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Ashgill bryozoans from the Iberian Chains (NE Spain) and their contribution to the Late Ordovician biodiversity peak in North Gondwana

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Abstract. In the lower-middle Ashgill Cystoid Limestone Formation of the Iberian Chains (NE Spain) twenty one bryozoan genera have been identified, which belong to the four Stenolaemata orders that were already spread worldwide by the Mid Ordovician: Cryptostomata, Cyclostomata, Cystoporata and Trepostomata. Five of them: *Cyclophaenopora* Spjeldnaes, *Glauconomella* Bassler, *Orbignyella* Ulrich and Bassler, *Phaenopora* Hall and *Pseudostictoporella* Ross have been identified here for the first time in the Mediterranean Province. This list increases the number of bryozoan genera known to sixty six, making it the most diversified group in the region for that period.

Resumen. Briozoos del Ashgill de las Cadenas Ibéricas (NE España) y su contribución al pico de biodiversidad del Ordovícico Superior en el norte de Gondwana. En la Formación Calizas de Cistideos, de edad Ashgill inferior-medio, de las Cadenas Ibéricas (NE de España) se han identificados veintiún géneros de briozoos pertenecientes a los cuatro órdenes Stenolaemata que ya se habían expandido a nivel mundial en el Ordovícico Medio: Cryptostomata, Cyclostomata, Cystoporata y Trepostomata. Cinco de ellos: *Cyclophaenopora* Spjeldnaes, *Glauconomella* Bassler, *Orbignyella* Ulrich y Bassler, *Phaenopora* Hall y *Pseudostictoporella* Ross son reconocidos por primera vez en la Provincia Mediterránea. Esta lista permite ampliar a sesenta y seis el número de géneros de briozoos conocidos allí, convirtiéndolos en el grupo más diversificado de la región para ese periodo.

Key words. Bryozoans. Cystoid Limestone. Late Ordovician. Iberian Chains. Mediterranean Province. Biodiversity.

Palabras clave. Briozoos. Calizas de Cistideos. Ordovícico Superior. Cadenas Ibéricas. Provincia Mediterránea. Biodiversidad.

Introduction

The Cystoid Limestone Formation (Dereims, 1898; Villas, 1983) of the Iberian Chains is one of the units where carbonate productivity and associated Upper Ordovician organisms are best recorded in the whole northern Gondwana margin. This production of carbonate follows a long period of siliciclastic sedimentation lasting from the Late Cambrian to the mid Late Ordovician. In the studied region this sedimentation did not start until the early Ashgill and suddenly ceased with the onset of the Hirnantian glaciation, representing a period of 4 My. There is a similar sedimentary pattern for most of the present southwest Europe and north Africa, where remains of the continental platforms of the northern Gondwana margin exist, and on which the Mediterranean Province (Spjeldnaes, 1961) was developed. At the end of the Ordovician, this region would have been placed at intermediate latitudes, allowing equatorial currents to reach it. These, besides warming the environment, account for the arrival to the region of a distinct benthic fauna previously restricted to tropical zones (Villas *et al.*, 2002). As a consequence, the biodiversity reached a peak in the region at this time, including large pelmatozoan and bryozoan meadows, over which, in some cases, small mud-mounds grew up (Vennin *et al.*, 1998). A great number of brachiopods, trilobites, echinoderms and conodonts are known to have thrived in this

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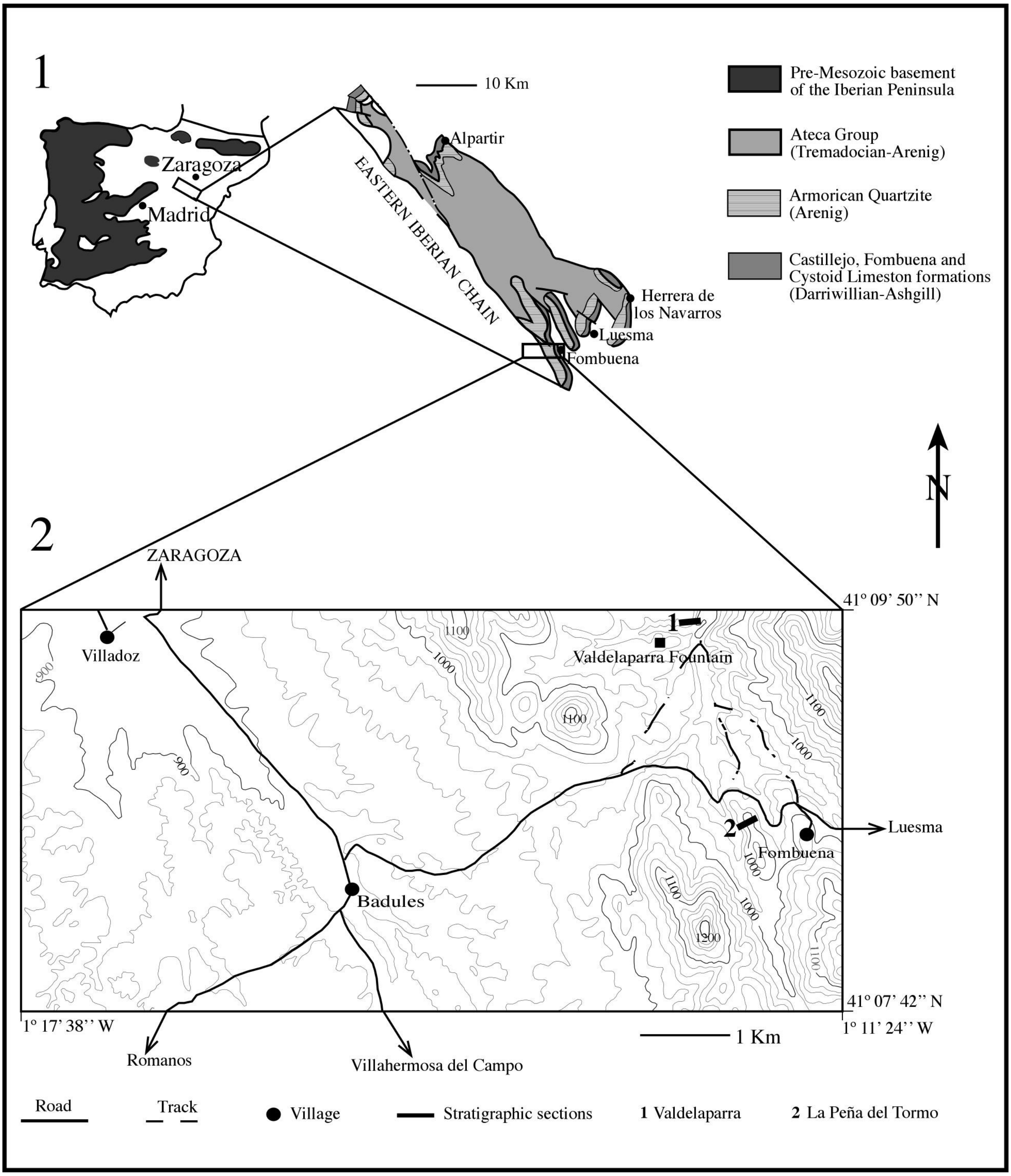


Figure 1. **1,** outcrops of Ordovician rocks on the Eastern Iberian Chain and their location on the Iberian Peninsula. **2,** location of the studied sections. / ***1,*** *afloramientos de rocas ordovícicas en la Cadena Ibérica oriental y su localización en la Península Ibérica.* ***2,*** *localización de las secciones estudiadas.*

environment, together with rare ostracodes, gastropods and cephalopods.

The chronostratigraphy, microfacies and geometry of the carbonate build-ups or mud-mound complexes are well known in the Cystoid Limestone Formation, as well as the systematics of brachiopods, trilobites and echinoderms. However, no detailed study of bryozoan systematics has been carried out, in spite of their role as one of the main producers of carbonates at that time and responsible for the development of small build-ups. The first mention of Ordovician bryozoans from the Iberian Chains appears in Meléndez (1944), who described the new species *Synocladia lluecae* and *Polypora camarensis* in the basal horizons of the Fombuena Formation, underlying the Cystoid Limestone; but these species will have to be verified in a future study as their identification was made exclusively from moulds. Spjeldnaes (1967) cited the genus *Chasmatoporella* Nekhoroshev, 1936, from horizons later included in the same Fombuena Formation, Caradoc in age (Villas, 1992). Hafenrichter (1979) identified the genera *Diplotrypa* in the localities of Alpartir and Fombuena, and *Hallopora* in Luesma, besides several undetermined trematoporid trepostomates and bifoliate cryptostomates, all of them from the Cystoid Limestone Formation.

This report identifies the bryozoan associations in one of the best exposed sections of the Cystoid Limestone of the Iberian Chains, and compares them with others described in the Mediterranean Province. It also undertakes an initial approximation of the diversity of the group during the early-mid Ashgill and compares it with the diversity of other benthic organisms.

