TREPOSTOME BRYOZOANS FROM THE LOWER - MIDDLE DEVONIAN OF NW SPAIN

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Abstract. The present paper presents descriptions of 11 trepostome bryozoan species from the material deposited at the Geological Centrum Göttingen, Germany, and National Natuurrhistorisch Museum (Natuur), 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: Leptostyphla maculata n. sp., Anomalocochius tabulatus n. sp. and Esethpora tenax n. sp. The genus Mongolocelma 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).


Introduction

Bryozoans 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 (Suárez 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 siliciclastic shelf sediments and carbonate platform rocks. The entire succession experienced only moderate deformation during the Variscan orogeny (e.g., Comte 1959;

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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 marls/bones, limestones and shales of Villayandre Member (serotinus conodont zone) in the uppermost part of the formation (Keller 1988, 1997; Keller & Gröttsch 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 Bedía 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 buildups 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 (Natuuris) 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 GZGIN.0510.512 and GZGIN.0510.529. Separate thin sections of the same sample are numbered by adding a subnumber suffix.

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

Fig. 2 - Stratigraphy of the Lower Devonian of the Astur-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 of 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).

Sample 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°48’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°56’N 5°09’W), Cantabrian Mountains, NW Spain” (= Esla Formation, Lower Devonian, Emsian).

Sample RGM 211 548-549 refer to “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 (1976). The following morphologic characters were measured and used for statistics in the studied material:

- Branch width, colony thickness, exo- (endo-) zone width, autozooecial aperture width, aperture spacing, acaustochyle diameter, meso- (exila-) zoocoe diameter, autozooecial (mesozooecial) diaphragm spacing, number of meso- (exila-) zoocoe and acaustochyles surrounding each autozooecial 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 Berg, 1926

Order Trepostomata Ulrich, 1882

Suborder Heteroporina Astrova, 1965

Family Heterotriphyidae Ulrich, 1890

Genus *Leioclema* Ulrich, 1882

[= *Liodema* Ulrich, 1882]

**Type species:** *Callopora puncrata* 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. Mesozooecia abundant, with abundant apertures, often beaded. Acanthostyles abundant, commonly large. Autozoecial walls thin in endzone; laminated, regularly thickened in exozones (modified after Astrova 1978).

**Comparison.** *Liodema* Ulrich, 1882 differs from *Heterotrypa* Nicholson, 1879 in having rare autozoecial diaphragms and abundant acanthostyles and mesozooecia, from *Stigmatella* Ulrich & Basdler, 1904 in having abundant mesozooecia.

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

*Leioclema elegans* Ernst, 2008

Pl. 1, figs 1-5; Appendix


**Material.** RGM 211 539-1-1, RGM 211 539-8, RGM 211 546, GZG.IN.0.010.512, b-(1-2), c-(1-3), c2-(1-2), f-(1-4), g-(3, 4, 8, 10), GZG.IN.0.010.529, e.

**Occurrence.** Koněprusy Limestone, Lower Devonian (Pragian); Zlatý Kůň, Czech Republic. Lower Devonian (Upper Emsian); Ménéz-Bélar 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 indented acanthostyles. Autozoecial basal diaphragms rare to absent, thin, straight or slightly
deflected proximally. Mesozoecia 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 exozones, often indenting autozoecia, having distinct calcite cores and dark laminated sheaths. Walls granular, 0.010-0.012 mm thick in exozones; distinctly laminated, merged, 0.03-0.05 mm thick in the exozone. Indistinct maculae consisting of slightly larger zooecia and more abundant mesozoecia.

Comparison. Leioiclama elegans Ernst, 2008 (Ernst 2008b) differs from L. abiettensis 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. abiettensis).

Suborder Amplesporina Astrova, 1965
Family Atactoetocheidae Duncan, 1939
Genus Leptotrypella Vinassa de Legry, 1921
Type species: Chaetetes kurnabei Nicholson, 1874. Middle Devonian; Ontario (Canada)


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

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 Lucia 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 exozones, bending at low angles in exozones. Autozoecial apertures oval. Autozoecial diaphragms abundant in exozone, thin, straight or slightly deflected proximally. Exilazoecia 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 zoecial boundaries, 0.03-0.07 mm thick in exozones. Secondary cingulum often developed, relatively thin, with laminated 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 endzone 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, 1963
Pl 2, figs 4-6, Pl. 3, figs 1-4; Appendix
1963 Leptotrypella (Leptotrypella) mesozoea provecta Boardman, p. 36, pl. 6, figs 7-8.

