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RESEARCH PAPER

Palaeoecology and palaeobiogeographic relationships of Lower Devonian bryozoans from the Guadámez and Peñón Cortado Sections of Sierra Morena (SW Spain)

Paleoecología y relaciones paleobiogeográficas de los briozoos del Devónico Inferior de las Secciones Guadámez y Peñón Cortado de Sierra Morena (SO de España)

Andrej ERNST & Sergio RODRÍGUEZ

Abstract: Bryozoan fauna from the Lower Devonian (Pragian–Emsian) deposits of the Ossa-Morena Zone (SW Spain) comprises twenty-eight species: one cyclostome, two cystoporates, sixteen trepostomes, five cryptostomes, and four fenestrates. Three new genera with one new species, respectively, are described: cyclostome *Diploclemella serenensis* n. gen. n. sp., trepostome *Cordobella tenuis* n. gen. n. sp., and cryptostome (rhabdomesine) *Serenella dubia* n. gen. n. sp. Three trepostome species are new: *Leptotrypa parva* n. sp., *L. modesta* n. sp., and *Boardmanella spinigera* n. sp. Ten species are described in open nomenclature. The studied bryozoan fauna shows high morphological and taxonomical diversity, comprising mostly species of moderate size. The assemblage is clearly dominated by branched ramose and encrusting growth forms. The studied bryozoan fauna shows some distinct palaeobiogeographic relations to the bryozoans from the Lower Devonian of NW Spain, Morocco, and Czech Republic.

Resumen: La fauna de briozoos de los depósitos del Devónico Inferior (Pragiense–Emsiense) de la Zona de Ossa-Morena (SO de España), comprende ventiocho especies: un ciclostomado, dos cystoporados, dieciséis trepostomados, cinco cryptostomados y cuatro fenestrados. Se describen respectivamente tres nuevos géneros con sus respectivas especies tipo: el ciclostomado *Diploclemella serenensis* n. gen. n. sp., el trepostomado *Cordobella tenuis* n. gen. n. sp., y el cryptostomado (rhabdomesino) *Serenella dubia* n. gen. n. sp. Tres especies de trepostomados son nuevas: *Leptotrypa parva* n. sp., *L. modesta* n. sp., y *Boardmanella spinigera* n. sp. Diez especies se describen en nomenclatura abierta. La fauna de briozoos muestra una alta diversidad morfológica y taxonómica, comprendiendo principalmente formas de tamaño moderado. La asociación está claramente dominada por formas ramosas e incrustantes. La fauna de briozoos muestra claras relaciones paleogeográficas con los briozoos del Devónico Inferior del norte de España, Marruecos y República Checa.

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INTRODUCTION

Lower to Middle Devonian rocks crop out at the Ossa-Morena Zone (SW Spain), between the Guadiana and Guadalquivir Valleys along 200 km (Fig. 1). The Devonian succession comprises more than 600 m of shales, sandstones, limestones and marls. The limestones show reefal features, but they have limited lateral and vertical development. The most complete successions of these reefal facies are located in five sections, Guadámez-2, Arroyo del Lobo, Zújar, Peñón Cortado and Arroyo del Pozo del Rincón (Rodríguez-García, 1978). Pragian reefal facies occur in most of these localities, being best exposed in the Peñón Cortado section. Emsian reefs are only developed in the Guadámez-2 section. During the field trip in 2007 rich bryozoan assemblages occurring in the reefal and peri-reefal facies were collected. The present paper aims the taxonomic description of the abundant and diverse Lower Devonian bryozoan fauna from the Peñón Cortado and Guadámez-2 sections at the Ossa-Morena Zone.

BACKGROUND

Febrel (1963) first mapped the Devonian outcrops near the Valsequillo village, southern from the Sierra del Pedroso. Herranz (1970) and Llopis-Lladó *et al.* (1970) described the regional stratigraphy of the Sierra del Pedroso and surrounding region, including Precambrian and Palaeozoic rocks. They provided the first description of the Devonian regional stratigraphy. Both papers indicated the presence of reefal facies and abundant fossils and assigned an Emsian age to the limestones. Rodríguez-García (1978) measured logs in several outcrops and described some rugose corals from the Chamorra, Guadámez and Peñón Cortado sections. Rodríguez and Soto (1979) described additional corals from the Arroyo del Pozo del Rincón section. After the new coral identifications, the age of the upper part of this section was regarded as Givetian. Herranz (1984) described the general stratigraphy of the Devonian between Hornachos and Mérida. Moreno-Eiris *et al*. (1995) described some sections for a field trip during the VII Fossil Cnidaria symposium without adding new data. May (1999) described some stromatoporoids collected during that field trip. Liao *et al*. (2003) identified Lochkovian–Pragian conodont assemblages in the lower part of the arroyo del Pozo del Rincón showing the existence of an important discontinuity in the limestone succession at that locality. Valenzuela-Ríos *et al*. (2006a, 2006b) added information on the brachiopods, conodonts, ostracods, fishes and stromatoporoids from the Guadámez-2 and Peñón Cortado sections. May (2004, 2006, 2007) and May and Rodríguez (2011, 2012) described new stromatoporoid and rugose corals assemblages. Pardo-Alonso and Valenzuela (2006) studied the structure and stratigraphy of several Devonian outcrops. Ernst and Rodríguez (2010) described the bryozoan assemblage of the Pajarejos section. Rodríguez *et al*. (2010) described the reefal processes shown in the Guadámez-2 section.

In contrast to the bryozoan faunas of SW Spain, those from the Lower–Middle Devonian of NW Spain were more intensively studied in a series of publications in more than two last decades (Suárez Andrés, 1998, 1999a, 1999b, 1999c, 2014; Suárez Andrés & González Álvarez, 2000; Suárez Andrés & McKinney, 2010; Ernst, 2010, 2011, 2012; Ernst *et al*., 2011, 2012; Ernst & Buttler, 2012; Suárez Andrés & Ernst, 2015; Suárez Andrés *et al*., 2014, 2020, 2021; Suárez Andrés & Wyse Jackson, 2014, 2017, 2018; Sendino *et al*., 2019). These studies show the high diversity and richness of bryozoans in the Lower to Middle Devonian sediments of Spain.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The studied sections provide a view of the Lower Devonian bryozoan assemblages in Sierra Morena, because they have different age and are the best exposed in the region.

Two main sections were studied at the rand of the Guadámez river, near the road from Campillo de Llerena to Higuera de la Serena, at the Badajoz province (Fig. 1) by Rodríguez-García (1978) who named them Guadámez-1 and Guadámez-2. The Guadámez-1 section is exposed in old quarries. The facies are monot-

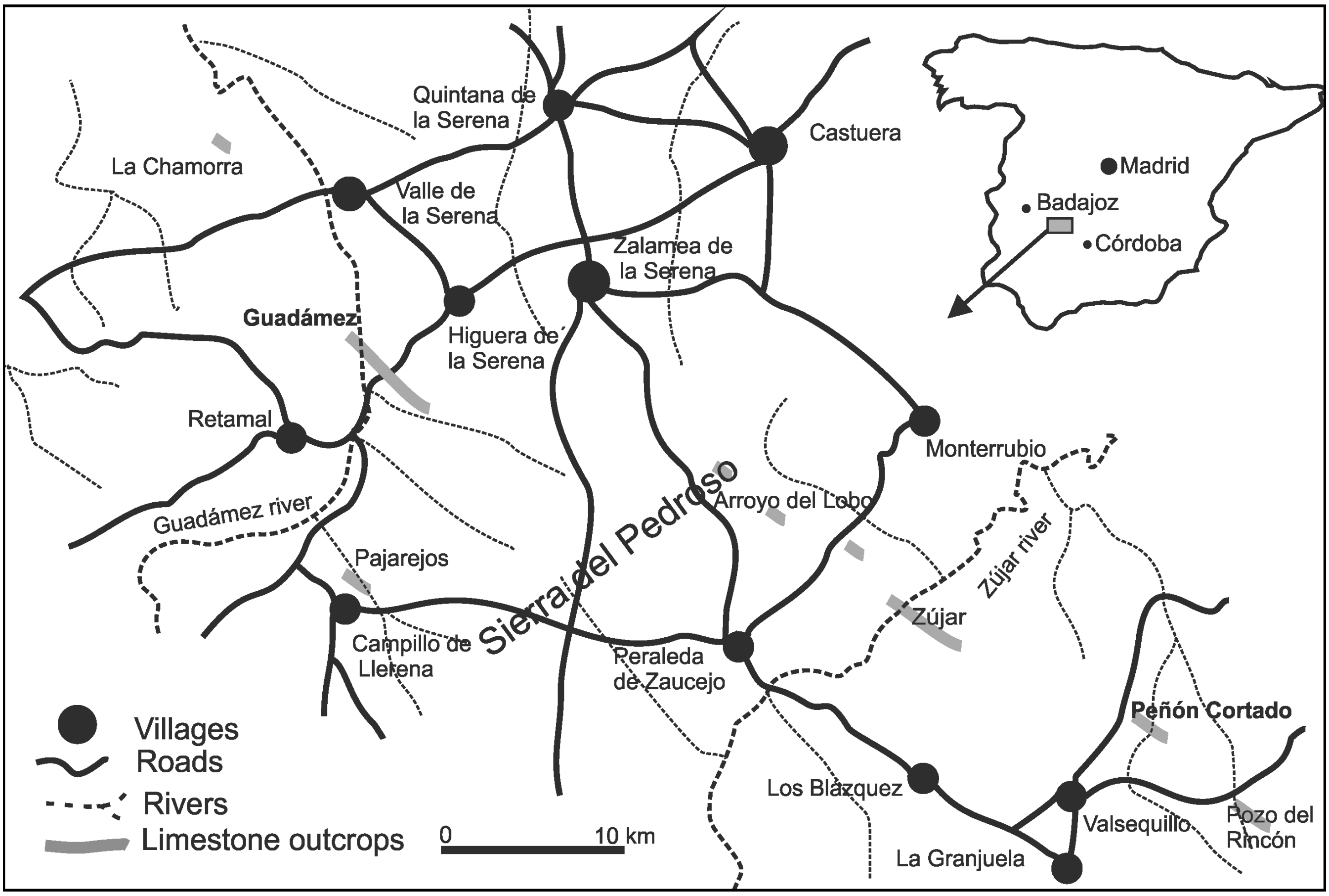


Figure 1. Outcrops of the Lower to Middle Devonian rocks at the Ossa-Morena Zone (SW Spain).

onous, composed of calcareous shales and crinoidal limestones. The Guadámez-2, on the contrary, shows a succession of limestones and marly limestones with a varied palaeontological content that includes corals, brachiopods, bryozoans, crioconarids, stromatoporoids, ostracods, conodonts, etc. (Fig. 2). The upper part of the section (units 15–19) shows bioherms composed mainly of stromatoporoids, tabulate corals and bryozoans (Rodríguez *et al*., 2010). The main facies containing bryozoans are tabulate coral rudstones (Fig. 4A, 4B) and stromatoporoid-tabulate coral boundstones.

The Peñón Cortado section was named by Herranz (1970). It is located 5 km northwest from the Valsequillo village (Fig. 1), at the Angostura valley, along the railway from Córdoba to Almorchón. It begins with alternation of shales and marls containing brachiopods, bryozoans, solitary rugosans and tabulate corals. The middle part of the section (units 12–14) contains massive rugose and tabulate corals, stromatoporoids and bryozoans. The upper part of the section contains ramose rugose and tabulate corals, bryozoans, brachiopods, etc. (Fig. 3). The old section was modified to introduce new units.

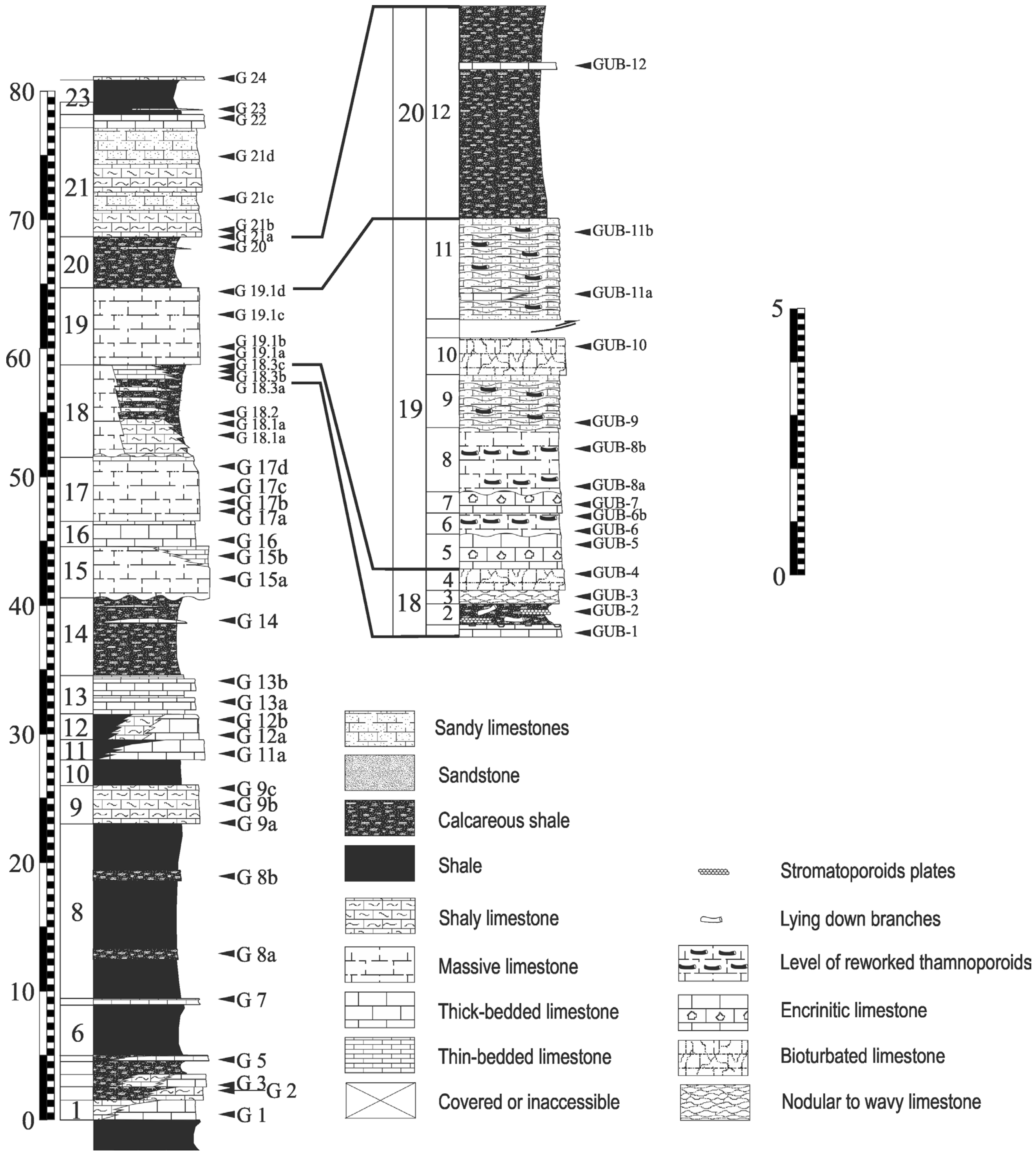


Figure 2. Lithostratigraphic succession at the Guadámez-2 section (modified from Rodríguez-García, 1978).

So, the old units 14b to 17 of Rodríguez-García (1978) were changed to units 15 to 20. The old samples of this part of the section are marked in gray and the new samples are marked in black and a B letter in the Figure 3. A fault above the old bed 17 (new 20) repeats a segment of the section in less calcareous facies. Bryozoans are especially abundant in the crinoid-bryozoan rudstones and packstones at the lower part of the section (Fig. 4C, 4D) and in the marly limestones at the upper part of the section (Fig. 4E, 4F).

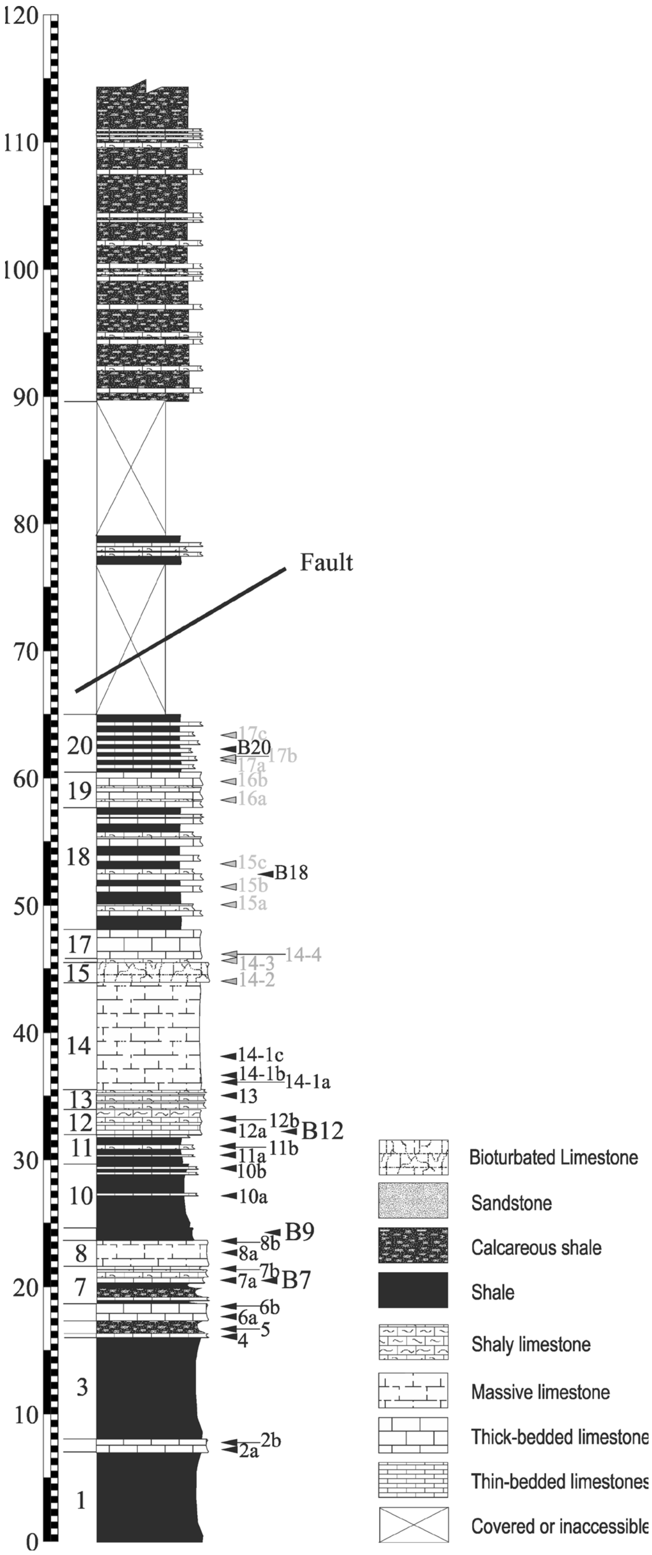


Figure 3. Lithostratigraphic succession at the Peñón Cortado section (modified from Rodríguez-García, 1978).

MATERIALS AND METHODS

The material for the study was collected in autumn 2007 and represents a series of samples taken from the outcrop. From these rock samples, 190 thin sections were made (24x48 mm, 50x50 mm). Studied material is housed at the Senckenberg Museum (Frankfurt am Main, Germany), numbers SMF 40200–SMF 40579.

Morphologic character terminology is partly adopted from Boardman (1960), Anstey and Perry (1970) for trepostomes, from Hageman (1991) for fenestrates, and Hageman (1993) for cryptostomes. The following morphologic characters were measured and used for statistics in the studied material: branch width, branch thickness, exo- (endo-) zone width, axial ratio (ratio of endozone width to the branch width), autozooecial aperture width (non-macular, macular), aperture spacing (non-macular, macular, along branch, diagonally) lunarium width (length, thickness), acanthostyle diameter, number of acanthostyles per aperture, mesozooecia (exilazooecia) diameter, number of mesozooecia (exilazooecia), wall thickness in exozone, vesicle diameter (spacing), number of vesicles per aperture, autozooecial budding angle in endozone (exozone), dissepiment width, fenestrule width (length), distance between branch (dissepiment) centres, apertures per fenestrule length, maximal chamber width, keel node diameter (spacing), thickness of reverse wall granular layer, thickness of reverse wall laminated layer, lateral wall budding angle. For branched bryozoans, the Bryozoan Skeletal Index (**BSI**) has been counted, using the formula ((Exozone Width*Exozonal Wall Width)/Aperture Width)*100 (Wyse Jackson *et al.*, 2020).

The spacing of structures is measured as a distance between their centres. Statistics were summarized using arithmetic mean, sample standard deviation, coefficient of variation, and minimum and maximum values.

SYSTEMATIC PALAEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder PALAEOTUBULIPORINA Brood, 1973
Family DIPLOCLEMIDAE Gorjunova, 1992
Genus *Diploclemella* n. gen.

Type-species. *Diploclemella serenensis* n. sp.

Etymology. The genus name points to the similarity of the new genus to the genus *Diploclema* Ulrich in Miller, 1889.

Diagnosis. Branched, rarely dichotomous colonies, branch transverse sections rounded to oval. Autozooecia budding from the exterior wall, elongated, having

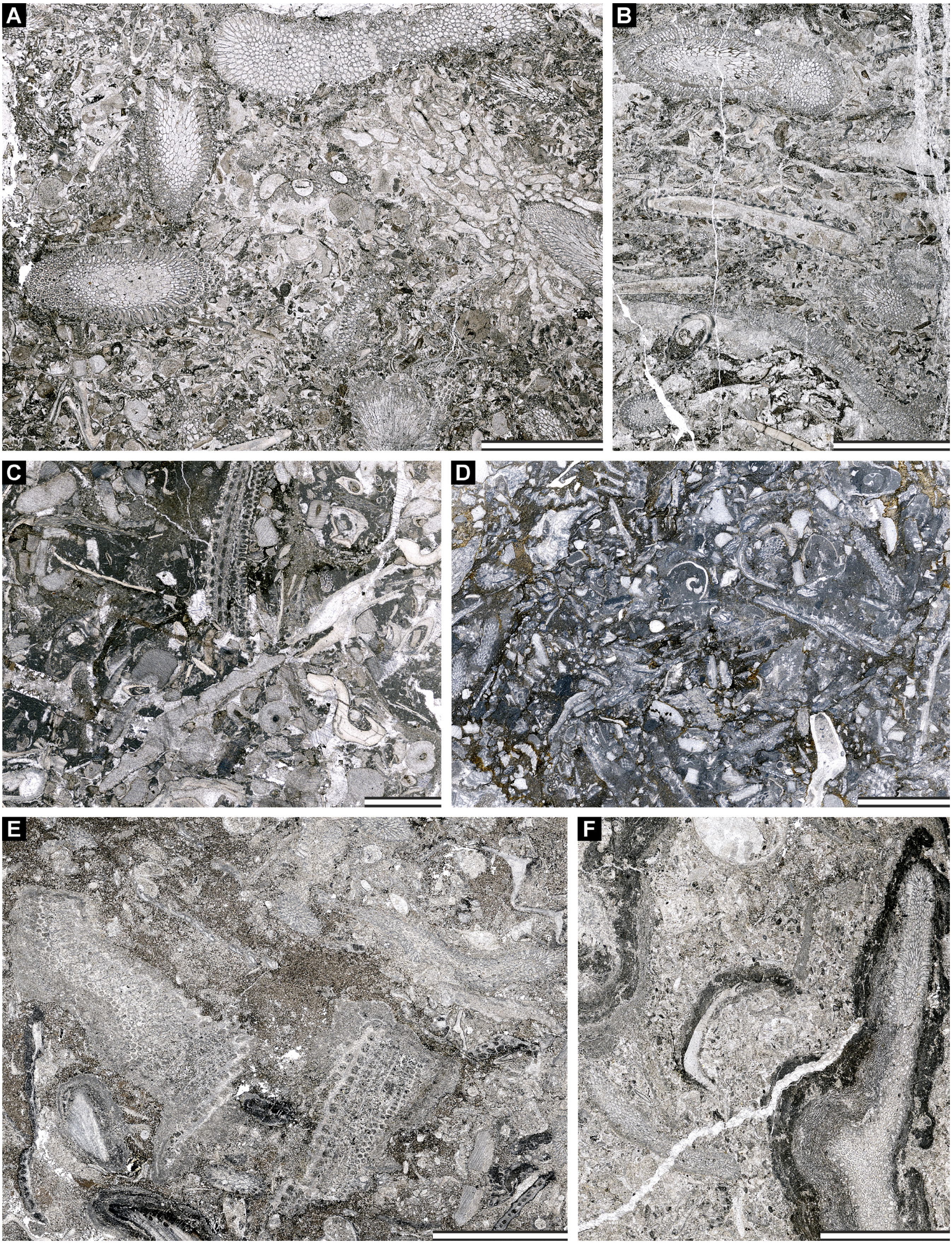


Figure 4. Microfacies of the studied rocks. **A**–**B,** Bryozoan-coral rudstone from Guadámez-2 bioherms, Unit 18, between G18.1 and G18.2, top of 18.1 (A, SMF 40200; B, SMF 40201); **C**–**D,** bryozoan-crinoid rudstone from the Peñón Cortado section (C, top of unit 7, SMF 40202; D, 12.2 m from the base of the profile, SMF 40203); **E**–**F,** bryozoan-rich marly limestone, Peñón Cortado section between beds 17 and 20 (E, SMF 40204; F, SMF 40205); scale bars = 5 mm.

long narrow proximal partitions, subtriangular to subpentagonal in transverse section, growing in tri-, tetra- or pentaradial pattern around branch axis. Interzooecial space in endozone not developed. Autozooecial apertures rounded to oval, peristomes not developed, opening distally on all sides of subcylindrical stems, arranged connately in oblique series on the colony surface. Autozooecial diaphragms absent. Interior skeletal walls thin, finely laminated, indistinctly divided; exterior autozooecial walls thin, indistinctly laminated. Heterozooecia, communication pores and pseudopores absent.

Remarks. *Diploclemella* n. gen. differs from *Diploclema* Ulrich in Miller, 1889 in absence of interzooecial space and arrangement of autozooecia in oblique fascicles.

Occurrence. Lower Devonian (Pragian–Emsian); Sierra Morena, southern Spain.

Diploclemella serenensis n. gen. n. sp.

Figure 5A–5K

Etymology. The new species is named after the region of La Serena, where the type locality is situated.

Holotype. SMF 40206.