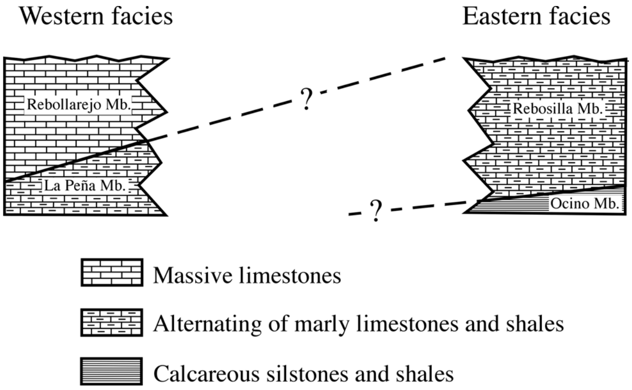


Figure 2. Relationships of facies and lithostratigraphic units of the Cystoid Limestone Formation. Based in Hammann (1992) and Vennin *et al.* (1998) / *relaciones de facies y unidades litoestratigráficas de la Formación Calizas de Cistideos. Basado en Hammann (1992) y Vennin* et al. *(1998).*

Geographic and geological setting

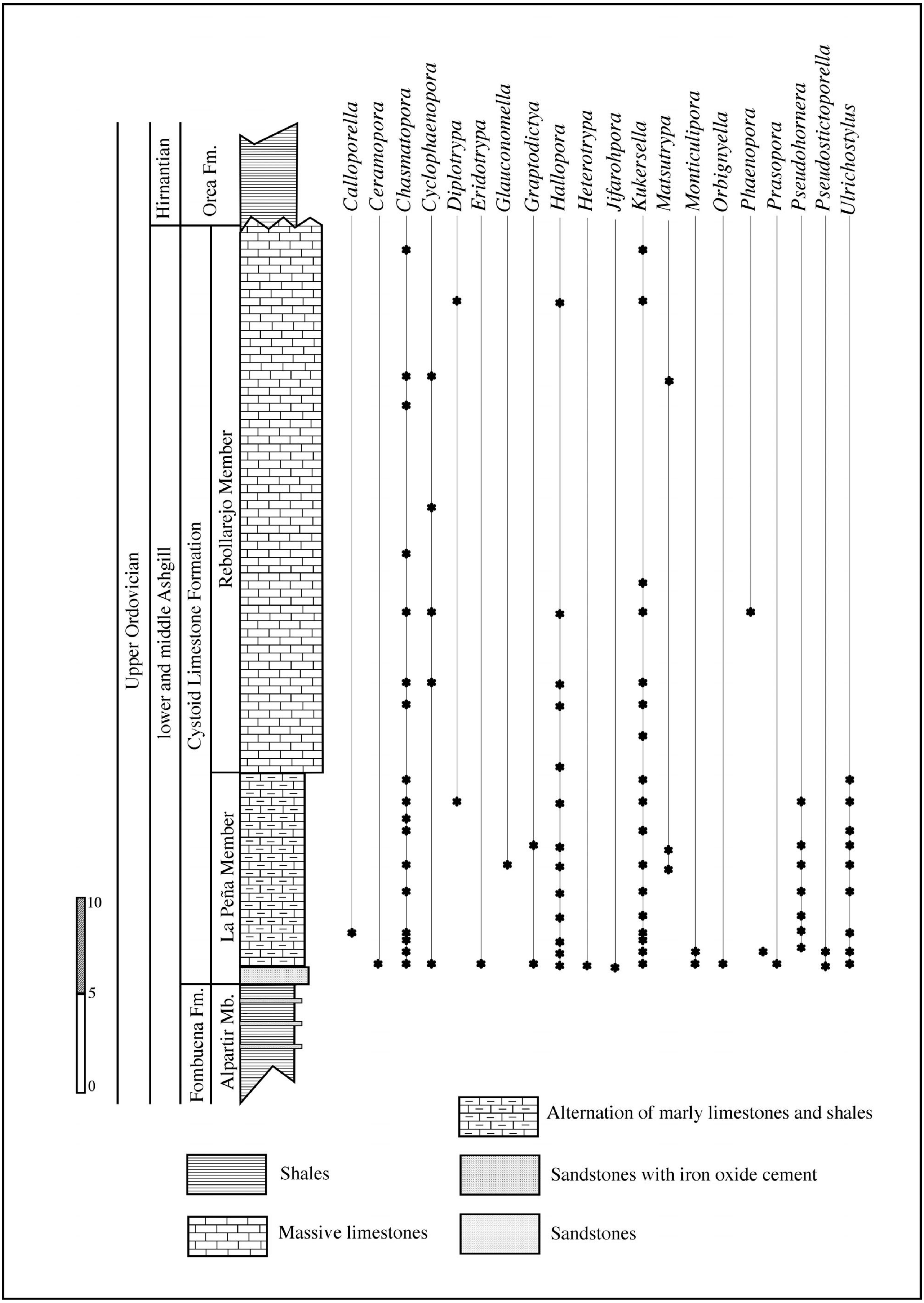
The studied section of the Cystoid Limestone Formation is located in the Eastern Iberian Chain (NE Spain), within the municipality of Fombuena (Zaragoza). It is situated 2,6 km northwest of the Fombuena village, in the gully of La Peña del Tormo and close to the Valdelaparra aspring (figure 1).

The Cystoid Limestone conformably overlies the Fombuena Formation and is characterized by the presence of a basal bed of fine-grained argillaceous sandstone with iron oxide cement and centimetre-thick lenses of ooidal packstones. The top of the formation is commonly dolomitized, and its upper boundary is an erosional unconformity overlain by the Orea Formation. The Cystoid Limestone Formation displays a maximum thickness of 50 m in its westernmost outcrops and 25 m in the easternmost. It is geographically restricted to the Eastern Iberian Chain.

Four members were distinguished in the Cystoid Limestone Formation by Hammann (1992) in order to characterize vertical and lateral facies changes (figure 2). Towards the east, where the formation shows a marly character, it was divided into the Ocino and Rebosilla Members. The massive limestones of the western area were divided into the La Peña and Rebollarejo Members. Prior to this division, Hafenrichter (1980) had distinguished the Rebosilla facies in the east, with a marly character, and the Rebollarejo facies in the west, with a mainly biomicritic character.

The La Peña and Rebosilla Members are composed of alternating shales, up to 2 cm thick, and marly limestones, varying from 10 to 25 cm in thickness, which consist mainly of thin-bedded packstones rich in pelmatozoans and bryozoans, and a pelmatozoan wackestone. The Ocino Member is made up of calcareous siltstones and shales rich in bryozoans, pelmatozoans and brachiopods. The Rebollarejo Member is characterized by the presence of mud-mound complexes composed of individual lens mounds; each mud-mound complex can reach up to 10 m in thickness and over 300 m in width (Vennin *et al.*, 1998).

The fauna, in order of abundance, consists of echinoderms (Meléndez, 1944, 1959; Meléndez and Hevia, 1947; Chauvel *et al.*, 1975; Chauvel and Le Men, 1979; Gutiérrez-Marco *et al.*, 1996), bryozoans (Hafenrichter, 1979), brachiopods (Villas, 1985), trilobites (Hammann, 1992), ostracodes, gastropods, sponges, cephalopods (Carls, 1975) and conodonts (Carls, 1975; Sarmiento, 2002; Del Moral, 2005).


Upper Ordovician
Hirnantian
lower and middle Ashgill
Orea Fm.
Cystoid Limestone Formation
Fombuena Fm.
Rebollarejo Member
La Peña Member
Alpartir Mb.
0
5
10
Calloporella
Ceramopora
Chasmatopora
Cyclophaenopora
Diplotrypa
Eridotrypa
Glauconomella
Graptodictya
Hallopora
Heterotrypa
Jifarohpora
Kukersella
Matsutrypa
Monticulipora
Orbignyella
Phaenopora
Prasopora
Pseudohornera
Pseudostictoporella
Ulrichostylus
Alternation of marly limestones and shales
Shales
Sandstones with iron oxide cement
Massive limestones
Sandstones

Based on the studies of conodonts (Carls, 1975; Sarmiento, 2002; Del Moral, 2005), brachiopods (Villas, 1985) and trilobites (Hammann, 1992), the Cystoid Limestone Formation is considered as Pusgillian-Rawtheyan in age (Vennin *et at.*, 1998).

Stratigraphy

In the Valdelaparra section the Cystoid Limestone Formation exhibits the typical western facies, where the La Peña and Rebollarejo Members can be recognised. At this exposure the formation is 39 m thick. From the base to the top it is composed sequentially of a bed of sandstones with iron oxide cement 1 m thick, alternating shales and marly limestones, with a total thickness of 10 m, all of which form the La Peña Member, and recrystallized massive limestones, 28 m thick, which make up the Rebollarejo Member (figure 3).

Most of the identified bryozoans come from the La Peña Member. This is due to the fact that a high degree of recrystallization has occurred in the massive limestones, which make up the Rebollarejo Member, and has erased for the most part the necessary diagnostic characters of the bryozoans.

Bryozoans with different growth habits have been found in the La Peña Member. Incrusting, massive and robust branching forms occur in the first 2 m of the member; upwards within the section they give way to more numerous forms with delicate branching, flexible erect and fenestrate growth habits. These latter forms are very fragmented, with the branch fragments arranged parallel to the stratification but with no preferential orientation. Fragmentation degree is considerably less in the robust branching forms, but like the previous ones, the long axes of the branch fragments are parallel to the stratification and likewise display no preferential orientation. Incrusting forms have preferentially grown on brachiopod shells, and bryozoan colonies incrusted by other colonies have also been found.

No mud-mound complexes, which characterize the Rebollarajo Member in other exposures, have been identified in this section due to the extensive diagenetic alteration of the massive limestones. This absence has also precluded observing the distribution of growth habits of colony forms. However, we have been able to observe a predominance of large sized massive forms preserved in life orientation, as well as delicate branching forms, which are less fragmented than in the lower member.

Cystoid Limestone bryozoans

In our analysis of the Upper Ordovician bryozoans of the Iberian Chains, 114 thin sections have been studied. They are stored in the Museo Paleontológico de la Universidad de Zaragoza and labelled with the prefix MPZ. In this preliminary stage of the work, a species-level identification of the bryozoans has not yet been attained in many cases, and the faunal list is given here on a generic level. In spite of this, the results achieved nevertheless effectively reveal the degree of diversification in the associations and their paleobiogeographical relationships.