PLATE 1

Figs 1-5 - Leioiclama elegans Ernst, 2008. Lower part of Esla Formation, Lower Devonian (Emsian); Villayandre, Cantabrian Mountains, NW Spain. 1-2: longitudinal sections. GZG-IN.010.512b-2; 3: branch oblique section. GZG-IN.010.512f-4; 4-5: tangential sections. GZG-IN.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 Ludlow 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. Autozoocoea long in endozones, bending at low angles in exozones. Autozoocoeal apertures oval. Autozoocoeal diafragms in exozone, thin, straight or slightly deflected proximally. Exilazoecia common, 1-5 surrounding each autozoocoeal aperture, locally absent, short, restricted to exozones, rounded to polygonal in cross section. Acanthostyles large, abundant, 2-4 surrounding each autozoocoeal aperture, originating in basal exozone, having distinct cores and laminated sheaths, protruding above colony surface. Autozoocoeal walls granular, 0.005-0.010 mm thick in endozones; laminated, merged, without distinct zoocoeal boundaries, 0.075-0.138 mm thick in exozones. Secondary cingulum often well developed, with laminated parallel autozoocoeal 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 zooecia, 1.35-2.10 mm in diameter, spaced 2.2-2.6 mm from centre to centre.

Comparison. Leptotrypella maculata n. sp is similar to L. acquisibilis 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. acquisibilis (average autozoocoea width 0.16 mm vs. 0.20 mm in L. acquisibilis). Duncan 1939 (224) mentioned no mural spines in walls of L. acquisibilis. However, the longitudinal section of L. acquisibilis (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 macula of the new species (from Latin "maculatus" - spotted).

Holotype: RGM 211 546-2.

Paratypes: RGM 211 546-1, 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; autozoocoeal diafragms 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 autozoocoeal walls present; maculae well defined, regularly spaced, consisting of larger zooecia 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 autozoocoeal walls and mural spines (arrows on Fig. 3). RGM 211 539-1-2.

Figs 4-6 - *Leptotrypella protracta* 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 exozones, 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* Boardman, p. 73-74, pl. 18, figs. 4-6.
1960 *Atactotoechus cartus* pilanes Boardman, p. 74, pl. 18, figs. 1-3.

Material: Two colonies GZG.1N.0.010.312F-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 (Emisian); 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, 0.025-0.040 mm thick in exozones. Maculae consisting of larger autozoecia, not well observed in present material.

Comparison. *Atactotoechus cartus* Boardman, 1960 differs from *A. acritos* 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. acritos*).

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


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 - *Leptotrypa proeicta* Boardman, 1960. ? Esla Formation, Lower Devonian (Emisian); Portilla de Luna, Cantabrian Mountains, NW Spain.
1: tangential section. RGM 211 536-5-1; 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 - *Leptotrypa maculata* n. sp. Santa Lucía Formation, Lower-Middle Devonian (Emisian-Eifelian); Cudás de Luna, Cantabrian Mountains, NW Spain.
5: holotype. Branch transverse section showing autozoecial walls and acanthostyles. RGM 211 540-2; 6: paratype. Branch transverse 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 - *Leptotrypa maculata* n. sp. Santa Lucía Formation, Lower-Middle Devonian (Emisian-Eifelian); Cudás de Luna, Cantabrian Mountains, NW Spain.
1: holotype. Tangential section of non-macular area. RGM 211 540-2; 2: holotype. Tangential section of macula 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.
**Anomalotoechus alpenensis** (Duncan, 1939)

