



Stenolaemate bryozoan fauna from the Mississippian of Guadiato Area, southwestern Spain

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ABSTRACT

Stenolaemate bryozoan fauna from the Lower Carboniferous (Mississippian) of southwestern Spain (Los Santos de Maimona Basin and Guadiato Area – Ossa Morena Zone) contains eight bryozoan species including three cystoporates, three trepostomes, and two cryptostomes. They range from Asbian (Upper Viséan) to Pendleian (Serpukhovian). This fauna displays distinct palaeobiogeographic relationships to the Mississippian of Europe, USA, Siberia, and Japan.

Keywords: Bryozoa, taxonomy, palaeobiogeography, Mississippian, Spain.

RESUMEN

Las asociaciones del briozoos estenolemados del Misisípico (Carbonífero inferior) del suroeste de España (Cuenca de los Santos de Maimona y Área del Guadiato, Zona de Ossa Morena) se componen de ocho especies de briozoos que incluyen tres cystoporados, tres trepostomados y dos cryptostomados. Su distribución se extiende desde el Asbiense (Visense superior) al Pendleense (Serpujoviense). Estas asociaciones muestran distintas relaciones biogeográficas con el Misisípico de Europa, Estados Unidos, Siberia y Japón.

Palabras clave: Briozoos, taxonomía, paleobiogeografía, Misisípico, España.

1. INTRODUCTION

Stenolaemate bryozoans are commonly abundant and diverse in Carboniferous deposits worldwide. They are important for biostratigraphy and palaeobiogeography (Ross, 1981; Bancroft, 1987). However, our knowledge about them is very uneven, and many of older data need to be revised. Well-studied bryozoan faunas are known from North America, certain parts of Australia, several regions in China and Mongolia, the British Isles, and the European part of Russia and Ukraine. In other regions the Carboniferous bryozoans are poorly studied.

The Lower Carboniferous (Mississippian) bryozoans in Europe were mainly recorded from the British Isles (e.g., Wyse Jackson, 1996), and from Poland and Germany (Nekhoroshev, 1932; Ernst, 2005). Mississippian bryozoans are also known from southern France, Montagne Noire (unpublished data) and southwestern Spain (present paper).

Bryozoans described in this paper have been recorded in two different basins in southwestern Spain (Sierra Morena): the Los Santos de Maimona Basin, and the Guadiato Area. These Mississippian basins contain upper Viséan and Serpukhovian deposits.

The Los Santos de Maimona Basin is located in the Badajoz province, between Los Santos de Maimona, Fuente del Maestre and Feria villages. Mississippian outcrops are 11 km long from SE to NW, and 1 to 3 km wide. Eight stratigraphic units have been defined in that basin (Fig. 1c) by Rodríguez *et al.* (1992). The bryozoans have been sampled from unit 1 (upper Asbian) in Los Santos Hill (SS) and El Almendro (AL) sections. Unit 1 is composed of biostromal limestones where rugose, and tabulate corals and gigantoproductid brachiopods are the most conspicuous elements in a very diverse assemblage (Rodríguez *et al.*, 1992, 1994). Bryozoans are common in this unit, mainly in the northern outcrops (AL). *Pseudonematopora planatus* Wyse Jackson, 1996, *Stenophragmidium crassimularis* (Lee, 1912), and *Nikiforovella multipitata* Trizna, 1958 have been recorded there (Fig. 2).

The Guadiato Area is a large and complex region in SW Spain that comprises Mississippian siliciclastics and limestones (Fig. 1b). It is divided into three bands (Cózar & Rodríguez, 1999): the Fresnedoso Unit, composed mainly of Viséan siliciclastic rocks described by Cózar & Rodríguez (2001); the San Antonio-La Juliana Unit, composed of Serpukhovian siliciclastic and limestone rocks (Cózar & Rodríguez, 2004); the Sierra del Castillo Unit, composed mainly of Viséan limestone rocks (Rodríguez *et al.*, 2007).

The El Collado Section (about 150 m in thickness) comprises the upper part of the stratigraphical succession in the Castillo Ridge (Sierra del Castillo Unit), SE from Espiel. It consists of massive and well bedded limestones deposited in shallow water of an inner shelf. Corals, algae

and foraminifera are common in this succession. The distribution of corals, foraminifera, algae and conodonts indicates a late Viséan age (Asbian-Brigantian). The Asbian/Brigantian boundary is located between units COL4 and COL/6 of El Collado section (Rodríguez *et al.*, 2007). *Nikiforovella multipitata* Trizna, 1958 and *Fistulipora incrustans* (Phillips, 1836) have been recorded in El Collado Section.

The Caleras Bajas and Antolín sections are located in the northern outcrops of the Sierra del Castillo Unit, near Peñarroya-Pueblonuevo. They comprise Brigantian siliciclastic and carbonate rocks deposited in a talus/ramp. Shales and sandstones in cyclic sequences dominate in these sections, but limestone boulders, microbial mounds and conglomerates also occur (Cózar & Rodríguez, 2000; Rodríguez & Rodríguez-Curt, 2002). The carbonate boulders contain reefal facies rich in corals, algae and cyanobacteria. *Pseudonematopora planatus* Wyse Jackson, 1996, *Nikiforovella multipitata* Trizna, 1958, and *Glyptopora michelinia* (Prout, 1860) have been recorded from these outcrops.

The La Cornuda Section is located in the San-Antonio-La Juliana Unit, about 3 km Northwest of Espiel, near La Cornuda Farm. The coordinates at the base of the section are 5° 6' 30" West and 38° 12' 40" North. It was first described by Cózar (1998), who analysed the age and paleoenvironment of each unit based on algae, foraminifera and microfacies. He identified foraminifera zones 17 and 18 of Mamet (1974), included in the Pendleian stage (lower Serpukhovian). The section is about 500 m thick, but only some limestones, calcareous sandstones and conglomerates are exposed. Cózar (1998) and Cózar & Rodríguez (2004) regarded the whole sequence having originated on a shallow platform where bioclastic limestones, calcareous sandstones and conglomerates represent shoals while the covered units (lutites, limolites and marls) represent surrounding lagoonal and shallow platform facies. Gómez-Herguedas & Rodríguez (2005) studied the coral assemblages and later analysed the palaeoenvironments (Gómez-Herguedas & Rodríguez, 2008). The following bryozoans have been recorded from the La Cornuda Section: *Stenophragmidium crassimularis* (Lee, 1912), *S. paramirandum* Ernst *et al.*, 2005, *Fistulipora* sp., and *Hinaclema hinaensis* Sakagami & Sugimura, 1987.

2. MATERIAL AND METHODS

Bryozoans were investigated in thin sections using a binocular microscope in transmitted light. Morphologic character terminology is partly adopted from Anstey & Perry (1970) for trepostomes and from Hageman (1993) for cryptostomes. Thin sections are deposited at the Universidad Complutense, Madrid.