Twenty genera belonging to the four Stenolaemata orders dispersed worldwide by the Mid Ordovician have been identified in the Valdelaparra section: the cryptostomates *Cyclophaenopora* Spjeldnaes, 1984, *Glauconomella* Bassler, 1952, *Graptodictya* Ulrich, 1882, *Matsutrypa* Gorjunova, 1985, *Phaenopora* Hall, 1851, *Pseudohornera* Roemer, 1876, *Pseudostictoporella* Ross, 1970 and *Urichostylus* Bassler, 1952; the cystoporate *Ceramopora* Hall, 1851; the cyclostomate *Kukersella* Toots, 1952; and the trepostomates *Calloporella* Ulrich, 1882, *Chasmatopora* Eichwald, 1860, *Chasmatoporella* Nekhoroshev, 1936, *Diplotrypa* Nicholson, 1879, *Eridotrypa* Ulrich, 1893, *Hallopora* Bassler, 1911, *Heterotrypa* Nicholson, 1879, *Jifarohpora* Buttler, Cherns and Massa, 2007, *Monticulipora* d'Orbigny, 1850, *Orbignyella* Ulrich and Bassler, 1904 and *Prasopora* Nicholson and Etheridge, 1877. To this list the cystoporate *Ceramoporella* must be added, identified in the La Peña Member of the La Peña del Tormo section, near Fombuena.

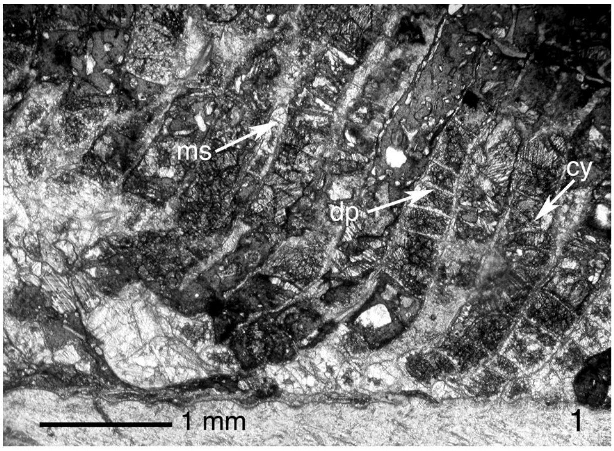
The genera *Chasmatopora*, *Cyclophaenopora*, *Diplotrypa*, *Hallopora*, *Kukersella* and *Matsutrypa*

Figure 3. Stratigraphic column of the Cystoid Limestone Formation at the Valdelaparra section, with the occurrence of the identified genera / *columna estratigráfica de la Formación Calizas de Cistideos en la sección de Valdelaparra, con la localización de los géneros identificados.*

Table 1. Occurrence of bryozoan genera in the Ashgill of the Mediterranean Province. After: **1,** Vinassa de Regny (1910, 1915); **2,** Schmidt (1931) and Spjeldnaes (in Hartevelt, 1970); **3,** this study and Hafenrichter (1979); **4,** Buttler and Massa (1995) and Buttler *et al.* (2007); **5,** Dreyfuss (1948), Boulange (1963) and Ernst and Key (in press); **6,** Termier and Termier (1950) and Destombes *et al.* (1971); **7,** Conti (1990). The circumscribed asterisk indicates the genera identified only in the Iberian Chains / *registro de los géneros de briozoos en materiales ashgillienses en la Provincia Mediterránea. Datos obtenidos de:* ***1,*** *Vinassa de Rengy (1910, 1915);* ***2,*** *Schmidt (1913) y Spjeldnaes (en Hartevelt, 1970);* ***3,*** *este estudio y Hafenrichter (1979);* ***4,*** *Buttler y Massa (1995) and Buttler* et al. *(2007);* ***5,*** *Dreyfuss (1948), Boulange (1963) y Ernst y Key (en prensa);* ***6,*** *Termier y Termier (1950) y Destombes* et al. *(1971);* ***7,*** *Conti (1990). El asterisco dentro del círculo indica los géneros identificados exclusivamente en las Cadenas Ibéricas.*

Mediterranean Regions / Genera	CARNIC ALPS (1)	EASTERN PYRENEES (2)	**IBERIAN CHAIN (3)**	LIBYA (4)	MONTAGNE NOIRE (5)	MOROCCO (6)	SARDINIA (7)
Acanthotrypa	*						
Amplexopora					*		*
Anaphragma							*
Arthropora						*	
Astrovidictya					*		
Atactoporella					*		
Batostoma	*				*?		*
Bythopora					*		*
Calloporella			*		*?		
Ceramophylla							*
Ceramopora	*		*		*		*
Ceramoporella			*		*		*
Chasmatopora			*		*		*
Chasmatoporella		*					
Corynotrypa					*		*
Crassaluna					*		*
Crepipora					*		
Cyclophaenopora			⊛				
Dekayia				*	*	*	*
Diamesopora							*
Dianulites							*
Diplotrypa	*		*		*		*
Dybowskites					*		
Eridotrypa			*		*		*
Fenestella	*						
Fistuliporina				*			
Glauconomella			⊛				
Graptodictya	*	*	*	*	*		*
Hallopora	*	*	*	*	*		*
Hemiphragma					*		*
Heterotrypa			*		*	*?	
Homotrypa		*			*		
Jifarahpora			*	*			
Kukersella			*	*	*		*
Lichenalia					*		
Matsutrypa			*		*		
Mesotrypa					*?		
Monotrypa	*			*	*		
Monotrypella	*						
Monticulipora	*	*	*				
Moorephylloporina					*		*
Nematopora	*				*		*
Nematotrypa					*		
Nicholsonella					*		
Orbignyella			⊛				
Orbipora				*			
Panderpora							*
Papillalunaria							*
Parvohallopora					*		
Phaenopora			⊛				
Ptilodictya		*					
Polypora	*						
Prasopora	*		*		*	*	*
Protocrisina (=*Enallopora*)	*						
Pseudohornera			*		*		
Pseudostictoporella			⊛				
Ptilodictya					*		
Ralfina					*		
Ralfinella					*		
Stellatodictya		*?			*		
Stereodictya							*
Stictoporella					*?		
Stictoporellina					*		
Stigmatella					*	*	*
Trematopora	*				*	*	*
Ulrichostylus			*		*		*