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

1939 *Stigmella 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, Genishaw 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 overgrowth common, separate sheets 1.9-8.0 mm thick. Exozones 1.05-1.44 mm wide. Autozoosoea long, prismatic, having polygonal cross sections. Autozoosoeal apertures rounded-polygonal. Autozoosoeal diaphragms widely spaced in exozones, common to abundant in exozones, usually straight or slightly curved distally, locally absent. Exilazoosoea rare, short, with rounded apertures. Acanthostyles moderately large, having narrow hyaline cores and indistinct laminated sheaths, 1-3 surrounding each autozoosoeal aperture, locally absent. Autozoosoeal walls granular, locally strongly crenulated, 0.005-0.010 mm thick in exozones; merged, showing reversal V-shaped lamination without distinct zoosoeal boundaries, irregularly thickened, with serial thickenings throughout the colony, 0.025-0.063 mm thick in exozones. Maculae large, elevated, consisting of large autozoosoea, 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 autozoosoeal 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 (autozoosoeal 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 cystiphagums in autozoosoea (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 endozoones; diaphragms and cystiphagums abundant in exozoones; exilazoosoea rare; acanthostyles common, moderately large.

**Description.** Encrusting (subramose) colonies, separate sheets 0.30-0.75 mm in thickness. Exozones indistinctly separated from endozoones. Autozoosoea long, bending gently in endozoones, having polygonal cross sections. Autozoosoeal apertures rounded-polygonal. Autozoosoeal diaphragms restricted to exozones, locally common, 2-5 occurring in each autozoosoeum; locally absent. Cystiphagums present in exozone, occupying about half space of the autozoosoeal chamber. Exilazoosoea rare, short, with rounded apertures. Acanthostyles moderately large, 3-6 surrounding each autozoosoeal aperture, having distinct cores and laminated sheaths. Autozoosoeal walls granular, 0.005-0.010 mm thick in endozoones; irregularly thickened, merged, showing reversal U-shaped lamination without distinct zoosoeal 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 cystiphagums.

Family Eridotrypellidae Morozova, 1960

Genus Eridotrypella Duncan, 1939

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


**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. Exozones 0.48-0.63 mm wide, endozones 2.74-2.44 mm wide. Exozones distinctly separated from endozones. Autozoococia long in endozones, bending sharply in exozones. Autozoococolial apertures polygonal with rounded corners. Autozoococcoal diaphragms absent to rare in endozones; usually thick, abundant in transition between endozoecium and exozone, straight or inclined. Exilazoecia rare, short, polygonal in cross section. Acanthostyles rare, moderately large, having distinct narrow cores and laminated sheaths. Autozoococial 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. spinierea* Duncan, 1939 in fewer acanthostyles and thicker autozoococial walls.

Genus Eifelpora Ernst, 2008

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

Diagnosis: Branched colonies; secondary overgrowths common; proximal hemisphragms common; autozoococial walls containing spherules in exozones; exilazoecia rare to common; acanthostyles locally abundant.

Comparison. Eifelpora Ernst, 2008 is similar to Eridotrypella Duncan, 1939, but differs in the presence of hemisphragms. The new genus differs also from Eridocamypus Duncan, 1939 in shape and arrangement of hemisphragms. Eridocamypus has curved and serrated hemisphragms which are arranged on all autozoococial chamber walls. Eifelpora differs from Stenophragmiidium Basler, 1952 in wall structure without monilae shaped thickenings and containing spherules.

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

Eifelpora tenus n. sp.

Pl. 8, figs 3-7; Appendix

Etymology: The specific name ‘tenus’ refers to the thin colonies of the new species (derived from Latin ‘tenus’ = thin).

Holotype: GZG.IN.001.512F-1.

Paratypes: GZG.IN.001.512F (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 Eda Formation, Lower Devonian (Emsian).

Diagnosis: Branched colonies; proximal hemisphragms common; autozoococial walls containing spherules in exozones; exilazoecia 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. Autozoococia tubular-prismatic, growing parallel to branch axes in endozone, bending abruptly in exozone and intersecting colony surface at angles of 78-80°. Autozoococial apertures rounded-polygonal. Basal diaphragms common to absent, restricted to exozone, straight or slightly curved distally, thin. Hemisphragms abundant in exozones, positioned on proximal wall, moderately thin, short to moderately long, straight to weakly curved proximally. Autozoococial walls granular, 0.005-0.010 mm thick in endozone; laminated, containing spherules, 0.030-0.055 mm thick in exozones. Exilazoecia abundant, 2-7 surrounding each autozoococial aperture, small, originating in basal exozone. Acanthostyles abundant, 2-7 surrounding each autozoococial aperture, having distinct cores and laminated sheaths, originating in basal exozone. Maculae absent.

