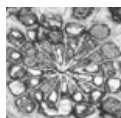


The upper Katian (Ordovician) bryozoans from the Eastern Iberian Chains (NE Spain)

ANDREA JIMÉNEZ-SÁNCHEZ



The upper Katian (Upper Ordovician) bryozoans from the Iberian Chains (NE Spain) are described. Twenty-three species are identified, five of them are new, seven were already identified in other paleocontinents and Mediterranean localities, four are provisionally referred to other known species, and seven are undetermined species. All of them belong to 22 genera assigned to 14 families, and to one incertae sedis genera. The five Stenolaemata orders (Cryptostomata, Cyclostomata, Cystoporata, Fenestrata and Trepostomata) are represented here, Trepostomata and Cryptostomata being the most abundant and diverse. The trepostome family Halloporidae is the one with the highest diversity, with 4 genera and 5 species described here. The five new species are the cryptostomes *Pseudostictoporella iberiensis* sp. nov., characterized by the presence of superior hemisepta in the autozooezia, and *Prophyllodictya javieri* sp. nov., also characterized by the presence of superior hemisepta in the autozooezia and by its small exilazooezia; the cystoporate *Ceramoporella inclinata* sp. nov., whose main diagnostic character is the constant autozooezial inclination; and the trepostomates *Dybowskites ernsti* sp. nov., easily recognizable by its large autozooezial and mesozooezial apertures, as well as by its large acanthostyles and *Trematopora acanthostylita* sp. nov., mainly characterized by the absence of diaphragms in its mesozooezia and numerous, large acanthostyles. • Key words: Stenolaemata, Bryozoans, upper Katian, Upper Ordovician, Iberian Chains, NE Spain.

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Andrea Jiménez-Sánchez, Área de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, C/ Pedro Cerbuna 12, 50009 Zaragoza (Spain); andrea.j@unizar.es

Bryozoans were one of the main invertebrate groups dominating the carbonate platforms during the Ordovician. They have been widely studied in North America, the Baltic and Scandinavian countries, Eastern Europe and Siberia, where they were strongly diversified by the Mid Ordovician. However, the Ordovician bryozoans from the Mediterranean margin of Gondwana have received much less attention in spite of their abundance in the Upper Ordovician carbonate units typical of the region. In the Cystoid Limestone Formation (Dereims 1898, Villas 1983), upper Katian (Upper Ordovician) in age, of the Iberian Chains (NE Spain), the five Stenolaemata orders, present since the Lower-Middle Ordovician transition, are represented [Cryptostomata, Cyclostomata, Cystoporata, Fenestrata and Trepostomata (Jiménez-Sánchez *et al.* 2007)]. This strongly contrasts with their extremely low diversity and very scarce occurrences in the underlying horizons. This fact is related to the Upper Ordovician environmental conditions, when the development of carbonate platforms on the Mediterranean margin of Gondwana allowed a massive faunal expansion (Vennin *et al.* 1998). Before the late

Katian and since the Mid Cambrian, the Mediterranean Region was occupied by large siliciclastic platforms (Gutiérrez-Marco *et al.* 2002).

The first descriptions of the Ordovician Mediterranean bryozoans are from Portugal (Sharpe 1853), Bohemia (Počta 1902, Kettner 1913, Röhlich 1957) and the Carnic Alps (Vinassa de Regny 1910, 1914, 1915, 1942), although this work now needs revision. The bryozoans occurring in rocks of the same age as the Cystoid Limestone Formation, from the Montagne Noire, France (Dreyfuss 1948, Boulange 1963, Ernst & Key 2007), and Sardinia (Conti 1990), have already been well studied. The contributions of Buttler & Massa (1996) and Buttler *et al.* (2007) describing a total of seven species in the Upper Ordovician of Libya, as well as the contributions of Termier & Termier (1950) and Destombes *et al.* (1971) identifying five genera in the Upper Ordovician of Morocco must also be acknowledged. In addition to the first report of Upper Ordovician bryozoans in the Cystoid Limestone Formation by Hafenrichter (1979), who identified the genera *Diplotrypa* and *Hallopora*, the preliminary study of Jiménez-Sánchez *et al.*

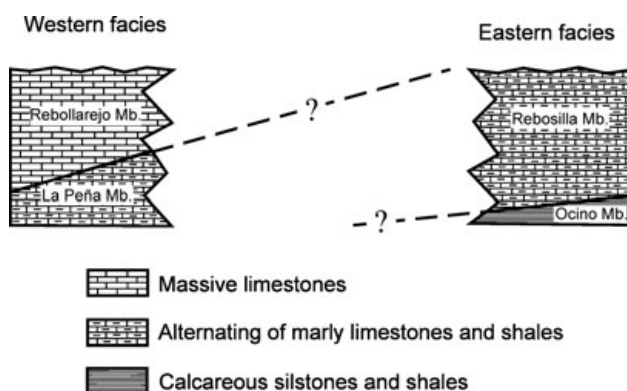


Figure 1. Relationships between facies and lithostratigraphic units of the Cystoid Limestone Formation. Taken from Jiménez-Sánchez *et al.* (2007).

(2007) should also be mentioned, in which 21 genera are added to those already known from the region. Jiménez-Sánchez (in press) described five Monticuliporidae species found in the Cystoid Limestone Formation. Jiménez-Sánchez & Villas (in press) conducted a paleobiogeographic study of the upper Katian bryozoan faunas, incorporating the taxonomic data from previous papers and using multivariate statistical methods. Finally, Jiménez-Sánchez *et al.* (in press) described a new genus and species from the family Rhinidictyidae using both the phenetic and cladistic systematic approaches.

The aim of the present study is to continue with the systematic description of the bryozoans from the Cystoid Limestone Formation, most of them preliminarily listed and figured in Jiménez-Sánchez *et al.* (2007). This study should contribute to knowledge of the Ordovician bryozoan fauna in the Mediterranean margin of Gondwana.

In this paper twenty three species are described, five of them are new, seven were already identified in other paleocontinents and Mediterranean localities, four are provisionally referred to other known species, and seven are undetermined species. All of them belong to 22 genera assigned to 14 families, and to one incertae sedis genera. The trepostome family Halloporidae is the one with the highest diversity, with 4 genera and 5 species described here.

A total of 29 species have now been identified in the Cystoid Limestone Formation, the orders Trepostomata, with 15 species (52%), and Cryptostomata, with 9 species (31%), are the most diverse. The other orders, Cystoporata (7%), Fenestrata (7%) and Cyclostomata (3%), are in the minority. Thirteen of these species are restricted to the Mediterranean Province, in which India has also been included (Jiménez-Sánchez & Villas in press). These species are *Ceramoporella inclinata* sp. nov., *Chasmatopora hypnoides* (Sharpe, 1853), *Dybowskites ernsti* sp. nov., *Diplotrypa gemmata* (Conti, 1990), *Eridotrypa obliqua* Conti, 1990, *Iberostomata fombuenensis* Jiménez-Sánchez

et al., to be published, *Monticulipora cystiphragmata* Jiménez-Sánchez, in press, *Prasopora carnica* Vinassa de Regny, 1915, *Prasopora spjeldnaesi* Jiménez-Sánchez, in press, *Prophyllodictya javieri* sp. nov., *Pseudostictoporella iberiensis* sp. nov., *Trematopora acanthostylita* sp. nov., and *Ulrichostylus radiatus* Conti, 1990. *Monticulipora kolaluensis* Jaroshinskaja, 1962 was previously known exclusively from the Upper Ordovician of Altai Sayan. *Ceramopora? lindströmi* Hennig, 1908, was also known exclusively from the Lower Silurian of Gotland (Sweden). *Pseudostictoporella iberiensis* sp. nov. and *Prophyllodictya javieri* sp. nov. are the first representatives of their genera known outside the palaeocontinents of Laurentia, the former, and of Baltica and South China, the latter. *Hallopora elegantula* (Hall, 1851) and *Kukersella borealis* (Bassler, 1911) are the most widely distributed of all the species found in Cystoid Limestone Formation, both in space and time. *Hallopora elegantula* has been identified in the palaeocontinents of Avalonia, Baltica, Laurentia, Gondwana and Siberia, as well as in South China, in horizons from the Upper Ordovician to the Middle-Upper Silurian. *Kukersella borealis* is known from the palaeocontinents of Avalonia, Baltica, Gondwana and Laurentia, in horizons from the Middle to the Upper Ordovician.

Geographical and geological setting

A detailed description of the geographical and geological setting of the studied sections, as well as complete information regarding the stratigraphic and sedimentary characteristics of the Cystoid Limestone Formation, can be found in Villas (1985), Hammann (1992), Vennin *et al.* (1998), Jiménez-Sánchez *et al.* (2007) and Jiménez-Sánchez (in press).

The bryozoans described here have been collected from four sections of the Cystoid Limestone Formation: the Valdelaparra and La Peña del Tormo sections, near the village of Fombuena (Zaragoza), and the Luesma 2 and Luesma 3 sections, near the village of Luesma (Zaragoza). The formation was divided into four members according to lateral and vertical facies changes (Hammann 1992). In the western sections, Valdelaparra and La Peña del Tormo, the La Peña and the Rebollarejo members can be recognized; while in the eastern sections, Luesma 2 and Luesma 3, the Ocino and Rebosilla members can be recognized (Fig. 1). The distribution of the species in the studied sections and lithostratigraphic units is not homogenous (Fig. 2). The La Peña Member was the most productive, having yielded the 29 known species; in the Rebollarejo Member, three species only are represented, the same as in the Rebosilla Member; and the Ocino Member has not yet yielded any taxa. Valdelaparra

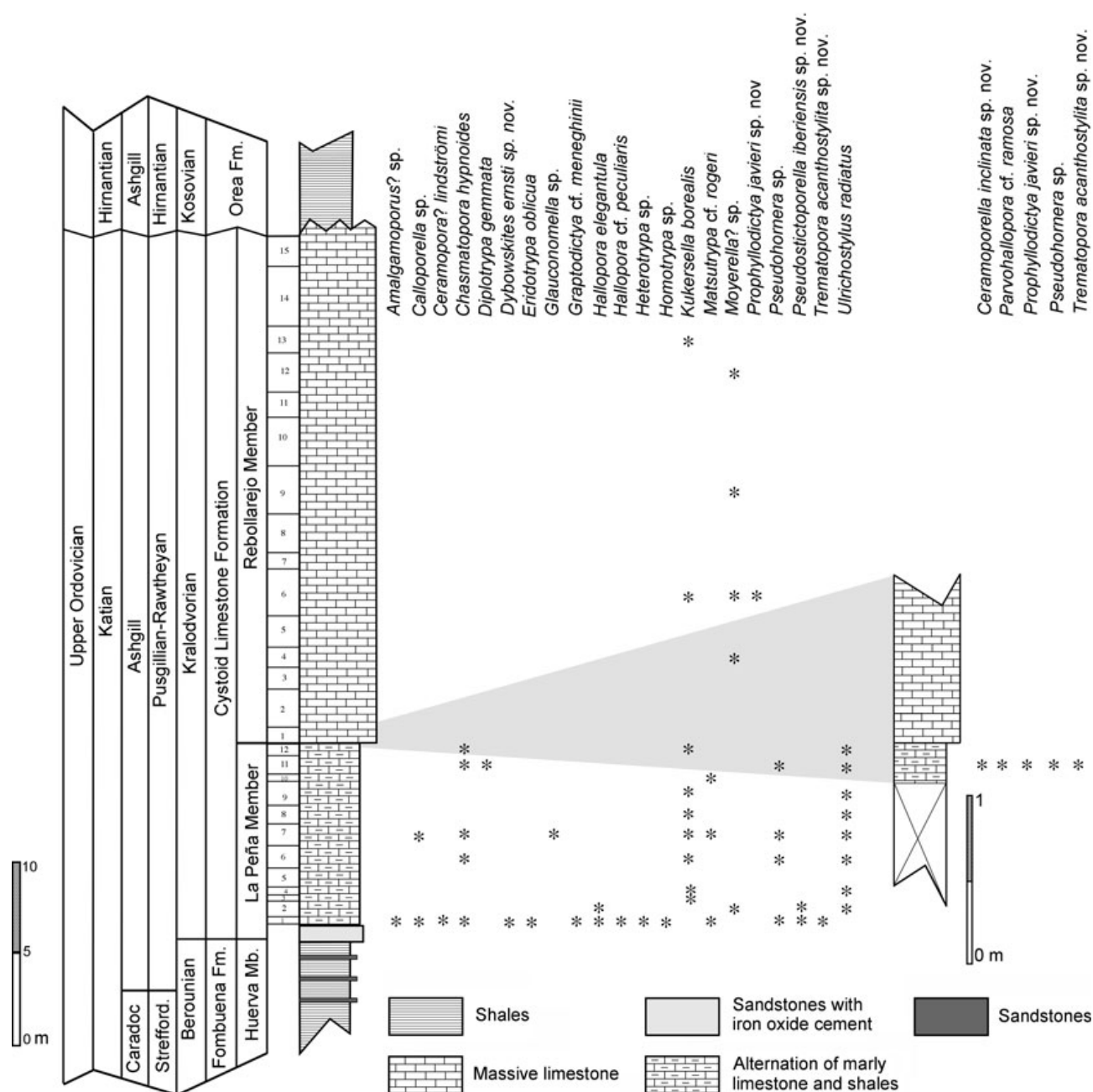


Figure 2. Stratigraphic distribution of the species described from the Valdelparra (on the left) and the La Peña del Tormo (on the right) sections.

is the section with a higher bryozoan diversity, with 26 recognized species.

Systematic palaeontology

To carry out this systematic study, 219 thin sections were observed under a transmitted light microscope. The measurements were taken directly from the thin section using the microscope with a micrometer, or from scaled photog-

raphs. The suprageneric classification is based on Karklins (1983) for the suborder Ptilodictyina, the web page: <http://bryozoa.net/iba.html>, edited by Phil Bock for the order Fenestrata and Ernst & Key (2007) for the rest of orders, suborders and families. The material described here is housed in the Museo de Paleontología de la Universidad de Zaragoza, specimen numbers MPZ 2006/100–107, 111, 112, 114–116, 118–125, 127, 128, 135–162, 164–167, 169–184, 186, 188–197, 199–201, 203–230, 233–238, 240–251, 253, 255–258, 261–272, 274–290 and MPZ 2008/169.

Phylum Bryozoa Ehrenberg, 1831
 Class Stenolaemata Borg, 1926
 Order Cryptostomata Vine, 1884
 Suborder Ptilodictyina Astrova & Morozova, 1956
 Family Escharoporidae Karklins, 1983

***Graptodictya* Ulrich, 1882**

Type species. – *Ptilodictya perelegans* Ulrich, 1878. Waynesville Formation, Upper Ordovician of Clarkville (Ohio, USA).

***Graptodictya* cf. *meneghinii* (Vinassa de Regny, 1942)**

Figures 3A, B, 4, 5, Table 1

- cf. 1942 *Pachydictya meneghinii* sp. nov.; Vinassa de Regny, pp. 1030, 1031, pl. 1, figs 6–8.
 cf. 1942 *Graptodictya* sp.; Vinassa de Regny, p. 1030, pl. 1, figs 4, 5.
 cf. 1942 *Pachydictya* (?) *sardona* sp. nov.; Vinassa de Regny, p. 1031, pl. 1, fig. 11.
 cf. 1988 *Graptodictya* sp.; Conti & Serpagli, p. 143, pl. 11, fig. 5, pl. 12, figs 2, 3.
 cf. 1990 *Graptodictya meneghinii* (Vinassa de Regny, 1942). – Conti, pp. 113, 114, pl. 20, figs 5–7.
 cf. 2007 *Graptodictya meneghini* (Vinassa de Regny, 1942). – Ernst & Key, p. 408, pl. 17, fig. 15, pl. 18, figs 1–3.
 2007 *Graptodictya* sp.; Jiménez-Sánchez *et al.*, fig. 7 (5, 6).

Material. – One zoarium (MPZ 2006/189) in tangential and longitudinal sections.

Description. – Zoaria branching and bifoliated, with a small diameter of 0.64 mm on average. Autozooeceia of length equal to between three and four times its diameter, budding

from the mesotheca, forming on average an angle of 44°, bending at the endozone-exozone limit and intersecting the external surface at an apparent angle of 71° on average; autozooeceal cross section oval with large diameter 0.14 mm and small diameter 0.06 mm on average, and with the large axis parallel to the zoarial growth direction; autozooeceal apertures arranged in longitudinal rows, separated by one or two grooves, but with a rhombic pattern overall; diagonal and longitudinal separation between autozooeceal apertures being 0.26 mm and 0.08 mm, respectively. Autozooeceal superior hemisepta short and blunt, always present in the exozone. Heterozooeceia absent. Mesotheca slightly sinuous in longitudinal section, without median rods and apparently formed by one layer of laminated microstructure. Walls laminated with an average thickness of 0.017 mm in the endozone and 0.095 mm in the exozone; pustules may be present. Extrazooeceal laminated skeleton also present in zoarial margins, forming longitudinal grooves.

Discussion. – This zoarium is closely related to *Graptodictya meneghinii* (Vinassa de Regny, 1942) as was described by Ernst & Key (2007) from the Montagne Noire, France. The two collections share the same relative size of the large and small diameter of the zoarial branches; the angle of autozooeceia with the mesotheca and the shape of the latter; the oval shape of the autozooeceal apertures and its separation, both longitudinally and diagonally; the presence of hemisepta and their shape; the distribution and the microstructure of the extrazooeceal skeleton, as well as the absence of heterozoeeceia and maculae. However, no transversal section is available and so, the shape of autozooeceia in the endozone, the way they are placed with respect to the mesotheca, and the transversal shape of the mesotheca can not be analyzed. Thus, this specimen can only be referred provisionally to *Graptodictya meneghinii*.

Table 1. Summary of the statistical analysis of *Graptodictya* cf. *meneghini* (Vinassa de Regny, 1942) including the observed range (Or), the mean value (X), the standard deviation (SD), the number of measurements (Nm), and the number of zoaria from which these measurements were made (Nsp).

Character	Or	X	DS	Nm	Nsp
Autozooeceal angle with mesotheca	30°–55°	44°	10	6	1
Autozooeceal angle with zoarial surface	70°–72°	71°	1	3	1
Autozooeceal large diameter (in mm)	0.09–0.19	0.14	0.04	10	1
Autozooeceal small diameter (in mm)	0.05–0.08	0.06	0.01	10	1
Autozooeceal separation in diagonal direction (in mm)	0.05–0.1	0.08	0.02	6	1
Autozooeceal separation in growth direction (in mm)	0.20–0.3	0.26	0.04	6	1
Autozooeceal wall thickness in endozone (in mm)	0.015–0.02	0.017	0.003	6	1
Autozooeceal wall thickness in exozone (in mm)	0.080–0.115	0.095	0.01	6	1
Endozone thickness (in mm)	0.11–0.3	0.2	0.10	5	1
Exozone thickness (in mm)	0.15–0.2	0.18	0.02	4	1
Zoarial small diameter (in mm)	0.60–0.7	0.64	0.05	4	1

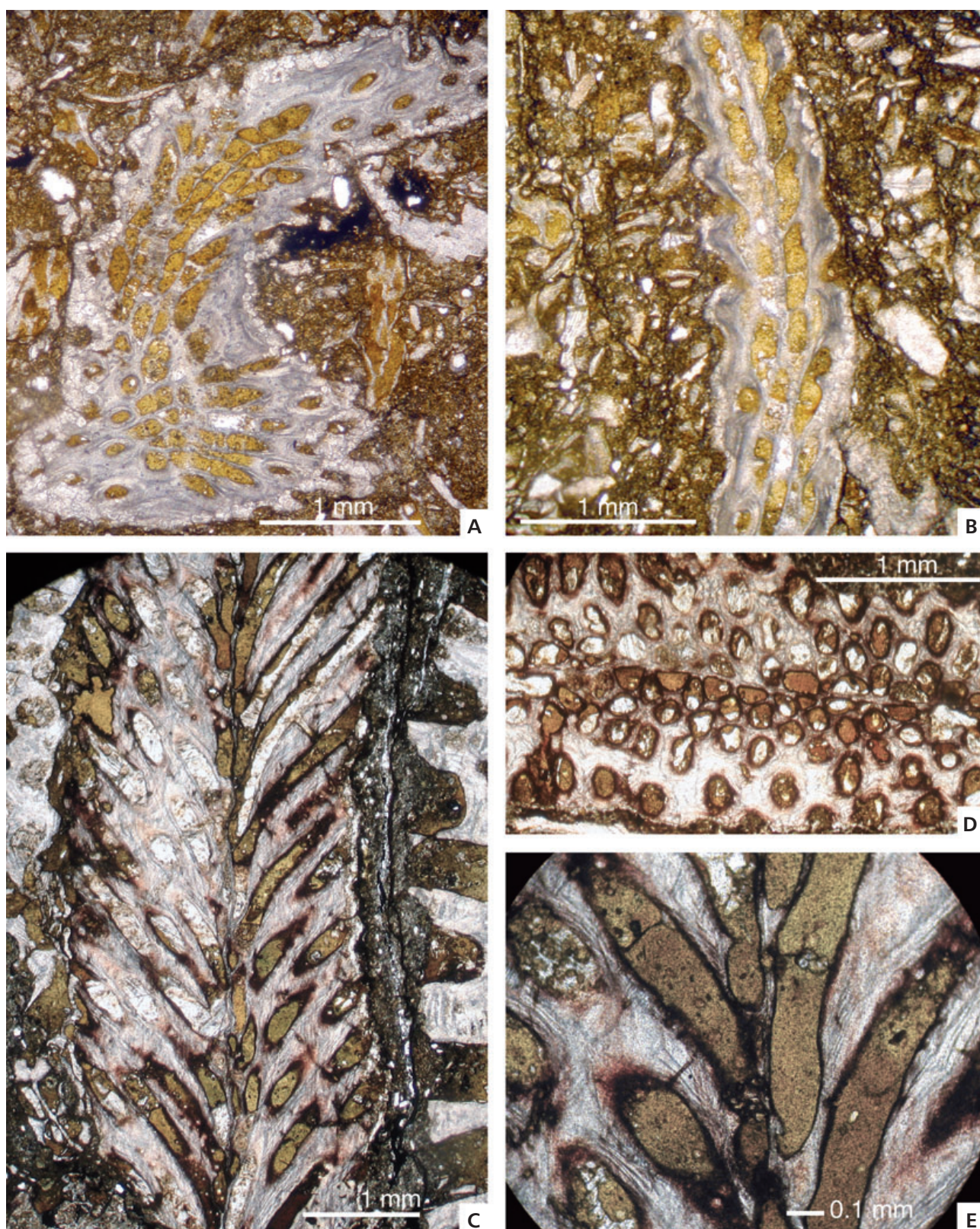


Figure 3. A, B – *Graptodictya cf. meneghinii* (Vinassa de Regny, 1942), MPZ 2006/189; A – oblique section; B – longitudinal section. • C–E – *Amalgamoporus?* sp., MPZ 2006/213; C – longitudinal section; D – transversal section; E – enlargement of the longitudinal section in C. All taxa from the La Peña Member, in the Valdelaparra section (Fombuena, Zaragoza).

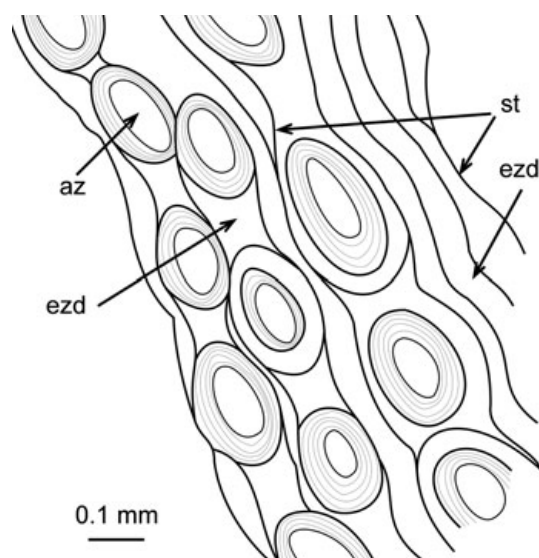


Figure 4. *Graptodictya* cf. *meneghinii* (Vinassa de Regny, 1942). Schematic tangential section showing oval autozooeal apertures (az), and thick extrazoeal laminated deposits (ezd) with longitudinal striae (st).

Occurrence. – The La Peña Member (layer 1), in the Valdelaparra section (Fombuena, Zaragoza).

Family Rhinidictyidae Ulrich, 1893

Genus *Amalgamoporus* Farmer, 1975

Type species. – *Amalgamoporus kecius* Farmer, 1975. Tulip Creek Formation, Middle Ordovician of Oklahoma (USA).

Amalgamoporus? sp.

Figures 3C–E, 6, 7, Table 2

Material. – One zoarium (MPZ 2006/213) in longitudinal and transversal sections.

Description. – Zoarium branching and bifoliated, with small diameter 1.95 mm on average and apparent large diameter 11 mm. Length of autozooea 2.1 mm on average, and with a constant diameter of 0.16 mm on average; budding from the mesotheca and forming an average angle of 20° with it, but at the endozone-exozone transition autozooea slightly bend to intersect the external surface at an angle of 41° on average; autozooea short and blunt, superior and inferior hemisepta can be present; in transversal section autozooeal subcircular to oval in the endozone and with straight contact with the mesotheca. Diaphragms present, but no more than one per autozooea, located in the inner exozone and usually concave. Mesotheca composed of two external laminated layers and a central granular layer, all of them continuous and slightly sinuous. Median rods present in granular layer, but less than

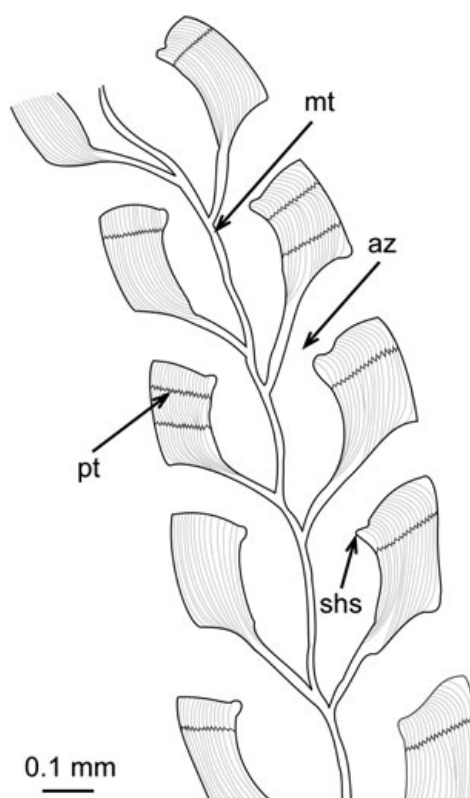


Figure 5. *Graptodictya* cf. *meneghinii* (Vinassa de Regny, 1942). Schematic longitudinal section showing autozooea (az), superior hemisepta (shs), mesotheca (mt), and pustules (pt).

one per mm; mesotheca with an average thickness of 0.03 mm. Autozooeal wall constituted of thick longitudinal lamina, 0.02 mm thick in the endozone and 0.20 mm thick in the exozone, on average; pustules may be present. Zoarial margins without autozooea.

Discussion. – This zoarium shares the following features with the genus *Amalgamoporus*; the rounded zoarial margins without autozooea; the longitudinal wall lamination, parallel to the autozooeal growth direction and the occurrence of pustules; the large size of the autozooea, with occasional diaphragms and its position in the exozone; as well as the angle that the autozooea form with the mesotheca and the zoarial surface. But this material has much fewer median rods than *Amalgamoporus*, as was described by Farmer (1975), and lacks the cystoidal spaces between autozooea, characteristic of this genus. On the other hand, it was not possible to study the arrangement pattern of autozooeal apertures on the colonial surface or to check if it corresponds with that of *Amalgamoporus*. In spite of the similarity with *Amalgamoporus* as stated above, this zoarium is only provisionally referred to this genus.

Occurrence. – The La Peña Member (layer 1), in the Valdelaparra section (Fombuena, Zaragoza).

