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## TREPOSTOME BRYOZOANS FROM THE LOWER - MIDDLE DEVONIAN OF NW SPAIN

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**Key words:** Bryozoa, taxonomy, Devonian, Spain, palaeobiogeography.

**Abstract.** The present paper presents descriptions of 11 trepostome bryozoan species from the material deposited at the Geological Centrum Göttingen, Germany, and Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Netherlands. The studied material comes from the Lower to Middle Devonian (Emsian-Eifelian) deposits of different localities in Cantabrian Mountains, NW Spain. Three species are new: *Leptotrypella maculata* n. sp., *Anomalotoechus tabulatus* n. sp. and *Eifelipora tenuis* n. sp. The genus *Mongoloclema* is reported for the first time from the Devonian of Europe. The described fauna displays palaeobiogeographic relations to the Lower Devonian (Pragian) of Bohemia and to the Middle Devonian of Kazakhstan and Michigan (USA).

**Riassunto.** Vengono descritte 11 specie di briozoi trepostomi su materiale depositato nel Geological Centrum Göttingen, Germania, e nel Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Olanda. Il materiale studiato proviene dal Devoniano Inferiore e Medio (Emsiano-Eifeliano) di diverse località dei monti Cantabrigi nel NO della Spagna. Tre sono le specie nuove: *Leptotrypella maculata* n. sp., *Anomalotoechus tabulatus* n. sp. e *Eifelipora tenuis* n. sp. Il genere *Mongoloclema* viene identificato per la prima volta nel Devoniano dell'Europa. La fauna descritta ha rapporti paleobiogeografici con il Devoniano Inferiore (Pragiano) della Bohemia e con il Devoniano Medio del Kazakhstan e del Michigan (USA).

### Introduction

Bryozoa are abundant and diverse in the Devonian worldwide (Cuffey & McKinney 1979). This period was a time of important changes in the structure and global composition of bryozoan faunas (Bigey 1985; Horowitz et al. 1996). However, despite their abundance and importance, Devonian bryozoan faunas in Europe have been scarcely investigated. Whereas the

bryozoans from the Lower Devonian of Bohemia and France are relatively well studied (Bigey 1972, 1980, 1981, 1986; McKinney & Kříž 1986; Ernst 2008b, 2009; Ernst & May 2009), the Lower Devonian bryozoans of Spain remain poorly known. A few recent publications have focused on the Devonian bryozoans of Spain (Suarez Andrés 1998, 1999a-c; Suárez Andrés & González 2000a, b). These papers contain descriptions of several species from the Moniello Formation (late Emsian - early Eifelian) of Cantabrian Zone (NW Spain), mainly fenestrate taxa were described.

The present paper provides taxonomic descriptions of trepostome bryozoans from the Lower to Middle Devonian (Emsian-Eifelian) of the Cantabrian Mountains, NW Spain (Fig. 1). This study is a part of a project supported by the Deutsche Forschungsgemeinschaft, titled "Evolution, palaeoecology and palaeobiogeography of the Devonian Bryozoa of Europe and adjacent areas" (ER 278/4-1 u. 2) which was conducted during 2006-2009. The aim of the project was to carry out a comprehensive study of regional bryozoan faunas and their evaluation in regarding evolution, palaeoecology and palaeobiogeography.

### Geological setting

In the Cantabrian Mountains of northern Spain, a well-developed succession of Palaeozoic rocks is exposed. This succession consists of an alternation of siliclastic shelf sediments and carbonate platform rocks. The entire succession experienced only moderate deformation during the Variscan orogeny (e.g., Comte 1959;



Fig. 1 - Position of study area in Cantabrian Mountains, NW Spain (rectangle).

Truyols et al. 1990). Carbonate platform deposits are prominent throughout the Devonian and Carboniferous. During the Devonian, a carbonate ramp (Abelgas Formation; Keller 1988, 1997) and two carbonate shelves became established in the Cantabrian Mountains, the Santa Lucía Formation and the Portilla Formation (Comte 1959), respectively. These carbonate platform deposits are highly fossiliferous and many different groups have been described from these rocks so far.

Most of the studied material for the present paper is labelled as “La Vid Formation (Emsian), Cantabrian Mountains, NW Spain”. These samples were collected before the modern understanding of the Devonian stratigraphy of NW Spain. The “La Vid Formation” as understood by collectors represents apparently the upper part of the La Vid Group corresponding to the Esla Formation (Keller 1988, 1997; Fig. 2). Another part of the material is clearly labelled as collected from the Santa Lucía Formation which overlies the Esla Formation (see chapter Material and methods).

The Esla Formation is represented by deposition of pelagic subtidal shales that gradually change into variegated marlstones, limestones and shales of Villayandre Member (*serotinus* conodont zone) in the uppermost part of the formation (Keller 1988, 1997; Keller & Grötsch 1990; Hoffman & Keller 2006). The base of the Esla Formation is dated as *gronbergi* conodont zone (Keller 1997). The Esla Formation reflects a successive shallowing of the depositional environment caused by eustatic sea-level changes. Above this succession, the carbonate platform of the Santa Lucía Formation was established.

The Emsian-Eifelian Santa Lucía Formation was deposited across a vast carbonate shelf (De Coo 1974; Méndez Bediá 1976; Buggisch et al. 1982; Hofmann & Keller 2006) from the *serotinus* through the *partitus* conodont zones (Buggisch et al. 1982; García López & Sanz López 2002). Three major facies belts were present on this shelf. In the north, restricted lagoonal deposits with peritidal facies are found that include abundant terrigenous siliciclastic mud. To the south and west, this lagoon was separated from open-marine influence by a reef belt in which major individual build-ups are aligned parallel to depositional strike. On the seaward side of this reef belt, open-marine limestones are found, either as autochthonous deposits or as debris derived from the reefs.

**Materials and methods**

Material for this study comes from collections of the Nationaal Natuurhistorisch Museum (Naturalis) in Leiden, Netherlands, and the Geological Centrum Göttingen. For the study, 130 randomly as well as precisely oriented thin sections were made from the extensive rock material. Two sets of thin sections were used. The first set was prepared from the rock material housed at the Geological Centrum Göttingen, Germany. These thin sections have collection numbers GZG.IN.0.010.512 and GZG.IN.0.010.529. Separate thin sections of the same sample are numbered by adding a subnumber suffix.

<b>Lower Devonian</b>	<b>Emsian</b>	<i>patulus</i>	Santa Lucía Fm.		<b>La Vid Group</b>	
		<i>serotinus</i>	Villayandre Member			
		<i>laticostatus</i>	Shale Unit	Sagüera Member		Esla Fm.
		<i>inversus</i>				
		<i>gronbergi</i>				
	<b>Pragian</b>	<i>dehiscens</i>	Millaró Limestone	Limestone / Marlstone Member		
		<i>pireneae</i>	Dolomite Member	Wavy Limestone Member upper part		
		<i>sulcatus</i>		Wavy Limestone Member lower part		
		<i>pesavis</i>		Lumajo Member		
	<i>delta</i>					
	<b>Lochkovian</b>	<i>eurekaensis</i>	transitional unit			
		<i>hesperius</i>	San Pedro Fm. (Mbr. C)			

Fig. 2 - Stratigraphy of the Lower Devonian of the Asturo-Leonese Basin (after Keller 1997).

Sample GZG.IN.0.010.512 refers to “La Vid Formation, profile SE Villayandre, units 9-11, Lower Devonian (Emsian)” (= lower part of the Esla Formation, Lower Devonian, Emsian), profile southeast the village of Villayandre, Cantabrian Mountains, NW Spain. From this sample 37 thin sections were prepared.

Sample GZG.IN.0.010.529 comes from the Marl Unit (? = Villayandre Member, serotinus conodont zone) of Esla Formation, Lower Devonian (Emsian), profile near the village of Villayandre, Cantabrian Mountains, NW Spain. From this sample 7 thin sections were prepared.

Another set of material includes rock samples housed at the Nationaal Natuurhistorisch Museum (Naturalis) in Leiden, Netherlands, registered under numbers RGM 211 536 - RGM 211549. Unfortunately, not all samples possess necessary information on locality and stratigraphy. From this material 86 thin sections were prepared.

Sample RGM 211 536 refers to “La Vid Formation (Lower Devonian, Emsian) in the vicinity of Portilla de Luna (42°56'N 5°49' W)” (? = Esla Formation, Lower Devonian, Emsian).

Samples RGM 211 537-541 and RGM 211 544 come from the Santa Lucía Formation (Lower Devonian, Emsian-Eifelian) of Caldas de Luna (42°56'N 5°52' W).

Sample RGM 211 542 refers to “La Vid Formation near Collada del Campo de la Puerta (42°55'N 5°02'W)” (? = Esla Formation, Lower Devonian, Emsian).

Samples RGM 211 543 and RGM 211 547 refer to “Middle part of the La Vid Formation (Lower Devonian, Emsian) near Puerto de la Cubilla (42°59'N 5°54'W)” (? = Esla Formation, Lower Devonian, Emsian).

Sample RGM 211 545 has no exact information, refers to “La Vid Formation of NW Spain” (? = Esla Formation, Lower Devonian, Emsian).

Sample RGM 211 546 refers to “La Vid Formation, section near the village of Villayandre (42°54'N 5°09'W), Cantabrian Mountains, NW Spain” (? = Esla Formation, Lower Devonian, Emsian).

Samples RGM 211 548-549 refer to the “La Vid Formation” (? = Esla Formation, Lower Devonian, Emsian), localities unknown, Cantabrian Mountains, NW Spain.

Bryozoans were investigated in thin sections using binocular microscope in transmitted light. Morphologic character terminology is partly adopted from Anstey & Perry (1970). The following morphologic characters were measured and used for statistics in the studied material:

Branch width, colony thickness, exo- (endo-) zone width, autozoecial aperture width, aperture spacing, acanthostyle diameter, meso- (exila-) zoecia diameter, autozoecial (mesozoecial) diaphragm spacing, number of meso- (exila-) zoecia and acanthostyles surrounding each autozoecial aperture, wall thickness in exozone, and macular diameter (spacing).

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 (see Appendix).

## Systematic palaeontology

Phylum **Bryozoa** Ehrenberg, 1831

Class **Stenolaemata** Borg, 1926

Order **Trepotomata** Ulrich, 1882

Suborder **Halloporina** Astrova, 1965

Family **Heterotrypidae** Ulrich, 1890

## Genus *Leioclema* Ulrich, 1882

[= *Lioclema* Ulrich, 1882]

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

**Diagnosis:** Encrusting, branched, less commonly massive colonies. Autozoecia with polygonal to rounded-polygonal, sometimes petaloid apertures. Autozoecial diaphragms rare. Mesozoecia abundant, with abundant diaphragms, often beaded. Acanthostyles abundant, commonly large. Autozoecial walls thin in endozone; laminated, regularly thickened in exozones (modified after Astrova 1978).

**Comparison.** *Leioclema* Ulrich, 1882 differs from *Heterotrypa* Nicholson, 1879 in having rare autozoecial diaphragms and abundant acanthostyles and mesozoecia, from *Stigmatella* Ulrich & Bassler, 1904 in having abundant mesozoecia.

**Occurrence.** Lower Silurian to Upper Carboniferous; worldwide.

## *Leioclema elegans* Ernst, 2008

Pl. 1, figs 1-5; Appendix

1981 *Eridotrypa* cf. *eximia* Yaroshinskaya, 1970 - Bigey, p. 114-116, pl. 11, figs 5-10.

2008b *Leioclema elegans* Ernst, 2008, p. 331-332, pl. 1, figs 1-7.

**Material:** RGM 211 539-1-(1-3), RGM 211 539-8, RGM 211 546, GZG.IN.0.010.512a, b-(1-2), d-(1-3), e-2,f-2, f-4, g-(3, 4, 8, 10), GZG.IN.0.010.529c, e.

**Occurrence.** Koněprusy Limestone, Lower Devonian (Pragian); Zlatý Kůň, Czech Republic. Lower Devonian (Upper Emsian); Ménez-Bélaire Syncline, Armorican Massif, France. Marl Unit of Esla Formation, Lower Devonian (Emsian); section near the village of Villayandre, Cantabrian Mountains, NW Spain. Lower part of Esla Formation, Lower Devonian (Emsian); section southeast of the village of Villayandre, Cantabrian Mountains, NW Spain. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.

**Description.** Ramose branching and encrusting colonies. Branched colonies 1.5-3.0 mm in diameter, with distinctly separated endozones and exozones. Endozones 1.00-1.04 mm wide, exozones 0.3-1.0 mm wide, encrusting sheets 0.60-1.95 mm in thickness. Secondary overgrowths occurring. In encrusting colonies, autozoecia budding from a thin epitheca, on short distances parallel to the substrate, then bending sharply and intersecting the colony surface at right angle. In branched colonies, autozoecia growing parallel to branch axis for short distance in endozones, bending in exozone and intersecting the colony surface at angles of 90°. Autozoecial apertures rounded-polygonal to petaloid due to indenting acanthostyles. Autozoecial basal diaphragms rare to absent, thin, straight or slightly

deflected proximally. Mesozooecia abundant, 4-10 surrounding each aperture, polygonal in cross section, often beaded, containing abundant and thick diaphragms, sometimes as large as autozoecia, usually sealed by skeleton at the colony surface. Acanthostyles moderately large, abundant, 2-6 surrounding each aperture, originating in the distal part of exozone, often indenting autozoecia, having distinct calcite cores and dark laminated sheaths. Walls granular, 0.010-0.012 mm thick in endozones; distinctly laminated, merged, 0.03-0.05 mm thick in the exozone. Indistinct maculae consisting of slightly larger zooecia and more abundant mesozooecia.

**Comparison.** *Leioclema elegans* Ernst, 2008 (Ernst 2008b) differs from *L. abuettensis* Ernst, 2008a from the Middle Devonian of Rhenish Massif in shorter distances between centres of autozoecial apertures (average distance 0.25 mm vs. 0.36 mm in *L. abuettensis*).

#### Suborder **Amplexoporina** Astrova, 1965

##### Family Atactotoechidae Duncan, 1939

##### Genus *Leptotrypella* Vinassa de Regny, 1921

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

**Diagnosis:** Branched colonies. Autozoecia with polygonal to rounded-polygonal apertures. Autozoecial diaphragms lacking in endozones; rare to common in exozones. Exilazooecia rare. Acanthostyles long, common to abundant. Autozoecial walls granular, thin in endozones; laminated, mainly merged but sometimes serrated, irregularly thickened in exozones (modified after Astrova 1978).

**Comparison.** *Leptotrypella* Vinassa de Regny, 1921 differs from *Leptotrypa* Ulrich, 1883 in having branched colony, and from *Anomalotoechus* Duncan, 1939 in having branched colonies and absence of diaphragms in endozones.