Paratypes. SMF 40207–SMF 40238.

Type locality. Peñón Cortado, Ossa-Morena Zone (SW Spain).

Type horizon. Lower Devonian (Pragian).

Other occurrences. Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Diagnosis. As for genus.

Description. Branched colonies, rarely dichotomous, 0.15–0.27 mm in diameter (0.20 mm at average, 33 measurements). Branch transverse sections rounded, oval or rhombic. Autozooecia budding from the exterior wall, elongated, having long narrow proximal partitions, subtriangular to subpentagonal in transverse section, growing in tri-, tetra- or pentaradial pattern around branch axis. Autozooecial apertures rounded to oval, peristomes not developed, opening distally on all sides of subcylindrical stems, arranged connately in oblique series on the colony surface, 0.09–0.11 mm in width. Autozooecial diaphragms absent. Interior skeletal walls 0.010–0.015 mm thick, finally laminated, indistinctly divided. Exterior autozooecial wall ca 0.003 mm thick, indistinctly laminated.

Remarks. As for genus.

Subclass PALAEOSTOMATA Ma *et al.*, 2014
Order CYSTOPORATA Astrova, 1964a
Suborder FISTULIPORINA Astrova, 1964a
Genus *Fistuliporella* Simpson, 1897

Type-species. *Lichenalia constricta* Hall, 1883. Silurian–Devonian; USA.

Diagnosis. Encrusting colonies. Autozooecia tubular, distal and lateral parts commonly made of superimposed vesicle walls. Diaphragms straight to curved. Lunaria in endozone and exozone, of dense hyaline calcite. Autozooecia isolated by vesicular skeleton. Vesicles high blisters in endozones, becoming low blisters in exozones. Vesicle roofs thin, containing small acanthostyles. Monticules elevated with central cluster of vesicles or stereom.

Comparison. *Fistuliporella* Simpson, 1897 differs from *Fistuliporidra* Simpson, 1897 in having autozooecial diaphragms and acanthostyles in vesicles.

Occurrence. Middle Silurian–Middle Devonian; North America, Europe.

Fistuliporella sp.

Figures 5L–5M, 6A–6F; Table 1

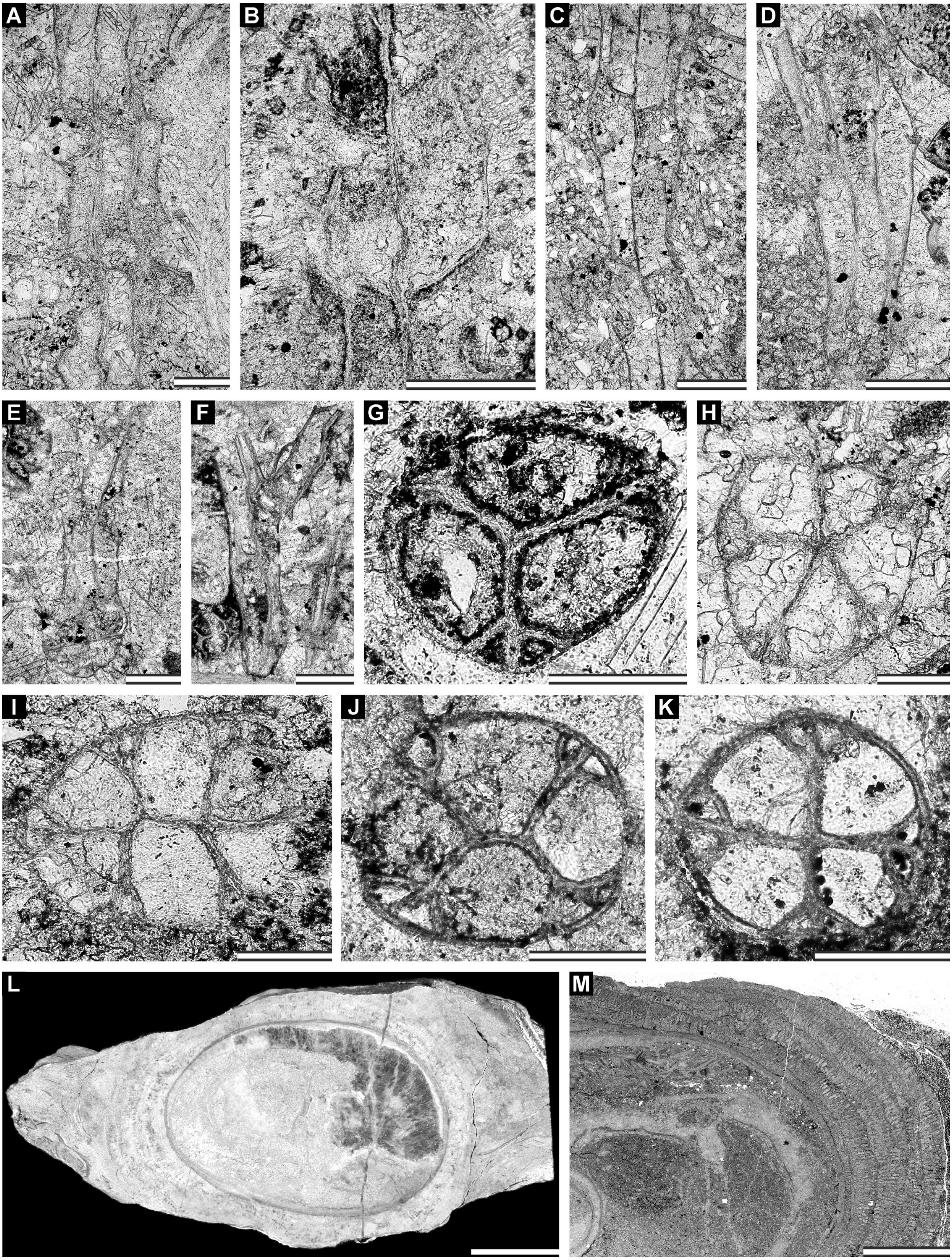
Material. Two colonies with six thin sections SMF 40239–SMF 40243 and SMF 40244.

Description. Colonies encrusting, often multilayered. Multilayered colonies 2.2–4.0 mm in thickness, separate layers 0.55–2.30 mm in thickness. Autozooecia prismatic, budding from the basal epitheca, recumbent in their proximal parts, then bending sharply and intersecting colony surface at right angles. Autozooecial diaphragms common to abundant, thin, straight to inclined, sometimes cystoidal. Autozooecial apertures rounded-polygonal. Lunaria small, horseshoe-shaped to triangular, consisting of hyaline material. Heterozooecia not observed. Vesicles abundant, usually isolating autozooecia, moderately large, polygonal, having thin roofs with single style in the centre (Fig. 6E); styles 0.015–0.030 mm in diameter. Autozooecial walls in the endozone granular, straight, 0.010–0.020 mm thick; in exozone irregularly thickened, showing indistinct granular microstructure, 0.015–0.035 mm thick. Granulated skeletal material on the colony surface weakly developed. Maculae not observed.

Remarks. The present material displays similarities to the genus *Fistuliporella* Simpson, 1897, especially in abundant vesicles with thin roofs and styles, as well

Figure on next page

Figure 5. A–K, *Diploclemella serenensis* n. gen. n. sp.; **A–B,** branch longitudinal section, holotype SMF 40206; **C,** branch longitudinal section, paratype SMF 40210; **D,** branch longitudinal section, paratype SMF 40224; **E,** longitudinal section of dichotomizing branch, paratype SMF 40225; **F,** longitudinal section of dichotomizing branch, paratype SMF 40224; **G,** branch transverse section, paratype SMF 40227; **H,** branch transverse section, holotype SMF 40206; **I,** branch transverse section, paratype SMF 40209; **J–K,** branch transverse section, paratype SMF 40226. **L–M,** *Fistuliporella* sp. **L,** external view of the colony cut in the middle, SMF 40239; **M,** transverse section of the colony, SMF 40242; scale bars = 10 mm (L), 5 mm (M), 0.2 mm (A–F), 0.1 mm (G–K).


A
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as in having abundant diaphragms. *Fistuliporella* sp. differs from *F. hladili* (Ernst & May, 2009) in having smaller autozooecia (average aperture width 0.18 mm *vs* 0.20 mm in *F. hladili*) and smaller distances between aperture centres (average distance 0.24 mm *vs* 0.30 mm in *F. hladili*). The present species differs from *Fistuliporella cumulata* Ulrich & Bassler, 1913 from the Lower Devonian of USA in having larger autozooecia (aperture width 0.15–0.22 mm *vs* 0.13–0.15 mm in *F. cumulata*).

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian). Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 1. Descriptive statistics of *Fistuliporella* sp. (single colony). 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	20	0.18	0.019	10.73	0.15	0.22
Aperture spacing, mm	20	0.24	0.022	9.15	0.20	0.28
Vesicle diameter, mm	20	0.07	0.023	32.44	0.03	0.11
Vesicles per aperture	20	9.4	1.188	12.63	8.0	12.0
Vesicle spacing, mm	20	0.07	0.014	18.92	0.05	0.10

Suborder CERAMOPORINA Astrova, 1964a
Family ANOLOTICHIIDAE Utgaard, 1968
Genus *Altshedata* Morozova, 1959

Type-species. *Fistulipora belgebaschensis* Nekhoroshev, 1948. Middle Devonian (Givetian); Altai, Russia.

Diagnosis. Colonies encrusting or massive. Autozooecia large, living chambers subangular to subrounded in transverse section, budding from the epitheca. Lunaria moderate to large in the inner exozone, large on the colony surface, rounded, deeply indenting autozooecia. Diaphragms few to abundant. Vesicular skeleton present. Heterozooecia absent. Autozooecial walls thick, undulatory, having indistinct granular microstructure. Monticules with large zooecia and more abundant interzooecial space.

Remarks. *Altshedata* Morozova, 1959 differs from *Anolotichia* Ulrich, 1890 in having rounded lunaria indenting autozooecia and vesicular skeleton, from *Crassaluna* Utgaard, 1968 in the shape of the lunaria which are rounded in *Altshedata* but irregular with nodes and ridges in *Crassaluna*.

Occurrence. Type species *Altshedata belgebaschensis* (Nekhoroshev, 1948) was described from the Middle Devonian (Givetian) of Russia. *Altshedata hispanica* Ernst *et al*., 2012 and *A. gracilis* Ernst *et al*., 2012 were described from the Middle Devonian (Emsian) of NW Spain. The latter species is reported in the present paper from the Emsian of southern Spain. *Altshedata parasitica* Yang & Lu, 1983 was reported from the Pennsylvanian of Xinjiang (China), and *A. xiacaiyuanensis* Fan, 1993 from the Permian of Yunnan (China). However, these species may not belong to the genus *Altshedata* Morozova, 1959 because they show significant differences in their internal morphology possessing large and abundant vesicles as well as hemiphragms.

Altshedata gracilis Ernst *et al*., 2012
Figure 6G–6J; Table 2

2012 *Altshedata gracilis* Ernst *et al*., p. 700–704, figs. 6D–6G, 7A–7D.

Material. SMF 40245–SMF 40258.

Description. Encrusting colonies, 1.20–1.35 mm thick. Autozooecia prismatic, budding from the basal epitheca, hemispherical to trapezoidal at their bases, becoming rhombic to hexagonal, recumbent in proximal parts, then bending sharply and intersecting colony surface at right angles. Autozooecial diaphragms common, straight, thin, locally absent. Autozooecial apertures rounded-polygonal. Lunaria well-developed, prominent, rounded, deeply indenting autozooecial cavity, originating from bases of autozooecia, consisting of hyaline material. Macrozooecia few, 0.32–0.35 mm in width. Vesicles rarely present, irregular in shape and size, occurring at the base of exozone. Autozooecial walls in the endozone granular, straight, 0.010–0.015 mm thick; in exozone irregularly thickened, showing indistinct granular microstructure with deep annulations, 0.05–0.09 mm thick. Short style-like projections present in autozooecial walls and in the granular skeleton on the colony surface. Communication pores absent. Maculae absent.

Remarks. *Altshedata gracilis* Ernst *et al*., 2012 differs from *A. hispanica* Ernst *et al*., 2012 in having smaller autozooecia (average autozooecial width 0.24 mm *vs* 0.30 mm in *A. hispanica*), as well as in presence of style-like projections in autozooecial walls.

Occurrence. Lebanza Formation, Lower Devonian (Pragian); Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 2. Descriptive statistics of *Altshedata gracilis* Ernst *et al*., 2012 (four colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	50	0.24	0.032	13.30	0.18	0.30
Aperture spacing, mm	50	0.29	0.042	14.33	0.20	0.40
Lunarium length, mm	30	0.09	0.022	23.70	0.05	0.14
Lunarium width, mm	50	0.09	0.016	18.25	0.06	0.13

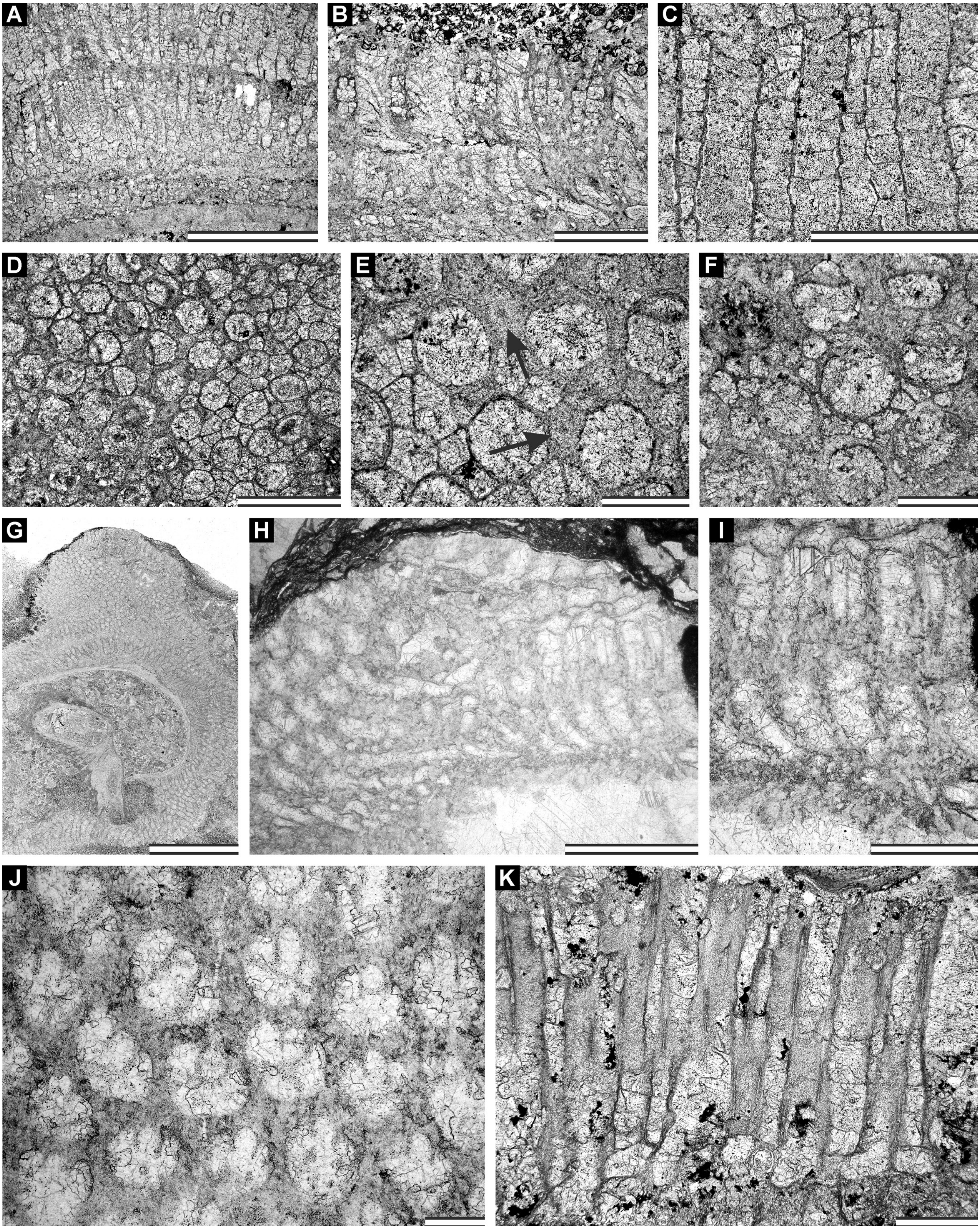

Figure 6. A–**F,** *Fistuliporella* sp.; **A**–**B,** longitudinal section showing autozooecia with diaphragms and vesicles, SMF 40242; **C,** longitudinal section showing autozooecia with diaphragms and vesicles, SMF 40241; **D**–**F,** tangential section showing autozooecial apertures and vesicles (arrows – styles in vesicle roofs), SMF 40243; **G**–**J,** *Altshedata gracilis* Ernst *et al*., 2012; **G,** longitudinal section of the colony, SMF 40255; **H**–**I,** longitudinal section showing autozooecia, SMF 40245; **J,** tangential section showing autozooecial apertures with lunaria, SMF 40245; **K,** *Leioclema arauzensis* Ernst *et al*., 2012; longitudinal section showing autozooecia and mesozooecia, SMF 40260; scale bars = 5 mm (G), 2 mm (A), 1 mm (H), 0.5 mm (B–D, I), 0.2 mm (E–F, J–K).

Order TREPOSTOMATA Ulrich, 1882
Suborder HALLOPORINA Astrova, 1965
Family HETEROTRYPIDAE Ulrich, 1890
Genus *Leioclema* Ulrich, 1882

Type-species. *Callopora punctata* Hall, 1858. Lower Carboniferous; Iowa (USA).

Diagnosis. Encrusting, branched, less commonly massive colonies. Autozooecia with polygonal to rounded-polygonal, sometimes petaloid apertures. Autozooecial diaphragms rare. Mesozooecia abundant, with abundant diaphragms, often beaded. Acanthostyles abundant, commonly large. Autozooecial walls thin in endozone; laminated, regularly thickened in exozones (modified from Astrova, 1978).

Remarks. *Leioclema* Ulrich, 1882 differs from *Heterotrypa* Nicholson, 1879 in having rare autozooecial diaphragms and abundant acanthostyles and mesozooecia, and from *Stigmatella* Ulrich & Bassler, 1904 in having abundant mesozooecia.

Occurrence. Lower Silurian–Upper Carboniferous; worldwide.

Leioclema arauzensis Ernst *et al.*, 2012
Figures 6H, 7A–7B; Table 3

2012 *Leioclema arauzensis* Ernst *et al.*, p. 710–712, fig. 11B–11G.

Material. Two colonies SMF 40259–SMF 40263.

Description. Encrusting colonies, 0.3–1.0 mm in thickness. Autozooecia budding from a thin epitheca, briefly oriented parallel to the substrate, then bending sharply and intersecting the colony surface at right angles. Epitheca 0.005–0.008 mm thick. Autozooecial apertures rounded-polygonal to petaloid due to indenting acanthostyles. Autozooecial diaphragms few to absent, thin, straight or slightly deflected proximally. Mesozooecia abundant, 4–6 surrounding each aperture, polygonal in cross section, slightly beaded, containing planar diaphragms. Acanthostyles moderately large, abundant, 3–5 surrounding each aperture, originating from the base of exozone, often indenting autozooecia, having distinct calcite cores and dark laminated sheaths. Walls granular, in endozone 0.005–0.013 mm thick; in exozone 0.015–0.025 mm thick, distinctly laminated. Maculae not observed.

Comparison. *Leioclema arauzensis* Ernst *et al.*, 2012 is similar to *L. passitabulatum* Duncan, 1939 from the Lower–Middle Devonian of USA and Europe, but differs in having fewer mesozooecia (4–6 *vs* 4–10 mesozooecia around autozooecial aperture in *L. passitabulatum*).

Occurrence. Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains); Lebanza Formation, Lower Devonian (Pragian). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian). Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 3. *Leioclema arauzensis* Ernst *et al.*, 2012 (single colony measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	10	0.14	0.014	10.35	0.12	0.16
Aperture spacing, mm	10	0.19	0.027	14.47	0.16	0.24
Acanthostyle diameter, mm	10	0.04	0.008	21.90	0.03	0.055
Mesozooecia width, mm	10	0.05	0.012	25.52	0.03	0.06

Leioclema cf. *incomposita* Duncan, 1939
Figure 7C–7H; Table 4

1939 Duncan, 1939, p. 250, 251, pl. 15, figs. 4–6.
2012 Ernst & May, p. 68, figs. 5.10, 5.11, 6.1–6.3.

Material. Three colonies SMF 40264–SMF 40270.

Description. Irregular massive (multilayered) colonies with branched outgrowths, 10x15 mm in size. Encrusting sheets 0.5–2.6 mm in thickness. Branched parts 2.9–4.4 mm in diameter, with 0.45–0.72 mm wide exozone and 2.00–3.04 mm wide endozone. Axial ratio is 0.65–0.72. BSI is equal 17.10. In encrusting colonies autozooecia budding from a thin epitheca, initially oriented parallel to the substrate, then bending sharply and intersecting the colony surface at right angles. In branched colonies autozooecia long in endozones bending sharply in exozones. Autozooecial apertures rounded-polygonal to petaloid due to indenting acanthostyles. Autozooecial diaphragms rare to common, thin, straight or slightly deflected proximally. Mesozooecia common, locally abundant, 5–7 surrounding each aperture, polygonal in cross section, slightly beaded, containing abundant planar diaphragms. Acanthostyles small, abundant, 2–4 surrounding each aperture, originating from the base of exozone, often indenting autozooecia, having distinct calcite cores and dark laminated sheaths. Walls granular, 0.003–0.005 mm thick in endozones; distinctly laminated, 0.04–0.08 mm thick in the exozone. Maculae not observed.

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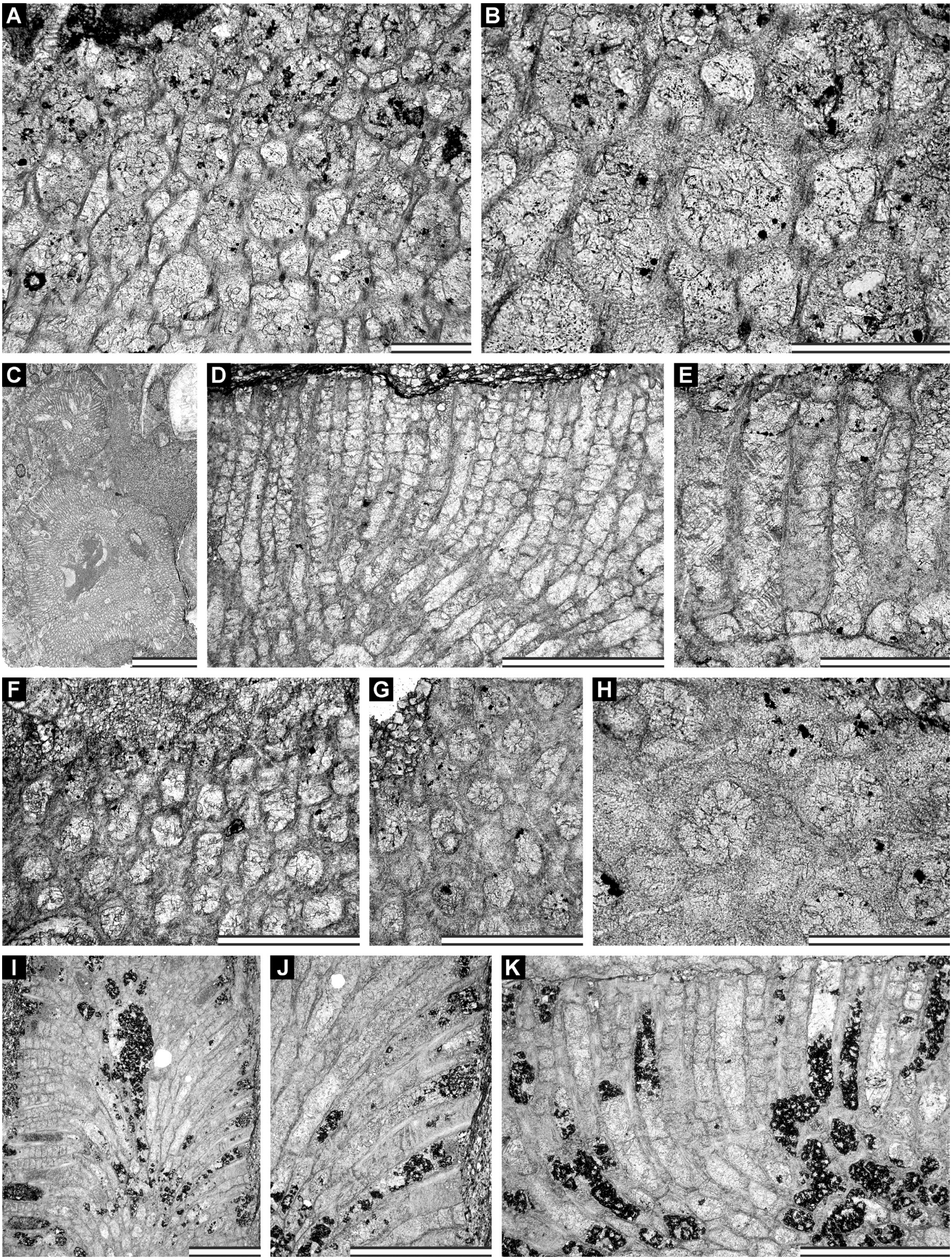
Figure 7. A–B, *Leioclema arauzensis* Ernst *et al.*, 2012; tangential section showing autozooecial apertures, mesozooecia and acanthostyles, SMF 40260. **C–H,** *Leioclema* cf. *incomposita* Duncan, 1939; **C,** longitudinal section of the colony, SMF 40270; **D–E,** longitudinal section showing autozooecia and mesozooecia, SMF 40269; **F,** tangential section showing autozooecial apertures, mesozooecia and acanthostyles, SMF 40270; **G–H,** tangential section showing autozooecia, mesozooecia and acanthostyles, SMF 40268. **I–K,** *Leioclema* sp.; **I–J,** branch longitudinal section showing autozooecia and mesozooecia, SMF 40271; **K,** longitudinal section showing autozooecia and mesozooecia, SMF 40272; scale bars = 5 mm (C), 1 mm (D, I–K), 0.5 mm (E–G), 0.2 mm (A–B, H).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Remarks. The present material is similar to the species identified as *Leioclema incomposita* Duncan, 1939 from the Lower Devonian (middle Lochkovian) of Sierra de Guadarrama, Spain (Ernst & May, 2012) but differs in having smaller autozooecial apertures (average aperture width 0.12 mm *vs* 0.14 mm in the material from Sierra de Guadarrama). The species *Leioclema incomposita* Duncan, 1939 was described from the Middle Devonian of Michigan, USA, and shows similarities to the Spanish material, both from Sierra de Guadarrama and Sierra Morena (present publication).