Figure 4. 1 and **2,** ***Orbignyella*** sp. MPZ 2006/110, longitudinal section of a zoarium; mesozooecia (ms) almost absent, diaphragms (dp) and false cystiphragms (cy) that collide with the diaphragms **(1),** and detail of previous zoarium in which the large sizes that acanthostyles (ac) reach can be observed **(2), 3** and **4,** ***Pseudohornera*** sp. **3,** MPZ 2006/105, longitudinal section of a zoarium; acanthostyles (ac) and very marked growth line (gl) on the reverse side. **4,** MPZ 2006/104, cross section of a zoarium in a two-branch point; obverse side with zooecial apertures and reverse side without them. **5, 6** and **7,** ***Pseudostictoporella*** sp., MPZ 2006/106, tangential section of a zoarium; autozooecia (au) with irregular hexagonal boundaries, in some cases separated by polygonal exilazoocia (ex) (**5**), and longitudinal section of previous zoarium, with mesotheca (mst) and superior hemiseptum (sh) (**7**). **6,** MPZ 2006/107, cross section of a zoarium; slightly sinuous mesotheca (mst). **1, 2** and **5-7**: specimens from the Valdelaparra section; **3** and **4**: specimens from the La Peña del Tormo section / **1** y **2, Orbingyella** *sp. MPZ 2006/110, sección longitudinal de un zoario; mesozoecios (ms) muy escasos, diafragmas (dp) y falsos cistifragmas (cy) que se apoyan en los diafragmas inferiores o en otros cistifragmas (**1**), un detalle del zoario anterior donde se observa el gran tamaño de los acantoestilos (**2**).* ***3*** *y* ***4,* Pseudohornera** *sp.* ***3,*** *MPZ 2006/105, sección longitudinal de un zoario; acantoestilos (ac) y líneas de crecimiento (gl) muy marcadas en el reverso.* ***4,*** *MPZ 2006/104, sección transversal de un zoario en un punto de ramificación; el lado frontal con aperturas autozoeciales y el reverso sin ellas.* ***5, 6*** *y* ***7,*** **Pseudostictoporella** *sp. MPZ 2006/106, sección tangencial de un zoario; autozoecios (au) con límites hexagonales irregulares, exilazoecios (ex) poligonales que, en ocasiones, separan a los autozoecios (**5**), y sección longitudinal del zoario anterior donde se observa la mesoteca (mst) y un hemisepto superior (sh) (**7**).* ***6,*** *MPZ 2006/107, sección transversal de un zoario que muestra una mesoteca (mst) ligeramente sinuosa.* ***1, 2*** *y* ***5 - 7,*** *ejemplares de la sección de Valdelaparra;* ***3*** *y* ***4,*** *ejemplares de la sección de La Peña del Tormo.*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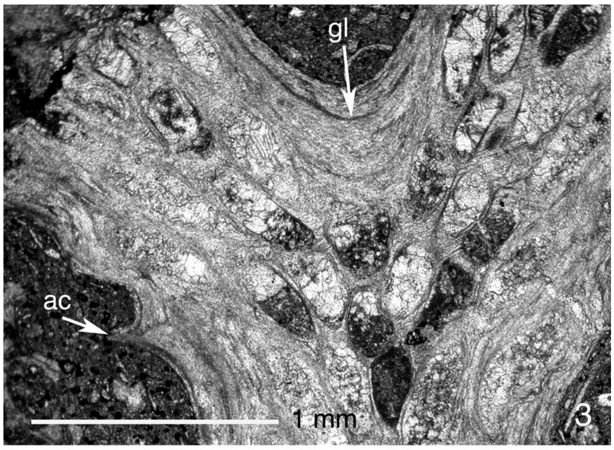
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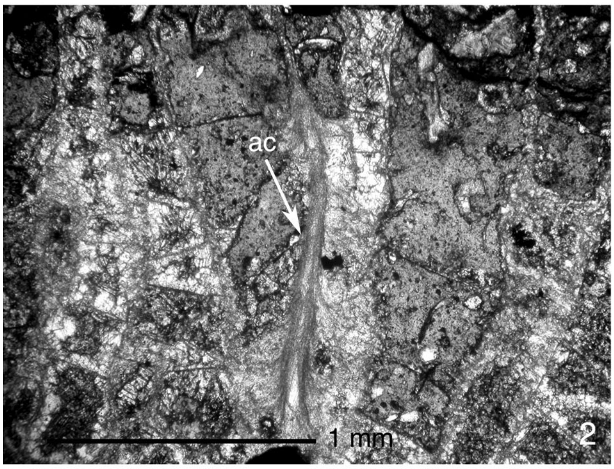
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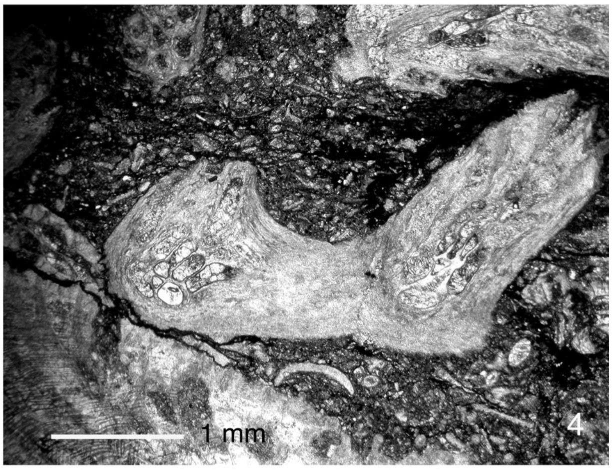
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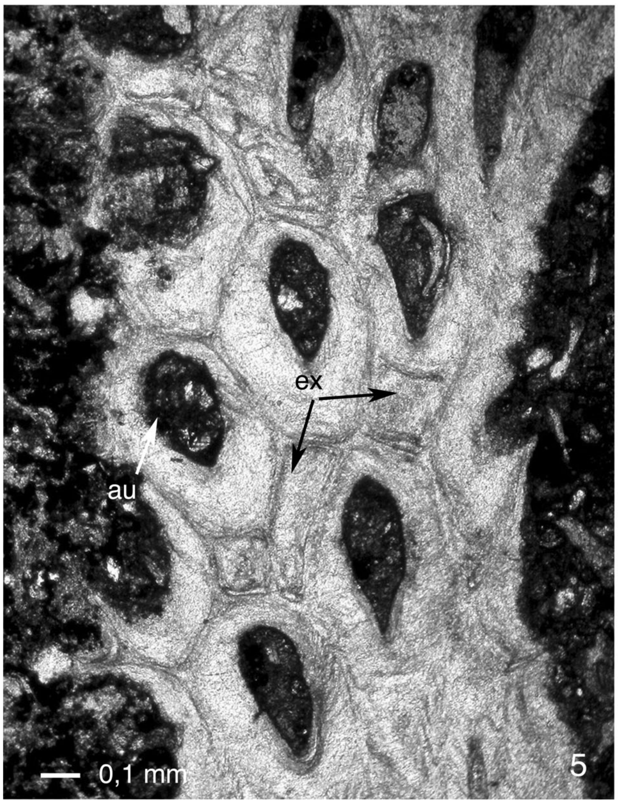
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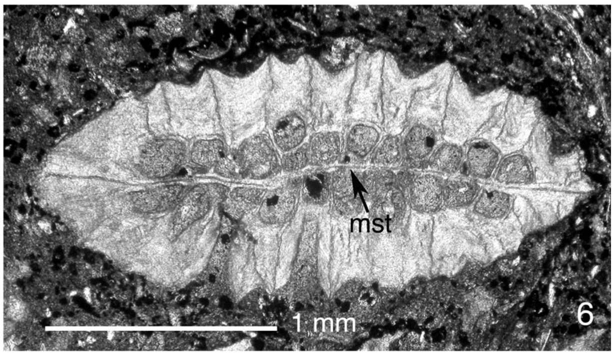
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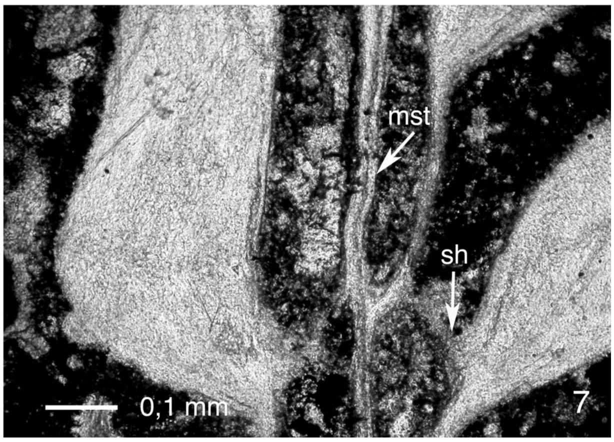
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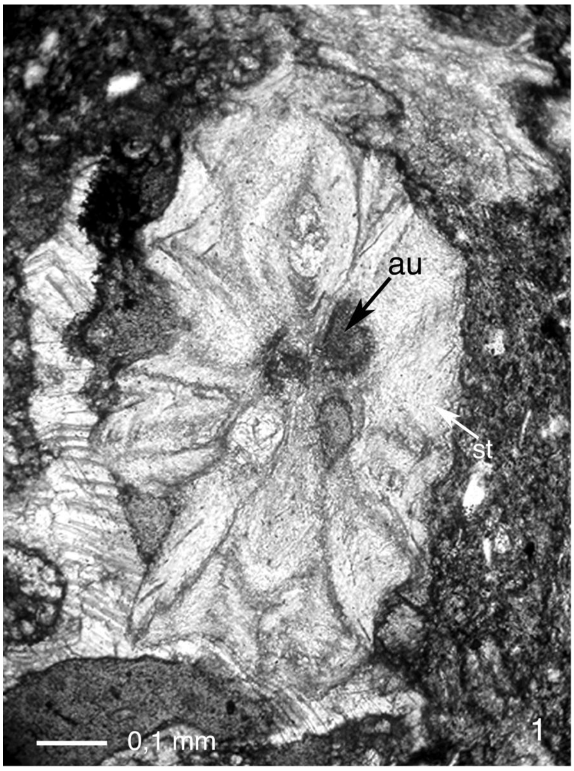
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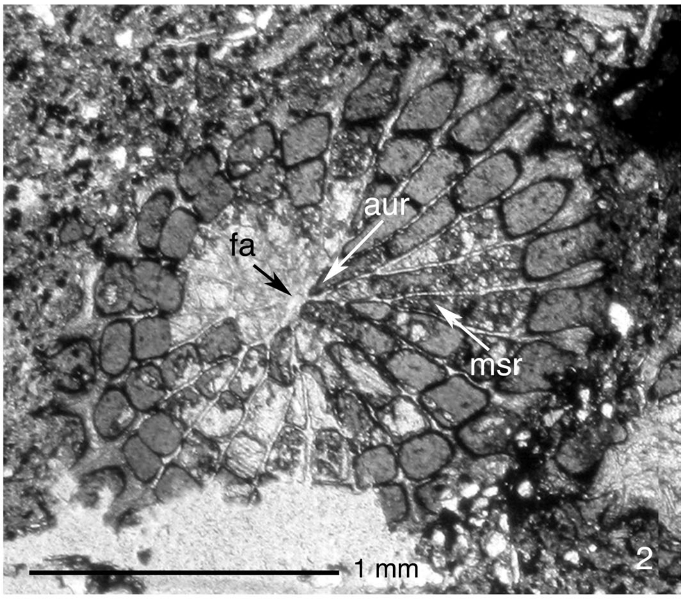
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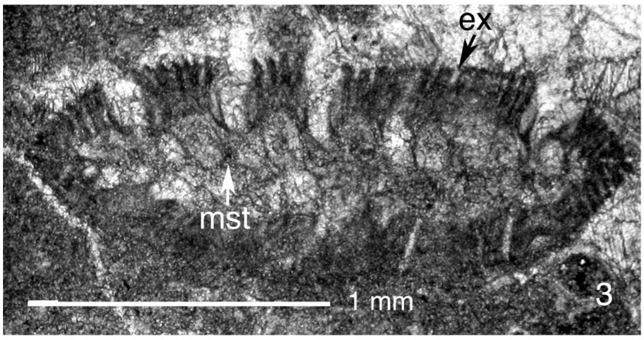
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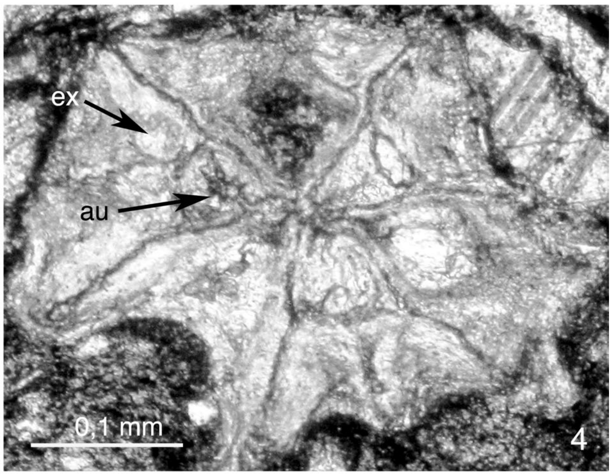
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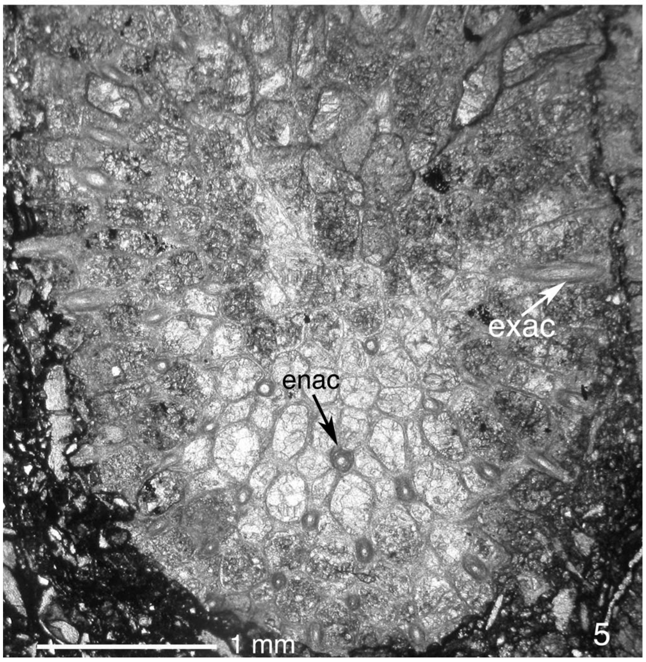
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have been recognized in both the La Peña and Rebollarejo Members (figure 3); of these, *Chasmatopora*, *Hallopora* and *Kukersella* are the most abundant and usually appear together, and in some beds they are accompanied by *Cyclophaenopora*. The genera *Calloporella*, *Ceramopora*, *Eridotrypa*, *Glauconomella*, *Graptodictya*, *Heterotrypa*, *Jifarohpora*, *Monticulipora*, *Orbignyella*, *Prasopora*, *Pseudohornera*, *Pseudostictoporella* and *Ulrichostylus* have been identified only in the La Peña Member; *Pseudohornera* and *Ulrichostylus* are the most abundant here. The genus *Phaenopora* has only been found in the Rebollarejo Member.