**Occurrence.** Middle Silurian to Lower Carboniferous; worldwide.

##### ***Leptotrypella parva*** Duncan, 1939

Pl 1, figs 5-6, Pl. 2, figs 1-3; Appendix

1939 *Leptotrypella parva* Duncan, p. 229-230, pl. 9, figs 4-5.

**Material:** RGM 211 536-3-(1-2), RGM 211 539-1-(1-2).

**Occurrence.** Traverse group, Gravel Point Stage (Middle Devonian, Givetian); Michigan, USA. ? Esla Formation, Lower Devonian (Emsian); Portilla de Luna, Cantabrian Mountains, NW Spain. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.

**Description.** Branched and encrusting colonies. Branches 3.4-3.8 mm in diameter. Exozones 0.75-0.84 mm wide, endozones 1.90-2.12 mm wide. Encrusting

sheets 1.11-1.35 mm thick. Autozoecia long in endozones, bending at low angles in exozones. Autozoecial apertures oval. Autozoecial diaphragms abundant in exozone, thin, straight or slightly deflected proximally. Exilazooecia locally common, 0-5 surrounding each autozoecial aperture, short, restricted to exozones, rounded to polygonal in cross section. Acanthostyles moderately large, common, locally absent, usually 2 surrounding each autozoecial aperture, originating in basal exozone, having distinct cores and laminated sheaths, protruding above colony surface. Autozoecial walls granular, 0.010-0.015 mm thick in endozones; laminated, merged, without distinct zooecial boundaries, 0.03-0.07 mm thick in exozones. Secondary cingulum often developed, relatively thin, with lamination parallel autozoecial wall surface. Mural spines common to abundant in exozone, 0.020-0.035 mm in diameter, curved proximally. Maculae consisting larger zooecia, 1.2-1.5 mm in diameter, spaced 1.8-2.0 mm from centre to centre.

**Comparison.** *Leptotrypella parva* Duncan, 1939 differs from *L. undans* Duncan, 1939 in fewer and smaller acanthostyles. Furthermore, Duncan (1939) identified *Leptotrypella undans* by axial ratio (ratio of endozone width to branch diameter) as 0.8:1. This ratio was given as 0.45:1 for *L. parva*, whereas the present material has axial ratio 0.55:1. No mural spines were reported from both species of Duncan (1939). *Leptotrypella parva* differs also from *L. vulgata* Astrova, 1964 from the Lower Devonian (Lochkovian) of Ukraine in having fewer acanthostyles per autozoecial aperture (0-2 vs. 4-6 in *L. vulgata*).

##### ***Leptotrypella provecta*** Boardman, 1960

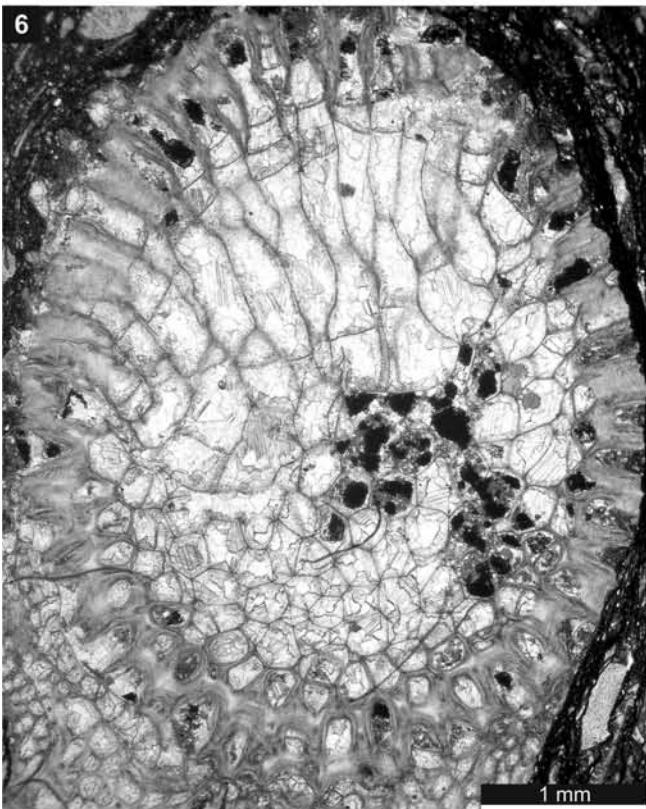
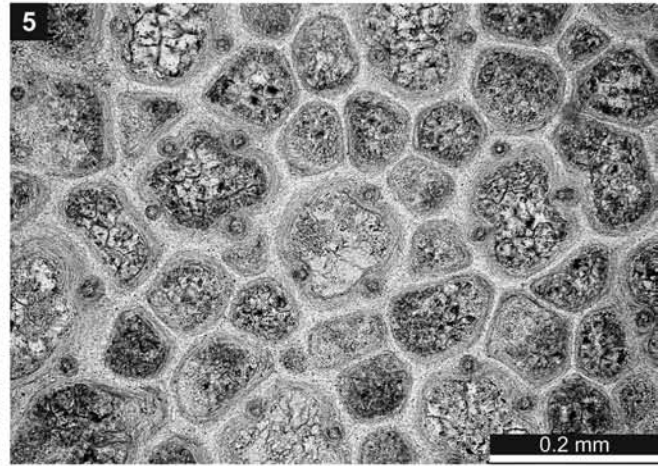
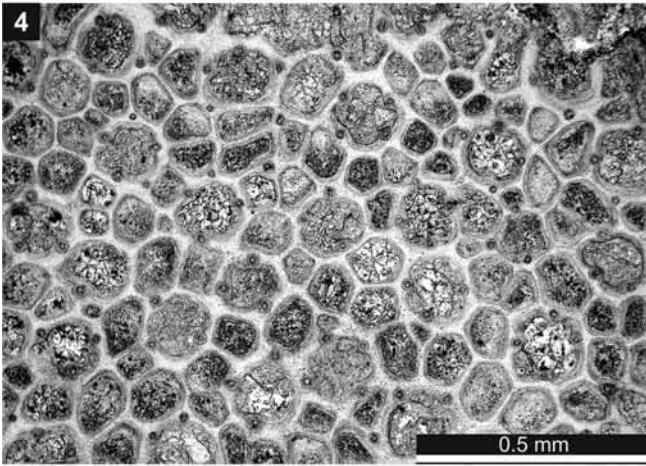
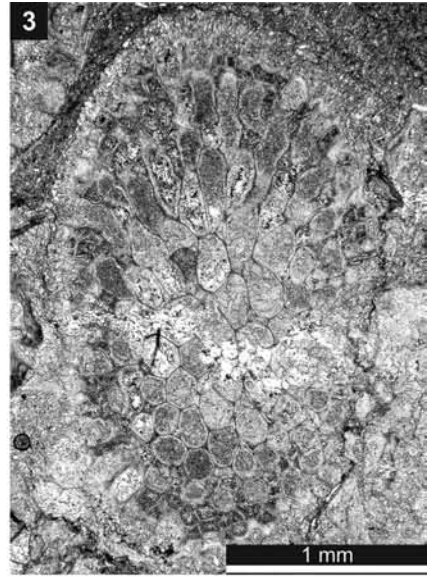
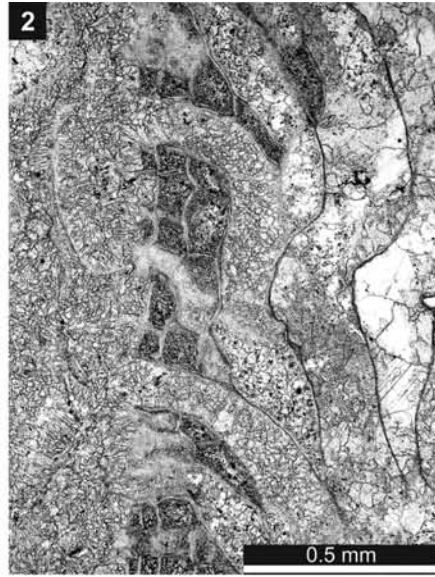
Pl. 2, figs 4-6, Pl. 3, figs 1-4; Appendix

1960 *Leptotrypella* (*Leptotrypella*) *mesostena provecta* Boardman, p. 56, pl. 6, figs 7-8.

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#### PLATE 1

- Figs 1-5 - *Leioclema elegans* Ernst, 2008. Lower part of Esla Formation, Lower Devonian (Emsian); Villayandre, Cantabrian Mountains, NW Spain.  
1-2: longitudinal sections. GZG.IN.0.010.512b-2; 3: branch oblique section. GZG.IN.0.010.512f-4; 4-5: tangential sections. GZG.IN.0.010.512b-2.
- Figs 6-7 - *Leptotrypella parva* Duncan, 1939. ? Esla Formation, Lower Devonian (Emsian); Portilla de Luna, Cantabrian Mountains, NW Spain.  
6: branch oblique section. RGM 211 536-3-2; 7: longitudinal section. RGM 211 536-3-1.



**Material:** RGM 211 536-1-3, RGM 211 536-1-9, RGM 211 536-8-1, RGM 211 536-2-4, RGM 211 536-2-5, RGM 211 536-2-13, RGM 211 543-4.

**Occurrence.** Hamilton Group, Ledyard member of Ludlowville shale (Middle Devonian, Givetian) of New York, USA. ? Esla Formation, Lower Devonian (Emsian); Portilla de Luna and Puerto de la Cubilla, Cantabrian Mountains, Spain.

**Description.** Branched and encrusting colonies. Secondary overgrowth occurring. Branches 3.4-4.5 mm in diameter. Exozones 0.7-0.9 mm wide, endozones 2.0-2.7 mm wide. Encrusting sheets 0.55-1.08 mm thick. Autozoecia long in endozones, bending at low angles in exozones. Autozoecial apertures oval. Autozoecial diaphragms abundant in exozone, thin, straight or slightly deflected proximally. Exilazoecia common, 1-5 surrounding each autozoecial aperture, locally absent, short, restricted to exozones, rounded to polygonal in cross section. Acanthostyles large, abundant, 2-4 surrounding each autozoecial aperture, originating in basal exozone, having distinct cores and laminated sheaths, protruding above colony surface. Autozoecial walls granular, 0.005-0.010 mm thick in endozones; laminated, merged, without distinct zoecial boundaries, 0.075-0.138 mm thick in exozones. Secondary cingulum often well developed, with lamination parallel autozoecial wall surface. Mural spines common to abundant in exozone, 0.020-0.025 mm in diameter, curved proximally. Maculae elevated, consisting larger, usually thick walled zoecia, 1.35-2.10 mm in diameter, spaced 2.2-2.6 mm from centre to centre.

**Comparison.** *Leptotrypella provecta* Boardman, 1960 is similar to *L. multitecta* Boardman, 1960 in having abundant mural styles and moderately large and abundant acanthostyles. However, it differs in having thicker autozoecial walls and smaller autozoecial apertures (autozoecia width 0.07-0.10 mm vs. 0.20-0.28 mm in *L. multitecta*).

**Description.** Branched and encrusting colonies. Branches 7-12 mm in diameter. Exozones 1.0-3.5 mm wide, endozones 5-6 mm wide. Encrusting sheets 3.1-3.6 mm thick. Autozoecia long in endozones, bending at low angles in exozones. Autozoecial apertures polygonal. Autozoecial diaphragms rare in endozone; common to absent in exozone, abundant in the transition between endo- and exozone, thin, straight or inclined. Exilazoecia rare, short, restricted to exozones, rounded to polygonal in cross section. Acanthostyles moderately large, common, locally absent, 1-6 surrounding each autozoecial aperture, originating in basal exozone, having distinct cores and laminated sheaths, protruding above colony surface. Massive megastyles present, having wide hyaline cores and relatively narrow laminated sheaths, originating repeatedly through the colony, concentrated usually in maculae. Autozoecial walls granular, 0.005-0.015 mm thick in endozones; laminated, merged, without distinct zoecial boundaries, 0.025-0.070 mm thick in exozones, often thickened in macular zoecia. Secondary cingulum not developed. Mural spines absent. Cyst-like spherical structures in autozoecial walls common, 0.08-0.10 mm in diameter. Maculae consisting of larger zoecia and megastyles, 1.1-1.9 mm in diameter, spaced 2.1-3.5 mm from centre to centre.

**Comparison.** *Leptotrypella maculata* n. sp. is similar to *L. aequabilis* Duncan, 1939 from the Traverse Group of Michigan, USA, in presence of thick acanthostyles in maculae. The new species has smaller apertures than those in *L. aequabilis* (average autozoecia width 0.16 mm vs. 0.20 mm in *L. aequabilis*). Duncan (1939: 224) mentioned no mural spines in walls of *L. aequabilis*. However, the longitudinal section of *L. aequabilis* (Duncan 1939, pl. 9, fig. 7) exhibits several apparent mural spines, which are absent in *L. maculata*.

### **Leptotrypella maculata** n. sp.

Pl. 3, figs 5-8, Pl. 4, figs 1-6; Appendix

**Etymology:** The specific name '*maculata*' refers to the presence of well-defined maculae of the new species (from Latin "*maculatus*" - spotted).