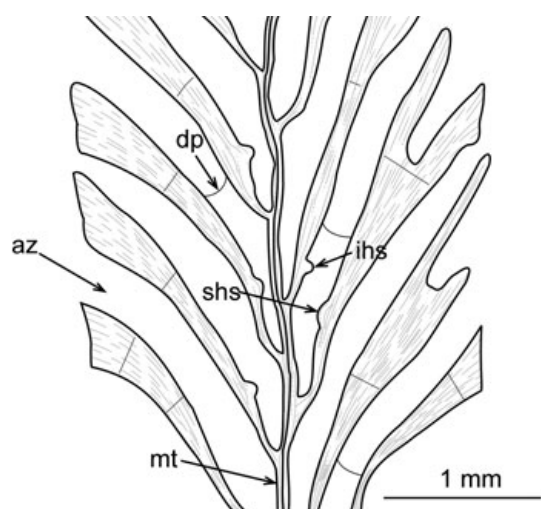


Figure 6. *Amalgamoporus?* sp. Schematic longitudinal section showing autozooezia (az), autozooezial diaphragms (dp), superior (shs) and inferior (ih) hemisepta, and mesotheca (mt) composed of three layers.

Family Stictoporellidae Nickles & Bassler, 1900

***Pseudostictoporella* Ross, 1970**

Type species. – *Pseudostictoporella typicalis* Ross, 1970. Rockland Formation, Middle Ordovician of Ontario (Canada) and New York (USA).

***Pseudostictoporella iberiensis* sp. nov.**

Figures 8A–C, 9, Table 3

2007 *Pseudostictoporella iberiensis* sp.; Jiménez-Sánchez et al., fig. 1 (5–7).

Holotype. – MPZ 2006/106.

Paratypes. – MPZ 2006/107 and MPZ 2006/195.

Type horizon. – La Peña Member of the Cystoid Limestone Formation, Upper Ordovician.

Type locality. – The Valdelaparra section (Fombuena, Zaragoza).

Material. – One zoarium in tangential, longitudinal and transversal sections (MPZ 2006/106) and two zoarial fragments in transversal section (MPZ 2006/107 and MPZ 2006/195).

Etymology. – After the Iberian Peninsula where the species has been described for the first time.

Diagnosis. – *Pseudostictoporella* characterized by superior hemisepta in autozooezia.

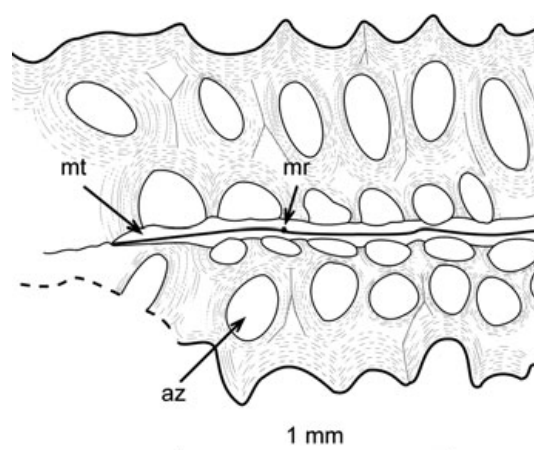


Figure 7. *Amalgamoporus?* sp. Schematic transversal section showing autozooezia (az) and mesotheca (mt) with median rods (mr) in central layer.

Description. – Zoaria branching and bifoliated, with large and small diameters of 2.5 mm and 1.1 mm on average, respectively. Autozooezia polygonal in shape with five or six sides and with the large axis parallel to the growth direction; apertures oval with large diameter 0.31 mm and small diameter 0.14 mm on average, and outline much smaller than the autozooezial outline; autozooezia long, about five times longer than its diameter; bedding from the mesotheca and forming an angle with it of 27° on average, but at the limit of the endozone-exozone, bending and intersecting the zoarial surface at an angle of 75° on average; two autozooezia per 1 mm and 5 autozooezia per 1 mm². Short, blunt superior hemisepta present in the exozone. Mesotheca slightly sinuous, composed of two external laminated layers and a central granular layer. Exilazooezia growing in the exozone, rhomboidal in shape with a large axis of 0.23 mm and small axis of 0.14 mm on average; one exilazooezium per 1 mm and 3 exilazooezia per 1 mm². Autozooezial wall obliquely laminated, with an inverse V pattern in the exozone in transversal section, 0.02 mm thick in the endozone and 0.2 mm thick in the exozone on average. With an extrazooezial laminated skeleton within the exilazooezia.

Discussion. – *Pseudostictoporella* Ross, 1970 is a genus known only from its type species *Pseudostictoporella typicalis* Ross, 1970. The material described here is closely related to this species, sharing all its diagnostic characters. However, the Iberian specimens have superior hemisepta in the autozooezia and a larger angle between the autozooezia and the mesotheca (27° in our material vs. 20° in *Pseudostictoporella typicalis*). The occurrence of the superior hemisepta is considered important enough to define it as a new species.

Occurrence. – This species is exclusively from its type horizon in layer 1 and 2.

Table 2. Summary of the statistical analysis of *Amalgamoporus?* sp. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeal angle with mesotheca	17°–27°	20°	5	4	1
Autozooeal angle with zoarial surface	33°–48°	41°	4	10	1
Autozooeal diameter (in mm)	0.135–0.21	0.16	0.022	10	1
Autozooeal length (in mm)	1.4–2.3	2.1	0.4	6	
Autozooeal wall thickness in endozone (in mm)	0.01–0.02	0.02	0.01	8	1
Autozooeal wall thickness in exozone (in mm)	0.15–0.23	0.2	0.03	6	1
Endozone thickness (in mm)	0.12–0.3	0.23	0.07	5	1
Exozone thickness (in mm)	0.51–0.63	0.58	0.04	5	1
Mesotheca thickness (in mm)	0.02–0.04	0.03	0.01	12	
Zoarial small diameter (in mm)	1.68–2.07	1.95	0.14	7	1

Table 3. Summary of the statistical analysis of *Pseudostictoporella iberiensis* sp. nov. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeal angle with mesotheca	20°–33°	27°	5	5	1
Autozooeal angle with zoarial surface	63°–81°	75°	8	5	1
Autozooeal large diameter (in mm)	0.24–0.36	0.31	0.03	18	1
Autozooeal small diameter (in mm)	0.09–0.18	0.14	0.02	19	1
Autozooeal wall thickness in endozone (in mm)	0.010–0.028	0.018	0.006	31	3
Autozooeal wall thickness in exozone (in mm)	0.08–0.22	0.2	0.17	17	1
Endozone thickness (in mm)	0.11–0.3	0.19	0.04	32	3
Exozone thickness (in mm)	0.22–0.5	0.34	0.08	24	3
Exilazooeal large axis	0.16–0.42	0.23	0.08	8	1
Exilazooeal small axis	0.09–0.16	0.14	0.03	10	1
Mesotheca thickness (in mm)	0.02–0.04	0.03	0.01	19	3
Number of autozooea per 1 mm	0.5–3.5	2	0.8	11	1
Number of autozooea per 1 square mm	3–6	5	1	3	1
Number of exilazooea per 1 mm	0–3	1	1	11	1
Number of exilazooea per 1 square mm	2–4	3	1	3	1
Zoarial large diameter (in mm)	2.3–3.1	2.5	0.3	5	3
Zoarial small diameter (in mm)	0.9–1.5	1.1	0.3	7	3

Family indet.

***Prophyllodictya* Gorjunova in Gorjunova & Lavrentjeva, 1987**

Type species. – *Prophyllodictya intermedia* Gorjunova in Gorjunova & Lavrentjeva, 1987. Volkhov and Kunda horizons, Middle Ordovician of Estonia and Saint Petersburg area.

Discussion. – Gorjunova (Gorjunova & Lavrentjeva, 1987) described the ptilodictyine genus *Prophyllodictya* and included it in the family Rhinidictyidae. Jiménez-Sánchez *et al.* (in press) cladistically analyzed this family, concluding that *Prophyllodictya* cannot be included within the Rhinidictyidae because it does not possess the two synapomorphies that characterize this family: presence of median rods in the mesotheca and presence of cystopores (or vesicular tissue) in the zooecia. *Prophyllodictya* does not have any apomorphic character among those considered by Jiménez-Sánchez *et al.* (in press) which could allow it to be included in any other known ptilodictyine family. So they consider this genus to be within a group of genera with an uncertain family relationship. This criterion is followed here.

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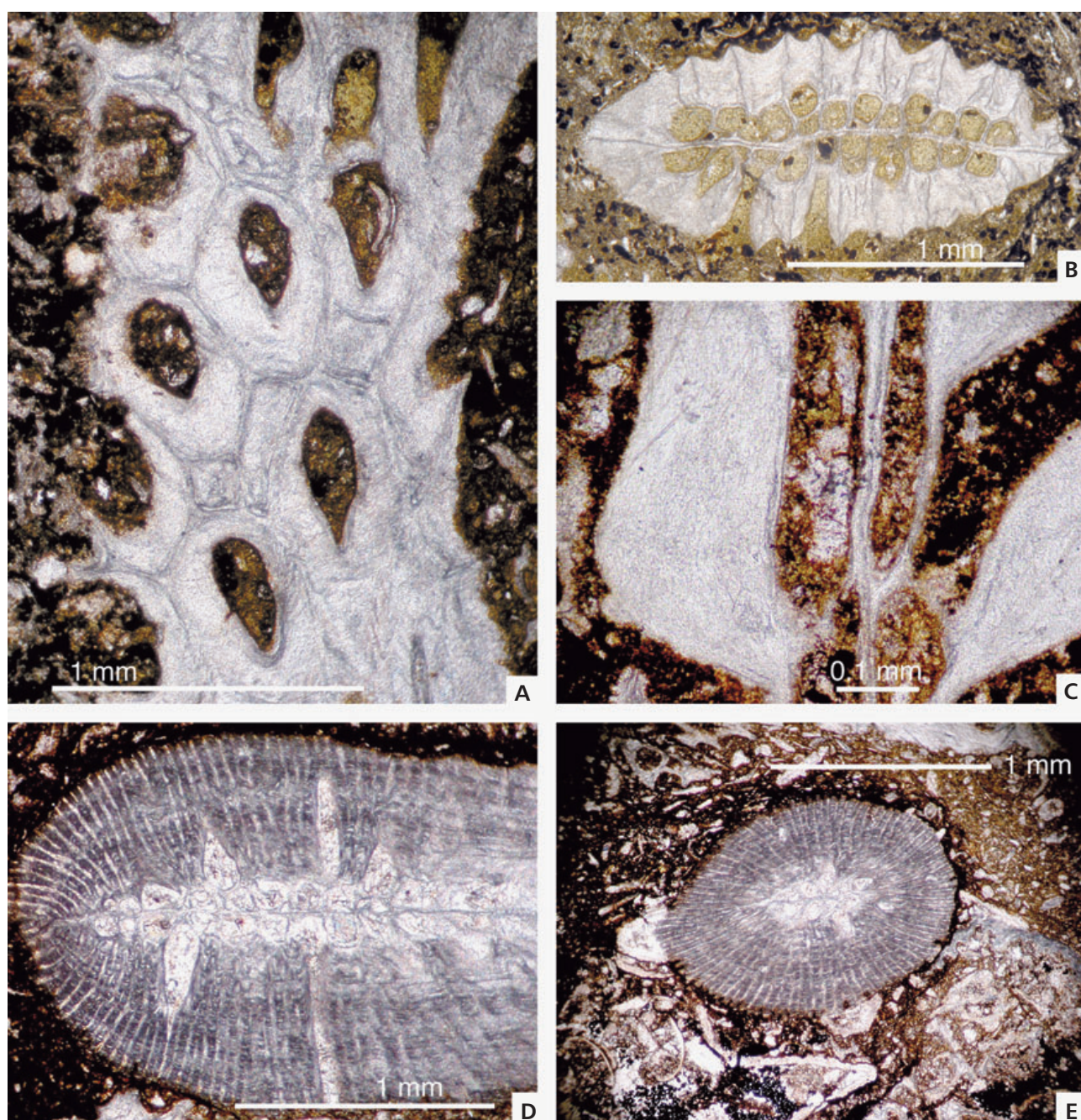


Figure 8. A–C – *Pseudostictoporella iberiensis* sp. nov. A, C – MPZ 2006/106 (holotype), A – tangential section, C – detail of longitudinal section. B – MPZ 2006/107, transversal section. • D, E – *Prophyllodictya javieri* sp. nov. D, MPZ 2006/114, transversal section in proximal zoarial zone; E, MPZ 2006/117 (holotype), transversal section. A–C from the La Peña Member in the Valdelaparra section, D and E from the La Peña Member in the La Peña del Tormo section (Fombuena, Zaragoza).

***Prophyllodictya javieri* sp. nov.**

Figures 8D, E, 10A, B, 11, Table 4

2007 *Phaenopora* sp.; Jiménez-Sánchez *et al.*, fig. 5 (3).

Holotype. – MPZ 2006/117.

Paratypes. – MPZ 2006/114–116 and MPZ 2006/118.

Type horizon. – La Peña Member of the Cystoid Limestone Formation, Upper Ordovician.

Type locality. – La Peña del Tormo Section (Fombuena, Zaragoza).

Material. – One zoarium in tangential, longitudinal and transversal sections (MPZ 2006/117); one zoarium in lon-

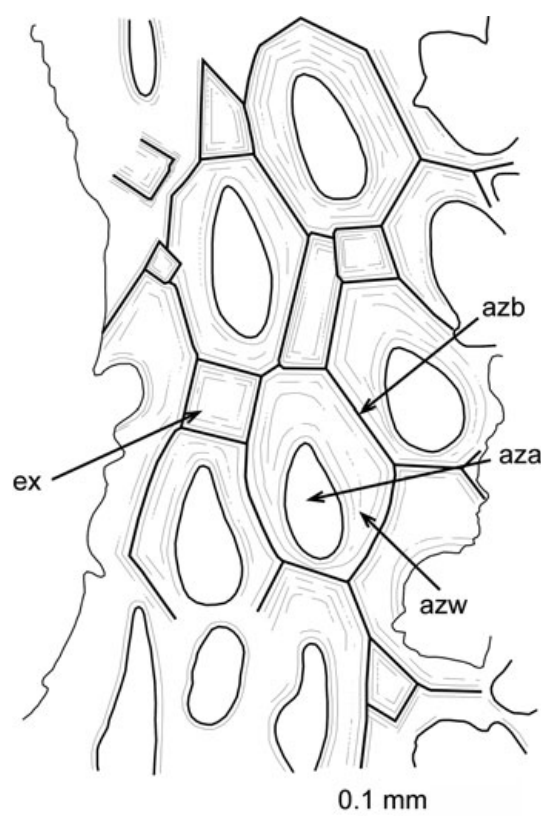


Figure 9. *Pseudostictoporella iberiensis* sp. nov. Schematic tangential section of the holotype (MPZ 2006/106) showing autozooeccia with oval apertures (aza) and polygonal boundaries (azb), laminated autozooeccial walls (azw) and exilazooecia (ex).

gitudinal and transversal sections (MPZ 2006/118); and three zoarial fragments in transversal sections (MPZ 2006/114, MPZ 2006/115 and MPZ 2006/116).

Etymology. – Named after my husband, Javier Gómez, thanking him for his academic and personal help.

Diagnosis. – *Prophyllodictya* characterized by the presence of superior hemisepta and by the small diameter of autozooeccia and exilazooecia.

Description. – Zoaria cribrate and bifoliate, ellipsoidal in cross section with large diameter 2.30 mm and small diameter 1.01 mm on average; zoarial base rounded in cross section. Autozooeccial apertures having rhombic pattern on the surface with a distance between them of 0.30 mm measured in the growth direction and 0.16 mm in a diagonal direction. Autozooeccial cross section oval with large diameter 0.18 mm and small diameter 0.10 mm on average; large axis parallel to the growth direction; autozooeccia long, roughly four times the small diameter; bedding from the mesotheca, forming an angle with it of 27° on average, and bending at the endozone-exozone transition until reaching

the zoarial surface at an average angle of 78°; superior hemisepta short and blunt present in almost all autozooeccia. Mesotheca sinuous, formed apparently of only one granular layer, with average thickness of 0.009 mm, but thickest at the zoarial margins. Exilazooecial apertures small, 0.014 mm diameter on average; budding in the exozone, reaching the external surface at the same angle as the autozooeccia and arranged in longitudinal rows between autozooeccia. Autozooeccial wall wavy, laminated with an average thickness of 0.008 mm in the endozone and 0.063 mm in the exozone; in transversal section significant changes in the colour of the wall waves occurs in adjacent laminae. Extrazooecial laminated skeleton present in zoarial base and zoarial margins.

Discussion. – This material displays all the characters included by Gorjunova in Gorjunova & Lavrentjeva (1987), within *Prophyllodictya* diagnosis, excluding the presence of superior hemisepta, a feature not considered diagnostic by Gorjunova in Gorjunova & Lavrentjeva (1987), since neither inferior nor superior hemisepta are present in any of the five known *Prophyllodictya* species: *Prophyllodictya gracilis* (Eichwald, 1840), *Prophyllodictya flabellaris* (Bassler, 1911), *Prophyllodictya intermedia* Gorjunova, 1987, *Prophyllodictya lauta* Lavrentjeva, 1987, and *Prophyllodictya prisca* Xia, Zhang & Wang, 2007.

The presence/absence of superior and/or inferior hemisepta in autozooeccia is an important character because hemisepta modify the internal structure of autozooeccia. However, it is not clear whether this character by itself is enough to define a new genus since there are polymorphic genera with respect to this character. So, the assignment of this material to *Prophyllodictya* is based on the remaining characters shared with this genus. In this case, the presence of superior hemisepta should be added to Gorjunova's diagnosis in Gorjunova & Lavrentjeva (1987).

The new species, *Prophyllodictya javieri*, is similar to *Prophyllodictya lauta* Lavrentjeva in Lavrentjeva & Gorjunova, 1987. Both species lack autozooeccial diaphragms and maculae, in addition the distance between adjacent autozooeccial apertures is similar.

Occurrence. – La Peña Member in la Peña del Tormo section and in the Rebollarejo Member (layer 6) in the Valde-laparra section (Fombuena, Zaragoza).

Suborder Rhabdomesina Astrov & Morozova, 1956
Family Arthrostylidae Ulrich, 1882

***Glauconomella* Bassler, 1952**

Type species. – *Glauconome disticha* Goldfuss, 1831. Upper Silurian, England.

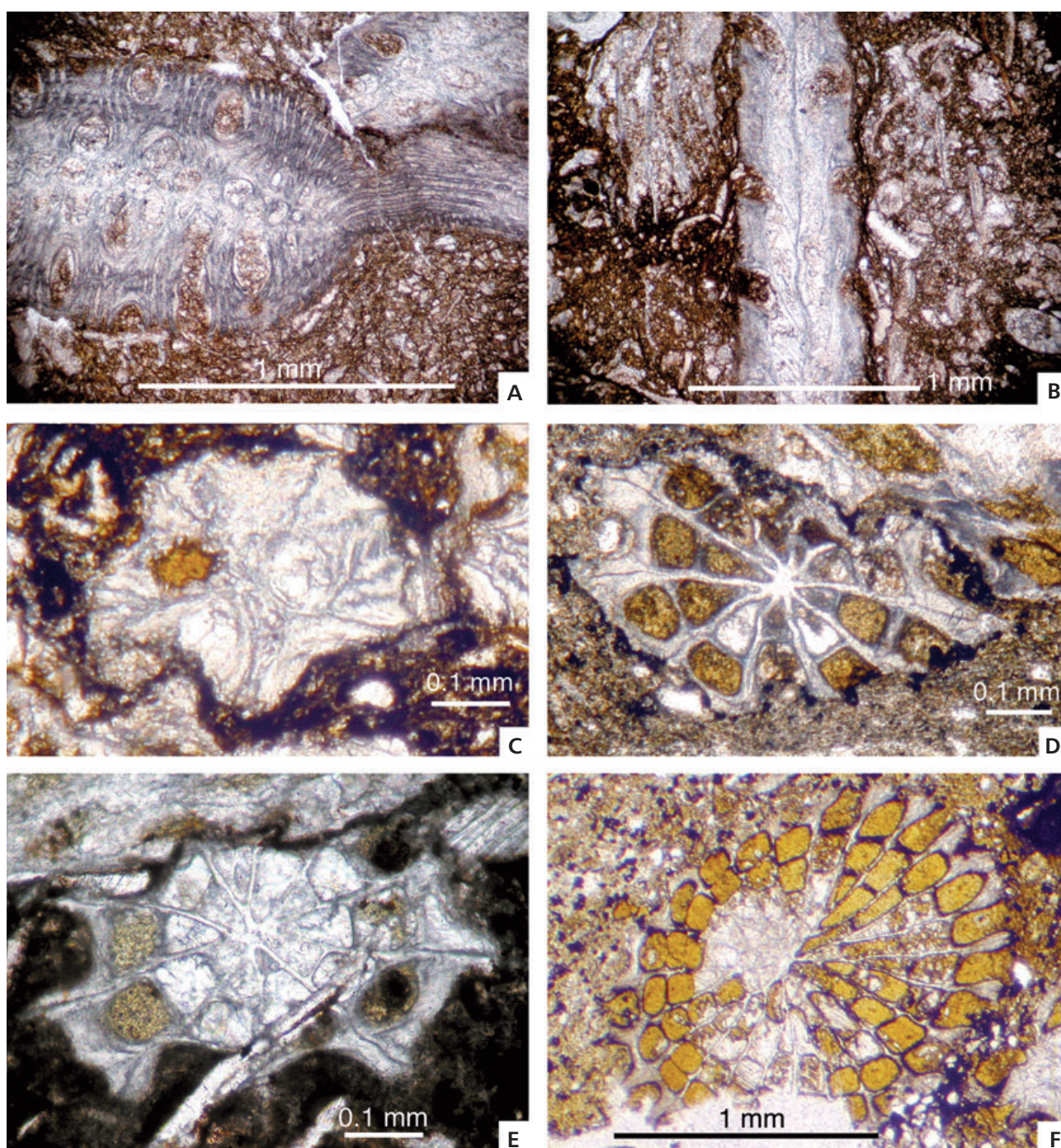


Figure 10. A, B – *Prophyllodictya javieri* sp. nov. A – MPZ 2006/118, oblique section; B – MPZ 2006/117 (holotype), longitudinal section. • C – *Glauconomella* sp. MPZ 2006/127, transversal section. • D, E – *Ulrichostylus radiatus* Conti, 1990. D – MPZ 2006/192, transversal section; E – MPZ 2006/227, transversal section. • F – *Moyerella?* sp. MPZ 2006/128, transversal section. A and B from the La Peña Member in the La Peña del Tormo section, C–F from the La Peña Member in the Valdelaparra section (Fombuena, Zaragoza).

***Glauconomella* sp.**

Figure 10C, Table 5

Material. – Two zoarial fragments in transversal section (MPZ 2006/127 and MPZ 2006/254).

Description. – Zoaria of slender, articulated branches, 0.42 mm average diameter; branch obverse side with auto-zooecial apertures distributed in four longitudinal rows and branch reverse side without apertures, but with longitudinal grooves; obverse side with a median keel and angular

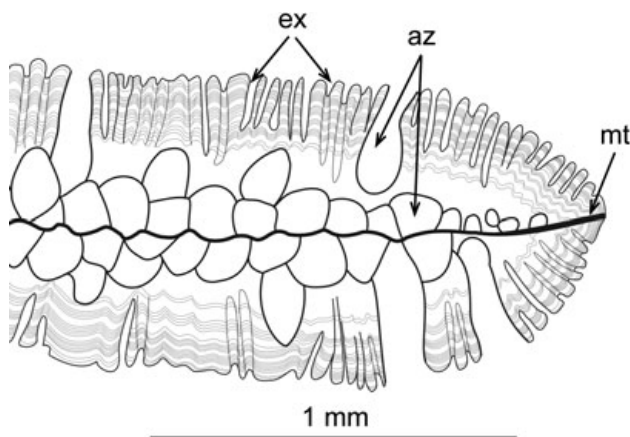


Figure 11. *Prophyllodictya javieri* sp. nov. Schematic transversal section of the zoarium MPZ 2006/115 showing autozooezia (az), exilazooezia (ex), and mesotheca (mt).

outline. Reverse autozooezia small and circular, front autozooezia large, 0.12 mm average diameter; autozooezia separated by a dark line; in the exozone, numerous dark, planar zones, similar to an autozooezial boundary, radiating from this boundary. Autozooezial wall laminated with inverse V pattern in the exozone and an average thickness of 0.034 mm. Extrazooezial laminated skeleton present in the distal side.

Discussion. – This material presents all the diagnostic characters of *Glauconomella*, but it cannot be assigned to a concrete species until a more complete specimen is found.

Occurrence. – La Peña Member (layer 7) in the Valdelparra section (Fombuena, Zaragoza).

Table 4. Summary of the statistical analysis of *Prophyllodictya javieri* sp. nov. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooezial angle with mesotheca	22°–32°	27	5	3	1
Autozooezial angle with zoarial surface	71°–84°	78°	7	3	1
Autozooezial large diameter (in mm)	0.16–0.21	0.18	0.19	13	2
Autozooezial small diameter (in mm)	0.08–0.13	0.1	0.017	13	2
Autozooezial separation in diagonal direction (in mm)	0.1–0.23	0.16	0.03	23	2
Autozooezial separation in growth direction (in mm)	0.26–0.35	0.3	0.03	8	2
Autozooezial wall thickness in endozone (in mm)	0.005–0.015	0.008	0.003	22	5
Autozooezial wall thickness in exozone (in mm)	0.04–0.1	0.063	0.02	15	5
Endozone thickness (in mm)	0.19–0.35	0.25	0.05	16	5
Exozone thickness (in mm)	0.21–0.44	0.35	0.07	24	5
Exilazooezia diameter (in mm)	0.005–0.025	0.014	0.004	38	5
Mesotheca thickness (in mm)	0.005–0.01	0.009	0.003	16	5
Zoarial large diameter (in mm)	1.4–2.6	2.3	0.7	5	5
Zoarial small diameter (in mm)	0.87–1.17	1.01	0.12	5	5

Ulrichostylus Bassler, 1952

Type species. – *Helopora divaricatus* Ulrich, 1886. Decorah Shale, Middle Ordovician of Minneapolis (USA).

Discussion. – Blake (1983) revised the genus *Ulrichostylus* and reduced its number of autozooezial rows from eight or more, as was considered by Bassler (1952), to between six and eight. Conti (1990) tacitly increased that number, including in the genus a species with twelve autozooezial rows. We follow Blake's (1983) diagnosis, but accept the increase in the number of autozooezial rows introduced by Conti (1990).

Ulrichostylus radiatus Conti, 1990

Figure 10D, E, Table 6

1990 *Ulrichostylus radiatus* sp. n.; Conti, p. 116, pl. 21, figs 7–12.

2007 *Ulrichostylus radiatus* Conti, 1990. – Ernst & Key, p. 401, pl. 15, figs 1–4.

2007 *Ulrichostylus* sp.; Jiménez-Sánchez, *et al.*, fig. 8 (2).

Material. – Seventeen zoarial fragments in transversal section (MPZ 2006/192, MPZ 2006/214–229).

Description. – Zoarium articulated and delicately branched; transversal section subpolygonal, 0.54 mm diameter on average. Axial region formed by well-defined linear axis, with autozooezia arranged radially around it; autozooezial apertures arranged on average in 8 longitudinal rows. Autozooezial cross section oval in the exozone, with

Table 5. Summary of the statistical analysis of *Glauconomella* sp. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeccial diameter (in mm)	0.10–0.15	0.12	0.02	4	2
Autozooeccial wall thickness in exozone (in mm)	0.030–0.040	0.034	0.005	4	2
Zoarial diameter (in mm)	0.41–44	0.42	0.02	2	2

a large diameter of 0.094 mm and a small diameter of 0.061 mm on average; a dark zone marking the boundary between adjacent autozooeccia. Autozooeccial cross section triangular and without visible boundary in the endozone. Exozonal walls 0.028 mm thick on average, composed of concentrically arranged layers around the autozooeccial aperture; endozonal walls 0.009 mm thick on average, composed of only one crystal. Dark zones bifurcated at the zoarial surface producing prominent longitudinal ridges separating apertural rows.

Discussion. – These characters have allowed the inclusion of this material in *Ulrichostylus*: the diameter of the transversal section and its subpolygonal shape; the radial arrangement of autozooeccial rows around one well defined central axis; the presence of prominent longitudinal ridges separating these autozooeccial rows; the well developed autozooeccial boundaries in the exozone and its absence in the endozone; the presence of dark zones; and the absence of mesozoeeccia. There are neither longitudinal nor tangential sections of this material to be compared with those described by Blake (1983). However, transversal sections of the Iberian material closely conform to *Ulrichostylus* diagnosis, therefore it can be confidently assigned to this genus.