Leioclema cf. *incomposita* Duncan, 1939 differs from *L. passitabulatum* Duncan, 1939 in less abundant acanthostyles and mesozooecia (2–4 acanthostyles per aperture *vs* 1–5 in *L. passitabulatum*; 5–8 mesozooecia per aperture *vs* 5–9 in *L. passitabulatum*).

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 4. *Leioclema* cf. *incomposita* Duncan, 1939 (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	4	3.65	0.759	20.81	2.90	4.40
Exozone width, mm	4	0.57	0.112	19.63	0.45	0.72
Endozone width, mm	4	2.51	0.573	22.86	2.00	3.04
Axial ratio	4	0.68	0.031	4.46	0.65	0.72
Aperture width, mm	60	0.12	0.013	11.43	0.09	0.15
Aperture spacing, mm	60	0.22	0.034	15.67	0.15	0.32
Acanthostyle diameter, mm	30	0.032	0.007	21.05	0.023	0.045
Mesozooecia width, mm	60	0.07	0.016	21.75	0.03	0.11
Acanthostyles per aperture	17	2.7	0.772	28.52	2.0	4.0
Mesozooecia per aperture	20	6.6	1.050	16.03	5.0	8.0
Mesozooecial diaphragm spacing, mm	45	0.08	0.029	36.53	0.04	0.18
Exozonal wall thickness, mm	10	0.036	0.009	25.19	0.025	0.050

Leioclema sp.

Figures 7I–7K, 8A–8C; Table 5

Material. Four thin sections of a single colony SMF 40271–SMF 40274.

Description. Branched colony, 4.00–4.75 mm in diameter, with 0.72–1.31 mm wide exozone and 1.48–2.96 mm wide endozone. Axial ratio is 0.37–0.62. BSI is equal 43.31. Autozooecial apertures rounded-polygonal to petaloid due to indenting acanthostyles. Autozooecial diaphragms rare to common, thin, straight or slightly deflected proximally. Mesozooecia abundant, 4–5 surrounding each aperture, polygonal in cross section, slightly beaded, containing abundant planar diaphragms. Acanthostyles small, abundant, 3–5 surrounding each aperture, originating from the base of exozone, often indenting autozooecia, having distinct calcite cores and dark laminated sheaths. Walls granular, 0.008–0.013 mm thick in endozones; distinctly laminated, 0.023–0.040 mm thick in the exozone. Maculae not observed.

Remarks. *Leioclema* sp. differs from *Leioclema* cf. *incomposita* Duncan, 1939 in having larger autozooecial apertures (average aperture width 0.15 mm *vs* 0.12 mm in the latter species). The present material differs from *Leioclema multiacanthoporum* (Astrova in Astrova & Yaroshinskaya, 1968) from the Lower Devonian (Emsian) of Russia in less abundant acanthostyles (3–5 per aperture *vs* up to 8 in *L. multiacanthoporum*).

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 5. *Leioclema* sp. (single colony measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	20	0.15	0.031	20.30	0.12	0.22
Aperture spacing, mm	20	0.24	0.030	12.51	0.19	0.29
Acanthostyle diameter, mm	20	0.06	0.010	16.91	0.04	0.08
Mesozooecia width, mm	20	0.08	0.023	28.41	0.04	0.13
Acanthostyles per aperture	10	3.8	0.789	20.76	3.0	5.0
Mesozooecia per aperture	10	4.6	0.516	11.23	4.0	5.0
Mesozooecial diaphragm spacing, mm	20	0.10	0.018	17.30	0.08	0.14

Suborder AMPLEXOPORINA Astrova, 1965
Family ATACTOTOECHIDAE Duncan, 1939
Genus *Atactotoechus* Duncan, 1939

Type-species. *Atactotoechus typicus* Duncan, 1939. Traverse Group (Middle Devonian); Michigan (USA).

Diagnosis. Encrusting, massive and branched colonies. Autozooecia with polygonal to rounded-polygonal apertures. Diaphragms abundant, straight or inclined. Cystiphragms singly or several in cluster. Exilazooecia rare. Acanthostyles absent or present in small numbers in maculae. Autozooecial walls thin in endozone; serrated, irregularly thickened, finely laminated in exozone (modified after Astrova, 1978).

Comparison. *Atactotoechus* Duncan, 1939 differs from *Orbignyella* Ulrich & Bassler, 1904 in having thickened autozooecial walls and absence of acanthostyles.

Occurrence. Lower Silurian–Upper Devonian; worldwide.

Atactotoechus cf. *casey* Duncan, 1939

Figure 8D–8I; Table 6

cf. 1939 *Atactotoechus casey* Duncan, p. 192, pl. 2, figs. 1–3.

Material. Single colony SMF 40275–SMF 40279.

Description. Massive, subramose colony, 8.8–10.6 mm in diameter, produced by several layers. Exozone distinct, 1.00–1.25 mm in width. Autozooecia prismatic, long in endozones, bending sharply in exozones.

Autozooecial apertures polygonal. Autozooecial diaphragms abundant in exozones, straight or inclined; absent to rare in endozones. Cystiphragms common. Exilazooecia absent. Acanthostyles absent. Autozooecial walls locally undulating, granular, 0.005–0.010 mm thick in endozones; serrated in the longitudinal view and merged in the tangential section of the outer exozone, 0.01–0.04 mm thick in exozones. Maculae consisting of macrozooecia, 1.5–1.9 mm in diameter. Macrozooecia 0.24–0.40 mm in width.

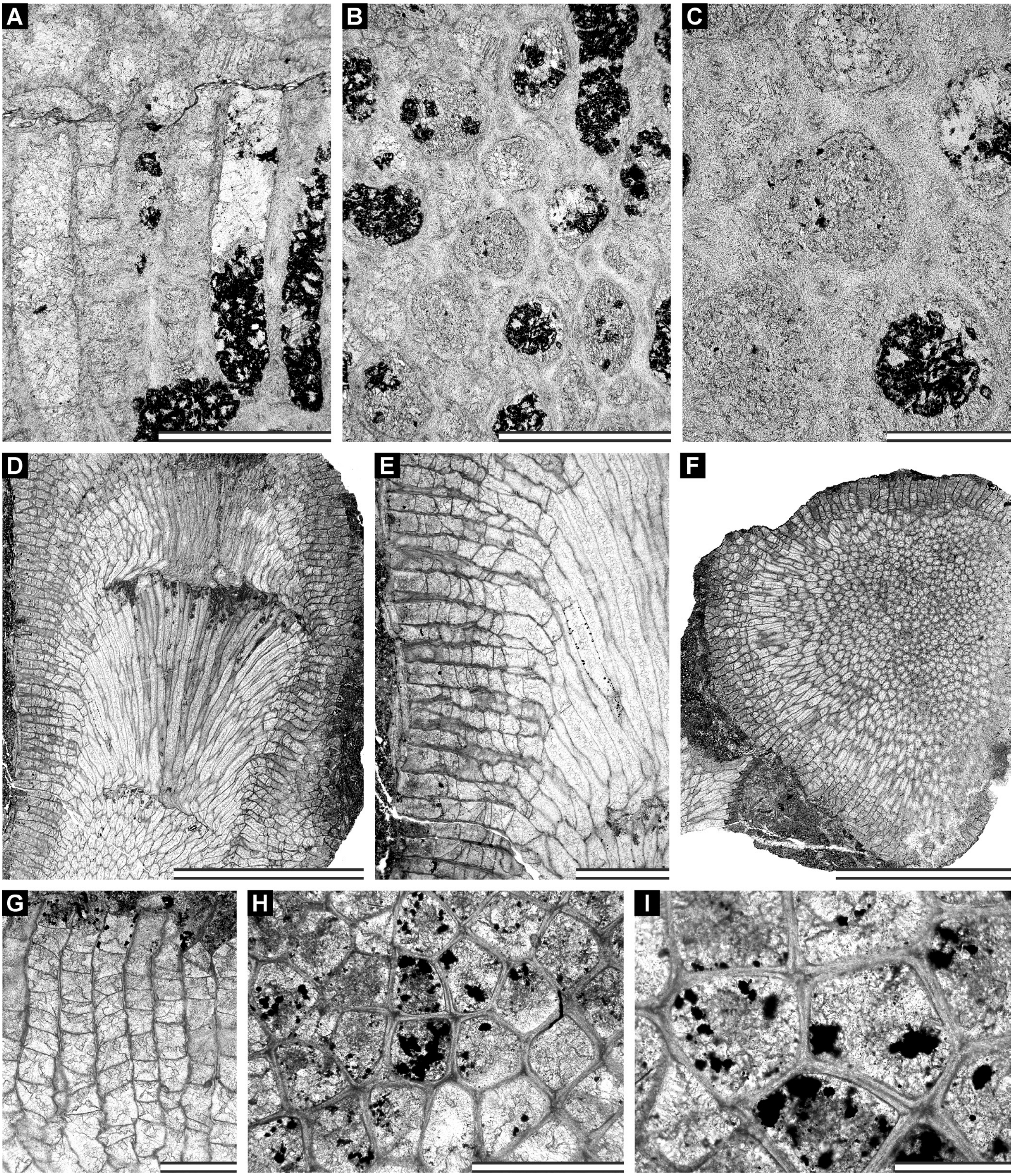

Figure 8. A–**C,** *Leioclema* sp.; **A,** longitudinal section showing autozooecia and mesozooecia, SMF 40272; **B**–**C,** tangential section showing autozooecia, mesozooecia and acanthostyles, SMF 40272; **D**–**I,** *Atactotoechus* cf. *casey* Duncan, 1939; **D**–**E**, longitudinal section, SMF 40276; **F,** transverse section, SMF 40279; **G,** longitudinal section, SMF 40277; **H**–**I,** tangential section, SMF 40275; scale bars = 5 mm (D, F), 1 mm (E), 0.5 mm (A–B, G–H), 0.2 mm (C, I).

Remarks. The present material is similar to *Atactotoechus casey* Duncan, 1939 from the Middle Devonian (Givetian) of USA. Boardman (1960, p. 75) mentioned maculae with acanthostyles which are absent in the present material. The present material differs from *A. inconditus* Bigey, 1986 from the Lower Devonian (Lochkovian) of France in absence of acanthostyles and slightly smaller autozooecial apertures (aperture

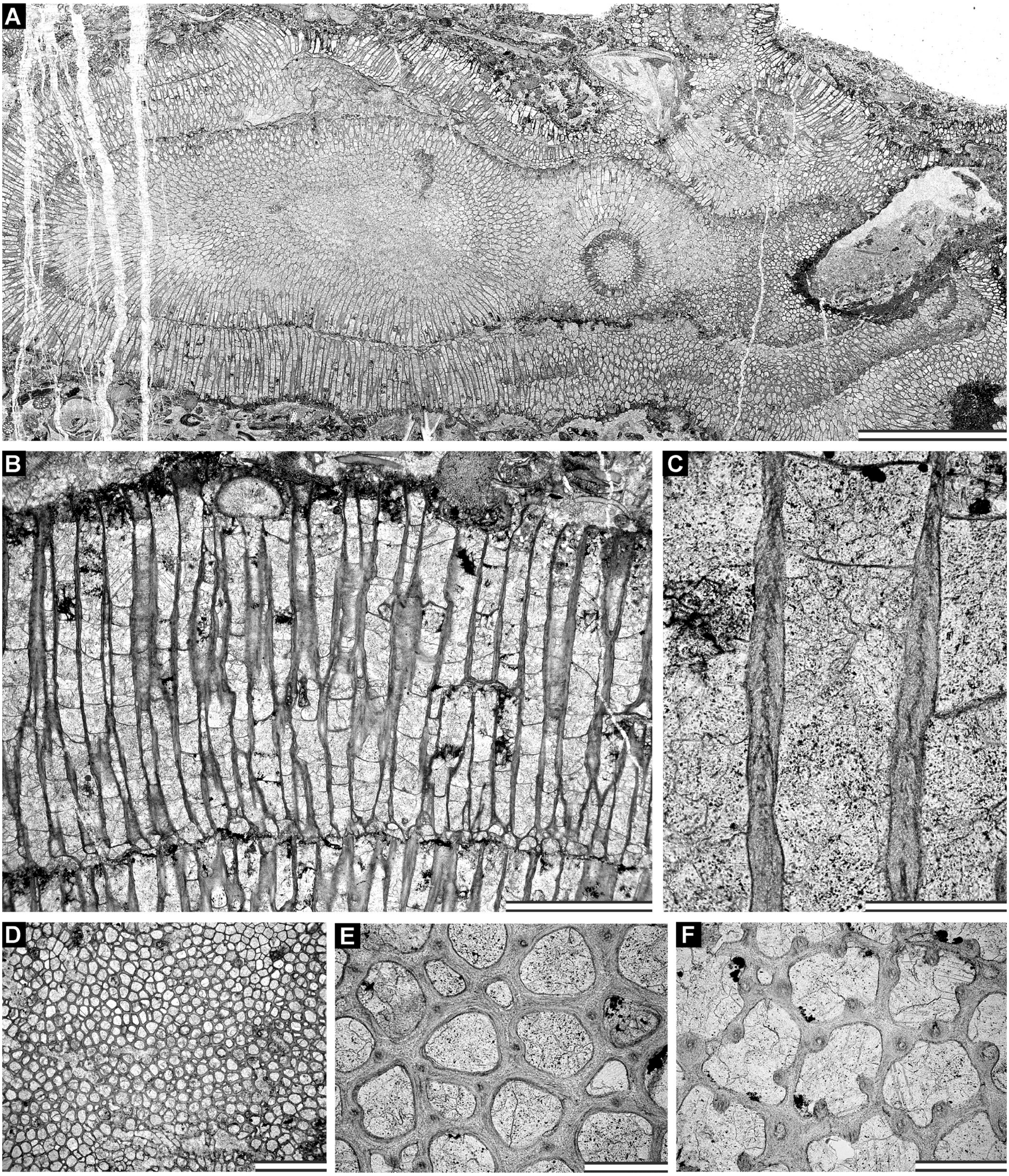

Figure 9. *Anomalotoechus* sp. **A,** Longitudinal section of the colony, SMF 40283; **B**–**C,** longitudinal section of the colony showing autozooecia with diaphragms, SMF 40283; **D**–**E,** tangential section showing autozooecial apertures, exilazooecia and acanthostyles, SMF 40284; **F,** tangential section showing autozooecial apertures, exilazooecia and acanthostyles, SMF 40283; scale bars = 5 mm (A), 1 mm (B, D), 0.2 mm (C, E–F).

width 0.14–0.21 mm *vs* 0.18–0.23 mm in *A. inconditus*). Moreover, *A. inconditus* Bigey, 1986 has strongly thickened autozooecial walls in exozone producing regular annulations.

Atactotoechus cf. *casey* Duncan, 1939 differs from *A. parallelus* Boardman, 1960 from the Middle Devonian (Givetian) of USA in massive (subramose) colony *vs* ramose one in the latter species, as well as in smaller autozooecial apertures (aperture width 0.14–0.21 mm *vs* 0.26–0.29 mm in *A. parallelus*).

Occurrence. Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Genus *Anomalotoechus* Duncan, 1939
[= *Stereotoechus* Duncan, 1939]

Type-species. *Anomalotoechus typicus* Duncan, 1939. Traverse Group (Middle Devonian); Michigan (USA).

Diagnosis. Encrusting, massive, less commonly branched colonies. Autozooecia with polygonal to rounded-polygonal apertures. Diaphragms abundant in exozones, straight or inclined. Exilazooecia rare, short. Acanthostyles abundant. Autozooecial walls thin in the endozone; merged, without visible zooecial boundaries, strongly and irregularly thickened in the exozone, often with monilae-shaped thickenings.

Remarks. *Anomalotoechus* Duncan, 1939 differs from *Leptotrypa* Ulrich, 1883 in having massive and branched colonies, thickened walls and abundant diaphragms, and from *Atactotoechus* Duncan, 1939 in having abundant acanthostyles.

Occurrence. Upper Silurian–Upper Devonian; North America, Eurasia.

Table 6. *Atactotoechus* cf. *casey* Duncan, 1939 (single colony measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.19	0.018	9.53	0.14	0.21
Aperture spacing, mm	25	0.23	0.029	12.55	0.18	0.30
Macrozooecia width, mm	10	0.29	0.055	18.92	0.24	0.40
Diaphragm spacing, mm	25	0.15	0.045	29.42	0.07	0.25

Anomalotoechus sp.
Figure 9A–9F; Table 7

Material. SMF 40280–SMF 40290.

Description. Encrusting multilayered and branched colonies. Branched colonies 2.95–8.82 mm in diameter, with 0.48–3.16 mm wide exozones and 1.50–3.40 wide endozones. Axial ratio is 0.28–0.67. BSI is equal 54.08. Encrusting multilayered colonies up to 3 mm in thickness, separate sheets 0.4–1.0 mm in thickness. Epitheca 0.008–0.015 mm in thickness. Autozooecia prismatic, long in endozones, bending sharply in exozones. Autozooecial apertures polygonal. Autozooecial diaphragms absent to rare in endozones; abundant in exozones, straight or inclined, locally absent. Exilazooecia few to abundant, 2–6 surrounding each autozooecial aperture. Acanthostyles common to abundant, 2–7 surrounding each autozooecial aperture, often indenting autozooecial apertures. Autozooecial walls straight, granular, 0.005–0.010 mm thick in endozones; serrated, 0.02–0.05 mm thick in exozones. Maculae consisting of macrozooecia and macrostyles, slightly elevated, 1.25–1.50 mm in diameter, spaced 2.0–2.4 mm from centre to centre.

Remarks. The present material differs from *Anomalotoechus typicus* Duncan, 1939 from the Middle Devonian (Givetian) of USA in having smaller autozooecia (autozooecial width 0.11–0.16 mm *vs* 0.15–0.20 mm in *A. typicus*), and in having more abundant acanthostyles which indent autozooecial apertures. The present material differs from *A. quasitypicus* Ernst, 2008a from the Middle Devonian (Eifelian) of Germany in having smaller autozooecia (average autozooecial width 0.13 mm *vs* 0.22 mm in *A. quasitypicus*) as well as in having more acanthostyles per aperture (at average 4.7 *vs* 2.5 in *A. quasitypicus*).

Occurrence. Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 7. *Anomalotoechus* sp. (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	5	6.18	2.436	39.42	2.95	8.82
Exozone width, mm	5	1.90	0.993	52.33	0.48	3.16
Endozone width, mm	5	2.38	0.708	29.69	1.50	3.40
Axial ratio	5	0.42	0.152	36.24	0.28	0.67
Aperture width, mm	45	0.13	0.014	10.50	0.11	0.16
Aperture spacing, mm	60	0.19	0.027	14.22	0.14	0.30
Acanthostyle diameter, mm	60	0.039	0.008	19.67	0.025	0.060
Acanthostyles per aperture	55	4.7	1.169	24.91	2.0	7.0
Exilazooecia width, mm	40	0.048	0.017	35.43	0.020	0.085
Exilazooecia per aperture	15	3.8	1.265	33.29	2.0	6.0
Exozonal wall thickness, mm	30	0.037	0.008	22.78	0.020	0.055
Macroacanthostyles diameter, mm	20	0.10	0.031	29.33	0.06	0.18
Macrozooecia width, mm	25	0.17	0.021	12.26	0.15	0.23

Genus *Leptotrypa* Ulrich, 1883
[= *Calacanthopora* Duncan, 1939]

Type-species. *Leptotrypa minima* Ulrich, 1883. Cincinnatian (Upper Ordovician); North America.

Diagnosis. Thin encrusting colonies. Autozooecia with polygonal apertures. Autozooecial walls irregularly thickened, throughout the colony or near the periphery, indistinctly laminated, usually integrated in initial parts and merged near the colony surface. Autozooecial diaphragms absent or rare. Exilazooecia rare. Acanthostyles small to moderately large, common to abundant.

Remarks. *Leptotrypa* Ulrich, 1883 differs from *Anomalotoechus* Duncan, 1939 in having thin encrusting colony and rare diaphragms.

Occurrence. Middle Ordovician–Middle Carboniferous; worldwide.

Leptotrypa parva n. sp.
Figure 10A–10D; Table 8

Etymology. The new species name refers to its small dimensions (from Latin "parva" – small).

Holotype. SMF 40292.

Paratypes. SMF 40291, SMF 40293–SMF 40296.

Type locality. Guadámez-2, Ossa-Morena Zone (SW Spain).

Type horizon. Lower Devonian (Emsian).

Diagnosis. Thin encrusting colonies; autozooecial diaphragms rare; exilazooecia few; acanthostyles small, 1–3 surrounding each autozooecial aperture, locally absent; maculae not observed.

Description. Encrusting colonies, 0.18–0.32 mm thick, often encrusting cylindrical ephemeral objects. Autozooecia budding from a thin epitheca, growing a short distance parallel to the substrate, then bending sharply to the colony surface. Autozooecial apertures polygonal. Autozooecial diaphragms rare, straight, thin. Acanthostyles small, common, 1–3 surrounding each autozooecial aperture, locally absent. Exilazooecia few, 0.06–0.08 mm in diameter. Autozooecial walls laminated, 0.015–0.020 mm thick in the endozone and 0.015–0.050 mm thick in the exozone. Maculae not observed.

Remarks. *Leptotrypa parva* n. sp. differs from *L. angustocrustata* Astrova, 1964b from the Lower Devonian (Lochkovian) of Ukraine in having smaller autozooecial apertures (aperture width 0.09–0.18 mm *vs*. 0.18–0.21 mm in *L. angustocrustata*) and in having less abundant acanthostyles (1–3 *vs* 4–6 per autozooecial aperture in *L. angustocrustata*). *Leptotrypa parva* differs from *L. simplex* Lavrentjeva, 2001 from the Middle Devonian (Eifelian) of Transcaucasia (Armenia) in smaller autozooecial apertures (aperture width 0.09–0.18 mm *vs* 0.17–0.20 mm in *L. simplex*). The species name *L. simplex* Lavrentjeva, 2001 represents a homonym because the species *L. simplex* was described by Liu (1980).

Table 8. *Leptotrypa parva* n. sp. (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	28	0.14	0.023	16.18	0.09	0.18
Aperture spacing, mm	23	0.17	0.022	13.09	0.13	0.22
Acanthostyle diameter, mm	9	0.034	0.008	23.46	0.020	0.045
Exozonal wall thickness, mm	9	0.031	0.011	35.14	0.015	0.050

Leptotrypa modesta n. sp.
Figure 10E–10H; Table 9

Etymology. The new species name refers to its simple morphology (from Latin "modesta" – plain, modest).

Holotype. SMF 40301.

Paratypes. SMF 40297–SMF 40300.

Type locality. Peñón Cortado, Ossa-Morena Zone (SW Spain).

Type horizon. Lower Devonian (Pragian).

Diagnosis. Thin encrusting colonies; autozooecial diaphragms rare; exilazooecia absent; acanthostyles small, 1–5 surrounding each autozooecial aperture, locally absent; maculae not observed.

Description. Encrusting colonies, often multilayered, 0.60–0.98 mm thick. Autozooecia budding from a thin epitheca, growing a short distance parallel to the substrate, then bending sharply to the colony surface. Autozooecial apertures polygonal. Autozooecial diaphragms rare, straight, thin. Acanthostyles small, common, 1–5 surrounding each autozooecial aperture, locally absent. Exilazooecia absent. Autozooecial walls laminated, 0.005–0.008 mm thick in the endozone and 0.025–0.050 mm thick in the exozone. Maculae not observed.

Remarks. *Leptotrypa modesta* n. sp. is similar to *L. circumtexta* Prantl, 1933 from the Lower Devonian (Pragian) of the Czech Republic. The latter species has not been illustrated. Its aperture width (0.1–0.3 mm) is slightly smaller than in the present species (0.14–0.42 mm). *Leptotrypa modesta* n. sp. differs from *L. parva* described above, in having larger autozooecial apertures (average aperture width 0.26 mm *vs* 0.14 mm in *L. parva*).

Table 9. *Leptotrypa modesta* n. sp. (two colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.26	0.072	27.53	0.14	0.42
Aperture spacing, mm	29	0.29	0.065	22.49	0.19	0.40
Acanthostyle diameter, mm	5	0.040	0.004	8.84	0.035	0.045

Genus *Leptotrypella* Vinassa de Regny, 1921

Type-species. *Chaetetes barrandei* Nicholson, 1874. Middle Devonian; Ontario (Canada).

Diagnosis. Branched colonies. Autozooecia with polygonal to rounded-polygonal apertures. Autozooecial diaphragms lacking in endozones; rare to common in exozones. Exilazooecia rare. Acanthostyles long, common to abundant. Autozooecial walls granular, thin in endozones; laminated, irregularly thickened in exozones (modified after Astrova, 1978).

Remarks. *Leptotrypella* Vinassa de Regny, 1921 differs from *Leptotrypa* Ulrich, 1883 in having branched colonies, and from *Anomalotoechus* Duncan, 1939 in having branched colonies and lacking diaphragms in endozones.

Occurrence. Middle Silurian–Lower Carboniferous; worldwide.

