New Monticuliporidae (Bryozoa, Trepostomata) from the Cystoid Limestone Formation (Upper Ordovician) of the Iberian Chains (NE Spain)

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ABSTRACT
Bryozoans are among the most abundant fossil groups in the cool water limestones that characterize the uppermost Katian (Upper Ordovician) of Southwestern Europe and North Africa. The Cystoid Limestone Formation, the representative unit of those widespread rocks in the Iberian Chains (NE Spain), yields one of the most diversified bryozoan faunas of the whole area. Herein the first systematic description of the trepostomate family Monticuliporidae is undertaken, this is one of the most diverse families within the associations collected. Four species of the genera Monticulipora and Prasopora are described, including the new species Monticulipora cystiphragmata n. sp. and Prasopora spjeldnæsii n. sp., and an indeterminate Monticuliporidae. Monticulipora and Prasopora have shown to be very similar genera, with several species that are difficult to distinguish between them. Their diagnoses include common features such as the wall microstructure, density of mesozooecia, and number of acanthostyles. Herein a new generic diagnosis of Monticulipora is proposed, putting special emphasis on the shape and distribution of cystiphrags. The species Monticulipora kolaluensis is identified for the first time out of Siberia. Although the record of these new taxa can indicate a certain isolation of the Iberian Chains region within the North Gondwana platform, the occurrence of Prasopora carnica shows a relation to the neighbouring Carnic Alps (Italy and Austria).

KEY WORDS
Bryozoa, Trepostomata, Monticuliporidae, Upper Ordovician, Cystoid Limestone Formation, Iberian Chains, new species.
INTRODUCTION

Bryozoans are among the most abundant fossil groups in the cool water limestones that characterize the uppermost Katian (Upper Ordovician) of Southwest Europe and Northern Africa. These are remnants of the northern Gondwana margin, which formed at paleolatitudes of 45-60°S (Vennin et al. 1998; Cocks & Torsvik 2002). Limestone deposition was rare during the Ordovician on the northern Gondwana platforms, with the only exception of the latest Katian times, immediately before the onset of the Hirnantian glaciation and coinciding with what has been called the Boda Event (Fortey & Cocks 2005).

By that time those platforms suddenly increased carbonate production, with the development of pelmatozoan-bryozoan meadows in mid-ramp setting and occasionally mud-mounds on the outer ramp (Vennin et al. 1998). These buildups were made up mainly by robust- and fragile-branching, and encrusting bryozoans associated with cystoid and crinoids (Jiménez-Sánchez et al. 2007). Both biofacies are devoid of microbialites, calcareous algae or corals and were compared by Vennin et al. (1998) with the bryomol faunas of Nelson et al. (1988), typical of temperate cool water carbonates in recent seas.

The Cystoid Limestone Formation of the Iberian Chains (NE Spain) is one of the units where carbonate productivity and associated late Ordovician organisms are best developed in the whole northern Gondwana margin. It has yielded one of the most diversified faunas of the area (Lifán et al. 1996) with the bryozoans revealing one of the highest species richness, along with trilobites and brachiopods (Jiménez-Sánchez et al. 2007). Bryozoans are the most diversified northern Gondwanan groups during the pre-Hirnantian (late Ordovician) and played a leading role in its shelly carbonate factories (Vennin...
et al. 2004). In spite of their importance, only a few detailed modern systematic studies on the bryozoans have been focused on the late Ordovician carbonate platforms of North Gondwana, particularly in Sardinia (Conti 1990), Libya (Buttler et al. 2007) and the Montagne Noire (Ernst & Key 2007). This work aims systematically to describe the late Ordovician bryozoans from the Iberian Chains, focusing on the trepostomate family Monticuliporidae, one of the most diverse within the associations.
A preliminary study of the bryozoan associations and one complete systematic description of the bryozoan fauna from the Cystoid Limestone Formation have been presented by Jiménez-Sánchez et al. (2007) and Jiménez-Sánchez (2009).

The material studied in the present work is deposits in the Museo Paleontológico de Zaragoza (MPZ), University of Zaragoza, Spain (numbers MPZ 2006/99, 2006/109, 2006/110, 2006/113, 2006/132, 2006/133, 2006/134).