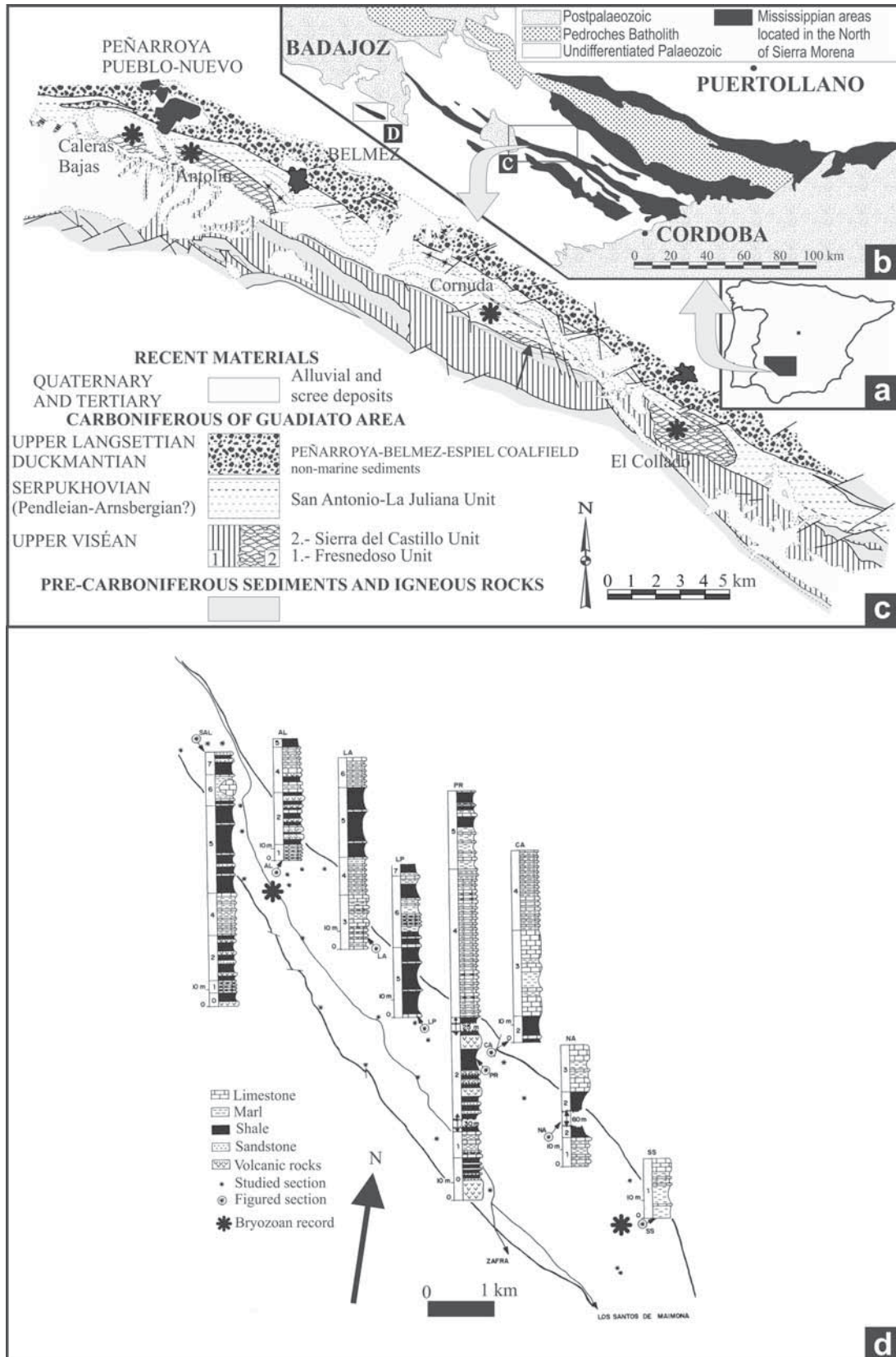


Figure 1. Location of the studied sections. **a)** Map of the Iberian Peninsula. **b)** Distribution of Carboniferous outcrops in the Ossa Morena Zone. **c)** Mississippian outcrops in the Guadiato Area. Asterisks show the position of the studied sections. **d)** Mississippian outcrops in the Los Santos de Maimona Basin. Asterisks show the position of the studied sections. SAL- Salamanca Chico Section. AL- El Almendro Section. LA- La Alameda Section. LP- Las Pilatas Section. PR- Portezuelo Section. CA- Cerro Almeña Section. NA- Navafría Section. SS- Los Santos Section.

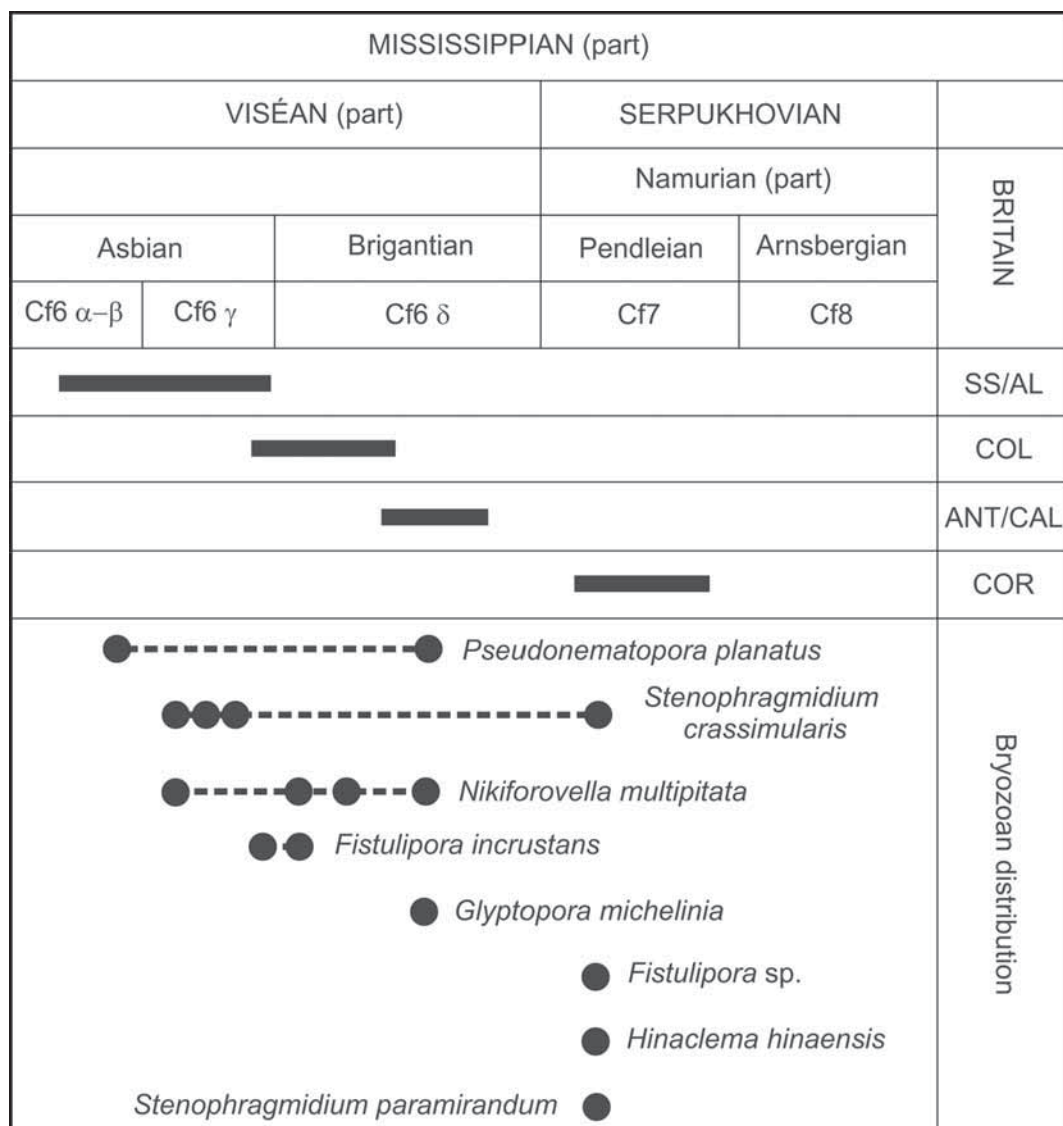


Figure 2. Stratigraphic distribution of the studied sections with location of the identified taxa. SS/AL – Los Santos and El Almendro Sections. COL – El Collado Section. ANT/CAL – Antolín and Caleras Bajas Sections. COR – La Cornuda Section.

3. SYSTEMATIC PALAEOLOGY

Phylum BRYOZOA Ehrenberg, 1831
 Class STENOLAEMATA Borg, 1926
 Order CYSTOPORATA Astrova, 1964
 Suborder FISTULIPORINA Astrova, 1964
 Family **Fistuliporidae** Ulrich, 1882
 Genus *Fistulipora* M'Coy, 1849

Type species. *Fistulipora minor* M'Coy, 1849.
 Carboniferous; England.

Diagnosis. Massive, encrusting or ramose colonies. Cylindrical autozoecia with thin walls and complete diaphragms. Apertures rounded, possessing horse-shoe shaped lunaria. Autozoecia separated by the extrazoooidal vesicular skeleton.

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

Stratigraphic and geographic range. Ordovician to Permian; worldwide.

Fistulipora sp.
 (Figs 3a-3d; Table 1)

Material. Cor/1-51, Cor/1-86.