**Holotype:** RGM 211 540-2.

**Paratypes:** RGM 211 540-1, RGM 211 538-1-(1-2).

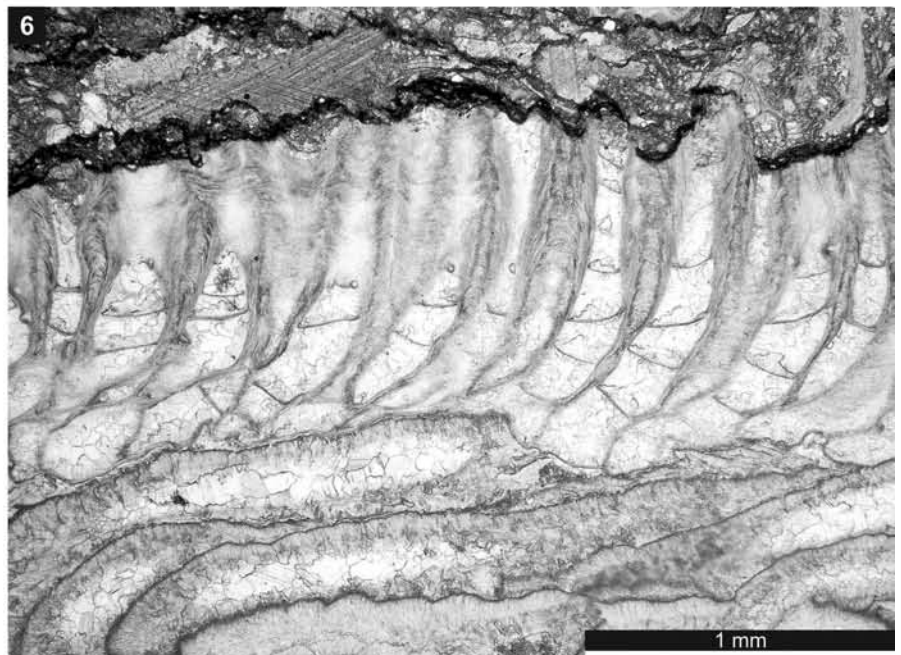
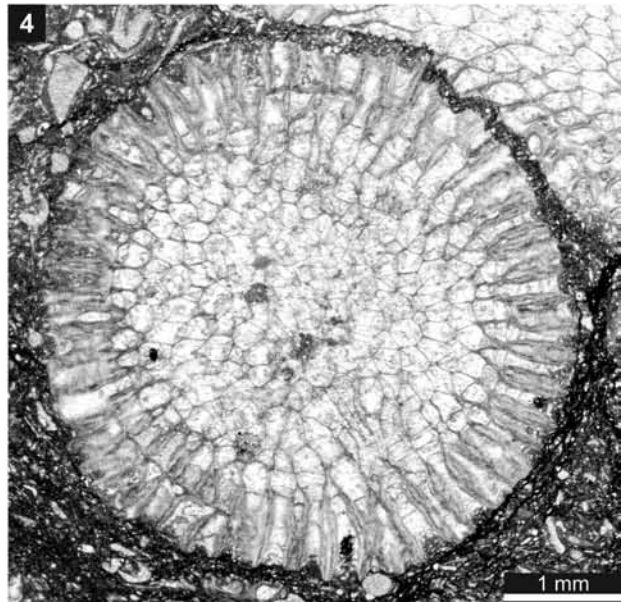
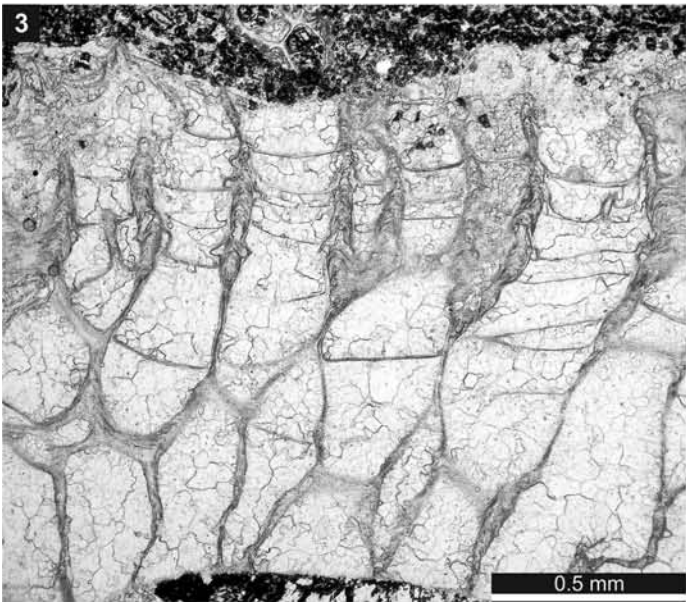
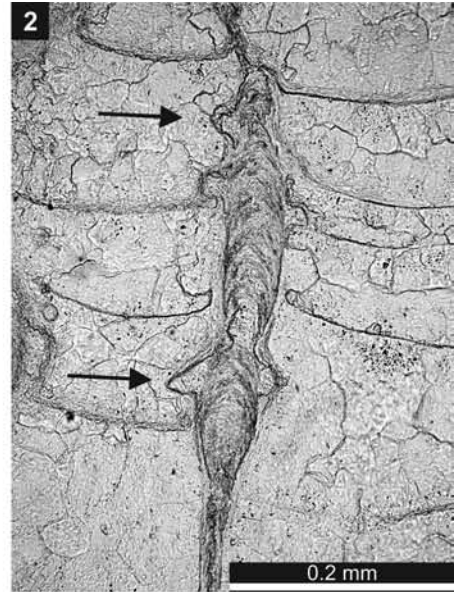
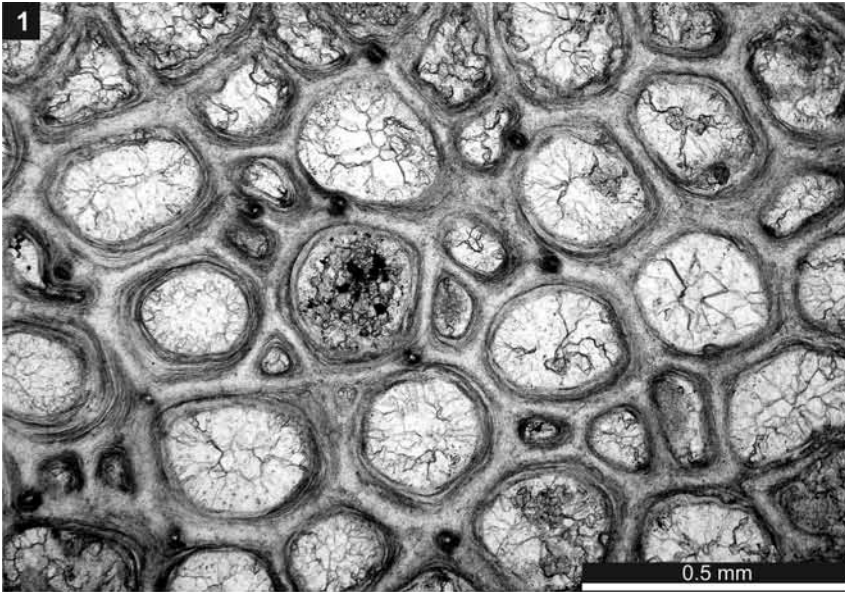
**Type locality:** Caldas de Luna, Cantabrian Mountains, NW Spain.

**Type stratum:** Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian).

**Diagnosis:** Branched and encrusting colonies; autozoecial diaphragms abundant to absent, straight or inclined; exilazoecia rare, small; acanthostyles common, locally absent, moderately large; megastyles present; mural spines absent; cyst-like spherical structures in autozoecial walls present; maculae well-defined, regularly spaced, consisting of larger zoecia with thickened walls and megastyles.

### PLATE 2

- Figs 1-3 - *Leptotrypella parva* Duncan, 1939. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.  
1: tangential section. RGM 211 539-1-1; 2-3: longitudinal sections showing autozoecial walls and mural spines (arrows on Fig. 3). RGM 211 539-1-2.
- Figs 4-6 - *Leptotrypella provecta* Boardman, 1960. ? Esla Formation, Lower Devonian (Emsian); Portilla de Luna, Cantabrian Mountains, NW Spain.  
4: branch transverse section. RGM 211 536-1-3; 5: branch longitudinal section. RGM 211 536-8-1; 6: longitudinal section of an encrusting colony. RGM 211 536-2-13.



Genus *Atactotoechus* Duncan, 1939

Type species: *Atactotoechus typicus* Duncan, 1939, by original designation. Traverse Group (Middle Devonian); Michigan (USA).

**Diagnosis:** Encrusting, massive and branched colonies. Autozoecia with polygonal to rounded-polygonal apertures. Diaphragms abundant, straight or inclined. Cystiphragms singly or several in cluster. Exilazoecia rare. Acanthostyles absent or present in small numbers in maculae. Autozoecial walls thin in endozones; serrated, irregularly thickened, finely laminated in exozones (modified after Astrova 1978).

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

**Occurrence.** Lower Silurian to Upper Devonian; worldwide.

***Atactotoechus cartus*** Boardman, 1960

Pl. 5, figs 1-4; Appendix

1960 *Atactotoechus cartus* Boardman, p. 73, pl. 18, figs. 1-6.

1960 *Atactotoechus cartus cartus* Boardman, p. 73-74, pl. 18, figs. 4-6.

1960 *Atactotoechus cartus pilatus* Boardman, p. 74, pl. 18, figs. 1-3.

**Material:** Two colonies GZG.IN.0.010.512f-3, g-14.

**Occurrence:** Hamilton Group, Wanakah member of the Ludlowville shale (Middle Devonian, Givetian) of New York, USA. Lower part of Esla Formation, Lower Devonian (Emsian); section southeast of the village of Villayandre, Cantabrian Mountains, NW Spain.

**Diagnosis:** Branched colonies; exozones distinctly separated from endozones; diaphragms abundant in exozones; cystiphragms few; exilazoecia absent; acanthostyles rare, small.

**Description.** Ramose branched colonies. Branches 1.7-2.3 mm in diameter. Exozones 0.36-0.63 mm wide, endozones 0.98-1.04 mm wide. Exozones distinctly separated from endozones. Autozoecia long in endozones, bending sharply in exozones. Autozoecial apertures polygonal with rounded corners. Autozoecial diaphragms abundant in exozones, straight or inclined; absent to rare in endozones. Cystiphragms common. Exilazoecia absent. Acanthostyles locally present, usually absent, small, having distinct narrow cores and laminated sheaths. Autozoecial walls granular, 0.010-0.015 mm thick in endozones; serrated in the longitudinal view and merged in the tangential section, 0.020-0.040 mm thick in exozones. Maculae consisting of larger autozoecia, not well observed in present material.

**Comparison.** *Atactotoechus cartus* Boardman, 1960 differs from *A. acritus* Boardman, 1960 in having smaller colonies, less abundant acanthostyles and smaller autozoecia (aperture width 0.12-0.24 mm vs. 0.20-0.29 mm in *A. acritus*).

Genus *Anomalotoechus* Duncan, 1939

[= *Stereotoechus* Duncan, 1939]

Type species: *Anomalotoechus typicus* Duncan, 1939, by original designation. Traverse Group (Middle Devonian); Michigan (USA)

**Diagnosis:** Encrusting, massive, less commonly branched colonies. Autozoecia with polygonal to rounded-polygonal apertures. Diaphragms abundant in exozones, straight or inclined. Exilazoecia rare, short. Acanthostyles abundant. Autozoecial walls thin in endozones; finely laminated, strongly and irregularly thickened in exozones (modified after Astrova, 1978).

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

## PLATE 3

Figs 1-4 - *Leptotrypella provecta* Boardman, 1960. ? Esla Formation, Lower Devonian (Emsian); Portilla de Luna, Cantabrian Mountains, NW Spain.

1: tangential section. RGM 211 536-8-1; 2: tangential section of a macula. RGM 211 536-2-13; 3: tangential section showing autozoecia, exilazoecia, acanthostyles and mural styles (arrows). RGM 211 536-2-5; 4: branch longitudinal section showing basal diaphragms and a mural spine inside of autozoecial chamber (arrow). RGM 211 536-8-1.

Figs 5-8 - *Leptotrypella maculata* n. sp. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.

5: holotype. Branch transverse section showing autozoecial walls and acanthostyles. RGM 211 540-2; 6: paratype. Branch longitudinal section showing autozoecial walls and basal diaphragms. RGM 211 540-1; 7: paratype. Branch tangential-transversal section. RGM 211 538-1-1; 8: holotype. Branch transverse section. RGM 211 540-2.

## PLATE 4

Figs 1-6 - *Leptotrypella maculata* n. sp. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.

1: holotype. Tangential section of non-macular area. RGM 211 540-2; 2: holotype. Tangential section of macular area. RGM 211 540-2; 3: holotype. Tangential section of macular area showing megastyles in thickened autozoecial walls (arrows). RGM 211 540-2; 4-5: paratype. Longitudinal section showing basal diaphragms and megastyles in autozoecial walls. RGM 211 538-4-3; 6: holotype. branch transverse section showing autozoecial wall with a cyst-like spherical structure. RGM 211 540-2.