The two most frequent associations include the genera *Chasmatopora*, *Hallopora*, *Kukersella*, *Pseudohornera* and *Ulrichostylus* in the La Peña Member, and *Chasmatopora*, *Hallopora*, *Kukersella* and *Cyclophaenopora* in both members.

Five of these genera: *Cyclophaenopora*, *Glauconomella*, *Orbignyella*, *Phaenopora* and *Pseudostictoporella*, have been identified here for the first time in the Mediterranean Province. These, together with the rest of the genera, are illustrated in figures 4 to 8.

In the pre-Ashgill horizons of the Iberian Chains bryozoans are well represented only at the base of the Fombuena Formation (Carls, 1975; Villas, 1985) whose age is mid Caradoc (Soudleyan-Longvillian in the British scale) according to Villas (1992). Though a study of these bryozoans has not yet been made in depth, the association seems to have an extremely low diversity, with only three taxa having been cited in the literature. Two of them are new species described by Meléndez (1944): *Synocladia lluecae* and *Polypora camarensis* which have never been revised after their definition. The former appears in great abundance and could be assigned to the genus *Chasmatopora* according to the emended diagnosis of this genus by Larent'yeva (1985). Besides them, only the genus *Chasmatoporella* has been found, cited by Spjeldnaes (1967).

This apparent low diversity of Caradoc bryozoans, compared with that given above for the Ashgill genera, emphasizes the importance of the biodiversification event, which took place during the Late Ordovician in this region. This diversity peak is also the highest of all the Ordovician for the bryozoans (Taylor and Ernst, 2004) and for most of the marine invertebrate groups throughout the world (Webby *et al.*, 2004). However, the great increase in the number of known bryozoan genera between the Caradoc and the Ashgill in the Iberian Chains (from 3 to 21 genera) could be reduced once an in-depth study on the Caradoc bryozoans is made.

Diversity of the bryozoans in the Mediterranean Region during the Upper Ordovician

Until now, Ordovician bryozoans have been studied in six areas of the Mediterranean Region: the Carnic Alps, Sardinia, Montagne Noire, eastern Pyrenees, Libya and Morocco. In all these cases the described bryozoans are from horizons correlative to the Cystoid Limestone Formation (Villas *et al.*, 2002: fig. 1).

Figure 5. 1 and **4,** ***Matsutrypa*** sp. **1,** MPZ 2006/125, cross section of a zoarium; development of very thick extrazooecial wall material (st), and **4,** MPZ 2006/191, cross section of a zoarium; triangular autozooecia (au) in the endozone, circular exilazoecia (ex) and extrazooecial skeleton strongly developed (st) in the exozone, as well as dark line (dl) marking zooecial boundary and occurring also inside of extrazooecial skeleton. **2,** ***Cyclophaenopora*** sp. MPZ 2006/128, cross section of a zoarium; filiform axis (fa) from which autozooecial rows (aur) radiate and with mesozooecial rows (mzr), placed between them, not radiating directly from the axis. **3,** ***Phaenopora*** sp. MPZ 2006/126, cross section of a zoarium; autozooecia at both sides of the mesotheca (mst) and exilazooecia (ex) between the autozooecial apertures. **5** and **6,** ***Heterotrypa*** sp. MPZ 2006/111, obliqued section of a zoarium; exozonal acanthostyles (exac) and endacanthoslyles (enac) of great diameter (**5**), and longitudinal section of previous zoarium (**6**). All specimens from the Valdelaparra section / **1** y **4** **Matsutrypa** *sp.* **1,** *MPZ 2006/125, sección transversal de un zoario; esqueleto extrazoecial (st) con un gran desarrollo y* **4,** *MPZ 2006/191, sección transversal de un zoario; autozoecios (au) triangulares en la endozona, exilazoecios (ex) circulares y esqueleto extrazoecial (st) con un gran desarrollo en la exozona, así como líneas oscuras (dl) marcando los límites zoeciales y extendiéndose también dentro del esqueleto extrazoecial.* **2,** **Cyclophaenopora** *sp. MPZ 2006/128, sección transversal de un zoario; eje filiforme (fa) a partir del cual radian las hileras de autozoecios (aur); las hileras mesozoeciales (mzr) se sitúan entre la de los autozoecios, pero no radian directamente desde el eje.* **3,** **Phaenopora** *sp. MPZ 2006/126, sección transversal de un zoario; autozoecios a ambos lados de la mesoteca (mst) y exilazoecios (ex) entre las aperturas autozoeciales.* **5** *y* **6,** **Heterotrypa** *sp. MPZ 2006/111, sección oblicua de un zoario; exozonal acantoestilos (exac) y endoacantoestilos de gran diámetro* **(5),** *y sección longitudinal del zoario anterior* (**6**). *Todos los ejemplares de la sección de Valdelaparra.*