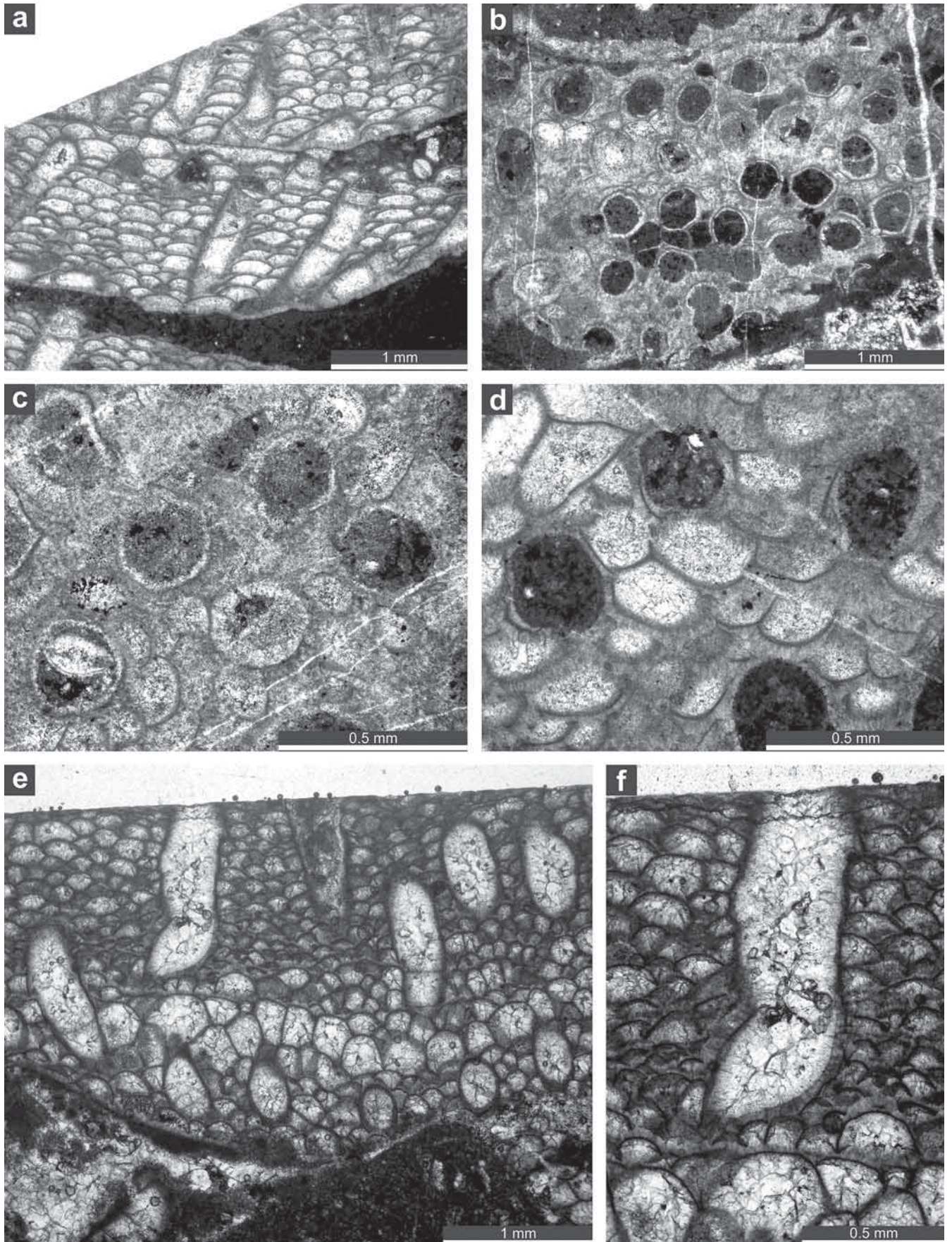


Figure 3. *Fistulipora sp. 1*: **a)** Longitudinal section, Cor/1-51. **b-c)** Tangential section, Cor/1-86. **d)** Tangential section, Cor/1-51. *Fistulipora incrustans* (Phillips, 1836): **e-f)** Longitudinal section, Col/1-11.

Table 1. Descriptive statistics of *Fistulipora* sp. Abbreviations: N = number of measurements, X = mean, SD = sample standard deviation, CV = coefficient of variation, MIN = minimal value, MAX = maximal value.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	10	0.23	0.030	12.93	0.19	0.29
Autozooeccial aperture spacing, mm	10	0.40	0.063	15.86	0.32	0.53
Vesicle diameter, mm	10	0.16	0.057	36.12	0.08	0.29
Vesicles per aperture	5	7.8	0.837	10.73	7.0	9.0

Description. Encrusting colony, 1.0-1.1 mm thick. Basal diaphragms common, 2-4 per autozooeccium. Autozooeccial apertures circular, 0.18-0.22 mm wide. Lunaria weakly developed. Vesicles large, flattened, 8-9 surrounding each autozooeccia aperture, with rounded roofs, polygonal in tangential section, separating the autozooeccia in single row, 11-12 per 1 mm line in longitudinal section.

Comparison. The present species differs from *Fistulipora incrustans* (Phillips, 1836) by having smaller autozooeccial apertures (0.18-0.22 mm vs. 0.25-0.36 mm in *F. incrustans*) and by fewer vesicles around autozooeccial apertures (8-9 instead of 10-14 in *F. incrustans*). It differs from *Fistulipora excelens* Ulrich, 1884 from the Mississippian of USA in having smaller autozooeccia (0.18-0.22 mm vs. 0.30-0.40 in *F. excelens*). The present material is inadequate for establishing a new species, however.

Stratigraphic and geographic range. Carboniferous, Mississippian, Serpukhovian (Pendleian); La Cornuda, southwestern Spain.

Fistulipora incrustans (Phillips, 1836)
(Figs 3e-3f, 4a-4b; Table 2)

Material. Val-1-7, Col/1-11, Col/2b-1, Col/7-11.

Table 2. Descriptive statistics of *Fistulipora incrustans* (Phillips, 1836). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	26	0.30	0.026	8.69	0.25	0.36
Autozooeccial aperture spacing, mm	25	0.49	0.060	12.33	0.36	0.63
Vesicle diameter, mm	20	0.13	0.022	17.07	0.10	0.18
Vesicle spacing, mm	20	0.10	0.025	25.27	0.05	0.13

Description. Encrusting colony, 1.5-3.1 mm thick. Diaphragms abundant in basal parts of autozooeccia, rare to common in distal exozone. Autozooeccial apertures circular to ovate. Lunaria weakly developed, horseshoe-shaped. Vesicles large, 10-14 surrounding each autozooeccia aperture, with rounded roofs, polygonal in tangential section, 1-3 rows separating the autozooeccia, 9-12 spaced per 1 mm line in longitudinal section.

Comparison. *Fistulipora incrustans* (Phillips, 1836) is similar to both *F. parvilabrum* Shulga-Nesterenko, 1955 and *F. steshevensis* Shulga-Nesterenko, 1955 from the Mississippian of the Russian Platform. *Fistulipora incrustans* differs from both species by having smaller vesicles (10-14 of them surrounding autozooeccial aperture versus 7-8 in *F. parvilabrum* and 8-9 in *F. steshevensis*). *Fistulipora incrustans* (Phillips, 1836) differs from *F. micidolamina* McKinney, 1972 from the Mississippian of USA (Serpukhovian) and Pennsylvanian of NW Spain (Bashkirian-Moscovian) by having larger autozooeccial apertures (average width 0.30 mm vs. 0.25 mm in *F. micidolamina*).

Remark. See full synonymy of *Fistulipora incrustans* (Phillips, 1836) in Bancroft & Jackson (1995, p. 131-133).

Stratigraphic and geographic range. Carboniferous, Mississippian, Viséan (Asbian-Brigantian); England, Scotland, Ireland. Carboniferous, Mississippian, Viséan (Asbian-Brigantian); El Collado, southwestern Spain.

Suborder HEXAGONELLINA Morozova, 1970
Family **Hexagonellidae** Crockford, 1947
Genus *Glyptopora* Ulrich, 1884

Type species. *Coscinium plumosum* Prout, 1860. Carboniferous, Mississippian; USA (Illinois).

Diagnosis. Colony consisting of erect bifoliate lobes. Mesotheca with dark, thin, middle layer and two light and thick outer layers, containing median rods and longitudinal ridges parallel to growth direction. Autozooeccia recumbent on the mesotheca or epitheca for a long distance, bending upwards abruptly or gently, intersecting the surface almost perpendicularly. Hemisepta absent. Thin, complete diaphragms common to abundant. Autozooeccial apertures circular to oval. Lunaria common. Autozooeccia separated by vesicular skeleton that is covered in distally by calcite material. Microacanthostyles in outer layer of calcite material. Maculae depressed, long, narrow, consisting of stereom.

Comparison. *Glyptopora* differs from *Evactinopora* Meek & Worthen, 1865 by lacking hemisepta, and from

Prismopora Hall, 1883 by possessing median tubuli in the mesotheca and lacking hemisepta.

Remark. *Prismopora* species described from the Carboniferous and Lower Permian deposits of Europe (Ernst, 2000; Ernst & Winkler Prins, 2008) differ significantly from the type species *Prismopora triquetra* Hall & Simpson, 1887 from the Middle Devonian of North America. The most important differences include the presence of long hemisepta, poorly developed vesicular skeleton consisting of small, rare, vesicles, and lacking rods. *Prismopora* species described by Crockford (1957) from the Lower Permian of Australia, are similar to the material from Europe (especially *Prismopora digitata* Crockford, 1957), and differ in the same manner from the type species. They may belong to the genus *Glyptopora*.

Stratigraphic and geographic range. Carboniferous-Permian; North America, Europe, Australia.

Glyptopora michelinia (Prout, 1860)
(Figs 4c-4e, 5a-5f, 6a-6d; Table 3)

1860 *Coscinium michelinia* Prout, p. 573.

1866 *Coscinium michelinia* Prout, 1860; Prout, p. 414, pl. 22, figs 4, 4o.

1890 *Glyptopora michelinia* (Prout, 1860); Ulrich, p. 515-516, pl. 78, figs 8-8b.

Material. Ant 2/1-1, Ant 2/1-9, Ant 2/1-25, Ant 2/1-1, Ant 2/1-45, Ant 2/1-47, Ant 2/1-F2, FE-A.

Table 3. Descriptive statistics of *Glyptopora michelinia* (Prout, 1860). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.14	0.019	13.84	0.10	0.18
Autozooeical aperture spacing, mm	30	0.37	0.045	12.10	0.30	0.48
Vesicle diameter, mm	30	0.09	0.020	21.31	0.06	0.13
Vesicles per aperture	15	8	1.134	14.17	6	10
Vesicle spacing, mm	10	0.07	0.007	10.69	0.06	0.08

Description. Colony initially encrusting, producing a series of erect bifoliate lobes. Lobes usually trifurcating radially and fused together forming a honeycomb-shaped structure. Lobes diverg radially from the central axis at angles of 86-148°. Bifoliate lobes up to 5 mm high and 0.6-0.9 mm thick. Mesotheca with a dark, thin, middle layer and two light, thick, outer layers, 0.025-0.050 mm thick, containing abundant median tubuli. Median tubuli of hyaline calcite, rounded in transverse section, 0.010-0.015

mm in diameter, developing short and densely spaced lateral projections (Figs 4c-4d). Autozooeicia recumbent on the mesotheca or epitheca for a relatively long distance, then bending upwards abruptly, intersecting the surface almost perpendicularly. Thin, complete diaphragms in autozooeicia occasionally present. Autozooeical apertures circular to oval. Lunaria weakly developed, horseshoe-shaped to triangular. Vesicular skeleton well developed, covered distally by calcite material. Vesicles moderately large, polygonal in tangential section, with 6-10 surrounding each autozooeical aperture, and 1-3 rows between autozooeicia in longitudinal sections, with rounded roofs. Longitudinal depressed maculae lacking autozooeicia apparently developed only near bases of erect lobes along the axis of fusion.