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

Although there are abundant outcrops of the Cystoid Limestone Formation throughout the Iberian Chains (Hafenrichter 1980; Villas 1985; Hammann 1992), most are recrystallized, becoming totally or partially dolomitized (Carls 1975) as well as intensively ferruginized in its lowermost horizons. These alterations preclude a detailed study of the bryozoans in most of the Cystoid Limestone Formation outcrops. The only exception has been some horizons of the La Peña del Torno and the Valdelaparra sections, described below. Nevertheless, even at these localities, it was not possible to obtain a number of adequately preserved samples, enough to get a complete assessment of the variability of many of the identified species, in spite of extensive collections during five field trips in 2004 and 2005, and resulting in more than 200 thin sections and a almost a thousand polished sections. An additional problem has been the difficulty to get isolated zoaria, since they are usually firmly cemented in hard matrix. As a consequence, it is difficult to get to a complete knowledge of the external shape and growth habit of many of the zoaria. Even more, it makes it extremely difficult to obtain orientated thin sections of the smallest zoaria.

The fauna described here was collected from the Cystoid Limestone Formation at outcrops in Valdelaparra and La Peña del Torno. Both are located in the Eastern Iberian Chain (NE Spain) within the municipality of Fombuena (Zaragoza province). The Valdelaparra section is situated 2.6 km northwest of the village of Fombuena, in the gully of La Peña del Torno and close to the Valdelaparra Fountain (Fig. 1). The La Peña del Torno section is situated 600 m west of the same village, south of the Badules-Luesma local road (Fig. 1).

The Cystoid Limestone Formation displays a maximum thickness of 50 m in its westernmost outcrops, 25 m in the east and it is geographically restricted to the eastern Iberian Chain. Four members (Ocino, Rebosilla, La Peña and Rebollarejo) were distinguished in this formation by Hammann (1992) in order to characterize vertical and lateral lithofacies changes. Based on conodonts (Carls 1975; Sarmiento 2002; Del Moral 2005), brachiopods (Villas 1985) and trilobites (Hammann 1992), this formation is considered as upper Katian (mid Ashgill) in age.

A detailed description of the Cystoid Limestone Formation can be found in Villas (1985), Hammann (1992), Vennin et al. (1998) and Jiménez-Sánchez et al. (2007).

In the two studied sections, only the La Peña and the Rebollarejo members are recognized. In the Valdelaparra section the formation is 39 m thick. From the base to the top it is composed of one-meter thick bed of sandstone with iron oxide cement, followed by alternating marly limestones and shales, with a total thickness of 11 m, all of which form the La Peña Member. It is overlain by 28 m of recrystallized massive limestones, making up the Rebollarejo Member (Fig. 2A). Bryozoans with different growth habits occur in the La Peña Member. Incrusting, massive and robust branching forms are found in the basal 2 m of the member; upwards within the section they are gradually replaced by more numerous forms with delicate branching, flexible erect and fenestrate growth habits. All the latter forms are fragmented, with branch fragments placed parallel to the bedding, but without preferential orientation. Robust branching forms are less fragmented, and their long axes lay parallel to the bedding, with no preferential orientation. Incrusting forms have preferentially grown on brachiopod shells and other bryozoan colonies. In the Rebollarejo Member the degree of recrystalization is higher...
than in the La Peña Member, but more large sized massive forms preserved in life orientation can be observed (Vennin et al. 1998), as well as delicate branching forms, which are less fragmented than those in the La Peña Member. All bryozoans described here, except Prasopora spjeldnaesi n. sp., not recorded in this locality, occur in the first two meters of alternating marly limestones and shales of the La Peña Member in the Valdelaparra section.

In the La Peña del Tormo section (Fig. 2B), the La Peña Member has yielded Prasopora spjeldnaesi n. sp. This member is poorly exposed, cropping out averagely 25 cm, but it displays a similar lithology (marly limestones alternating with thin shale beds) and bryozoan record (growth habit and fragment orientation) as in the Valdelaparra section. The Rebollarejo Member is formed by a series of mud-mound complexes composed of individual lenticular mounds with a range of 0.2 to 1.8 m high and 0.4 to 6.0 m wide (Vennin et al. 1998). The degree of recrystalization of these mud-mounds is extensive, but massive colonies (up to 20 cm in diameter and 10 cm in height) preserved in life position can be observed within them (Vennin et al. 1998).