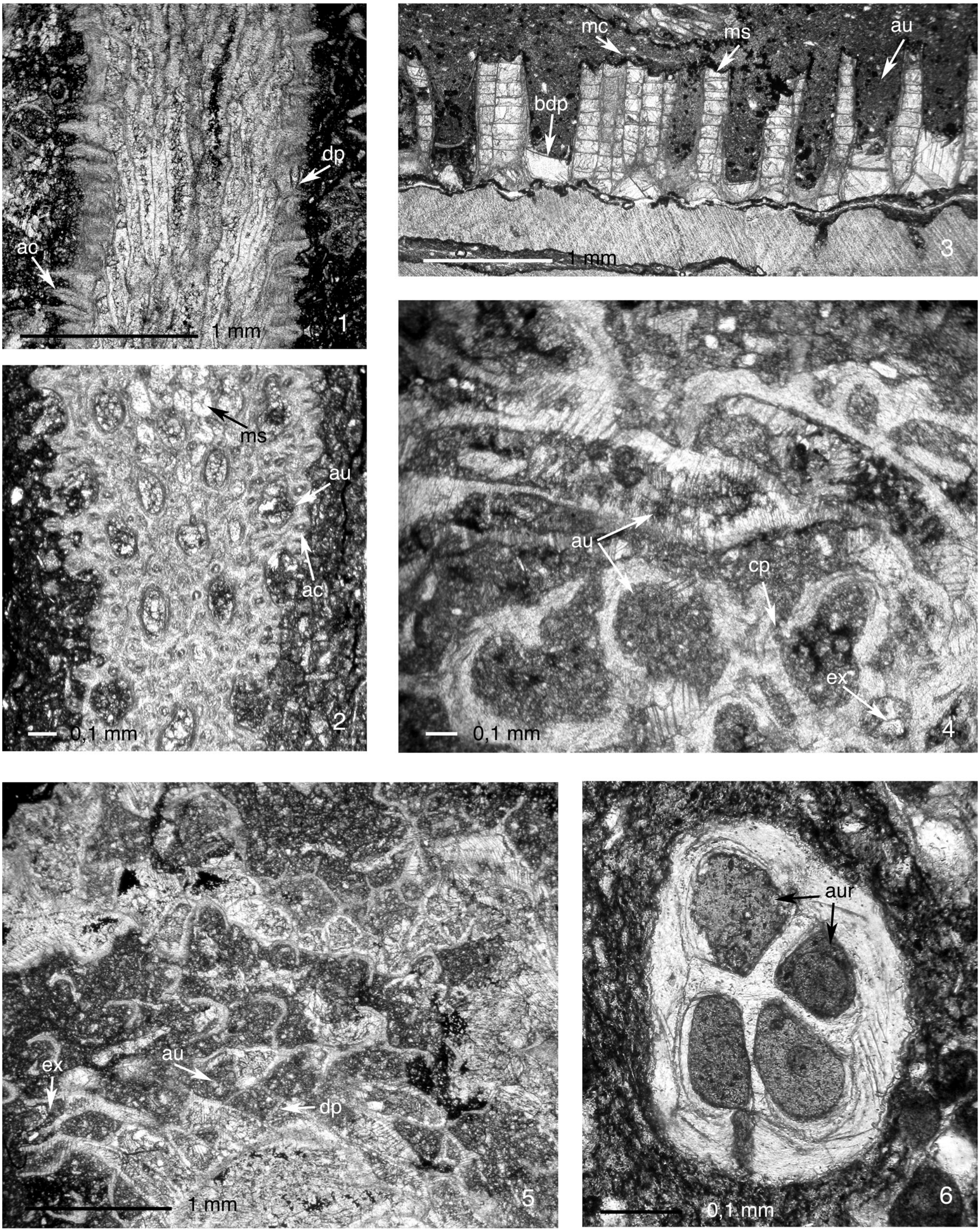


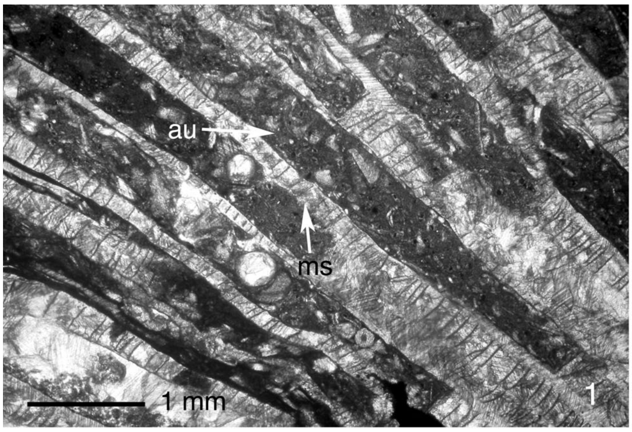
Figure 6. 1 and **2,** ***Jifarohpora*** sp. **1,** MPZ 2006/172, longitudinal section of a zoarium; acanthostyles (ac) protruding from the zoarial surface and autozooecia tabulated by diaphragms (dp). **2,** MPZ 2006/165, tangential section of a zoarium; mesozooecia (ms) grouped forming a macula, some of them also between autozooecia (au), and acanthostyles (ac) modifying the autozooecial apertures. **3,** ***Calloporella*** sp. MPZ 2006/175, longitudinal section of a zoarium; autozooecia (au) with basal diaphragms (bdp) and some mesozooecia (ms)

Vinassa de Regny (1910, 1915) studied the bryozoan fauna of the Carnic Alps identifying 15 genera, of which *Protocrisina* has been synonymized in recent publications with the genus *Enallopora*. Conti (1990), in his study of Sardinian bryozoans, gave an extensive listing with 28 recognized genera. Dreyfuss (1948), Boulange (1963), and Ernst and Key (in press) in their studies on the Montagne Noire, give the most extensive list, with a total of 42 genera. Referring to North Africa, Buttler and Massa (1995) and Buttler *et al.* (2007) recognized 8 genera in carbonate build-ups of Tripolitania (Libya); Termier and Termier (1950) and Destombes *et al.* (1971) identified 6 genera in Morocco. In the eastern Pyrenees Schmidt (1931) and Spjeldnaes (in Hartevelt, 1970) cited 7 genera. To date, as a result of this combined work, 61 Ashgill genera have been identified from North Gondwana.

With the 21 genera identified in this study it is evident that during the Ashgill bryozoans underwent a significant diversification in the region. This initial evaluation of the Cystoid Limestone bryozoans gives diversity figures slightly lower than for other fossil groups in the same formation, such as trilobites or brachiopods, which have 28 genera identified in each group (see Liñán *et al.*, 1996). Nevertheless, they largely exceed the biodiversity reached by echinoderms, with 15 genera (Liñán *et al.*, 1996), and conodonts, with 10 identified genera (Del Moral, 2005). Their diversity is also slightly lower than that of the bryozoans in Sardinia (Conti, 1990), but it adds an important datum because 8 of the genera have been identified here for the first time in the whole Mediterranean Province. This means extending to 66 the number of known bryozoan genera, making it the most diversified group in the region for that period (table 1).

The 21 genera that during the Ashgill dispersed into the carbonate platform represented in the Iberian Chains were mainly of Avalonian-Baltican and Laurentian origin, because they have been recorded in materials older than the Ashgill in these regions. Some have also been identified beyond those palaeocontinents, as in the Altai Sayan, Kazakhstania and Siberia, in older materials than those studied here (Tuckey, 1990). These five palaeocontinents were at tropical positions during the Late Ordovician. Although some of the studied genera could have reached the North Gondwana margin prior to the Ashgill, most of them did it during that time, coinciding with an eustatic rise of sea level and with what has been considered a global warming event (Boucot *et al.,* 2003; Fortey and Cocks, 2005). A detailed analysis of the migration and extinction patterns in the original sites of these bryozoans will allow contrasting the global warming hypothesis with the one that postulates just a local warming of the Mediterranean Region (Villas *et al.*, 2002), and with the hypothesis by Cherns *et al.* (2004) and Cherns and Wheeley (2006) that suggest a cool climate at times of regional or wider lowstand. The suggested amelioration of the local climate would be related to a change in ocean currents, joined to a northward displacement of the Gondwana northern edge (Villas *et al.,* 2002). This displacement agrees with the identification of the Montagne Noire bryozoans as belonging to the North Estonia II Biome