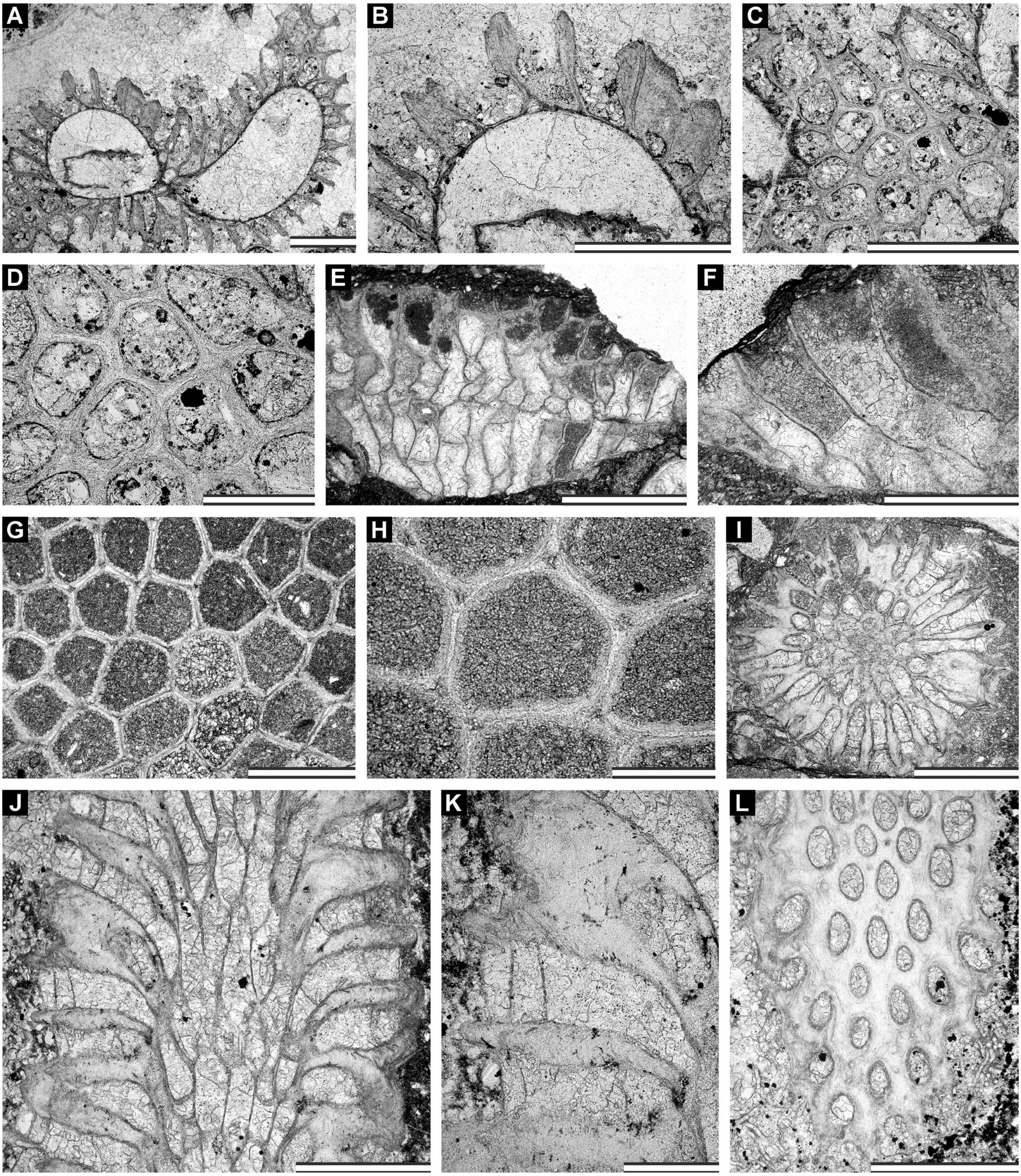

Figure 10. A–**D,** *Leptotrypa parva* n. sp., holotype SMF 4029; **A**–**B,** transverse section of a tubular colony; **C**–**D,** tangential section showing autozooecial apertures and acanthostyles; **E**–**H,** *Leptotrypa modesta* n. sp., holotype SMF 40301; **E**–**F**, longitudinal section of the colony; **G**–**H,** tangential section showing apertures and acanthostyles; **I**–**L,** *Leptotrypella armata* Ernst *et al*., 2012; **I,** branch transverse section, SMF 40309; **J**–**K,** longitudinal section, SMF 40317; **L,** tangential section, SMF 40318; scale bars = 1 mm (E), 0.5 mm (A–C, F–G, I–J, L), 0.2 mm (D, H, K).

Leptotrypella armata Ernst *et al.*, 2012

Figures 10I–10L; Table 10

2012 *Leptotrypella armata* Ernst *et al.*, p. 714–716, figs. 13D, 13E, 14A–14F.

Material. SMF 40302–SMF 40324.

Description. Branched colonies 0.82–1.63 mm in diameter with 0.17–0.35 mm wide exozones and 0.42–1.05 mm wide endozones. Axial ratio is 0.36–0.64. BSI is equal 21.27. Autozooecia long, having a polygonal shape in transverse section in endozones, bending sharply in exozones. Autozooecial apertures oval to slightly polygonal. Autozooecial diaphragms absent in endozones; common to abundant, thin, straight in exozones. Exilazooecia generally few, short, restricted to exozones, rounded to oval in cross section. Acanthostyles moderately large, varying in size, abundant, 7–10 surrounding each autozooecial aperture, growing from the base of the exozone, having distinct cores and laminated sheaths. Autozooecial walls in endozones granular, 0.010–0.015 mm thick; in exozones laminated, merged, without distinct zooecial boundaries, 0.040–0.088 mm thick. Mural spines abundant, 0.005–0.015 mm in diameter. Maculae not observed.

Remarks. *Leptotrypella armata* Ernst *et al.*, 2012 differs from *L. elliptica* Kopajevich, 1984 from the Middle–Upper Devonian of Mongolia, in having thinner branches (branch width 0.82–1.63 mm *vs* 2.0–2.2 mm in *L. elliptica*), smaller apertures (aperture width 0.07–0.12 mm *vs* 0.07–0.13 mm in *L. elliptica*) as well as in having more abundant acanthostyles per autozooecial aperture (7–10 *vs* 1–4 in *L. elliptica*).

Occurrence. Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains); Lebanza Formation, Lower Devonian (Pragian). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 10. *Leptotrypella armata* Ernst *et al.*, 2012 (eight colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	15	1.21	0.294	24.34	0.8	1.63
Exozone width, mm	15	0.29	0.068	23.67	0.17	0.4
Endozone width, mm	15	0.63	0.205	32.45	0.36	1.05
Axial ratio	15	0.52	0.076	14.64	0.36	0.64
Aperture width, mm	35	0.09	0.013	14.08	0.07	0.12
Aperture spacing, mm	30	0.18	0.031	17.77	0.11	0.25
Acanthostyle diameter, mm	10	0.03	0.003	10.93	0.03	0.04
Acanthostyles per aperture	10	7.7	0.949	12.32	7.0	10.0
Exozonal wall thickness, mm	20	0.066	0.015	22.09	0.040	0.088

Leptotrypella sp. 1

Figure 11A–11D; Table 11

Material. Single colony, two serial thin sections SMF 40325–SMF 40326.

Description. Branched colony 2.8 mm in diameter, with 0.9 mm wide exozone and 1 mm wide endozone. Axial ratio is 0.36. BSI is equal 25.71. Autozooecia long, having a polygonal shape in transverse section in endozone, bending sharply in exozone. Autozooecial apertures polygonal. Autozooecial diaphragms absent in endozone; rare, thin, straight in exozone. Exilazooecia few, short, restricted to exozones, rounded to oval in cross section. Acanthostyles moderately large, varying in size, abundant, 2–6 surrounding each autozooecial aperture, growing from the base of the exozone, having distinct cores and laminated sheaths. Autozooecial walls in endozones granular, 0.005–0.008 mm thick; in exozones laminated, merged, without distinct zooecial boundaries, 0.03–0.05 mm thick. Mural spines abundant in the transition between endo- and exozone. Maculae not observed.

Remarks. *Leptotrypella* sp. 1 differs from *L. multitecta* Boardman, 1960 from the Middle Devonian of New York, USA in having smaller autozooecial apertures (average aperture width 0.14 mm *vs* 0.20 mm in *L. multitecta*) and fewer autozooecial diaphragms. The present material differs from *Leptotrypella amplectens* (Grabau, 1899) from the Middle Devonian of USA in in having smaller autozooecial apertures (average aperture width 0.14 mm *vs* 0.26 mm in *L. amplectens*).

Occurrence. Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 11. *Leptotrypella* sp. 1 (single colony measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.14	0.020	13.79	0.11	0.19
Aperture spacing, mm	25	0.21	0.030	14.40	0.15	0.28
Acanthostyle diameter, mm	25	0.05	0.010	19.37	0.03	0.07
Acanthostyles per aperture	20	4.1	1.099	27.14	2.0	6.0
Exilazooecia width, mm	25	0.052	0.018	34.64	0.025	0.100
Exozonal wall thickness, mm	10	0.04	0.007	18.38	0.03	0.05

Leptotrypella sp. 2

Figures 11E–11G, 12A; Table 12

Material. Two colonies, three thin sections SMF 40327–SMF 40329.

Description. Branched colonies, 1.75–2.00 mm in diameter, with 0.38–0.60 mm wide exozones and 0.99–1.40 mm wide endozone. Axial ratio is 0.57–0.70. BSI is equal 13.65. Autozooecia long, having a polygonal shape in transverse section in endozone, bending sharply in exozone. Autozooecial apertures polygonal. Autozooecial diaphragms absent in endozone; rare, thin, straight in exozone. Exilazooecia few, short, restricted to exozones, rounded to oval in cross section. Acanthostyles moderately large, varying in size, abundant, 3–6 surrounding each autozooecial aperture, growing from the base of the exozone, having

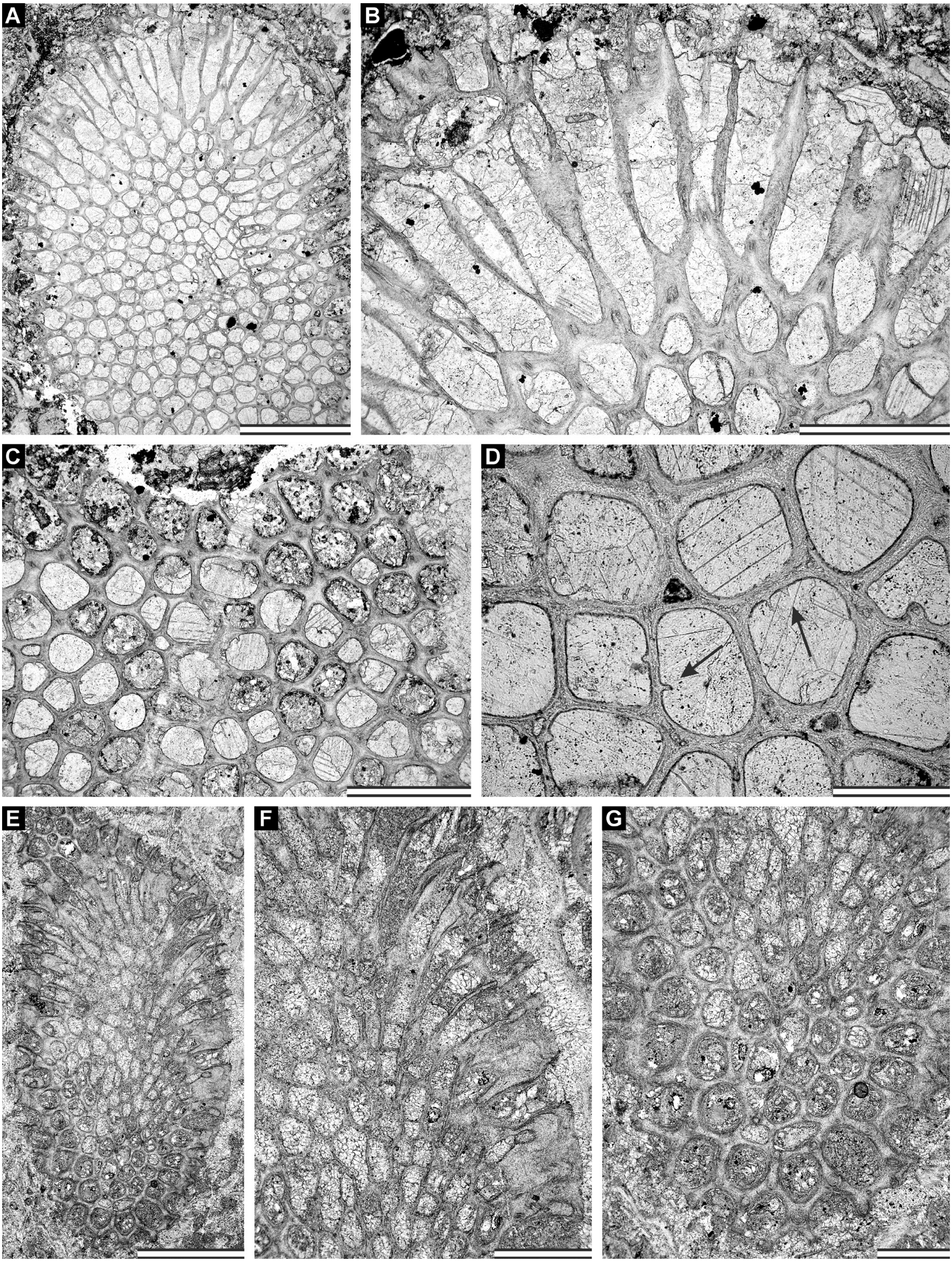

Figure 11. A–**D,** *Leptotrypella* sp. 1, SMF 40325; **A**–**B,** branch longitudinal section; **C**–**D,** tangential section showing autozooecial apertures and acanthostyles (arrows – mural spines). **E**–**G,** *Leptotrypella* sp. 2, SMF 40327; **E**–**F,** longitudinal section; **G,** tangential section showing autozooecial apertures and acanthostyles; scale bars = 1 mm (A, E), 0.5 mm (B–C, F), 0.2 mm (D, G).

distinct cores and laminated sheaths. Smaller styles (0.015–0.033 mm in diameter) occasionally occurring between larger ones. Autozooecial walls in endozones granular, 0.005–0.015 mm thick; in exozones laminated, merged, without distinct zooecial boundaries, 0.030–0.055 mm thick. Mural spines absent. Maculae not observed.

Remarks. *Leptotrypella* sp. 2 differs from *L. furcata* (Hall, 1876) from the Middle Devonian of New York, USA, in having smaller autozooecial apertures (average aperture width 0.14 mm *vs* 0.17 mm in *L. furcata*) and fewer autozooecial diaphragms.

Occurrence. Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 12. *Leptotrypella* sp. 2 (two colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	26	0.14	0.020	13.67	0.11	0.18
Aperture spacing, mm	26	0.21	0.024	11.87	0.16	0.25
Acanthostyle diameter, mm	19	0.05	0.010	18.46	0.04	0.075
Acanthostyles per aperture	18	4.8	0.808	16.92	3.0	6.0
Exozonal wall thickness, mm	8	0.039	0.009	22.51	0.030	0.055

Leptotrypella sp. 3
Figure 12B–12F; Table 13

Material. SMF 40330–SMF 40338.

Description. Ramose branched colonies, branches 2.70–4.25 mm in diameter, with 0.37–1.26 mm wide exozones and 1.13–1.73 mm wide endozones. Exozones distinctly separated from endozones. Axial ratio is 0.33–0.69. BSI is equal 55.27. Secondary overgrowths occurring, 0.52–0.60 mm in thickness. Autozooecia polygonal in transverse section, long in endozones, bending sharply in exozones. Autozooecial apertures rounded-polygonal in exozones. Autozooecial diaphragms absent to rare, straight, thin, occurring mainly in the outermost exozone. Exilazooecia rare to common, restricted to exozone, rounded-polygonal in transverse section. Acanthostyles abundant, 3–6 surrounding each autozooecial aperture, varying strongly in diameter, having distinct narrow cores and laminated sheaths. Autozooecial walls in endozones granular, 0.005–0.008 mm thick; in exozones finely laminated, merged, 0.04–0.13 mm thick. Maculae consisting of acanthostyles locally developed, 0.40 mm in diameter.

Remarks. *Leptotrypella* sp. 3 differs from *L. magninodosa* Duncan, 1939 from the Middle Devonian (Givetian) of USA in having smaller autozooecial apertures (average aperture width 0.11 mm *vs* 0.20 mm in *L. magninodosa*) as well as in having rare diaphragms instead of abundant ones in the latter species. *Leptotrypella* sp. 3 differs from *L. gemmata* Duncan, 1939 from the Middle Devonian (Givetian) of USA in having smaller autozooecial apertures (average aperture width 0.11 mm *vs* 0.20 mm in *L. gemmata*) as well as in having fewer diaphragms.

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 13. *Leptotrypella* sp. 3 (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	7	3.00	0.765	25.46	2.20	4.25
Exozone width, mm	7	0.76	0.415	54.90	0.37	1.26
Endozone width, mm	7	1.49	0.227	15.21	1.13	1.73
Axial ratio	7	0.53	0.159	30.11	0.33	0.69
Aperture width, mm	40	0.11	0.018	15.69	0.08	0.14
Aperture spacing, mm	40	0.20	0.020	10.24	0.15	0.25
Acanthostyle diameter, mm	38	0.05	0.021	46.90	0.02	0.10
Acanthostyles per aperture	30	4.6	0.809	17.45	3.0	6.0
Exilazooecia width, mm	27	0.04	0.015	36.69	0.02	0.07
Exozonal wall thickness, mm	35	0.08	0.027	32.02	0.04	0.13

Leptotrypella sp. 4
Figures 12G–12I, 13A–13C; Table 14

Material. Single colony, three serial thin sections SMF 40339–SMF 40341.

Description. Ramose branched colonies, branches 2.0–3.0 mm in diameter. Exozones 0.41–0.59 mm wide, endozones 1.12–1.82 mm wide. Exozones distinctly separated from endozones. Axial ratio is 0.59. BSI is equal 25.39. Secondary overgrowths unknown. Autozooecia polygonal in transverse section, long in endozones, bending sharply in exozones. Autozooecial apertures polygonal. Autozooecial diaphragms absent in endozone; rare to common, straight, thin in exozone. Exilazooecia slightly beaded, containing 1–2 diaphragms, abundant, 4–6 surrounding each autozooecial aperture, restricted to exozone, rounded-polygonal in transverse section. Acanthostyles common to abundant, 3–6 surrounding each autozooecial aperture, moderately large, having distinct narrow cores and laminated sheaths, often indenting autozooecial apertures. Autozooecial walls in endozones granular, locally crenulated, 0.005–0.010 mm thick; in exozones

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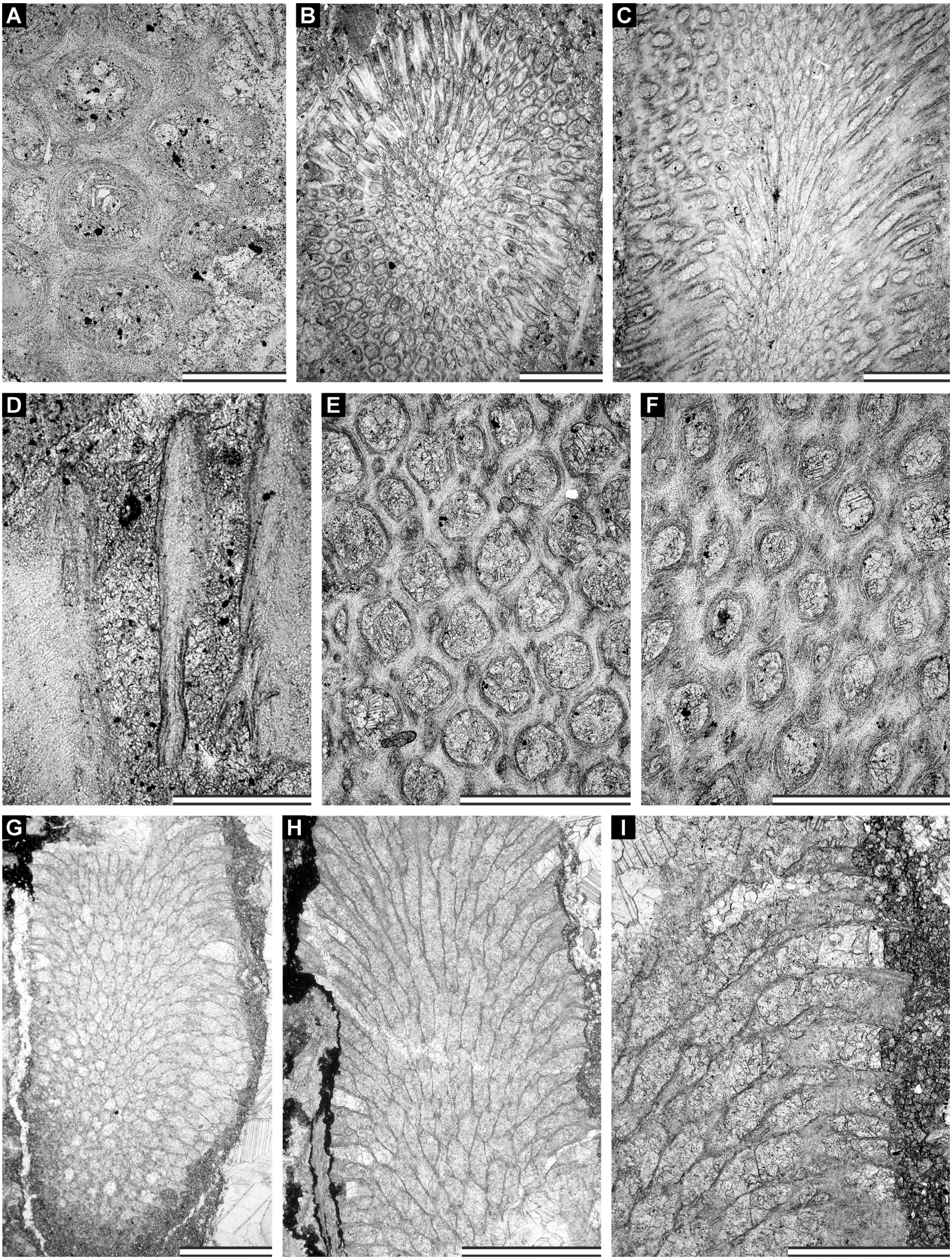
Figure 12. A–F, *Leptotrypella* sp. 2, SMF 40327; **A,** tangential section showing autozooecial apertures and acanthostyles. *Leptotrypella* sp. 3; **B,** branch transverse section, SMF 40336; **C,** branch longitudinal section, SMF 40331; **D,** longitudinal section of exozone showing autozooecial walls, SMF 40336; **E,** tangential section showing autozooecial apertures and acanthostyles, SMF 40336; **F,** tangential section showing autozooecial apertures and acanthostyles, SMF 40331. **G–I,** *Leptotrypella* sp. 4, SMF 40339; longitudinal section; scale bars = 1 mm (B–C, G–H), 0.5 mm (A, E–F, I), 0.2 mm (D).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finely laminated, irregularly thickened, merged, 0.025–0.050 mm thick.

Remarks. *Leptotrypella* sp. 4 differs from other species of the genus *Leptotrypella* in having abundant acanthostyles and exilazooecia. It differs from *L. pervulgata* Yaroshinskaya, 1970 from the Lower Devonian (Lochkovian–Eifelian) of Siberia in having more abundant mesozooecia and in smaller autozooecial apertures (aperture width 0.10–0.17 mm *vs* 0.20–0.25 mm in *L. pervulgata*).

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 14. *Leptotrypella* sp. 4 (single colony measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	20	0.13	0.022	16.96	0.10	0.17
Aperture spacing, mm	20	0.20	0.035	17.83	0.14	0.28
Acanthostyle diameter, mm	20	0.032	0.004	12.04	0.025	0.04
Exilazooecia width, mm	20	0.05	0.015	28.32	0.03	0.08
Acanthostyles per aperture	10	4.0	0.943	23.57	3.0	6.0
Exilazooecia per aperture	10	4.7	0.675	14.36	4.0	6.0
Exozonal wall thickness, mm	10	0.033	0.008	23.54	0.023	0.050

Genus *Loxophragma* Boardman, 1960
[= *Multiphragma* Yang & Hu, 1981]

Type-species. *Loxophragma lechrium* Boardman, 1960. Hamilton Group (Middle Devonian); New York (USA).

Diagnosis. Branched and encrusting colonies. Autozooecia with polygonal apertures. Autozooecial diaphragms abundant in exozones, often inclined, non-parallel, thickened. Exilazooecia rare to common. Acanthostyles small, variable in number. Autozooecial walls thin in endozones, irregularly thickened in exozones (modified after Astrova, 1978).

Comparison. *Loxophragma* Boardman, 1960 differs from *Atactotoechus* Duncan, 1939 in having irregularly thickened walls and abundant and complicated diaphragms.
Genus *Multiphragma* Yang & Hu, 1981 is a junior synonym of *Loxophragma* Boardman, 1960 (Boardman, pers. comm., 2008).

Occurrence. Lower Devonian of Europe (France and Czech Republic), Middle Devonian of Northern America and Upper Devonian of China and Canada.

Loxophragma sp.
Figure 13D–13I; Table 15

Material. Single colony (four serial thin sections SMF 40342–SMF 40345).

Description. Branched colony, 2.38–2.60 mm in diameter. Exozone 0.49–0.70 mm wide, distinctly separated; endozone 1.00–1.62 mm wide. Axial ratio is 0.42–0.62. BSI is equal 18.07. Secondary overgrowth occurring, 0.9 mm in thickness. Autozooecia long in endozones, bending sharply in exozones. Autozooecial apertures polygonal with rounded corners. Autozooecial diaphragms abundant in exozones, straight or inclined, originating from the secondary lining of autozooecial walls. Exilazooecia rare to common, short, having polygonal apertures. Acanthostyles moderately large, common, restricted to exozone. Autozooecial walls granular, 0.005–0.010 mm thick in endozones; regularly thickened, finely laminated, often with secondary lining, showing reversal V-shaped lamination without distinct zooecial boundaries, 0.030–0.075 mm thick in exozones. Indistinct maculae consisting of slightly larger autozooecia present.

Remarks. *Loxophragma* sp. differs from *L. rarispinosum* Bigey, 1986 from the Lower Devonian (Lochkovian) of France in having more abundant acanthostyles and larger autozooecial apertures (aperture width 0.12–0.25 mm *vs* 0.12–0.16 mm in *L. rarispinosum*). The present species differs from *L. varium* (Duncan, 1939) from the Middle Devonian (Givetian) of USA in having regularly thickened autozooecial walls in exozone.

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 15. *Loxophragma* sp. (single colony measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	5	2.48	0.089	3.59	2.38	2.60
Exozone width, mm	5	0.59	0.084	14.26	0.49	0.70
Endozone width, mm	5	1.30	0.242	18.54	1.00	1.62
Axial ratio	5	0.52	0.081	15.40	0.42	0.62
Aperture width, mm	20	0.16	0.035	21.76	0.12	0.25
Aperture spacing, mm	20	0.21	0.042	20.26	0.15	0.32
Acanthostyle diameter, mm	10	0.046	0.007	15.92	0.030	0.055
Exilazooecia width, mm	10	0.06	0.017	27.27	0.04	0.10
Exozonal wall thickness, mm	10	0.049	0.015	29.96	0.030	0.075

Family ERIDOTRYPELLIDAE Morozova, 1960
Genus *Eridotrypella* Duncan, 1939

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

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

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

Occurrence. Silurian–Upper Devonian; worldwide.