Comparison. *Glyptopora michelinia* (Prout, 1860) differs from *Glyptopora plumosa* (Prout, 1860) by mode of lobe divergence. *Glyptopora michelinia* produced cups by lobes attached to a substrate, whereas lobes in *G. plumosa* arose from a common base, bifurcating and trifurcating to produce cups. Furthermore, maculae are less strongly developed, diaphragms less common and autozooeical apertures are smaller (0.10-0.18 mm vs. 0.15-0.20 mm in *G. plumosa*).

Stratigraphic and geographic range. Carboniferous, Mississippian, Viséan; USA Illinois, Missouri, Virginia. Carboniferous, Mississippian, Viséan (Brigantian); Antolin section, southwestern Spain. Las Llacerias Formation, Carboniferous, Pennsylvanian, Kasimovian; Asturias, Cantabrian Mountains, NW Spain.

Order TREPOSTOMATA Ulrich, 1882

Family **Stenoporidae** Waagen & Wentzel, 1886

Genus *Stenophragmidium* Bassler, 1952

Type species. *Stenophragma lobatum* Munro, 1912. Carboniferous, Mississippian, Viséan; England.

Diagnosis. Encrusting, rarely ramose, colonies. Autozooeicia possessing rounded-polygonal and oval apertures. Hemiphragms short, often curved proximally, positioned on one side of autozooeicia. Exilazooeicia rare. Acanthostyles both large and small, rarely one size. Exozonal walls laminated, merged, without distinct autozooeical boundaries, with moniliform thickenings.

Comparison. *Stenophragmidium* Bassler, 1952 is similar to *Tabulipora* Young, 1883 in having moniliform walls and acanthostyles of two sizes, but differs from it by having hemiphragms instead of ring septa. *Stenophragmidium* differs from *Stenopora* Lonsdale, 1844 by having both hemiphragms and diaphragms: *Stenopora* lacks any kind of diaphragms.

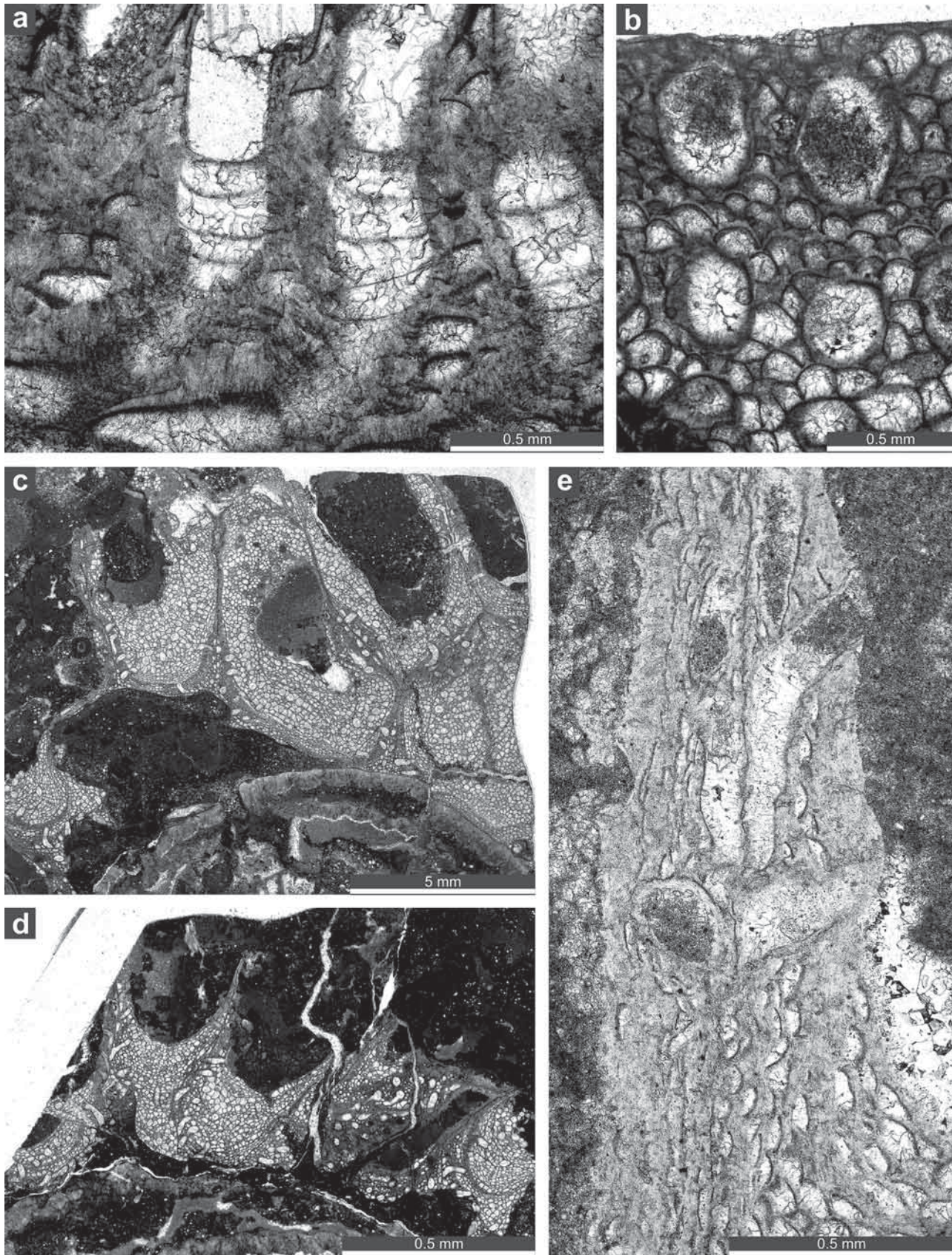


Figure 4. *Fistulipora incrustans* (Phillips, 1836): **a)** Longitudinal section showing abundant diaphragms in basal parts of zooecia, Col/7-11. **b)** Tangential section, Col/1-11. *Glyptopora michelinia* (Prout, 1860): **c)** Tangential section showing trifurcating lobes, Ant 2-1-45. **d)** Oblique section showing arising lobes, Ant 2-1-45. **e)** Longitudinal section of a lobe showing autozoecia and vesicular skeleton, Ant 2-1-25.