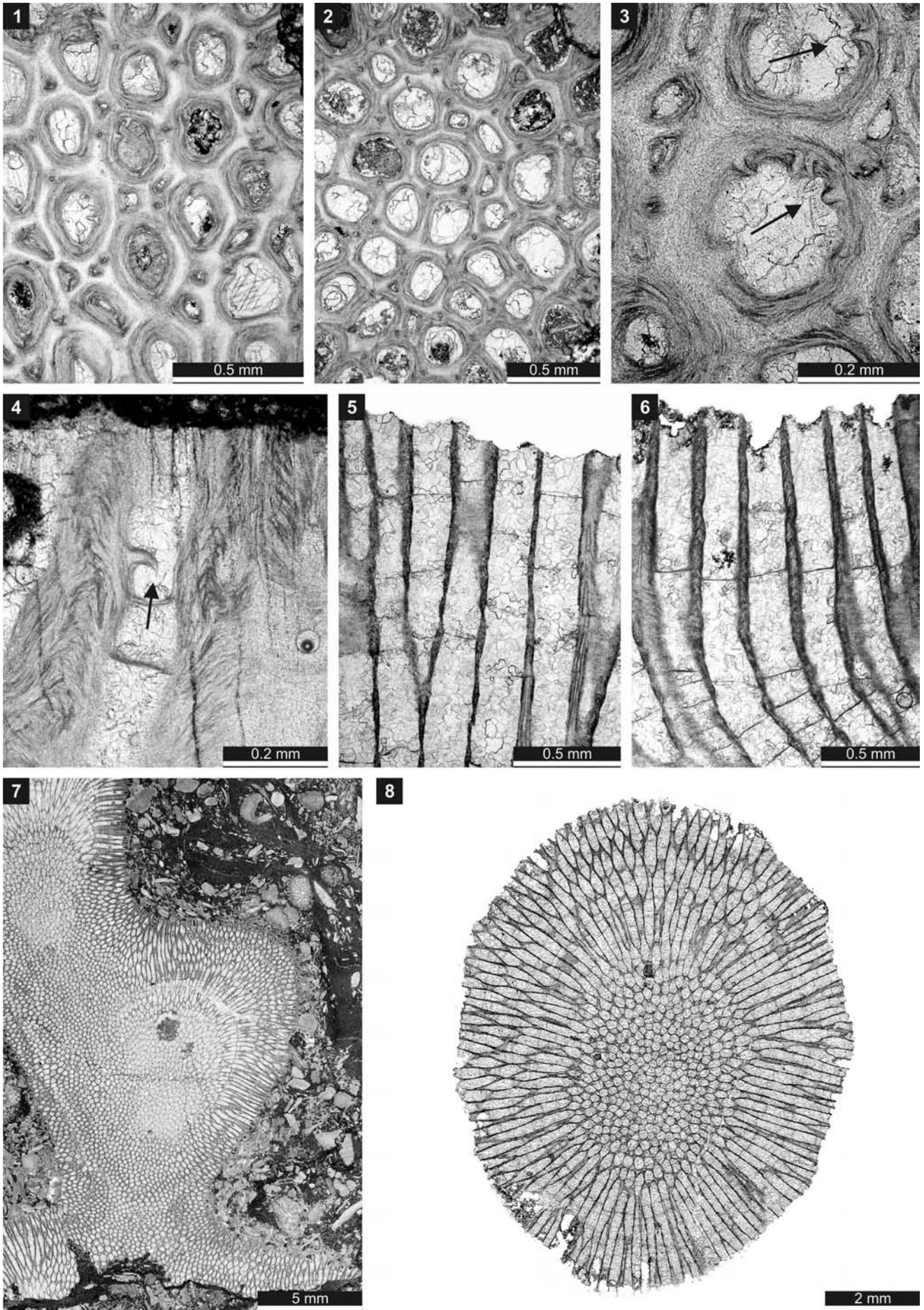


PLATE 3

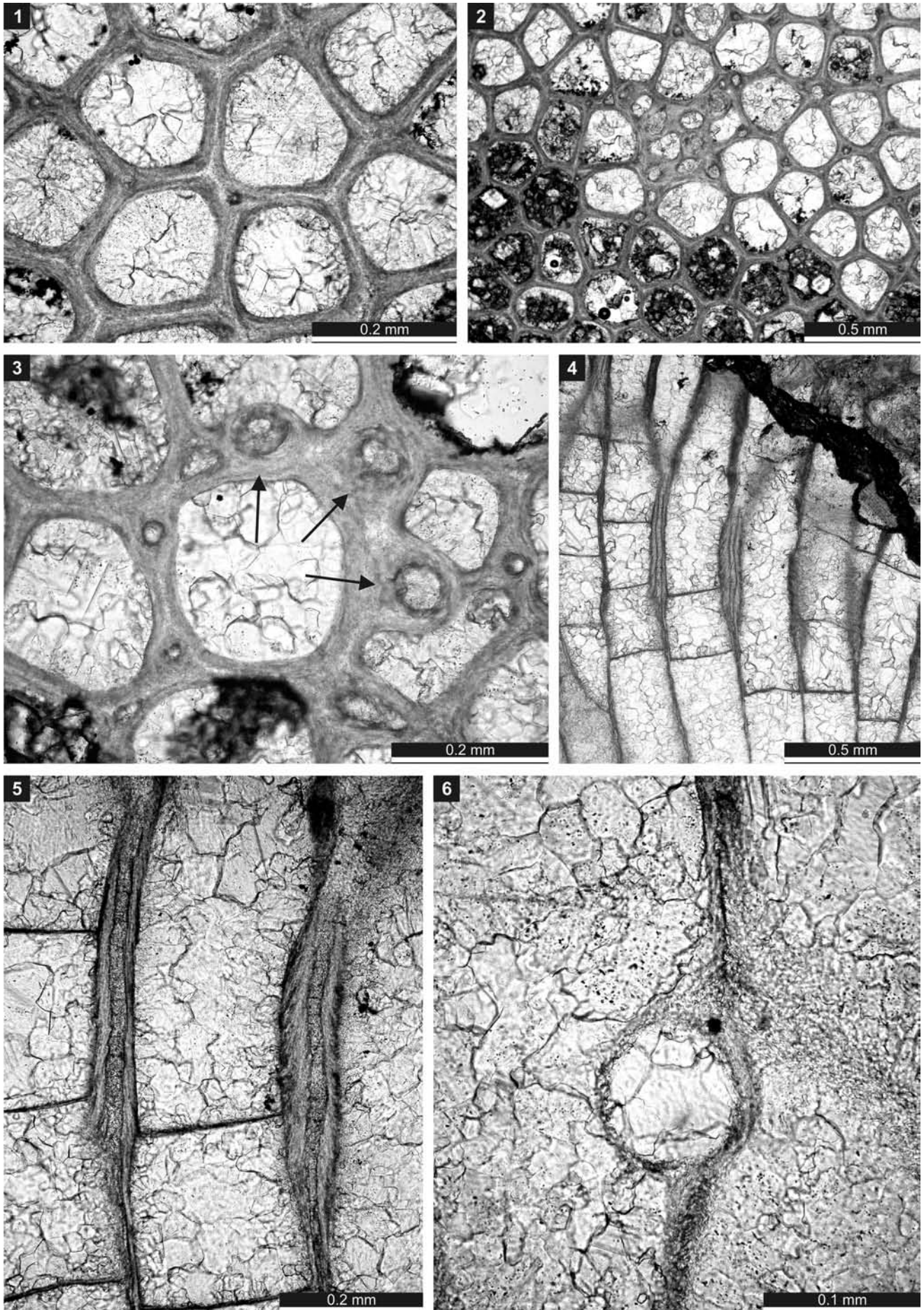


PLATE 4

**Anomalotoechus alpenensis** (Duncan, 1939)

Pl. 5, figs 5-8, Pl. 6, figs 1-5; Appendix

1939 *Stigmatella alpenensis* Duncan, p. 233-234, pl. 4, figs. 4-6.**Material:** RGM 211 536-1-9, RGM 211 538-4-3, RGM 211 540-2-(1-3), RGM 211 547.**Occurrence.** Traverse group, Genshaw Formation (Middle Devonian, Givetian); Michigan, USA. ? Esla Formation, Lower Devonian (Emsian); Puerto de la Cubilla, Portilla de Luna, Cantabrian Mountains, NW Spain. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.**Description.** Massive colonies up to 35 mm in thickness. Secondary overgrowths common, separate sheets 1.9-8.0 mm thick. Exozones 1.05-1.44 mm wide. Autozoecia long, prismatic, having polygonal cross sections. Autozoecial apertures rounded-polygonal. Autozoecial diaphragms widely spaced in endozones, common to abundant in exozones, usually straight or slightly curved distally, locally absent. Exilazooecia rare, short, with rounded apertures. Acanthostyles moderately large, having narrow hyaline cores and indistinct laminated sheaths, 1-3 surrounding each autozoecial aperture, locally absent. Autozoecial walls granular, locally strongly crenulated, 0.005-0.010 mm thick in endozones; merged, showing reversal V-shaped lamination without distinct zoecial boundaries, irregularly thickened, with serial thickenings throughout the colony, 0.025-0.063 mm thick in exozones. Maculae large, elevated, consisting of large autozoecia, 1.95-2.75 mm in diameter, spaced 2.65-3.70 mm from centre to centre.**Comparison.** *Anomalotoechus alpenensis* (Duncan, 1939) differs from *A. traversensis* (Duncan, 1939) in having fewer autozoecial diaphragms. *Anomalotoechus alpenensis* is also similar to *A. corrugatus* (Nekhoroshev, 1948) from the Middle Devonian (Givetian) of Altay, but differs from it in having smaller apertures (autozoecial aperture width 0.13-0.25 mm vs. 0.25-0.36 mm in *A. corrugatus*).**Anomalotoechus tabulatus** n. sp.

Pl. 6, fig. 6, Pl. 7, figs 1-3; Appendix

**Etymology:** The specific name 'tabulatus' refers to the presence of abundant diaphragms and cystiphagms in autozoecia (from Latin "tabulatus" - floor).**Holotype:** RGM 211 536-1-11.**Paratypes:** RGM 211 536-1-6, RGM 211 536-2-9, RGM 211 539-1-(1-2).**Type locality:** Portilla de Luna, Cantabrian Mountains, NW Spain.**Type stratum.** ? Esla Formation, Lower Devonian (Emsian).**Another occurrence:** Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian).**Diagnosis:** Encrusting (subramose) colonies; exozones indistinctly separated from endozones; diaphragms and cystiphagms

abundant in exozones; exilazooecia rare; acanthostyles common, moderately large.

**Description.** Encrusting (subramose) colonies, separate sheets 0.30-0.75 mm in thickness. Exozones indistinctly separated from endozones. Autozoecia long, bending gently in endozones, having polygonal cross sections. Autozoecial apertures rounded-polygonal. Autozoecial diaphragms restricted to exozones, locally common, 2-5 occurring in each autozoecium; locally absent. Cystiphagms present in exozone, occupying about half space of the autozoecial chamber. Exilazooecia rare, short, with rounded apertures. Acanthostyles moderately large, 3-6 surrounding each autozoecial aperture, having distinct cores and laminated sheaths. Autozoecial walls granular, 0.005-0.010 mm thick in endozones; irregularly thickened, merged, showing reversal U-shaped lamination without distinct zoecial boundaries, 0.04-0.07 mm thick in exozones. Maculae not observed.**Comparison.** *Anomalotoechus tabulatus* n. sp. differs from *A. typicus* Duncan, 1939 in more abundant and well-defined cystiphagms.

## Family Eridotrypella Morozova, 1960

Genus *Eridotrypella* Duncan, 1939Type species: *Batostomella obliqua* Ulrich, 1890. Middle Devonian; Michigan (USA)**Diagnosis:** Branched colonies. Autozoecial apertures irregularly polygonal. Autozoecial walls laminated, without distinct zoecial boundaries, irregularly thickened, containing spherulites. Diaphragms complete, varying in number. Exilazooecia rare. Acanthostyles varying in size and number.**Comparison.** *Eridotrypella* Duncan, 1939 differs from *Eostenopora* Duncan, 1939 in colony form (ramose branched vs. encrusting or massive colonies).**Stratigraphic and geographic range.** Silurian-?Carboniferous; worldwide.**Eridotrypella valida** Duncan, 1939

Pl. 7, figs 4-6, Pl. 8, figs 1-2; Appendix

1939 *Eridotrypella valida* Duncan, p. 219-220, pl. 7, figs 12-14.**Material:** Two thin sections of a single colony RGM 211 538-1-(4-5).**Occurrence.** Traverse group, Bell shale, Ferron Point Formation (Middle Devonian, Givetian); Michigan, USA. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.

**Description.** Ramose branched colony, 3.7 mm in diameter. Exozone 0.48-0.63 mm wide, endozones 2.74-2.44 mm wide. Exozones distinctly separated from endozones. Autozoocelia long in endozones, bending sharply in exozones. Autozoocelial apertures polygonal with rounded corners. Autozoocelial diaphragms absent to rare in endozones; usually thick, abundant in transition between endozones and exozones, straight or inclined. Exilazoocelia rare, short, polygonal in cross section. Acanthostyles rare, moderately large, having distinct narrow cores and laminated sheaths. Autozoocelial walls granular, locally weakly crenulated, 0.005-0.010 mm thick in endozones; serrated in the longitudinal view and merged in the tangential section, 0.055-0.110 mm thick in exozones. Maculae not observed.

**Comparison.** *Eridotrypella valida* Duncan, 1939 differs from *E. spinifera* Duncan, 1939 in fewer acanthostyles and thicker autozoocelial walls.

#### Genus *Eifelipora* Ernst, 2008

Type species: *Eifelipora ramosa* Ernst, 2008 (Ernst, 2008a), by original designation. Middle Devonian (Givetian); eastern Rhenish Massif, Germany.

**Diagnosis:** Branched colonies; secondary overgrows common; proximal hemiphragms common; autozoocelial walls containing spherules in exozones; exilazoocelia rare to common; acanthostyles locally abundant.

**Comparison.** *Eifelipora* Ernst, 2008 is similar to *Eridotrypella* Duncan, 1939, but differs in the presence of hemiphragms. The new genus differs also from *Eridocampylus* Duncan, 1939 in shape and arrangement of hemiphragms. *Eridocampylus* has curved and serrated hemiphragms which are arranged on all autozoocelial chamber walls. *Eifelipora* differs from *Stenophragmidium* Bassler, 1952 in wall structure without monilae shaped thickenings and containing spherules.

**Occurrence.** Middle Devonian (Eifelian-Givetian) of Rhenish Massif, Germany. Lower Devonian (Emsian) of Spain.

#### *Eifelipora tenuis* n. sp.

Pl. 8, figs 3-7; Appendix

**Etymology:** The specific name 'tenuis' refers to the thin colonies of the new species (derived from Latin 'tenuis' = thin).

**Holotype:** GZG.IN.0.010.512f-1.

**Paratypes:** GZG.IN.0.010.512 (a, b-1, b-3, c-5, c-8, e-1, e-3, e-4, d-4, f-5, g-3, g-12, g-15).

**Type locality:** Section southeast of the village of Villayandre, Cantabrian Mountains, NW Spain.

**Type stratum:** Lower part of Esla Formation, Lower Devonian (Emsian).

**Diagnosis:** Branched colonies; proximal hemiphragms common; autozoocelial walls containing spherules in exozones; exilazoocelia rare to common; acanthostyles abundant.

**Description:** Ramose colonies with relatively narrow, distinctly separated exozones; secondary overgrowths occurring. Branches 0.81-1.29 mm in diameter, endozones 0.42-0.54 mm wide, exozones 0.13-0.20 mm wide. Autozoocelia tubular-prismatic, growing parallel to branch axes in endozones, bending abruptly in exozones and intersecting colony surface at angles of 78-80°. Autozoocelial apertures rounded-polygonal. Basal diaphragms common to absent, restricted to exozones, straight or slightly curved distally, thin. Hemiphragms abundant in exozones, positioned on proximal wall, moderately thin, short to moderately long, straight to weakly curved proximally. Autozoocelial walls granular, 0.005-0.010 mm thick in endozones; laminated, containing spherules, 0.030-0.055 mm thick in exozones. Exilazoocelia abundant, 2-7 surrounding each autozoocelial aperture, small, originating in basal exozones. Acanthostyles abundant, 2-7 surrounding each autozoocelial aperture, having distinct cores and laminated sheaths, originating in basal exozones. Maculae absent.

**Comparison.** *Eifelipora tenuis* n. sp. differs from *E. ramosa* Ernst, 2008 (Ernst, 2008a) from the Middle Devonian of Rhenish Massif in thinner branches (average branch diameter 1.01 mm vs. 1.67 mm in *E. ramosa*) and more abundant acanthostyles and exilazoocelia.