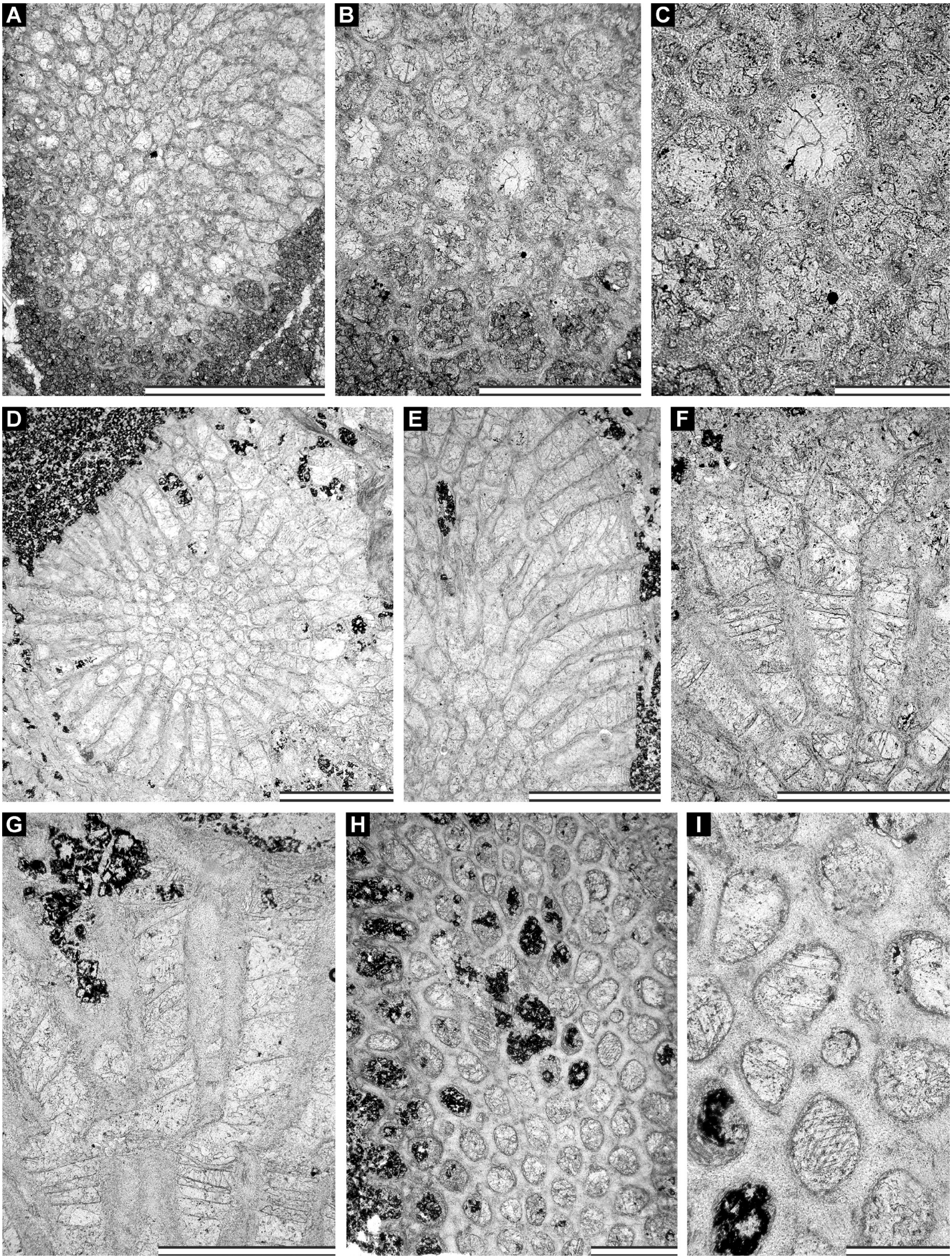


Figure 13. A–**C,** *Leptotrypella* sp. 4, SMF 40339; tangential section showing autozooecial apertures, exilazooecia, and acanthostyles. **D**–**I,** *Loxophragma* sp.; **D,** branch transverse section, SMF 40343; **E,** longitudinal section, SMF 40345; **F,** longitudinal section of exozone with secondary overgrowth, SMF 40343; **G,** transverse section of exozone with secondary overgrowth, SMF 40344; **H**–**I,** tangential section showing autozooecial apertures, exilazooecia, and acanthostyles, SMF 40343; scale bars = 1 mm (A, D–E), 0.5 mm (B, F–G, H), 0.2 mm (C, I).

Eridotrypella sp.

Figure 14A–14D; Table 16

Material. Two colonies (four thin sections SMF 40346–SMF 40349).

Description. Ramose branched colonies, branches 2.50–2.75 mm in diameter. Exozones 0.52–0.60 mm wide, endozones 1.43–1.65 mm wide. Exozones distinctly separated from endozones. Axial ratio is 0.54–0.60. BSI is equal 21.54. Secondary overgrowths occurring. Autozooecia polygonal in transverse section, long in endozones, bending sharply in exozones and intersecting colony surface at angles of 78–90°. Autozooecial apertures polygonal with rounded corners. Autozooecial diaphragms rare to common, straight, thin, occurring mainly in the transition between endo- and exozone. Exilazooecia slightly beaded, containing 1–2 diaphragms, common to abundant, 1–6 surrounding each autozooecial aperture, restricted to exozone, rounded-polygonal in transverse section. Acanthostyles common to abundant, 3–6 surrounding each autozooecial aperture, moderately large, having distinct narrow cores and laminated sheaths, often indenting autozooecial apertures. Autozooecial walls in endozones granular, locally crenulated, 0.005–0.010 mm thick; in exozones finely laminated, irregularly thickened, merged, containing spherules, 0.03–0.07 mm thick. Laminated cingulum locally developed, 0.008–0.015 mm thick. Maculae consisting of slightly larger autozooecia present.

Remarks. *Eridotrypella* sp. differs from *E. vilis* Duncan, 1939 from the Middle Devonian (Givetian) of USA in having more abundant exilazooecia as well as in having smaller autozooecial apertures (aperture width 0.09–0.16 mm *vs* 0.21–0.25 mm in *E. vilis*).

Occurrence. Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 16. *Eridotrypella* sp. (two colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	3	2.63	0.125	4.76	2.50	2.75
Exozone width, mm	3	0.56	0.040	7.26	0.52	0.60
Endozone width, mm	3	1.51	0.119	7.88	1.43	1.65
Axial ratio	3	0.58	0.029	5.03	0.54	0.60
Aperture width, mm	40	0.13	0.019	14.69	0.09	0.16
Aperture spacing, mm	40	0.20	0.031	15.54	0.14	0.25
Acanthostyle diameter, mm	40	0.04	0.007	20.47	0.02	0.05
Exilazooecia width, mm	40	0.04	0.011	26.56	0.02	0.07
Acanthostyles per aperture	30	4.1	0.937	22.67	3.0	6.0
Exilazooecia per aperture	21	3.7	1.617	43.53	1.0	6.0
Exozonal wall thickness, mm	22	0.05	0.009	17.81	0.03	0.07

Family ANISOTRYPIDAE Dunaeva & Morozova, 1967

Genus *Boardmanella* Gorjunova & Weis, 2003

Type-species. *B. richardi* Gorjunova & Weiss, 2003. Middle Devonian (Givetian); Mongolia.

Diagnosis**.** Branched colonies with distinct exozones; autozooecia prismatic, growing parallel to the branch axis in endozones, then bending in exozones at moderate angles, polygonal in transverse section; autozooecial apertures rounded to oval or rounded-polygonal; basal diaphragms usually absent, locally present, thin, straight; exilazooecia rare to abundant, short, varying in size; paurostyles (cf. Gorjunova & Weis, 2003) always covered by skeletal material, restricted to exozone; varying in size and number; autozooecial walls regularly thickened in exozones, straight, merged without distinct zooecial boundaries and showing reverse U-shaped lamination.

Remarks. *Boardmanella* Gorjunova & Weis, 2003 is superficially similar to *Dyscritella* Girty, 1911 in having rare to absent diaphragms and regularly thickened autozooecial walls. However, the styles in *Boardmanella* are different to those in *Dyscritella*. resembling rather paurostyles *sensu* Blake (1983a, p. 538–539). The main difference between acanthostyles and paurostyles is that acanthostyles usually protrude upon the colony surface and have wide, well-developed laminated sheaths, whereas paurostyles are largely embedded in the skeletal wall of the exozone.

Occurrence. Lower–Upper Devonian; North America, Eurasia.

Boardmanella spinigera n. sp.

Figures 14E–14J, 15A–15C; Table 17

Etymology. The species name refers to the abundant paurostyles of the new species (from Latin “*spinigera*” – spiny, spinose).

Holotype. SMF 40350.

Paratypes. SMF 40351–SMF 40368.

Type locality. Guadámez-2, Ossa-Morena Zone (SW Spain).

Type horizon. Lower Devonian (Emsian).

Diagnosis. Branched colonies, moderately robust, with relatively narrow, distinct exozones; axial ratio 0.33–0.70; BSI 37.33; autozooecia long in endozone, bending sharply in exozones; autozooecial apertures oval to slightly polygonal; autozooecial diaphragms thin, concentrated in the transition between endozone and exozone; exilazooecia few; paurostyles moderately large, varying in size, abundant; maculae not observed.

Description. Branched colonies, 1.30–3.50 mm in diameter, with 0.30–1.15 mm wide exozones and 0.70–2.05 mm wide endozones. Axial ratio is 0.33–0.70.

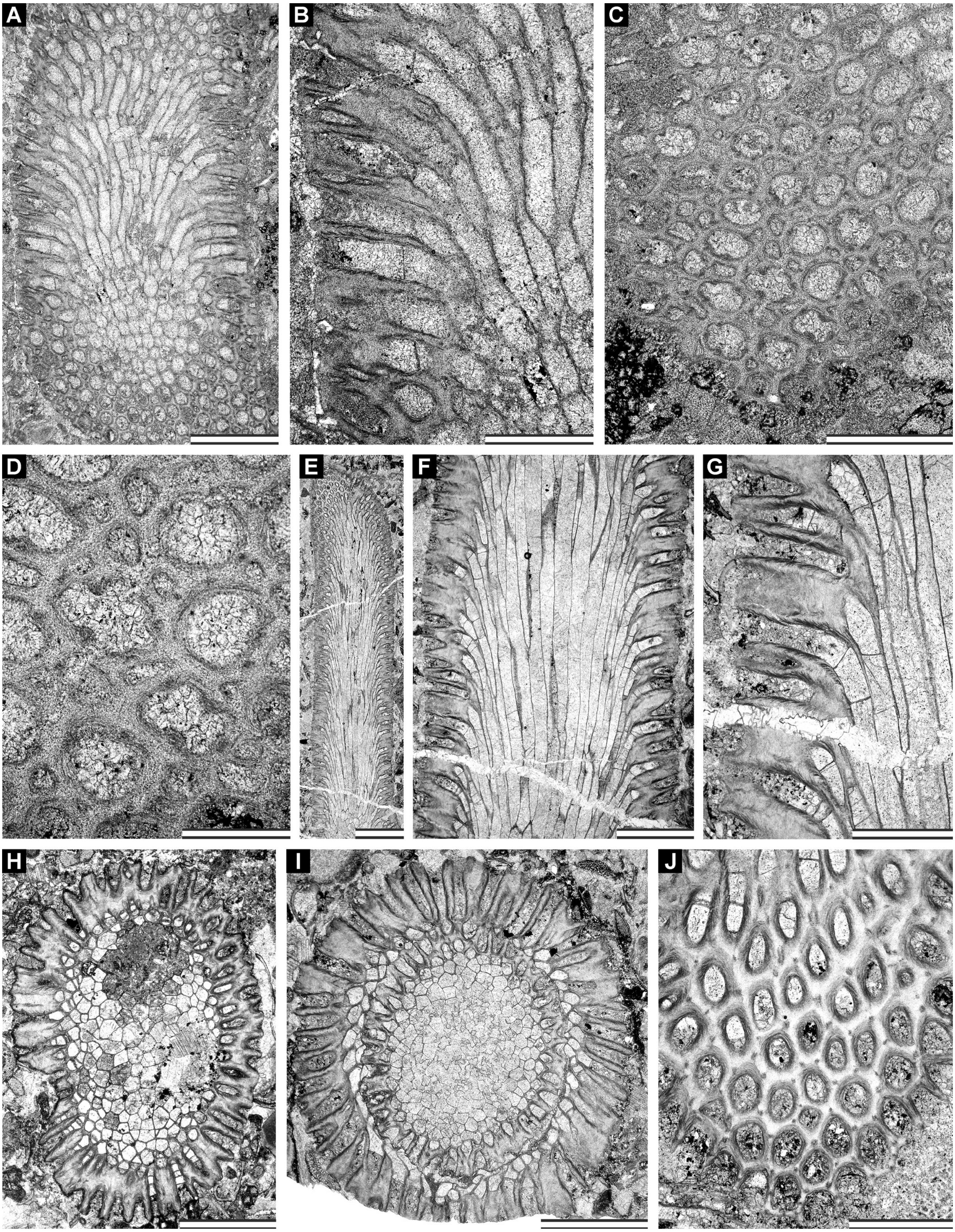


Figure 14. *Eridotrypella* sp., SMF 40348. **A**–**B,** Longitudinal section; **C**–**D,** tangential section showing autozooecial apertures, exilazooecia, and acanthostyles. *Boardmanella spinigera* n. sp.; **E**–**G,** branch longitudinal section, holotype SMF 40350; **H,** branch transverse section, paratype SMF 40361; **I,** branch transverse section with secondary overgrowth, paratype SMF 40365; **J,** tangential section showing autozooecial apertures, exilazooecia, and paurostyles, holotype SMF 40350; scale bars = 2 mm (E), 1 mm (A, F, H–I), 0.5 mm (B–C, G, J), 0.2 mm (D).

BSI is equal 37.33. Secondary overgrowth occurring, 0.62–1.75 mm in thickness. Autozooecia long, having a polygonal shape in transverse section in endozones, bending sharply in exozones and intersecting colony surface at angles of 63–77°. Autozooecial apertures oval to slightly polygonal. Autozooecial diaphragms thin, straight to slightly deflected proximally, concentrated mainly in the transition between endozone and exozone. Exilazooecia few, small, short, restricted to exozones, rounded to oval in cross section. Paurostyles moderately large, varying in size, abundant, 2–6 surrounding each autozooecial aperture, growing from the base of the exozone, having distinct cores and laminated sheaths. Autozooecial walls in endozones granular, 0.003–0.010 mm thick; in exozones laminated, merged, without distinct zooecial boundaries, 0.04–0.07 mm thick. Maculae not observed.

Remarks. *Boardmanella spinigera* n. sp. differs from *B. elliptica* (Kopajevich, 1984) from the Middle Devonian of Mongolia in having more abundant paurostyles (2–6 per autozooecial aperture *vs*. 1–4 in *B. elliptica*) and in having less abundant exilazooecia. The new species differs from *B. devonica* (Volkova, 1968) from the Middle Devonian of Altai, Russia, in having smaller autozooecial apertures (aperture width 0.07–0.12 mm *vs* 0.15–0.21 mm in *B. devonica*). It differs from *B. interporosa* (Ulrich & Bassler, 1913) from the Lower Devonian (Lochkovian) of USA in narrower exozones and less abundant exilazooecia.

Table 17. *Boardmanella spinigera* n. sp. (*ca*. 20 colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	26	2.54	0.555	21.85	1.30	3.50
Exozone width, mm	26	0.56	0.223	40.05	0.30	1.15
Endozone width, mm	26	1.42	0.310	21.74	0.70	2.05
Axial ratio	26	0.57	0.096	16.86	0.33	0.70
Aperture width, mm	20	0.09	0.014	14.35	0.07	0.12
Aperture spacing, mm	20	0.17	0.023	13.28	0.13	0.20
Paurostyle diameter, mm	20	0.053	0.012	22.24	0.030	0.075
Paurostyles per aperture	20	4.2	0.933	22.49	2.0	6.0
Exilazooecia width, mm	10	0.04	0.013	35.46	0.02	0.06
Exozonal wall thickness, mm	20	0.06	0.010	18.09	0.04	0.07

Family uncertain
Cordobella n. gen

Type- species. *Cordobella tenuis* n. gen. n. sp.

Etymology. The genus name refers to the Cordoba province in which the type locality is situated.

Diagnosis. Encrusting colonies; secondary overgrowth not observed; autozooecia prismatic; endozones short; autozooecial diaphragms absent; 1–2 hood-shaped cystiphragms in each autozooecium, situated at the proximal wall of zooecial chambers; acanthostyles small, abundant; maculae not observed.

Remarks. The new genus differs from other trepostomes in the presence of hood-shaped cystiphragms. Those are closed chambers attached to the proximal wall, one or two in a series. Roofs of the chambers are planar or rounded. Sometimes the cystiphragms are not completely closed at their proximal ends. In that case they are filled with micrite, otherwise the interior part of cystiphragms is sparitic (Figs. 15E–15F, 16A). Such a morphology is unknown in trepostome bryozoans. Monticuliporid bryozoans have singular or multiple cystiphragms which are hemispheric in shape (*e.g.*, Boardman, 1971).

Occurrence. Lower Devonian (Pragian); Cordoba, southern Spain.

Cordobella tenuis n. gen. n. sp.
Figures 15D–15F, 16A–16F; Table 18

Etymology. The species name refers to the thin encrusting colony of the new species (from Latin "*tenuis*" thin).

Holotype. SMF 40369.

Paratypes. SMF 40370–SMF 40379.

Type locality. Peñón Cortado, Ossa-Morena Zone (SW Spain).

Type horizon. Lower Devonian (Pragian).

Diagnosis. As for genus.

Description. Encrusting tubular colonies (encrusting ephemeral cylindrical objects), 0.17–0.30 mm in thickness. Autozooecia budding from a thin epitheca, firstly oriented parallel to the substrate, then bending sharply and intersecting the colony surface at right angles. Epitheca 0.008–0.015 mm thick. Autozooecial apertures rounded-polygonal. Autozooecial diaphragms absent. Hood-shaped cystiphragms present, situated at the proximal wall of zooecial chambers, shaped semilunar in the shallow tangential section, becoming triangular near their bases. Hood-shaped cystiphragms 0.07–0.11 mm in height and 0.05–0.10 mm in width, restricting about a half of the chamber space in the exozone, having planar or rounded roofs. Usually one, rarely two cystiphragms in each autozooecium. Cystiphragm walls 0.005–0.008 mm thick. Heterozooecia absent. Acanthostyles small, abundant, 4–6 surrounding each aperture, originating from the base of exozone, having distinct calcite cores and dark laminated sheaths. Walls granular, in endozone 0.005–0.013 mm thick;

Table 18. *Cordobella tenuis* n. gen. n. sp. (six colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.13	0.023	17.61	0.10	0.17
Aperture spacing, mm	25	0.18	0.025	13.82	0.14	0.23
Acanthostyle diameter, mm	23	0.025	0.007	29.13	0.015	0.048

in exozone 0.02–0.03 mm thick, distinctly laminated. Maculae not observed.

Remarks. As for genus.

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

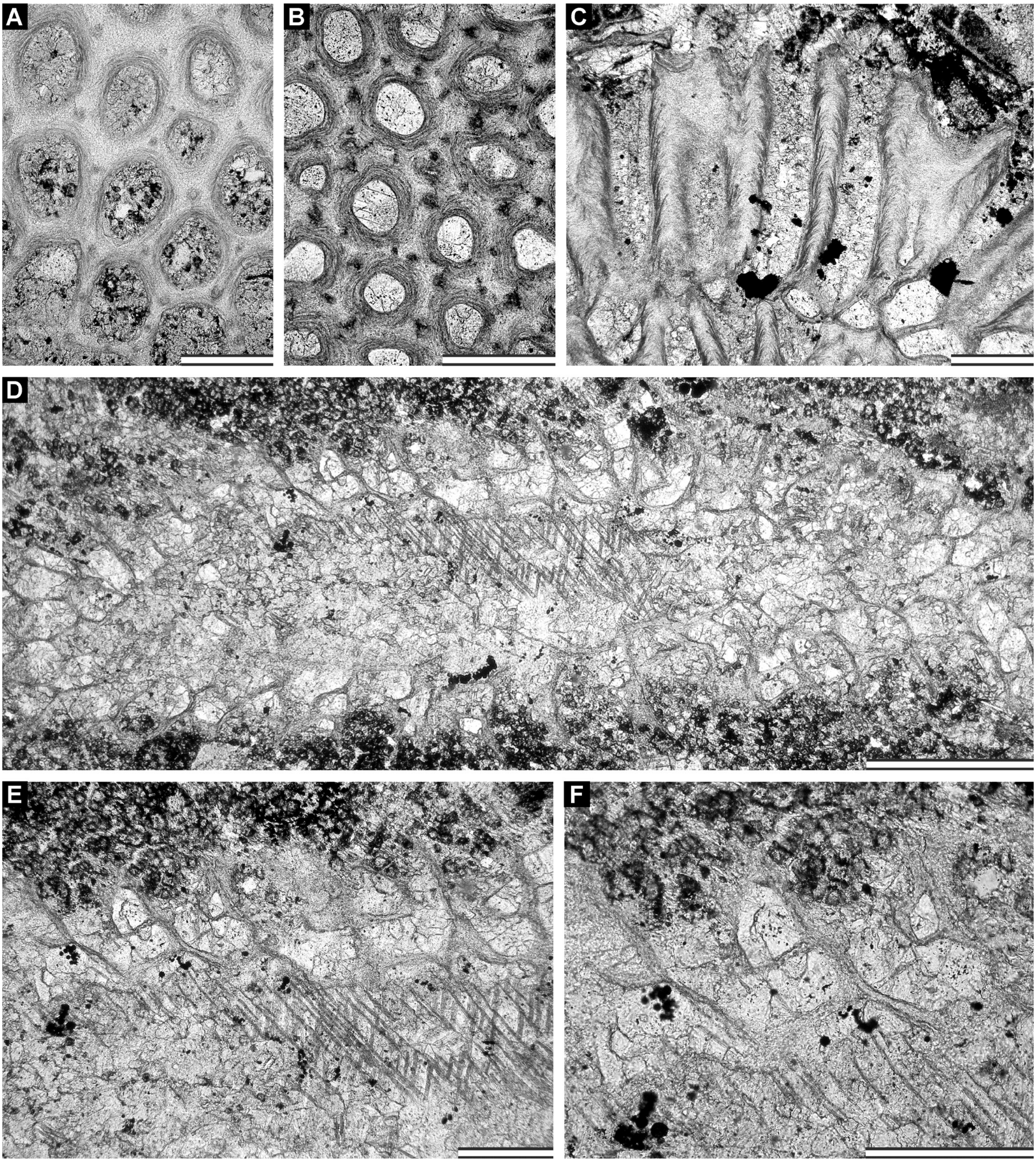


Figure 15. A–**C,** *Boardmanella spinigera* n. sp.; **A,** tangential section showing autozooecial apertures and paurostyles; holotype SMF 40350; **B,** tangential section showing autozooecial apertures, exilazooecia, and paurostyles, paratype SMF 40351; **C,** branch transverse section with secondary overgrowth, paratype SMF 40365; **D**–**F,** *Cordobella tenuis* n. gen. n. sp., holotype SMF 40369; **D,** longitudinal section of the colony; **E**–**F,** longitudinal section showing autozooecia with “cystiphragms”; scale bars = 0.5 mm (D), 0.2 mm (A–C, E–F).

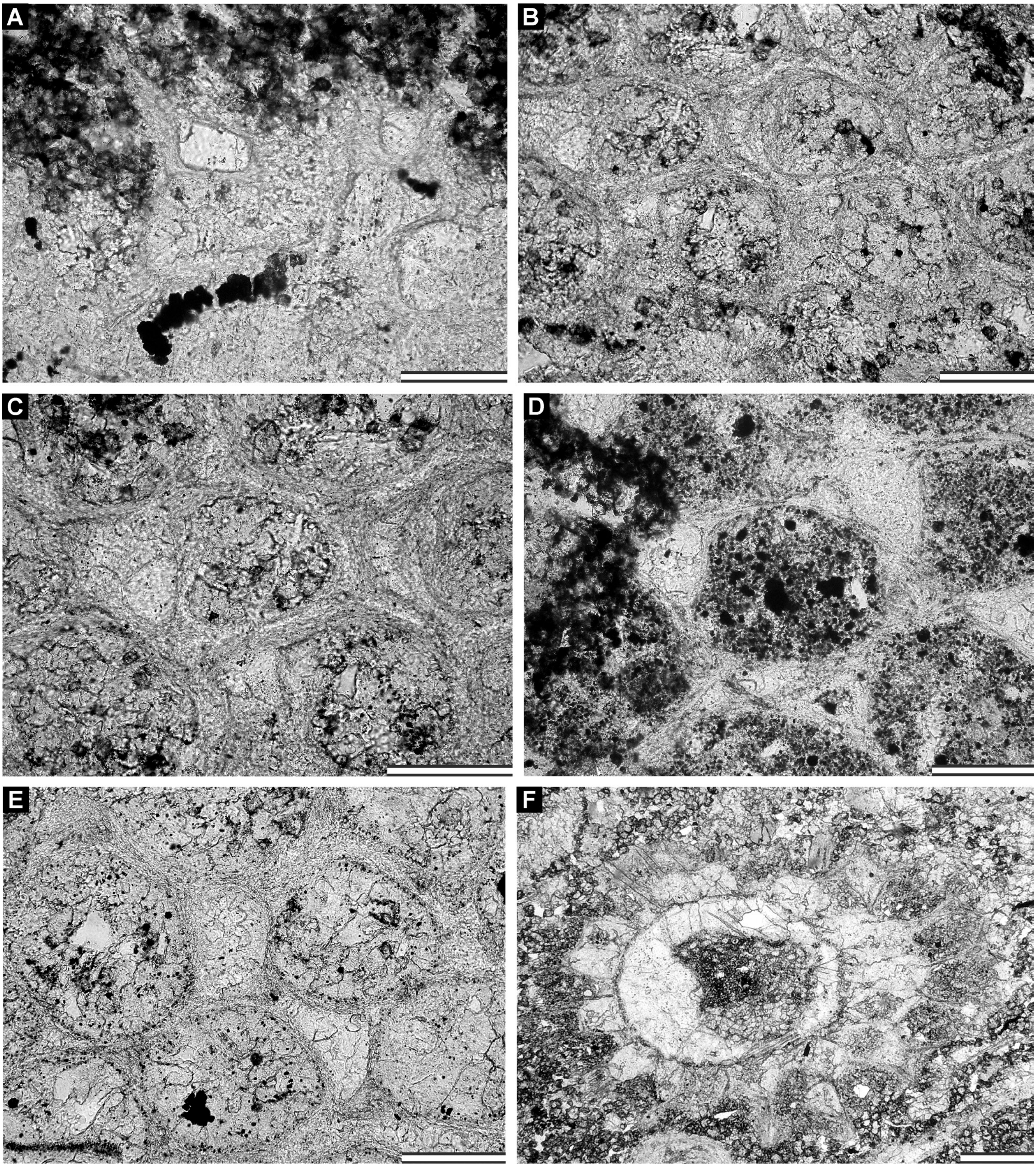


Figure 16. *Cordobella tenuis* n. gen. n. sp. **A,** Longitudinal section showing autozooecia with “cystiphragms”, holotype SMF 40369; **B**–**C,** tangential section showing autozooecial apertures, acanthostyles and “cystiphragms”, holotype SMF 40369; **D,** deep tangential section showing autozooecial chambers and “cystiphragms”, holotype SMF 40369; **E,** tangential section showing autozooecial apertures, acanthostyles and “cystiphragms”, paratype SMF 40377; **F,** transverse section showing autozooecia with cystiphragms, paratype SMF 40374; scale bars = 0.1 mm (A–E), 0.2 (F).