**TAXONOMIC REMARKS**

In the Cystoid Limestone Formation, 29 species of Bryozoa have been identified; 55% of them belong to Trepostomata, 35% to Cryptostomata, 7% to Cystoporata and 3% to Cyclostomata. The trepostome family Monticuliporidae is one of the most diverse although it is represented by a reduced number of zoaria. This family is one of the oldest Trepostomata families in the fossil record, including the genus Monticulipora d’Orbigny, 1850 known since Floian times (Early Ordovician), the age in which the first bryozoans are reported (Ernst et al. 2007), and no member of the family is recorded after the late Silurian (Modzalevskaya 1978; Hu & Wang 1983). This family displayed a very wide geographic distribution, most genera being cosmopolitans (Tuckey 1990). Members of the family Monticuliporidae are characterized by having incrusting, ramose, frondescent, or massive zoaria, with usually regularly spaced monticles. The main internal shared diagnostic characters are polygonal or subpolygonal autozooecial apertures and presence of cystiphragms and diaphragms. Densely tabulated mesozooecia and acanthostyles can also be present in some of its most characteristic genera.

Four species of two genera belonging to this family have been identified in the Cystoid Limestone Formation: Monticulipora cystiphragmata n. sp., Monticulipora kolaluensis Jaroshinskaja.
1962, Prasopora carnica Vinassa de Regny, 1915 and Prasopora spjeldnaesi n. sp., besides one monticuliporid left in open nomenclature.

Monticulipora has been previously described in upper Katian horizons from the eastern Pyrenees, Spain (Schmidt 1931), and from the Carnic Alps, Italy and Austria (Vinassa de Regny 1910, 1915). Prasopora Nicholson & Etheridge, 1877 has much wider geographical distribution in the Mediterranean region, reported in the Montagne Noire, Carnic Alps and Sardinia, always in correlative horizons to the Cystoid Limestone Formation (Villas et al. 2002).

The two Monticulipora species described in this paper have few mesozooecia and lack cystiphrags and diaphragms in the outer exozone, but with different microstructure of the zooecial wall (laminated vs granular). The two Prasopora species described have abundant mesozooecia, but one of them having approximately at the same depth within the colony two clearly different zones, one of them with autozoecia completely surrounded by mesozooecia, and the other one with mesozooecia located in the corners of some autozoecia. The extensive area of this colony shown in thin section rules out the possibility that this unequal distribution of mesozooecia is a consequence of maculae.

Herein I propose an emended diagnosis of Monticulipora not considering the microstructure of the wall as a valid diagnostic character, although a revision of those Prasopora species with a low number of mesozooecia will be necessary, checking if this character is present in the whole colony.

**SYSTEMATIC PALEONTOLOGY**

Order TEREPOSTOMATA Ulrich, 1882

Family MONTICULIPORIDAE Nicholson, 1881

Genus Monticulipora d’Orbigny, 1850

Type species. — Monticulipora mammulata d’Orbigny, 1850; Upper Ordovician of Ohio.

Emended diagnosis. — Genus characterized by a massive growth habit formed by multiple layers, but frondescent or branching habits can be present; autozoecia with polygonal or subpolygonal apertures, less commonly subcircular; with simple cystiphrags larger in endozone than in inner exozone; autozoecial diaphragms join cystiphrags to the opposite wall; mesozooecia not abundant, located in autozoecial corners and monticules, and densely tabulated by diaphragms; acanthostyles mainly developed in exozone; monticules present and formed by mesozooecia and autozoecia larger than those in the intermonticular area.

**DISCUSSION**

Astrova (1978) characterized Monticulipora as having autozoecia with polygonal apertures, numerous cystiphrags and diaphragms in all autozoecia, few mesozooecia, presence of acanthostyles, and zooecial walls with granular microstructure. Ross (1967) had described Prasopora as having autozoecia with rounded or subpolygonal apertures, isolated and superimposed autozoecial diaphragms and cystiphrags, abundant closely spaced mesozooecia, and sporadic acanthostyles. According to Astrova (1978) these two genera are similar, but can be distinguished because Monticulipora has fewer mesozooecia, walls with granular microstructure, and cystiphrags always attached to the wall side nearest to the maculae. However, after a detailed study of the species assigned to these genera, I have observed no clear separation between them as these characters used by Astrova (1978) to distinguish between these genera are mixed up in some species. Prasopora fritzae Loeblich, 1942, from the Upper Ordovician of Oklahoma, Monticulipora mammulata d’Orbigny, 1850, as described by Singh (1979) from the Upper Ordovician of Indiana and Kentucky, and by Boardman & Utgaard (1966) in the Upper Ordovician of Ohio, and finally Monticulipora parallela McKinney, 1971 (Middle Ordovician of Alabama), were all characterized as having the same laminated-granular microstructure wall.