The absence of diaphragms and acanthostyles is characteristic of *Ulrichostylus radiatus* Conti, 1990, as was described in the type material from Sardinia (Italy) (Conti 1990) and by Ernst & Key (2007) in the Montagne Noire (France), in both cases Late Ordovician in age. The absence of these characters also in the Iberian material, as well as the number of autozooeccial rows and an autozooeccial diameter similar to that of *Ulrichostylus radiatus* has allowed assigning of these specimens to this species.

Ulrichostylus radiatus is similar to *Ulrichostylus castatus* Lobdell, 1992, but they differ in that the former species has more autozooeccial longitudinal rows (7–12 in *Ulrichostylus radiatus* vs. 7–8 in *Ulrichostylus castatus*) and a smaller autozooeccial diameter (0.06–0.13 mm in *Ulrichostylus radiatus* vs. 0.1–0.2 mm in *Ulrichostylus castatus*).

Occurrence. – Maciurru and Punta S'Argiola members in the Domus-Novas Formation (Sardinia, Italy), upper Katian (Conti 1990); carbonate and clastic sequence from the Montagne Noire (France), upper Katian (Ernst & Key 2007); Pin Formation, upper Katian, in India (Suttner & Ernst 2007); and the La Peña Member (layers 4, 6–9, 11 and 12), in the Valdelaparra section (Fombuena, Zaragoza).

Family Hyphasmoporidae Vine, 1886

Matsutrypa Gorjunova, 1985

Type species. – *Matsutrypa mera* Gorjunova, 1985. Lower Silurian (Llandovery) of Estonia.

Matsutrypa cf. *rogeri* Ernst & Key, 2007

Figures 12C–E, 13, Table 7

cf. 2007 *Matsutrypa rogeri* sp. nov.; Ernst & Key, p. 45, pl. 15, figs 16, 17, pl. 16, figs 1–3.

2007 *Matsutrypa* sp.; Jiménez-Sánchez *et al.*, fig. 5 (1 and 4).

Material. – Eighteen zoarial fragments in transversal section (MPZ 2006/125, MPZ 2006/191, MPZ 2006/235–238, MPZ 2006/240–251); two zoarial fragments in longitudinal section (MPZ 2006/233 and MPZ 2006/234); one zoarial fragment in tangential section (MPZ 2006/253); and one zoarial fragment in oblique section (MPZ 2006/230).

Description. – Zoarium with erect growth habit, with segments of different sizes; transversal section subcircular, 0.50 mm diameter on average; axial region formed by well-defined linear axis, sometimes substituted by a thin layer; autozooeccial apertures with small peristome, arranged

Table 6. Summary of the statistical analysis of *Ulrichostylus radiatus* Conti, 1990. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeccial large diameter (in mm)	0.06–0.13	0.094	0.016	68	18
Autozooeccial small diameter (in mm)	0.04–0.09	0.061	0.012	59	18
Autozooeccial rows number	7–11	8	1	17	18
Autozooeccial wall thickness in endozone (in mm)	0.005–0.015	0.009	0.002	73	18
Autozooeccial wall thickness in exozone (in mm)	0.015–0.06	0.028	0.008	67	18
Zoarial diameter (in mm)	0.36–0.82	0.54	0.13	18	18

in longitudinal rows and separated by a small ridge. Autozooecia budding from the central axis, or central layer, at an average angle of 38° , but suddenly bending to grow parallel to the segment growth direction; autozooecial apertures oval with large diameter 0.102 mm on average, and separated by a pair of small metazooecia, triangular in shape, observed only in the exozone; a well developed dark line marks the autozooecial boundaries. Autozooecial walls laminated, 0.02 mm thick on average in the exozone and much thinner in the endozone, but with a high degree of recrystallization preventing exact measurement. Extrazooecial laminated deposits present, separating autozooecia.

Discussion. – The main diagnostic characters of the studied zoaria that allow their assignment to *Matsutrypa* Gorjunova, 1985 (see emended diagnosis by Ernst & Key 2007) are the following: erect growth habit with different sizes of segments; axial region with a lineal axis, less commonly a central layer, from which the autozooecia bud; the oval shape of the autozooecia and the triangular shape of the metazooecia; the arrangement of autozooecia in longitudinal rows on the zoarial surface; clearly visible autozooecial boundaries; the development of a thick extrazooecial skeleton, and the absence of acanthostyles.

The study of different species included in *Matsutrypa* shows that the characters used to distinguish them are mainly the diameter of the zoarial segments, the number of autozooecial longitudinal rows, the density of autozooecial apertures per mm, the thickness of the extrazooecial skeleton and the presence/absence of diaphragms. The poor preservation of this material prevented measurement of autozooecia density. Nevertheless, in most of the other features, the Iberian material is similar to *Matsutrypa rogeri* Ernst & Key, 2007 (upper Katian of the Montagne Noire) with the exception that Ernst & Key (2007) described occasional diaphragms in the autozooecia, not observed in the Iberian material. Therefore, these specimens are only provisionally assigned to *Matsutrypa rogeri*.

Specimens MPZ 2006/235–238, 240–243, 245, 247, 249, 250, all in transversal section, have some characteristics different from those in the remaining specimens. They have a smaller zoarial and autozooecial diameter, thinner autozooecial walls, and only in one section a pair of metazooecia between autozooecia can be seen. In spite of these differences these specimens have also been included in the same taxon referred here to as *Matsutrypa rogeri*, because they seem to be secondary segments. The fact that most sections lack the pair of metazooecia could be a consequence of the orientation of the thin section. Metazooecia are very small structures and they are longitudinally separated, therefore they are difficult to see in randomly cut thin sections.

Occurrence. – La Peña Member (layers 1, 7 and 10), in the Valdelaparra section (Fombuena, Zaragoza).

Table 7. Summary of the statistical analysis of *Matsutrypa* cf. *rogeri* Ernst & Key, 2007. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooecial angle respect central axis	19° – 51°	38°	11	10	3
Autozooecial large diameter (in mm)	0.01–0.04	0.02	0.01	39	15
Autozooecial wall thickness in exozone (in mm)	0.01–0.04	0.02	0.01	39	15
Zoarial diameter (in mm)	0.33–0.84	0.50	0.13	19	19

Family Nematotrypidae Spjeldnaes, 1984

Genus *Moyerella* Nekhoroshev, 1956

Type species. – *Moyerella stellata* Nekhoroshev, 1956. Lower Silurian (Llandovery) of Russia.

Moyerella? sp.

Figures 10F, 12A, B, 14–21, Tables 8, 9

Material. – Twenty zoarial fragments in transversal section (MPZ 2006/128, MPZ 2006/143–145, MPZ 2006/147–162); and one zoarial fragment in oblique section (MPZ 2006/146).

Description. – Zoaria with erect growth habit, with circular cross section, 0.93 mm diameter on average. Axial region formed by well-defined axis, with two types of autozooecia: the most numerous (type 1) directly radiating from the central axis, and the other (type 2) developed between the former. Autozooecial apertures circular with an average diameter of 0.10 mm and laminated cingulum, 0.04 mm thick; autozooecial apertures laterally separated 0.15 mm on average, and arranged on average in 16 longitudinal rows, with a dark layer separating each row. Autozooecial

Table 8. Summary of the statistical analysis of *Moyerella?* sp. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooecial aperture separation (in mm)	0.11–0.23	0.15	0.04	8	1
Autozooecial diameter (in mm)	0.08–0.14	0.10	0.02	1	1
Autozooecial rows number	13–25	16	3	21	21
Autozooecial wall thickness in endozone (in mm)	0.005–0.015	0.009	0.003	89	21
Autozooecial wall thickness in exozone (in mm)	0.01–0.06	0.03	0.01	135	21
Cingulum thickness (in mm)	0.03–0.07	0.04	0.01	11	1
Zoarial diameter (in mm)	0.59–1.41	0.93	0.31	21	21

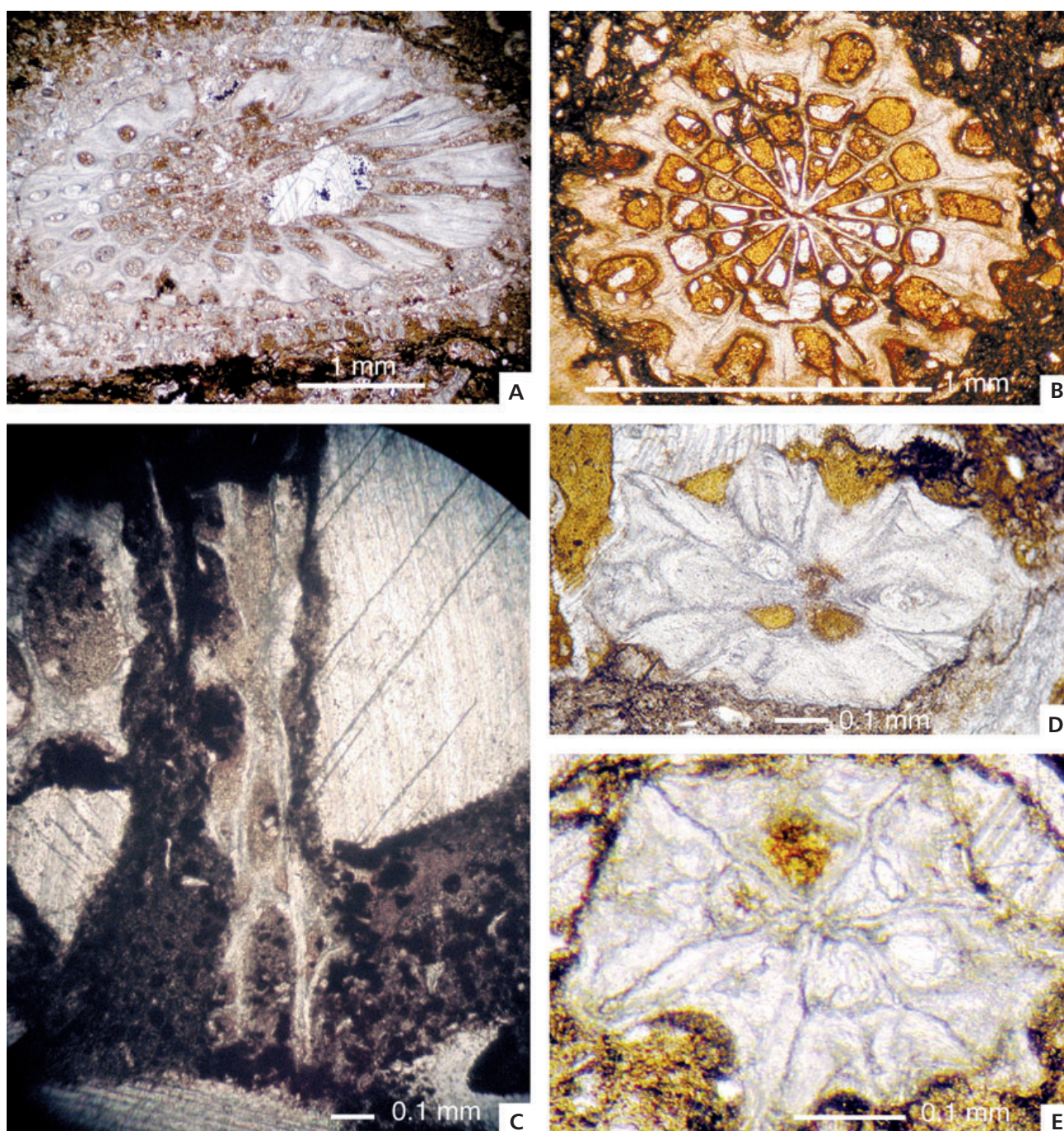


Figure 12. A, B – *Moyerella?* sp. A – MPZ 2006/146, transversal section; B – MPZ 2006/144, transversal section. • C–E – *Matsutrypa* cf. *rogeri* Ernst & Key, 2007. C – MPZ 2006/253, tangential section; D – MPZ 2006/125, transversal section; E – MPZ 2006/191, transversal section. A from the La Peña Member in the La Peña del Tormo section, B–E from the La Peña Member in the Valdelaparra section.

cross section triangular in the endozone. Autozooeical walls laminated, with an inverse V pattern, 0.030 mm thick in the exozone; in the endozone autozooeical walls composed of a single crystal 0.009 mm thick.

Discussion. – According to Ernst & Carrera (2007), these taxa are closer to *Moyerella* Nekhoroshev, 1956, sharing

with it the zoarial growth habit, the axial region in the zoarium composed of a well defined central axis, the shape of autozooeicia in the endozone and the exozone, and the arrangement of autozooeicia in longitudinal rows. But neither heterozooeicia nor acanthostyles can be seen in the Iberian material. Nevertheless, neither tangential nor longitudinal sections are available to confirm the absence of these features.

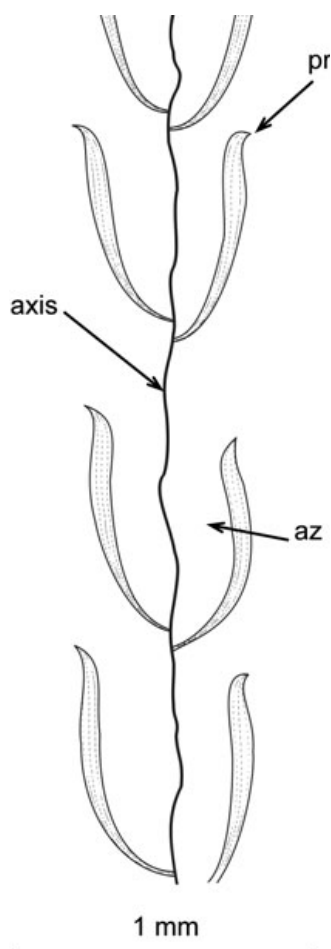


Figure 13. *Matsutrypa* cf. *rogeri* Ernst & Key, 2007. Schematic longitudinal section of the zoarium MPZ 2006/233 showing the central axis with autozooeal apertures (pr) around it and autozooeal apertures (az).

So, I provisionally refer this material to *Moyerella* while waiting for new data which can confirm this assignment.

The absence of tangential and longitudinal sections has hindered classifying this material to species level because some characters cannot be described. However, with the large number of transversal sections studied, coming from several localities and stratigraphic levels, statistical analysis to determine the degree of homogeneity of the samples and check whether all sections indeed belong to the same species have been performed. For this purpose, different univariate and multivariate analyses with PAST (Hammer *et al.* 2008) was carried out.

The analyzed characters are: zoarial diameter (ZoD), number of autozooeal longitudinal rows ($N^{\circ}AzR$), autozooeal diameter in the exozone (Az_1DEX for autozooeal type 1; Az_2DEX for autozooeal type 2), and autozooeal wall thickness in the exozone ($AzWthEx$).

A histogram of the number of autozooeal longitudinal rows (Fig. 15) shows the fragments can be divided into three groups: the first one is composed of the zoaria with

12–14 autozooeal rows (33.3% of the sample); the second one is composed of the zoaria with 16–21 autozooeal rows (57.14%); and the third one is composed of the zoaria with 24–25 autozooeal rows (9.5%). All the zoaria coming from the Rebosilla Member (Luesma 2 section) are included in the first group, and more than 80% of the zoaria coming from the Rebollarejo Member (Valdelaparra section) are included in the second group; the zoaria coming from the La Peña Member (Valdelaparra and Peña del Tormo sections) are distributed among the three groups. There is no relationship between the number of autozooeal longitudinal rows and the stratigraphic position.

Considering the autozooeal wall thickness in the exozone (Fig. 16), the zoaria are also divided into three groups: the first one is composed of zoaria with a wall thickness range of 0.011–0.016 mm (38.1% of the sample); the second group is composed of zoaria with wall thickness ranging from 0.018–0.021 mm (38.1%); and the third one is composed of zoaria with wall thickness ranging from 0.023–0.028 mm (23.8%). According to the provenance of zoaria, 100% of those coming from the Rebollarejo Member in the Valdelaparra section are included in the first and second groups, and 100% of the zoaria coming from the La Peña Member in the Valdelaparra and La Peña del Tormo sections are included in the third group. The zoarial fragments with thinner walls have been recorded in the upper stratigraphic member of the formation (Rebollarejo and Rebosilla members), while all zoarial fragments with thicker walls have been recorded in the basal member of the formation (La Peña Member) in the Valdelaparra and La Peña del Tormo sections.

There is no significant correlation between zoarial diameter and autozooeal wall thickness in the exozone ($r = 0.3$). But the Fig. 17 shows that most zoarial fragments with a diameter smaller than 1 mm have autozooeal walls of thickness less than 0.018 mm, while those zoaria with a zoarial diameter greater than 1 mm have autozooeal walls of thickness greater than 0.020 mm. However, no conclusion can be made from this analysis in connection with the stratigraphic and geographic distribution.

Nevertheless, characters ZoD and $N^{\circ}AzR$ have a good positive correlation index, with $r = 0.82$ (Fig. 18), although the zoarial fragment MPZ 2006/128 plot is at some distance from the regression line. This specimen does not have an especially large diameter (1.17 mm), but it does have the largest number of autozooeal longitudinal rows (25 rows). Superficial erosion is not significant in this fragment, so it can be assumed that the original diameter is similar to the measured one. This anomaly could be the consequence of anomalous colonial growth, which instead of attaining a larger diameter with a proportional increase in autozooeal diameter and number of autozooeal longitudinal rows, produced an increase in size with only an increase in the number of autozooeal longitudinal rows.

Table 9. Characters analyzed in *Moyerella?* sp. with the software PAST. N°AzR (Number of autozooeceia rows), Az₁DEx (Autozooeceial diameter type 1 in the exozone), Az₂DEx (Autozooeceial diameter type 2 in the exozone), AzWthEx (autozooeceial wall thickness in exozone), and ZoD (zoarial diameter).

Specimen	N°AzR	Az ₁ DEx	Az ₂ DEx	AzWthEx	ZoD
MPZ 2006/128	25	0.097	0.101	0.019	1.17
MPZ 2006/143	13	0.008	0.085	0.019	0.63
MPZ 2006/144	12	0.087	0.077	0.024	0.63
MPZ 2006/145	16	0.115	0.113	0.025	1.2
MPZ 2006/146	24	0.118	0.118	0.024	1.86
MPZ 2006/147	14	0.075	0.067	0.012	0.65
MPZ 2006/148	13	0.089	0.075	0.024	0.66
MPZ 2006/149	13	0.074	0.077	0.018	0.59
MPZ 2006/150	18	0.114	0.11	0.02	1.41
MPZ 2006/151	17	0.081	0.076	0.014	0.84
MPZ 2006/152	16	0.088	0.097	0.012	0.87
MPZ 2006/153	14	0.090	0.09	0.012	0.72
MPZ 2006/154	17	0.092	0.11	0.011	1.05
MPZ 2006/155	13	0.090	0.09	0.016	0.75
MPZ 2006/156	16	0.087	0.09	0.019	0.81
MPZ 2006/157	19	0.114	0.114	0.016	0.96
MPZ 2006/158	16	0.081	0.08	0.014	0.87
MPZ 2006/159	16	0.1	0.1	0.018	0.87
MPZ 2006/160	18	0.11	0.1	0.019	0.96
MPZ 2006/161	21	?	?	0.023	1.2
MPZ 2006/162	16	0.09	0.115	0.028	0.81

The multivariate analyses included cluster analysis, a Principal Components analysis and a Discriminant analysis, using the characters previously mentioned. The zoarial diameter (ZoD) has not been used for these analyses because this character is related to the other ones.

In the cluster analysis (Fig. 19), the euclidean distance and UPGMA (unweighted pair-group average, Hammer *et al.* 2008) algorithm have been used to define the distance between the groups. In the obtained dendrogram, the zoarial fragments are separated into two groups clearly correlated with their stratigraphic position. The first group, on the left, is composed of eight fragments mainly belonging to the La Peña Member. The second group, on the right, is composed of thirteen fragments mainly belonging to the Rebollarejo and Rebozilla Members. The fragments MPZ 206/150, MPZ 2006/157 and MPZ 2006/160 from the Rebollarejo Member are included in the first group. The study of the different characters in these zoarial fragments show that they have more autozooeceial longitudinal rows and a larger autozooeceial diameter than the other fragments

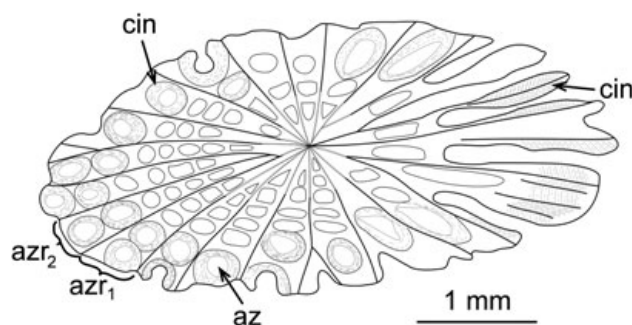


Figure 14. *Moyerella?* sp. Schematic oblique section of the zoarium MPZ 2006/146 showing autozooeceial apertures (az) with a thick cingulum (cin), and the different types of autozooeceial rows: those radiating directly from the central axis (azr₁) and those growing between the other rows (azr₂).

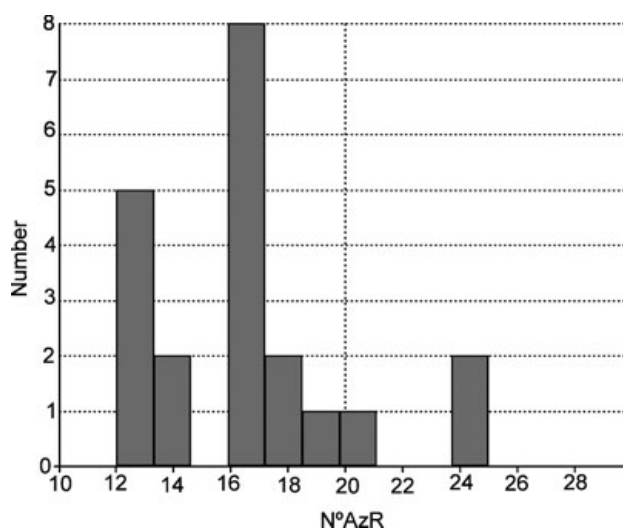


Figure 15. Histogram showing the frequency of the number of autozooeceial rows in *Moyerella?* sp.

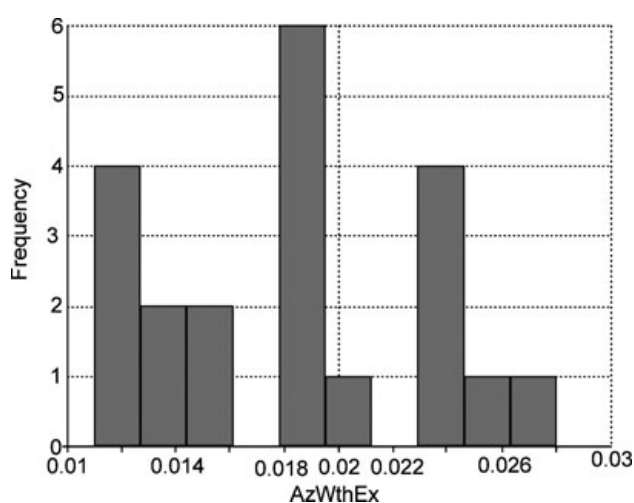


Figure 16. Histogram showing the frequency of autozooeceial wall thickness in *Moyerella?* sp.

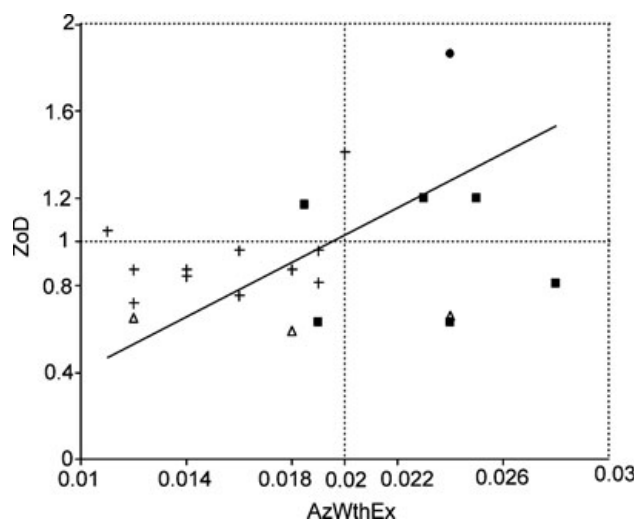


Figure 17. Autozooeal wall thickness in the exozone (AzWthEx) vs. zoarial diameter (ZoD) in *Moyerella?* sp. The regression line is shown, although the correlation coefficient is low ($r = 0.3$). n – zoarial fragments from the La Peña Member, + – zoarial fragments from the Rebollarejo Member, both in the Valdelaparra section, l – zoarial fragments from the La Peña Member in La Peña del Tormo section, Δ – zoarial fragments from the Reboquilla Member in the Luesma 2 section.

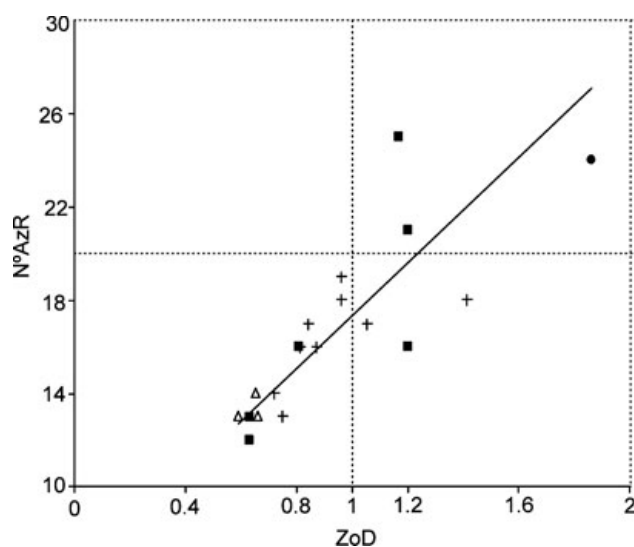


Figure 18. Zoarial diameter (ZoD) vs. number of longitudinal autozooeal rows (N°AzR) in *Moyerella?* sp. The regression line has a correlation coefficient (r) of 0.82. Symbols as in Fig. 17.

belonging to the Rebollarejo Member. The zoarial fragments MPZ 2006/143 and 144 come from the La Peña Member, but are included in the second group (on the right). They have fewer autozooeal longitudinal rows and a smaller autozooeal diameter than the other fragments belonging to the La Peña Member.

To see the strength of this grouping, a Principal Component analysis (Fig. 20) and a Discriminant analysis (Fig. 21) were carried out. In both analyses, the result was that the

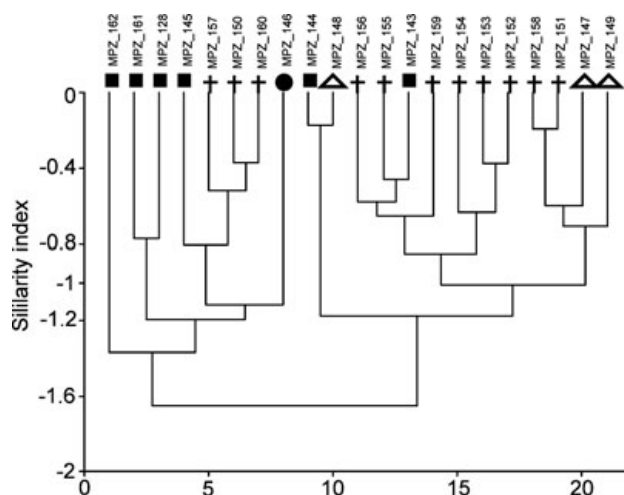


Figure 19. Dendrogram of the cluster analysis of *Moyerella?* sp. with the euclidean distance and UPGMA algorithm. n and l represent the zoarial fragments from the La Peña Member, + and Δ the zoarial fragments from the Rebollarejo and Reboquilla members, respectively.

zoarial fragments were divided into two groups, composed of the same zoarial fragments as in the dendrogram.