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

Family Anisotrypidae Dunaeva & Morozova, 1967

Genus Boardmanella Gorjunova & Weis, 2003

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

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

PLATE 5

Figs 1-4 - Atactotrichus artsis Boardman, 1960. Lower part of Eda Formation, Lower Devonian (Emsian); Villayandre, Cantabrian Mountains, NW Spain. 1-3: branch oblique section showing basal diaphragms and cystiphragms. GZG.IN.001.512F-3; 4: tangential section. GZG.IN.001.512G-14.

Figs 5-7 - Anomalotoechus alpensis (Duncan, 1939). Santa Lucia Formation (Lower Devonian, Emsian-Eifelian); Caldas de Luna, Cantabrian Mountains, NW Spain. 5: longitudinal section of encrusting colony. RGM 211 538A-4; 6: transverse section of encrusting colony. RGM 211 541-2; 7: transverse section of massive colony. RGM 211 539-1.

Fig. 8 - Anomalotoechus alpensis (Duncan, 1939). ? Eda Formation, Lower Devonian (Emsian); Puerto de la Cubilla, Cantabrian Mountains, NW Spain. Longitudinal section of massive colony. RGM 211 547.
endzones, then bending in endzones at moderate angles, polygonal in transverse section; autozooidal apertures rounded to oval or rounded-polygonal; basal diaphragms usually absent, locally present, thin, straight; exulazooecia rare to abundant, short, varying in size; paurostyles (Gorjunova & Weis, 2003) always covered by skeletal material; varying in size and number; autozooidal walls regularly thickened in endzones, straight, merged without distinct zooidal 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 autozooidal 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 & Weis, 2003 from the Middle Devonian (Givetian) of Mongolia, B. interporosa (Ulrich & Bassler, 1904) from the Lower Devonian of USA, B. antigua (Nekhoroshev, 1977) from the Lower Devonian (Pragian-Emnian) of Kazakhstan, B. bohemia (Ernst, 2008) (Ernst 2008b) from the Lower Devonian (Pragian) of Bohemia and Lower-Middle Devonian (Emnian-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. universalis (Kopajevich, 1984) from the Middle Devonian (Eifelian-Givetian) of Mongolia, B. elliptica (Kopajevich, 1984) from the Middle-Upper Devonian (Givetian-Prasian) of Mongolia, B. indistincta (Nekhoroshev, 1977) from the Upper Devonian (Famennian) of Kazakhstan.

Boardmanella bohemia (Ernst, 2008)
Pl. 9, figs 1-8. Appendix
2008b Dyscritella bohemia 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, RGM 211 541-1(5, 6, 7, 8, 9), RGM 211 543-3(2-6), RGM 211 541-4.

Occurrence. Zlatý Kůň, Czech Republic; Koněprusy Limestone, Frigian (Lower Devonian)? Esła 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 exozones. Secondary overgrowth occurring. Branches 1.9-4.1 mm in diameter. Endzones 1.1-3.3 mm wide, exozones 0.4-1.4 mm wide. Autozoocoea long in endzone, bending at low angles in exozone. Autozooidal apertures rounded-polygonal. Autozooidal diaphragms rare to absent. Exulazooecia rare, short, rounded to oval in cross section. Paurostyles of two distinct sizes. 3-6 large paurostyles surrounding each autozooidal aperture; having indistinct cores and laminated sheaths. Commonly 1-2 small paurostyles spaced in a single row between large paurostyles. Autozooidal walls granular, 0.005-0.015 mm thick in endzones; thick, merged, laminated without distinct zooidal boundaries, 0.05-0.10 mm thick in exozones. Indistinct maculae consisting of larger autozoocoea.

