles. Possible reproductive heterozooecia (brood chambers). Aviculomorphs (McKinney 1998) on the reverse of branches, obverse of dissepiments and possibly also occupying lateral positions in the superstructure.

**Remarks.** – *F. occidentalis* differs from *F. transcaucasica* Morozova & Lavrentjeva, 1998 from the upper Eifelian of Transcaucasia, in having smaller fenestrules and shorter, narrower fenestrules.

**Occurrence.** – Middle Devonian (Hamilton), USA; Emsian–lower Eifelian, Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

Family Septoporidae Morozova, 1962

### **Genus *Paraseptopora* Lisitsyn, 1991**

**Type species.** – *Pinnatopora uralica* Nikiforova, 1938; Lower Permian, Urals (URSS).

### ***Paraseptopora geometrica* sp. nov.**

Figure 7A–E, Table 11

1999 *Septopora* sp. A. – Suárez Andrés, pp. 186–187, pl. 1, figs 4–6, pl. 2, fig. 1.

**Holotype.** – DGO 12968.

**Paratypes.** – DGO 12969–12972.

**Type horizon and locality.** – Upper Emsian–lower Eifelian. Moniello Formation, Arnao.

**Material.** – Five specimens, DGO 12968–12972.

**Etymology.** – The name refers to the regular arrangement and growth of pinnae. Gender feminine.



**Table 11.** Measurements of *Paraseptopora geometrica* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.70	0.082	0.0068	0.76	0.51	8
Branch width (mm)	0.44	0.060	0.0036	0.54	0.32	10
Distance between branch centres (mm)	1.03	0.354	0.1251	1.47	0.51	11
Aperture spacing across branch (mm)	0.29	0.039	0.0015	0.37	0.21	27
Aperture spacing along branch (mm)	0.29	0.027	0.0007	0.36	0.23	28
Aperture width (mm)	0.12	0.012	0.0001	0.15	0.10	21
Maximal chamber width (mm)	0.14	0.012	0.0001	0.16	0.12	8
Chamber depth (mm)	0.18	0.009	0.0001	0.19	0.18	3
Chamber length (mm)	0.25	0.019	0.0003	0.28	0.22	8
Angle transverse wall-basal plate (degrees)	63.69	1.48	2.19	64.73	62.64	2
Pinnae width, mm	0.42	0.047	0.0022	0.51	0.36	15
Distance between pinnae centers (mm)	0.97	0.125	0.0156	1.19	0.71	19
Aperture spacing across pinna (mm)	0.28	0.048	0.0023	0.35	0.22	9
Aperture spacing along pinna (mm)	0.27	0.018	0.0003	0.31	0.24	12
Aperture width in pinnae (mm)	0.11	0.015	0.0002	0.14	0.09	9
Maximal chamber width in pinnae (mm)	0.13	0.006	0.0000	0.13	0.12	3
Chamber length in pinnae (mm)	0.23	0.019	0.0004	0.25	0.21	3
Angle branch-pinna (degrees)	53.65	8.81	77.56	70.02	34.03	19

**Diagnosis.** – *Paraseptopora* with straight main branches and short, straight, regularly arranged pinnae.

**Description.** – Exterior: Zoarium reticulate, fan-shaped. Main branches straight or widely curved; pinnae short and straight. Some pinnae change growth direction paralleling main growth direction and become main branches. Keel very low, nodes absent. Two rows of autozoecia per branch, apertures rounded, with peristome. Fenestrules moderately large, regular.

Interior: Autozoecial chambers subrectangular, sac-shaped in longitudinal section, vestibule wide, subvertical. Axial wall straight. Hemisepta lacking. Basal plate concave, with few reverse ridges. Granular skeleton thin and short in the keel; microstyles abundant. Heterozooecia not observed.

**Remarks.** – *P. geometrica* sp. nov. differs from *P. irregularis* sp. nov. in the regular arrangement of the meshwork,

**Table 12.** Measurements of *Paraseptopora irregularis* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.69	0.081	0.0066	0.78	0.56	5
Branch width (mm)	0.51	0.065	0.0043	0.60	0.41	13
Distance between branch centres (mm)	1.32	0.310	0.0958	1.85	0.87	22
Aperture spacing across branch (mm)	0.29	0.040	0.0016	0.35	0.18	28
Aperture spacing along branch (mm)	0.30	0.038	0.0014	0.37	0.22	28
Aperture width (mm)	0.12	0.011	0.0001	0.14	0.10	26
Maximal chamber width (mm)	0.13	0.012	0.0001	0.15	0.11	20
Chamber length (mm)	0.28	0.024	0.0006	0.31	0.23	20
Angle transverse wall-basal plate (degrees)	58.62	3.89	15.16	61.37	55.86	2
Pinnae width (mm)	0.41	0.078	0.0061	0.58	0.30	14
Distance between pinnae centres (mm)	1.03	0.155	0.0239	1.28	0.69	23
Aperture spacing across pinna (mm)	0.28	0.019	0.0004	0.30	0.26	3
Aperture spacing along pinna (mm)	0.32	0.011	0.0001	0.33	0.31	2
Maximal chamber width in pinnae (mm)	0.15	0.054	0.0030	0.27	0.12	7
Chamber length in pinnae (mm)	0.25	0.056	0.0031	0.31	0.15	7
Angle branch-pinna (degrees)	53.09	7.47	55.72	67.41	34.95	31

straight pinnae, and slightly narrower main branches with a shorter spacing. *P. geometrica* is similar to *P. variabilis* (Nekhoroshev, 1977) in the absence of nodes, but differs in having wider branches and pinnae, somewhat larger fenestrules and larger spacing of zooidal apertures.

**Occurrence.** – Upper Emsian–lower Eifelian, Arnao, Cantabrian Zone, NW Spain.

***Paraseptopora irregularis* sp. nov.**

Figure 7F–J, Table 12

**Holotype.** – DGO 12973.

**Paratypes.** – DGO 12975, 12977, 12978.

**Type horizon and locality.** – Upper Emsian–lower Eifelian, Moniello Formation, Arnao.

**Material.** – Seven specimens, DGO 12973–12979.

**Etymology.** – From Latin, referring to the irregular arrangement of pinnae. Gender feminine.

**Table 13.** Measurements of *Penniretopora bohémica* (Prantl, 1932). Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	1.42	0.443	0.1964	2.40	0.96	8
Branch width (mm)	0.94	0.461	0.2126	2.21	0.52	12
Aperture spacing across branch (mm)	0.33	0.054	0.0030	0.46	0.23	64
Aperture spacing along branch (mm)	0.28	0.033	0.0011	0.35	0.21	57
Aperture width (mm)	0.11	0.015	0.0002	0.14	0.08	50
Maximal chamber width (mm)	0.14	0.013	0.0002	0.16	0.11	42
Chamber depth (mm)	0.13	0.025	0.0006	0.19	0.10	10
Chamber length (mm)	0.23	0.032	0.0011	0.30	0.17	42
Angle transverse wall-basal plate (degrees)	74.22	3.62	13.07	80.70	69.77	7
Keel node spacing (mm)	0.95	0.230	0.0531	1.29	0.61	7
Pinnae width (mm)	0.43	0.062	0.0039	0.53	0.34	8
Distance between pinnae centres (mm)	0.78	0.113	0.0128	0.97	0.56	24
Aperture spacing across pinna (mm)	0.27	0.036	0.0013	0.35	0.21	15
Aperture spacing along pinna (mm)	0.29	0.086	0.0073	0.53	0.22	17
Maximal chamber width in pinnae (mm)	0.14	0.035	0.0012	0.26	0.11	38
Chamber length in pinnae (mm)	0.19	0.025	0.0006	0.25	0.12	38
Angle branch-pinna (degrees)	61.77	5.55	30.83	70.79	51.28	31

**Diagnosis.** – *Paraseptopora* with sinuous main branches and curved pinnae producing irregular or heart-shaped fenestrules.

**Description.** – Exterior: Zoarium reticulate, fan-shaped; main branches straight or widely arched. Pinnae short, curved, irregular in length; some become main branches and develop pinnae. Keel very low, without nodes, separating two rows of autozoecia; zooecial apertures circular, with peristome. Fenestrules large, irregular in shape.

Interior: Autozoecial chambers rounded rectangular-pentagonal, sac-shaped in longitudinal section, vestibule wide and tilted towards fenestrule. Axial wall straight or

slightly sinuous. Hemisepta absent. Basal plate concave, with 2–3 prominent reverse ridges. Microstyles thin, macrostyles absent. Heterozooecia not observed.

**Remarks.** – *P. irregularis* sp. nov. differs from *P. geometrica* sp. nov. in having larger, irregular or heart-shaped fenestrules, curved pinnae and a larger branch spacing.

**Occurrence.** – Emsian–lower Eifelian, Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

Family Acanthocladiidae Zittel, 1880

### Genus *Penniretopora* d'Orbigny, 1849

**Type species.** – *Retepora pluma* Phillips, 1836; Visean, Yorkshire, England and Ireland.

### *Penniretopora bohémica* (Prantl, 1932)

Figure 8A–D, Table 13

1932 *Glauconome bohémica*; Prantl, pp. 29–30, pl. 3, figs 15–16.

1986 *Penniretopora bohémica* (Prantl, 1932). – McKinney & Kříž, p. 78, fig. 48.

1999 *Penniretopora* sp. A. – Suárez Andrés & González Álvarez, p. 646, pl. 1, figs 8–10.