These analyses show that it is possible to group the zoarial fragments using the characters selected here. The first group, composed of the zoarial fragments coming from the La Peña Member, is characterized by having more autozooeal longitudinal rows, a larger autozooeal diameter, and thicker autozooeal walls than those zoarial fragments coming from the Rebollarejo and Reboquilla Members, the two stratigraphic upper members in the Cystoid Limestone Formation. So, the zoaria in the lower members are more robust than those in the upper members.

A good correlation between zoarial diameter (ZoD) and the number of autozooeal longitudinal rows (N°AzR), and the consequences of this correlation (increase in the autozooeal diameter with the increase in autozooeal wall thickness), suggest that all the studied fragments belong to the same species. The difference in robustness here is interpreted as an environmental adaptation. The La Peña and the Reboquilla Member represent a high energy environment near the coast, while the Rebollarejo Member represents a calm environment, further from the coast, where complex mud-mounds were developed. This difference can explain the presence of robust forms in the La Peña Member and of more delicate forms in the Rebollarejo Member. The delicate forms found in the Reboquilla Member would have come from distal, calm environments (represented by the Rebollarejo Member) and would have been transported during the storm episodes that characterize it.

Occurrence. – The La Peña Member (layer 1) in Valdelaparra and La Peña del Tormo sections, in the Rebollarejo Member (layers 4, 6, 9 and 12) in the Valdelaparra

section (Fombuena, Zaragoza); in the Rebozilla Member (layers 22 and 23) in the Luesma 2 section (Luesma, Zaragoza).

Order Cystoporata Astrova, 1964
Suborder Ceramoporina Bassler, 1913
Family Ceramoporidae Ulrich, 1882

Ceramopora Hall, 1851

Type species. – *Ceramopora imbricata* Hall, 1852. Niagara Limestone Formation (Lock-port, New York), Lower Silurian of USA.

Discussion. – Utgaard (1969) made a comprehensive study of *Ceramopora*, emending its diagnosis; this diagnosis is followed here.

Ceramopora? lindströmi Hennig, 1908

Figures 22A–C, 23, 24, Table 10

1908 *Ceramopora lindströmi* n. sp.; Hennig, pp. 2–5, pl. 1, figs 1–3, pl. 4, figs 1, 2, text-figs 1–3.

2007 *Ceramopora* sp.; Jiménez-Sánchez *et al.*, fig. 6 (4).

Material. – Two zoaria in tangential and longitudinal section (MPZ 2006/176 and MPZ 2006/178); and one zoarium in longitudinal section (MPZ 2006/177).

Description. – Zoaria with encrusting growth habit, composed of one or two layers with an average thickness of 0.77 mm per layer. Autozooezia 1.14 mm long, budding from thick basal layer at an angle of 40° on average; this angle increases until forming an average angle of 67° with the external surface. Basal layer 0.047 mm thick. Autozooezial cross section asymmetrically oval, with small diameter 0.29 mm on average and 3 autozooezia per mm on average. Lunaria sickle shaped and located in the autozooezium narrower side, radially arranged. Lunarial deposits 0.1 mm thick on average, only present in the outer exozone. Exilazooezia cross-section circular or polygonal in shape, 0.11 mm diameter on average and 0.8 exilazooezia per mm. Interzooezial pores present and situated on the opposite side of the lunarium, 0.05 mm diameter on average. Zooezial walls 0.075 mm thick in the exozone and 0.03 mm thick in the endozone, on average, completely recrystallized. Another polymorph, wedge shaped, present in the zoarium, situated between the autozooezia and exilazooezia, but with irregular distribution; composed of thick skeletal structures, with perpendicular orientation with respect to autozooezial growth direction and circular holes between them, resembling large vesicular structures.

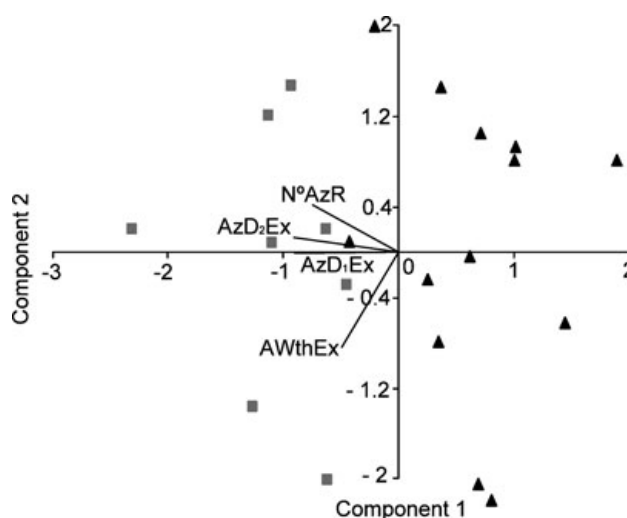


Figure 20. Principal Component Analysis of the main measurements made on *Moyerella?* sp. The graph shows that the separation between the first (■) and the second (▲) groups obtained by cluster analysis is very distinct. The character with less influence on these groups is the autozooezial wall thickness (AzWth).

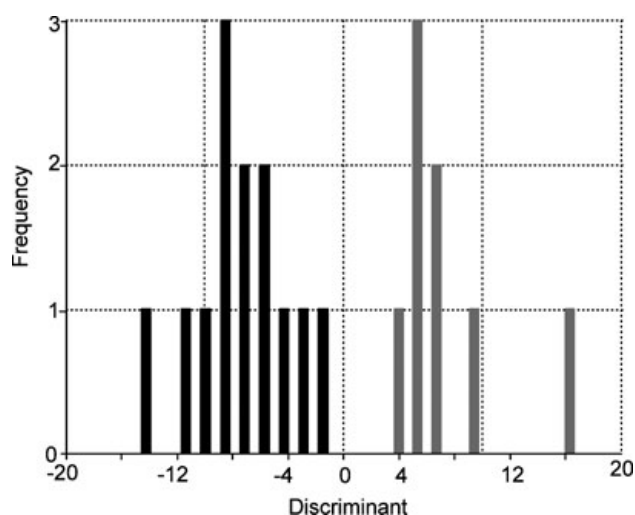


Figure 21. Discriminant analysis of the main measurements made on *Moyerella?* sp. The graph shows two well-differentiated groups. The group formed by gray bars corresponds to the first group in the dendrogram (on the left) and the group formed by black bars corresponds to the second one, on the right in the dendrogram.

Discussion. – The Iberian material shares several features with *Ceramopora* species: the growth habit; the angle at which the autozooezia bud from the epitheca and reach the zoarial external surface; the shape and arrangement of the autozooezia; the thickness of the walls in the exozone and the endozone; the presence of interzooezial pores; the shape, size and arrangement of lunaria; the absence of diaphragms and acanthostyles; as well as the presence of exilazooezia. However Utgaard (1969) in his emended diagnosis of the genus did not mention any polymorph apart

from the exilazooecia. The material studied here has another large, wedge shaped polymorph and similar structures were described by Hennig (1908) in *Ceramopora armata* Hennig, 1908 and *Ceramopora lindströmi* Hennig, 1908 from the Lower Silurian of Sweden. This type of polymorph could be important enough to define a new genus, since it considerably changes the internal structure of the colony. Nevertheless, there are only three specimens from the Iberian Chains, and it has not been possible to describe their external surface, so Hennig's (1908) generic assignment of *Ceramopora lindströmi* is followed here until further study of this species can be made to clarify the situation.

The presence of the large polymorphs with vesicular structure, the budding angle of the autozooecia and its oval shape, the wall thickness and the occasional interzooecial pores are characters that the Iberian material shares with *Ceramopora lindströmi*, thus this material is included in this species.

Along the Mediterranean margin of Gondwana *Ceramopora discoidalis* (Vinassa de Regny, 1942) was previously described by Conti (1990), and *Ceramopora italica* (Vinassa de Regny, 1942), by Conti (1990) and Ernst & Key (2007) from the upper Katian of the Montagne Noire and Sardinia, respectively. *Ceramopora? lindströmi* is similar to both species, but can be easily distinguished from them because neither *Ceramopora discoidalis* nor *Ceramopora italica* have any polymorphs apart from exilazooecia and both have more interzooecial pores. It can be also distinguished from *Ceramopora discoidalis* because this species has a constant wall thickness; and from *Ceramopora italica* because this species has larger lunaria deposits that reach the endozone.

Occurrence. – Lower Silurian of Gotland (Sweden) (Hen-

nig, 1908); and in the La Peña Member (layer 1), in the Valdelaparra section (Fombuena, Zaragoza).

***Ceramoporella* Ulrich, 1882**

Type species. – *Ceramoporella distincta* Ulrich, 1890. Cincinnati Group (Upper Ordovician of Cincinnati, USA).

***Ceramoporella inclinata* sp. nov.**

Figures 22D–F, 25A, 26, 27, Table 11

2007 *Ceramoporella* sp.; Jiménez-Sánchez *et al.*, fig. 6 (5).

Holotype. – MPZ 2006/212.

Paratype. – MPZ 2006/179–184.

Type horizon. – La Peña Member of the Cystoid Limestone Formation, Upper Ordovician.

Type locality. – La Peña del Tormo section (Fombuena, Zaragoza).

Material. – Seven zoaria in tangential and longitudinal section (MPZ 2006/179–184 and MPZ 2006/212).

Etymology. – After the constant inclination of the autozooecia during its growth.

Diagnosis. – *Ceramoporella* characterized by the constant inclination of its autozooecia, by the presence of only one diaphragm per autozooecium, by its large lunaria, and by the limited number of exilazooecia.

Table 10. Summary of the statistical analysis of *Ceramopora? lindströmi* Hennig, 1908. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooecial angle with basal zoarial layer	26°–60°	40°	12	9	3
Autozooecial angle with superior zoarial surface	47°–85°	67°	11	9	3
Autozooecial length	0.88–1.4	1.14	0.21	9	3
Autozooecial small diameter (in mm)	0.24–0.45	0.29	0.05	33	2
Autozooecial wall thickness in endozone (in mm)	0.015–0.045	0.03	0.009	18	3
Autozooecial wall thickness in exozone (in mm)	0.06–0.09	0.075	0.014	24	3
Basal layer thickness (in mm)	0.015–0.09	0.047	0.018	24	3
Exilazooecia diameter (in mm)	0.045–0.15	0.11	0.038	20	2
Interzooecial pores diameter (in mm)	0.03–0.08	0.05	0.01	23	3
Lunaria deposit thickness (in mm)	0.02–0.21	0.1	0.04	21	2
Number of autozooecia per 1 mm	2–4	3	0.6	13	2
Number of exilazooecia per 1 mm	0–2	0.8	0.7	13	2
Zoarial layer thickness (in mm)	0.53–0.9	0.77	0.14	11	3

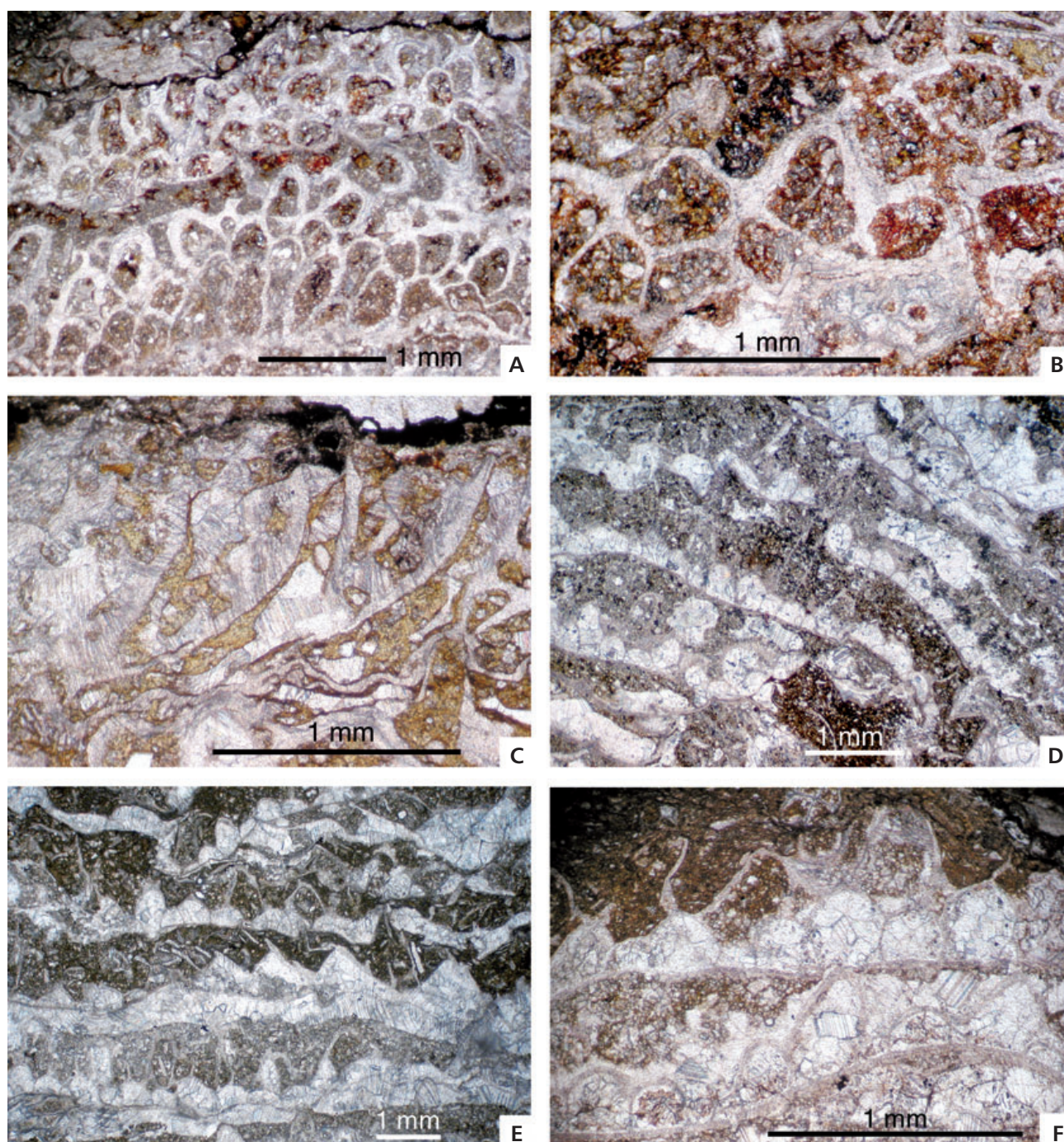


Figure 22. A–C – *Ceramopora? lindströmi* Hennig, 1908. A, C – MPZ 2006/178; A – tangential section; C – longitudinal section; B – MPZ 2006/176, tangential section. • D–F – *Ceramoporella inclinata* sp. nov. D – MPZ 2006/184; E – MPZ 2006/212 (holotype); F – MPZ 2006/180; superimposed zoarial layers, sectioned in different orientations. A–C from the La Peña Member in the Valdelaparra section, D–F from the La Peña Member in the La Peña del Tormo section.

Description. – Zoaria with encrusting growth habit composed of several layers, 0.66 mm thick on average. Autozooezia tubular in shape, 1.15 mm long on average, budding from the laminated basal layer, 0.04 mm thick, at a constant angle of 32° on average; autozooezia adjacent to exilazooezia sigmoid in shape and with thickened basal zone. Auto-

zooezial cross section asymmetrically oval, with large diameter 0.26 mm on average and an average of 4 autozooezia per mm. Lunaria sickle shaped and located in the autozooezium narrower side, all of them with the same orientation. Lunarial end penetrates into the autozooezial wall producing two small indentations; lunarial deposits 0.07 mm

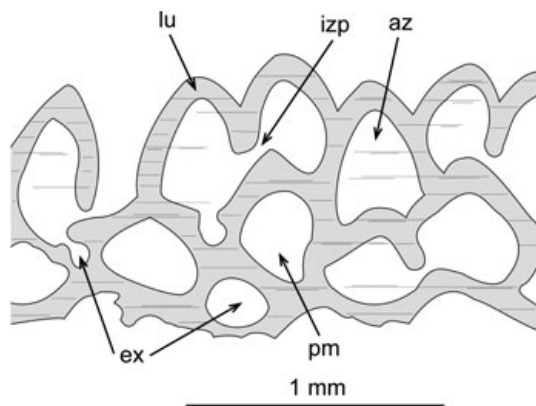


Figure 23. *Ceramoporella? lindströmi* Hennig, 1908. Schematic tangential section of the zoarium MPZ 2006/178 showing semioval autozooeceal apertures (az) with lunaria (lu), exilazooecia (ex) and large polymorphs (pm), as well as interzooeceal pores (izp).

thick on average, also present in the outer endozone, apparently being formed by single crystal. Only one diaphragm present per autozooeceum, always at the same autozooeceal level. Exilazooecia developed as small wedges in the inner exozone, some of them with one diaphragm; exilazooecial cross section four-sided polygonal, with average diameter of 0.15 mm and 0.7 exilazooecia per mm on average. Zooecial walls laminated with a constant thickness of 0.018 mm on average.

Discussion. – The characters shared between the Iberian material and the genus *Ceramoporella*, following Utgaard’s (1968) emended diagnosis are: the encrusting growth habit; the shape of autozooeceia in tangential and longitudinal section; the presence of exilazooecia growing between autozooeceia from the inner exozone; the presence of only one autozooeceal diaphragm and its position inside the autozooeceia; the presence of only one occasional diaphragm in exilazooecia; the microstructure of the lunarial deposits,

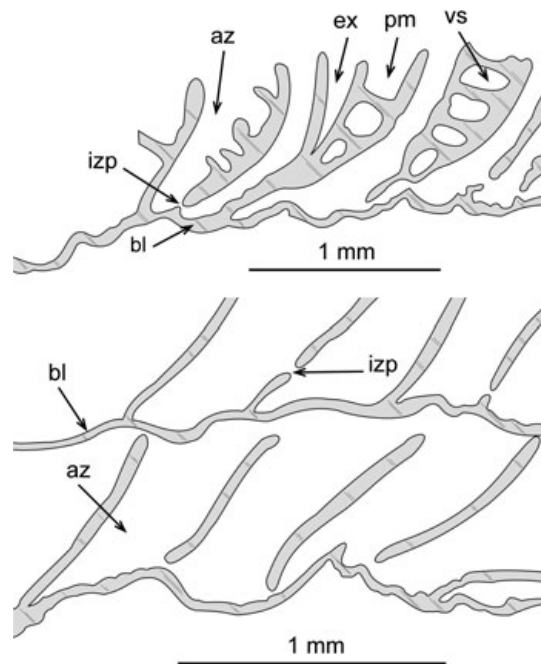


Figure 24. *Ceramoporella? lindströmi* Hennig, 1908. Schematic longitudinal sections of the zoaria MPZ 2006/178 (A) and MPZ 2006/176 (B), showing large polymorphs with vesicular structures (vs) and small exilazooecia (ex) in (A) and a zoarial zone without them in (B). Both figures show autozooeceia (az), interzooeceal pores (izp), and the basal layer (bl).

zooecial walls and epitheca; the absence of interzooeceal pores; as well as the position of the lunaria sometimes indenting the autozooeceal chambers. But Utgaard (1968) included in his diagnosis the presence of macula with radially arranged lunaria, and this feature was not seen in the Iberian material. In spite of this, the shared characters have enough importance to assign these specimens to *Ceramoporella*.

The studied zoaria have a series of diagnostic characters valid for defining them as *Ceramoporella inclinata* sp.

Table 11. Summary of the statistical analysis of *Ceramoporella inclinata* sp. nov. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeceal angle with inferior zoarial surface	21°–40°	32°	8	5	2
Autozooeceal length	0.7–1.5	1.15	0.28	9	3
Autozooeceal large diameter (in mm)	0.18–0.3	0.26	0.03	59	6
Autozooeceal wall thickness (in mm)	0.015–0.03	0.018	0.007	24	6
Basal layer thickness (in mm)	0.03–0.06	0.04	0.01	33	6
Exilazooecia diameter (in mm)	0.09–0.21	0.15	0.03	20	6
Lunaria deposit thickness (in mm)	0.04–0.1	0.07	0.02	31	6
Number of autozooeceia per 1 mm	2–5	4	1	16	5
Number of exilazooecia per 1 mm	0–2	0.7	0.7	16	5
Zoarial total height (in mm)	4–12	9.5	3.3	5	5
Zoarial layer thick (in mm)	0.28–1.2	0.66	0.3	12	3

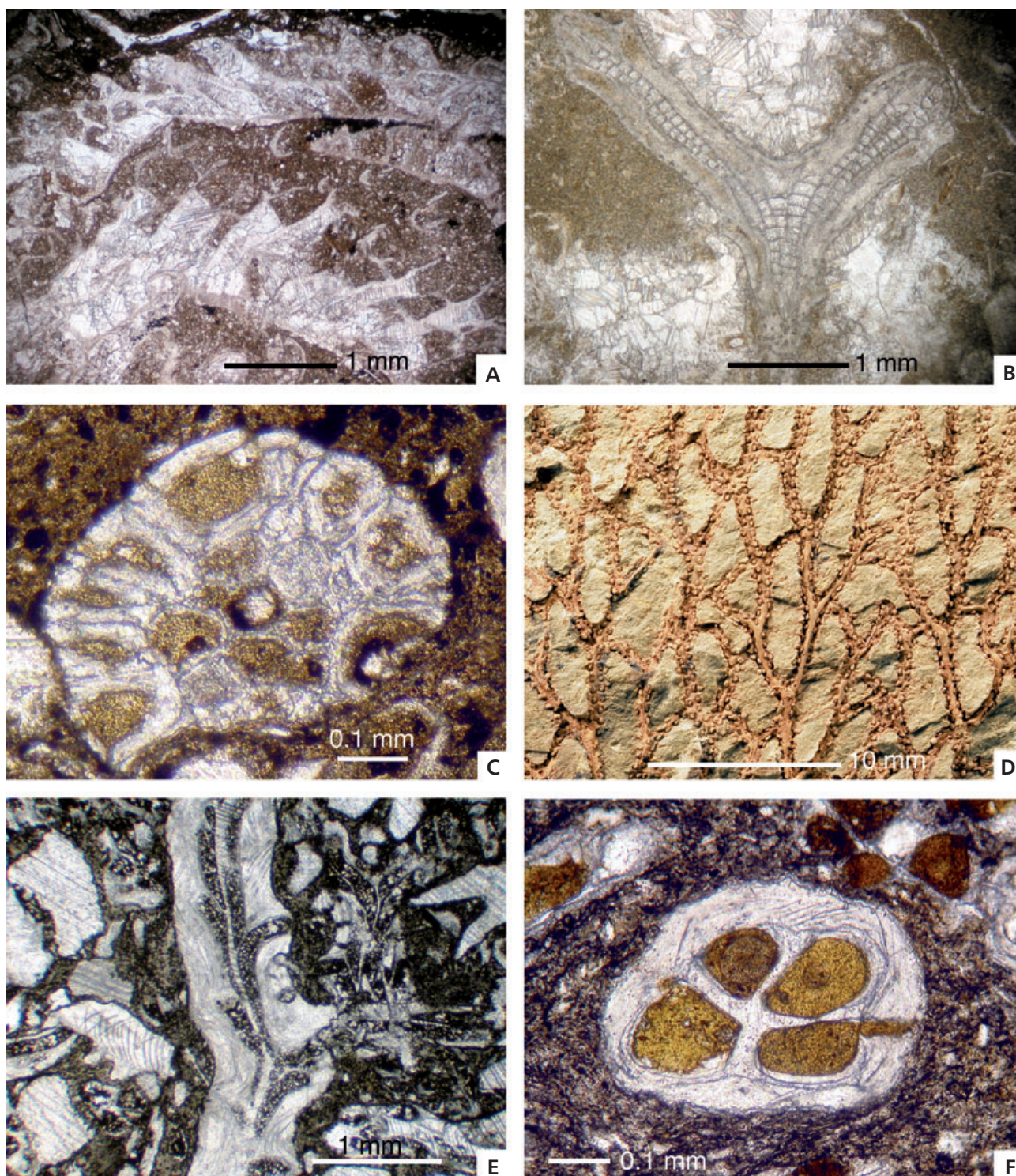


Figure 25. A – *Ceramoporella inclinata* sp. nov. MPZ 2006/179, longitudinal section. • B, C – *Kukersella borealis* (Bassler, 1911). B – MPZ 2006/193, longitudinal section; C – MPZ 2006/194, transversal section. • D–F – *Chasmatopora hypnoides* (Sharpe, 1853). D – MPZ 2008/196, general view of the zoarial internal mold; E – MPZ 2006/260, longitudinal section; F – MPZ 2006/186, transversal section. A from the La Peña Member in the La Peña del Tormo section, B from the Rebollarejo Member in the Valdelaparra section, C and F from the La Peña Member in the Valdelaparra section (Fombuena, Zaragoza); D from the Reboquilla Member in Luesma 3 section, and E from the Reboquilla Member in Luesma 2 section (Luesma, Zaragoza).

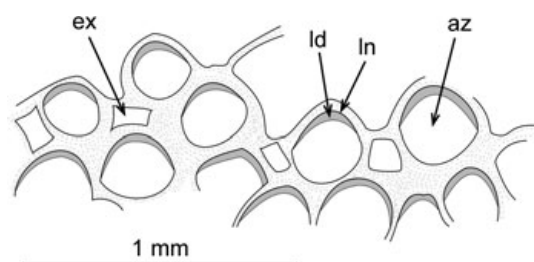


Figure 26. *Ceramoporella inclinata* sp. nov. Schematic tangential section of the zoarium MPZ 2006/182 showing autozooeal apertures (az) with lunaria (ln) and lunarial deposits (ld), and small exilazooecia (ex).

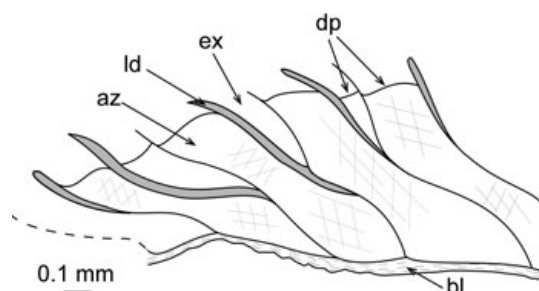


Figure 27. *Ceramoporella inclinata* sp. nov. Schematic longitudinal section of the zoarium MPZ 2006/179 showing autozooealia (az) and exilazooecia (ex) with a single diaphragm (dp) and the basal layer (bl).

nov. The new species is most similar to the specimens studied by Karklins (1984) from the Eden Formation (Upper Ordovician of Cincinnati), and by Buttler (1991b) in the Llanbedrog Limestone (Upper Ordovician of Wales), included in *Ceramoporella distincta* Ulrich, 1890. Both species share the same general shape of the zoarium composed of a group of encrusting zooecial layers, the autozooeal wall thickness, the shape of the lunarial deposits, the absence of cores (spines) in the lunaria, and the absence of interzooeal pores. But the new species can be distinguished from *Casmatoporella distincta* because its autozooealia have a constant inclination, contain fewer exilazooecia and no basal diaphragm.

Along the Mediterranean margin of Gondwana *Ceramoporella discoidalis* Conti, 1990 [upper Katian of Sardinia (Italy), Conti (1990), and the Montagne Noire (France), Ernst & Key (2007)] and *Ceramoporella grandis* Ernst & Key, 2007, in the same Katian beds from the Montagne Noire have been previously described. *Ceramoporella inclinata* sp. nov. shares with both species the shape of lunarial deposits, adapted to the sinuous autozooeal walls. But it can be distinguished from both because in *Ceramoporella discoidalis* and *Ceramoporella grandis* the autozooealia reach the zoarial external surface at an angle of 90°, but the angle is more acute in the new species, they contain more exilazooecia, interzooeal pores are present in the autozooeal walls and cores (spines) are present in the lunaria.

Occurrence. – This species occurs exclusively in its type locality and horizon.

Order Cyclostomata Busk, 1852

Suborder Paleotubuliporina Brood, 1973

Family Crownoporidae Ross, 1967a

Genus *Kukersella* Toots, 1952

Type species. – *Kukersella bassleri* Toots, 1952. Kuckers Shales Formation (Middle Ordovician of Käva, Estonia).