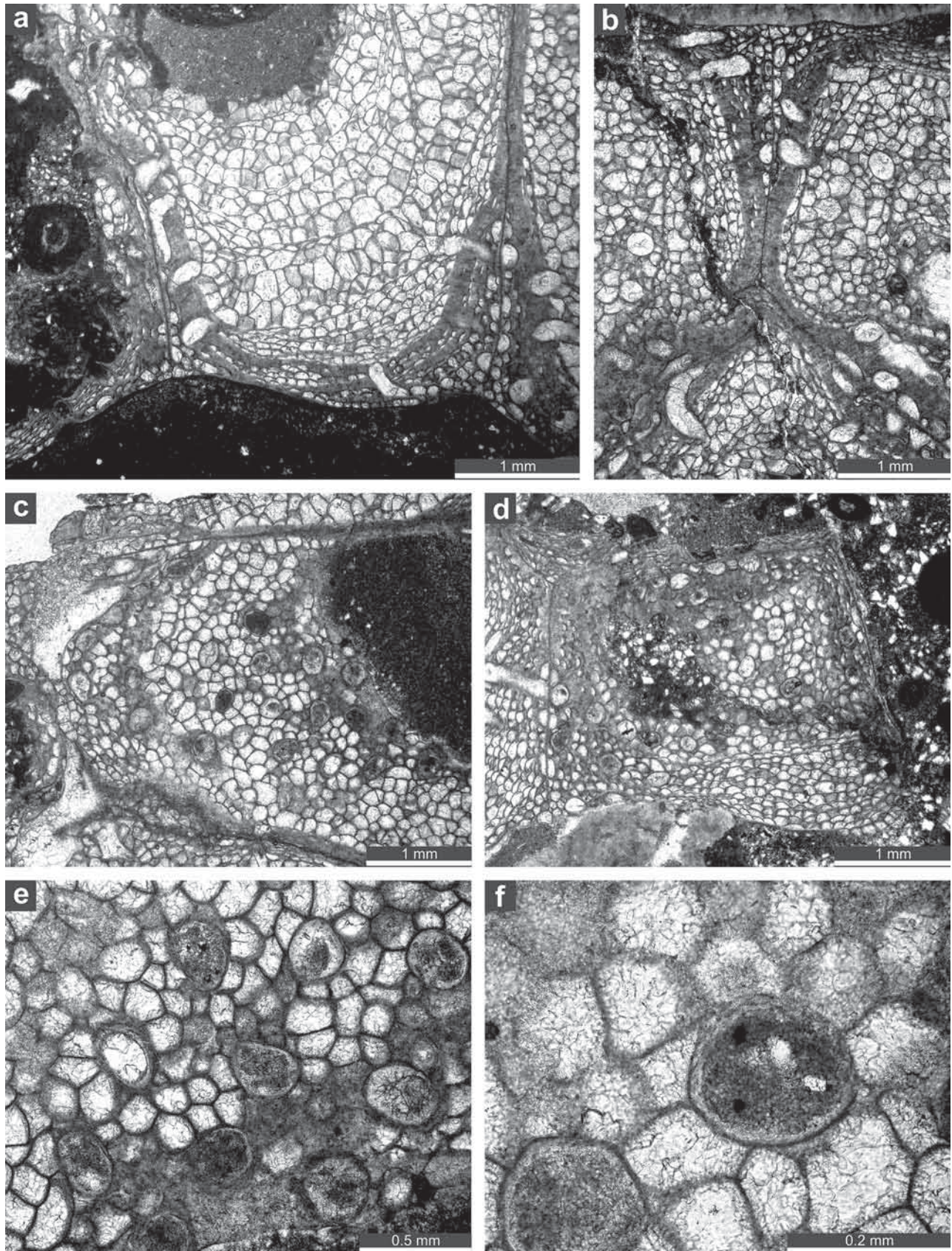


Figure 5. *Glyptopora michelinia* (Prout, 1860): **a)** Oblique section showing arising lobes and vesicular skeleton, Ant 2-1-45. **b)** Tangential section showing place of trifurcation, Ant 2-1-45. **c)** Tangential section showing part of the colony between lobes, Ant 2-1-45. **d)** Tangential section showing sector between fusing lobes, Ant 2-54. **e-f)** Tangential section showing autozoecial apertures, Ant 2-1-45.

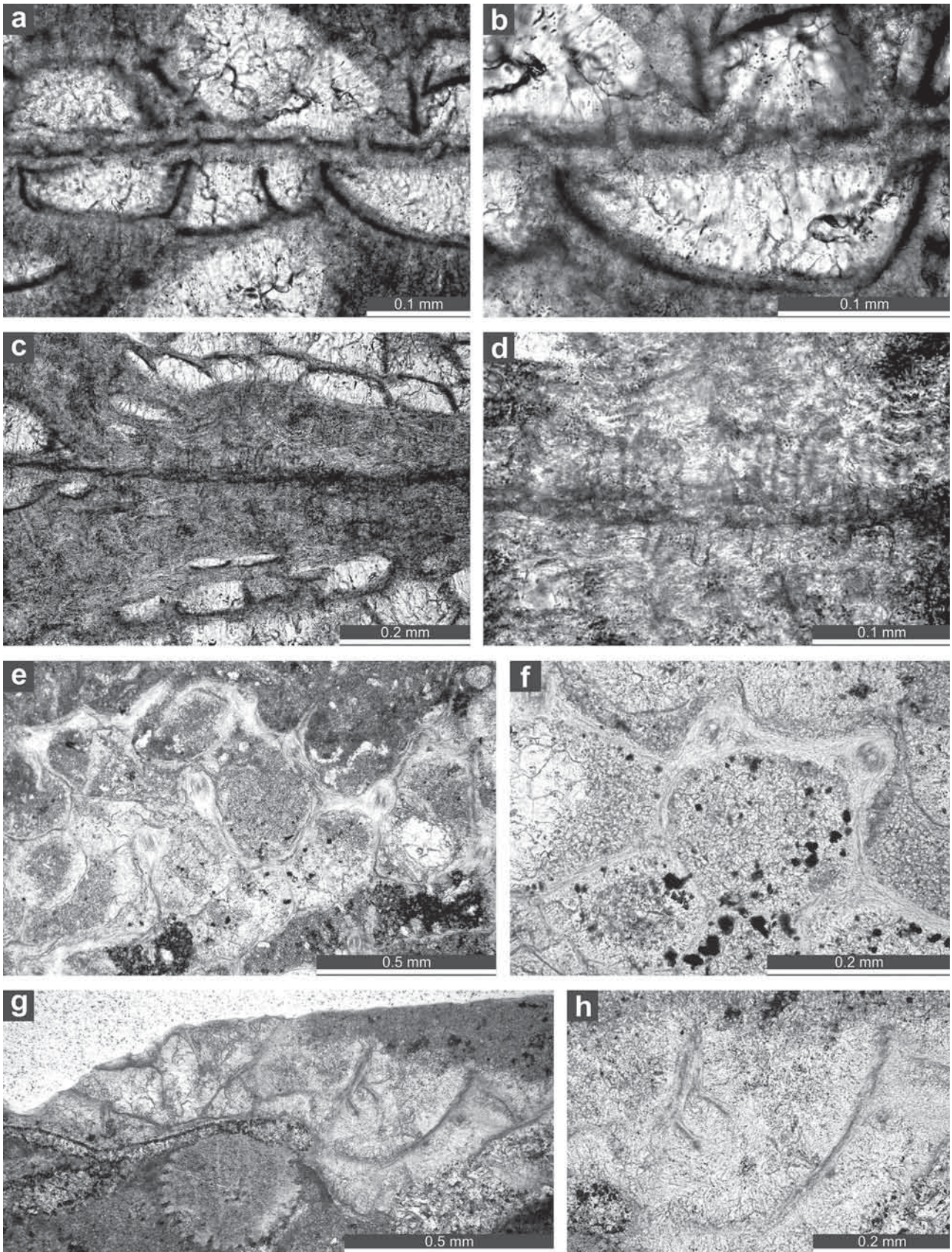


Figure 6. *Glyptopora michelinia* (Prout, 1860): **a-b**) Transverse section of a lobe showing three-layered mesotheca with median tubuli, Ant 2-1-45. **c-d**) Longitudinal section showing median tubuli with lateral projections, Ant 2-1-45. *Stenophragmidium paramirandum* Ernst *et al.* 2005: **e-f**) Oblique section showing autozooeical apertures and acanthostyles, Cor/1-60. **g-h**) Longitudinal section showing hemiphragms in autozooeia, Cor/1-62.

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

Stenophragmidium paramirandum Ernst *et al.*, 2005
(Figs 6e-6h)

2005 *Stenophragmidium paramirandum* Ernst *et al.*, p. 306, pl. 1, fig. 7, pl. 2, fig. 1, pl. 3, fig. 4

Material. Cor/1-46, Cor/1-60, Cor/1-62.

Description. Thin encrusting colonies, 0.27-0.45 mm thick. Autozoecia bud from a thin epitheca, bending gently in their deeper portion and intersecting the colony surface at angles of 80-90°. Hemiphragms thick, on proximal side of autozoecia, typically 3-4 per autozoecium. Autozoecial apertures polygonal, 0.18-0.22 mm wide. Exilazoecia not observed. Acanthostyles large, having hyaline cores and wide laminated sheaths, located in autozoecial corners, 0.06-0.09 mm in diameter, 2-5 per autozoecial aperture. Smaller styles occur between acanthostyles. Autozoecial walls laminated, 0.03-0.04 mm thick in exozone.

Comparison. *Stenophragmidium paramirandum* Ernst *et al.*, 2005 differs from *S. mirandum* Dunaeva, 1964 from the Lower Carboniferous (Namurian) of the Ukraine by forming thinner colonies with strongly differentiated acanthostyles and smaller autozoecial aperture widths (0.18-0.22 mm in present material and 0.12-0.21 mm in type material vs. 0.27-0.30 mm in *S. mirandum*). *Stenophragmidium paramirandum* differs from *S. lobatum* (Munro, 1912) by having encrusting colony form rather than hollow erect and lobate one in the latter species, and in smaller autozoecial apertures (0.18-0.22 mm vs. 0.18-0.31 mm in *S. lobatum*).

Stratigraphic and geographic range. San Emiliano Formation, Pennsylvanian, Bashkirian; NW Spain. Mississippian, Serpukhovian (Pendleian); La Cornuda, southwestern Spain.

Stenophragmidium crassimularis (Lee, 1912)
(Figs 7a-7f; Table 4)

1912 *Tabulipora crassimularis* Lee, pp. 172-173, pl. 16, figs. 5-6.

1912 *Stenophragma grandense* Munro, pp. 576-577.

2007 *Stenophragmidium crassimularis* (Lee, 1912); Cleary & Wyse Jackson, pp. 12-15, figs 3C-D.

Material. AL/1-3, AL/1-7, AL/1-5, AL/1-15, Ex-1, Cor/1-51, Cor/1-96.