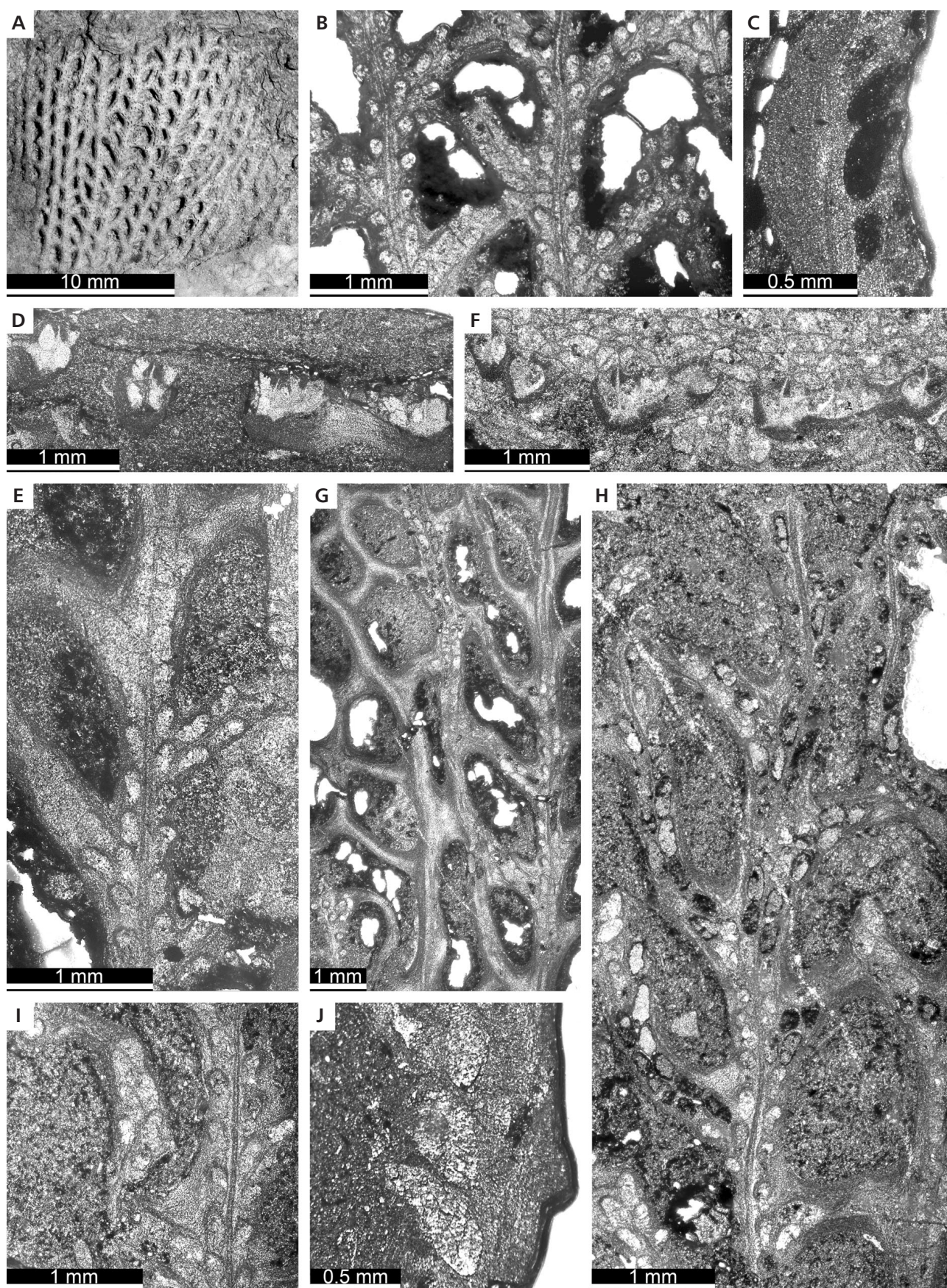
**Description.** – Exterior: Zoarium pinnate, main branch straight or arched; pinnae short and straight. Some pinnae may become secondary main branches. Keel low with a single row of regularly spaced nodes, separating two rows of autozoecia. Zooecial apertures rounded, with a complete peristome.

Interior: Autozoecial chambers pentagonal or barrel-shaped, low, with a long vestibule. Proximal hemiseptum weak. Axial wall zigzag, transverse walls well developed. Basal plate concave with several small reverse ridges. Microstyles numerous, macrostyles absent on the reverse. Strong thickening of laminar skeleton in main branches. Heterozooecia not observed.

**Remarks.** – The studied material is assigned to the species *P. bohémica* on account of the arrangement of pinnae,

**Figure 7.** A–E – *Paraseptopora geometrica* sp. nov., Moniello Formation. • A – obverse surface of a colony, DGO 12971. • B – shallow tangential section, holotype, DGO 12968. • C – longitudinal section of a main branch, DGO 12970. • D – transverse section of a colony cutting four main branches, holotype, DGO 12968. • E – tangential section showing autozoecial morphology, DGO 12968. • F–J – *Paraseptopora irregularis* sp. nov. Moniello Formation. • F – transverse section cutting main branches and pinnae, DGO 12975. • G–J – holotype, DGO 12973; G – tangential section showing the irregular meshwork; H – tangential section; chamber morphology and curved pinnae can be observed; I – shallow tangential section; J – longitudinal section of a main branch.







**Table 14.** Measurements of *Kalvariella antiqua* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.82	0.207	0.0429	0.97	0.67	2
Branch width (mm)	0.60	0.008	0.0001	0.60	0.59	3
Aperture spacing across branch (mm)	0.34	0.021	0.0004	0.38	0.30	23
Aperture spacing along branch (mm)	0.33	0.019	0.0004	0.37	0.30	22
Aperture width (mm)	0.10	0.009	0.0001	0.12	0.087	24
Maximal chamber width (mm)	0.15	0.011	0.0001	0.17	0.13	11
Chamber length (mm)	0.29	0.019	0.0004	0.32	0.25	11
Pinnae width (mm)	0.57	0.039	0.0015	0.62	0.53	4
Distance between pinnae centres (mm)	0.82	0.108	0.0117	0.94	0.61	7
Aperture spacing across pinna (mm)	0.18	0.021	0.0004	0.21	0.14	11
Aperture spacing along pinna (mm)	0.19	0.020	0.0004	0.21	0.16	6
Maximal chamber width in pinnae (mm)	0.15	0.008	0.0001	0.15	0.14	3
Chamber length in pinnae (mm)	0.30	0.051	0.0026	0.35	0.25	3
Angle branch-pinna (degrees)	58.60	4.78	22.80	65.26	50.86	6

distance between apertures, and chamber shape and width. *P. bohémica* differs from *P. spinosa* (Počta, 1894) from the Lower Devonian of Prague, in the shape and dimensions of autozoecial chambers, as well as in having wider pinnae (McKinney & Kříž 1986).

**Occurrence.** – Emsian, Prague Basin, Czech Republic. Emsian–lower Eifelian, Arnao, Cantabrian Zone, NW Spain.

### Genus *Kalvariella* Morozova, 1970

**Type species.** – *Kalvariella typica* Morozova, 1970; Upper Permian, Lithuania.

#### *Kalvariella antiqua* sp. nov.

Figure 8E–H, Table 14

**Holotype.** – DGO 12871.

**Paratypes.** – DGO 12989–12991.

**Type horizon and locality.** – Upper Emsian–lower Eifelian, Moniello Formation, Arnao.

**Material.** – Five specimens, DGO 12871, 12988–12991.

**Etymology.** – From Latin *antiqua*, ancient. Gender feminine.

**Diagnosis.** – *Kalvariella* forming small zoaria with relatively thin biserial main branch and very short multiserial pinnae.

**Description.** – Exterior: Zoarium pinnate, main branch relatively thin, with very short opposite or alternating pinnae. Keel low in main branch, with a single row of nodes; keel absent in pinnae. Two rows of autozoecia in main branch, 3–4 in pinnae. Zooecial apertures stellate, peristome well defined.

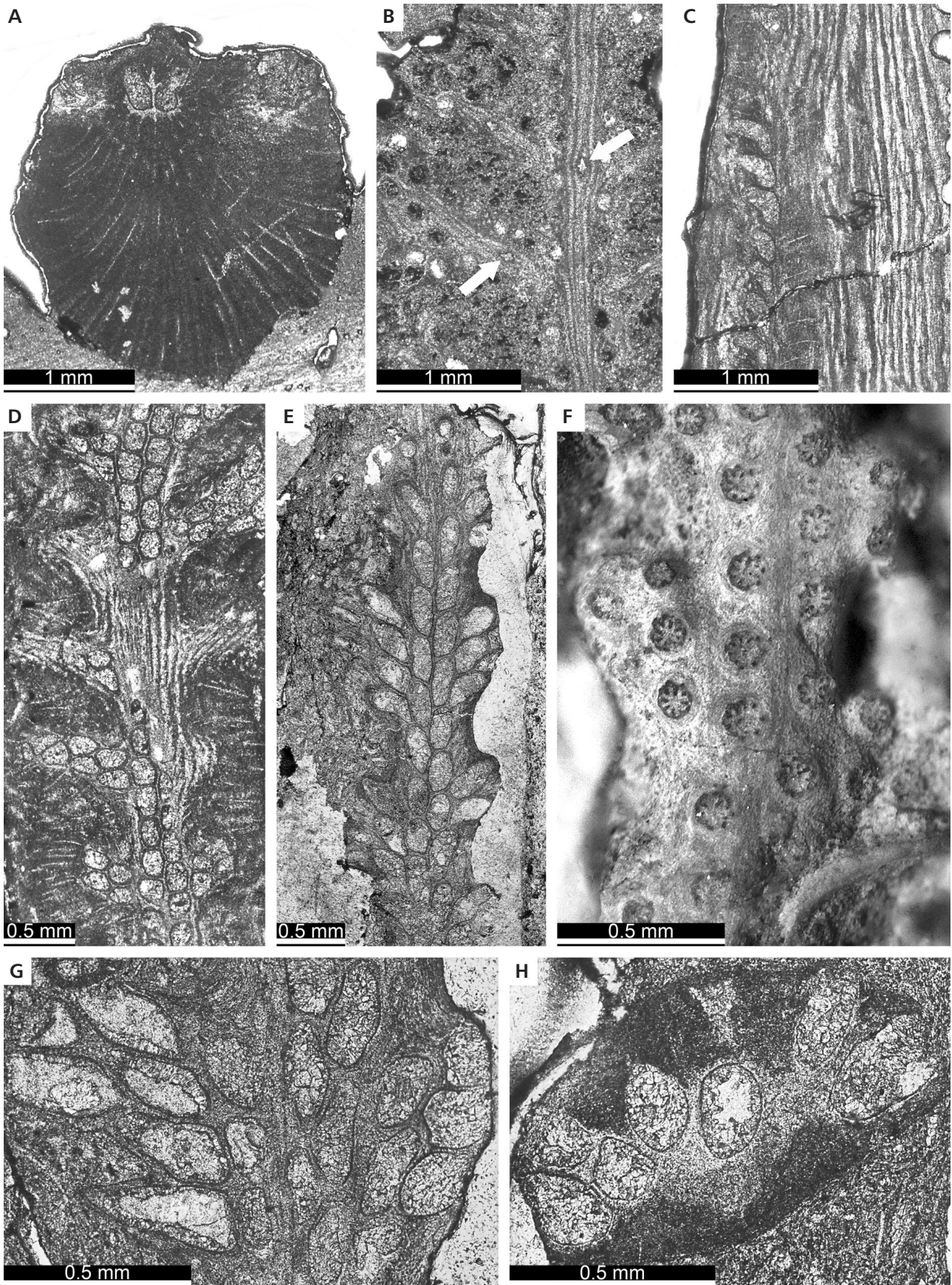
Interior: Autozoecial chambers rectangular or parallelogram-shaped in main branch, locally pentagonal; axial wall straight, locally zigzag. Chambers elongate hexagonal or rhombic in pinnae, irregular in the first generation close to main branch. Hemisepta absent. Basal plate concave, very short and curved towards the reverse in pinnae, bearing few generations of autozoecia. Microstyles common, thin. Laminar skeleton thickened in main branch. Heterozooecia not observed.