Discussion. – Toots (1952) included the genus *Kukersella* in the family Diastoporidae (order Cyclostomata), considering significant the absence of large peristomes, mesozooecia and acanthostyles, as well as its narrow autozooeal apertures. Ross (1967a) described the new genus *Crownopora*, with *Crownopora singularis* as the type species, and the family *Crownoporidae* to include this genus, in addition to *Diploclema* Ulrich, 1889, *Kukersella* Toots, 1952, *Mitoclema* Ulrich, 1882, and *Mitoclemella* Bassler, 1952, which were previously included in the family Diastoporidae. Ross (1967a) included the new family in the order Cryptostomata based on the presence of vestibules. Brood (1975a) considered the external and internal structures of *Crownopora* and *Kukersella* to be identical, putting both genera as synonymous. Furthermore, Brood (1975a) proposed changing the name of the family *Crownoporidae* to *Kukersellidae* and assigning it to the order Cyclostomata. This change of order was based on the zooecial wall structure, the presence of front pseudopores and interzooeal pores, as well as the zoaria growth pattern. Buttler (1989) accepted the synonymy between the genera *Kukersella* and *Crownopora*, but she returned to *Crownoporidae* as the family name. Her criteria are followed here.

Kukersella borealis (Bassler, 1911)

Figures 25B, C, 28, 29, Table 12

- 1911 *Mitoclema boreale* new species; Bassler, p. 69, pl. 6, fig. 8, text-fig. 15.
- 1952 *Kukersella bassleri* n. sp.; Toots, p. 117, pl. 7, figs 1 and 9.
- 1967a *Crownopora singularis* n. sp.; Ross, p. 645, pl. 72, figs 4–11, pl. 73, figs 1–4, pl. 74, figs 1–4, text-fig. 4.
- 1973 *Crownopora singularis* Ross, 1967a. – Boardman & Cheetham, p. 145, fig. 34.
- 1973 *Kukersella boreale* (Bassler, 1911). – Brood, p. 254, fig. 2.
- 1974 *Kukersella boreale* (Bassler, 1911). – Brood, p. 425, fig. 2A.

- 1975a *Kukersella bassleri* Toots, 1952. – Brood, p. 113, pl. 8, figs 6, 7, pl. 12, figs 1, 2.
 1975b *Kukersella boreale* (Bassler, 1911). – Brood, p. 114, pl. 8, figs 1, 5, pl. 12, figs 1, 2.
 1987 *Kukersella* cf. *boreale* (Bassler, 1911). – Hillmer & Schallreuter, fig. 2N.
 1987 *Kukersella* n. sp.; Gorjunova, pl. 4, fig. 3a–c.
 1989 *Kukersella borealis* (Bassler, 1911). – Buttler, pp. 222–225, figs 4A–F, 5A–F, 6A, B.
 1990 *Kukersella borealis* (Bassler, 1911). – Conti, p. 117, pl. 22, figs 7–11.
 1991a *Kukersella borealis* (Bassler, 1911). – Buttler, pp. 104, 105, pl. 7, figs 7, 8.
 1991b *Kukersella borealis* (Bassler, 1911). – Buttler, p. 167, fig. 20.
 1996 *Kukersella borealis* (Bassler, 1911). – Buttler & Massa, fig. 4h.
 2007 *Kukersella borealis* (Bassler, 1911). – Buttler, Cherns & Massa, p. 490, text-fig. 5D.
 2007 *Kukersella borealis* (Bassler, 1911). – Suttner & Ernst, p. 6, pl. 2, fig. 5.
 2007 *Kukersella borealis* (Bassler, 1911). – Ernst & Key, p. 365, pl. 1, figs 3, 4, 6.
 2007 *Kukersella* sp.; Jiménez-Sánchez *et al.*, fig. 8 (8, 9).

Material. – One zoarial fragment in longitudinal and transversal section (MPZ 2006/201); four zoarial fragments in longitudinal section (MPZ 2006/193, MPZ 2006/199, 200); and ten zoarial fragments in transversal section (MPZ 2006/194, MPZ 2006/203, 211).

Description. – Zoaria with branching growth habit, dichotomously bifurcated; branch transversal section circular, 0.52 mm diameter on average. Exozone composed of only one autozooeal ring, 0.16 mm thick on average. Endo-

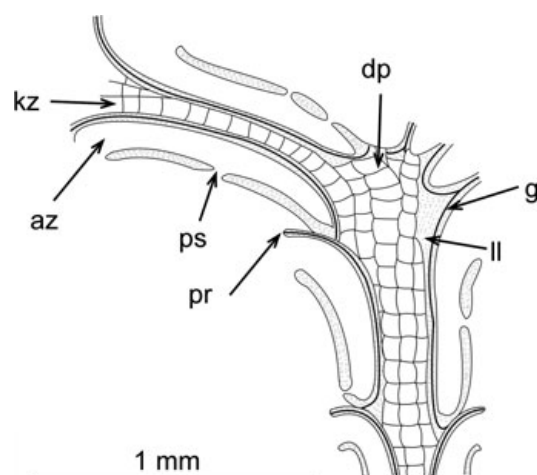


Figure 28. *Kukersella borealis* (Bassler, 1911). Schematic longitudinal section of the zoarium MPZ 2006/199 showing long autozooea (az) with peristome (pr) and pseudopores (ps), kenozooea (kz) divided by numerous diaphragms (dp), and autozooeal walls composed of two laminated layers (ll) and one granular layer (gl).

zone with 0.20 mm diameter on average, composed of kenozooea, laminated skeletal material, or a hollow with neither kenozooea nor laminated skeletal material. Autozooea very long, developed only in the exozone; parallel to the branch growth direction, but near the external surface bending to reach it at an average angle of 36°; autozooeal apertures widely separated and with small peristome; autozooeal cross section subrectangular or sub-circular in shape, with a chamber of average diameter 0.11 mm; interzooeal pores, situated at the lateral-distal wall junction. Kenozooea long and narrow, only open to the zoarial surface at the branch ends and densely tabulated by diaphragms, 13 per mm on average; without any physical continuity between kenozooea and autozooe-

Table 12. Summary of the statistical analysis of *Kukersella borealis* (Bassler, 1911). Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeal angle with zoarial surface	22°–60°	36°	14	6	3
Autozooeal diameter (in mm)	0.04–0.16	0.11	0.11	52	10
Autozooeal distal wall thickness (in mm)	0.015–0.06	0.03	0.01	33	10
Autozooeal proximal and lateral wall thickness (in mm)	0.01–0.03	0.019	0.004	63	10
Endozone diameter (in mm)	0.07–0.35	0.2	0.08	22	11
Exozone thickness (in mm)	0.11–0.28	0.16	0.03	68	14
Kenozooeal diameter	0.05–0.12	0.08	0.02	12	3
Kenozooeal wall thickness (in mm)	0.005–0.015	0.008	0.003	48	7
Number of kenozooea	5–12	8	3	3	3
Number of kenozooeal diaphragm per 1 mm	9–16	13	2	19	5
Pseudopores diameter	0.005–0.04	0.017	0.01	33	9
Zoarial diameter (in mm)	0.38–1.03	0.52	0.18	11	11

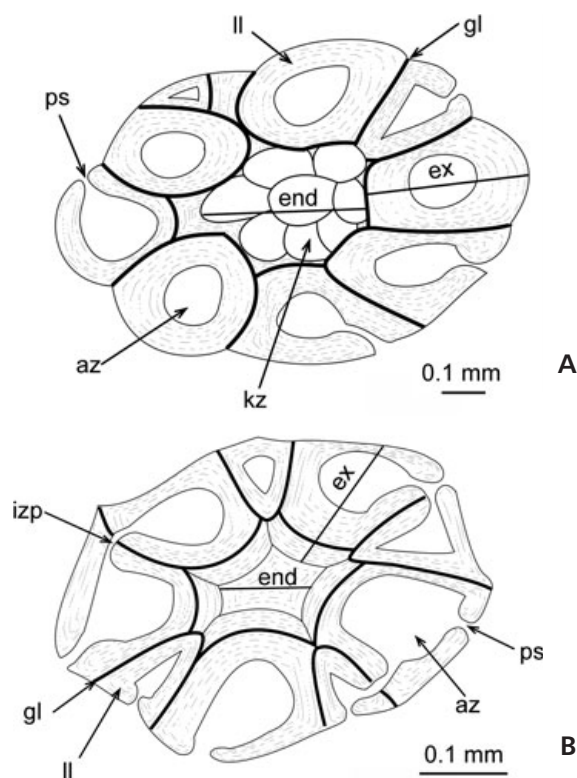


Figure 29. *Kukersella borealis* (Bassler, 1911). Schematic transversal sections of the zoaria MPZ 2006/201 (A) and MPZ 2006/206 (B). The two figures show autozooeceal (az), pseudopores (ps), laminar (ll) and granular (gl) layers in autozooeceal walls and the relative size of the endozone (end) and exozone (ex). In (A) the endozone is composed of kenozooeceal and in (B) it is composed of skeletal material; interzooeceal pores (izp) can also be observed in (B).

cia; kenozooeceal cross section subhexagonal or subcircular, 0.08 mm diameter on average and with 8 kenozooeceal on average in the endozone, this number increases just before branch bifurcation and then reduces in the resulting branches; kenozooeceal seem to be absent in the zoarial base. Autozooeceal proximal and lateral walls composed of two layers, 0.019 mm thick on average, with a thin internal layer of granular microstructure and an external layer thickened by laminated microstructure; distal wall composed of only a thickened laminated layer, 0.030 mm thick on average; large pseudopores, 0.017 mm diameter on average, present in distal autozooeceal walls. Kenozooeceal walls composed of a single granular layer, 0.008 mm thick on average.

Discussion. – Following Buttler's (1989) emended diagnosis, the Iberian material shares with *Kukersella* the zoarium size and growth habit, the autozooeceal and kenozooeceal development patterns in the exozone and endozone, respectively, the presence of peristomes in autozooeceal apertures, as well as interzooeceal pores and pseudopores in the autozooeceal walls.

The features seen in this material correspond with the description given by Buttler (1989) of *Kukersella borealis* (Bassler 1911). I am in agreement with her regarding the impossibility of distinguishing it from *Kukersella bassleri* Toots, 1952 and *Kukersella singularis* (Ross 1967a) taking into account the generally used characters of pseudopore diameters and number of kenozooeceal in the endozone. In the material from the Iberian Chains, the diameter of the pseudopores is not constant, ranging from 0.005 mm to 0.04 mm, and the number of kenozooeceal in the endozone depends on the position along the branch.

Occurrence. – Orthoceras Limestone (Darriwilian) in Port Kunda (Bassler 1911); in the Wassalem bed (lower Katian) in Uxnorn (Bassler 1911); Kukers Shale and Wesenberg Limestone (upper Darriwilian-lower Katian) (Toots 1952); all of them in Estonia. Rockland and Kirkland Formations (Sandbian-lower Katian) in New York (Ross 1967a). In erratic blocks in North and Central Poland and the Mójcza Limestone (Poland), Floian-Katian in age (Dzik 1981). Llanbedrog Limestones (upper Sandbian) in Gwynedd, Wales (Buttler 1991b). Punta S'Agliola Member, lower Domus-Novas Formation (upper Katian) in Sardinia, Italy (Conti 1990). Crug Shale and Slade and Redhill beds (Hirnantian) in Dyfed, Wales (Buttler 1991a). Tripolitania Formation (upper Katian) in Djeffara, Libya (Buttler *et al.* 2007). Pin Formation, Upper Katian, in India (Suttner & Ernst 2007). The siltstone/sandstone member of the Uggwa Formation (upper Katian) in Valbertad, Carnic Alps, Italy, and the carbonate and clastic sequence from Montagne Noire, France (Ernst & Key 2007). La Peña (layers 3, 4, 6–9 and 12) and Rebollarejo (layers 6 and 12) members, the Valdelaparra section, Fombuena, and Rebovilla Member (layer 6), Luesma 2 section, Luesma; both sections in the Zaragoza province.

Order Fenestrata Astrova & Morozova, 1956
Family Phylloporinidae Ulrich, 1890

Genus *Chasmatopora* Eichwald, 1855

Type species. – *Retepora tenella* Eichwald, 1855. Upper Ordovician of Vormsi (Estonia).

Chasmatopora hypnoides (Sharpe, 1853)

Figure 25D–F, Table 13

- 1853 *Synocladia hypnoides* n. sp.; Sharpe, p. 147, pl. 7, fig. 10.
- 1880 *Dictyonema? corniculata* sp. nov.; Meneghini, p. 216, pl. 1, 6.
- 1910 *Fenestella (Reteporina) carnica* n. sp.; Vinassa de Regny, p. 17, pl. 2, figs 12–14.

- 1936 *Chasmatoporella metzi* sp. nov.; Nekhoroshev, p. 7, pl. 1, fig. 1.
- 1940 *Chasmatoporella metzi* Nekhoroshev, 1936. – Prantl, p. 87, l. 1, figs 2, 3.
- 1942 *Fenestella (Reteporina) corniculata* (Meneghini, 1880). – Vinassa de Regny, pp. 1033, 1034, pl. 2, figs 5, 6.
- 1942 *Protocrisina sardoa* n. sp.; Vinassa de Regny, p. 1027, pl. 1, fig. 10, text-fig. A.
- 1948 *Phylloporina hypnoides* (Sharpe, 1853). – Dreyfuss, p. 33, pl. 4, figs 11, 11a, 12, pl. 9, fig. 11.
- 1968 *Chasmatoporella* sp.; Annoscia, p. 221, pl. 7, fig. 1.
- 1985 *Chasmatopora metzi* (Nekhoroshev, 1936). – Lavrentjeva, p. 45, pl. 17, fig. 2.
- 1988 *Graptodictya* sp.; Conti & Serpagli, pl. 11, figs 4–6.
- 1990 *Chasmatopora corniculata* (Meneghini, 1880). – Conti, pp. 112, 113, pl. 19, figs 3–12, pl. 22, fig. 6.
- 2001 *Moorephyloporina hypnoides* (Sharpe, 1853). – Morozova, p. 41.
- 2007 *Chasmatopora hypnoides* (Sharpe, 1853). – Ernst & Key, p. 56, pl. 21, figs 9–15, pl. 22, figs 1–3.
- 2007 *Chasmatopora* sp.; Jiménez-Sánchez *et al.*, fig. 6 (6).

Material. – Two external zoarial molds (MPZ 2008/169); eleven zoarial fragments in transversal section (MPZ 2006/186, MPZ 2006/256, MPZ 2006/261, MPZ 2006/266–272 and MPZ 2006/274); five zoarial fragments in longitudinal section (MPZ 2006/257, 258, MPZ 2006/264, 265 and MPZ 2006/275); one zoarium in longitudinal and transversal section (MPZ 2006/263); and one zoarium in tangential section (MPZ 2006/262).

Description. – Zoaria with cribated growth habit, anastomosed in shape, 120 mm wide and 201 mm tall. Fenestrulae irregularly elongated, with large axis 5 mm long on average and small axis 2.3 mm long on average, with large axis parallel to zoarium growth direction. Fenestrula components (or zoarial fragments) four-sided polygonal or circular, with 0.55 mm diameter on average. Autozooezia without internal structures, arranged in four longitudinal rows, two median and two lateral, open to the obverse side; reverse side with longitudinal narrow grooves. Autozooezial apertures oval in shape with large diameter of 0.15 mm on average and with large peristome around them; autozooezial length almost eight times its average diameter; growing parallel to the zoarial growth direction during the majority of their development but suddenly bending and terminating at the external surface at an angle of 81° on average; autozooezia budding from a central axis in two series: the initial one forming central longitudinal rows, and the later one forming lateral longitudinal rows. Heterozooezia present, but scarce. Autozooezial walls laminated, 0.019 mm thick on average in the endozone, in the exozone 0.15 mm thick on the obverse side

Table 13. Summary of the statistical analysis of *Chasmatopora hypnoides* (Sharpe, 1853). Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooezial angles with zoarial surface	65°–88°	81°	8	6	4
Autozooezial large diameter (in mm)	0.09–0.03	0.15	0.05	91	19
Autozooezial wall thickness (in mm)	0.01–0.04	0.019	0.006	68	18
Fenestrula large axis (in mm)	6–3	5	1	21	2
Fenestrula small axis (in mm)	1.5–4	2.3	0.6	21	2
Obverse thickness (in mm)	0.04–0.27	0.15	0.07	18	
Reverse thickness (in mm)	0.05–0.3	0.12	0.06	22	11
Zoarial wide (in mm)	120	120	0	2	2
Zoarial fragment diameter (in mm)	0.34–1.32	0.55	0.2	31	15
Zoarial height	198–205	201	5	2	2

and 0.12 mm thick on average on the reverse side, respectively.

Discussion. – The following features have allowed the inclusion of the studied material in *Chasmatopora*, according to Ernst & Key's (2007) emended diagnosis: the zoaria growth habit and its anastomosed shape; the autozooezia budding from a central axis, arranged in four longitudinal rows; the autozooezial apertures with peristomes, frontally and laterally open; the presence of grooves on the reverse side; as well as the autozooezial cross sections being oval in shape. Up to now, only a single species of *Chasmatopora* has been identified from the Mediterranean margin of Gondwana: *Chasmatopora hypnoides* (Sharpe, 1853). This species was originally described from the upper Katian of Portugal (Sharpe 1853) and subsequently identified from the Montagne Noire in France (Dreyfuss 1948 and Ernst & Key 2007), in Sardinia (Conti 1990) and in the Carnic Alps (Vinassa de Regny 1942) with different names (see synonymies). The fenestrula irregular shape, the size and shape of the fenestrula components, the large length of autozooezia without internal structures, the presence of a well-developed peristome, and the presence of heterozooezia clearly allow the inclusion of the Iberian material in the same species.

Occurrence. – Porto do Santa Anna Formation, upper Katian of Buçaco (Portugal), Sharpe (1853); carbonate and clastic sequence from the Montagne Noire (France), upper Katian, Dreyfuss (1948) and Ernst & Key (2007); Uggwa Formation, upper Katian of Carnic Alps, Vinassa de Regny (1942); c and e beds, upper Ordovician, Sardinia (Italy),

Conti (1990); the La Peña Member (layers 1, 6, 7, 11 and 12) in the Valdelaparra section (Fombuena, Zaragoza) and the Rebosilla Member (layer 23) in Luesma 2 section (Luesma, Zaragoza), Iberian Chains.

Genus *Pseudohornera* Roemer, 1876

Type species. – *Retepora diffusa* Hall, 1852. Niagara Limestone Formation, Lower Silurian of New York and Canada.

Pseudohornera sp.

Figures 30A–D, 31, 32, Table 14

Material. – One zoarial fragment in tangential and longitudinal section (MPZ 2006/105); three zoarial fragments in longitudinal section (MPZ 2006/100, MPZ 2006/135 and MPZ 2006/137); four zoarial fragments in transversal section (MPZ 2006/138, 139, MPZ 2006/141, 142); and six zoarial fragments in oblique section (MPZ 2006/101–104, MPZ 2006/136 and MPZ 2006/140).

Description. – Zoaria with a branching growth habit, with branches being circular in cross section, 0.99 mm diameter on average. Obverse side with autozooeical apertures arranged in four to six longitudinal rows and with prominent peristome; reverse side without apertures and composed of a succession of zoarial growth stages; growth stages with light, thickened, laminated internal zone and dark, thin, laminated external zone; 4 growth stages on average in reverse, with a thickness of 0.06 mm on average per growth stages. Autozooeical apertures subcircular to oval, with large diameter 0.22 mm and small diameter 0.14 mm, on average; large axis parallel to zoarial growth direction; autozooeical boundaries marked by a thick dark layer. Two

types of autozooeicia: those situated near the reverse side growing parallel to the branch, but suddenly bending to terminate at the zoarial surface; and those situated on the front side initially growing at an angle of 13° on average, and then slightly bending to form a 21° angle on average with the external surface; autozooeical cross section irregularly polygonal in the endozone and subelliptical in the exozone. Acanthostyles composed of light massive calcite, developed at the autozooeical boundaries where the autozooeicia bend, 0.02 mm diameter on average. Autozooeical walls concentrically laminated around the autozooeical apertures, 0.07 mm thick in the exozone; autozooeical walls composed of three layers in the endozone: one granular central layer and two laminated external layers, 0.017 mm thick on average. Small pore-like structures may be present on the reverse side.

Discussion. – According to Brood's (1970) and Ernst & Key's (2007) emended diagnoses, the following characters allow this Iberian material to be included in *Pseudohornera* Roemer, 1876: zoaria with branching growth habit; the autozooeicia open only to the obverse side; the wall microstructure in the exozone and the endozone; and the presence of small acanthostyles. In spite of the numerous thin sections studied, it is preferable not to assign this material to any precise species due to lack of certainty that all the fragments belong to a single species. Nevertheless, this material is similar to *Pseudohornera dimitrii* Ernst & Key, 2007, described from the upper Katian of the Montagne Noire (France), but they can be distinguished because in the Iberian material the acanthostyles are only present on the obverse side, while in *Pseudohornera dimitrii* the acanthostyles are also present on the reverse side.

Occurrence. – The La Peña Member, in the Valdelaparra section (layers 1, 6, 7 and 11) and in La Peña del Tormo section (Fombuena, Zaragoza).

Table 14. Summary of the statistical analysis of *Pseudohornera* sp. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Acanthostyles diameter (in mm)	0.01–0.03	0.02	0.01	31	8
Autozooeical angle in endozone	3°–32°	13°	10	7	3
Autozooeical angle with zoarial surface	13°–32°	21°	7	10	3
Autozooeical large diameter (in mm)	0.16–0.33	0.22	0.06	33	8
Autozooeical small diameter (in mm)	0.11–0.19	0.14	0.02	43	8
Autozooeical wall thickness in endozone (in mm)	0.010–0.035	0.017	0.004	94	14
Autozooeical wall thickness in exozone (in mm)	0.02–0.18	0.07	0.1	53	12
Growth stage thickness (in mm)	0.03–0.13	0.06	0.02	77	10
Number of growth stages	3–7	4	1	10	10
Zoarial diameter (in mm)	0.60–1.47	0.99	0.28	41	13

Order Trepotomata Ulrich, 1882
Family Halloporidae Bassler, 1911

Genus *Calloporella* Ulrich, 1882

Type species. – *Calloporella harrisi* Ulrich, 1882. Richmond Formation, Upper Ordovician of Ohio and Indiana (USA).

Calloporella sp.

Figure 30E, Table 15

Material. – One zoarium in longitudinal section (MPZ 2006/175); and one zoarium in longitudinal-oblique section (MPZ 2006/255); all sections are perpendicular to the zoarial growth direction.

Description. – Zoarium with encrusting growth habit, composed of a single layer 1.5 mm thick on average and with apparent diameter 22.5 mm. Autozooezia tubular with apparent diameter of 0.35 mm on average and 1.4 autozooezia per mm on average; autozooezia growing obliquely with respect to the basal surface, but in initial stages bending to form a 90° angle with the zoarial external surface. Diaphragms scarce, with no more than one per autozooezium. Mesozooezia tubular, with apparent diameter of 0.18 mm on average and 3 mesozooezia per mm, on average, densely tabulated by diaphragms, with 6 of these structures per mm on average; mesozooezia growing from the basal surface isolating autozooezia or in small groups forming maculae. Zooecial walls finely laminated, slightly thickened in the exozone; with autozooezial-mesozooezial wall 0.012 mm thick and mesozooezial-mesozooezial wall 0.01 mm thick, on average.

Discussion. – According to Pushkin's (1981) diagnosis the following characters allow these zoaria to be included in *Calloporella*: the zoarial encrusting growth habit, the thickness and microstructure of zooecial walls, and the abundance of mesozooezia, densely tabulated by diaphragms. Although, there are no transversal sections that permit classifying these zoaria at the species level, their longitudinal sections have been compared with these other species described by Pushkin (1981) as Upper Ordovician in age. The Iberian *Calloporella* can be distinguished from *Calloporella schmidtii* Pushkin, 1981, and from *Calloporella septata* Pushkin, 1981, because their autozooezial diaphragms are more numerous and autozooezia are larger than average in the maculae, while in the Iberian material maculae are exclusively composed of mesozooezia. In addition, *Calloporella septata* has less mesozooezia than the two zoaria studied here. The Iberian material can be distinguished from *Calloporella serotina* Pushkin, 1981, because in the latter the autozooezia grow forming an angle of

90° with the basal surface and the mesozooezia do not isolate autozooezia as in the Iberian *Calloporella*. It can be distinguished from *Calloporella concinna* Pushkin, 1981, because the latter has more autozooezial diaphragms and also the mesozooezia do not isolate autozooezia. Finally, *Calloporella tauchenisensis* Pushkin, 1981, can be distinguished from all other species, including the Iberian *Calloporella*, because its zoarium is composed of two symmetrical layers.

Occurrence. – The La Peña Member (layers 4 and 7) in the Valdelaparra section (Fombuena, Zaragoza).

Genus *Diplotrypa* Nicholson, 1879

Type species. – *Favosites petropolitanus* Pander, 1830. Middle Ordovician of Sweden.

Discussion. – Nicholson (1879) described *Diplotrypa* as a subgenus of *Monticulipora* d'Orbigny, 1850, with *Favosites petropolitanus* Pander, 1830, as the type species. Ulrich (1890) defined the family Diplotrypidae to include *Diplotrypa*, which was elevated to genus level, plus *Batostoma* Ulrich, 1882, and *Monotrypa* Nicholson, 1879. Nickles & Bassler (1900) moved all these genera into the family Trematoporidae. Astrova (1978) made a revision of *Diplotrypa* including it into the family Halloporidae but without giving any reason for this change. Conti (1990), following McKinney's (1971) revision of the family Diplotrypidae, moved *Diplotrypa* back into this family. Conti (1990) based the reallocation on the reduced thickness of the zooecial walls both in the endozone and the exozone, which distinguishes *Diplotrypa* from the Trematoporidae genera, and in the astogenetic pattern of *Diplotrypa*, with autozooezia budding from mesozooezia in the endozone, which distinguishes it from the Halloporidae genera. Key (1991) emended the diagnosis of *Diplotrypa* and moved it back again into the family Halloporidae, emending the diagnosis of this family.

Diplotrypa gemmata (Conti, 1990)

Figures 33A–C, 34, Table 16

1990 *Panderpora gemmata* n. sp.; Conti, p. 102, pl. 10, figs 4–8, pl. 11, figs 1, 2.

2007 *Diplotrypa* sp.; Jiménez-Sánchez, Spjeldnaes & Vilas, fig. 7 (1, 2).

Material. – One zoarium in longitudinal and tangential section (MPZ 2006/112).

Description. – Zoarium with massive growth habit, hemispherical in shape and with slightly concave basal surface,

Table 15. Summary of the statistical analysis of *Calloporella* sp. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeal diameter (in mm)	0.27–0.40	0.35	0.04	19	2
Autozooeal-mesozoeeal wall thickness (in mm)	0.01–0.02	0.012	0	15	2
Mesozoeeal diameter (in mm)	0.12–0.27	0.18	0.04	25	2
Mesozoeeal-mesozoeeal wall thickness (in mm)	0.005–0.01	0.01	0.002	19	2
Number of autozooea per 1 mm	0.5–2	1.4	0.6	12	2
Number of mesozoeeal diaphragms per 1 mm	2–9	6	2	16	2
Number of mesozoeeal per 1 mm	1–4	3	1	11	2
Zoarial apparent length (in mm)	21–24	22.5	2.1	2	2
Zoarial height (in mm)	1–2.3	1.5	0.5	8	2

Table 16. Summary of the statistical analysis of *Diplotrypa gemmata* (Conti, 1990). Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeal diameter (in mm)	0.49–0.66	0.57	0.06	18	1
Zooeeal wall thickness (in mm)	0.01–0.03	0.02	0	19	1
Brown body diameter (in mm)	0.13–0.24	0.17	0.04	8	1
Mesozoeeal diameter (in mm)	0.09–0.39	0.19	0.08	20	1
Number of autozooea per 1 square mm	3–4	3.3	0.6	3	1
Number of autozooea per 2 mm	2–4	2.7	0.7	7	1
Number of mesozoeeal diaphragms per 1 mm	6–11	8.5	1.5	20	1
Number of mesozoeeal per 1 square mm	6–11	8.2	2.5	3	1
Number of mesozoeeal per 2 mm	3–4.5	3.7	0.6	7	1
Zoarial diameter (in mm)	32	32	0	1	1
Zoarial height (in mm)	18.5	18.5	0	1	1

with a maximum diameter of 32 mm and a maximum height of 18.5 mm. Autozoeeal apertures subpolygonal or sub-circular, 0.57 mm diameter on average, isolated by mesozoeeal; 2.7 autozoeeal apertures per 2 mm and 3.3 autozoeeal apertures per mm², on average. Autozoeeal tubular with two astogenetic patterns. (1) Autozoeeal radiating directly from the zoarium base, characterized by a larger diameter, sinuous walls and occasional diaphragms, only present in the proximal autozoeeal zone in some autozoeeal. (2) Autozoeeal budding from mesozoeeal. This second autozoeeal pattern occurs in two ways: first and most common in the proximal mesozoeeal zone, consisting of the termination of mesozoeeal diaphragms and progressive increase in zooeeal diameter; and second one occurs in the distal mesozoeeal zone where autozoeeal develop from two or three small mesozoeeal; this transformation occurs at a point where a group of mesozoeeal have the diaphragm at the same level; here, diaphragm production ceases and a small autozoeeum with a pair of basal diaphragms develops.