In spite of Astrova’s (1978) assertion of the scarcity of mesozooecia in Monticulipora, some of its species have mesozooecia in similar densities to Prasopora. Even more, some species assigned to Prasopora have fewer mesozooecia per mm² than Monticulipora cystiphragmata n. sp. or Monticulipora epidermata Ulrich & Bassler, 1904 (as was described by Utgaard & Perry [1964] in the Upper Ordovician from Indiana and Ohio) for example...
Prasopora fritzae, P. prismatica Fritz, 1957, P. similis Fritz, 1957 (the two last species from the Middle Ordovician of Ottawa), P. fistuliporides Vinassa de Regny, 1910 (Upper Ordovician from Sardinia [Italy], Conti [1990]), and P. thorali Prantl, 1940 (Upper Ordovician from Wales, Buttler [1991]). Nevertheless, the same Prasopora colony can have a variable number of mesozooecia in different parts or at different depth of the zoarium. But some of these differences in mesozooecia density, of the species mentioned above, could be due to incomplete measurements.

It seems that the most constant character in Monticulipora is the arrangement of cystiphragms around maculae, but still there are some species that do not follow this. In this study most of the Monticulipora species recognized have neither cystiphragms nor diaphragms in the outer exozone, and the former are bigger in the inner endozone. However, this character is not persistent in all species, because the following ones have been described as having diaphragms, and sometimes cystiphragms, throughout the autozooecial: Monticulipora epidermata Ulrich & Bassler, 1904 as described by Utgaard & Perry (1964) from the Middle Ordovician of Indiana and Ohio, and by Brown & Daly (1985) in the Upper Ordovician from Indiana; Monticulipora multipora Dyer, 1925 as described by Utgaard & Perry (1964), also in the Middle Ordovician from Indiana and Ohio, and by Fritz (1976) in the Upper Ordovician from Ontario and Toronto; and Monticulipora grandis Ulrich, 1886, as described by Bork & Perry (1968) in the Middle Ordovician from Illinois, Iowa and Wisconsin. One of these species, Monticulipora grandis, has been alternatively assigned to Monticulipora and Prasopora (Nickles & Bassler [1900] assigned it to Prasopora, and Bork & Perry [1968] assigned it back to Monticulipora).

After a comprehensive review of the type species of Monticulipora and Prasopora (Monticulipora mammulata as described by Ulrich [1882], Boardman & Utgaard [1966], Singh [1979], and Brown & Daly [1985], and Prasopora grayae as described by Nicholson & Etheridge [1877] and by Buttler [1991]) and of a large number of species belonging to these genera it is concluded that Monticulipora has fewer mesozooecia, more polygonal autozooecial apertures and simpler cystiphragms (isolated cystiphragms or cystiphragms forming a single row) than Prasopora. Cystiphragms and diaphragms in the endozone and the inner exozone, as well as acanthostyles are common to almost all Monticulipora species, while in Prasopora cystiphragms and diaphragms are equally distributed in the autozooecia, and acanthostyles are rare.