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

Genus Mongolocolema Shishova, 1970
Type species: Mongolocolema ignotum Shishova, 1970. Middle-Late Devonian; Mongolia

1970 Mongolocolema Shishova, p. 29.

PLATE 6

Figs 1-4 - Amonaloctoechus alperenius (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; 4: tangential section of a macula. RGM 211 547.

Fig. 5 - Amonaloctoechus alperenius (Duncan, 1939). ? Esła Formation, Lower Devonian (Emsian); Puerto de la Cubilla, Cantabrian Mountains, NW Spain. Longitudinal section showing crenulated walls of endozone. RGM 211 547.

Fig. 6 - Amonaloctoechus 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; autozooecia 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 autozooecia, sometimes containing thin diaphragms; styles absent; autozoocelial walls finely laminated, without visible boundaries, irregularly thickened in exzone; fine tubules present in outermost parts of exozonal walls.

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

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

*Mongololecma sincera* Troitzkaya, 1976

Pl. 10, figs 1-6; Appendix

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


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

Description. Colony shape apparently ramose, ca 10 mm wide. Exozoone narrow, distinctly separated, 0.48–0.90 mm wide. Secondary overgrowths not observed. Autozoocelia tubular; bending in exozoone at angles of 57–70° and intersecting colony surface at angles of 90°. Autozoocelial apertures circular to oval and slightly polygonal. Basal diaphragms abundant in exozoone, thin, straight or inclined; absent in endozoone. Autozoocelial walls granular, 0.010–0.015 mm thick in exozoone; finely laminated, without visible boundaries, 0.020–0.055 mm thick in exozones. Exilazoecia abundant, 8–14 surrounding each autozoocelial aperture, small, originating in basal exozoone, occasionally containing diaphragms. Acanthostyles absent. Indistinct
maculae consisting of larger zooecia and abundant exilazoecia, 0.9–1.2 mm in diameter, spaced 2.5–3.1 mm from centre to centre.

Comparison. *Mogoloclema 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 exilazoecia. Troitzkaya (1976) and Kopajevich (1984) distinguished *Mogoloclema sincera* from *M. ignotum* by smaller autozooecial apertures. However, these authors used only the range of measurements, what makes the comparison difficult:

Autozooecia width (shorter diameter):

*M. sincera* Troitzkaya, 1976 0.12–0.18 mm
Present material 0.14–0.20 mm
*M. ignotum* Shishova, 1970 0.10–0.15 mm
*M. ignotum* 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 autozooecial widths (for intermural 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 (intermural 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 autozooecial apertures than *M. sincera*.

Conclusions

The described bryozoan fauna shows palaeobiogeographic relations to the Lower Devonian (Fragi) of Bohemia (*Boardmanella bohemia* Ernst, 2008), *Letioclava elegans* Ernst, 2008), Lower Devonian (Upper Emsian) of the Armorican Massif, France (*Leoclema elegans* Ernst, 2008), Middle Devonian (Givetian) of Kazakhstan (*Mogoloclema sincera* Troitzkaya, 1976), and Middle Devonian (Givetian) of USA (*Leptotrypeilla para* Duncan, 1939, *L. provecta* Boardman, 1960, *Atactotoechus carus* Boardman, 1960, *Anomalotoechus alpenensis* (Duncan, 1939), *Eridotrypella valida* Duncan, 1939). On the genus level, the genus *Mogoloclema* 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. *Leptotrypeilla*, *Atactotoechus*, *Anomalotoechus*, and *Eridotrypella* are widely distributed genera.

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References


## Appendix

### Descriptive statistics

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

**Leiodema eleanu Ernst, 2008**

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**Leptospyrella parae Duncan, 1989**

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**Leptospyrella prosect Boardman, 1960**

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**Leptostrygella maculata n. sp.**

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**Atutozoeciodus cartus Boardman, 1960**

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**Anomalotoecieidus alpenensis (Duncan, 1939)**

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**Anomalotoecaidus tabulata n. sp.**

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**Endodrypsella valida** Duncan, 1939

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**Eisfelopa tenuis** n. sp.

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**Boardmanella bohemica** (Ernst, 2008b)

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**Mongolomela sinica** Troitskaya, 1976

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