Brown body structures, 0.17 mm diameter on average, are present in some autozoeeal. Mesozoeeal apertures polygonal or subcircular, 0.19 mm diameter on average, but with a large variability, 0.09–0.39 mm, isolating autozoeeal or forming small maculae; 3.7 mesozoeeal apertures per 2 mm and 8.2 mesozoeeal apertures per mm², on average. Three types of mesozoeeal astogenetic patterns were found: (1) mesozoeeal developed at the zoarium base, characterised by a large diameter and either reaching the external zoarial surface, or transforming into autozoeeal; (2) mesozoeeal budding from other mesozoeeal, when situated above a mesozoeeal diaphragm, another mesozoeeal wall is generated; and (3) mesozoeeal budding from other mesozoeeal, but in this process also generating an autozoeeum. All mesozoeeal densely tabulated by diaphragms, 8.5 of these structures per mm on average. Zooeeal walls laminated, 0.02 mm thick on average, with layers parallel to the zoarium growth direction and without any thickness change between the exozone and endozone.

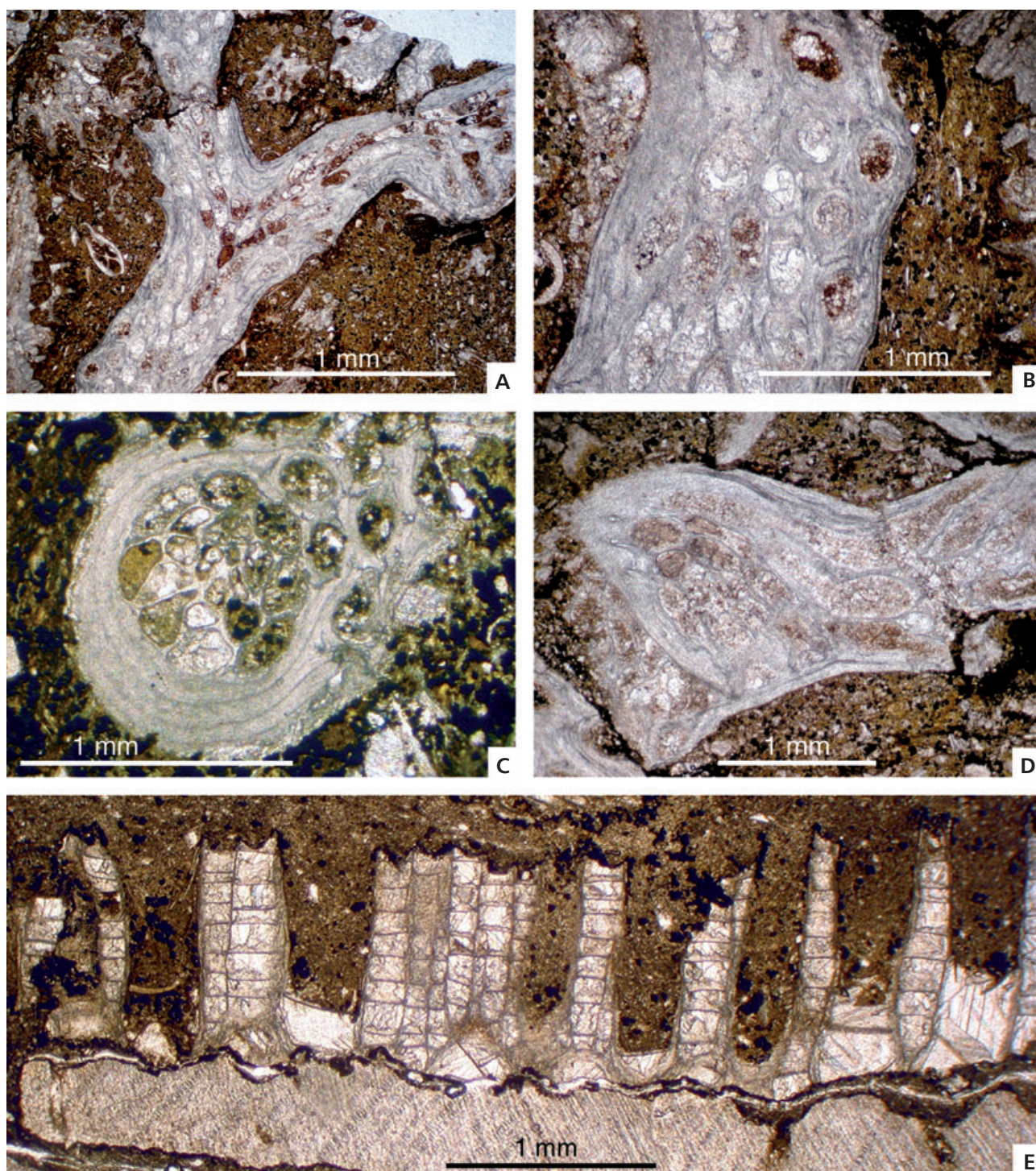


Figure 30. A–D – *Pseudohornera* sp. A, B – MPZ 2006/105; A – longitudinal section; B – tangential section; C – MPZ 2006/136, transversal section; D – MPZ 2006/102, oblique section in which small acanthostyles (on the left) can be observed. • E – *Calloporella* sp. MPZ 2006/175, longitudinal section. A, B and C from the La Peña Member in the La Peña del Tormo section, C and E from the La Peña Member in the Valdelaparra section (Fombuena, Zaragoza).

Discussion. – Bassler (1952) described the new genus *Panderpora*, including in it species closely related to *Hallopora* Bassler, 1911. Astrova (1978) considered *Pander-*

pora as a junior synonym of *Diplotrypa*. Conti (1990) drew freehand astogenetic patterns of the genera *Hallopora*, *Panderpora* and *Diplotrypa*, showing the way in which au-

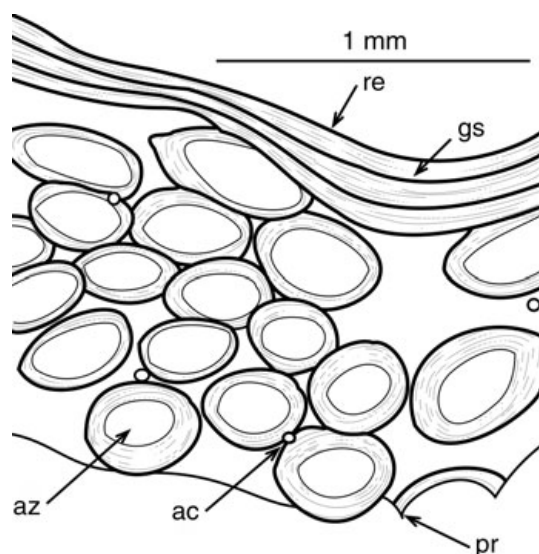


Figure 31. *Pseudohornera* sp. Schematic tangential section of the zoarium MPZ 2006/105 showing oval to subcircular autozooeal apertures (az) with peristome (pr), small acanthostyles (ac), and reverse with growth stages (gs).

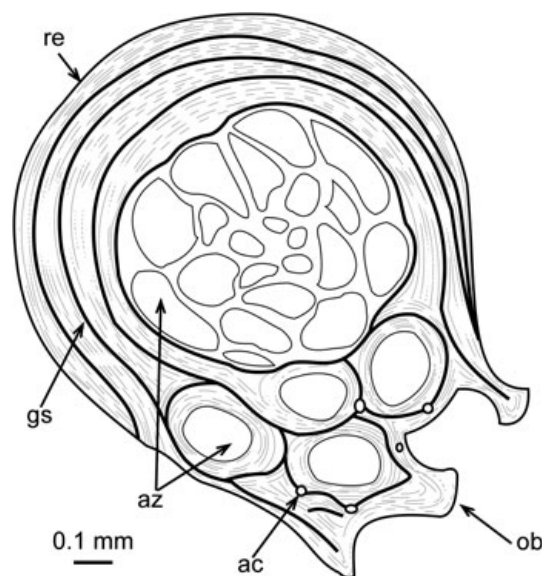


Figure 32. *Pseudohornera* sp. Schematic transversal section of the zoarium MPZ 2006/136 showing obverse (ob) with autozooeal apertures, autozooea (az) sections irregular in endozone and regular in exozone, small acanthostyles (ac), and reverse (re) with growth stages (gs).

tozooea bud from mesozooea and vice versa. *Diplotrypa* and *Panderpora* show a different astogenetic pattern and Conti (1990), based on this fact, considered them as two different genera. Key (1991) also considered *Panderpora* as a junior synonym of *Diplotrypa*, including in it species with the typical growth habit of the halloporids, where autozooea arise from mesozooea by astogenetic transformation. In the zoarium studied here, the astogenetic pat-

terns described by Conti (1990) for *Diplotrypa* and *Panderpora* are both present. This fact can indicate that the astogenetic pattern is not a valid diagnostic generic feature and thus, *Panderpora* is here also considered as a junior synonym of *Diplotrypa*.

The Iberian zoarium shows two of the three diagnostic characters of *Diplotrypa gemmata* (Conti, 1990), defined from the upper Katian of Sardinia: endozone-exozone boundary well defined and the astogenetic patterns of autozooea and mesozooea. No phosphatic autozooeal diaphragm has been found in the Iberian zoarium, this being the third diagnostic feature according to Conti (1990). However, since the phosphatic composition of autozooeal diaphragms is a product of diagenesis, this feature should not be considered as diagnostic. The Iberian material and *Diplotrypa gemmata* share the same shape, the diameter and the height of the zoarium; the same astogenetic pattern characterized by budding of autozooea from mesozooea; the rare autozooeal diaphragms; as well as the distribution of mesozooeal diaphragms and the winding of its walls. Due to these shared characters, the Iberian material can be clearly assigned to *Diplotrypa gemmata*.

Following Key's (1991) emended diagnosis, *Diplotrypa gemmata* can be included in *Diplotrypa* because it shares with it the main diagnostic characters. They are: the massive growth habit and the hemispherical shape of the zoarium; the presence of maculae composed of larger mesozooea; the astogenetic patterns of the autozooea and mesozooea; the distribution of the mesozooea isolating the autozooea or in small groups, forming maculae; the composition and thickness of zooeal walls; the large autozooeal apertures; and the absence of acanthostyles. The Mediterranean species differs from Key's (1991) emended diagnosis in that its autozooeal diaphragms are really scarce and the endozone-exozone boundary is very clear. But the species included in *Diplotrypa* have a wide range in number and shape of the autozooeal diaphragm. Therefore, this species is assigned to *Diplotrypa* without any doubt.

Diplotrypa sardoa Conti, 1990, and *Diplotrypa languedociana* Dreyfuss, 1948, were previously described from the Mediterranean margin of Gondwana in the upper Katian of Sardinia (Conti 1990) and the Montagne Noire (Dreyfuss 1948, Ernst & Key 2007), respectively. *Diplotrypa gemmata* can be distinguished from *Diplotrypa sardoa* and *Diplotrypa languedociana* because in the latter two species there are no differences between the endozone and the exozone. In addition, *Diplotrypa gemmata* can be distinguished from *Diplotrypa sardoa* because in the latter the autozooea are bottle-shaped and has cystoidal diaphragms and cystiphragms; *Diplotrypa gemmata* can be distinguished from *Diplotrypa languedociana* by the presence of acanthostyles.

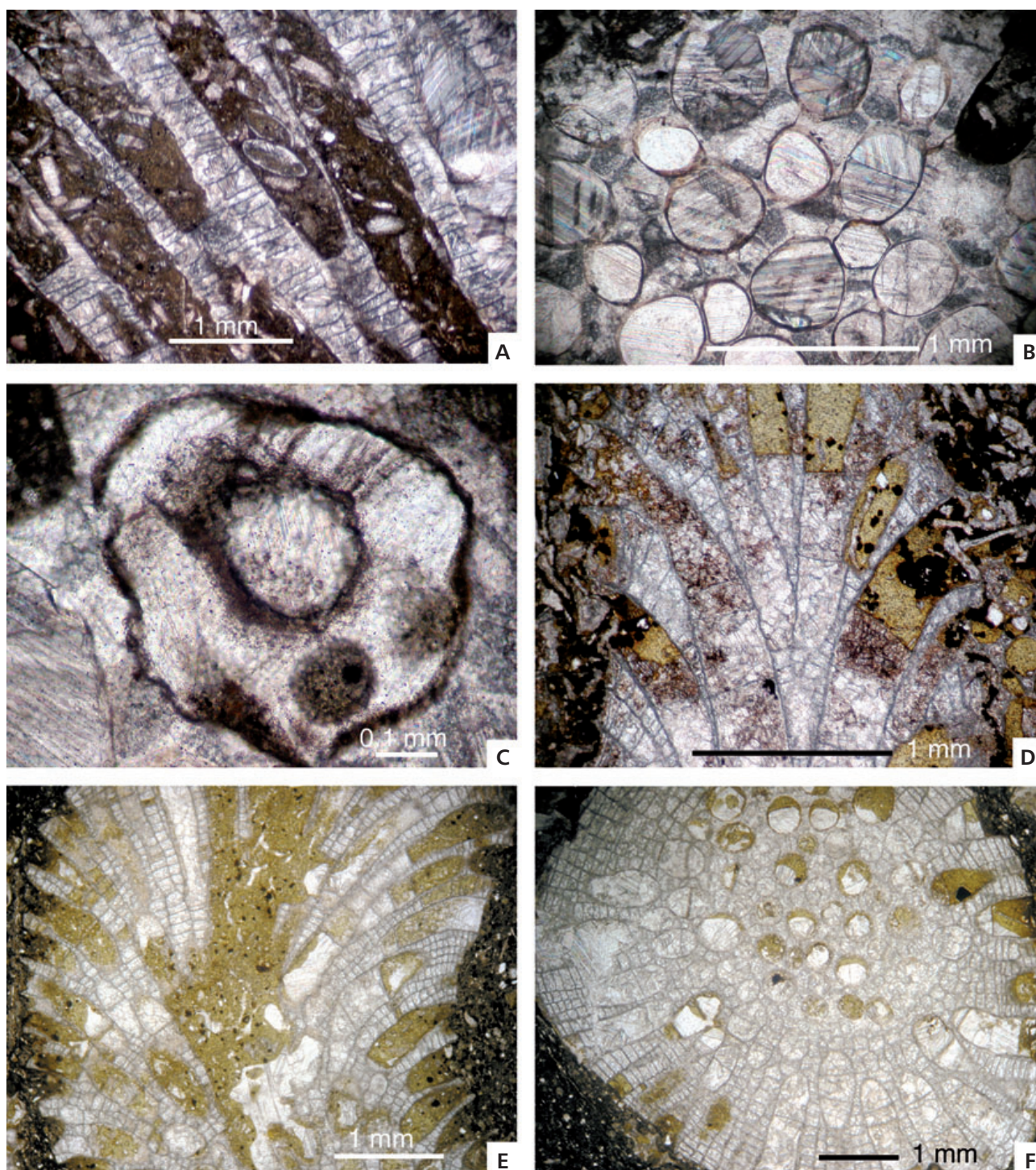


Figure 33. A–C – *Diplotrypa gemmata* (Conti, 1990), MPZ 2006/112. A – longitudinal section; B – transversal section; C – brown body in an autozoecium. • D–F – *Hallopora elegantula* (Hall, 1851). D – MPZ 2006/280, longitudinal section; E, F – MPZ 2006/190; E – longitudinal section; F – transversal section. All specimens from the La Peña Member in the Valdelaparra section (Fombuena, Zaragoza).

Occurrence. – Punta S'Argiola Member, lower beds of Domus-Novas Formation, upper Katian (Sardinia, Italy) (Conti 1990); the La Peña Member (layer 11), in the Valdelaparra section (Fombuena, Zaragoza).

Genus *Hallopora* Bassler, 1911

Type species. – *Calopora elegantula* Hall, 1851. Niagara Limestone Formation, Lower Silurian of Lockport and New York (USA).

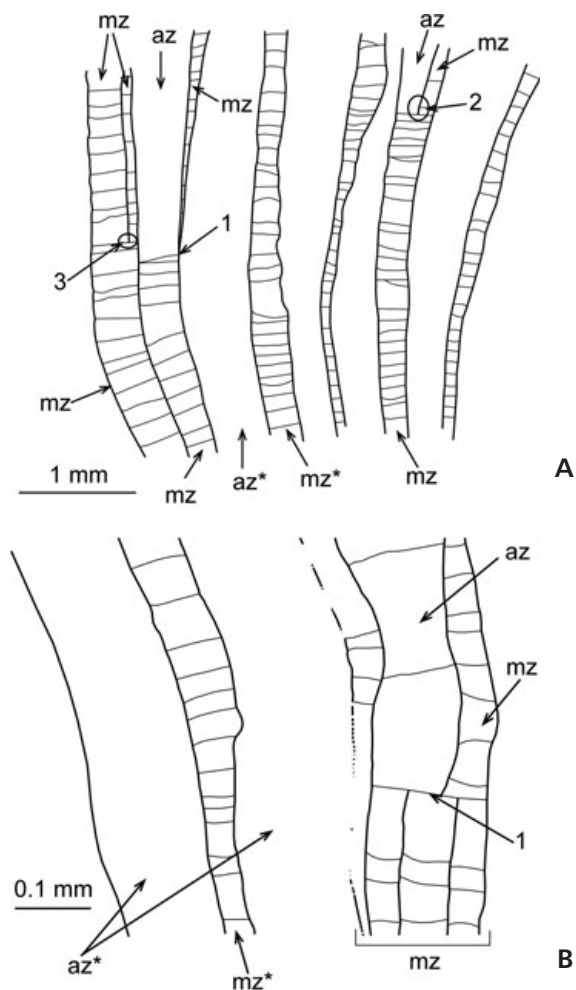


Figure 34. *Diplotrypa gemmata* (Conti, 1990). Schematic longitudinal sections showing the different types of autozooecia and mesozooecia. In both, the large tubes without diaphragms represent the autozooecia growing from the zoarial base (az*) while the large tubes densely tabulated by diaphragms represent the mesozooecia growing from the zoarial base and reaching the zoarial surface (mz*). In (A) numbers 1 and 2 show the generation of autozooecia from mesozooecia by the mechanism of termination of diaphragms and development of an associated mesozooecium, conical in 1 and tubular in 2; and number 3 shows the generation of one mesozooecium from a preexisting one. In (B) number 1 shows the development of an autozooecium and one associated mesozooecium from three mesozooecia.

Hallopora elegantula (Hall, 1851)

Figures 33D–F, 35, Table 17

1851 *Calopora elegantula* n. sp.; Hall, p. 400.

1990 *Hallopora elegantula* (Hall, 1851). – Conti, p. 100, pl. 8, fig. 8, pl. 9, figs 1–6; and synonymy there cited.

2007 *Hallopora elegantula* (Hall, 1851). – Ernst & Key, p. 382, pl. 7, figs 4–8.

2007 *Hallopora* sp.; Jiménez-Sánchez *et al.*, fig. 7 (7, 8).

Material. – One zoarium in longitudinal and transversal section (MPZ 2006/190); four zoarial fragments in trans-

versal and oblique section (MPZ 2006/278, MPZ 2006/281, 282 and MPZ 2006/285); and six zoarial fragments in transversal section (MPZ 2006/279, 280, MPZ 2006/283, 284, MPZ 2006/287 and MPZ 2006/290).

Discussion. – There is no tangential section available and autozooecial and mesozooecial diameters have been measured in longitudinal and transversal sections only, so these values are estimates and the real values could be higher. The linear density of autozooecia and mesozooecia has been measured in longitudinal sections, therefore real density also may be less than the value obtained here.

Description. – Zoaria with branching growth habit, branches with circular cross section, 3.4 mm diameter on average. Autozooecia tubular, 0.33 mm diameter on average, budding in the endozone and growing parallel to the zoarial growth direction, but bending slightly in the outer endozone; in the inner exozone, autozooecia bend strongly to reach the external zoarial surface at an angle of 60° on average; autozooecial diaphragms mainly in the inner exozone and irregularly distributed; autozooecial cross section circular to subpolygonal in the endozone; 3.2 autozooecia per 2 mm. Mesozooecia develop in the outer endozone where autozooecia bend towards the external zoarial surface; wedge-shaped proximally and progressively becoming tubular distally, with an average diameter of 0.16 mm; mesozooecial diaphragms abundant, 14 per mm on average, with clear laminated microstructure; mesozooecia isolating autozooecia or in groups forming maculae; 7.3 mesozooecia per 2 mm. Astogenetic budding of autozooecia from mesozooecia and also vice versa; budding of autozooecia from mesozooecia occurs in the inner exozone by termination of mesozooecial diaphragms and an increase in autozooecial diameter. Budding of mesozooecia from autozooecia occurs in the outer exozone by the development of cap-like structures (Conti & Serpagli 1987). Autozooecial walls laminated with layers parallel to autozooecial growth direction, without any change in thickness at the endozone-exozone boundary, 0.011 mm thick on average; mesozooecial walls laminated with an inverse V pattern, slightly thinner than autozooecial walls. Lamination forming mesozooecial diaphragms also including part of mesozooecial wall lamination. Endozone and exozone well defined, with similar diameter and width.

Discussion. – The branching growth habit of the zoarium, the presence of cap-like structures (present in many species of the genus), well defined endozone and exozone, the distribution of autozooecial and mesozooecial diaphragms, and the absence of acanthostyles, are the characters that have allowed this material to be included in the genus *Hallopora* following Ernst & Key's (2007) emended diagnosis.

The features described in the Iberian material correspond with those described by Conti (1990) and Ernst & Key (2007) in *Hallopora elegantula* (Hall, 1851) from the upper Katian of Sardinia (Italy) and the Montagne Noire (France), respectively, but the Iberian zoaria lack mural spines in the autozooeceia. However, not all the material assigned to *Hallopora elegantula* have these structures (Spjeldnaes 1984, from the Upper Ordovician of the Baltic); therefore, the mural spines do not appear to have diagnostic value and the zoaria studied are thus included in *Hallopora elegantula*.

Hallopora cystoidalis Conti, 1990, *Hallopora edonis* Bassler, 1927, *Hallopora furumjuliensis* (Vinassa de Regny 1910) and *Hallopora gracilens* Bassler, 1927 are other species of the genus described previously from the Mediterranean margin of Gondwana [see Conti (1990) and Ernst & Key (2007)]. This Iberian material assigned to *Hallopora elegantula* can be distinguished from *Hallopora cystoidalis* because in the latter the zoarium is larger, the autozooeceia bud from mesozooecea also in the endozone, the autozooeceial diaphragms are more numerous in the exozone, and the cap-like structures are absent. From *Hallopora edonis* it can be distinguished because in this species the autozooeceia reach the external surface at a broader angle, the autozooeceia lack cap-like structures, the mesozooecea are restricted to the exozone and are more numerous, and have thicker autozooeceial walls in the exozone. From *Hallopora furumjuliensis* it can be distinguished because in this species the autozooeceia bud from mesozooecea also in the endozone, and the autozooeceia reach the external surface at a broader angle. And, finally, the Iberian material can be distinguished from *Hallopora gracilens* because in the latter the zoaria are smaller, the autozooeceia reach the external surface at a broader angle, the cap-like structures are absent, and the autozooeceial walls are thicker in the exozone.

Occurrence. – *Hallopora elegantula* is a species with a broad geographic distribution in the Upper Ordovician of Southern Europe and Scandinavia, as well as in the Lower

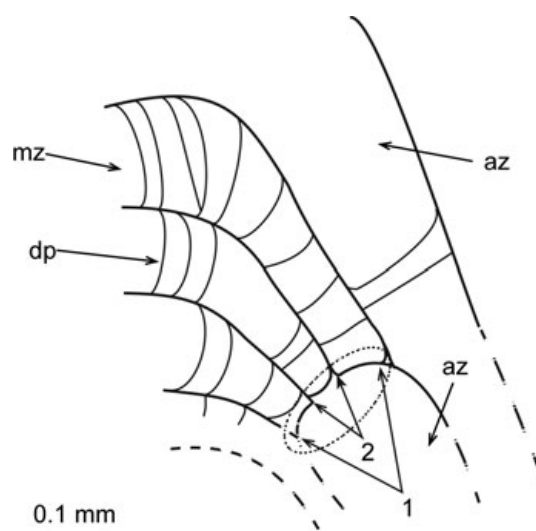


Figure 35. *Hallopora elegantula* (Hall, 1851). Schematic longitudinal section of the zoarium MPZ 2006/281 showing a cap-like structure (contained in the ellipse) in one autozooeceium (az); numbers 1 and 2 show the outer and inner mesozooeceial (mz) ring. The mesozooecea are densely tabulated by diaphragms (dp).

and Middle Silurian of North America. In the Mediterranean Region it has been identified in the Maciurru and Punta S' Argiola Member from the Domus-Novas Formation in Sardinia (Italy) (Conti 1990); in the carbonate and clastic sequence from the Montagne Noire (France) (Ernst & Key 2007) both upper Katian in age; in La Peña Member (layers 1 and 2) in the Valdelaparra section (Fombuena, Zaragoza).

***Hallopora cf. peculiaris* (Pushkin, 1987)**

Figures 36A–C, Table 18

cf. 1987 *Hallopora peculiaris* n. sp.; Pushkin, p. 153, pl. 8, fig. 5, pl. 9, fig. 1.

cf. 1991a *Hallopora peculiaris* Pushkin, 1987. – Buttler, pp. 86–88, pl. 3, figs 3–8.

Table 17. Summary of the statistical analysis of *Hallopora elegantula* (Hall, 1851). Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeceial angle with zoarial surface	43°–85°	60°	11	15	2
Autozooeceial diameter (in mm)	0.21–0.45	0.33	0.05	97	11
Autozooeceial wall thickness in exozone (in mm)	0.005–0.02	0.011	0.004	74	10
Mesozooeceial diameter (in mm)	0.09–0.27	0.16	0.04	92	11
Number of autozooeceia per 2 mm	2–4	3.2	0.6	4	10
Number of mesozooeceial diaphragms per 1 mm	8–20	14	3	63	10
Number of mesozooecea per 2 mm	4.5–12	7.3	2.3	4	10
Zoarial diameter (in mm)	5–1.8	3.4	1.1	11	11

Table 18. Summary of the statistical analysis of *Hallopora* cf. *peculiaris* (Pushkin, 1987). Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeccial angle with zoarial surface	60°–90°	83°	8	15	2
Autozooeccial diameter (in mm)	0.21–0.45	0.34	0.05	31	1
Autozooeccial wall thickness (in mm)	0.005–0.01	0.009	0.001	15	3
Cingulum thickness (in mm)	0.025–0.12	0.042	0.020	24	3
Mesozooeccial large diameter (in mm)	0.12–0.24	0.18	0.04	24	1
Number of autozooeccia per 1 square mm	3–5.5	4.2	1.2	4	1
Number of autozooeccia per 2 mm	0.5–4.5	3	1	13	1
Number of mesozooeccial diaphragms per 1 mm	7–18	13	3	11	3
Number of mesozooeccia per 1 square mm	13–16	14.5	1.3	4	1
Number of mesozooeccia per 2 mm	2–7	5	1.5	13	1
Zoarial diameter (in mm)	3–5.5	4	1.3	3	2

Material. – One zoarium in tangential, longitudinal and transversal section (MPZ 2006/286); one zoarial fragment in longitudinal section (MPZ 2006/276); and one zoarial fragment in transversal section (MPZ 2006/277).