**Remarks.** – *K. antiqua* sp. nov. can be distinguished from the pinnate fauna among which it occurs in the presence of multiserial pinnae. From the five known species of *Kalvariella* it differs in having very short, backward curved pinnae. One of the specimens corresponds to the basal part of a mature colony with astogenetic thickening of laminar skeleton and shows bioclastration structures identified as *Caupokeras* caused by growth of a modular symbiont organism on the obverse surface of the bryozoan colony. This is the only reported case of *Caupokeras* developed on a superstructure-lacking fenestrate (Suárez Andrés 2014).

**Occurrence.** – Emsian–lower Eifelian, Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

**Figure 8.** A–D – *Penniretepora bohémica* (Prantl, 1932), Moniello Formation. • A–C – DGO 12980; A – transverse section of a heavily thickened main branch; B – shallow tangential section showing zooecial apertures and keel nodes (arrows); C – longitudinal section of a main branch. • D – deep tangential section cutting through zooecial chambers and basal plate, DGO 12985. • E–H – *Kalvariella antiqua* sp. nov., Moniello Formation. • E – deep tangential section showing short multiserial pinnae, DGO 12990. • F – obverse surface of a secondary main branch with multiserial pinnae, holotype, DGO 12871. • G – deep tangential section, DGO 12990. • H – transverse section cutting a main branch; the basal plate of pinnae is curved towards the reverse, DGO 12990.







**Table 15.** Measurements of *Filites robustus* sp. nov. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.85	0.107	0.0115	0.99	0.67	9
Branch width (mm)	0.73	0.129	0.0166	0.96	0.56	34
Aperture spacing across branch (mm)	0.27	0.031	0.0010	0.34	0.21	43
Aperture spacing along branch (mm)	0.40	0.053	0.0028	0.55	0.29	47
Aperture width (mm)	0.13	0.017	0.0003	0.16	0.08	56
Maximal chamber width (mm)	0.15	0.020	0.0004	0.20	0.11	93
Chamber depth (mm)	0.23	0.011	0.0001	0.24	0.23	2
Chamber length (mm)	0.28	0.037	0.0014	0.39	0.21	93
Angle transverse wall-basal plate (degrees)	74.77	3.96	15.64	77.57	71.98	2
Pinnae width (mm)	0.54	0.098	0.0096	0.79	0.43	22
Aperture spacing across pinna (mm)	0.84	0.086	0.0073	1.09	0.67	46
Aperture spacing along pinna (mm)	0.23	0.009	0.0001	0.24	0.23	2
Maximal chamber width in pinnae (mm)	0.24	0.044	0.0020	0.34	0.15	55
Chamber length in pinnae (mm)	0.13	0.025	0.0006	0.18	0.09	55
Chamber depth in pinnae (mm)	0.33	0.043	0.0019	0.40	0.24	22
Angle branch-pinna (degrees)	71.69	6.48	42.00	81.41	56.91	30

**Genus *Filites* Barrande, 1894 in Pořta (1894)**

*Type species.* – *Filites bohemicus* Barrande, 1894 in Pořta (1894); Early Devonian, Czech Republic.

*Remarks.* – One of the most evident characters of *Filites bohemicus* is the unusual backward recurved morphology of pinnae, which was included by McKinney & Kříž (1986) in the diagnosis of the genus. Morozova (2001) emended these authors' diagnosis and assigned to *Filites* species previously attributed to *Penniretepora* with triangular autozoöecial chambers, none of which showed vestigial, backward recurved pinnae. This is rejected here, and the specific composition of *Filites* is restricted to taxa in which zooecial chambers in pinnae exhibit a very different shape to that of chambers in main branch, as in the type

species *Filites bohemicus*. This generic diagnostic characteristic can also be observed in the species *Filites robustus* sp. nov. defined herein.

***Filites robustus* sp. nov.**

Figure 9A–E, Table 15

1999 *Filites* sp. A. – Suárez Andrés, pp. 190–192, pl. 2, figs 6–10.

*Holotype.* – DGO 12941.

*Paratypes.* – DGO 12942–12950.

*Type horizon and locality.* – Upper Emsian–lower Eifelian, Moniello Formation, Arnao.

*Material.* – Fifteen specimens, DGO 12941–12955.

*Etymology.* – From Latin *robustus*, robust. Gender masculine.

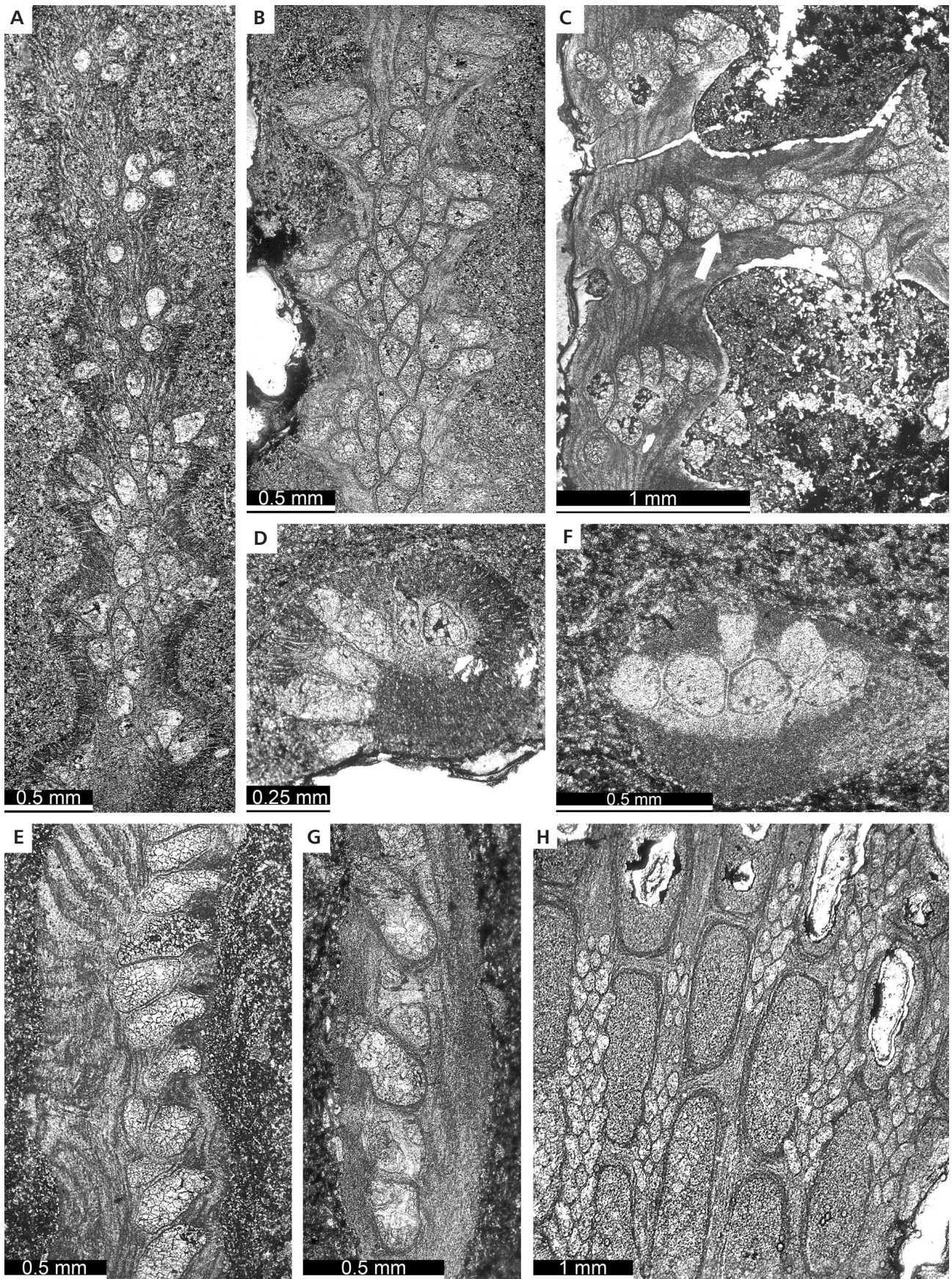
*Diagnosis.* – *Filites* with wide main branch, pinnae short and recurved with zooecia morphologically differentiated from those of main branch.