Table 4. Descriptive statistics of *Stenophragmidium crassimularis* (Lee, 1912). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Colony thickness, mm	10	1.25	0.482	38.50	0.75	2.50
Aperture width, mm	35	0.16	0.032	19.59	0.10	0.24
Autozoecial aperture spacing, mm	35	0.31	0.046	14.48	0.20	0.42
Exilazoecia width, mm	15	0.047	0.010	21.08	0.030	0.065
Exozonal wall thickness, mm	19	0.14	0.036	25.46	0.08	0.19
Macroacanthostyle diameter, mm	6	0.071	0.006	8.25	0.060	0.075

Description. Colonies tubular-shaped, 4-8 mm in diameter, produced by encrusting of ephemeral cylindrical objects (sheets 0.75-2.50 mm thick). Secondary overgrowth occur. Autozoecia bud from thick epitheca, bending gently in their deeper portion and intersecting the colony surface at angles of 80-90°. Thick hemiphragms common, 1-3 in each autozoecium, positioned on proximal side of autozoecia, and curved proximally, concentrated in the early exozone. Autozoecial apertures polygonal. Basal diaphragms rare, thin. Exilazoecia usually absent, locally rare to common. Macroacanthostyles usually absent; locally common, large (0.060-0.075 mm in diameter), having hyaline cores and wide laminated sheaths, positioned in autozoecial corners. Abundant microacanthostyles (heterostyles) protruding from exozonal walls perpendicular to skeletal laminations, and irregularly arranged, 0.015-0.030 mm in diameter. Autozoecial walls finely laminated, 0.005-0.015 mm thick in the endozone; laminated, merged, displaying inverted U-shaped laminations, with local monilae-like thickenings, 0.08-0.19 mm thick in the exozone.

Comparison. *Stenophragmidium crassimularis* (Lee, 1912) is similar to *S. multitabulata* (Lee, 1912) from the Mississippian of the British Isles, but differs from it in forming hollow ramose instead of solid ramose colonies, in having fewer abundant hemiphragms (1-6 vs. 6-7 hemiphragms per autozoecium, in autozoecial walls that are distinctly moniliform; walls in *S. multitabulata* lack moniliform thickenings. *Stenophragmidium crassimularis* is similar to *S. isospinosum* Ernst *et al.*, 2005 from the Pennsylvanian of NW Spain, but differs from it by having two types of acanthostyles, instead of just microacanthostyles in *S. isospinosum*, and in smaller autozoecial diameters (average width 0.16 mm vs. 0.21 mm in *S. isospinosum*).

Stratigraphic and geographic range. Lower Carboniferous, Mississippian, Viséan (?Courseyan/Chadian-Brigantian sub-stages); Pembrokeshire, Wales.

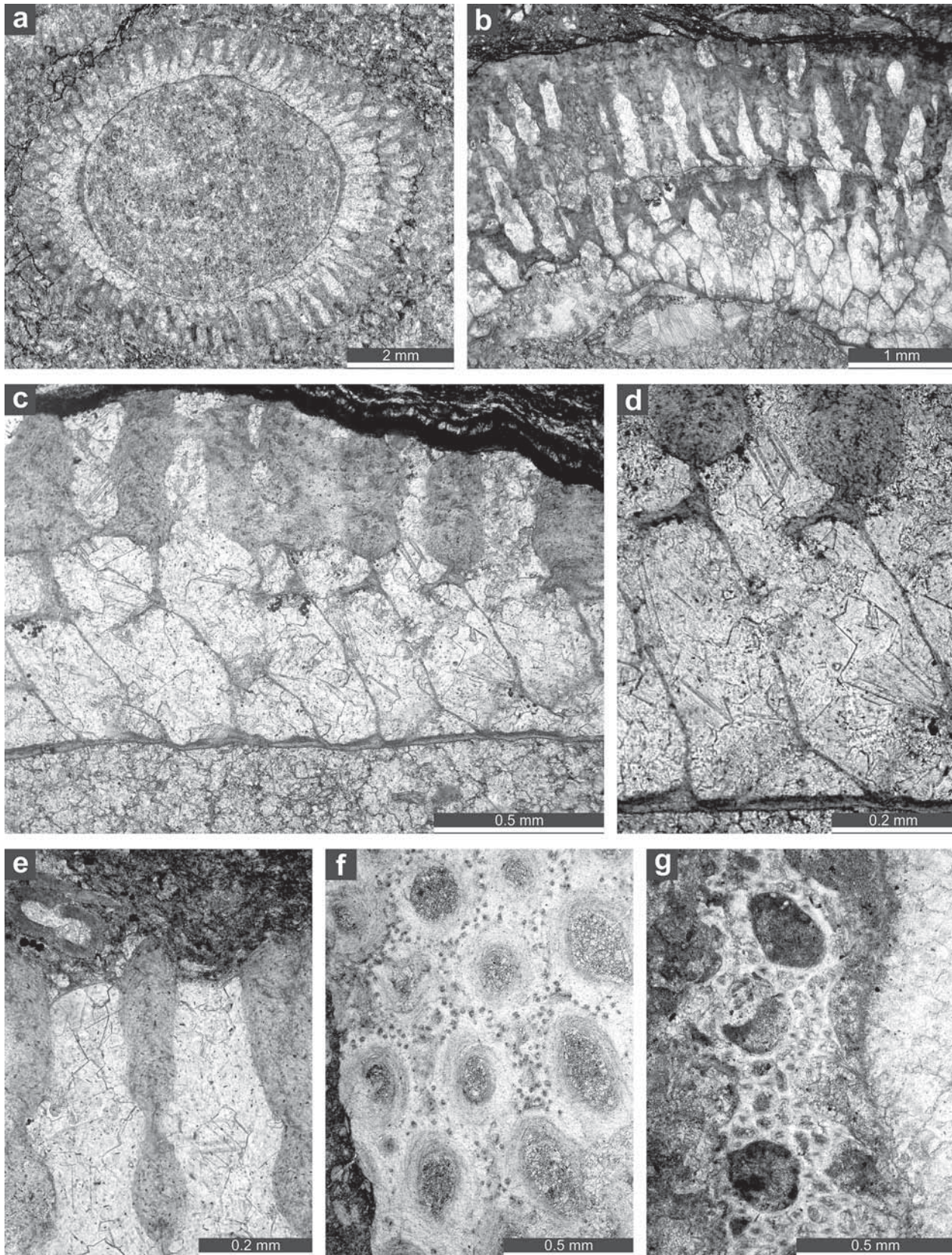


Figure 7. *Stenophragmidium crassimularis* (Lee, 1912): **a)** Transverse section of a tubular colony, Al/1-15. **b)** Longitudinal section of a multilayered encrusting colony, Al/1-7. **c-d)** Longitudinal section showing autozoecia with hemiphragms, Al/1-7. **e)** Longitudinal section showing monilae-shaped thickenings, Al/1-7. **f)** Tangential section showing autozoecial apertures, microacanthostyles and a few macroacanthostyles (arrow), Al/1-5. *Hinaclema hinaensis* Sakagami & Sugimura, 1987: **g)** Tangential section showing autozoecia, mesozoecia, and acanthostyles, Cor/1-51.

North Yorkshire, Westmorland and Cumbria, northern England. Lower Carboniferous, Mississippian, Viséan (upper Asbian); El Almendro section, southwestern Spain. Mississippian, Serpukhovian (Pendleian); La Cornuda, southwestern Spain.

Family **Crustoporidae** Dunaeva & Morozova, 1967
Genus *Hinaclema* Sakagami & Sugimura, 1987

Type species. *Hinaclema hinaensis* Sakagami & Sugimura, 1987. Mississippian, Viséan; Japan.

Diagnosis. Colony lamellar, encrusting with secondary overgrowth. Cylindrical autozooezia recumbent at their bases, bending sharply in exozones, intersecting the colony surface at right angles. Basal diaphragms in autozooezia rare to common. Exilazooezia abundant, separating autozooezia in multiple rows. Acanthostyles abundant throughout the colony, usually large, originating at the base of exozone. Autozooezial walls finely laminated, merged, without visible boundaries.

Comparison. *Hinaclema* Sakagami & Sugimura, 1987 differs from *Crustopora* Dunaeva, 1964 by having large acanthostyles, instead of small needle-like ones, and displaying abundant exilazooezia. *Toulopora* Nakrem et al., 2009 differs in having of acanthostyles of two sizes: sparsely distributed large ones, and a row of regularly distributed small ones inflecting each zooezial aperture.

The affinity of *Hinaclema* is disputable because of its cylindrical zooezia with rounded apertures and finely laminated walls. Sakagami & Sugimura (1987) placed their genus in the Family Heterotrypidae Nicholson, 1881. However, the merged wall structure, without distinct boundaries, and exilazooezia (not mesozooezia as in the original diagnosis) are not characteristic of heterotrypid bryozoans. Gorjunova (1996) placed *Hinaclema* in the Order Cystoporata based on its oval to circular autozooezial apertures and argued that its exilazooezia represented a special type of heterozooezia, called neozooezia. However, neozooezia have circular shape in transverse section, whereas *Hinaclema*'s exilazooezia are polygonal, and its wall structure differs from that of cystoporata bryozoans. Schastlivtseva (1991) put *Hinaclema* in the Family Crustoporidae Dunaeva & Morozova, 1967, and compared it with *Crustopora* Dunaeva, 1964. This assignment appears to be valid and is followed in this paper.

Stratigraphic and geographic range. Mississippian, Viséan; Japan, Uzbekistan. Mississippian, Serpukhovian (Pendleian); La Cornuda, southwestern Spain.

Hinaclema hinaensis Sakagami & Sugimura, 1987
(Figs 7g, 8a-8c)

1987 *Hinaclema hinaensis* Sakagami & Sugimura, pp. 247-249, figs 1-6.