Order CRYPTOSTOMATA Vine, 1884
Suborder RHABDOMESINA Astrova & Morozova, 1956
Family RHABDOMESIDAE Vine, 1884
Genus *Orthopora* Hall, 1886

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

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

Remarks. *Orthopora* Hall, 1886 differs from *Trematella* Hall, 1886 in lacking metazooecia and in the presence of well-developed hemisepta.

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

Orthopora spinosa Ernst *et al.*, 2012

Figure 17A–17E; Table 19

1980a *Orthopora* sp. Bigey, p. 189–191, pl. 26, figs. 1–9.
1980b *Orthopora* sp. Bigey, pl. 55, figs. 3, 6, 7.
2012 *Orthopora spinosa* Ernst *et al.*, p. 716, figs. 14G–14I, 15A–15C.

Material. SMF 40380–SMF 40434.

Description. Branches 0.48–0.95 mm in diameter, with 0.11–0.25 mm wide endozones and 0.18–0.51 mm wide exozones. Axial ratio is 0.28–0.68. Branch bifurcations common. Transverse sections of branches circular. Autozooecia short, growing in spiral pattern from the distinct median axis at angles of 28–34° in endozones, abruptly bending in exozones and intersecting colony surface at angles of 46–75°; having polygonal, tear-drop shape in transverse sections of endozone. Autozooecial diaphragms rare to absent. Long superior hemisepta present, curved proximally; inferior hemisepta long, positioned beneath superior hemisepta, curved distally. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls in the endozone granular, 0.008–0.010 mm thick; in exozone laminated. Acanthostyles abundant, arranged in longitudinal rows between apertures, slightly varying in size, having narrow hyaline cores and wide laminated sheaths. Heterozooecia absent.

Remarks. *Orthopora spinosa* Ernst *et al.*, 2012 is similar to *O. sincera* Ernst, 2011 from the Lower to Middle Devonian of NW Spain but differs in having thinner branches. *Orthopora spinosa* differs from *O. tenuis* Ernst, 2008b from the Lower Devonian (Pragian) of the Czech Republic, in having smaller autozooecial apertures (average aperture width 0.060 mm *vs* 0.076 mm in *O. tenuis*).

Occurrence. Arauz Sur (Arroyo section), Palencia, NW Spain (Cantabrian Mountains); Lebanza Formation, Lower Devonian (Pragian). Bretagne, France; Lower Devonian (Emsian). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian). Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 19. *Orthopora spinosa* Ernst *et al.*, 2012 (*ca*. 45 colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	50	0.72	0.161	22.46	0.48	1.10
Exozone width, mm	50	0.19	0.062	33.01	0.10	0.38
Endozone width, mm	50	0.34	0.089	26.02	0.18	0.58
Axial ratio	50	0.48	0.097	20.20	0.28	0.68
Aperture width, mm	50	0.056	0.009	15.90	0.040	0.075
Aperture spacing along branch, mm	16	0.33	0.046	13.82	0.25	0.40
Aperture spacing diagonally, mm	23	0.20	0.030	15.08	0.12	0.25
Acanthostyle diameter, mm	50	0.03	0.004	14.15	0.02	0.04

Genus *Vidronovella* Gorjunova, 2006

Type-species. *Vidronovella fastigiata* Gorjunova, 2006. Late Devonian (Famennian); Afghanistan.

Diagnosis. Colonies branched. Autozooecia tubular, short, budding from indistinct medial axis or short mesotheca in spiral order around the branch, oriented at high angles to the branch axis. Autozooecial diaphragms absent. Proximal part of autozooecia thickened in the outermost exozone ("fastigia" *sensu* Gorjunova, 2006). Both superior and inferior hemisepta present, located in the distal part of autozooecia. Superior hemiseptum moderately long, hook-shaped, curved distally, positioned at the base of the thicken exozone ("fastigium" *sensu* Gorjunova, 2006); inferior hemiseptum long, slender, occupying two-thirds of body cavity of autozooecia, positioned beneath superior hemisepta, curved distally. Secondary blunt hemisepta may occur, one proximally to the superior hemiseptum, and another one distally to the inferior hemiseptum. Autozooecial apertures oval to rounded-rhombic, arranged regularly in alternating rows on the colony surface. Acanthostyles large and blunt, with narrow hyaline cores and wide laminated sheaths, embedded in the skeleton. Single or two acanthostyles positioned between two longitudinally successive autozooecial apertures. Paurostyles occur in one species, irregularly distributed between acanthostyles. Heterozooecia absent. Walls granular in the endozone; laminated in exozone, becoming structureless near the colony surface. Mural spines may occur.

Remarks. *Vidronovella* Gorjunova, 2006 is similar to *Orthopora* Hall, 1886, but differs from in the short autozooecia and the higher budding angle of the autozooecia in the axial area.

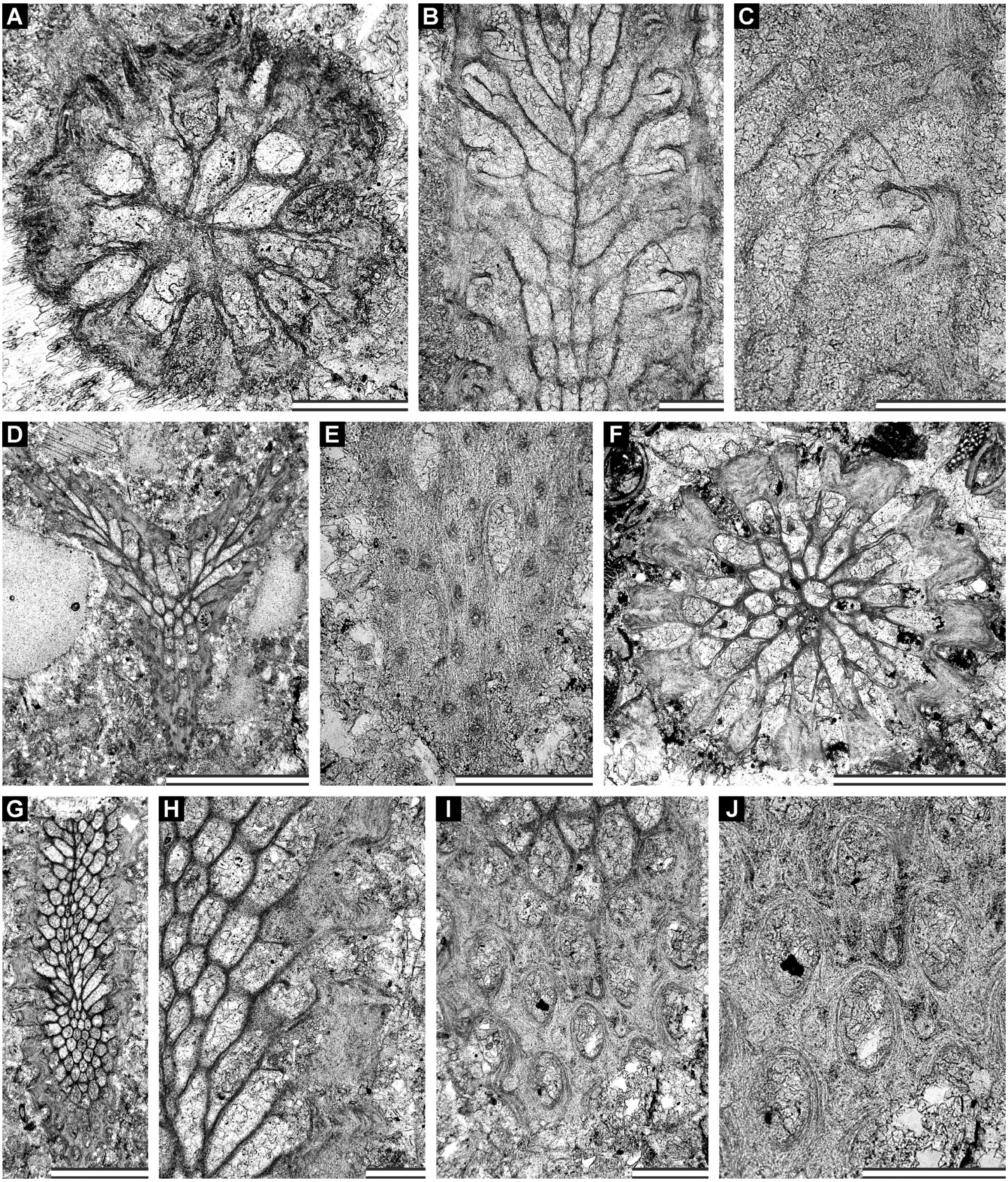


Figure 17. A–**E,** *Orthopora spinosa* Ernst *et al*., 2012; **A,** branch transverse section, SMF 40399; **B**–**C,** branch longitudinal section showing autozooecial chambers with hemisepta, SMF 40414; **D,** branch longitudinal section in place of dichotomy, SMF 40401; **E,** tangential section showing autozooecial apertures and acanthostyles, SMF 40400; **F**–**J,** *Vidronovella elegantula* Ernst *et al*., 2012; **F,** branch transverse section, SMF 40435; **G**–**H,** branch longitudinal section showing autozooecial chambers with hemisepta, SMF 40436; **I**–**J,** tangential section showing autozooecial apertures and acanthostyles, SMF 40436; scale bars = 1 mm (D, G), 0.5 mm (E–F), 0.2 mm (A–C, H–J).

Occurrence. Lower Devonian; Spain. Middle Devonian; Western Sahara and Germany. Upper Devonian; Afghanistan.

Vidronovella elegantula Ernst *et al.*, 2012

Figure 17F–17J; Table 20

2012 *Vidronovella elegantula* Ernst *et al.*, p. 718, figs. 15D–15I, 16A.

Material. SMF 40435–SMF 40458.

Description. Branches 1.50–1.75 mm in diameter, with 0.29–0.40 mm wide exozones and 0.90–1.05 mm wide endozones. Axial ratio is 0.38–0.60. Branch bifurcation common. Transverse sections of branches circular. Autozooecia short, budding from distinct medial axis in spiral order at angles of 41–50°, abruptly bending in exozones and intersecting colony surface at angles of 86–90°. Autozooecial diaphragms absent. Superior hemiseptum moderately long, hook-shaped, curved proximally; inferior hemiseptum long, slender, occupying two-thirds of body cavity of autozooecia, positioned beneath superior hemisepta, inclined distally, widened laterally. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls in the endozone granular, 0.005–0.008 mm thick; laminated in exozone. Acanthostyles having distinct hyaline cores and wide laminated sheaths, regularly sized, single or two positioned between two longitudinally successive autozooecial apertures, 4–6 surrounding each aperture. Acanthostyles often sealed by a thick layer of laminated skeleton on the colony surface. Mural spines absent.

Remarks. *Vidronovella elegantula* Ernst *et al.*, 2012 differs from *V. fastigiata* Gorjunova, 2006 in having of 4–6 instead of 4 acanthostyles surrounding each autozooecial aperture, and from *V. intricata* Ernst, 2011 in the absence of mural spines and in the presence of single hemisepta instead of the double hemisepta found in *V. intricata*.

Occurrence. Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains); Lebanza Formation, Lower Devonian (Pragian). Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 20. *Vidronovella elegantula* Ernst *et al.*, 2012 (twelve colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	15	0.91	0.140	15.42	0.70	1.15
Exozone width, mm	15	0.23	0.042	18.68	0.15	0.30
Endozone width, mm	15	0.46	0.124	27.15	0.26	0.72
Axial ratio	15	0.50	0.085	17.12	0.33	0.65
Aperture width, mm	50	0.07	0.015	19.40	0.05	0.11
Aperture spacing along branch, mm	45	0.26	0.032	12.20	0.20	0.35
Aperture spacing diagonally, mm	45	0.17	0.018	10.82	0.13	0.20
Acanthostyle diameter, mm	45	0.030	0.004	14.02	0.025	0.040

Family ARTHROSTYLIDAE Ulrich, 1882
Genus *Paracuneatopora* Ernst, 2008b

Type-species. *Paracuneatopora striata* Ernst, 2008b. Lower Devonian (Pragian); Czech Republic.

Diagnosis. Branched colonies, rarely dichotomous. Autozooecia short, growing from a distinct medial axis, abruptly bending, having triangular cross sections in endozones. Hemisepta absent. Autozooecial diaphragms occurring. Heterozooecia absent. Paurostyles abundant, densely spaced, arranged in regular strait rows between apertures, forming low ridges on colony surface. Extrazooecial skeleton well developed, laminated.

Remarks. *Paracuneatopora* Ernst, 2008b differs from *Cuneatopora* Siegfried, 1963 in having shorter autozooecia and in absence of metazooecia, as well as in having of dichotomously branching colonies instead of non-branching in the latter genus.

Occurrence. Lower Devonian (Pragian); Morocco, Czech Republic, Spain.

Paracuneatopora striata Ernst, 2008b

Figure 18A–18G

1994 *Cuneatopora* sp. Bigey, p. 18, pl. 1, fig. 15.
2008b *Paracuneatopora striata* Ernst, p. 342, pl. 6, figs. 1–6.

Material. Six transverse sections SMF 40459–SMF 40463, and one longitudinal section SMF 40464.

Description. Branches 0.27–0.45 mm in diameter, with 0.04–0.13 mm wide exozones and 0.18–0.27 mm wide endozones. Axial ratio is 0.42–0.70. Autozooecia short, growing from medial axis; triangular in transverse section at their base; having short narrow vestibule; arranged in 6–9 rows on branches. Autozooecial apertures 0.05 mm in width. Paurostyles abundant, densely spaced, arranged in regular strait rows between apertures, forming low ridges on colony surface, 0.025-0.030 mm in diameter. Autozooecial walls in endozone finely laminated, with distinct zooecial boundaries, 0.010–0.015 mm in thickness.

Remarks. The present material has thinner branches than the material from the Koněprusy Limestone: branch diameter 0.27–0.45 mm *vs* 0.42–0.84 mm. Transverse section of the specimen from Morocco depicted by Bigey (1994, pl. 1, fig. 15) is 0.50 mm in diameter. Otherwise, the compared specimens are identical.

Occurrence. Safi area, Morocco; Lower Devonian (Pragian). Czech Republic; Koněprusy Limestone, Lower Devonian (Pragian). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Family uncertain
Serenella n. gen.

Type-species. *Serenella dubia* n. gen. n. sp.

Etymology. The genus name refers to the region La Serena, in which the type locality is situated.

Diagnosis. Branched colonies; axial ratio 0.36–0.64; branch bifurcation not observed; autozooecia long, budding from indistinct median axis in spiral order; autozooecial diaphragms few to absent, rarely common; hemisepta absent; 1–2 acanthostyles positioned between two longitudinally successive autozooecial apertures; mural spines absent.

Remarks. *Serenella dubia* n. gen. shows distinct spiral budding pattern and regular arrangement of autozooecial apertures and acanthostyles typical for cryptostome (rhabdomesine) bryozoans (*e.g.*, Blake, 1983b; Gorjunova, 1985). However, its wall structure is rather typical for leptotrypid bryozoans (Trepostomata) and not known with the Cryptostomata. The new genus can be compared to the subgenus *Klaucena* (*Spira*) Trizna, 1958 in general shape of autozooecia and presence of acanthostyles. However, the latter genus has distinct median axis and one acanthostyle between autozooecial apertures.

Occurrence. Lower Devonian (Pragian–Emsian); Cordoba, southern Spain.

Serenella dubia n. gen. n. sp.
Figure 19A–19I; Table 21

Etymology. The species name refers to the indistinct relations of the new species.

Holotype. SMF 40466.

Paratypes. SMF 40465, SMF 40467–SMF 40473.

Type locality. Guadámez-2, Ossa-Morena Zone (SW Spain).

Type horizon. Lower Devonian (Emsian).

Diagnosis. As for genus.

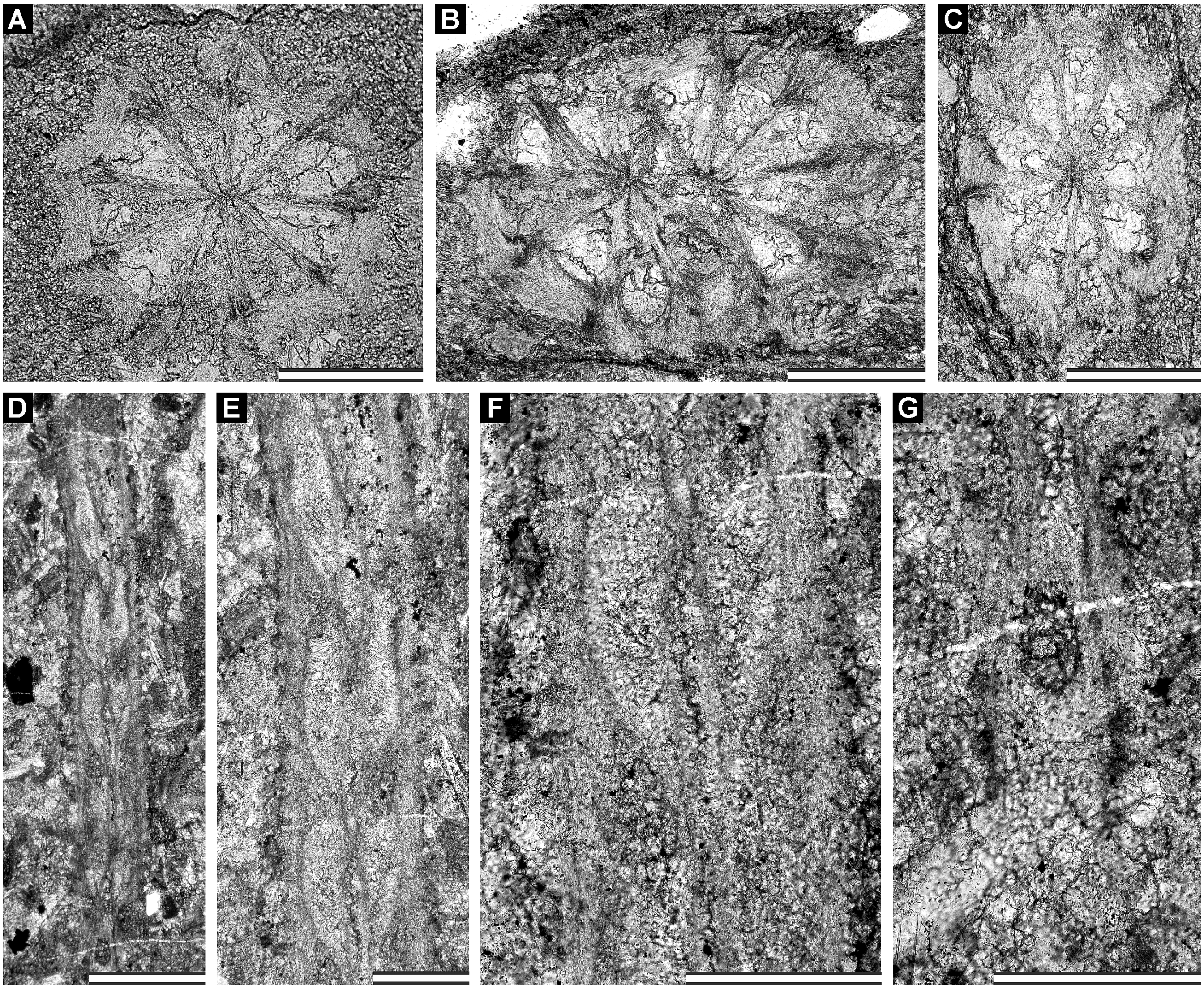


Figure 18. *Paracuneatopora striata* Ernst, 2008b, branch transverse sections. **A,** SMF 40460; **B,** SMF 40461 (place of dichotomy); **C,** SMF 40461; **D**–**F,** SMF 40464, longitudinal section showing autozooecial chambers and paurostyles; **G,** SMF 40464, oblique section showing paurostyles and an autozooecial aperture; scale bars = 0.5 mm for D and 0.2 mm for A–C, E–G.

Description. Branched colonies, 0.82–1.15 mm in diameter, with 0.20–0.26 mm wide exozones and 0.36–0.69 mm wide endozones. Axial ratio is 0.36–0.64. Branch bifurcation not observed. Transverse sections of branches circular. Autozooecia long, budding from indistinct medial axis in spiral order, growing parallel to the axis for long distances, then bending at low angles in exozones. Autozooecial diaphragms straight, usually few to absent, sometimes common in the outermost exozone. Hemisepta absent. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Acanthostyles having distinct hyaline cores and wide laminated sheaths, regularly sized,1–2 positioned between two longitudinally successive autozooecial apertures, 4–6 surrounding each aperture. Acanthostyles sealed by a thick layer of laminated skeleton on the colony surface. Mural spines absent. Walls in the endozone granular, 0.008–0.010 mm thick; laminated, 0.030–0.55 mm thick in exozone.

Other occurrences. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 21. *Serenella dubia* n. gen. n. sp. (four colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	4	0.96	0.146	15.14	0.82	1.15
Exozone width, mm	4	0.25	0.047	18.76	0.20	0.31
Endozone width, mm	4	0.46	0.154	33.23	0.36	0.69
Axial ratio	4	0.48	0.101	21.17	0.38	0.60
Aperture width, mm	10	0.08	0.013	16.29	0.06	0.10
Aperture spacing along branch, mm	5	0.22	0.013	5.98	0.20	0.23
Aperture spacing diagonally, mm	5	0.15	0.008	5.50	0.14	0.16
Acanthostyle diameter, mm	5	0.030	0.003	9.73	0.025	0.033

Suborder PTILODICTYINA Astrova & Morozova, 1956
Family INTRAPORIDAE Simpson, 1897
Genus *Intrapora* Hall, 1883

Type-species. *Intrapora puteolata* Hall, 1883. Middle Jeffersonville Limestone, Middle Devonian; Eastern USA.

Diagnosis. Bifoliate colonies consisting of dichotomous branches, leaf-like, frondose. Mesotheca straight or slightly undulating. Autozooecia subelliptical in transverse section, abruptly bending in exozones, with rounded or rounded-polygonal apertures. Superior hemisepta indistinct, short, present or absent. Diaphragms occasionally occurring. Metazooecia usually abundant, often separating autozooecia, containing abundant, closely spaced diaphragms. Acanthostyles present or absent, varying in number.

Remarks. *Intrapora* Hall, 1883 differs from *Ensiphragma* Astrova in Astrova & Yaroshinskaya, 1968 in arrangement of metazooecia. Metazooecia in *Intrapora* are arranged more or less irregularly, whereas metazooecia of *Ensiphragma* are arranged in pairs between apertures. *Intrapora* differs also from *Coscinella* Hall, 1887 in the presence of acanthostyles and colony shape: dichotomous branched, leaf-like, or frondose versus reticular colony consisting of anastomosing branches in *Coscinella*.

Occurrence. Lower Devonian–Lower Carboniferous; North America, Eurasia.

Intrapora sp.
Figure 20A–20D; Table 22

Material. SMF 40474–SMF 40479.

Description. Bifoliate, leaf-like colonies. Branches 1.00–1.25 mm thick. Mesotheca 0.02–0.04 mm thick, zigzag shaped in transverse section. Rods in mesotheca absent. Autozooecia relatively long, growing from a mesotheca, semicircular at the base in transverse section, becoming rounded-polygonal in the exozone, arranged in indistinctly alternating rows on branches. Autozooecial diaphragms rare, hemisepta absent. Metazooecia abundant, polygonal to subcircular in transverse section, sometimes nearly as large as autozooecia, often sealed at colony surface by skeletal material, commonly separating autozooecia, 4–6 occurring between neighbouring autozooecia. Metazooecial diaphragms abundant, thick. Acanthostyles abundant, 2–4 constantly surrounding each autozooecial aperture and occurring randomly between autozooecia, having narrow hyaline cores and wide laminated sheaths, often originating from the level of mesotheca. Autozooecial walls granular, 0.018–0.030 mm thick in endozone; finely laminated, 0.07–0.11 mm thick in exozone. Maculae not observed.

Remarks. *Intrapora* sp. is similar to *I. traversensis* McNair, 1937 from the Traverse Group (Middle Devonian) of Michigan, USA, but differs from it in having smaller autozooecial apertures (average width 0.11 mm *vs* 0.18 mm in *I. traversensis*). The present species differs from *Intrapora armata* Ernst, 2011 from the Lower–Middle Devonian (Emsian–Eifelian) of NW Spain in having more abundant acanthostyles (at average 3 acanthostyles per aperture *vs* 2 in *I. armata*), and in absence of megastyles.