*Description.* – Exterior: Zoarium pinnate, pinnae short and curved backward, alternating on both flanks of main branch. Pinnae vestigial, short, curved backwards, rapidly tapering distally and merged with the reverse of main branch. Pinnae seldom grow straight and become secondary main branches approximately transversal to the parental one. Keel absent or very low and blunt. Two rows of autozoöecia in main branches and pinnae; zooecial apertures rounded, with thin, very low peristome.

Interior: Autozoöecial chambers dimorphic according to their placement in main branches or pinnae. Chambers triangular, triangular-pentagonal or trapezoidal, high and with a well developed vestibule in main branch. Chambers tubular, high, vesicular in tangential section, with a poorly differentiated vestibule. Hemisepta absent. Basal plate thin and concave; granular skeleton of axial wall not prolonged towards obverse. Microstyles very abundant, macrostyles absent. Laminar skeleton thickened, especially in main branch. Heterozooecia not observed.

**Figure 9.** A–E – *Filites robustus* sp. nov., Moniello Formation. • A – oblique tangential section, DGO 12951. • B – deep tangential section, DGO 12953. • C – longitudinal section of a colony cutting through three pinnae; autozoöecial morphology progressively changed in the central pinna as it became a secondary main branch (arrow), DGO 12952. • D – transverse section cutting autozoöecia in the main branch and in a pinna (left), DGO 12951. • E – longitudinal section, DGO 12953. • F–H – *Polypora inusitata* McKinney & Kříž, 1986, Moniello Formation. • F – transverse section of a branch prior to bifurcation, DGO 12999. Arnao. • G – longitudinal section of a branch, DGO 13000. • H – tangential section, DGO 12995.







**Remarks.** – *F. robustus* sp. nov. differs from the type species, *F. bohemicus*, in having colonies with wider branches and pinnae, larger chambers and a greater spacing between zooecial apertures. Both species share the retrograde morphology of pinnae; Ernst & Winkler Prins (2008) described and figured an undetermined fenestrate from the Carboniferous of the Cantabrian Zone (p. 46–47, pl. 29, figs 2–3) with a very similar external morphology, but unfortunately information about its internal organization is not available.

The growth pattern of *F. robustus* sp. nov. produced delicate colonies with main branches a few cm long, from which occasionally secondary main branches occur. The total lack of regularity in this aspect of colony growth contrasts with the internal organization of pinnae that become secondary main branches: the tubular chambers characteristic of pinnae gradually turned into the main branch type before the first secondary pinnae were formed.

**Occurrence.** – Emsian–lower Eifelian, Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

Family Polyporidae Vine, 1880

### Genus *Polypora* M'Coy, 1844

**Type species.** – *Polypora dendroides* M'Coy, 1844; Tournaian, Ireland.

### *Polypora inusitata* McKinney & Kříž, 1986

Figure 9F–H, Table 16

1986 *Polypora inusitata*; McKinney & Kříž, 75–77, fig. 46a–f.

1999 *Polypora* aff. *inusitata* McKinney & Kříž, 1986. – Suárez Andrés, 187, pl. 1, figs 4–6, pl. 2, fig. 1.

**Material.** – Fourteen specimens, DGO 12992–13005.

**Description.** – Exterior: Zoarium reticulate, fan-shaped. Branches straight or slightly sinuous, dissepiments thin; 3–4 rows of zooecia per branch, zooecial apertures lobulated, arranged in rhombic pattern, peristome complete. Fenestrules moderately wide, very long.

Interior: Autozooecial chambers tubular, elongate rhomb- or hexagon-shaped in deep tangential section, proximal region recumbent. Hemisepta and diaphragms not observed. Basal plate concave, thin, with numerous small, thin reverse ridges. Laminar skeleton well developed, thickened on the reverse of branches, mainly along the axial plane. Microstyles abundant, macrostyles absent. Heterozooecia not observed.

**Remarks.** – The studied material resembles *P. inusitata* McKinney & Kříž, 1986 in branch width and fenestrule length. The rectangular geometry of fenestrules in the Asturian colonies cannot be observed in the specimens figured by McKinney & Kříž (1986). Nevertheless, the spacing of apertures is very similar, as well as chamber dimensions, for which reason the Asturian specimens have been assigned to this species. *P. inusitata* is similar to *P. una* Morozova, 1960 from the Givetian of the Kuznets Basin, but branches and zooecial apertures are more widely spaced.

**Occurrence.** – Emsian–lower Eifelian, Prague Basin, Czech Republic; Arnao and Moniello Inlet, Cantabrian Zone, NW Spain.

### Genus *Anastomopora* Simpson, 1897

**Type species.** – *Fenestella cinctuta* Hall, 1884; Middle Devonian, Canada and USA.

### *Anastomopora* sp.

**Material.** – Ten fragmentary specimens, DGO 13037–13046. All specimens are recrystallized and partially silicified, producing evident loss of detail in both external and internal features. Sectioned specimens did not yield sections suitable for microscopic study of internal characters. Morphometric characters are provided in this description as a basic quantitative approach to the species, but it must be stressed that the bad preservation prevents accurate measurements. The description below is the result of partial observations of both external and internal characters in different specimens.

**Description.** – Exterior: Zoarium reticulate, shape unknown. Branches sinuous, robust, connected by short, wide dissepiments. Branch width 0.45–0.64 mm. Zooecia arranged in 3–4 rows, up to 6 prior to branch bifurcation and 2–3 rows after bifurcation. Apertures circular, inflected by minute radial styles producing lobulated aspect, peristome thick. Fenestrules oval, 0.88–1.16 mm long. Branch spacing 0.77–1.05 mm. Sparse, irregularly spaced spine-like styles between zooecial apertures and on the reverse of branches. Distinct longitudinal ridge on the reverse surface of branches.

Interior: Autozooecial chambers elongate hexagonal. Heterozooecia not observed.

**Remarks.** – The studied material has been assigned to *Anastomopora* on the basis of the morphology of branches, presence of a longitudinal ridge on the reverse of branches, number of zooecial rows and shape of chambers, but the accessory pores characteristic of this genus have not been



observed. Ernst *et al.* (2011) described *Anastomopora adnata* (Hall, 1883) from the Santa Lucía Formation, which is the lateral equivalent to the Moniello Formation on the southern slope of the Cantabrian Mountains. These authors did not report accessory pores in *A. adnata*, the material figured by them is morphologically comparable to that described herein, and also shows a blurry recrystallized aspect that contrasts with the good preservation of other species described in their work. Despite the apparent similarity, and consequently with the poor preservation of the Asturian specimens, it is convenient to keep this species in open nomenclature.

**Occurrence.** – Upper Emsian–lower Eifelian, Arnao, Cantabrian Zone, NW Spain.

### Palaeobiography of fenestrate bryozoans from the Moniello Formation

Biogeographic studies are strongly conditioned by the accuracy in the identification of taxa, the uneven knowledge of the faunas from different regions of the world, the discontinuity of the fossil record and the degree of association of the studied faunas with facies. Palaeogeographic analyses of Palaeozoic bryozoans are significantly biased by these factors, and conclusions must be assumed as approaches subject to modifications according to the progress of knowledge. Updated taxonomic work has been carried out recently on the fenestrate bryozoans from the Moniello Formation; Suárez Andrés & Wyse Jackson (2014) described the rare *Ernstipora mackinneyi*, Suárez Andrés & Ernst (2015) reported thirteen species of Fenestellidae and eighteen more belonging to other families have been identified in the present work. These data provide a rather detailed insight into the morphological and taxonomic diversity developed by fenestrates from NW Spain during the transition between the Early and Middle Devonian.

Boucot *et al.* (1967, 1969) set the existence of three geographic realms during the Lower Devonian, based on the distribution of brachiopods: the Malvinokafric, the Eastern Americas and the Old World Realm. Oliver (1976) and Bigey (1980) used these divisions in their biogeographic studies of Devonian rugose corals and bryozoans, respectively. The upper Emsian–lower Eifelian Moniello Formation was deposited in a carbonate platform belonging to the Rhenish-Bohemian Province of the Old World Realm, at the septentrional margin of Gondwana.

Many fenestrate genera from the Moniello Formation are cosmopolite or have very wide distributions, indicating a low degree of provincialism. Spanish fenestrates clearly show Gondwanan affinities, but a few taxa shared with American faunas also occur. This fact has already been observed in other groups from the Devonian from NW Spain,

**Table 16.** Measurements of *Polypora inusitata* McKinney & Kříž, 1986. Abbreviations as in Table 1.

	X	SD	CV	MAX	MIN	N
Branch thickness (mm)	0.50	0.043	0.0018	0.59	0.36	30
Branch width (mm)	0.55	0.053	0.0034	0.69	0.46	55
Fenestrule length (mm)	1.74	0.310	0.0871	2.27	1.23	63
Fenestrule width (mm)	0.58	0.142	0.0198	0.82	0.24	63
Dissepiment width (mm)	0.23	0.031	0.0013	0.29	0.16	65
Distance between branch centres (mm)	1.02	0.277	0.0662	1.38	0.13	76
Aperture spacing across branch (mm)	0.25	0.022	0.0009	0.33	0.20	103
Aperture spacing along branch (mm)	0.31	0.037	0.0012	0.39	0.23	91
Aperture width (mm)	0.11	0.016	0.0002	0.17	0.09	117
Maximal chamber width (mm)	0.15	0.016	0.0004	0.19	0.11	114
Chamber length (mm)	0.24	0.037	0.0011	0.31	0.18	114
Chamber depth (mm)	0.17	0.012	0.0004	0.20	0.14	24
Angle transverse wall-basal plate (degrees)	57.02	5.43	20.56	70.22	40.64	17

such as rugose (Soto 1979, 1982) and tabulate corals (Fernández-Martínez 1993), which show a high degree of cosmopolitanism in the Emsian, or trilobites (Arbizu 1978). Recent studies (May 2005, Rachebouf *et al.* 2012) report affinities between tabulate corals from NW Spain and Bolivia. Ernst (2010, 2011), Ernst *et al.* (2011) and Ernst & Buttler (2012) reported bryozoan species previously known from North America in the Emsian and Eifelian of NW Spain. Affinities of the fenestrates from the Moniello Formation with Laurentian forms are supported by the presence of *Fenestella* aff. *parallela*, *F. vera* and *Ptylopora* aff. *nodosa* (Suárez Andrés & Ernst 2015), but most significantly by *Fenestrapora occidentalis*. According to the reported occurrences, *Fenestrapora* was a short-lived genus (upper Emsian to Givetian) with few known species, but its geographic distribution was relatively wide, ranging from US to Spain, Germany and Azerbaijan (Ernst 2016). The number of species shared with the Devonian of North America is probably underestimated, partly due to the great number of taxa described in early taxonomic works, which largely lack information on their inner morphology. Most of these taxa have not been restudied according to updated procedures, what hampers reasonably accurate assessment of faunal similarities.