Description. – Zoarial growth habit branching with circular branches, 4.0 mm diameter on average. Autozooeccia tubular, budding in the endozone with only slight inclination, but bending at the endozone-exozone boundary to reach the external zoarial surface at an average angle of 83°; autozooeccia rarely budding from mesozooeccia. Autozooeccial apertures irregularly circular and without any specific arrangement pattern, 0.34 mm diameter on average, and with laminated cingulum, 0.042 mm thick; three autozooeccia per 2 mm and 4.2 autozooeccia per 1 mm². Autozooeccial diaphragms scarce in the endozone and inner exozone and absent in the outer exozone. Autozooeccial cross section circular or subpolygonal in the endozone. Mesozooeccial apertures irregular in shape, placed in gaps between autozooeccia; mesozooeccial large diameter 0.18 mm on average, with a frequency of 5 mesozooeccia per 2 mm and 14.5 mesozooeccia per mm². Mesozooeccia also present in the inner endozone, distinguishable from autozooeccia by smaller diameter and more numerous diaphragms; mesozooeccial diaphragms numerous, 13 per mm on average, increasing in number in the outer exozone, where cystoidal diaphragms are also present. Zooeal walls thin, 0.009 mm on average, with laminated microstructure parallel to the zooeal growth direction. Endozone and exozone well defined, with endozonal diameter twice the exozonal width.

Discussion. – According to Ernst & Key's (2007) emended diagnosis the following characters allow this material to be included in the genus *Hallopora*: the branching growth habit of the zoarium; the well defined endozone and exozone;

the distribution of autozooeccia and mesozooeccia; and the absence of acanthostyles.

The Iberian zoaria are similar to *Hallopora peculiaris*, a species well represented in the Upper Ordovician of Wales (Buttler 1991a). The Iberian material shares with it the broad angle made by the autozooeccia at the external zoarial surface, the shape and size of autozooeccial and mesozooeccial apertures, the budding of mesozooeccia also in the endozone, and the presence of a cingulum in the autozooeccia. However, in the Iberian material the branch diameter is much smaller, the cingulum is thinner, and the autozooeccial diaphragms are absent in the outer exozone. So, the Iberian material is only provisionally referred to *Hallopora peculiaris* until new material is found.

Hallopora cf. *peculiaris* can be distinguished from *Hallopora elegantula*, described above, because in the former the autozooeccial tubes have a cingulum, the mesozooeccia are also developed in the inner endozone, cap-like structures are absent, the autozooeccial diaphragms are absent in the outer exozone and the mesozooeccial cystoidal diaphragms are more numerous.

Occurrence. – The La Peña Member (layer 1), in the Valdelaparra section (Fombuena, Zaragoza).

Genus *Parvohallopora* Singh, 1979

Type species. – *Monticulipora ramosa* d'Orbigny, 1850. Lower Silurian of Cincinnati (Ohio, USA).

Discussion. – The genus *Hallopora* Bassler, 1911, include a group of morphologically heterogeneous species, with a wide age range (Middle Ordovician–Upper Silurian), characterized by the presence of diaphragms in the endozone and in the exozone, by the abundance of diaphragms in the inner endozone



Figure 36. A–C – *Hallopore* cf. *peculiaris* (Pushkin, 1987). A, C – MPZ 2006/276; A – longitudinal section, C – detail of a mesozooecial group; B – MPZ 2006/286, transversal section. • D–F – *Parvohallopore* cf. *ramosa* (d’Orbigny, 1850). D – MPZ 2006/119, oblique section; E – MPZ 2006/121, transversal section; F – MPZ 2006/124, transversal section showing the wall units in the mesozooecia. A–C from the La Peña Member in the Valdelaparra section, D–F from the La Peña Member in the La Peña del Tormo section (Fombuena, Zaragoza).

and less abundance in the outer endozone, by the abundance of mesozooecia, by the circular autozooecial apertures, and by the absence of acanthostyles (Singh 1979).

Singh (1979) proposed segregating from this heterogeneous group the species displaying the following features: smaller autozooecial diameter, mural spines absent in the

autozooeceia, numerous, small mesozooecea between the autozooeceia, cystoidal diaphragms rare to absent in autozooeceia and absent in mesozooecea, and laminated zooecial walls with inverse U or V patterns which in *Hallopore* are rarely present. To accommodate these species Singh (1979) erected the genus *Parvohallopore*.

***Parvohallopore cf. ramosa* (d'Orbigny, 1850)**

Figures 36D–F, Table 19

cf. 1850 *Monticulipore ramosa* sp. nov.; d'Orbigny, p. 25.

cf. 1979 *Parvohallopore ramosa* (d'Orbigny, 1850). – Singh, p. 228, pl. 41, figs 1–3, 4a–c, pl. 42, figs 1, 2, 3a–c, pl. 43, figs 1a–c, 2, 3. Synonymies also included.

Material. – Four zoarial fragments in transversal section (MPZ 2006/121–124); one zoarial fragment in longitudinal section (MPZ 2006/120); and one zoarial fragment in oblique section (MPZ 2006/119).

Description. – Zoaria with branching growth habit, circular branches with 2.3 mm diameter on average. Autozooeceia tubular, budding in the endozone with an inclination of 13° on average; at the endozone-exozone boundary they suddenly bend to terminate at the external zoarial surface at an angle of 87° on average; autozooeceial apertures completely isolated by mesozooecea, circular in shape with 0.24 mm diameter on average and with a cingulum 0.017 mm thick on average; autozooeceial cross section irregularly six-sided polygonal in the endozone. Autozooeceia budding also at the endozone-exozone boundary. Autozooeceial dia-

phragms present in the endozone and exozone, with 9.5 diaphragms per mm, and laminated microstructure with layers discontinuous with cingulum layers. Mesozooecea tubular, developing in the outer endozone and with the same inclination as autozooeceia; mesozooeceial apertures subcircular or four-sided polygonal, 0.11 mm diameter on average, isolating autozooeceia or in small groups forming maculae; mesozooecea densely tabulated by diaphragms, 22.5 per mm; diaphragms with laminated microstructure, with clear wall units continuing through adjacent mesozooecea and terminating at the mesozooeceial-autozooeceial boundary. Zooecial walls laminated with an inverse V pattern; laminae concentrically arranged around autozooeceial and mesozooeceial apertures in the exozone; autozooeceial walls 0.024 mm thick and mesozooeceial walls 0.017 mm thick in the exozone, but in the endozone 0.009 mm thick and 0.008 mm thick, respectively. Endozone and exozone well defined, but with the exozone more developed than the endozone (0.70 mm thick exozone vs. 1.04 mm diameter endozone).

Discussion. – According to Singh's (1979) diagnosis: the presence of a large exozone, the zooecial angle with respect to the zoarial surface, the shape of autozooeceia in the endozone and exozone, the wall units in mesozooeceial diaphragms, the inverse V laminated pattern of the zooecial walls, the presence of autozooeceial and mesozooeceial diaphragms, both in the endozone and exozone, the abundance, shape and size of mesozooecea, and the high density of diaphragms, are the characters which allow this material to be included in the genus *Parvohallopore*.

The Iberian material is similar to *Parvohallopore*

Table 19. Summary of the statistical analysis of *Parvohallopore cf. ramosa* (d'Orbigny, 1850). Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeceial angle with zoarial surface	83°–90°	87°	4	3	1
Autozooeceial angle in endozone	20°–8°	13°	5	5	2
Autozooeceial diameter (in mm)	0.19–0.27	0.24	0.02	19	2
Autozooeceial wall thickness in endozone (in mm)	0.005–0.02	0.009	0.004	19	4
Autozooeceial wall thickness in exozone (in mm)	0.01–0.04	0.024	0.008	17	2
Cingulum thickness (in mm)	0.01–0.025	0.017	0.004	20	6
Endozone diameter (in mm)	0.9–1.44	1.04	0.2	6	6
Exozone thickness (in mm)	0.48–1.05	0.7	0.15	25	6
Mesozooeceial diameter (in mm)	0.05–0.16	0.11	0.03	15	2
Mesozooeceial wall thickness in endozone (in mm)	0.005–0.01	0.008	0.003	13	2
Mesozooeceial wall thickness in exozone (in mm)	0.005–0.03	0.017	0.008	13	2
Number of autozooeceial diaphragms per mm	2–18	9.5	4.1	31	5
Number of mesozooeceial diaphragms per 1 mm	13.5–30	22.5	4.4	42	6
Zoarial diameter (in mm)	1.7–2.5	2.3	0.5	7	6

Table 20. Summary of the statistical analysis of *Heterotrypa* sp. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Acanthostyles diameter (in mm)	0.04–0.2	0.11	0.03	39	1
Autozooeccial angle with zoarial surface	72°–82°	77°	3	11	1
Autozooeccial diameter (in mm)	0.18–0.28	0.24	0.03	17	1
Autozooeccial wall thickness in endozone (in mm)	0.005–0.02	0.01	0.005	13	1
Autozooeccial wall thickness in exozone (in mm)	0.035–0.08	0.05	0.015	13	1
Endozone diameter (in mm)	1.29–1.71	1.47	0.16	5	1
Exozone thickness (in mm)	0.51–0.81	0.7	0.14	6	1
Mesozooeccial diameter (in mm)	0.07–0.13	0.1	0.02	16	1
Number of acanthostyles per 1 mm	1–3	1.7	0.9	10	1
Number of acanthostyles per 1 square mm	9–14	12	3	3	1
Number of autozooeccia per 1 mm	1.5–3	2.2	0.5	10	1
Number of autozooeccia per 1 square mm	9.5–10	9.8	0.3	3	1
Number of autozooeccial diaphragms per mm	1–7	4	2	8	1
Number of mesozooeccial diaphragms per 1 mm	2–12	7	4	6	1
Number of mesozooeccia per 1 mm	0–2	0.4	0.9	10	1
Number of mesozooeccia per 1 square mm	0–3	2	2	3	1
Zoarial diameter (in mm)	2.7–3.3	3	0.2	5	1

ramosa (d'Orbigny, 1850), widely distributed during the Upper Ordovician in the palaeocontinents of Baltica and Laurentia. In addition to the diagnostic characters of the genus, both share the following features: the development of autozooeccia at the endozone-exozone boundary, the presence of diaphragms throughout the endozone and exozone, as well as the high density of diaphragms in the exozone, and the presence of a cingulum in the autozooeccia. But the zoarial surface of *Parvohallopora ramosa* is completely covered by monticules. These monticules vary from conical protuberances to rings completely encircling the branches. In the Iberian material there is no evidences of such structures, and in spite of the few available zoaria, these structures are of sufficient size to have been visible in some of the studied sections. So, the Iberian material is only provisionally referred to *Parvohallopora ramosa*.

Occurrence. – The La Peña Member in the La Peña del Tormo section (Fombuena, Zaragoza).

Family Heterotrypidae Ulrich, 1890

Genus *Heterotrypa* Nicholson, 1879

Type species. – *Monticulipora frondosa* d'Orbigny, 1850. Upper Ordovician of USA.

Heterotrypa sp.

Figures 37A–C, 38, Table 20

Material. – One zoarium (MPZ 2006/111) in tangential, longitudinal, transversal and oblique section.

Description. – Zoaria with branching growth habit, branch cross section being circular, 3 mm diameter on average. Autozooeccial apertures circular, with 0.24 mm diameter on average, frequently modified by extremely abundant acanthostyles so that they acquire petal shape due to the inclusion of large acanthostyles in their walls; 2.2 autozooeccial apertures per mm and 9.8 autozooeccial apertures per mm². Autozooeccia tubular, budding in the endozone and developing parallel to branch growth direction up to the outer endozone where they slightly bend; in the inner exozone they strongly bend to reach the external zoarial surface at an angle of 77° on average; some autozooeccia develop at the endozone-exozone boundary. Autozooeccial diaphragms present in the exozone, 4 diaphragms per mm on average, but almost absent in the endozone. Mesozooeccial apertures subcircular or irregularly polygonal, with 0.10 mm diameter on average; mesozooeccia scarce, 0.4 per mm and 2.0 per mm², on average. Wedge shaped mesozooeccia developed in the outer endozone, with 7 diaphragms per mm. Mesozooeccial diaphragms with walls units. Acanthostyles characterized by a large diameter, 0.11 mm on average (with a range of

0.04–0.20 mm), composed of a large central lumen of hyaline calcite and dark laminae concentrically arranged around the lumen; most acanthostyles develop at the endozone-exozone boundary, but some of them develop in the inner endozone parallel to autozooeceia; four or five acanthostyles around each autozooeceal aperture, 1.7 per mm and 12.0 per mm². Autozooeceal walls laminated with laminae altered by acanthostyles; with a thickness of 0.05 mm in the exozone and 0.01 mm in the endozone, on average, wavy and with nodular thickenings. Endozone and exozone well defined, with an average diameter of 1.47 mm and an average width of 0.70 mm, respectively.

Discussion. – According to Ernst & Key's (2007) emended diagnosis of the genus *Heterotrypa* Nicholson, 1879, the following characters have allowed this zoarium to be included in *Heterotrypa*: the zoarial growth habit, the endozonal walls with nodular thickenings, the distribution of autozooeceal and mesozooeceal diaphragms, the wedge shape of the mesozooeceia, and the presence of acanthostyles in both the exozone and the endozone.

The large diameter of the acanthostyles and the distortion that they produce in the autozooeceal apertures are characters not described before in other *Heterotrypa* species. However, since there is only one zoarium here and it is not possible to study the external surface, it cannot be assigned to a precise species.

Along the Mediterranean margin of Gondwana *Heterotrypa magnopora* Boulange, 1963, has been previously identified and described by Ernst & Key (2007) from the upper Katian of the Montagne Noire (France). The Iberian *Heterotrypa* shares with it the absence of autozooeceal

diaphragms in the endozone and also the low number of mesozooeceia, plus the fact that mesozooeceia are only present in the exozone. But they can be distinguished because in *Heterotrypa magnopora* the autozooeceia reach the external zoarial surface at an angle of 90° while in the presently studied zoarium it is at an angle of 77°, and the acanthostyles are much smaller.

The Iberian *Heterotrypa* is similar to *Heterotrypa sladei* Buttler, 1991, described by Buttler (1991a) in the Upper Ordovician of Wales. But they can also be distinguished because in the Welsh species autozooeceal diaphragms develop in both the endozone and the exozone, the mesozooeceia are also present in endozone and are abundant, and the acanthostyles are smaller than in the Iberian species.

Occurrence. – The La Peña Member (layer 1) in the Valdelaparra section (Fombuena, Zaragoza).

Family Monticuliporidae

Genus *Homotrypa* Ulrich, 1882

Type species. – *Homotrypa curvata* Ulrich, 1882. Upper Ordovician (Ashgill) of North America.

Homotrypa sp.

Figures 39E, Table 21

Material. – One zoarial fragment in tangential section (MPZ 2006/196); and one zoarial fragment in transversal and oblique section (MPZ 2006/197).

Table 21. Summary of the statistical analysis of *Homotrypa* sp. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Autozooeceal angle with zoarial surface	22°–72°	42°	17	9	2
Autozooeceal large diameter (in mm)	0.3–0.45	0.36	0.05	8	1
Autozooeceal small diameter (in mm)	0.17–0.27	0.22	0.03	8	1
Autozooeceal wall thickness in endozone (in mm)	0.005–0.015	0.009	0.003	24	2
Autozooeceal wall thickness in exozone (in mm)	0.025–0.04	0.033	0.006	8	2
Endozonal diameter	1.2–2.2	1.7	0.4	6	2
Exozonal thickness (in mm)	0.39–0.66	0.5	0.08	15	2
Mesozooeceal diameter (in mm)	0.05–0.15	0.11	0.04	5	1
Number of autozooeceia per 1 mm	3–6	4.2	0.9	17	2
Number of autozooeceia per 1 square mm	15–18	16.7	1.2	5	2
Number of autozooeceal cystiphragms per mm	10–17	13	3	3	1
Number of autozooeceal diaphragms per mm	7–12	11	3	8	2
Number of mesozooeceal diaphragms per mm	10–20	15	7	2	1
Zoarial diameter (in mm)	2.67–3.3	2.93	0.21	7	2

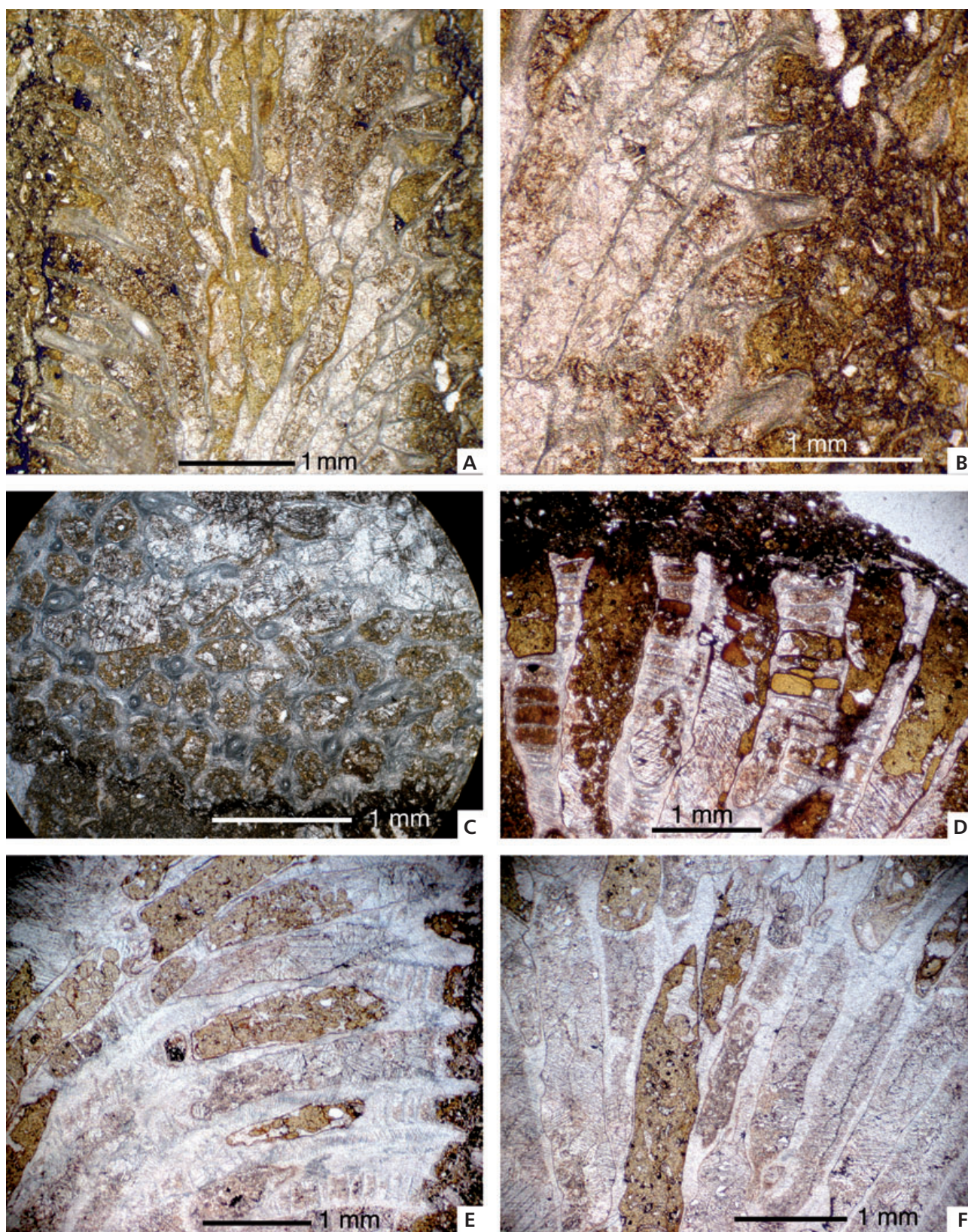


Figure 37. A–C – *Heterotrypa* sp., MPZ 2006/111; A – longitudinal section; B – detail of the longitudinal section; C – tangential section. • D–F – *Dybowskites ernsti* sp. nov. D – MPZ 2006/289 (holotype), transversal section; E, F – MPZ 2006/288, longitudinal sections. All specimens from the La Peña Member in the Valdelaparra section (Fombuena, Zaragoza).

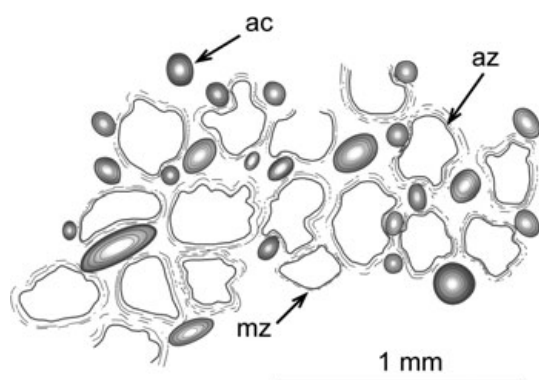


Figure 38. *Heterotrypa* sp. Schematic tangential section showing the large acanthostyles (ac) modifying autozooeal apertures (az), and the irregular mesozooeal sections (mz).

Description. – Zoarial growth habit branching, branches with circular cross section, 2.93 mm diameter on average. Autozooeal apertures elongated polygonal, with five or six sides, with the long axis parallel to branch growth direction; large diameter 0.36 mm and small diameter 0.22 mm, on average, and 4.2 autozooea per mm and 16.7 autozooea per mm²; autozooea tubular, budding in the axial zone, parallel to the growth direction of the branch in the inner endozone, but narrowing and bending slightly in the outer endozone to reach the external zoarial surface at an average angle of 42°. Endozone-exozone boundary marked by budding of new autozooea and development of autozooeal cystiphragms on one side of their walls; 13 autozooeal cystiphragms per mm on average. Autozooeal diaphragms absent or scarce in the inner endozone and numerous in the outer endozone and exozone (7 to 12 diaphragms per mm), some of them with cystiphragms joined to the opposite wall. Mesozooea with apertures irregularly polygonal, with an average diameter of 0.11 mm, developing in the outer exozone; mesozooea scarce (less than one per mm²), wedge shaped and densely tabulated by diaphragms, averaging 15 diaphragms per mm. Autozooeal wall microstructure lost due to diagenesis, 0.033 mm thick in the exozone and 0.009 mm thick in the endozone, on average. Small structures similar to acanthostyles thickening autozooeal walls in the exozone. Endozone and exozone well defined, but the endozone being larger than the exozone (1.7 mm diameter on average in the endozone and average width 0.5 mm in the exozone).

Discussion. – The characters which allow these zoaria to be included in the genus *Homotrypa*, following Ernst & Key's (2007) diagnosis, are: the zoarial branching growth habit, the polygonal autozooeal cross section, the presence of cystiphragms only in the outer exozone, more numerous diaphragms in the exozone, the presence of mesozooea and acanthostyles, and the thickness of zooeal walls both in the endozone and the exozone.

Homotrypa sp. is similar to *Homotrypa oweni* Ross, 1965, but they can be distinguished because the latter has less autozooeal diaphragms but more numerous mesozooea.

In the Mediterranean Province (Jiménez-Sánchez & Villas in press) *Homotrypa miqueli* (Prantl, 1940) has been described from the upper Katian of the Montagne Noire (France) [Ernst & Key (2007)]. *Homotrypa* sp. can be distinguished from *Homotrypa miqueli* because the former has slimmer zoaria, diaphragms both in the endozone and exozone, and abundant mesozooeal diaphragms.

Occurrence. – La Peña Member (layer 1), in the Valdelparra section (Fombuena, Zaragoza).

Family Ralfimartitidae Gorjunova, 2005

Genus *Dybowskites* Pushkin, 1987

Type species. – *Lioclemella clava* Bassler, 1911. Jewe Shale (Baron toll), in Kegel' beds (Habbinem), and in Wassalem's beds (Uxnorn); Upper Ordovician of Estonia.

Dybowskites ernsti sp. nov.

Figures 37D–F, 39A, 40, 41, Table 22

Holotype. – MPZ 2006/289.

Paratypes. – MPZ 2006/288.

Type horizon. – La Peña Member of the Cystoid Limestone Formation, Upper Ordovician.

Type locality. – The Valdelaparra section (Fombuena, Zaragoza).

Material. – Two zoaria in tangential, longitudinal and transversal section (MPZ 2006/288, 289).

Etymology. – After Andrej Ernst thanking him for his help with my doctoral thesis.

Diagnosis. – *Dybowskites* characterized by the large size of the autozooeal and mesozooeal apertures, as well as by its large acanthostyles.

Description. – Zoaria with branching growth habit, branches circular in cross section, 13 mm diameter on average, and dichotomously divided. Autozooeal apertures circular or subpolygonal, 0.49 mm diameter on average and without any apparent arrangement on the zoarial external surface; autozooeal apertures at a frequency of 2.5 per 2 mm and 2.7 per mm², on average. Autozooea tubular, bud-

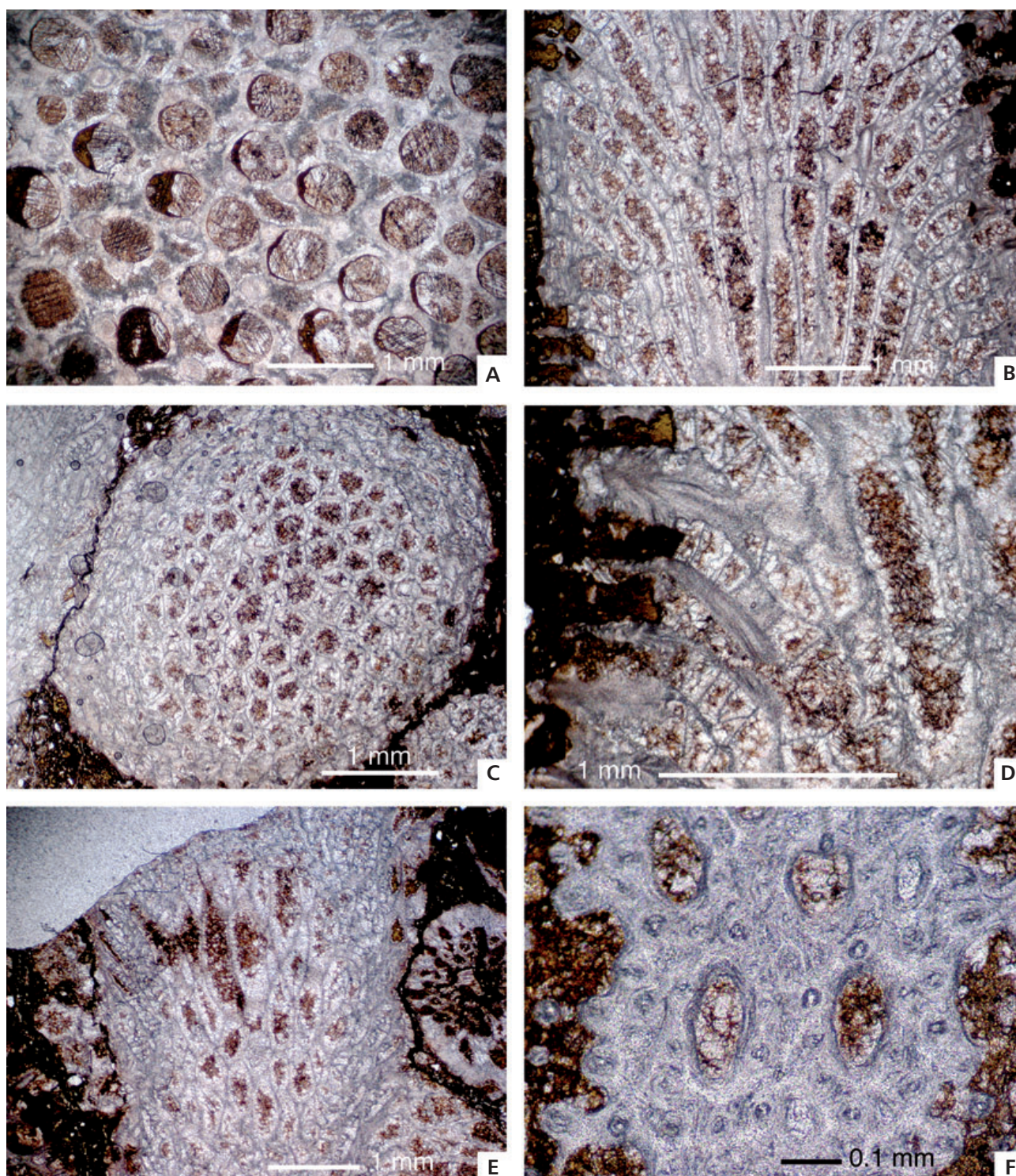


Figure 39. A – *Dybowskites ernsti* sp. nov., MPZ 2006/289 (holotype), transversal section. • B–D – *Eridotrypa obliqua* Conti, 1990, MPZ 2006/188. B – longitudinal section; C – transversal section; D – detail of the longitudinal section. • E – *Homotrypa* sp., MPZ 2006/197, longitudinal section. • F – *Trematopora acanthostylita* sp. nov., MPZ 2006/165, tangential section. A–E from the La Peña Member in the Valdelaparra section, F from the La Peña Member in the La Peña del Tormo section.

ding in the endozone, parallel to the branch growth direction; in the outer endozone they bend slightly up towards the endozone-exozone boundary where they strongly bend

to reach the zoarial external surface at an angle of almost 90°. Autozooeical diaphragms frequent in the endozone, reduced to one or two in the exozone. Mesozooeical aper-

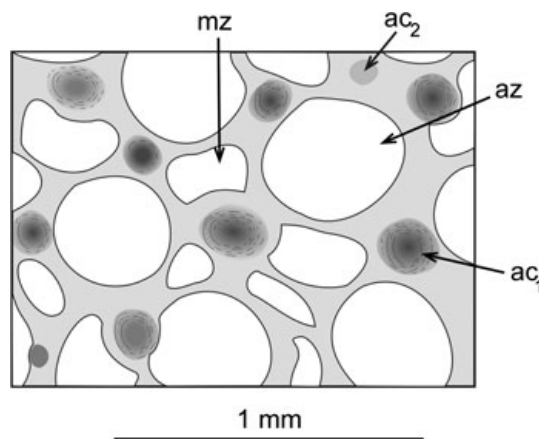


Figure 40. *Dybowskites ernsti* sp. nov. Schematic tangential section of the zoarium MPZ 2006/289 showing large autozoecia (az), irregular mesozooecia (mz), and the two types of acanthostyles: the larger ones with laminated microstructure (ac_1) and the smaller ones with massive microstructure (ac_2).

tures irregular in shape due to large acanthostyles, with a large diameter of 0.25 mm on average; mesozooecia scarce, 1.4 per 2 mm and 2.1 per mm^2 , on average. Mesozooecia developed at the endozone-exozone boundary, wedge-shaped in its proximal part and tubular in its distal part; mesozooecial tubes sometimes narrowed due to acanthostyles; mesozooecial diaphragms abundant, 9 per mm, and varied in shape. Two types of acanthostyles: the largest ones composed of a large dark lumen with laminae concentrically arranged around it, larger than some mesozooecia in cross section and developed close to them; smaller acanthostyles with massive microstructure, commonly protruding above the external zoarial surface. Considering both types of acanthostyle, they range from 0.13 mm to

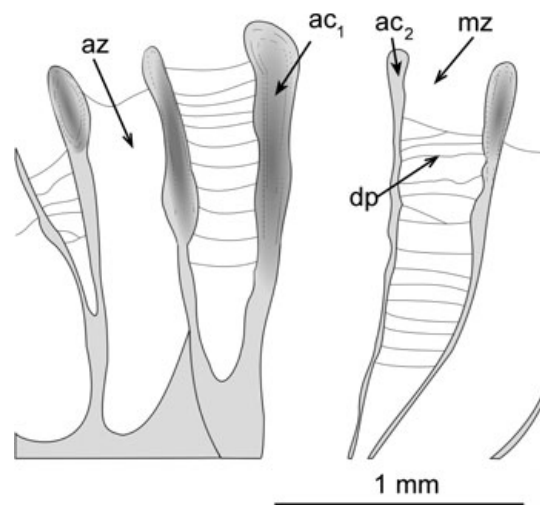


Figure 41. *Dybowskites ernsti* sp. nov. Schematic transversal section of the zoarium MPZ 2006/289 showing autozoecia (az), mesozooecia (mz) densely tabulated by diaphragms (dp), and the two types of acanthostyles (ac_1 and ac_2).