#### Family Anisotrypidae Dunaeva & Morozova, 1967

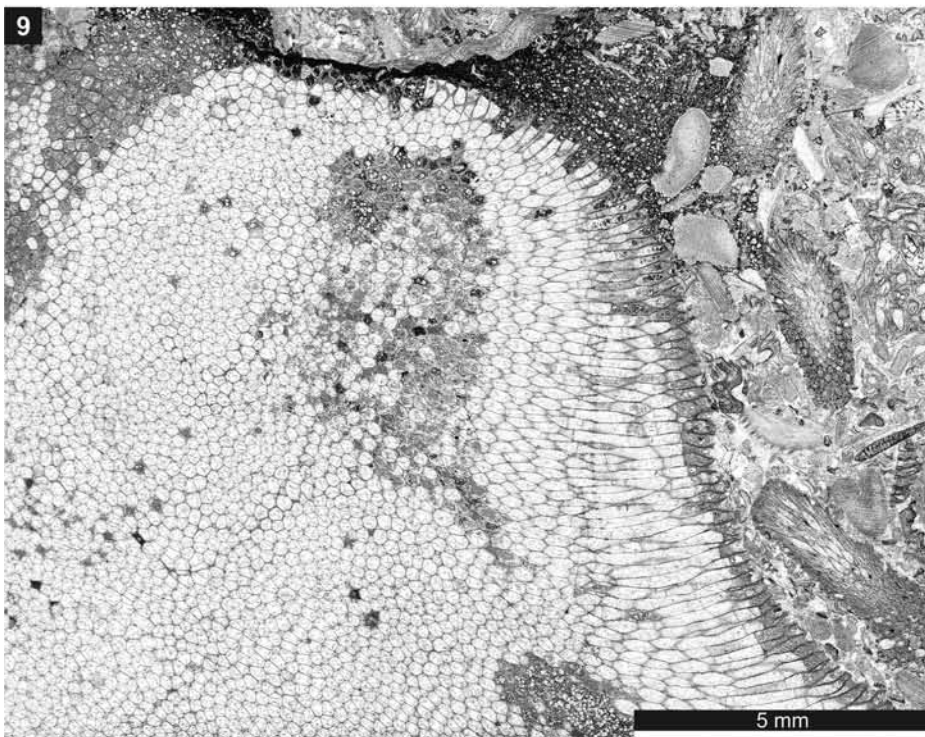
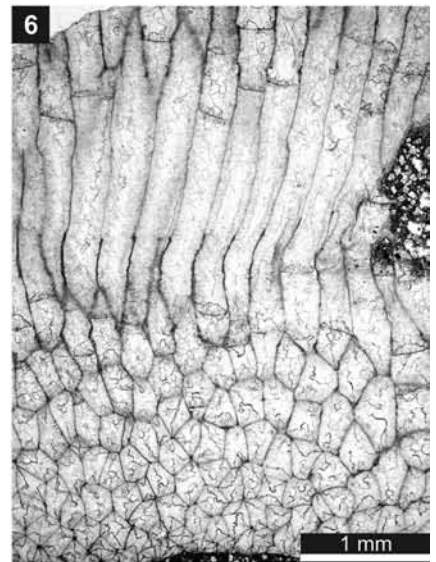
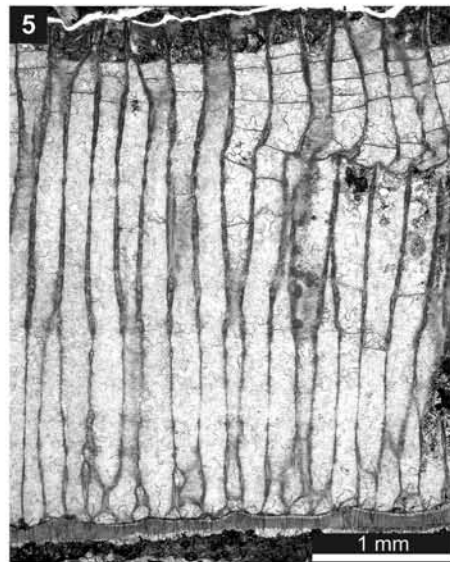
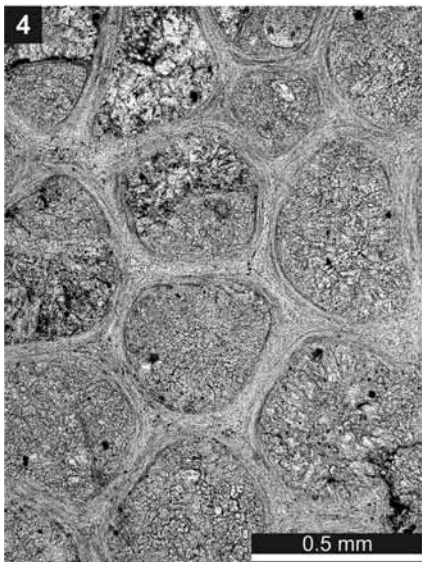
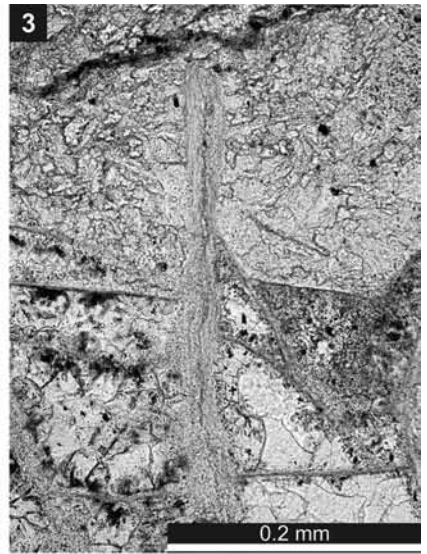
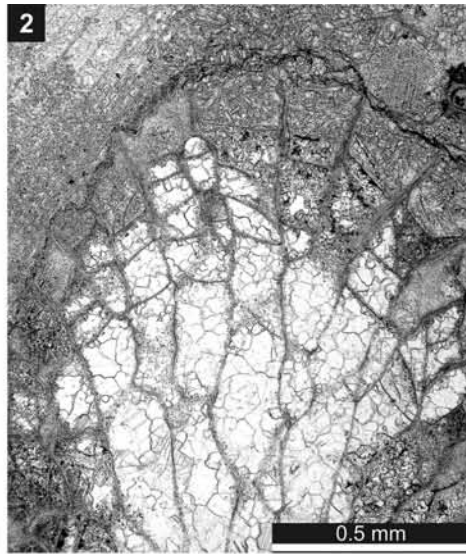
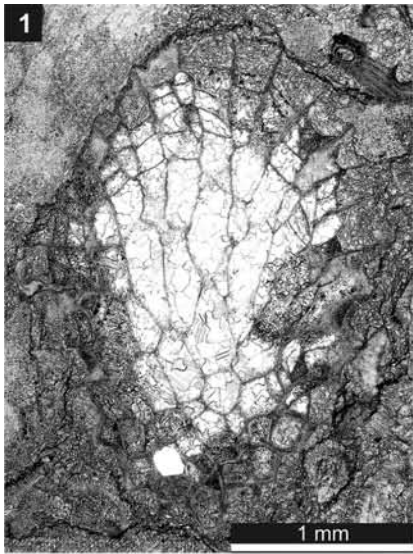
##### Genus *Boardmanella* Gorjunova & Weiss, 2003

Type species: *B. richardi* Gorjunova & Weiss, 2003, by original designation. Middle Devonian (Givetian); Mongolia.

**Diagnosis (emended):** Branched colonies with distinct exozones; autozoocelia prismatic, growing parallel to the branch axis in

#### PLATE 5

- Figs 1-4 - *Atactotoechus cartus* Boardman, 1960. Lower part of Esla Formation, Lower Devonian (Emsian); Villayandre, Cantabrian Mountains, NW Spain.  
1-3: branch oblique section showing basal diaphragms and cystiphragms. GZG.IN.0.010.512f-3; 4: tangential section. GZG.IN.0.010.512g-14.
- Figs 5-7 - *Anomalotoechus alpenensis* (Duncan, 1939). Santa Lucía Formation (Lower Devonian, Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.  
5: longitudinal section of encrusting colony. RGM 211 538-4-2; 6: transverse section of encrusting colony. RGM 211 541-2-3; 7: transverse section of massive colony. RGM 211 539-1-9.
- Fig. 8 - *Anomalotoechus alpenensis* (Duncan, 1939). ? Esla Formation, Lower Devonian (Emsian); Puerto de la Cubilla, Cantabrian Mountains, NW Spain. Longitudinal section of massive colony. RGM 211 547.



endozones, then bending in exozones at moderate angles, polygonal in transverse section; autozoocial apertures rounded to oval or rounded-polygonal; basal diaphragms usually absent, locally present, thin, straight; exilazooecia rare to abundant, short, varying in size; paurostyles (Gorjunova & Weis, 2003) always covered by skeletal material; varying in size and number; autozoocial walls regularly thickened in exozones, straight, merged without distinct zoocial boundaries and showing reverse U-shaped lamination.

**Comparison.** *Boardmanella* Gorjunova & Weis, 2003 is superficially similar to *Dyscritella* Girty, 1911 in having rare to absent diaphragms and regularly thickened autozoocial walls. However, the styles in *Boardmanella* are different to those in *Dyscritella*. Gorjunova & Weis (2003) correctly noted the similarity of these styles to paurostyles of Blake (1983). However, the styles in *Boardmanella* do not correspond completely to the terminus “paurostyle” *sensu stricto*. Species placed by Gorjunova & Weis (2003) to the genus *Boardmanella* have a typical combination of morphological characters (wall structure, rare or lacking diaphragms), and they also have styles varying in size and number, but always covered by skeletal material. Blake (1983: 538-539) regarded paurostyles as the simplest kind of styles consisting of small rods, usually 0.02-0.04 mm in diameter, and with narrow laminated sheaths. The main difference between acanthostyles and paurostyles is that acanthostyles usually protrude upon the colony surface and have wide, well-developed laminated sheaths. For aims of the present paper, the terminus “paurostyles” is used in the description, although the need for the new name is obvious.

**Occurrence.** Following species of *Boardmanella* are known from the Devonian worldwide: *B. richardi* Gorjunova & Weiss, 2003 from the Middle Devonian (Givetian) of Mongolia, *B. interporosa* (Ulrich & Bassler, 1904) from the Lower Devonian of USA, *B. antiqua* (Nekhoroshev, 1977) from the Lower Devonian (Pragian-Emsian) of Kazakhstan, *B. bohémica* (Ernst, 2008) (Ernst 2008b) from the Lower Devonian (Pragian) of Bohemia and Lower-Middle Devonian (Emsian-Eifelian) of Spain, *B. inermis* (Kopajevich, 1984) from the Middle Devonian (Eifel) of Mongolia, *B. devonica* (Volkova, 1974) from the Middle Devonian (Givetian) of Altai, *B. uniserialis* (Kopajevich, 1984) from the Middle Devonian (Eifelian-Givetian) of Mongolia, *B. elliptica* (Kopajevich, 1984) from the Middle-Upper Devonian (Givetian-Frasnian) of Mongolia, *B. indistincta* (Nekhoroshev, 1977) from the Upper Devonian (Famennian) of Kazakhstan.

#### **Boardmanella bohémica** (Ernst, 2008)

Pl. 9, figs 1-8; Appendix

2008b *Dyscritella bohémica* Ernst, p. 341-342, pl. 5, figs 5-9.

**Material.** RGM 211 536-2-(1, 3, 7, 8, 10, 11, 12), RGM 211 538-1-(3, 4, 5), RGM 211 538-2-(1, 3, 4, 6), RGM 211 538-4-3, RGM 211 541-1-(1-4), RGM 211 541-3-(2-6), RGM 211 541-4-1.

**Occurrence.** Zlatý Kůň, Czech Republic; Koněprusy Limestone, Pragian (Lower Devonian). ? Esla Formation, Lower Devonian (Emsian); Portilla de Luna, Cantabrian Mountains, NW Spain. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.

**Description.** Branched colonies with distinct exozone. Secondary overgrowth occurring. Branches 1.9-4.1 mm in diameter. Endozones 1.1-1.3 mm wide, exozones 0.4-1.4 mm wide. Autozoocia long in endozone, bending at low angles in exozone. Autozoocial apertures rounded-polygonal. Autozoocial diaphragms rare to absent. Exilazooecia rare, short, rounded to oval in cross section. Paurostyles of two distinct sizes. 3-6 large paurostyles surrounding each autozoocial aperture; having indistinct cores and laminated sheaths. Commonly 1-2 small paurostyles spaced in a single row between large paurostyles. Autozoocial walls granular, 0.005-0.015 mm thick in endozones; thick, merged, laminated without distinct zoocial boundaries, 0.05-0.10 mm thick in exozones. Indistinct maculae consisting of larger autozoocia.

**Comparison.** *Boardmanella bohémica* (Ernst, 2008) (Ernst 2008b) differs from *B. elliptica* (Kopajevich, 1984) from the Middle-Upper Devonian (Givetian-Frasnian) of Mongolia in presence of paurostyles of two different sizes.

#### Genus *Mongoloclema* Shishova, 1970

Type species: *Mongoloclema ignotum* Shishova, 1970. Middle-Late Devonian; Mongolia

1970 *Mongoloclema* Shishova, p. 29.