Among the Old World regions, the fenestrate bryozoans of the Moniello Formation show the highest affinities with the fauna from the Lower Devonian of the Prague Basin, Czech Republic, as detailed below, but apparently lower numbers of species shared with intermediate regions should be discussed.

Descriptions on Devonian fenestrates from France generally provide limited information, which hinders species-level comparisons; nevertheless, and beyond cosmopolitan genera, a few genera with less widespread distributions in the Lower–Middle Devonian are shared with the Moniello Formation. Bigey (1972a, b) reported the presence of *Ptylopora* and *Utopora* from the Armorican Massif, the latter being a relatively restricted genus identified in Spain (herein), Bohemia, Transcaucasia (Morozova & Lavrentjeva 1998) and the Lower Carboniferous of China (Xia & Lu 1986). Bigey & Feist (1975) described silicified upper Emsian fenestrates from the Armorican Massif including *Fenestella*, *Hemitrypa*, *Ptylopora* and *Penniretepora*, but species are not common with the Spanish fauna. Babin *et al.* (1980) reported species of *Hemitrypa*, *Semicoscinium* or *Fenestella* (*sensu lato*) in open nomenclature, all three widely distributed genera, but according to the illustrations and morphometric characters provided by the authors, these species have not been found in the Moniello Formation. Babin *et al.* (1981) illustrate transverse sections of bryozoan species assigned to undetermined fenestrates, which at present can be undoubtedly assigned to the Semicosciniidae. The species named as “Fenestellid 1” (Babin *et al.* 1981, pl. 13, figs 1–2) might belong to *Fenestrapora*. No rigorous identification can be made for “Fenestellid 2”, and “Fenestellid 3” could be assigned to *Bigeyina* on the basis of the bifurcation of the keel top (Babin *et al.* 1981, pl. 13, fig. 4). This would be reasonable, as *Bigeyina* has been reported from Bohemia, Germany and Spain.

Little is known about the Devonian fenestrates of Belgium. Dessilly & Kräusel (1962) described two species in open nomenclature belonging to *Hemitrypa* and *Semicoscinium*. Dessilly & Kräusel (1963) named the new genus *Speotrypa*, which nowadays is considered a junior synonym of *Semicoscinium* (McKinney 2009). Dessilly (1967) identified for the first time a Devonian phylloporinid species in Belgium, “*Phylloporina*” *devonica*, later assigned to *Bashkirella* by Lavrentjeva (1985) and found in the Rhenish Slate Massif (Germany) by Ernst & Schroeder (2007).

The Devonian fenestrate faunas from Germany share several genera with the Moniello Formation, most of them having little palaeobiogeographic significance due to their wide geographic and stratigraphic distributions, except for *Fenestrapora* and *Bigeyina*. The latter was first described in the Middle Devonian of Germany (Bornemann 1884) but the earliest species have been found in the Lower Devonian of Bohemia (McKinney & Kříž 1986). Besides these two regions and the possible case in France discussed above, *Bigeyina* has only been reported from the Emsian–lower Eifelian of NW Spain (Suárez Andrés 1998, Ernst 2012, Suárez Andrés & Wyse Jackson 2015, herein). After the transfer and restitution of *B. bohémica*

Prantl, 1932 as the type species of the genus *Pseudoisotrypa* (Suárez Andrés & McKinney 2010), new taxa described in Spain, including *B. cantabrica* and *B. spinosa* from the Moniello Formation, increased the known composition of *Bigeyina* from four to seven species. This short-lived genus underwent increasing diversity and disparity in the upper Emsian, as indicated by the number of species present in Spain and the occurrence of structural innovations, *i.e.* the bridged keels and the composite tubular morphology developed by *B. ibera*.

The revision made by McKinney & Kříž (1986) of the Bohemian fauna described by Barrande (Počta 1894) and Prantl (1932) is a thorough systematic work that stressed the diversity of the Lower Devonian fenestrates from the Prague Basin. Clear affinities have been established between the Bohemian and Spanish fenestrates on the basis of this study. Significant similarities comprise seven shared species, most of them belonging to genera with wide geographic and stratigraphic distributions, such as *Polypora inusitata* or *Spinofenestella strigilla*, but also the common presence of *Bigeyina*, *Utopora* and *Filites*, which have shorter distributions. Until this research *Filites*, originally described from Bohemia, was a monotypic genus, if one accepts that Morozova (2001) erroneously included species with triangular chambers previously assigned to *Penniretepora* from different stages and regions. Unlike these taxa, which the current authors consider to belong to *Penniretepora*, the Spanish *F. robustus* described here shares with the type species, *F. bohemicus*, diagnostic vestigial, backward recurved pinnae bearing zooecia morphologically different from those on the main branch.

Few affinities have been observed between fenestrates from the Moniello Formation and eastern faunas beyond Bohemia, except for the common presence of widespread genera. Only two common species have been found, *Fenestella vera* Ulrich, 1890 and *Rectifenestella pioneri* (Krasnopeeva, 1935). The former is a widely distributed species that has been identified in the Middle Devonian Hamilton Group, Buffalo, USA (Ulrich 1890), Lake Winnipegosis, Canada (Whiteaves 1892), and the Givetian of Mongolia (Nekhoroshev 1926), Altai (Krasnopeeva 1935, Volkova 1974) and Kuznets Basin (Morozova 1960). *Rectifenestella pioneri* has been reported from the Middle Devonian of Altai (Krasnopeeva 1935, Nekhoroshev 1948, Volkova 1974) and Kuznets Basin (Morozova 1960).

Though palaeogeographic links with other regions are supported by the affinities discussed above, the bryozoans of the Order Fenestrata of the Moniello Formation comprise fourteen new species (Suárez Andrés & Wyse Jackson 2014, Suárez Andrés & Ernst 2015, herein), which represent almost 50% of the identified fauna. It might be interpreted as the evidence of a high degree of provincialism, but this apparent endemism is possibly overestimated,



due to the confluence of circumstances such as the degree of knowledge of the regions subject to comparison. The active research on Devonian bryozoans carried out by several authors in recent years continuously increases the number of new taxa, but also the geographic distributions of some previously known species; much work has to be done in the field and restudying historical collections, so the present knowledge is not likely to become balanced in a short term. Among the new taxa, five species represent the earliest and westernmost occurrence of their “Lazarus genera”, and significantly increase their geographic and stratigraphic distributions. This fact has also been observed in rugose corals belonging to the *Cyathaxonia* fauna, some of which occurred for the first time in the Lower Devonian of the Cantabrian Range and later expanded becoming even cosmopolite taxa (Soto 1982). In his study of the Devonian *Cyathaxonia* fauna, Wrzolek (2002) named “silent taxa” those supposedly monophyletic that show significant gaps in their total distributions. The author considered two possible causes for these gaps, either lack of knowledge of the taxon in a given interval (“Lazarus taxa”), or extinction and further occurrence of a misidentified “Elvis taxon”.

*Bashkirella* has been reported from the upper Eifelian of Belgium, Germany and Armenia, as well as from the Carboniferous of Russia and China and early Permian of Russia. *Paraseptopora* has a relatively complete stratigraphic record from the Famennian (Upper Devonian) of Kazakhstan up to the Permian in different regions of the former USSR (Morozova 2001), but no species have been reported from Central or Western Europe. *Kalvariella* is a rare genus with only five known species including *K. antiqua* sp. nov.; previously reported species occurrences range from the Carboniferous of the Arctic region of Kolyma to the Permian of Thailand (Sakagami 1970, Morozova 2001), so *K. antiqua* sp. nov. greatly expands its distribution and stratigraphic range downwards into the Devonian. The occurrence of *Permofenestella*, a Permian genus from Russia and Mongolia, in the Mississippian (lower Carboniferous) of Ireland (Wyse Jackson 2001) seems to reflect the same downward stratigraphic trend. As a possible explanation to this gap, the delicate structure of *Kalvariella* possibly reduced its preservation potential when compared to reticulate forms; furthermore, this genus closely resembles *Penniretepora*, and can be easily misidentified if multiserial pinnae cannot be clearly observed. *Cavernella* also shows a wide gap in its stratigraphic record between the Lower Devonian of NW Spain and the Carboniferous of Hungary (Zágoršek 1993). It can be reasonably assumed that it should occur in intermediate sections, though specimens can be erroneously assigned to *Rectifenestella* if heterozooecia are not noticed in an appropriate tangential section.

Early occurrences of fenestrate genera have been reported in the Emsian of NW Spain beyond the Moniello

Formation. Ernst (2012) described *Fenestrapora occidentalis* from the Emsian of León, increasing the stratigraphic distribution of the species and the genus at a time: *Fenestrapora* had been previously described only from the Middle Devonian of USA, Transcaucasia and Germany. Ernst (2012) also reported two new species of *Prolixicella* that are the earliest known representatives of their genus and the only ones of Early Devonian age. Ernst & Königshof (2010) named the new genus *Dissotrypa* from the Givetian (Middle Devonian) of West Sahara, and Ernst (2012) defined two new species from the Emsian of León, Spain, thus placing in the Early Devonian the first appearance of both *Dissotrypa* and the Family Septatorporidae.