Material. Cor/1-51, Cor/1-90, PR-19.

Description. Colony lamellar, encrusting, 0.31-0.34 mm thick. Cylindrical autozooezia recumbent at their bases, bending sharply in exozones and intersecting the colony surface at right angles. Basal diaphragms common, 1-3 in each autozooezium. Autozooezial apertures rounded to oval, 0.18-0.22 mm wide. Exilazooezia abundant, 1-4 rows separating autozooezia, rounded-polygonal in tangential section, originating at the base of the exozone, 0.03-0.08 mm in diameter. Acanthostyles abundant throughout the colony, originating at the base of the exozone, having narrow hyaline cores and wide laminated sheaths, 0.03-0.04 mm in diameter. Autozooezial walls finely laminated, merged, without visible boundaries and monilae-shaped thickenings, 0.015-0.030 mm thick.

Comparison. *Hinaclema hinaensis* Sakagami & Sugimura, 1987 differs from *H. sakagamai* Schastlivtseva, 1991 from the Mississippian (Viséan) of Uzbekistan by having smaller autozooezial widths (0.18-0.22 mm in our material, 0.19-0.28 mm in Japanese material, vs. 0.35-0.40 mm in *H. sakagamai*).

Stratigraphic and geographic range. Mississippian, Viséan; Japan. Mississippian, Serpukhovian (Pendleian); La Cornuda, southwestern Spain.

Order CRYPTOSTOMATA Vine, 1884
Suborder RHABDOMESINA Astrova & Morozova, 1956
Family **Arthrostylidae** Ulrich, 1882
Genus *Pseudonematopora* Balakin, 1974

Type species. *Nematopora? turkestanica* Nikiforova, 1948. Lower Carboniferous of the Middle Asia.

Diagnosis. Ramose colonies with occasional dichotomous branches. Branches width constant, circular to semicircular in transverse section. Autozooezia arranged in 6 to 16 longitudinal rows, budding in an annular manner from a central axis or median wall. Autozooezial apertures circular to oval shaped, with proximal peristomes. Vesicular skeleton may be present in the exozone. Diaphragms and acanthostyles absent, terminal diaphragms common.

Comparison. *Pseudonematopora* Balakin, 1974 differs from *Nematotrypa* Bassler, 1911 by lacking both hemidiaphragms in autozooezia and nodes on colony surfaces.

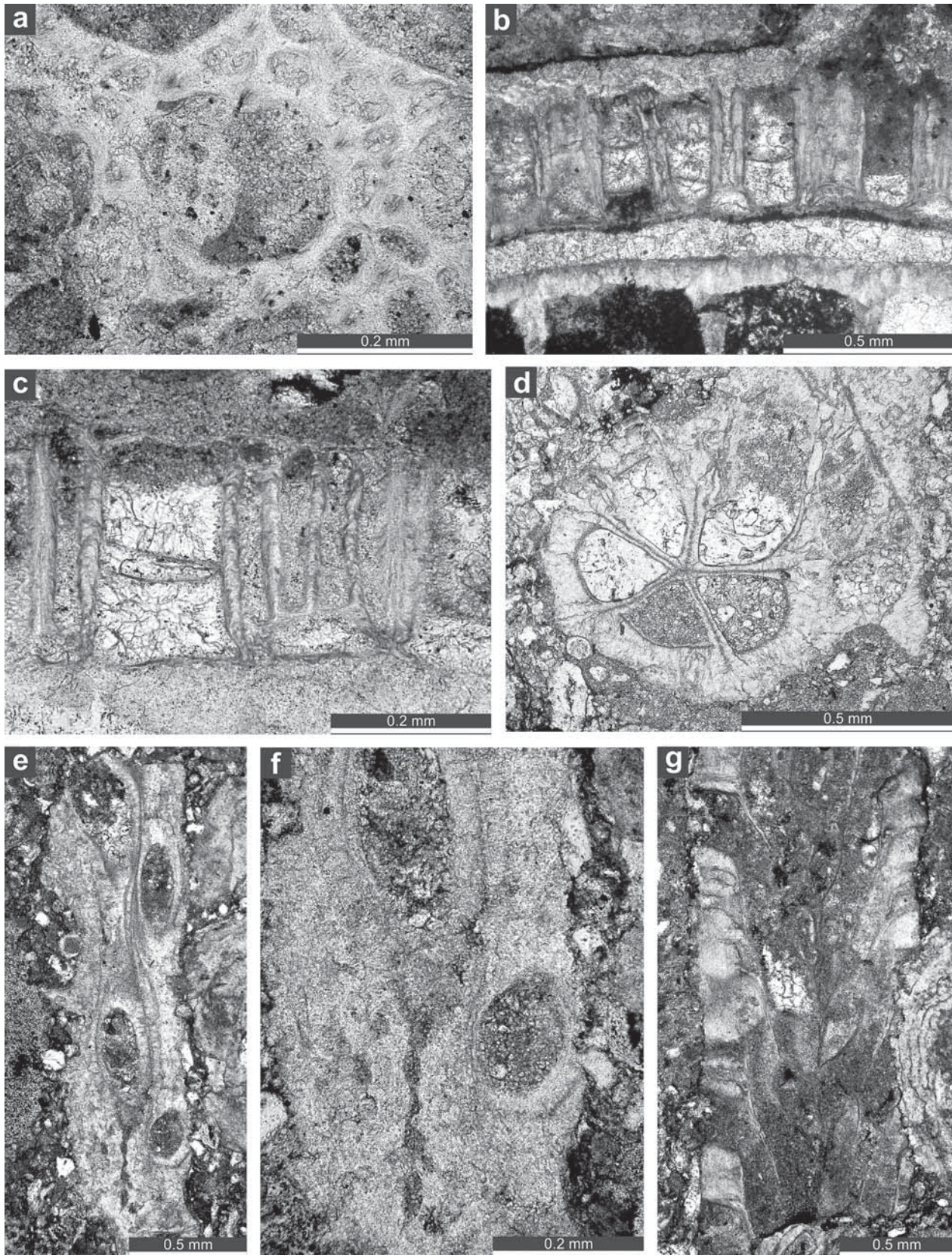


Figure 8. *Hinaclema hinaensis* Sakagami & Sugimura, 1987: **a)** Tangential section showing autozoecia, mesozoecia, and acanthostyles, Cor/1-51. **b)** Longitudinal section showing autozoecia and mesozoecia, Cor/1-51. **c)** Longitudinal section showing autozoecia and mesozoecia, Cor/1-90. *Pseudonematopora planatus* Wyse Jackson, 1996: **d)** Transverse section, Col/2b. **e-f)** Tangential section showing autozoecial apertures, Col/2b. *Nikiforovella multipitata* Trizna, 1958: **g)** Longitudinal section, Cal/2b.

Stratigraphic and geographic range. Upper Devonian (Famennian) to Pennsylvanian (Bashkirian); Europe, Russia, Kazakhstan, China, Mongolia.

Pseudonematopora planatus Wyse Jackson, 1996
(Figs 8d-8f)

1996 *Pseudonematopora planatus* Wyse Jackson, p. 126-127, fig 3c, 10-15.

2005 *Pseudonematopora planatus* Wyse Jackson, 1996; Ernst, p. 59, figs 4C-G.

Material. 36894, Cal/2b-10, SSc 1/14-1.

Description. Ramose colony, circular or slightly angular in cross-section, 0.66-0.72 mm in diameter. Short autozoecia budding in spiral order from the central axis. Hemisepta absent; terminal diaphragms common. Autozoecial apertures oval to teardrop-shaped, 0.12-0.13 mm wide, arranged in regular diagonal rows. Autozoecia displaying two types of walls – inner, bright, granular-prismatic walls and outer, dark, laminated walls. The inner granular-prismatic walls building three-layered endozones consisting of two bright outer layers and the dark inner one. No heterozoecia or styles present.

Comparison. *Pseudonematopora planatus* Wyse Jackson, 1996 differs from *P. turkestanica* (Nikiforova, 1948) from the Mississippian (Viséan) of Kazakhstan by having thinner branches (0.66-0.72 mm vs. 0.80-2.80 mm), smaller apertures (0.12-0.13 mm vs. 0.17-0.22 mm), and by lacking heterozoecia. *Pseudonematopora planatus* differs also from *P. balakini* Gorjunova, 1988 from the Pennsylvanian (Bashkirian) of Mongolia in having thinner branches (0.66-0.72 mm vs. 0.88-1.10 mm), smaller apertural width (0.12-0.13 mm vs. 0.18-0.22 mm), and by lacking heterozoecia.

Stratigraphic and geographic range. Mississippian, Viséan; Ireland (Wyse Jackson, 1996), Germany (Ernst, 2005), France (unpublished data). Mississippian, Viséan (upper Asbian); Los Santos Hill section, southwestern Spain. Mississippian (Brigantian); Caleras Bajas section, southwestern Spain.

Family **Nikiforovellidae** Gorjunova, 1975
Genus *Nikiforovella* Nekhoroshev, 1948

Type species. *Nikiforovella alternata* Nekhoroshev, 1948, by original designation. Lower Carboniferous; Altai, Russia.