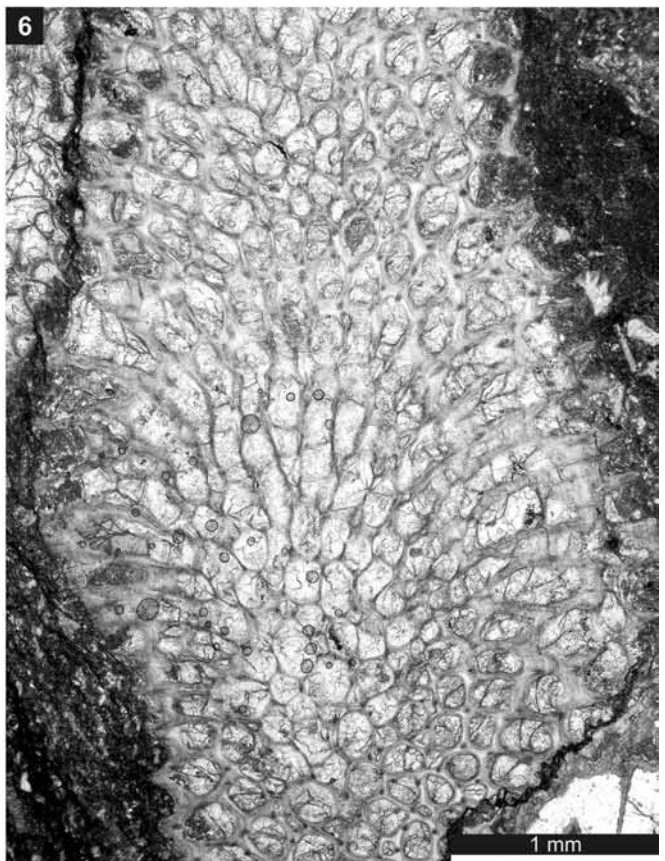
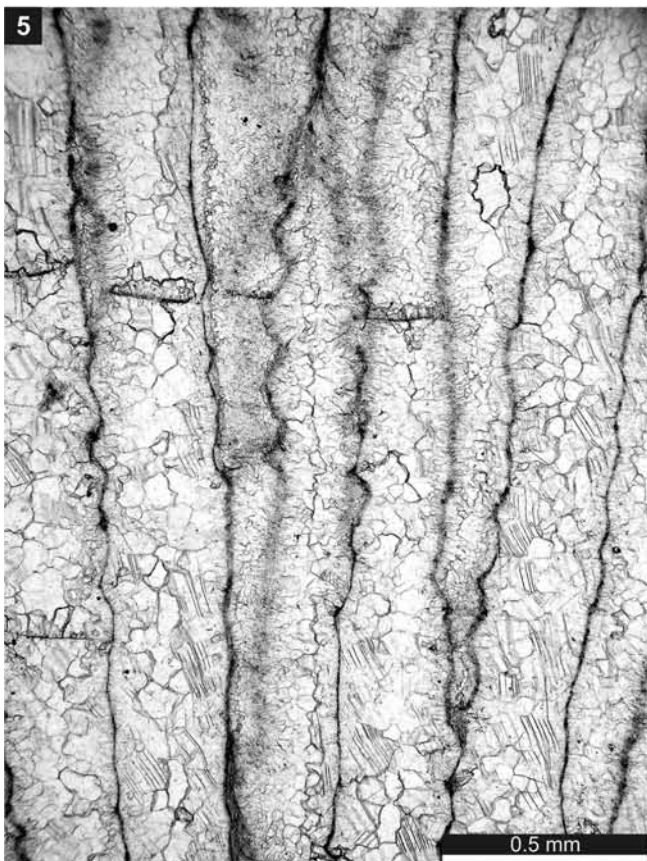
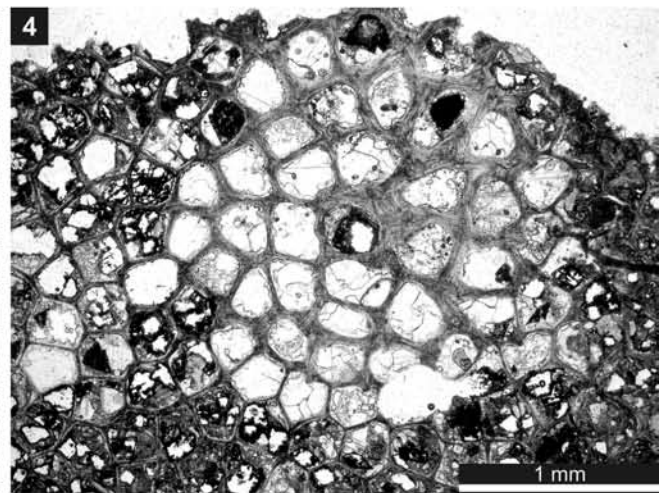
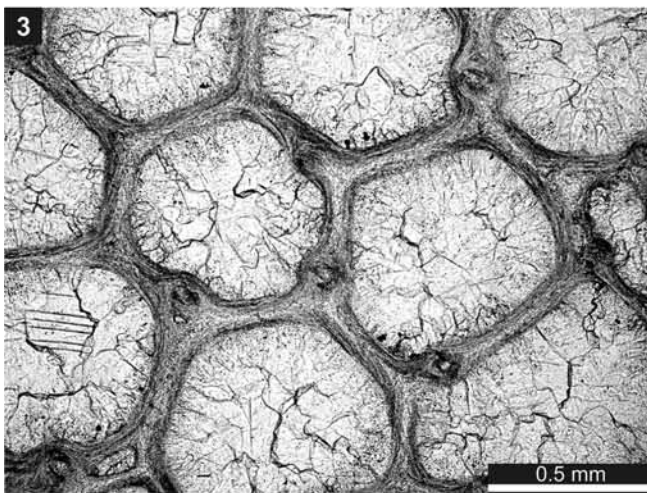
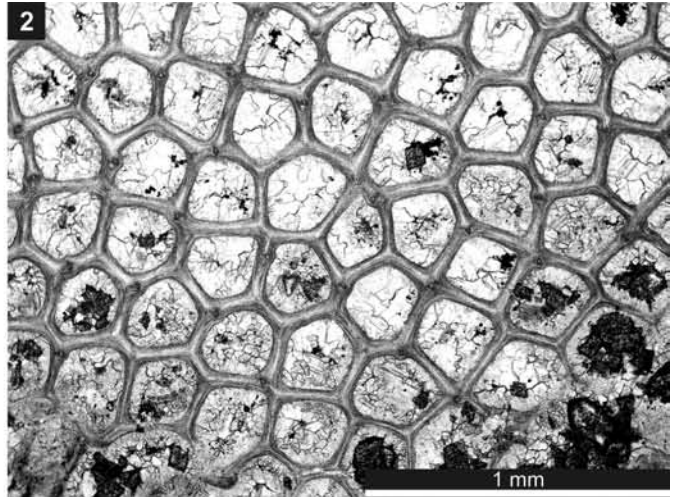
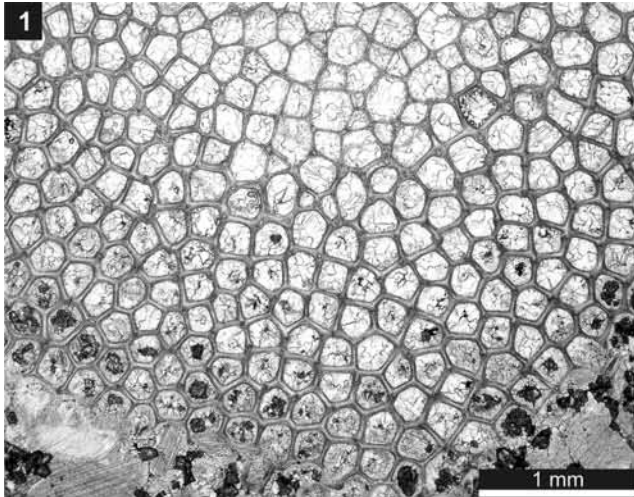
1976 *Mongoloclema* Shishova, 1970 - Troitzkaya, p. 148.

1984 *Mongoloclema* Shishova, 1970 - Kopajevich, p. 128-129.

2003 *Mongoloclema* Shishova, 1970 - Morozova, Gorjunova & Ariunchimeg, p. 93.

#### PLATE 6

- Figs 1-4 - *Anomalotoechus alpenensis* (Duncan, 1939). Santa Lucía Formation Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain. 1-3: tangential sections. RGM 211 541-4-3; 4: tangential section of a macula. RGM 211 547.
- Fig. 5 - *Anomalotoechus alpenensis* (Duncan, 1939). ? Esla Formation, Lower Devonian (Emsian); Puerto de la Cubilla, Cantabrian Mountains, NW Spain. Longitudinal section showing crenulated walls of endozone. RGM 211 547.
- Fig. 6 - *Anomalotoechus tabulatus* n. sp. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain. Holotype. Branch oblique section. RGM 211 536-1-11.



**Diagnosis:** Ramose colonies with distinct exozones; autozoecia long, growing parallel to branch axis then bending at moderately high angles to the colony surface; basal diaphragms common to abundant, thin, straight, inclined or cystiphragmoid; exilazoecia abundant, often separating autozoecia, sometimes containing thin diaphragms; styles absent; autozoecial walls finely laminated, without visible boundaries, irregularly thickened in exozone; fine tubules present in outermost parts of exozonal walls.

**Comparison.** Systematic position of *Mongoloclema* is uncertain. Shishova (1970) placed this genus in the rhabdomesine family Hyphasmoporidae Vine, 1886. However, *Mongoloclema* lacks typical regular budding pattern of autozoecia, which is usually observed in rhabdomesine cryptostomes. Furthermore, inclined and cystiphragmoid diaphragms are not characteristic for cryptostome bryozoans. Gorjunova (1992: 37) and Morozova et al. (2003: 93) placed *Mongoloclema* in the trepostome family Anisotrypidae Dunaeva & Morozova, 1967, apparently because of the absence of styles and presence of tubules (capillaries of authors). However, typical representatives of Anisotrypidae have autozoecial walls with distinct boundaries (serrated), whereas *Mongoloclema* possesses merged autozoecial walls.

**Occurrence.** Two species of *Mongoloclema* are known: *Mongoloclema ignotum* Shishova, 1970 from the Early-Middle Devonian (Emsian-Eifelian) of Mongolia, and *M. sincera* Troitzkaya, 1976, from the Middle Devonian (Givetian) of Kazakhstan (Dzungarian Alatau).

***Mongoloclema sincera* Troitzkaya, 1976**

Pl. 10, figs 1-6; Appendix

1976 *Mongoloclema sincera* Troitzkaya, p. 148-149, fig. 1.

**Material:** Single specimen RGM 211 544-8.

**Occurrence.** Middle Devonian (Givetian); Dzungarian Alatau, Kazakhstan. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.

**Description.** Colony shape apparently ramose, ca 10 mm wide. Exozone narrow, distinctly separated, 0.48-0.90 mm wide. Secondary overgrowths not observed. Autozoecia tubular, bending in exozone at angles of 57-70° and intersecting colony surface at angles of 90°. Autozoecial apertures circular to oval and slightly polygonal. Basal diaphragms abundant in exozone, thin, straight or inclined; absent in endozone. Autozoecial walls granular, 0.010-0.015 mm thick in endozone; finely laminated, without visible boundaries, 0.020-0.055 mm thick in exozones. Exilazoecia abundant, 8-14 surrounding each autozoecial aperture, small, originating in basal exozone, occasionally containing diaphragms. Acanthostyles absent. Indistinct

PLATE 7

- Figs 1-3 - *Anomalotoechus tabulatus* n. sp. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.  
1: paratype. Longitudinal section showing basal diaphragms and cystiphragms. RGM 211 539-1-2; 2: paratype. Longitudinal section showing cystiphragms. RGM 211 539-1-2; 3: holotype. Tangential section. RGM 211 536-1-11.
- Figs 4-6 - *Eridotrypella valida* Duncan, 1939. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.  
4: tangential section. RGM 211 538-1-4; 5: branch oblique section. RGM 211 538-1-5; 6: branch longitudinal section showing autozoecial walls and basal diaphragms. RGM 211 538-1-4.

PLATE 8

- Figs 1-2 - *Eridotrypella valida* Duncan, 1939. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.  
1: tangential section. RGM 211 538-1-4; 2: branch longitudinal section showing autozoecial wall with secondary cortex. RGM 211 538-1-4.
- Figs 3-7 - *Eifelipora tenuis* n. sp. Lower part of Esla Formation, Lower Devonian (Emsian); Villayandre, Cantabrian Mountains, NW Spain.  
3: holotype. Branch longitudinal section. GZG.IN.0.010.512f-1; 4-5: paratype. Tangential sections. GZG.IN.0.010.512c-5; 6: holotype. Branch longitudinal section showing hemiphragms. GZG.IN.0.010.512f-1; 7: paratype. Branch transverse section. GZG.IN.0.010.512f-5.

PLATE 9

- Figs 1-8 - *Boardmanella bohémica* (Ernst, 2008). Santa Lucía Formation (Lower Devonian, Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.  
1-2: branch longitudinal section. RGM 211 536-2-7; 3-4: tangential section. RGM 211 536-2-11; 5: branch transverse section. RGM 211 541-1-4; 6-7: branch transverse sections showing basal diaphragms, styles and autozoecial wall structure. RGM 211 541-1-4; 8: Branch longitudinal section. RGM 211 536-2-7.

PLATE 10

- Figs 1-6 - *Mongoloclema sincera* Troitzkaya, 1976. Santa Lucía Formation, Lower-Middle Devonian (Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain.  
1-3: tangential sections. RGM 211 544-8; 4-6: branch longitudinal sections. RGM 211 544-8.