The fenestrate fauna of the Moniello Formation is highly diverse but not only new taxa occurred; uncommon growth habits have been reported that could be framed in a peak of disparity within the evolution of fenestrates, as reported by Suárez Andrés & Wyse Jackson (2015). Besides zoarial morphology, other innovations seem to indicate an important episode of the evolutionary history of fenestrate bryozoans occurring in the Lower Devonian: the presence of *Cavernella* and *Fenestrapora* in this Emsian–Eifelian fauna, together with the occurrence of *Dissotrypa* and *Iberofenestella* in the Emsian of León (Ernst 2012) point to a high diversification of heteromorphs, while most of these structures are known to occur in Late Palaeozoic taxa. *Dissotrypa* is also meaningful due to the development of proximal pores (McKinney & Wyse Jackson 2015, pp. 49–51), a puzzling structure that has been described in other Carboniferous (Engel 1975, Tavener-Smith 1971) and Permian forms (Gautier *et al.* 2013).

## Conclusions

Eighteen species of non-Fenestellidae fenestrate bryozoans, nine of which are new, have been described from the upper Emsian–lower Eifelian Moniello Formation. Considering the previously reported ones belonging to the Fenestellidae, (Suárez Andrés & Wyse Jackson 2014, Suárez Andrés & Ernst 2015), the known fenestrate fauna of the Moniello Formation is composed of thirty-two species, thus representing a highly diverse group.

The fenestrate bryozoans of the Moniello Formation show strong affinities with the Early Devonian fauna from Bohemia within the Old World Realm, but species shared with the Eastern America Realm also exist.

In contrast with Bohemia, affinities of the Moniello Formation fenestrates with those from other close regions within the Old World Realm are possibly underestimated due to insufficient knowledge of these local faunas.

Among the high diversity of the Moniello Formation fauna, several species represent the earliest reported record

of their genera and their most western distribution, including *Bashkirella*, *Calvariella*, *Kavernella* and *Paraseptopora*. Hitherto all of them mostly were composed of Carboniferous and Permian species, and their presence in the Devonian of Spain significantly extends their stratigraphic and geographic distributions.

Innovative features of some fenestrates of the Moniello Formation, together with those of contemporary faunas from other regions, depict a period of high diversity and disparity within the evolutionary history of the Order Fenestrata that took place in the Emsian–Eifelian.

## Acknowledgements

This research received support from the SYNTHESYS Project <http://www.synthesys.info/> which is financed by European Community Research Infrastructure Action under the FP7 “Capacities” Programme, through a grant awarded to J.S. in 2012 (GB-TAF 2129) to visit the Natural History Museum, London. Cova González is thanked for assisting with graphic work. We thank the reviewers for their valuable and constructive comments. Andrej Ernst (Hamburg) is thanked for his help providing Russian references.

## References

- ALONSO, J.L., MARCOS, A. & SUÁREZ, A. 2009. Paleogeographic inversion resulting from large out of sequence breaching thrust: The León Fault (Cantabrian Zone, NW Iberia). A new picture of the external Variscan thrust belt in the Ibero-Armorican Arc. *Geologica Acta* 7, 451–473.
- ARBIZU, M. 1978. Trilobites Synphoriidae del Devónico de la Cordillera Cantábrica: Malladiinae nov. subfam. *Trabajos de Geología* 10, 37–65.
- ARBIZU, M. & MÉNDEZ-BEDIA, I. 2006a. Patrimonio natural y cultural de Castrillón, Asturias, 18. In GARCÍA RAMOS, J.C. et al. (eds) *Resúmenes VII Reunión de la Comisión para el Patrimonio Geológico*. Colunga. Sociedad Geológica de España.
- ARBIZU, M. & MÉNDEZ-BEDIA, I. 2006b. El Patrimonio Natural y Cultural de Castrillón (Asturias): Geología, Fósiles e Historia Minera. *Trabajos de Geología* 26, 73–91.
- ARBIZU, M., GARCÍA-ALCALDE, J.L., GARCÍA-LÓPEZ, S., MÉNDEZ-BEDIA, I., SÁNCHEZ DE POSADA, L.C., SOTO, F.M., TRUYOLS, M., TRUYOLS, J., ÁLVAREZ, F., MÉNDEZ, C. & MENÉNDEZ, J.R. 1979. Biostratigraphical study of the Moniello Formation (Cantabrian Mountains, Asturias, NW Spain). A contribution to the Lower/Middle Devonian boundary problem. *Geologica et Palaeontologica* 13, 103–124.
- ARBIZU, M., MÉNDEZ-BEDIA, I. & SOTO, F. 1991. Desarrollo arrecifal en el Devónico Inferior de los alrededores de Arnao, Costa Asturiana. *Guía de campo de la excursión n°1, VII Jornadas de Paleontología*. Universidad de Oviedo, 1–30.
- ASTROVA, G.G. & MOROZOVA, I.P. 1956. New order of Paleozoic Bryozoa. *Paleontologicheskii Zhurnal* 1, 22–31. [in Russian]
- BABIN, C., BIGEY, F., BRICE, D., CARLS, P., DEUNFF, J., GOUJET, D., HEDDEBAUT, C., JAHNKE, H., LAFUSTE, J., LARDEUX, H., LEJAL-NICOL, A., LE MENN, J., MOREAU-BENOIT, A., MORZADEC, P., PARIS, F., PELHATE, A., PLUSQUELLEC, Y., PONCET, J., RACHEBOEUF, P. & WEYANT, M. 1980. Les Schistes et Calcaires de l’Armorique (Devonien Inférieur, Massif Armoricain). Sédimentologie, paléontologie, stratigraphie. Bryozoans, 181–193. In PLUSQUELLEC, Y. (ed.) *Mémoires de la Société Géologique et Minéralogique de Bretagne* 23.
- BABIN, C., BIGEY, F., BRICE, D., COPPER, P., COQUEL, R., GOUJET, D., HEDDEBAUT, C., JAHNKE, H., LARDEUX, H., LE MENN, J., MELOU, M., MORZADEC, P., PARIS, F., PEHATE, A., PLUSQUELLEC, Y., RACHEBOEUF, P. & WEYANT, M. 1981. La Tranchée de La Lezais. Emsien Supérieur du Massif Armoricain. Sédimentologie, paléontologie, stratigraphie. Bryozoans, 109–124. In MORZADEC, P., PARIS, F. & RACHEBOEUF, P. (eds) *Mémoires de la Société Géologique et Minéralogique de Bretagne* 24.
- BIGEY, F.P. 1972a. Présence de *Utopora* aff. *nobilis* (Bryozoaire Cryptostome) dans le Dévonien du Sud Est du Massif Armoricain. *Bulletin de la Société géologique de France* XIV, 315–319. DOI 10.2113/gssgfbull.S7-XIV.1-5.315
- BIGEY, F.P. 1972b. Présence de *Ptilopora* aff. *bohemica* (Bryozoaire Cryptostome) dans le Dévonien du Sud Est du Massif Armoricain. *Bulletin de la Société d’Etudes Scientifiques de l’Anjou* VIII, 15–22.
- BIGEY, F.P. 1980. Biogeography of Devonian Bryozoa, 9–23. In NIELSEN, C., LARWOOD, G.P. (eds) *Bryozoa: Ordovician to Recent*. Olsen & Olsen, Fredensborg.
- BIGEY, F.P. & FEIST, R. 1975. Cryptostomata (Bryozoaires) des “Calcaires à Polypiers siliceux” (Dévonien Inférieur de la Montagne Noire, France Meridionale). Note préliminaire, 257–271. In POUYET, S. (ed.) *Bryozoa, 1974. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon H.S.* 3(2).
- BORG, F. 1926. Studies on Recent cyclostomatous Bryozoa. *Zoologiska Bidrag från Uppsala* 10, 181–507.
- BORNEMANN, J.G. 1884. *Cyclopelta winteri*, eine Bryozoe aus dem Eifeler Mitteldevon. *Zeitschrift der Deutschen Geologischen Gesellschaft* 36, 864–865.
- BOUCOT, A.J., JOHNSON, J.G. & TALENT, J.A. 1967. Lower and Middle Devonian faunal provinces based on Brachiopoda, 1239–1254. In OSWALD, D.H. (ed.) *International Symposium on the Devonian System* 2.
- BOUCOT, A.J., JOHNSON, J.G. & TALENT, J.A. 1969. Early Devonian brachiopod zoogeography. *Geological Society of America Special Papers* 119, 1–113.
- COMTE, P. 1936. Le Dévonien Inférieur du Léon. *Comptes Rendus de l’Académie des Sciences de Paris* 202, 771–773.
- DESSILLY, E. 1967. Les bryozoaires dévoniens de la Belgique: la présence du genre “*Phylloporina*” dans le Couvinien de la Belgique. *Bulletin de l’Institut Royal des Sciences Naturelles de Belgique* 43(3), 1–6.
- DESSILLY, E. & KRÄUSEL, W. 1962. Les Bryozoaires Dévoniens de