Table 22. *Intrapora* sp. (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	40	0.11	0.020	17.53	0.08	0.17
Aperture spacing along branch, mm	40	0.47	0.070	14.93	0.35	0.60
Aperture spacing diagonally, mm	40	0.26	0.044	16.93	0.19	0.35
Acanthostyle diameter, mm	40	0.05	0.016	35.54	0.03	0.07
Metazooecia width, mm	40	0.08	0.020	25.72	0.04	0.15
Acanthostyles per aperture	30	3.0	0.765	25.78	2.0	4.0
Metazooecia per aperture	10	4.6	0.699	15.20	4.0	6.0
Maximal chamber width, mm	20	0.11	0.011	9.87	0.09	0.13

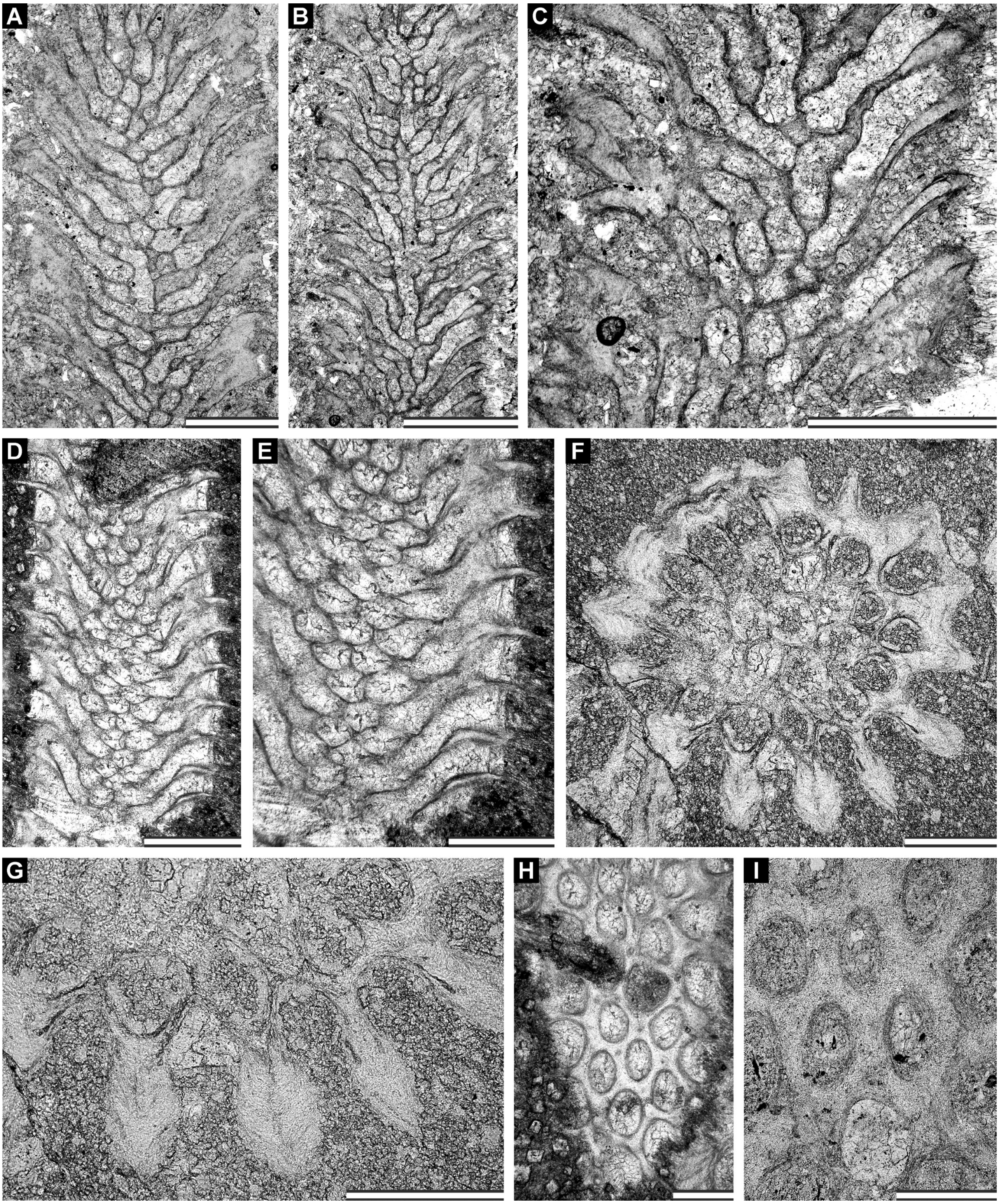


Figure 19. *Serenella dubia* n. gen. n. sp. **A**–**C,** Branch longitudinal section, holotype SMF 40466; **D**–**E,** branch longitudinal section, paratype SMF 40471; **F**–**G,** branch transverse section, paratype SMF 40473; **H,** tangential section showing autozooecial apertures, paratype SMF 40471; **I,** tangential section showing autozooecial apertures, holotype SMF 40466; scale bars = 0.5 mm (A–E), 0.2 mm (F–I).

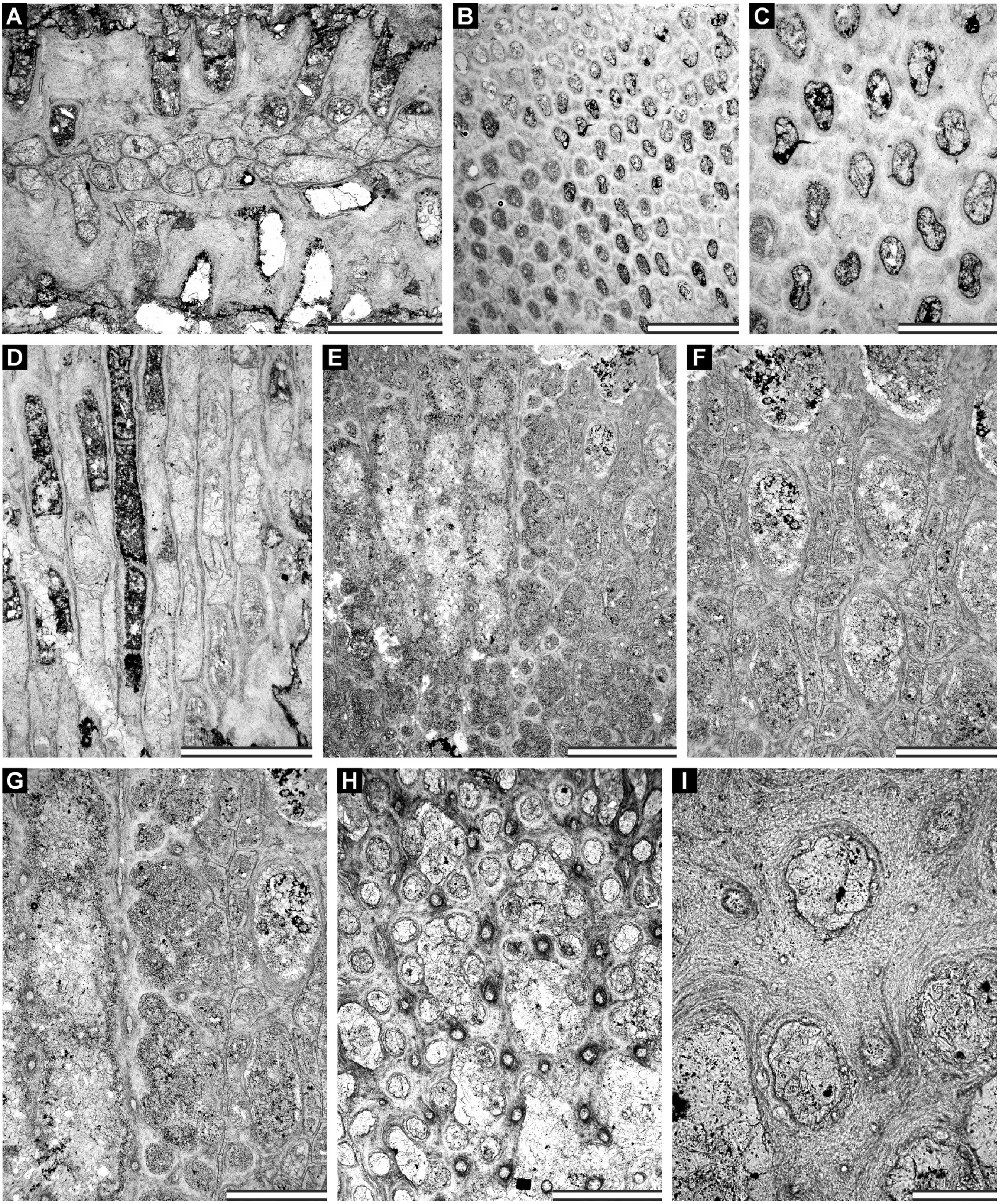


Figure 20. A–**D,** *Intrapora* sp.; **A,** branch transverse section, SMF 40474; **B**–**C,** tangential section showing autozooecial apertures, metazooecia, and acanthostyles, SMF 40475; **D,** deep tangential section showing autozooecial chambers, SMF 40475. **E**–**I,** *Fenestella* sp.; **E**–**G,** tangential section, SMF 40480; **H**–**I,** tangential section showing autozooecial apertures and nodes; scale bars = 1 mm (B, E), 0.5 mm (A, C–D, F–H), 0.1 mm (I).

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian). Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Order FENESTRATA Astrova & Morozova, 1956
Suborder FENESTELLINA Astrova & Morozova, 1956
Family FENESTELLIDAE King, 1849
Genus *Fenestella* Lonsdale, 1839

Type-species. *Fenestella subantiqua* d'Orbigny, 1849. Lower Silurian (Wenlockian); England.

Diagnosis. Conical or fan-shaped colonies. Branches typically intermediate width, linear, essentially parallel, closely to intermediately spaced, dichotomously divided; dissepiments narrow to intermediate width, regularly spaced at intermediate distance; fenestrules oval to rectangular. Two rows of autozooecia per branch except three proximal to bifurcations; low central obverse keel with granular-cored nodes aligned in a single row. Superstructure not developed. Axial wall straight to zigzag; autozooecial chamber size small-end intermediate; autozooecia rectangular, parallelogram-shaped, or pentagonal in tangential section deep in endozone and parallelogram- to bean-shaped in section in shallow endozone, chamber length greater than width, chamber height greater than width and may equal length, chamber elongation varying from parallel with branch axis to angled from reverse proximal to frontal distal portions of chamber; superior hemiseptum present, inferior hemiseptum and diaphragms absent. Autozooecial apertures small to intermediate in diameter, short, variable in length depending on proximity to dissepiment, inclined laterally or distolaterally away from axial wall; peristome absent or partial, lacking prominent stylets or stellate structure; older autozooecia may be closed by planar terminal diaphragm. Polymorphs in form of isolated zooecia with enlarged chamber (?gynozooecia) occurring in some species. Granular skeleton present in reverse and axial walls of autozooecia but locally absent in transverse and lateral walls; extrazooecial skeleton laminated, traversed by abundant, moderate-size microstyles (modified after McKinney, pers. comm., 2007).

Remarks. *Fenestella* Lonsdale, 1839 differs from *Archaeofenestella* Miller, 1962 in absence of cystose diaphragms in autozooecia.

Occurrence. Silurian–Permian; worldwide.

Fenestella sp.

Figures 20E–20I, 21A–21B; Table 23

Material. SMF 40480–SMF 40484.

Exterior Description. Reticulate colonies with straight branches, bifurcated, joined by dissepiments. Autozooecia arranged in 2 alternating rows on branches, having circular apertures with moderately high peristomes, 2–4 spaced per length of a fenestrule. Peristomes containing 10–15 variously sized nodes, from which 3–6 are significantly larger than the others. Peristomal nodes 0.015–0.025 mm in diameter. Fenestrules oval shaped. Keel low. Keel nodes closely spaced, rounded to oval in shape. Microacanthostyles on the reverse colony surface abundant, regularly spaced in longitudinal rows, 0.005–0.010 mm in diameter. Single node in the centre of each dissepiment present.

Interior Description. Autozooecia rectangular to pentagonal in the mid tangential section; with well-developed short vestibule; axial wall straight; aperture positioned at distal end of chamber. Both superior and inferior hemisepta absent. Internal granular skeleton thin, continuous with obverse keel, nodes, peristome and across dissepiments. Outer lamellar skeleton thick.

Remarks. The present material differs from *Fenestella constricta* Waschurova, 1964 from the Lower Devonian (?Emsian) of Tajikistan in having wider branches (average branch width 0.29 mm *vs* 0.20 mm in *F. constricta*), and in the presence of nodes on dissepiments. The present material differs from *Fenestella vera* Ulrich, 1890 from the Middle Devonian (Givetian) of USA in slightly narrower branches (branch width 0.29 mm *vs*. 0.35 mm in *F. vera*), shorter fenestrules (fenestrule length 0.38 mm *vs* 0.50 mm in *F. vera*), and in presence of nodes on dissepiments.

Occurrence. Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian). Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Table 23. *Fenestella* sp. (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	25	0.29	0.018	6.38	0.25	0.32
Dissepiment width, mm	25	0.26	0.042	15.85	0.20	0.35
Fenestrule width, mm	25	0.19	0.042	22.70	0.12	0.30
Fenestrule length, mm	25	0.38	0.081	21.21	0.20	0.50
Distance between branch centres, mm	25	0.57	0.160	28.24	0.31	0.88
Distance between dissepiment centres, mm	25	0.56	0.097	17.31	0.40	0.85
Aperture width, mm	30	0.09	0.014	15.88	0.07	0.12
Aperture spacing along branch, mm	30	0.23	0.020	9.02	0.19	0.28
Aperture spacing diagonally, mm	30	0.20	0.019	9.73	0.16	0.24
Maximal chamber width, mm	30	0.09	0.006	6.64	0.08	0.11
Keel node diameter, mm	30	0.06	0.011	18.97	0.05	0.09
Keel node spacing, mm	30	0.30	0.044	14.68	0.22	0.42
Apertures per fenestrule length	30	2.4	0.568	23.36	2.0	4.0

Genus *Hemitrypa* Phillips, 1841

Type-species. *Hemitrypa oculata* Phillips, 1841. Devonian; Barton, South Devon, England.

Diagnosis. Reticulate colonies, conical or fan-shaped, planar or longitudinally pleated, frontal surface exterior if conical. Branches intermediate in width, linear to moderately sinuous, closely or intermediately spaced, dichotomously divided. Two rows of autozooecia per branch, increasing to four rows proximal of branch bifurcations in some species; low straight to sinuous central keel on obverse side of branch with high nodes, composed of core of granular skeleton and sheath of laminar skeleton. Laminar wall extensions of keel nodes fused together forming a fine meshwork of polygonal openings, each opening centred over a zooecial aperture

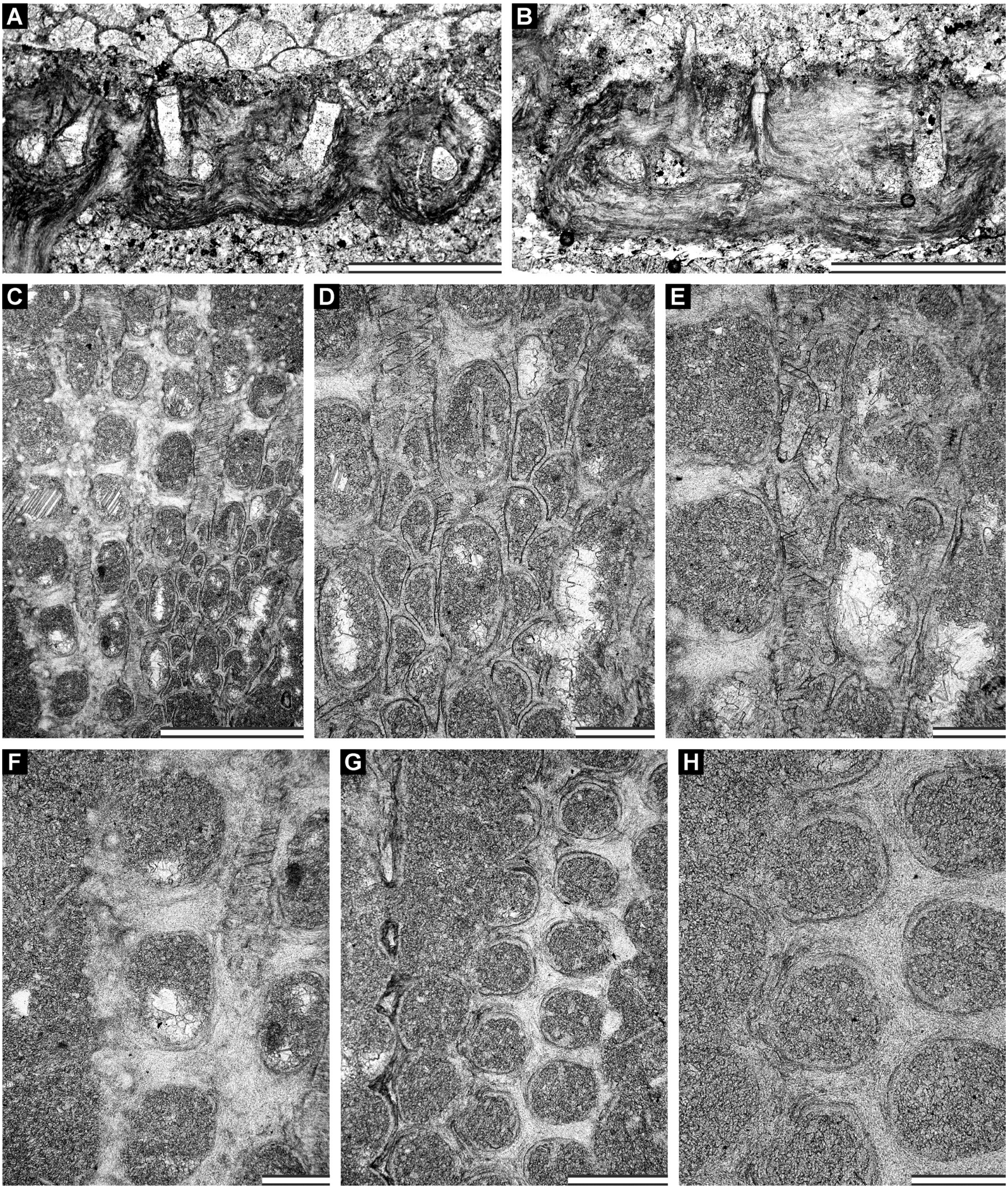


Figure 21. *Fenestella* sp., SMF 40481. **A**–**B,** Branch transverse section; *Hemitrypa lasutkiniae* Waschurova, 1964, SMF 40497; **C**–**E,** tangential section showing branches, fenestrules, autozooecial chambers and apertures; **F,** tangential section showing nodes on the reverse side of branches; **G**–**H,** tangential section showing protective superstructure, SMF 40497; scale bars = 1 mm (C), 0.5 mm (A–B), 0.2 mm (D–G), 0.1 mm (H).

in the branch below. Axial wall between autozooecial rows zigzag in tangential sections; zooecia not strongly inflated laterally, commonly quadrangular or pentagonal in tangential section deep within endozone, less commonly elongate triangular or semicircular, pentagonal to bean-shaped in shallower endozone; maximum diameter of zooecia corresponds with either length or height; transverse walls at intermediate or high angle to reverse wall; superior hemisepta absent or weakly developed, other interior structures absent. Small- to large-diameter distal tube typically short, opening frontally or slightly inclined laterally and perhaps distally; apertural peristome present or absent; terminal diaphragms planar where present, with central boss in some species. Heterozooecia are isolated zooecia with enlarged endozonal chambers (?gynozooecia) present in proximal parts of colonies, or spherically inflated distal tubes with diameters greater than branch width (?brood chambers). Zooecial walls of granular material that may be absent on obverse side near apertures; laminar extrazooecial skeleton traversed by small to moderate microstyles (modified after F. K. McKinney, pers. comm., 2007).

Remarks. *Hemitrypa* Phillips, 1841 is similar to *Pseudounitrypa* Nekhoroshev, 1926, but differs from it in the composition of the superstructure. The superstructure of *Hemitrypa* is produced by laminar wall extensions of keel nodes forming a meshwork of polygonal openings which are centred over zooecial apertures in the branch below, whereas openings in *Pseudounitrypa* are centred over the branches and terminate laterally over the centres of the fenestrules where the superstructural elements from adjacent branches meet and fuse.

Occurrence. Lower Devonian–Upper Carboniferous; worldwide.

Hemitrypa lasutkiniae Waschurova, 1964

Figures 21C–21H, 22A–22C; Table 24

1964 *Hemitrypa devonica* Nekhoroshev subsp. *lasutkiniae* Waschurova, p. 85, pl. 27, figs. 3–5.

2012 *Hemitrypa lasutkiniae* Waschurova, 1964 – Ernst *et al*., p. 725, figs. 18D, 18E, 19A–19F.

Material. SMF 40485–SMF 40533.

Description. Reticulate colonies with straight branches joined by dissepiments, forming cones with autozooecia opening to outside. Autozooecia arranged in two alternating rows on branches, having circular apertures with low peristomes, 2–3 spaced per length of a fenestrule. Peristomes smooth. Fenestrules oval to rectangular, varying in size. Openings in the superstructure irregularly shaped, rounded to petaloid, corresponding to positions of apertures, 0.12–0.17 mm in diameter. Superstructure containing small styles, 0.010–0.015 mm in diameter. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments, 0.05–0.07 mm thick on the branch reverse wall. Outer lamellar skeleton well developed, 0.07–0.12 mm thick on the branch reverse wall. Reverse colony surface containing large, irregularly sized nodes, 0.04–0.08 mm in diameter. Heterozooecia not observed.

Interior description. Autozooecia trapezoidal or pentagonal in mid tangential section; low and elongated, with short vestibule in longitudinal section. Axial wall between autozooecial rows zigzag in tangential sections; aperture positioned at distal end of chamber. Hemisepta absent.

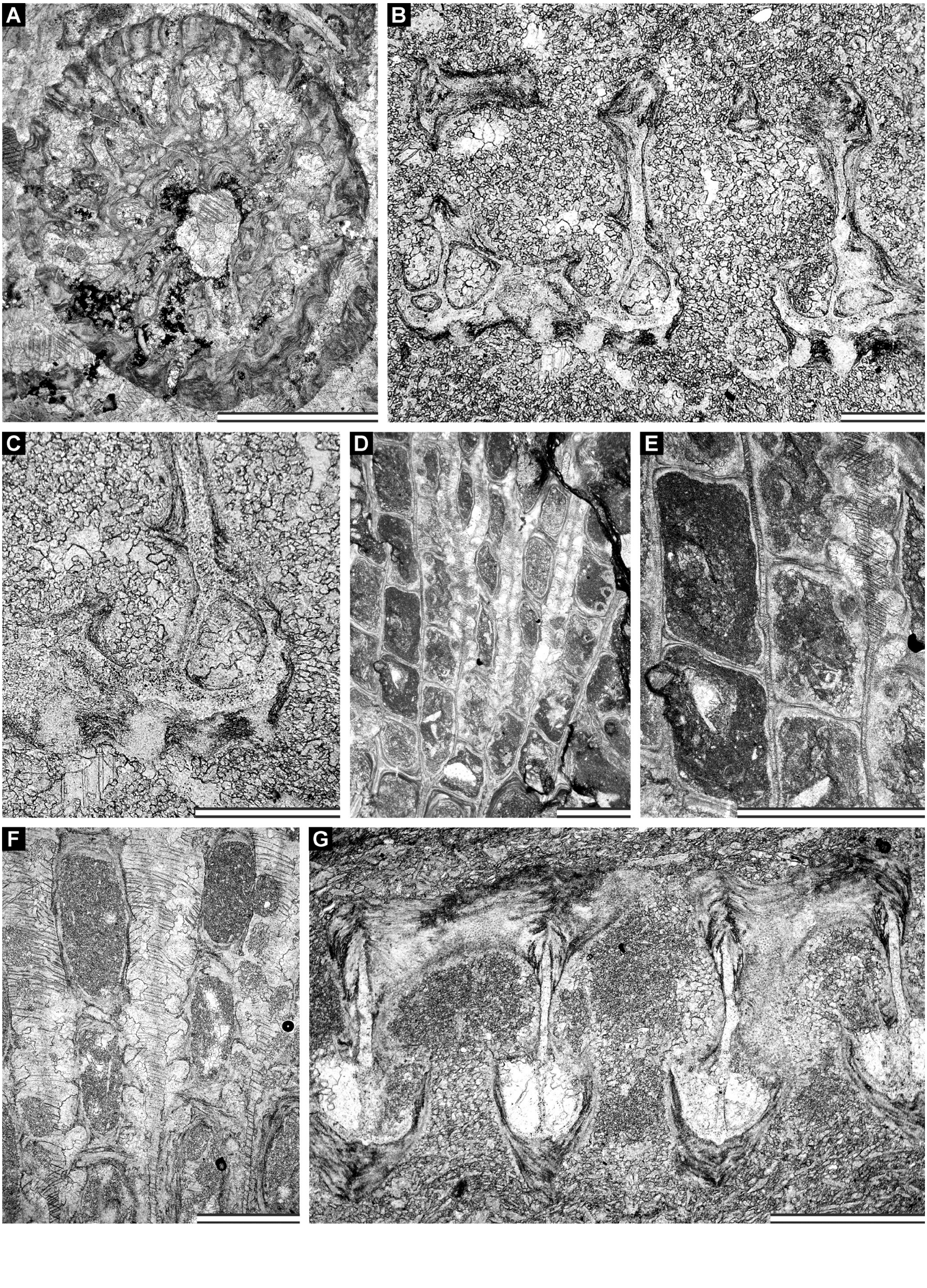
Remarks. The present material is similar to *Hemitrypa lasutkiniae* Waschurova, 1964 from the Lower Devonian (?Emsian) of Tajikistan, in having large nodes on the reverse side, the shape of the autozooecia and the size of the elements of the meshwork. *Hemitrypa lasutkinae* is similar to *H. kulalica* Waschurova, 1964 (p. 83–84, pl. 6, fig. 4) in general morphology and the presence of nodes on the reverse surface, but differs in having slightly larger fenestrules (fenestrule width 0.13–0.30 mm *vs* 0.15–0.25 mm in *H. kulalica*; fenestrule length 0.26–0.52 mm *vs* 0.25–0.35 mm in *H. kulalica*). *Hemitrypa lasutkinae* is similar to *H. mimicra* McKinney & Kříž, 1986 from the Lower Devonian

Table 24. *Hemitrypa lasutkiniae* Waschurova, 1964 (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	24	0.24	0.028	11.63	0.19	0.29
Dissepiment width, mm	30	0.15	0.023	15.48	0.09	0.18
Fenestrule width, mm	30	0.20	0.039	19.63	0.13	0.30
Fenestrule length, mm	30	0.37	0.062	16.80	0.26	0.52
Distance between branch centres, mm	30	0.42	0.057	13.42	0.30	0.51
Distance between dissepiment centres, mm	30	0.51	0.048	9.47	0.44	0.65
Aperture width, mm	15	0.09	0.014	15.30	0.07	0.11
Aperture spacing along branch, mm	8	0.22	0.023	10.59	0.18	0.25
Maximal chamber width, mm	30	0.10	0.008	7.92	0.09	0.12
Apertures per fenestrule length	20	2.6	0.510	20.02	2.0	3.0
Node diameter, mm (reverse surface)	20	0.07	0.010	15.38	0.04	0.08
Superstructure opening diameter, mm	30	0.15	0.015	9.95	0.12	0.17

Figure on next page

Figure 22. A–C, *Hemitrypa lasutkiniae* Waschurova, 1964; **A,** transverse section of the colony, SMF 40517; **B–C,** transverse section of branches showing autozooecial chambers, protective superstructure and nodes on the reverse surface, SMF 40496; **D–G,** *Tectulipora pannosa* (Počta, 1894); **D–E,** tangential section showing branches with autozooecia and protective superstructure, SMF 40539; **F,** tangential section showing branches with autozooecia, SMF 40543; **G,** transverse branch section showing autozooecial chambers and protective superstructure, SMF 40549; scale bars = 1 mm (A, D–E), 0.5 mm (F–G), 0.2 mm (B–C).