0.30 mm, with 0.21 mm diameter on average; 2 acanthostyles per 2 mm and 4 per mm^2 . Autozooeical walls laminated, 0.051 mm thick on average in the exozone and 0.019 mm thick on average in the endozone.

Discussion. – According to Ernst & Key's (2007) emended diagnosis the following characters allow this Iberian material to be included in the genus *Dybowskites*: the branching growth habit, the shape of the autozoecia and the mesozooecia, their budding pattern, the distribution of autozooeical and mesozooecial diaphragms, as well as the presence of two types of acanthostyles.

The presence of autozoecia, mesozooecia and

Table 22. Summary of the statistical analysis of *Dybowskites ernsti* sp. nov. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Acanthostyles diameter (in mm)	0.13–0.3	0.21	0.07	38	2
Autozooeical diameter (in mm)	0.36–0.6	0.49	0.06	47	2
Autozooeical wall thickness in endozone (in mm)	0.01–0.03	0.019	0.005	20	2
Autozooeical wall thickness in exozone (in mm)	0.02–0.06	0.051	0.01	13	2
Mesozooecial large diameter (in mm)	0.18–0.36	0.25	0.05	26	2
Number of acanthostyles per 1 square mm	2–6	4	1	21	2
Number of acanthostyles per 2 mm	0–4	2	1.2	12	2
Number of autozoecia per 1 square mm	2–4.5	2.7	0.6	21	2
Number of autozoecia per 2 mm	0.5–2.5	2.5	0.9	12	2
Number of mesozooecial diaphragms per 1 mm	6–13	9	2	15	2
Number of mesozooecia per 1 square mm	0–4	2.1	1.7	21	2
Number of mesozooecia per 2 mm	0–3	1.4	1	12	2
Zoarial diameter (in mm)	10–15	13	2	4	2

acanthostyles with a larger diameter than those present in other species of *Dybowskites*, even in those with larger branch diameter, prevent assigning these zoaria to any of the known species. So, *Dybowskites ernsti* sp. nov. is defined to include in it this Iberian material.

Dybowskites orbicularis (Modzilevskaya, 1953) was previously described from the upper Katian of the Montagne Noire (Ernst & Key 2007). *Dybowskites ernsti* sp. nov. and *Dybowskites orbicularis* can be distinguished because the former has less mesozooecia and acanthostyles with respect to autozoecia (a relationship slightly greater than 1 : 1 between autozoecia and mesozooecia in the new species vs. a relationship of almost 1 : 3 in *Dybowskites orbicularis*; and of 2 to 6 acanthostyles per mm² in the new species vs. 5 to 8 acanthostyles in the French species). The mesozooecial shape in cross sections is also different in both species (irregular in the Iberian species and polygonal in the French species). Additionally, the number of mesozooecial diaphragms per mm is higher in the French species.

Dybowskites ernsti sp. nov. can be distinguished from *Dybowskites clavus* (Bassler, 1911) described by Gorjunova (2005) and from *Dybowskites hispidus* Gorjunova, 2005, because these two have branches with smaller diameter and thinner autozoecial walls than the Iberian species. It can be also distinguished from *Dybowskites clavus* because in the latter the mesozooecial apertures are strongly distorted by the acanthostyles, while in the Iberian material there is much less distortion; and it can also be distinguished from *Dybowskites hispidus* because in the latter the autozoecia have several hemiphagms in the endozone that are absent in *Dybowskites ernsti* sp. nov.

Occurrence. – This species is known exclusively from its type locality: the La Peña Member (layer 1) in the Valdelparra section (Fombuena, Zaragoza).

Family Trematoporidae Miller, 1889

Genus *Eridotrypa* Ulrich, 1893

Type species. – *Eridotrypa mutabilis* Ulrich, 1893. Galena Shales, Upper Ordovician of Minnesota; Trenton Group, Upper Ordovician of Kentucky; Middle and Upper Ordovician of Iowa and Wisconsin (USA).

Discussion. – Ulrich (1893) included the new genus *Eridotrypa* in the family Batostomellidae. Ross (1967b) emended the diagnosis of *Eridotrypa* and assigned it to the family Aisenvergiidae, based on the constriction in the autozoecial tubes at the endozone-exozone boundary. McKinney (1971) assigned *Eridotrypa* to the family Trematoporidae following the Russian school (e.g., Astrova 1965), and suggesting that the constriction of the autozoecial wall in the inner exozone is a convergent character and, thus, it does not indicate any phylogenetic relationship between taxa. Conti (1990) considered that *Eridotrypa* is closely related to the genus *Batostomella* Ulrich, 1882, and *Bythopora* Miller & Dyer, 1878, because they share the same astogenetic pattern (McKinney 1977) as well as the appearance of the autozoecial walls, and therefore included *Eridotrypa* in the family Batostomellidae as Ulrich (1893) did originally. It is not clear what is the phylogenetic significance of the astogenetic pattern, since one specimen can have more than one; so I follow McKinney's (1971) proposal and *Eridotrypa* is assigned here to the family Trematoporidae.

Eridotrypa obliqua Conti, 1990

Figures 39B–D, 42, Table 23

1990 *Eridotrypa obliqua* n. sp.; Conti, p. 106, pl. 14, figs 5–8.

Table 23. Summary of the statistical analysis of *Eridotrypa obliqua* Conti, 1990. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Acanthostyles diameter (in mm)	0.04–0.15	0.09	0.03	26	1
Autozoecial angle with zoarial surface in adult zone of colony	85°–90°	89°	2	8	1
Autozoecial angle with zoarial surface in young zone of colony	46°–68°	58°	11	3	1
Autozoecial large diameter (in mm)	0.28–0.5	0.39	0.08	10	1
Autozoecial small diameter (in mm)	0.17–0.3	0.23	0.04	13	1
Autozoecial wall thickness in endozone (in mm)	0.005–0.02	0.015	0.013	20	1
Autozoecial wall thickness in exozone (in mm)	0.03–0.08	0.05	0.01	17	1
Endozonal diameter	1.65–2.7	2.2	0.4	5	1
Exozonal thickness (in mm)	0.36–0.9	0.6	0.15	12	1
Mesozooecial diameter (in mm)	0.04–0.09	0.07	0.02	4	1
Number of autozoecial diaphragms per mm	5–11	8	3	9	1
Zoarial diameter (in mm)	2.8–4.2	3.6	0.5	6	1

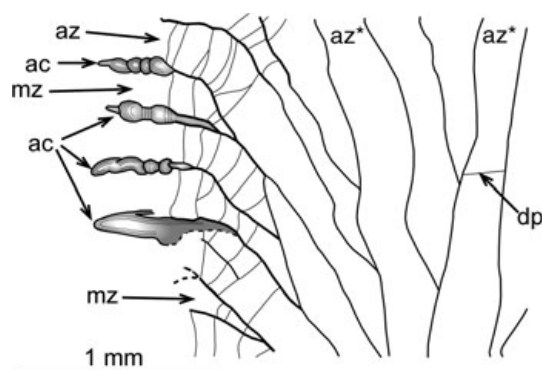


Figure 42. *Eridotrypa obliqua* Conti, 1990. Schematic longitudinal section showing autozooecia budding in the axial zone (az*), with occasional diaphragms (dp), and autozooecia developed in the inner exozone (az), small mesozooecia (mz), and “moniliform” acanthostyles (ac).

2007 *Eridotrypa* sp.; Jiménez-Sánchez *et al.*, fig. 7 (3, 4).

Material. – One zoarium in longitudinal, transversal and oblique section (MPZ 2006/188).

Description. – Zoarial growth habit branching with branches circular in cross section, 3.6 mm diameter on average and with overgrown surfaces. Autozooecial apertures oval or elongate polygonal with the large diameter being parallel to the branch growth direction, 0.39 mm on average, and small diameter 0.23 mm on average; autozooecia budding in the endozone with two size ranges: the most numerous are those with the larger diameter (0.18–0.50 mm, measurements from longitudinal section), and developed parallel to the axial zone, the second type having a smaller diameter (0.17–0.30 mm, measurements from longitudinal section); both types of autozooecia gently bending and their diameter slightly decreasing in the outer endozone; autozooecia reach the external zoarial surface at the same inclination as in the endozone (58° on average) in the young zoarial zones; in the old zone of the zoarium, autozooecia suddenly bend at the endozone-exozone boundary to reach the zoarial external surface at an average angle of 89°. Autozooecial diaphragms absent or scarce in the endozone and outer exozone, but abundant in the inner exozone, with 8 diaphragms per mm on average; autozooecial cross section hexagonal or four-sided polygonal in the inner endozone, with two size ranges of diameter; autozooecia homogeneous in size in the outer endozone. Mesozooecial apertures three or four sided polygonal with an average diameter of 0.07 mm; mesozooecia scarce, developed in the outer exozone as small wedges and with diaphragms separated by a distance equal to one mesozooecial diameter. Acanthostyle cross section circular, 0.09 mm diameter on average, composed of a large, light central lumen with laminae concentrically arranged around it; acanthostyles developed in the outer exozone, mainly in the zoarium old zone; irregularly

moniliform in longitudinal section and thickening autozooecial walls. Autozooecial walls laminated, with autozooecial boundary marked by dark granular layer, with a thickness of 0.05 mm on average in the exozone; autozooecial walls slightly wavy in the endozone with a thickness of 0.015 mm on average. Endozone and exozone well defined, with the endozone larger than the exozone (endozone with 2.2 mm diameter on average and exozone width 0.6 mm on average).

Discussion. – According to Ross’s (1967b) emended diagnosis this zoarium can be placed in *Eridotrypa* because it shares with it the slender and circular zoarial branches with overgrowth, the oval or polygonal elongated autozooecial apertures, the mesozooecia developed in the exozone, the autozooecial angle with respect to the zoarial external surface, the distribution of the autozooecial diaphragms, and the number of mesozooecial diaphragms. However, the Iberian zoarium does not fit Ross’s (1967b) emended diagnosis in having large acanthostyles in the exozone of the old zone of the zoarium, but I suggest adding this feature to *Eridotrypa*’s diagnosis, since acanthostyles with similar diameter were described by Conti (1990) in *Eridotrypa obliqua* Conti, 1990, from the upper Katian of Sardinia. Moreover, the Iberian zoarium shares with this species the average angle with which autozooecia reach the external zoarial surface in the old zone of the colony (almost 90°), the distribution and density of the autozooecial diaphragms, and the low number of mesozooecia. Due to these shared characters, the Iberian zoarium is assigned to the Sardinian species.

Eridotrypa obliqua is similar to *Eridotrypa abrupta* Loeblich, 1942. Both species share the autozooecial angle with respect to the zoarial external surface and the presence of a dark layer marking the autozooecial boundary. But the two species can be distinguished because the autozooecia in *Eridotrypa abrupta* have cystiphragms, the mesozooecia are more numerous, and lack large acanthostyles.

Along the Mediterranean margin of Gondwana the following are also known: *Eridotrypa constans* Conti, 1990, described by Conti (1990) and Ernst & Key (2007) from the upper Katian of Sardinia and the Montagne Noire (France), respectively; and *Eridotrypa spicata* Dreyfuss, 1948, identified by Dreyfuss (1948) and Ernst & Key (2007) in the same Ordovician levels in the Montagne Noire. *Eridotrypa constans* can be distinguished from the Iberian *Eridotrypa obliqua* because the former has smaller zoaria, autozooecia with irregular cross sections in the inner endozone, and a higher density of autozooecial diaphragms in the endozone, but both species share the wavy autozooecial walls in the endozone. *Eridotrypa spicata* can be distinguished from the Iberian material because the former has smaller zoaria and more abundant acanthostyles.

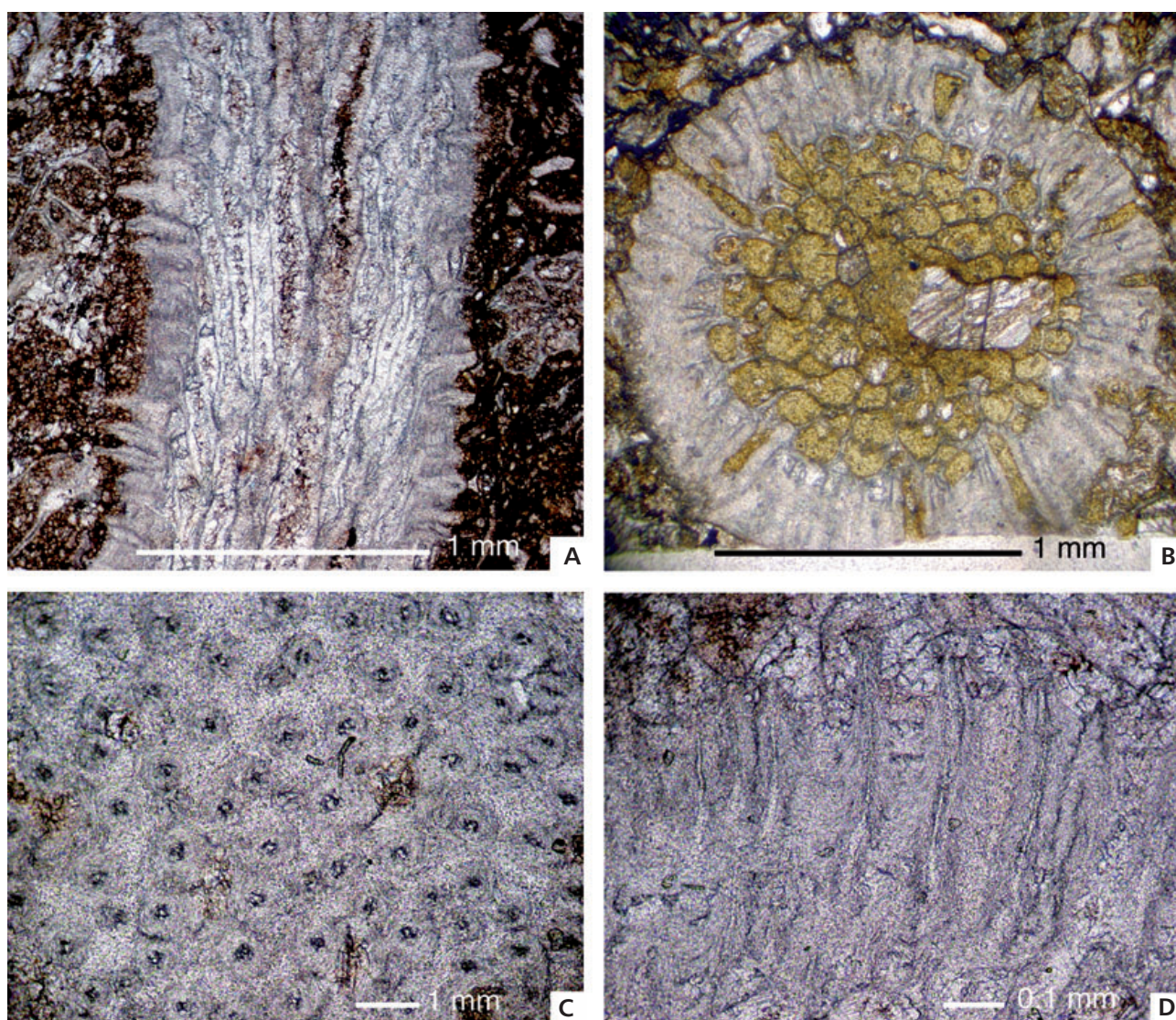


Figure 43. *Trematopora acanthostylita* sp. nov. • A – MPZ 2006/172 (holotype), longitudinal section. • B – MPZ 2006/173, transversal section. • C – MPZ 2006/169, detail of acanthostyles in tangential section. • D – MPZ 2006/170, detail of acanthostyles in longitudinal section. A, C and D from the La Peña Member in the La Peña del Tormo section, B from the La Peña Member in the Valdelaparra section (Fombuena, Zaragoza).

Occurrence. – Punta S' Argiola Member, lower part of the Domus-Novas Formation, upper Katian of Sardinia, Italy (Conti, 1990); the La Peña Member (layer 1), in the Valdelaparra section (Fombuena, Zaragoza).

Genus *Trematopora* Hall, 1852

Type species. – *Trematopora tuberculosa* Hall, 1852; Lower Silurian of North America.

Trematopora acanthostylita sp. nov.

Figures 39F, 43A–D, 44, 45, Table 24

2007 *Jifarahpora* sp.; Jiménez-Sánchez *et al.*, fig. 6 (1, 2).

Holotype. – MPZ 2006/172.

Paratypes. – MPZ 2006/164–167, MPZ 2006/169, MPZ 2006/170, 171 and MPZ 2006/173, 174.

Type horizon. – La Peña Member of the Cystoid Limestone Formation, Upper Ordovician.

Type locality. – La Peña del Tormo Section (Fombuena, Zaragoza).

Material. – Five zoarial fragments in tangential section (MPZ 2006/164, 165, MPZ 2006/168, 169 and MPZ 2006/172); four zoarial fragments in transversal section (MPZ 2006/166, 167, MPZ 2006/170 and MPZ 2006/174);

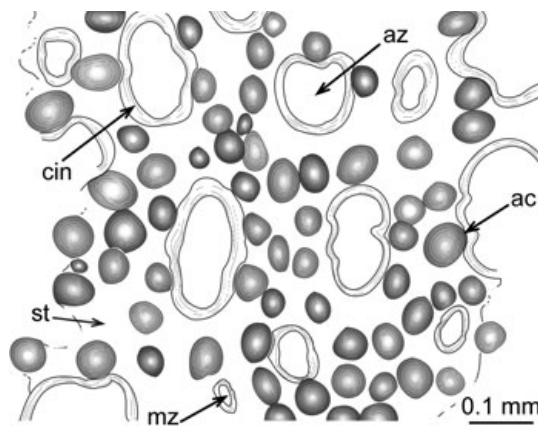


Figure 44. *Trematopora acanthostylita* sp. nov. Schematic tangential section of the zoarium MPZ 2006/165 showing the large, abundant acanthostyles (ac) modifying autozooeal apertures (az) that are separated by an extensive extrazoeal skeleton (st), thickened cingulum in autozooeia (cin), and small mesozoeia (mz).

one zoarial fragment in transversal/tangential section (MPZ 2006/171); and one zoarial fragment in longitudinal section (MPZ 2006/173).

Etymology. – After the numerous, large acanthostyles present.

Diagnosis. – *Trematopora* characterized by the presence of numerous, large acanthostyles, by the small number of autozooeal diaphragms (absent in almost all autozooeia), and by the absence of diaphragms in mesozoeia.

Description. – Zoarial growth habit branching with branch cross section circular, 1.7 mm diameter on average. Num-

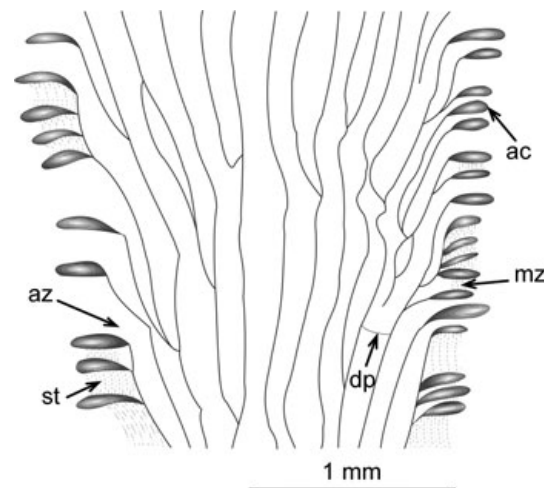


Figure 45. *Trematopora acanthostylita* sp. nov. Schematic longitudinal section of the holotype (MPZ 2006/172) showing the autozooeia (az) with occasional diaphragms (dp), the small mesozoeia (mz) covered by extrazoeal skeleton (st), and numerous acanthostyles (ac).

rous acanthostyles protruding from the external zoarial surface. Autozooeal apertures irregularly oval, some of them with petaloidal outline due to the acanthostyles, with large diameter of 0.09 mm on average; 1.3 autozooeal apertures per mm and 13 autozooeal apertures per mm², separated by thickened extrazoeal laminated skeleton which is more than 0.09 mm thick; cingulum, 0.022 mm thick on average, present in autozooeal tubes. Autozooeia tubular, budding mainly in the axial zone, but with secondary budding in the outer endozone; autozooeia parallel to the growth direction of the branches in the endozone, at the endozone-exozone boundary, they strongly bend to

Table 24. Summary of the statistical analysis of *Trematopora acanthostylita* sp. nov. Abbreviations as in Table 1.

Character	Or	X	DS	Nm	Nsp
Acanthostyles diameter (in mm)	0.035–0.085	0.07	0.02	47	6
Autozooeal large diameter (in mm)	0.07–0.1	0.09	0.01	67	6
Autozooeal wall thickness in endozone (in mm)	0.005–0.015	0.009	0.003	83	10
Autozooeal wall thickness in exozone (in mm)	0.033–0.057	0.041	0.008	26	6
Cingulum thickness (in mm)	0.015–0.028	0.022	0.004	25	7
Endozone diameter	0.74–1.35	1.1	0.2	39	10
Exozona thickness (in mm)	0.24–0.54	0.4	0.1	82	10
Mesozoeal diameter (in mm)	0.05–0.07	0.058	0.007	6	1
Number of acanthostyles per 1 mm	6–11	7.5	1.4	15	3
Number of acanthostyles per 1 square mm	72–109.5	90	17	5	3
Number of autozooeia per 1 mm	0.5–1.5	1.3	0.4	14	3
Number of autozooeia per 1 square mm	12–14.5	13	1	4	3
Number of mesozoeia per 1 square mm	11–18	18	12	3	1
Zoarial diameter (in mm)	1.2–2.67	1.7	0.4	36	10

reach the zoarial external surface at an angle of 90°. Autozooeccial diaphragms absent or scarce. Autozooeccial cross section irregularly polygonal in the endozone. Mesozooecia developed at the endozone-exozone boundary, overlaid by a thick extrazooecial skeleton and only observed in deep tangential section; mesozooecia with subcircular or subpolygonal shapes and 0.058 mm diameter on average, located between autozooeccia or in small groups forming maculae with an average density of 18 mesozooecia per mm²; mesozooecial diaphragms absent. Acanthostyles with large diameter (0.07 mm on average), composed of a light central hyaline lumen surrounded by dark laminae; high density of acanthostyles (90 acanthostyles per mm² and 7.5 acanthostyles per mm), mostly developed in the inner exozone, but some in the outer endozone. Autozooeccial walls in the exozone 0.041 mm thick on average, with an inverse V pattern, but with laminae strongly influenced by the presence of acanthostyles; autozooeccia walls in the endozone slightly wavy with a thickness of 0.009 mm on average. Endozone with an average diameter of 1.1 mm and the exozone with an average width of 0.4 mm, both well defined.

Discussion. – Following Ernst & Key's (2007) diagnosis, these zoaria share with the genus *Trematopora* the branching growth habit, the autozooeccial oval cross section and the scarce number of diaphragms in the autozooeccia, the presence of mesozooecia covered by a laminated skeleton, the abundance of acanthostyles around autozooeccial apertures, and the thickness of zooecial walls both in the endozone and exozone. The Iberian zoaria mesozooecia lack diaphragms, a feature included in Ernst & Key's (2009) diagnosis, although they defined *Trematopora gracile* as a species lacking mesozooecial diaphragms. So, I suggest changing "Abundant mesozooecia with abundant diaphragms..." to "Abundant mesozooecia, which may have diaphragms..." in the diagnosis of the genus by Ernst & Key's (2009).

Trematopora tuberculosa Hall, 1852, *Trematopora sardoa* (Vinassa de Regny, 1942), and *Trematopora gracile* Ernst & Key, 2007 from the upper Katian of Montagne Noire (France), Sardinia and the Carnic Alps (Italy) [see Conti (1990) and Ernst & Key (2007)] as well as *Trematopora minima* Suttner & Ernst, 2007 from the upper Katian of India, are other species of the genus previously described from the Mediterranean Province (Jiménez-Sánchez & Villas in press). *Trematopora acanthostylita* sp. nov. is most similar to *Trematopora gracile* but they can be distinguished because in the former the autozooeccial diaphragms are practically absent both in the endozone and in the exozone and it has a larger zoarial diameter (1.20–2.67 mm in *Trematopora acanthostylita* sp. nov. vs. 0.44–1.68 mm in *Trematopora gracile*). *Trematopora acanthostylita* sp. nov. is also similar to *Trematopora sardoa*, but they can be easily distinguished because the latter has abundant diaphragms in the mesozooecia.

Occurrence. – This species is known from its type locality and in the La Peña Member (layer 1) in the Valdelaparra section (Fombuena, Zaragoza).

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