Diagnosis. Branched colonies. Autozoecia diverging at low angles from distinct median axis. Hemisepta absent, diaphragms rare. Autozoecial walls laminated,

with dark zooecial boundaries. Metazoecia few between longitudinally successive autozoecial apertures; acanthostyles common to abundant. Longitudinal ridges absent.

Comparison. *Nikiforovella* Nekhoroshev, 1948 is similar to *Streblotrypella* Nikiforova, 1948, but differs from it mainly in the shape of autozoecia, that bend at higher angles in the exozone, the lack of longitudinal ridges, and in possessing of styles that can be absent in *Streblotrypella*.

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

Nikiforovella multipitata Trizna, 1958
(Figs 8g, 9a-9d; Table 5)

1958 *Nikiforovella multipitata* Trizna; p. 226-228, pl. 62, figs 7-15.

Material. Cal 2b/10, Col/7-8, Col/13-1, AL/1-3.

Table 5. Descriptive statistics of *Nikiforovella multipitata* Trizna, 1958. Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	5	0.10	0.014	14.14	0.08	0.12
Autozoecial aperture spacing along branch, mm	5	0.38	0.023	5.97	0.36	0.41
Metazoecia diameter, mm	15	0.025	0.005	20.38	0.015	0.035
Acanthostyle diameter, mm	15	0.028	0.004	14.41	0.020	0.035

Description. Colonies branched, 0.63-1.05 mm in diameter, with endozones 0.31-0.55 mm and exozones 0.16-0.30 mm wide. Autozoecia tubular, growing in a spiral pattern from a distinct median axis at angles of 23-26° in endozones, abruptly bending in exozones and intersecting colony surface at angles of 72-77° with triangular to rhombic transverse section in the endozone. Autozoecial apertures oval, arranged in regular diagonal rows on branches. Autozoecial diaphragms absent. Autozoecial walls granular, 0.005-0.015 mm thick in endozone; finely laminated, merged, in exozone. Metazoecia originating at the base of the exozone, 5-8 arranged in clusters between longitudinally successive autozoecial apertures. Acanthostyles large with distinct hyaline cores and laminated sheaths, 3-5 arranged between longitudinally successive autozoecial apertures.

Comparison. *Nikiforovella multipitata* Trizna, 1958 differs from *N. ulbensis* Nekhoroshev, 1956 from the

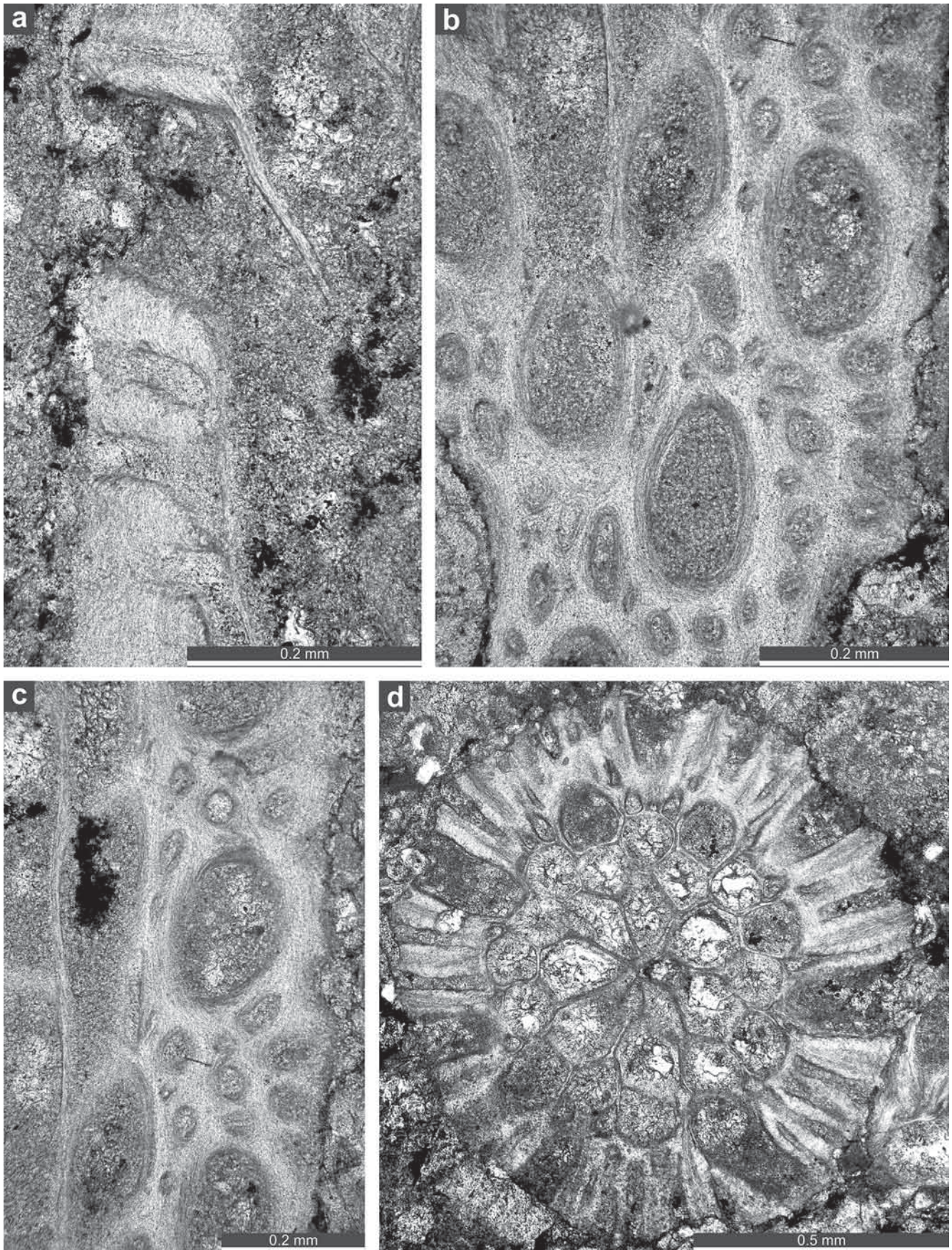


Figure 9. *Nikiforovella multipitata* Trizna, 1958: **a)** Branch longitudinal section, Cal/2b. **b-c)** Tangential section showing autozooeal apertures, metazooea, and acanthostyles, Cal/2b. **d)** Branch transverse section, Cal/2b.

Mississippian of Altai and Northern Russia by having less abundant metazooecia, fewer acanthostyles, and more closely spaced autozoecial apertures along branches (0.36-0.41 mm vs. 0.50-0.60 mm in *N. ulbensis*). *Nikiforovella multipitata* differs from *N. alternata* Nekhoroshev, 1956 from the Mississippian of Altai in having 5-8 metazooecia and 3-5 acanthostyles between longitudinally successive autozoecial apertures, whereas in *N. alternata* 2 metazooecia and 2 acanthostyles occur between apertures.

Stratigraphic and geographic range. Mississippian, Tournaisian-Viséan; Russia, Siberia (Kuznetzk Basin). Mississippian (upper Asbian); El Almendro section, southwestern Spain. Mississippian, Viséan (Asbian-Brigantian); El Collado, southwestern Spain. Mississippian (Brigantian); Caleras Bajas section, southwestern Spain.

4. DISCUSSION

The Lower Carboniferous (Mississippian) bryozoan fauna of southwestern Spain contains eight species: the cystoporates *Fistulipora* sp., *Fistulipora incrustans* (Phillips, 1836), and *Glyptopora michelinia* (Prout, 1860), the trepostomes *Stenophragmidium paramirandum* Ernst *et al.*, 2005, *Stenophragmidium crassimularis* (Lee, 1912), and *Hinaclema hinaensis* Sakagami & Sugimura, 1987, and the cryptostomes *Pseudonematopora planatus* Wyse Jackson, 1996 and *Nikiforovella multipitata* Trizna, 1958.

Carboniferous bryozoans can be important in biostratigraphy (Bancroft, 1987) and are certainly useful in palaeobiogeographic reconstructions (Ross, 1981). Some species described herein, are indicative of the Mississippian in Europe, including *Fistulipora incrustans* (Phillips, 1836) and *Pseudonematopora planatus* Wyse Jackson, 1996, both of which are restricted to the Viséan. *Stenophragmidium crassimularis* (Lee, 1912) also occurs in Viséan deposits of the British Isles, but we found this species in the lower Serpukhovian (Pendleian) of southwestern Spain.

Glyptopora michelinia (Prout, 1860) was originally recorded from the Mississippian (Viséan) of the USA. The genus *Glyptopora* is known primarily from the Mississippian of the USA, with ranges of three species extending into the Pennsylvanian (Bashkirian-Kasimovian). One species, *G. kasakhstanica* Nekhoroshev, 1953, is known from Viséan-Serpukhovian deposits of Kazakhstan.

The genus *Hinaclema* is also indicative of the Viséan, with both known species (*H. hinaensis* and *H. sakagamai*) from the Viséan of Japan and Tajikistan, respectively.

Finally, *Nikiforovella multipitata* Trizna, 1958 is known from the Mississippian (Viséan) of Siberia and *Stenophragmidium paramirandum* Ernst *et al.*, 2005 from the Pennsylvanian (Westphalian A/B) of NW Spain.

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