A
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(Pragian) of Czech Republic, but differs by presence of nodes on the reverse side of branches.

Occurrence. Tajikistan; Lower Devonian (?Emsian). Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains); Lebanza Formation, Lower Devonian (Pragian). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian). Guadámez-2, Ossa-Morena Zone (SW Spain); Lower Devonian (Emsian).

Family SEMICOSCINIIDAE Morozova, 1987
Genus *Tectulipora* Hall, 1888

Typespecies. *Fenestella* (*Hemitrypa*) *lata* Hall, 1883. Middle Devonian; Canada, Ontario.

Diagnosis. Reticulate colonies, conical or fan-shaped, planar or longitudinally pleated, frontal surface exterior if conical. Branches wide, moderately sinuous, closely or intermediately spaced, dichotomously divided. Two rows of autozooecia per branch. Straight to sinuous, high club-shaped median keel on obverse side of branch, composed of core of granular skeleton and sheath of laminar skeleton. Axial wall between autozooecial rows straight in tangential sections, continuing unbroken in superstructure; superstructure corresponding with underlying branches and dissepiments or with autozooecial apertures, consisting of laterally expanded laths borne on continuous skeletal sheets from branches and dissepiments. Autozooecia not strongly inflated laterally, commonly rectangular in deep tangential section; transverse walls at intermediate or high angle to reverse wall; hemisepta absent. Intermediate- to large-diameter short distal tube, opening frontally or slightly inclined laterally; apertural peristome present or absent; terminal diaphragms planar where present, with central boss in some species. Laminar extrazooecial skeleton traversed by small to moderate microstyles.

Remarks. *Tectulipora* Hall, 1888 differs from *Loculipora* Hall, 1885 in having less sinuous branches which are joined by dissepiments instead of anastomoses in *Loculipora*. Transverse connections in the superstructure of *Tectulipora* do not contact with dissepiments, whereas the superstructure in *Loculipora* is produced by extensions of both median keels and dissepiments.

Occurrence. Lower–Upper Devonian; North America and Eurasia.

Tectulipora pannosa (Počta, 1894)

Figure 22D–22G; Table 25

for full synonymy see McKinney & Kříž (1986, p. 47)

Material. SMF 40534–SMF 40557.

Exterior Description. Reticulate colonies, conical, frontal surface exterior. Branches intermediate in width, straight, intermediately spaced, dichotomously divided, joined by straight wide dissepiments. Autozooecia arranged in two weakly alternating rows on branches, having circular apertures with low peristomes, 3–5 spaced per length of a fenestrule. Fenestrules oval to rectangular, varying in size. Straight high club-shaped median keel on obverse side of branches, composed of core of granular skeleton and sheath of laminar skeleton; superstructure corresponding with underlying branches, consisting of laterally expanded laths borne on continuous skeletal sheets from branches. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments, 0.02–0.04 mm thick on the branch reverse wall. Outer lamellar skeleton well developed, 0.10–0.22 mm thick on the branch reverse wall, traversed by small microstyles. Reverse colony smooth. Heterozooecia not observed.

Interior description. Autozooecial chambers rectangular in mid tangential section, short and relatively high, with moderately short vestibules. Axial wall between autozooecial rows straight in tangential sections, continuing unbroken in superstructure. Hemisepta absent. Terminal diaphragms planar.

Remarks. *Tectulipora pannosa* (Počta, 1894) is similar to *T. tuberculata* Ernst *et al*., 2012 from the Lebanza Formation of northwestern Spain, but differs from it in absence of tubercles on the reverse side and the protective structure, as well as in having fewer autozooecial apertures per fenestrule length (3–5 *vs* 4–7 in *T. tuberculata*).

Occurrence. Czech Republic; Koněprusy Limestone, Lower Devonian (Pragian). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

Table 25. *Tectulipora pannosa* (Počta, 1894) (three colonies measured). Abbreviations as for Table 1.

	N	X	SD	CV	MIN	MAX
Branch width, mm	20	0.35	0.041	11.65	0.29	0.42
Dissepiment width, mm	20	0.23	0.048	20.58	0.15	0.30
Fenestrule width, mm	20	0.28	0.061	21.60	0.17	0.40
Fenestrule length, mm	10	0.87	0.307	35.21	0.50	1.25
Distance between branch centres, mm	30	0.55	0.088	16.08	0.33	0.78
Distance between dissepiment centres, mm	30	1.09	0.256	23.56	0.73	1.60
Aperture width, mm	20	0.10	0.008	8.51	0.08	0.12
Aperture spacing along branch, mm	20	0.25	0.027	10.74	0.21	0.30
Apertures per fenestrule length	17	3.8	0.664	17.64	3.0	5.0
Maximal chamber width, mm	20	0.13	0.014	10.79	0.10	0.15

Family ACANTHOCLADIIDAE Ulrich, 1890
Genus *Penniretepora* d`Orbigny, 1849
[=*Acanthopora* Young & Young, 1875; *Pinnatopora* Vine, 1883]

Type-species. *Retepora pluma* Phillips, 1836. Mississippian; Yorkshire, England.

Diagnosis. Colonies consisting of straight main branches with frequent lateral branches (pinnate); two rows of autozooecia both on main and lateral branches; autozooecia rectangular to pentagonal or trapezoid in mid-tangential section; hemisepta absent; superstructure absent; keel low with or without nodes.

Remarks**.** *Penniretepora* d`Orbigny, 1849 differs from *Filites* Počta, 1894 in the shape of autozooecia in mid-tangential section (rectangular to pentagonal or trapezoid *vs* triangular in *Filites*). Moreover, the pinnae in *Filites* are recurved proximally, whereas pinnae in *Penniretepora* are diverting in the distal direction (Suárez Andrés & Wyse Jackson, 2017). *Penniretepora* differs from *Gorjunopora* Ernst *et al*., 2015 in absence of hemisepta.

Occurrence. Devonian–Permian; worldwide.

Penniretepora spinosa (Počta, 1894)
Figure 23A–23I; Table 26

1894 *Filites spinosus* Počta, p. 112, pl. 10, figs. 30, 31.
1986 *Penniretepora spinosa* (Počta, 1894) – McKinney & Kříž, p. 77–78, fig. 47.

Material. SMF 40558–SMF 40579.

Exterior Description**.** Pinnate colonies consisting of straight main branches with frequent lateral branches. Main branches 0.40–0.77 mm wide, lateral branches 0.21–0.32 mm wide, diverging at angles 61–78° from main branches, spaced 0.45–0.80 mm from centre to centre. Autozooecia having circular apertures surrounded by apertural nodes, arranged in two rows both on main and lateral branches; regularly one aperture at the base of each lateral branch and one aperture between two neighbouring lateral branches. Median keels low, undulating, nodes moderate in size, closely spaced. Reverse side smooth.

Interior Description**.** Autozooecial chambers arranged in two alternating rows on branches, pentagonal to trapezoidal in mid-tangential section both on main and secondary branches, short, inflated, with moderately long vestibules. Axial wall straight on the main branches; strongly undulating to zigzag from base to crest on the lateral branches. Hemisepta absent. Apparent reproductive heterozooecia in form of isolated zooecia with enlarged endozonal chambers present. Chambers rounded, 0.13–0.15 mm in diameter. Nanozooecia absent. Extrazooecial skeleton moderately developed, traversed by abundant microstyles. Microstyles 0.005–0.010 mm in diameter.

Table 26. *Penniretepora spinosa* (Počta, 1894) (seven colonies measured). Abbreviations as for Table 1.

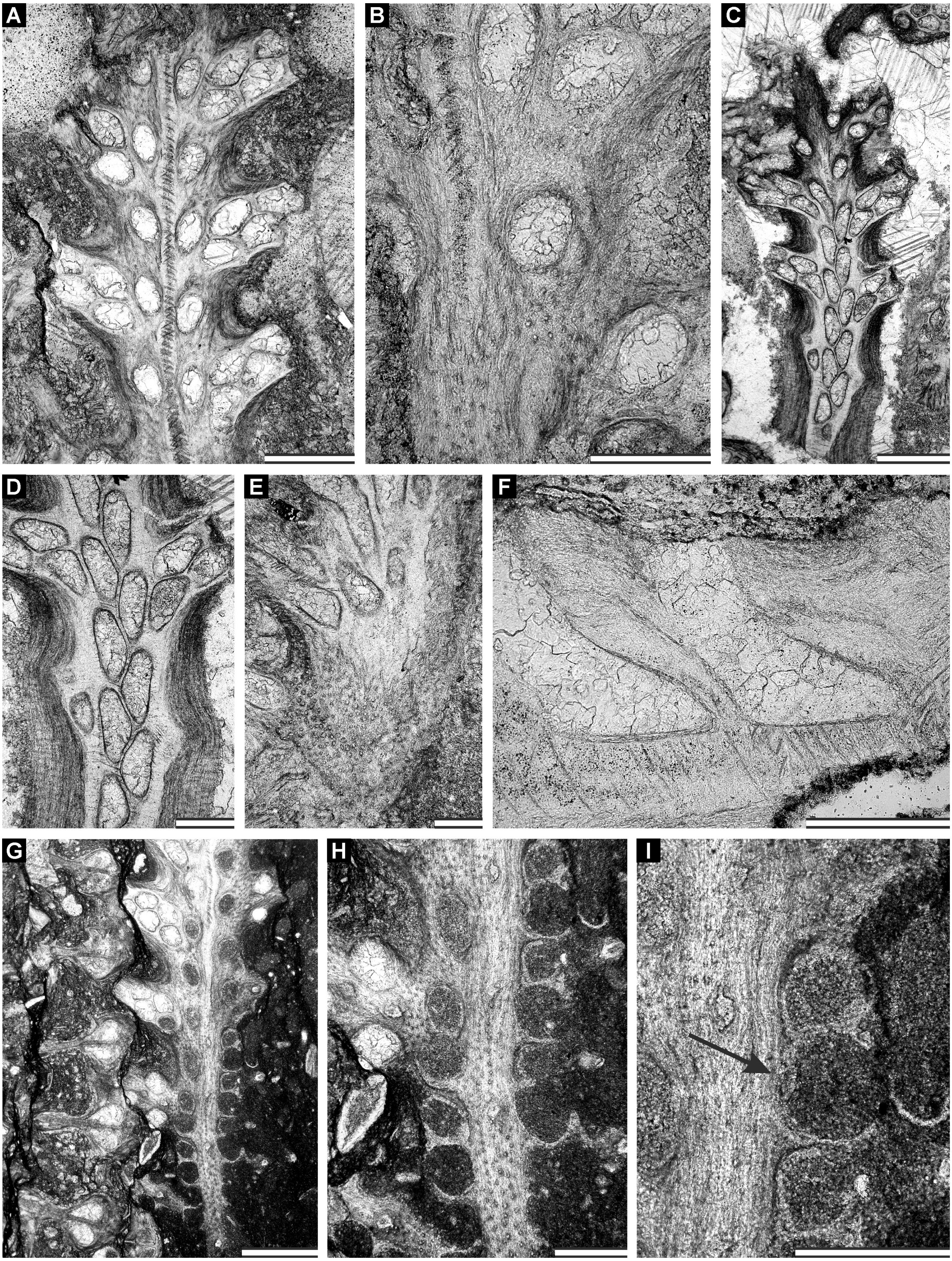
	N	X	SD	CV	MIN	MAX
Main branch width, mm	10	0.55	0.102	18.48	0.40	0.77
Lateral branch width, mm	25	0.28	0.040	14.32	0.21	0.40
Lateral branch spacing, mm	25	0.59	0.080	13.57	0.45	0.80
Aperture width, mm	25	0.10	0.010	10.11	0.08	0.11
Aperture spacing along branch, mm	25	0.29	0.037	12.63	0.24	0.40
Aperture spacing diagonally, mm	16	0.29	0.023	7.88	0.23	0.31
Maximal chamber width, mm	15	0.10	0.012	11.90	0.09	0.13
Keel node diameter, mm	14	0.04	0.010	22.66	0.03	0.06
Keel node spacing, mm	8	0.28	0.063	22.56	0.19	0.37

Remarks. *Penniretepora spinosa* (Počta, 1894) differs from *P. bohemica* (Prantl, 1932) from the Lower Devonian (Emsian–Eifelian) of Czech Republic and NW Spain in having thinner branches (average main branch width 0.54 mm *vs* 0.94 mm in *P. bohemica*) as well as in smaller autozooecial apertures (average aperture width 0.09 mm *vs* 0.11 mm in *P. bohemica*).

Occurrence. Czech Republic; Koněprusy Limestone, Lower Devonian (Pragian). Peñón Cortado, Ossa-Morena Zone (SW Spain); Lower Devonian (Pragian).

DISCUSSION

Twenty-eight bryozoan species are described from the Lower Devonian (Pragian–Emsian) deposits of the Ossa-Morena Zone (SW Spain): one cyclostome *Diploclemella serenensis* n. gen. n. sp., two cystoporates *Altshedata gracilis* Ernst *et al*., 2012 and *Fistuliporella* sp., sixteen trepostomes *Leioclema arauzensis* Ernst *et al*., 2012, *Leioclema* cf. *incomposita* Duncan, 1939, *Leioclema* sp., *Atactotoechus* cf. *casey* Duncan, 1939, *Anomalotoechus* sp., *Leptotrypa parva* n. sp., *L. modesta* n. sp., *Leptotrypella armata* Ernst *et al*., 2012, *L.* spp. (1–4), *Loxophragma* sp., *Eridotrypella* sp., *Boardmanella spinigera* n. sp., *Cordobella tenuis* n. gen. n. sp., five cryptostomes *Orthopora spinosa* Ernst *et al*., 2012, *Vidronovella elegantula* Ernst *et al*., 2012, *Paracuneatopora striata* Ernst, 2008b, *Serenella dubia* n. gen. n. sp., and *Intrapora* sp., four fenestrates *Fenestella* sp., *Hemitrypa lasutkiniae* Waschurova, 1964, *Tectulipora pannosa* (Počta, 1894), and *Penniretepora spinosa* (Počta, 1894).
From this fauna (Fig. 24), twelve species are restricted to the sediments of the Peñón Cortado section (Pragian): *Altshedata gracilis* Ernst *et al*., 2012, *Leioclema* cf. *incomposita* Duncan, 1939, *Leioclema* sp., *L. modesta* n. sp., *Leptotrypella armata* Ernst *et al*., 2012, *Leptotrypella* spp. (3–4), *Loxophragma* sp., *Cordobella tenuis* n. gen. n. sp., *Paracuneatopora striata* Ernst, 2008b, *Tectulipora pannosa* (Počta, 1894), and *Penniretepora spinosa* (Počta, 1894). Seven species occur in the Guadámez-2 section (Emsian) only: *Atactotoechus* cf. *casey* Duncan, 1939, *Anomalotoechus* sp., *Leptotrypa parva* n. sp., *Leptotrypella* spp. (1–2), *Eridotrypella* sp., and *Boardmanella spinigera* n. sp. Both profiles share the distribution of nine species: *Diploclemella serenensis* n. gen. n. sp., *Fistuliporella* sp., *Leioclema arauzensis* Ernst *et al*., 2012, *Orthopora spinosa* Ernst *et al*., 2012, *Vidronovella elegantula* Ernst *et al*., 2012, *Serenella dubia* n. gen. n. sp., *Intrapora* sp., *Fenestella* sp., *Hemitrypa lasutkiniae* Waschurova, 1964.
The studied fauna is dominated by the trepostome taxa (16 species). Cystoporate bryozoans are remarkably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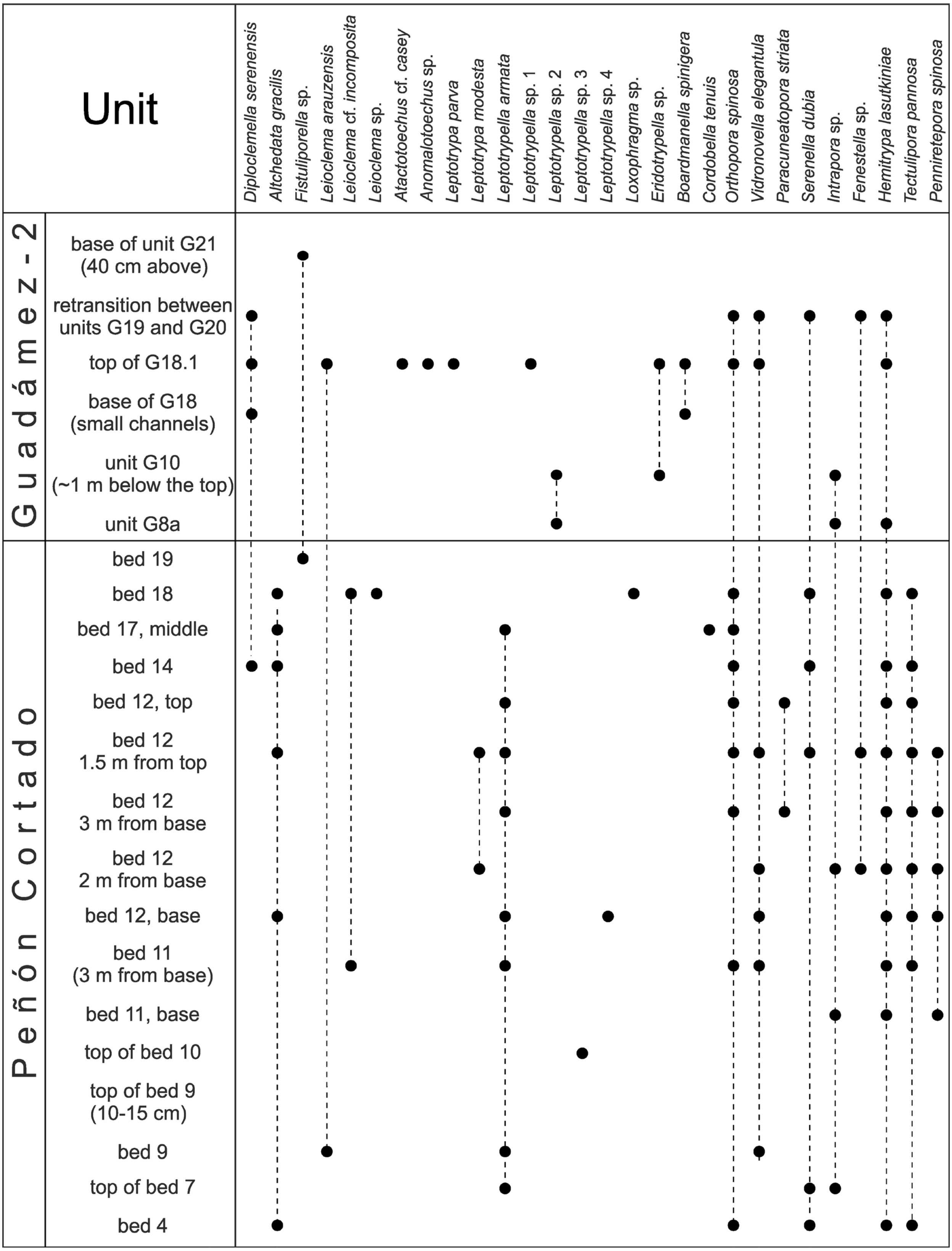

Figure 24. Distribution of bryozoan species within the sampled units of the Guadámez-2 and Peñón Cortado sections.

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Figure 23. *Penniretepora spinosa* (Počta, 1894). **A–B,** Tangential section showing autozooecial chambers and apertures, SMF 40573; **C–D,** tangential section showing autozooecial chambers and apertures, SMF 40571; **E,** tangential section showing styles on the reverse side, SMF 40564; **F,** longitudinal section showing autozooecial chambers, SMF 40568; **G–I,** SMF 40579, tangential section showing apertures with apparent reproductive heterozooecia (arrow); scale bars = 0.5 mm (A, C, G), 0.2 mm (B, D–F, H, I).

rare, represented by only two species. Fenestrates and cryptostomes (rhabdomesines and ptilodictyines) are represented by four and five species, respectively, showing moderate diversity. Rhabdomesines *Orthopora spinosa* Ernst *et al.*, 2012 and *Vidronovella elegantula* Ernst *et al.*, 2012 occur abundantly within the studied sections.

Bryozoan species from the studied fauna show high diversity of growth forms. Their sizes are rather moderate, only the species *Leioclema* cf. *incomposita* Duncan, 1939, *Atactotoechus* cf. *casey* Duncan, 1939 and *Anomalotoechus* sp. produced colonies approaching the diameters of 5–10 mm. Other species do not exceed thicknesses of 3 mm.

The majority of species developed branched ramose colonies with cylindrical stems (Tab. 27): *Diploclemella serenensis* n. gen. n. sp., *Leioclema* sp., *Leptotrypella armata* Ernst *et al.*, 2012, *L.* spp. (1–4), *Anomalotoechus* sp., *Loxophragma* sp., *Eridotrypella* sp., *Boardmanella spinigera* n. sp., *Orthopora spinosa* Ernst *et al.*, 2012, *Vidronovella elegantula* Ernst *et al.*, 2012, *Paracuneatopora striata* Ernst, 2008b, *Serenella dubia* n. gen. n. sp.

Six species are encrusting: *Altshedata gracilis* Ernst *et al.*, 2012, *Fistuliporella* sp., *Leioclema arauzensis* Ernst *et al.*, 2012, *Leptotrypa parva* n. sp., *L. modesta* n. sp., *Cordobella tenuis* n. gen. n. sp., *Leioclema* cf. *incomposita* Duncan, 1939 and *Atactotoechus* cf. *casey* Duncan, 1939 developed irregular massive colonies, with abundant secondary overgrowths.

Table 27. Distribution of growth forms in the studied bryozoan fauna of Sierra Morena.

	branched	encrusting	massive	leaf-like	reticulate	pinnate
Diploclemella serenensis	x					
Altchedata gracilis		x				
Fistuliporella sp.		x				
Leioclema arauzensis		x				
Leioclema cf. *incomposita*			x			
Leioclema sp.	x					
Atactotoechus cf. *casey*			x			
Anomalotoechus sp.	x					
Leptotrypa parva		x				
Leptotrypa modesta		x				
Leptotrypella armata	x					
Leptotrypella sp. 1	x					
Leptotrypella sp. 2	x					
Leptotrypella sp. 3	x					
Leptotrypella sp. 4	x					
Loxophragma sp.	x					
Eridotrypella sp.	x					
Boardmanella spinigera	x					
Cordobella tenuis		x				
Orthopora spinosa	x					
Vidronovella elegantula	x					
Paracuneatopora striata	x					
Serenella dubia	x					
Intrapora sp.				x		
Fenestella sp.					x	
Hemitrypa lasutkiniae					x	
Tectulipora pannosa					x	
Penniretepora spinosa						x

Intrapora sp. possesses bifoliate, leaf-like colonies. Fenestrates developed mostly reticulate colonies of various appearance: *Fenestella* sp., *Hemitrypa lasutkiniae* Waschurova, 1964, *Tectulipora pannosa* (Počta, 1894). *Penniretepora spinosa* (Počta, 1894) developed pinnate (feather-shaped) colonies.

The studied bryozoan fauna shows some distinct relations to the bryozoan faunas from contemporary sediments. Five species are previously known from the Lebanza Formation (Pragian) of Arauz Sur (Cantabrian Mountains, NW-Spain): *Altshedata gracilis* Ernst *et al.*, 2012, *Leioclema arauzensis* Ernst *et al.*, 2012, *Orthopora spinosa* Ernst *et al.*, 2012, *Vidronovella elegantula* Ernst *et al.*, 2012, and *Hemitrypa lasutkiniae* Waschurova, 1964 (Ernst *et al.*, 2012). The latter species was originally described from the Lower Devonian (probably Emsian) of Tajikistan. *Orthopora spinosa* has also been recorded from the Lower Devonian (Emsian) of Bretagne (France). Two species are previously known from the Lower Devonian (Pragian) of the Czech Republic: *Tectulipora pannosa* (Počta, 1894) and *Penniretepora spinosa* (Počta, 1894). The species *Paracuneatopora striata* Ernst, 2008b is known from the Lower Devonian (Pragian) of Morocco and Czech Republic.

Two species are compared with Middle Devonian bryozoans of USA: *Leioclema* cf. *incomposita* Duncan, 1939 and *Atactotoechus* cf. *casey* Duncan, 1939. Moreover, *Leioclema* cf. *incomposita* Duncan, 1939 shows similarity to the species identified as *Leioclema incomposita* Duncan, 1939 from the Lower Devonian (middle Lochkovian) of Sierra de Guadarrama, Spain (Ernst & May, 2012).

CONCLUSIONS

Twenty-eight bryozoan species are described from two sections of the Lower Devonian deposits of the Ossa-Morena Zone (SW Spain) including one cyclostome, two cystoporates, sixteen trepostomes, four cryptostomes, and four fenestrates.

Three genera with one new species, respectively, as well as three species are new.

Twelve species are restricted to the sediments of the Peñón Cortado section (Pragian), seven species occur in the Guadámez-2 section (Emsian), and nine species occur in both sections.

The majority of species developed branched ramose colonies with cylindrical stems (15), followed by encrusting (6), reticulate (3), irregular massive (2), leaf-like (1) and pinnate (1) growth forms.

The studied bryozoan fauna shows some distinct palaeobiogeographic relations to the bryozoans from the Lower Devonian of NW Spain, Morocco, and Czech Republic.

Supplementary information. There are no supplementary files for this publication. New taxonomic names proposed in this paper, and the nomenclatural acts it contains, have been registered in ZooBank, the online registration system for the ICZN: http://zoobank.org/References/A021FBED-D870-4FFE-B740-3AD7820AD321

Authors contributions. AE and SR collected the bryozoan material during the field trip. SR wrote Introduction and Geological Background chapters, created Figures 1–3, and provided selection of thin sections for study. AE made thin sections from the collected material, conducted the taxonomic descriptions and evaluation of the fauna. He created Figures 4–24.

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