- la Belgique. La découverte des genres *Hemitrypa* et *Semicoscinium* dans le Dévonien de la Belgique. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 38(20), 1–5.
- DESSILLY, E. & KRÄUSEL, W. 1963. Les Bryozoaires Dévoniens de la Belgique. *Speotrypa*, nouveau genre du Couvinien de la Belgique. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 39(31), 1–13.
- EHRENBERG, C.G. 1831. *Symbolae Physicae, seu Icones et descriptiones. Pars Zoologica, IV, Animalia Evertebrata exclusis Insectis*. Berolini ex Officina Academica, Berlin.
- ELIAS, M.K. & CONDRA, G.E. 1957. *Fenestella* from the Permian of West Texas. *The Geological Society of America Memoir* 70, 1–158.
- ENGEL, B.A. 1975. A new ? bryozoan from the Carboniferous of Eastern Australia. *Palaeontology* 18(3), 571–605.
- ERNST, A. 2010. Trepostome bryozoans from the Lower–Middle Devonian of NW Spain. *Rivista Italiana di Paleontologia e Stratigrafia* 116, 283–308.
- ERNST, A. 2011. Cryptostome (ptilodictyine and rhabdomesine) Bryozoa from the Lower Devonian of NW Spain. *Palaeontographica Abteilung A: Paläozoologie-Stratigraphie* 293, 147–183.
- ERNST, A. 2012. Fenestrate bryozoan fauna of the Lower–Middle Devonian of NW Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 264(3), 205–247.
- ERNST, A. 2013. Diversity dynamics and evolutionary patterns of Devonian Bryozoa. *Palaeobiodiversity and Palaeoenvironments* 93, 45–63.
- ERNST, A. 2016. *Fenestrapora* (Fenestrata, Bryozoa) from the Middle Devonian of Germany. *Paläontologische Zeitschrift* 90, 19–32. DOI 10.1007/s12542-016-0284-x
- ERNST, A. & BUTTLER, C. 2012. Cystoporate bryozoans from the Lower–Middle Devonian of NW Spain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 263, 261–285.
- ERNST, A. & KÖNIGSHOF, P. 2010. Bryozoan fauna and microfacies from a Middle Devonian reef complex (Western Sahara, Morocco). *Abhandlungen der Senckenberg Gesellschaft für Naturforschung* 568, 1–191.
- ERNST, A. & SCHROEDER, S. 2007. Stenolaemate bryozoans from the Middle Devonian of the Rhenish Slate Massif (Eifel, Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 246(2), 205–233.
- ERNST, A. & WINKLER PRINS, C.F. 2008. Pennsylvanian bryozoans from the Cantabrian Mountains (northwestern Spain). *Scripta Geologica* 137, 1–123.
- ERNST, A., DORSCH, T. & KELLER, M. 2011. A bryozoan fauna from the Santa Lucia Formation (Lower–Middle Devonian) of Cantabrian Mountains, NW Spain. *Facies* 57, 301–329.
- FERNÁNDEZ, L.P., NOSE, M., FERNÁNDEZ-MARTÍNEZ, E., MÉNDEZ-BEDIA, I., SCHRÖDER, S. & SOTO, F. 2006. Reefal and mud mound facies development in the Lower Devonian La Vid Group at the Colle outcrops (León province, Cantabrian Zone, NW Spain). *Facies* 52, 307–327. DOI 10.1007/s10347-005-0042-0
- FERNÁNDEZ-MARTÍNEZ, E. 1993. *Tabulados y Chaetétidos de las Formaciones Moniello-Santa Lucía y Candás-Portilla (Devónico, Cordillera Cantábrica, NO de España)*. 420 pp. Ph.D. thesis, Universidad de Oviedo, Spain.
- FERNÁNDEZ-MARTÍNEZ, E., FERNÁNDEZ, L.P., GARCÍA-ALCALDE, J., MÉNDEZ-BEDIA, I. & SOTO, F. 2006. Excursión A. El Devónico arrecifal de la Zona Cantábrica. *XXII Jornadas de la Sociedad Española de Paleontología*, 1–62.
- GARCÍA-LÓPEZ, S. & SANZ-LÓPEZ, J. 2002. Devonian to Lower Carboniferous conodont biostratigraphy of the Bernesga Valley section (Cantabrian Zone, NW Spain), 163–205. In GARCÍA-LÓPEZ, S. & BASTIDA, F. (eds) *Palaeozoic conodonts from northern Spain. 8<sup>th</sup> International Conodont Symposium held in Europe. Publicaciones del Instituto Geológico y Minero de España, Cuadernos del Museo Geominero* 1.
- GARCÍA-LÓPEZ, S., SANZ-LÓPEZ, J. & SARMIENTO, G.N. 2002. The Palaeozoic succession and conodont biostratigraphy of the section between Cape Peñas and Cape Torres (Cantabrian coast, NW Spain), 125–161. In GARCÍA-LÓPEZ, S., BASTIDA, F. (eds) *Palaeozoic conodonts from northern Spain. 8<sup>th</sup> International Conodont Symposium held in Europe. Publicaciones del Instituto Geológico y Minero de España, Cuadernos del Museo Geominero* 1.
- GAUTIER, T.G., WYSE JACKSON, P.N. & MCKINNEY, F.K. 2013. *Adlatipora*, a distinctive new acanthocladiid bryozoan from the Glass Mountains, Texas, USA, and its bearing on fenestrate astogeny and growth. *Journal of Paleontology* 87, 444–455. DOI 10.1666/12-128.1
- GORJUNOVA, R.V. 1966. On a new genus of the bryozoan Family Phylloporinidae. *Paleontologicheskii Zhurnal* 2, 127–130. [in Russian]
- HALL, J. 1883. Bryozoans of the Upper Helderberg and Hamilton groups. *Transactions of the Albany Institute* 10, 145–197.
- HALL, J. 1884. Bryozoa (Fenestellidae) of the Hamilton Group. *36<sup>th</sup> Annual report on the New York State Museum of Natural History*, 57–72.
- HALL, J. 1885. Bryozoans of the Hamilton Group. *Report of the State geologist for the year 1883*, 5–61.
- KOPEJEVICH, G.V. 1975. Silurian bryozoans from Estonia and Podolia. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 171, 1–155. [in Russian]
- KRASNOPEEVA, P.S. 1935. Bryozoans of the Middle and Upper Devonian of Altai. *Materialy po Geologii Zapadno-Sibirskogo Kraia* 2, 43–84. [in Russian]
- LAVRENTJEVA, V.D. 1979. Phylloporinina – A new Suborder of Paleozoic Bryozoa. *Paleontological Zhurnal* 1, 59–68.
- LAVRENTJEVA, V.D. 1985. Bryozoans of the suborder Phylloporinina. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 214, 1–101. [in Russian]
- LISITSYN, D.V. 1991. New Permian bryozoans from the Northern Urals. *Paleontological Journal* 25(4), 88–99.
- MAY, A. 2005. A new *Parastriatopora* species (Anthozoa, Tabulata) from the Lower Devonian of Colle (Spain, Cantabrian Mountains). *Bulletin of Geosciences* 80, 287–290.
- M'COY, F. 1844. *A synopsis of the character of the Carboniferous Limestone fossils of Ireland*. 207 pp. University Press, Dublin. DOI 10.5962/bhl.title.11559