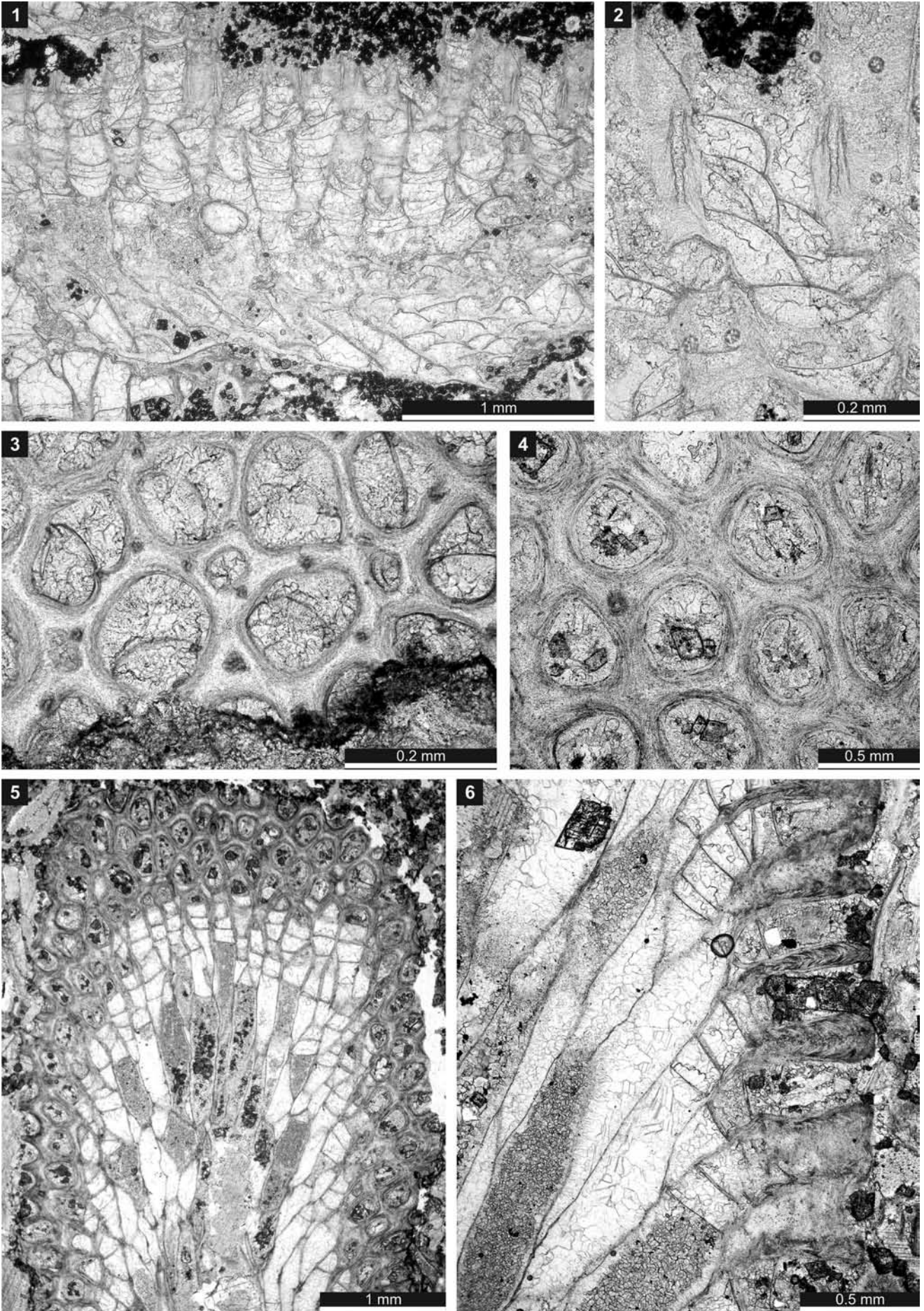


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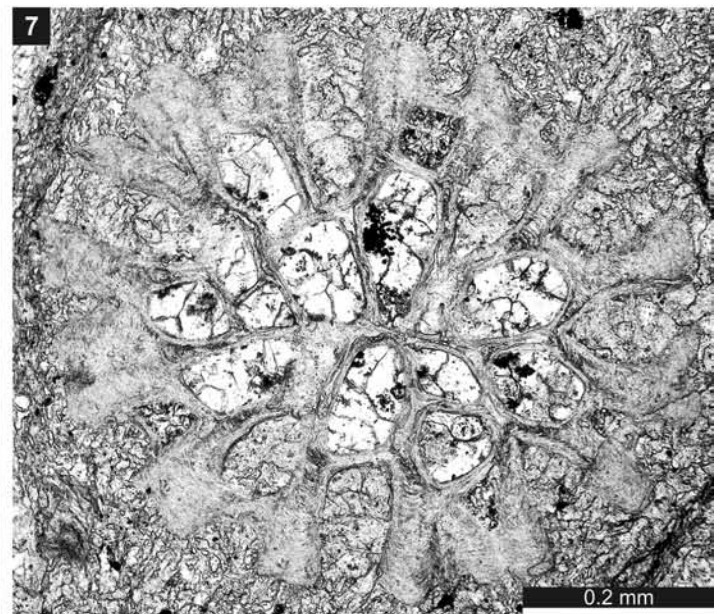
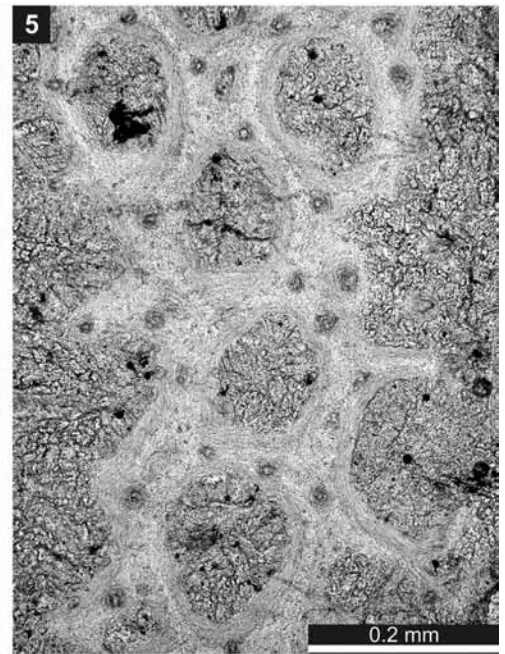
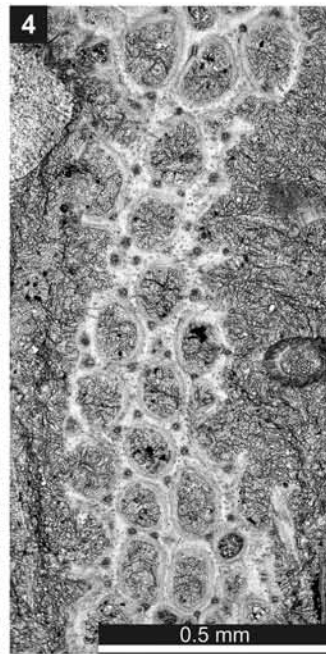
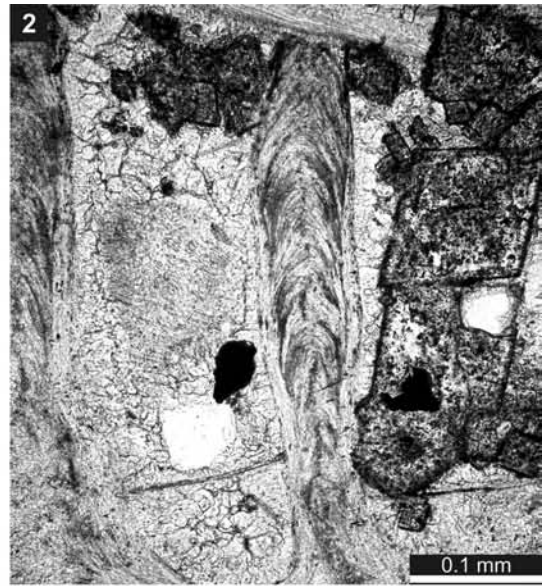
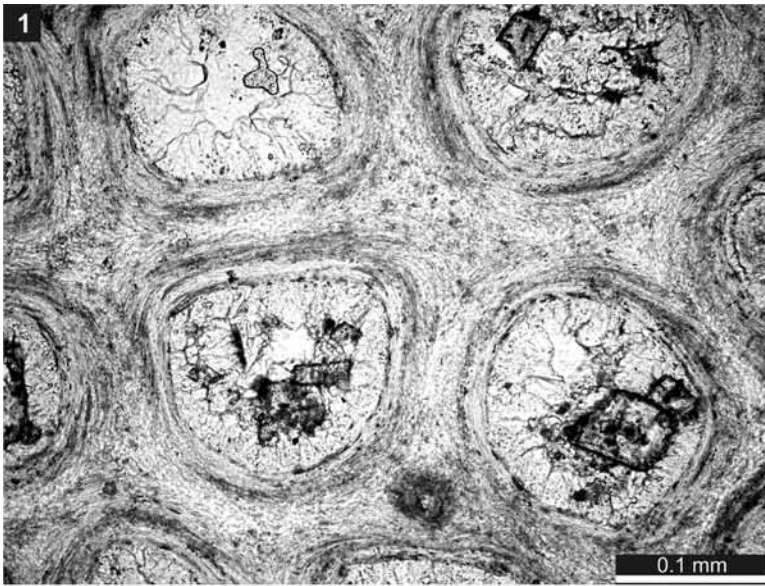


PLATE 8

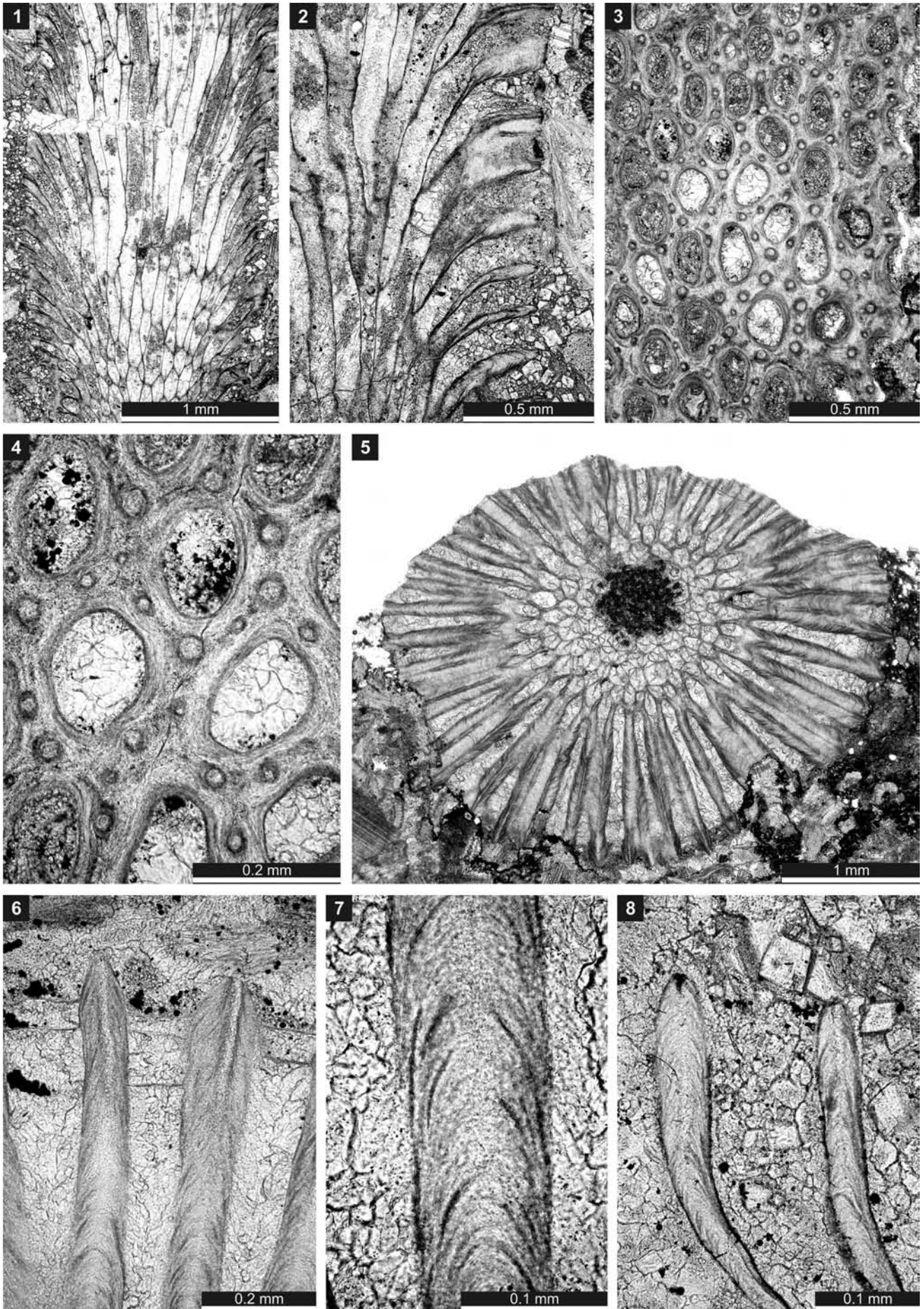


PLATE 9

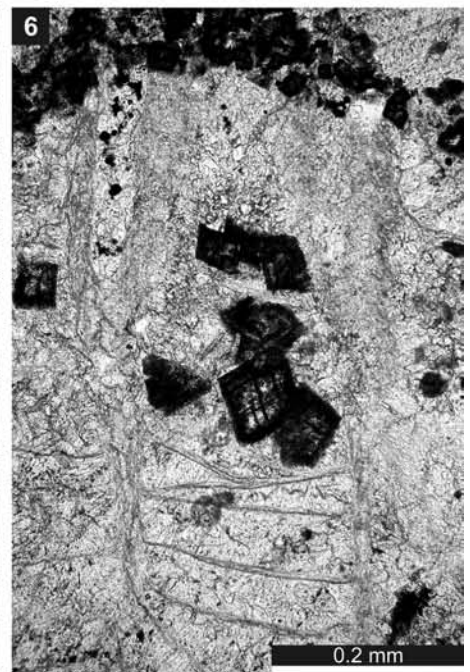
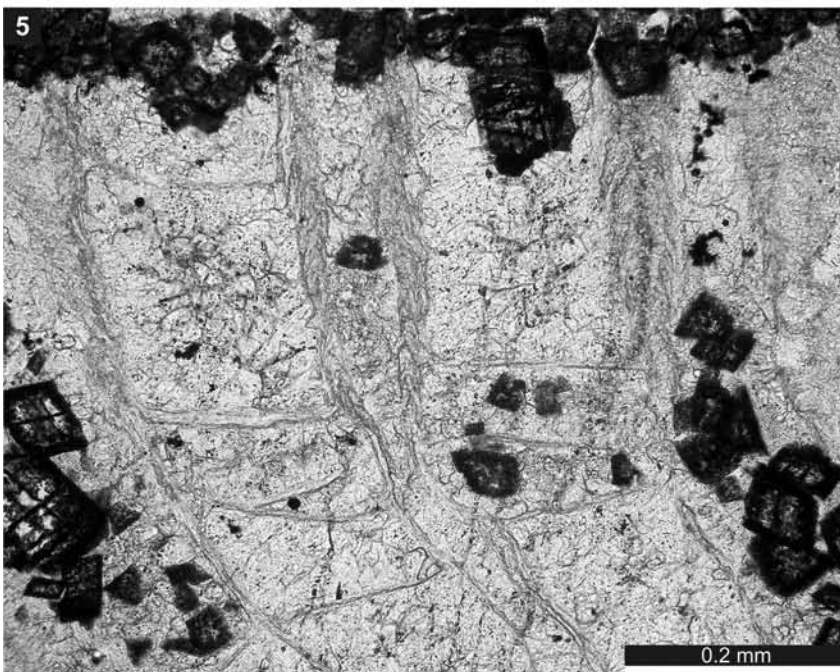
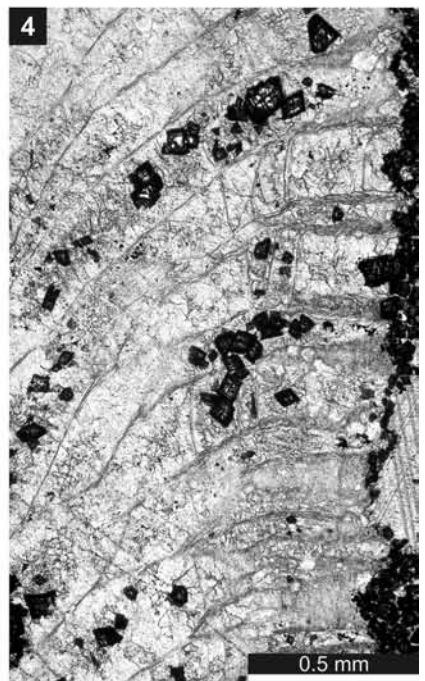
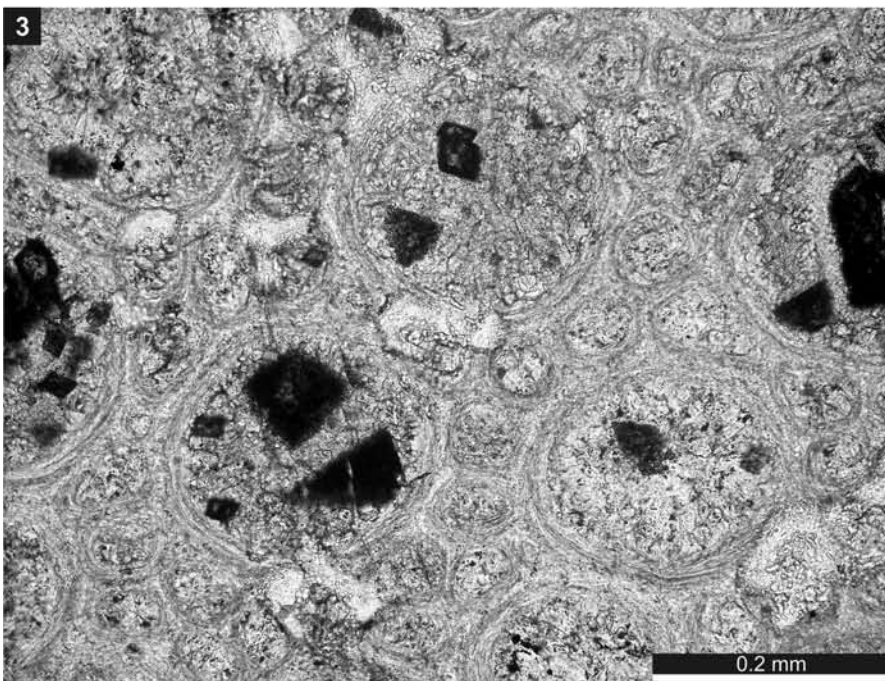
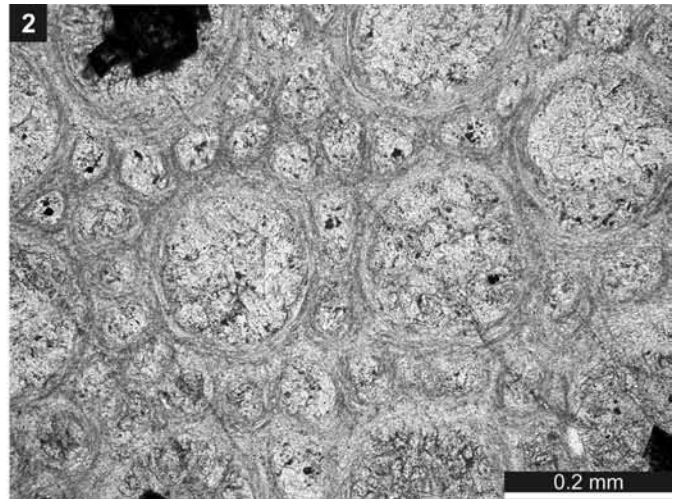
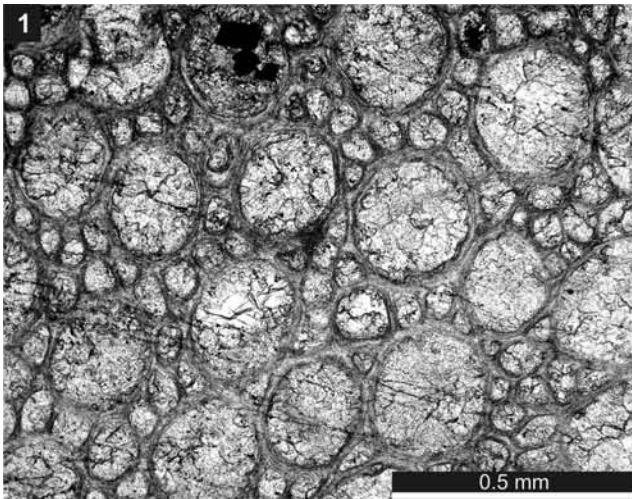