grouped forming a macula (mc). **4,** ***Ceramopora*** sp. MPZ 2006/178; longitudinal and cross section of the same zoarium; autozooecia (au) with communication pores (cp) and exilazooecia (ex) between them. **5,** ***Ceramoporella*** sp. MPZ 2006/179; longitudinal and cross section of the same zoarium; all autozooecia (au) with a single diaphragm (dp) at similar level and exilazooecia (ex) budding between them. **6,** ***Chasmatopora*** sp. MPZ 2006/186, cross section of a zoarium showing four autozooecial rows (aur). **1, 2** and **5**: specimens from the La Peña del Tormo section; **3, 4** and **6**: specimens from the Valdelaparra section / **1** y **2, Jifarohpora** *sp.* **1,** *MPZ 2006/172, sección longitudinal de un zoario; acantoestilos (ac) proyectándose sobre la superficie zoarial y autozoecios tabulados por diafragmas (dp).* **2,** *MPZ 2006/165, sección tangencial de un zoario; mesozoecios (ms) agrupados formando máculas, algunos de ellos también separando autozoecios (au), y acantoestilos (ac) modificando las aperturas autozoeciales.* **3, Calloporella** *sp. MPZ 2006/175, sección longitudinal de un zoario; autozoecios (au) con diafragmas basales (bdp) y grupos de mesozoecios (ms) formando máculas (mc).* **4, Ceramopora** *sp. MPZ 2006/178, sección longitudinal y transversal del mismo zoario; autozoecios (au) con poros de comunicación (cp) y exilazoecios (ex) entre ellos.* **5, Ceramoporella** *sp. MPZ 2006/179, sección longitudinal y transversal de mismo zoario; todos los autozoecios (au) tienen un único diafragma (dp) situado en un nivel similar en autozoecios adyacentes y exilazoecios (ex) desarrollados entre ellos.* **6, Chasmatopora** *sp. MPZ 2006/186, sección transversal de un zoario donde se observan cuatro hileras de autozoecios (aur).* **1, 2** *y* **5**: *ejemplares de la sección de La Peña del Tormo;* **3, 4** *y* **6**: *ejemplares de la sección de Valdelaparra.*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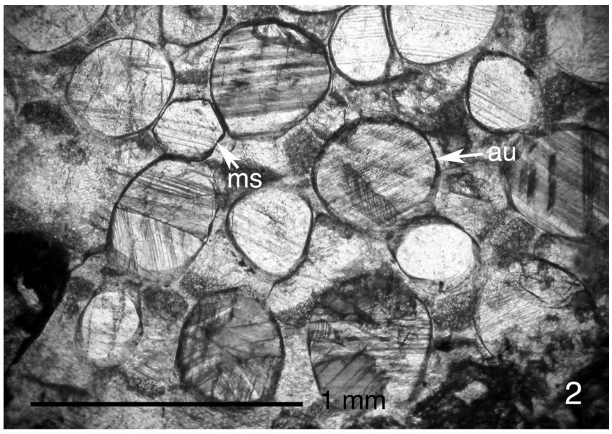
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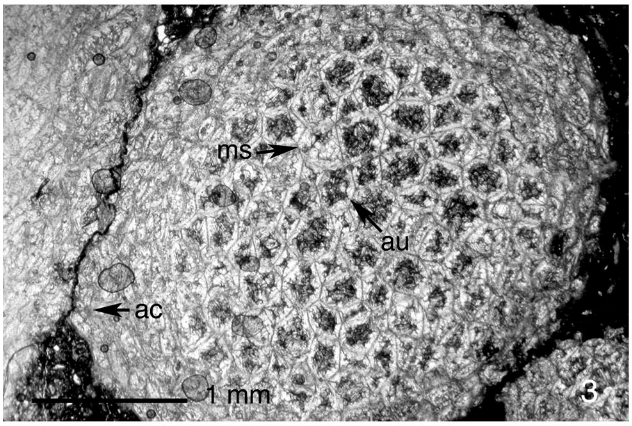
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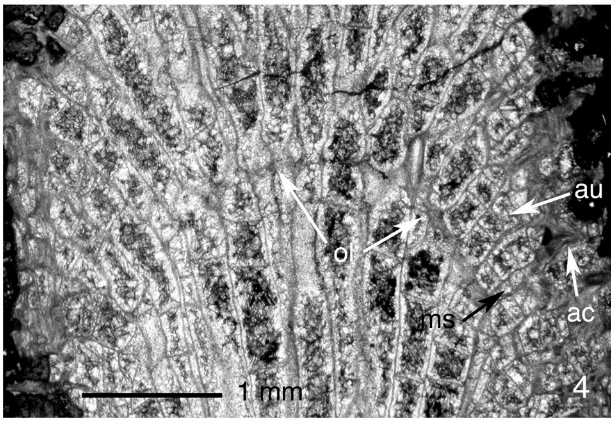
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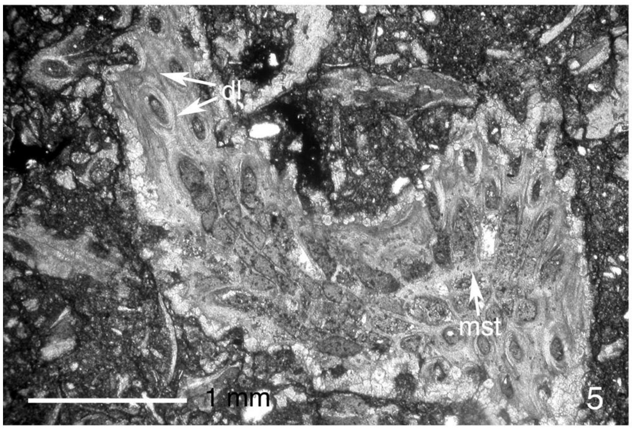
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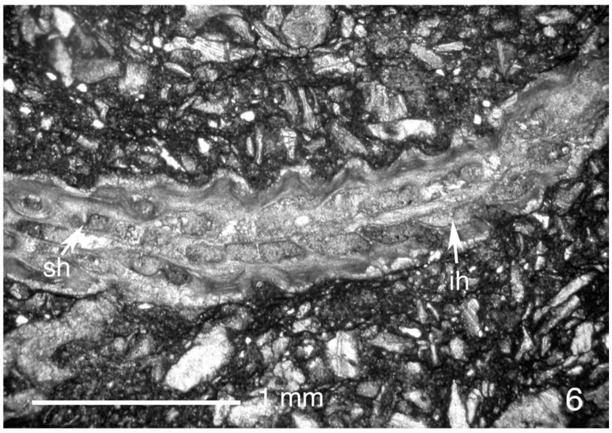
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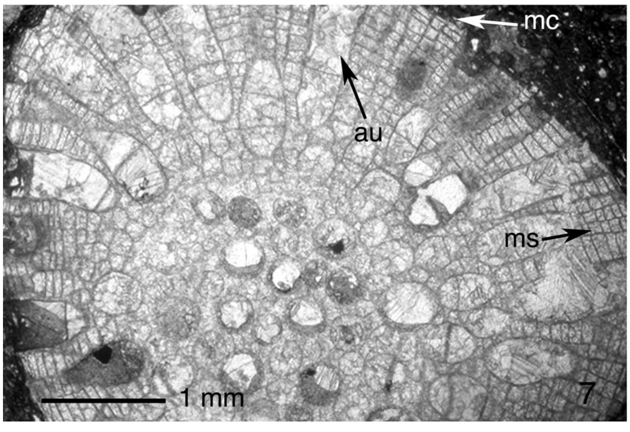
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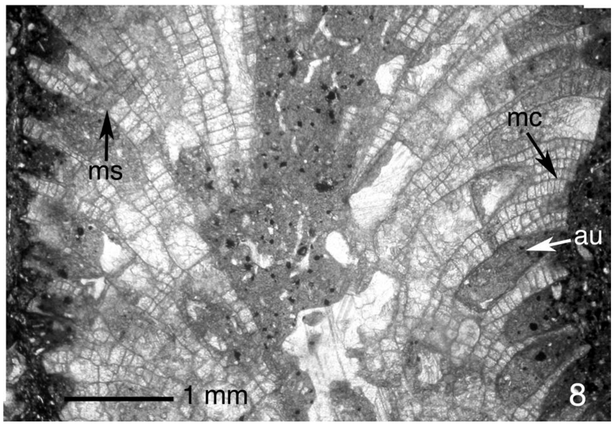
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of the Baltic Province I by Anstey *et al.* (2003); they also suggest that the South of Europe and Baltica should have been close enough to support this affinity between the two faunas.