- McKINNEY, F.K. 1998. Avicularia-like structures in a Paleozoic fenestrate bryozoan. *Journal of Paleontology* 72(5), 819–826. DOI 10.1017/S0022336000027177
- McKINNEY, F.K. 2009. Bryozoan-hydroid symbiosis and a new ichnogenus, *Caupokeras*. *Ichnos* 16, 193–201. DOI 10.1080/10420940802686160
- McKINNEY, F.K. & KRÍŽ, J. 1986. Lower Devonian Fenestrata (Bryozoa) of the Prague Basin, Barrandian Area, Bohemia, Czechoslovakia. *Fieldiana Geology n. s.* 15, 1–90.
- McKINNEY, F.K. & WYSE JACKSON, P.N. 2015. Part G, Revised, Volume 2, Chapter 8A: Order Fenestrata: Morphology and growth. *Treatise Online* 66, 1–91.
- MÉNDEZ-BEDIA, I. 1976. Biofacies y litofacies de la Formación Moniello-Santa Lucía (Devónico de la Cordillera Cantábrica, NO de España). *Trabajos de Geología* 9, 1–93.
- MÉNDEZ-BEDIA, I. & SOTO, F. 1984. Paleocological succession in a Devonian organic buildup (Moniello Fm., Cantabrian Mountains, NW Spain). *Geobios* 8, 151–157. DOI 10.1016/S0016-6995(84)80168-0
- MÉNDEZ-BEDIA, I., SOTO, F. & FERNÁNDEZ-MARTÍNEZ, E. 1994. Devonian reef types in the Cantabrian Mountains, (NW Spain) and their faunal composition. *Courier Forschungsinstitut Senckenberg* 172, 161–183.
- MOROZOVA, I.P. 1960. Devonian bryozoans from the Kuznets and Minusin Basins. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 86, 1–172. [in Russian]
- MOROZOVA, I.P. 1962. Systematics and phylogeny of Fenestelloidea. *Paleontologicheskii Zhurnal* 4, 104–115. [in Russian]
- MOROZOVA, I.P. 1970. Late Permian bryozoans. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 122, 1–347. [in Russian]
- MOROZOVA, I.P. 1987. Morphogenesis, system and colonial integration in Bryozoa of the Order Fenestrata. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 222, 70–88. [in Russian]
- MOROZOVA, I.P. 2001. Bryozoans of the Order Fenestellida. *Trudy Paleontologicheskogo Instituta* 277, 1–176. [in Russian]
- MOROZOVA, I.P. & LAVRENTJEVA, V.D. 1998. New bryozoans of the Family Semicosiniidae. *Paleontological Journal*, 32(2), 154–162.
- NEKHOROSHEV, V.P. 1926. Bryozoans of the Middle Devonian of NE Mongolia, with description of a microscopic method of study for fenestellids. *Trudy Geologicheskii Muzei Akademii Nauk SSSR* 1, 1–28. [in Russian]
- NEKHOROSHEV, V.P. 1948. Bryozoans of the Devonian of Altai. *Paleontologiya SSSR* 3(2-1). *Izdatel'stvo Akademii Nauk SSSR Paleontologicheskii Institut*, 1–172. [in Russian]
- NEKHOROSHEV, V.P. 1977. Devonian bryozoans of Kazakhstan. *Ministerstvo Geologii SSSR Vsesoyuznyy Ordena Lenina Nauchno-Issledovatel'skiy Geologicheskii Institut Trudy (n.s.)* 186, 1–192. [in Russian]
- NIKIFOROVA, A.I. 1938. Types of Carboniferous Bryozoa from the European part of the USSR. *Izdatel'stvo Akademii Nauk SSSR, Paleontology of USSR* 4, part 5(1), 1–290. [in Russian]
- NIKIFOROVA, A.I. 1939. New species of the Upper Palaeozoic bryozoans of the Bashkirian Urals. *Trudy Neftyanogo Geologo-razvedochnogo Instituta, (A)* 115, 70–102. [in Russian]
- OLIVER, W.A. 1976. Biogeography of Devonian rugose corals. *Journal of Paleontology* 50, 365–373.
- ORBIGNY, M.A. 1849. Descriptions de quelques genres nouveaux de mollusques bryozoaires. *Revue et magasin de Zoologie* 1(2), 499–501.
- PÉREZ-ESTAÚN, A., BASTIDA, F., ALONSO, J.L., MARQUÍNEZ, J., ALLER, J., ÁLVAREZ-MARRÓN, J., MARCOS, A. & PULGAR, J.A. 1988. A thin-skinned tectonics model for an arcuate fold and thrust belt: the Cantabrian Zone. *Tectonics* 7, 517–538. DOI 10.1029/TC007i003p00517
- PÉREZ-ESTAÚN, A., BEA, F., BASTIDA, F., MARCOS, A., MARTÍNEZ-CATALÁN, J.R., MARTÍNEZ-POYATOS, D., ARENAS, F., DÍAZ-GARCÍA, F., AZOR, A., SIMANCAS, J.F., GONZÁLEZ-LODEIRO, F. 2004. La Cordillera Varisca Europea. El Macizo Ibérico, 19–230. In VERA, J.A. (ed.) *Geología de España*, SGE – IGME, Madrid.
- PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire. 2. The Mountain Limestone District*, 253 pp. John Murray, London.
- PLAMENSKAYA, A. 1991. Bryozoans of the Lower and Upper Devonian of Kazakhstan, 91–111. In DUBATOLOV, V.N. & STUKALINA, G.A. (eds) *Biostratigraphy of the Lower and Upper Devonian of the Dzhulgaro-Balkhash provinces*. Akademiya Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Novosibirsk. [in Russian]
- POČTA, P. 1894. *Système Silurien du Centre de la Bohême par Joachim Barrande. Première Partie: Recherches Paleontologiques VIII (1)*. 230 pp. Privately published, Prague & Paris.
- PRANTL, F. 1932. Revision of the fenestellids from the Devonian of Bohemia. *Palaeontographica Bohemiae* XV, 1–70.
- PROUT, H.A. 1859. Third series of descriptions of Bryozoa from the Palaeozoic rocks of western states and territories. *Transactions of St. Louis Academy of Sciences (S. 3)*, 443–452.
- RACHEBOEUF, P.R., CASIER, J.G., PLUSQUELLEC, Y., TORO, M., MENDOZA, D., PIRES DE CARVALHO, M.G., LE HERISSÉ, A., PARIS, F., FERNÁNDEZ-MARTÍNEZ, E., TOURNEUR, F., BROUTIN, J., CRASQUIN, S. & JANVIER, P. 2012. New data on the Silurian–Devonian paleontology and biostratigraphy of Bolivia. *Bulletin of Geosciences* 86, 1–46. DOI 10.3140/bull.geosci.1248
- SAKAGAMI, S. 1970. Addition to the Permian Bryozoa from Ko Muk, peninsular Thailand. *Geology and Palaeontology of Southeast Asia* 8, 43–68.
- SÁNCHEZ DE LA TORRE, L. & MANJÓN, M. 1976. Facies de la Caliza de Moniello en la zona de Arnao, Asturias. *Trabajos de Geología* 8, 109–129.
- SHULGA-NESTERENKO, M.I. 1955. Carboniferous Bryozoa of the Russian Platform. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 57, 1–191. [in Russian]
- SIMPSON, G.B. 1897. A handbook of the genera of the North American Paleozoic Bryozoa. *14<sup>th</sup> Annual report of the state geologist (of New York) for the year 1894*, 407–608.



- SOTO, F. 1979. Considérations paléobiogéographiques sur les Streptelasmatina (Coelenterata, Rugosa) solitaires du Dévonien des Monts Cantabriques (NE de l'Espagne). *Geobios* 3, 399–409. DOI 10.1016/S0016-6995(79)80119-9
- SOTO, F. 1982. Plerophyllidae y Pentaphyllidae (Coelenterata, Rugosa) del Devónico de la Cordillera Cantábrica (NO de España). *Trabajos de Geología* 12, 49–61.
- SOTO, F. & MÉNDEZ-BEDIA, I. 1985. Estudio de una asociación coral rugoso-estromatopórido en el arrecife de Arnao (Fm. Moniello, Asturias, NO de España). *Trabajos de Geología* 15, 203–209.
- SOTO, F., MÉNDEZ-BEDIA, I. & FERNÁNDEZ-MARTÍNEZ, E. 1994. Construcciones arrecifales del Devónico de la Cordillera Cantábrica (NO de España). *Revista Española de Paleontología* 9, 29–36.
- SUÁREZ ANDRÉS, J.L. 1998. Briozoos Fenestrados de la Formación Moniello (Devónico) en el área de Arnao (Asturias, España) I: Fenestellidae. *Revista Española de Paleontología* 13(2), 187–196.
- SUÁREZ ANDRÉS, J.L. 1999. Briozoos Fenestrados de la Formación Moniello (Devónico) en el área de Arnao (Asturias, España) II: Septoporidae, Polyporidae y Acanthocladiidae. *Revista Española de Paleontología Numero Extraordinario Homenaje al Profesor Truyols*, 185–193.
- SUÁREZ ANDRÉS, J.L. 2014. Bioclaustration in Devonian fenestrate bryozoans. The ichnogenus *Caupokeras* McKinney, 2009. *Spanish Journal of Paleontology* 29, 5–14.
- SUÁREZ ANDRÉS, J.L. & ERNST, A. 2015. Lower-Middle Devonian Fenestellidae (Bryozoa) of NW Spain: Implication for fenestrate paleobiogeography. *Facies* 61(415), 1–29. DOI 10.1007/s10347-014-0415-3
- SUÁREZ ANDRÉS, J.L. & GONZÁLEZ ÁLVAREZ, M.C. 1999. Nuevos datos sobre los briozoos Devónicos de la Zona Cantábrica, 643–646. In RABANO, I. (ed.) *Actas de las XV Jornadas de la Sociedad Española de Paleontología y Simposios de los proyectos PICG 393, 410 y 421, Colección Temas Geológico-Mineros* 26. Instituto Tecnológico Geominero de España, Madrid.
- SUÁREZ ANDRÉS, J.L. & MCKINNEY, F.K. 2010. Revision of the Devonian Fenestrate bryozoan genera *Cyclopelta* Bornemann, 1884 and *Pseudoisotrypa* Prantl, 1932, with description of a rare growth habit. *Revista Española de Paleontología* 25(2), 123–138.
- SUÁREZ ANDRÉS, J.L. & WYSE JACKSON, P.N. 2014. *Ernstipora mackinneyi*, a new unique fenestrate bryozoan genus and species with an encrusting growth habit from the Emsian (Devonian) of NW Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 271(3), 229–242. DOI 10.1127/0077-7749/2014/0384
- SUÁREZ ANDRÉS, J.L. & WYSE JACKSON, P.N. 2015. Feeding currents: a limiting factor for disparity of Palaeozoic fenestrate bryozoans. *Palaeogeography, Palaeoclimatology, Palaeoecology* 433, 219–232. DOI 10.1016/j.palaeo.2015.05.015
- SUÁREZ ANDRÉS, J.L., WYSE JACKSON, P.N. & SENDINO, C. 2014. First record of a Palaeozoic fenestrate with a secondary zooid-bearing meshwork. *Studi Trentini delle Scienze Naturali* 94, 241–247.
- TAVENER-SMITH, R. 1971. *Polypora stenostoma*, a Carboniferous bryozoan with cheilostomatous features. *Palaeontology* 14(1), 178–187.
- ULRICH, E.O. 1890. Palaeozoic Bryozoa. *Illinois Geological Survey Bulletin* 8, 283–688.
- VINE, G.R. 1880. On the Carboniferous Polyzoa. *Geological Magazine II (VII)*, 501–512. DOI 10.1017/S0016756800151532
- VOLKOVA, K.N. 1974. Devonian Bryozoa from the Southeast Altai. *Trudy Institut Geologii i Geofiziki* 199, 1–182. [in Russian]
- WHITEAVES, J.F. 1892. The fossils of the Devonian rocks of the islands, shores or immediate vicinity of Lakes Manitoba and Winnipegosis. *Contributions to Canadian Palaeontology* 1(4), 255–359.
- WRZOLEK, T. 2002. Devonian history of diversity of the rugosan Cyathaxonia fauna. *Acta Palaeontologica Polonica* 47, 397–404.
- WYSE JACKSON, P.N. 2001. *Permofenestella* Morozova, 1974 (Fenestrata, Bryozoa): first record from the Lower Carboniferous of Ireland and Western Europe. *Irish Naturalists' Journal* 26 (11), 420–423.
- XIA, F.S. & LIU, X.L. 1986. Late Carboniferous bryozoans from the vicinity of Urumqi, Xinjiang. *Memoirs of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* 22, 145–180. [in Chinese]
- ZÁGORSEK, K. 1993. New Carboniferous Bryozoa from Nagyvisnyó (Bükk Mts., Hungary). *Földtani Közlöny* 123(4), 417–440.
- ZITTEL, K.A. VON 1880. *Handbuch der Palaeontologie. 1. Band. Palaeozoologie. I. Abtheilung. Protozoa, Coelenterata, Echinodermata und Molluscoidea*. 765 pp. Oldenburg, München & Leipzig.