PLATE 10

maculae consisting of larger zooecia and abundant exilazooecia, 0.9-1.2 mm in diameter, spaced 2.5-3.1 mm from centre to centre.

**Comparison.** *Mongoloclema sincera* Troitzkaya, 1976 differs from *M. ignotum* Shishova, 1970 in having larger colonies (branch width up to 10 mm vs. 1-4 mm in *M. ignotum*), and less abundant exilazooecia. Troitzkaya (1976) and Kopajevitch (1984) distinguished *Mongoloclema sincera* from *M. ignotum* by smaller autozoecial apertures. However, these authors used only the range of measurements, what makes the comparison difficult:

Autozoecia width (shorter diameter):

<i>M. sincera</i> Troitzkaya, 1976	0.12-0.18 mm
Present material	0.14-0.20 mm
<i>M. ignotum</i> Shishova, 1970	0.10-0.15 mm
<i>M. ignotum</i> Shishova, 1970 (in Kopajevich, 1984)	0.12-0.22 mm

Measurements on illustrations from available publications of *M. ignotum* Shishova, 1970 (Shishova 1970; Kopajevich 1984; Morozova et al. 2003) produced the range of autozoecial widths (for intermacular zooecia) by 0.13-0.30 mm, whereas the illustration of the type specimen (Shishova 1970, fig. 12, 2a) showed the range by 0.20-0.30 mm (intermacular zooecia). Even if the true range of aperture widths of *M. ignotum* is not consequently calculated yet, it is obvious that *M. ignotum* has larger autozoecial apertures than *M. sincera*.

## Conclusions

The described bryozoan fauna shows palaeobiogeographic relations to the Lower Devonian (Pragian) of Bohemia (*Boardmanella bohémica* (Ernst, 2008), *Leioclema elegans* Ernst, 2008),

Lower Devonian (Upper Emsian) of the Armorican Massif, France (*Leoclema elegans* Ernst, 2008), Middle Devonian (Givetian) of Kazakhstan (*Mongoloclema sincera* Troitzkaya, 1976), and Middle Devonian (Givetian) of USA (*Leptotrypella parva* Duncan, 1939, *L. provecta* Boardman, 1960, *Atactotoechus cartus* Boardman, 1960, *Anomalotoechus alpenensis* (Duncan, 1939), *Eridotrypella valida* Duncan, 1939). On the genus level, the genus *Mongoloclema* shows restricted distribution. It was previously reported from the Middle - Late Devonian of Kazakhstan and Mongolia. *Boardmanella* is known from the Lower Devonian of USA, Kazakhstan and Europe, Middle Devonian of Mongolia and Altay and from the Late Devonian of Kazakhstan and Mongolia. *Leptotrypella*, *Atactotoechus*, *Anomalotoechus*, and *Eridotrypella* are widely distributed genera.

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## Appendix

### Descriptive statistics

Abbreviations: N = number of measurements, X = mean, SD = sample standard deviation, CV = coefficient of variation, MIN = minimal value, MAX = maximal value.

#### *Leioclema elegans* Ernst, 2008

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Branch Width, mm	19	2.3	0.481	21.05	1.5	3.0
Exozone Width, mm	19	0.6	0.196	34.54	0.3	1.0
Autozooeical Aperture Width, mm	60	0.12	0.016	12.81	0.08	0.16
Aperture Spacing, mm	60	0.25	0.040	15.75	0.18	0.38
Mesozooeica Width, mm	60	0.068	0.021	31.58	0.025	0.125
Mesozooeica per Aperture	60	7.6	1.198	15.84	4.0	10.0
Acanthostyle Diameter, mm	60	0.029	0.005	17.60	0.020	0.045
Acanthostyles per Aperture	60	4.1	0.821	20.18	2.0	6.0
Mesozooeical Diaphragm Spacing	60	0.07	0.030	42.02	0.03	0.16
Exozonal Wall Thickness, mm	20	0.04	0.007	19.42	0.03	0.05

#### *Leptotrypella parva* Duncan, 1939

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozooeical Aperture Width, mm	20	0.16	0.031	18.96	0.12	0.24
Aperture Spacing, mm	20	0.24	0.035	14.75	0.18	0.30
Autozooeical Aperture Width, mm (macular)	10	0.23	0.030	12.80	0.19	0.30
Aperture Spacing, mm (macular)	8	0.34	0.054	15.70	0.30	0.46
Exilazooeica Width, mm	20	0.062	0.022	35.63	0.025	0.100
Acanthostyle Diameter, mm	20	0.042	0.007	17.92	0.030	0.060
Exozonal Wall Thickness, mm	19	0.05	0.011	21.60	0.03	0.07
Mural Spine Diameter, mm	10	0.027	0.005	19.91	0.020	0.035

#### *Leptotrypella propecta* Boardman, 1960

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozooeical Aperture Width, mm	30	0.10	0.021	20.17	0.07	0.16
Aperture Spacing, mm	30	0.25	0.036	14.35	0.18	0.32
Autozooeical Aperture Width, mm (macular)	30	0.21	0.033	15.92	0.15	0.28
Aperture Spacing, mm (macular)	24	0.36	0.048	13.36	0.30	0.45
Exilazooeica Width, mm	30	0.048	0.019	39.83	0.023	0.095
Acanthostyle Diameter, mm	30	0.043	0.009	20.47	0.030	0.063
Exilazooeica per Aperture	30	2.4	1.189	50.22	1.0	5.0
Acanthostyles per Aperture	30	3.0	0.830	27.68	2.0	4.0
Exozonal Wall Thickness, mm	20	0.101	0.021	20.58	0.075	0.138
Mural Spine Diameter, mm	10	0.024	0.002	8.75	0.020	0.025



*Leptotrypella maculata* n. sp.

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozooeical Aperture Width, mm	95	0.16	0.021	12.85	0.10	0.20
Aperture Spacing, mm	95	0.19	0.020	10.61	0.15	0.24
Autozooeical Aperture Width, mm (maculae)	75	0.22	0.030	14.10	0.17	0.31
Aperture Spacing, mm (maculae)	75	0.28	0.048	17.23	0.20	0.41
Acanthostyle Diameter, mm	95	0.03	0.007	20.56	0.03	0.05
Acanthostyles per Aperture	85	3.4	1.223	36.36	1.0	6.0
Megastyle diameter, mm	50	0.070	0.017	24.35	0.045	0.120
Exilazoecia Width, mm	10	0.067	0.025	36.76	0.04	0.120
Autozooeical Diaphragm Spacing, mm	25	0.102	0.026	25.20	0.05	0.15
Exozonal Wall Thickness, mm	65	0.046	0.011	22.75	0.025	0.070
Cyst Diameter, mm	10	0.09	0.008	9.12	0.08	0.10

*Atactotoechus cartus* Boardman, 1960

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozooeical Aperture Width, mm	20	0.17	0.030	18.27	0.12	0.24
Aperture Spacing, mm	20	0.20	0.023	11.43	0.17	0.24
Exozonal Wall Thickness, mm	15	0.03	0.005	17.02	0.02	0.04

*Anomalotoechus alpenensis* (Duncan, 1939)

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozooeical Aperture Width, mm	40	0.20	0.030	14.95	0.13	0.25
Aperture Spacing, mm	40	0.21	0.032	14.91	0.17	0.27
Autozooeical Aperture Width, mm (maculae)	30	0.28	0.031	11.07	0.23	0.36
Aperture Spacing, mm (maculae)	30	0.35	0.050	14.34	0.25	0.45
Exilazoecia Width, mm	10	0.042	0.015	35.50	0.025	0.068
Acanthostyle Diameter, mm	20	0.03	0.010	33.48	0.02	0.05
Exozonal Wall Thickness, mm	20	0.038	0.011	28.96	0.025	0.063
Maculae Diameter, mm	6	2.41	0.302	12.54	1.95	2.75
Maculae Spacing, mm	6	3.27	0.393	12.02	2.65	3.70

*Anomalotoechus tabulatus* n. sp.

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozooeical Aperture Width, mm	30	0.16	0.028	17.83	0.11	0.20
Aperture Spacing, mm	30	0.24	0.036	14.70	0.16	0.30
Acanthostyle Diameter, mm	30	0.033	0.005	15.43	0.025	0.045
Acanthostyles per Aperture	20	4.7	0.988	21.25	3.0	6.0
Exilazoecia Width, mm	15	0.052	0.016	31.18	0.035	0.080
Exozonal Wall Thickness, mm	10	0.05	0.010	20.29	0.04	0.07

*Eridodrypella valida* Duncan, 1939

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozoecial Aperture Width, mm	30	0.13	0.022	16.55	0.10	0.19
Aperture Spacing, mm	30	0.22	0.039	17.52	0.18	0.30
Acanthostyle Diameter, mm	6	0.06	0.009	16.27	0.05	0.075
Exilazooecia Width, mm	6	0.057	0.015	26.57	0.040	0.075
Exozonal Wall Thickness, mm	10	0.08	0.011	13.40	0.07	0.10
Autozoecial Diaphragm Spacing, mm	20	0.086	0.019	21.95	0.055	0.110

*Eifelipora tenuis* n. sp.

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Branch Width, mm	7	1.01	0.170	16.93	0.81	1.29
Endozone Width, mm	7	0.47	0.043	9.02	0.42	0.54
Autozoecial Aperture Width, mm	40	0.09	0.018	19.99	0.06	0.13
Aperture Spacing, mm	40	0.17	0.034	19.96	0.11	0.23
Exilazooecia Width, mm	40	0.032	0.012	36.81	0.015	0.060
Acanthostyle Diameter, mm	40	0.029	0.004	14.40	0.020	0.035
Exilazooecia per Aperture	20	3.3	1.333	41.01	2.0	7.0
Acanthostyles per Aperture	20	4.2	1.322	31.47	2.0	7.0
Exozonal Wall Thickness, mm	20	0.043	0.007	16.62	0.030	0.055

*Boardmanella bohémica* (Ernst, 2008b)

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Branch Width, mm	15	3.0	0.873	29.02	1.9	4.1
Exozone Width, mm	15	0.9	0.306	35.34	0.4	1.4
Autozoecial Aperture Width, mm	35	0.10	0.020	19.74	0.07	0.17
Aperture Spacing, mm	40	0.17	0.024	13.69	0.14	0.22
Macroacanthostyle Diameter, mm	40	0.04	0.009	20.74	0.03	0.07
Microacanthostyle Diameter, mm	20	0.017	0.002	12.61	0.013	0.020
Acanthostyles per Aperture	40	5.7	0.905	15.82	4.0	8.0
Exozonal Wall Thickness, mm	35	0.07	0.015	20.50	0.05	0.10

*Mongoloclema sincera* Troitzkaya, 1976

	<b>N</b>	<b>X</b>	<b>SD</b>	<b>CV</b>	<b>MIN</b>	<b>MAX</b>
Autozoecial Aperture Width, mm	20	0.17	0.014	8.21	0.14	0.20
Aperture Spacing, mm	20	0.27	0.040	15.06	0.20	0.34
Autozoecial Aperture Width, mm (maculae)	10	0.23	0.010	4.30	0.22	0.25
Exilazooecia Width, mm	20	0.05	0.015	29.60	0.03	0.08
Exilazooecia per Aperture	20	11.3	1.803	16.02	8.0	14.0
Exozonal Wall Thickness, mm	10	0.032	0.010	30.90	0.020	0.055