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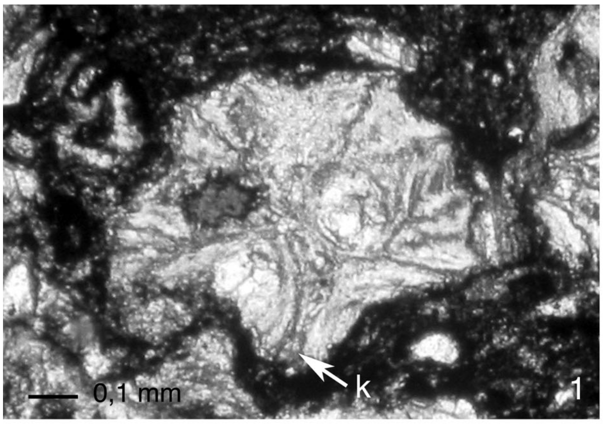
Figure 7. 1 and **2,** ***Diplotrypa*** sp. MPZ 2006/112, longitudinal and cross section of a zoarium; long and narrow mesozooecia (ms) strongly tabulated by diaphragms and autozooecia (au) without them. The endozone-exozone boundary is marked by the budding of autozooecia from mesozooecia **(1)**, and autozooecia (au) and mesozooecia (ms) in cross section **(2)**. **3** and **4,** ***Eridotrypa*** sp. MPZ 2006/188, cross and longitudinal section of the same zoarium; autozooecia (au), mesozooecia (ms) and acanthostyles (ac) in cross section (**3**); autozooecia (au) and mesozooecia (ms) tabulated by diaphragms both in endozone and exozone, and acanthostyles (ac) above overgrowth line (ol) (**4**). **5** and **6,** ***Graptodictya*** sp. MPZ 2006/189, two oblique section of the same zoarium; mesotheca (mst) and dark line (dl) around autozooecial apertures and between autozooecial rows (**5**), and superior (sh) and inferior (ih) hemiseptum (**6**). **7** and **8,** ***Hallopora*** sp. MPZ 2006/190, cross and longitudinal section of the same zoarium; large autozooecia (au) with some diaphragms separated by strongly tabulated mezozooecia (ms) that are also grouped forming maculas (mc) (**7**), and the same elements of the zoarium in longitudinal section (**8**). All specimens from the Valdelaparra section / **1 y 2, Diplotrypa** sp. *MPZ 2006/112, sección longitudinal y transversal del mismo zoario; mesozoecios (ms) largos y estrechos, con una gran densidad de diafragmas (dp), y autozoecios (au) carente de ellos. El límite endozona-exozona se sitúa donde los mesozoecios se transforman en autozoecios* (**1**)*, y autozoecios (au) y mesozoecios (ms) en sección transversal* (**2**)*.* ***3 y 4,*** **Eridotrypa** *sp. MPZ 2006/188, sección transversal y longitudinal del mismo zoario; autozoecio (au), mesozoecios (ms) y acantoestilo (ac) en sección transversal* (**3**)*; autozoecios (au) y mesozoecios (ms) tabulados por diafragmas tanto en la endozona como en la exozona y acantoestilos (ac) por encima de la línea de recrecimiento (ol)* (**4**)*.* ***5 y 6,*** **Graptodictya** *sp, MPZ 2006/189, dos secciones oblicuas del mismo zoario; mesoteca (mst) y líneas oscuras (dl) alrededor de las aperturas autozoeciales y entre las hileras de autozoecios* (**5**)*; hemisepto superior (sh) y hemisepto inferior (ih)* (**6**)*.* ***7 y 8,*** **Hallopora** *sp. MPZ 2006/190, sección longitudinal y transversal del mismo zoario; grandes autozoecios (au) con algunos diafragmas, separados por mesozoecios (ms) densamente tabulados; los mesozoecios también se agrupan formando máculas (mc)* (**7**)*; los mismos elementos en sección longitudinal* (**8**)*. Todos los ejemplares de la sección de Valdelaparra.*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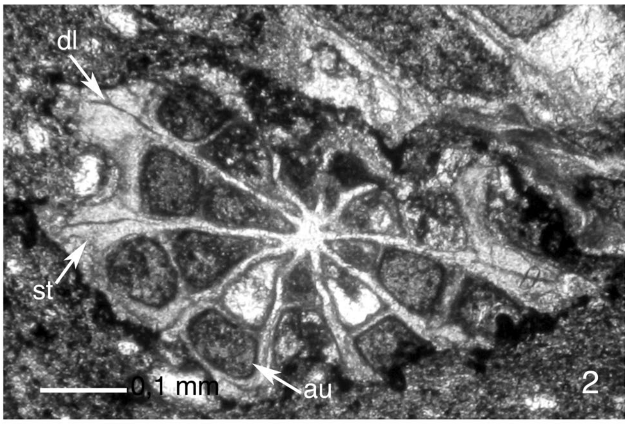
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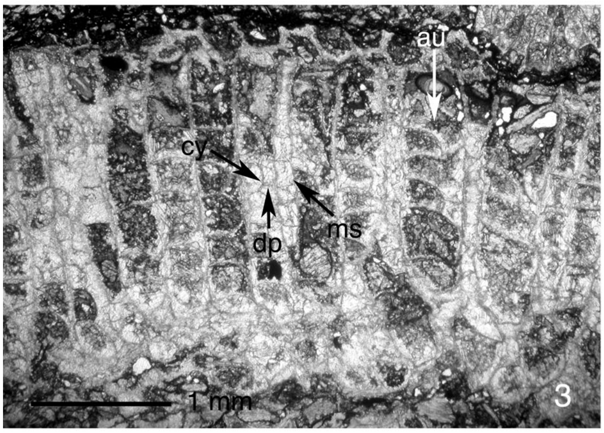
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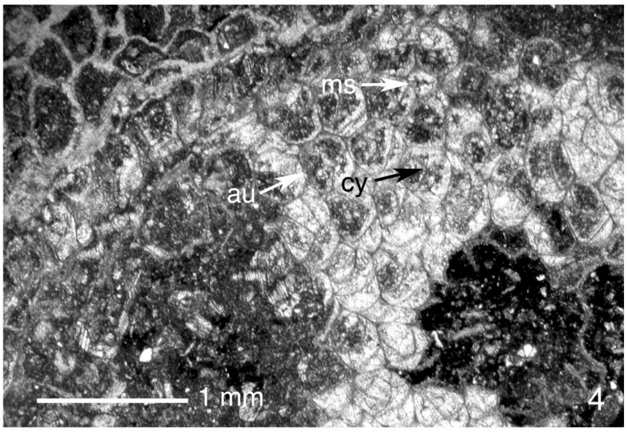
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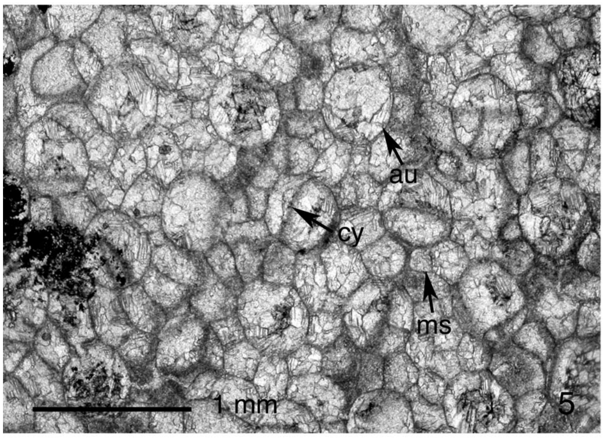
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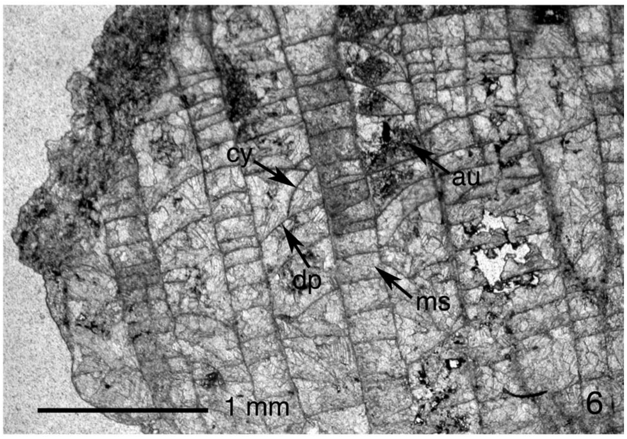
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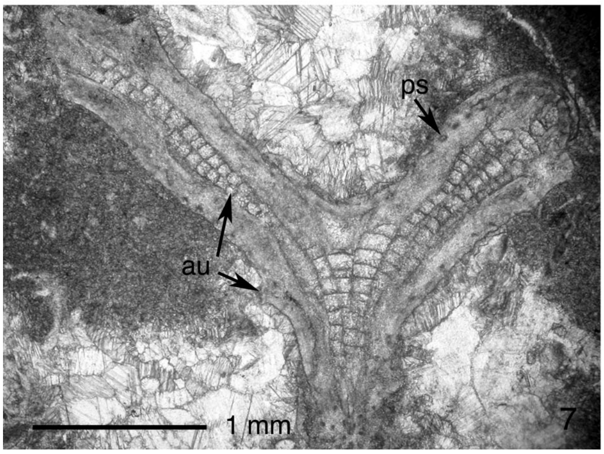
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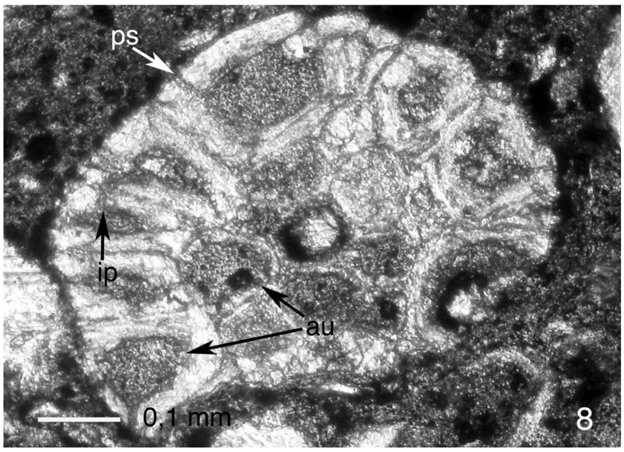
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Figure 8. 1, ***Glauconomella*** sp. MPZ 2006/127, cross section of a zoarium; reverse side rounded without zooecial apertures and obverse side keeled (k) with two front rows of zooecial apertures. **2,** ***Ulrichostylus*** sp. MPZ 2006/192, cross section of a zoarium; triangular autozooecia (au) in the endozone and subelliptical in the exozone; extrazooecial skeleton (st) and dark lines (dl) in the exozone. **3** and **4,** ***Monticulipora*** sp. MPZ 2006/132, longitudinal and cross section of the same zoarium; autozooecia (au) with large cystiphragms (cy), some of them touching the opposite wall; the smaller ones joined to the opposite wall by diaphragms (dp); and narrow mesozooecia (ms) with diaphragms (**3**), autozooecia (au) and mesozooecia (ms) in cross section; most autozooecial apertures are crossed by one or two cystiphragms (cy) (**4**). **5** and **6,** ***Prasopora*** sp. MPZ 2006/99, cross and longitudinal section of the same zoarium; autozooecia (au) and mesozooecia (ms) in cross section; some autozooecial apertures are crossed by one cystiphragm (cy) (**5**); autozooecia (au) with false cystiphragms (cy) leant on oblique diaphragms (dp) and mesozooecia (ms) tabulated by diaphragms (**6**). **7** and **8,** ***Kukersella*** sp. **7,** MPZ 2006/193, longitudinal section of a zoarium; two kinds of autozooecia (au): in endozone with diaphragms and in exozone without them; pseudopores (ps) in autozooecial walls. **8,** MPZ 2006/194, cross section of a zoarium; autozooecia (au) in cross section with pseudopores (ps) and interzooecial pores (ip) in the exozone. **1-4** and **7-8**: specimens from Valdelaparra section; **5** and **6**: specimens from La Peña del Tormo section / **1, Glauconomella** *sp. MPZ 2006/127, sección transversal de un zoario; reverso redondeado y sin aperturas autozoeciales, lado frontal con dos hileras de aperturas autozoeciales y una quilla (k) separándolas.* **2, Ulrichostylus** *sp. MPZ 2006/191, sección transversal de un zoario; autozoecios (au) triangulares en la endozona y subelípticos en la exozona; esqueleto extrazoecial (st) y líneas oscuras (dl) en la exozona.* **3** *y* **4, Monticulipora** *sp. MPZ 2006/132, sección longitudinal y transversal del mismo zoario; autozoecios (au) con grandes cistifragmas (cy), algunos de ellos llegan a tocar el lado opuesto de la pared; los cistifragmas más pequeños se unen a la pared opuesta mediante diafragmas (dp); y estrechos mesozoecios (ms) con diafragmas (*__*3*__*); autozoecios (au) y mesozoecios (ms) en sección transversal; la mayor parte de las aperturas autozoeciales están atravesadas por uno o dos cistifragmas (cy) (*__*4*__*).* **5** *y* **6, Prasopora** *sp. MPZ 2006/99, sección transversal y longitudinal del mismo zoario; autozoecios (au) y mesozoecios (ms) en sección transversal; algunas aperturas autozoeciales están atravesadas por un cistifragma (cy) (*__*5*__*); autozoecios con falsos cistifragmas (cy) que se apoyan en los diafragmas o en otros cistifragmas inferiores y mesozoecios (ms) tabulados por diafragmas (*__*6*__*).* **7** *y* **8, Kukersella** *sp.* **7,** *MPZ 2006/193, sección longitudinal de un zoario; dos clases de autozoecios (au): en la endozona con diafragmas y en la exozona sin ellos; pseudoporos (ps) en las paredes autozoeciales.* **8,** *MPZ 2006/194, sección transversal de un zoario; autozoecios (au) con pseudoporos (ps) y poros interzoeciales (ip) en la exozona.* **1-4** *y* **7-8***: ejemplares de la sección de Valdelaparra;* **5** *y* **6***: ejemplares de la sección de La Peña del Tormo.*

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