### Table 1

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthostyle diameter (in mm)</td>
<td>0.015-0.060</td>
<td>0.030</td>
<td>0.005</td>
<td>30</td>
<td>3</td>
</tr>
<tr>
<td>Autozooecial angle with basal colony surface</td>
<td>28-35°</td>
<td>32°</td>
<td>3</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Autozooecial angle with exterior colony surface</td>
<td>78-87°</td>
<td>84°</td>
<td>3</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>Autozooecial wall thickness in exozone (in mm)</td>
<td>0.005-0.030</td>
<td>0.014</td>
<td>0.006</td>
<td>48</td>
<td>3</td>
</tr>
<tr>
<td>Intermacular autozooecial diameter (in mm)</td>
<td>0.20-0.42</td>
<td>0.30</td>
<td>0.07</td>
<td>68</td>
<td>3</td>
</tr>
<tr>
<td>Macular autozooecial diameter (in mm)</td>
<td>0.36-0.48</td>
<td>0.43</td>
<td>0.04</td>
<td>38</td>
<td>2</td>
</tr>
<tr>
<td>Mesozooecial macular and intermacular diameter (in mm)</td>
<td>0.07-0.18</td>
<td>0.11</td>
<td>0.02</td>
<td>71</td>
<td>3</td>
</tr>
<tr>
<td>Number of acanthostyles per mm²</td>
<td>2.5-5.5</td>
<td>4.0</td>
<td>1.2</td>
<td>18</td>
<td>2</td>
</tr>
<tr>
<td>Number of autozooecia per mm</td>
<td>0.5-5.0</td>
<td>2.9</td>
<td>0.2</td>
<td>212</td>
<td>3</td>
</tr>
<tr>
<td>Number of autozooecial cystiphragms per mm</td>
<td>2.0-6.0</td>
<td>4.0</td>
<td>0.5</td>
<td>41</td>
<td>3</td>
</tr>
<tr>
<td>Number of autozooecial diaphragms per mm</td>
<td>0.0-7.0</td>
<td>2.0</td>
<td>1.2</td>
<td>23</td>
<td>3</td>
</tr>
<tr>
<td>Number of autozooecia per mm²</td>
<td>7.5-11.5</td>
<td>9.2</td>
<td>1.2</td>
<td>60</td>
<td>3</td>
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<tr>
<td>Number of mesozooecial diaphragms per mm</td>
<td>5.0-8.0</td>
<td>6.0</td>
<td>0.3</td>
<td>15</td>
<td>3</td>
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<tr>
<td>Number of mesozooecia per mm</td>
<td>0.0-5.0</td>
<td>1.0</td>
<td>0.2</td>
<td>212</td>
<td>3</td>
</tr>
<tr>
<td>Number of mesozooecia per mm²</td>
<td>2.5-18.5</td>
<td>7.0</td>
<td>3.6</td>
<td>60</td>
<td>3</td>
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</table>
FIG. 3. — A-D, Monticulipora cystiphragmata n. sp.; A, C, longitudinal thin sections of the holotype (MPZ 2006/134) and paratype (MPZ 2006/132), respectively, showing the autozooecia (az), the large cystiphragms (cy) joined in some cases to the opposite wall by diaphragms (dp), and the narrow mesozooecia (mz); B, D, tangential thin sections of the holotype and the same paratype as in C showing square and triangular mesozooecia (mz) in B, and the cystiphragms (cy) cross sections inside autozooecial (az) sections in D; E, F, Monticulipora kolaluensis Jaroshinskaja, 1962, MPZ 2006/109; E, longitudinal thin section showing the stylolitic contact with another monticuliporid bryozoan; F, tangential thin section showing the macular autozooecia (maz), the mesozooecia (mz), the acanthostyles (ac) in the common vertex of three autozooecia, and a cross section of a cystiphragm (cy) inside an autozooecial (az) section. Scale bars: 1 mm.
Monticulipora cystiphragmata n. sp.
(Figs 3A-D; 4; Table 1)

Monticulipora sp. – Jiménez-Sánchez et al. 2007: 694, fig. 8 (3-4).

**Type Material.** — One colony, holotype (MPZ 2006/134).

**Etymology.** — Refers to the large globular cystiphragms occurring in all autozooecia.

**Material Examined.** — Three colonies (MPZ 2006/132-134).

**Type Horizon.** — La Peña Member of the Cystoid Limestone Formation, Upper Ordovician.

**Type Locality.** — Valdelaparra section (Zaragoza, Spain).

**Stratigraphic and Geographic Range.** — Monticulipora cystiphragmata n. sp. is only known from its type locality, at the La Peña Member of the Cystoid Limestone Formation in the Valdelaparra section (Zaragoza, Spain).

**Diagnosis.** — *Monticulipora* characterized by a lens-shaped zoarium composed of only one layer, by the presence of large globular cystiphragms in the endzone that tangentially touch the opposite autozooecial wall to which they are attached, and by their centrifugal arrangement, always attached to the farthest autozooecial wall from the center of the colony, and arrangement not related with maculae.

**Description**

**General Characters**
Zoarium lens-shaped, composed of a single layer. Upper zoarial surface convex and lower one concave. The holotype zoarium is 3.60 mm high in the central part, 2.25 mm high in the extremes, and 6.50 mm in diameter. Specimen MPZ 2006/132 encrusts a zoarium of *Ceramopora* sp.

**Tangential Section**
Autozooecial apertures regularly or irregularly hexagonal, some of them irregularly pentagonal, with an average diameter of 0.30 mm. Intermacular autozooecia usually separated by a pair of small mesozooecia. Maculae composed of either a small group of mesozooecia surrounded by autozooecia or by a group of densely packed autozooecia with some mesozooecia between them. In monticular area autozooecial apertures have an average diameter of 0.43 mm. In total, including both macular and intermacular areas, nine complete autozooecia are spaced per mm² and 2.9 autozooecia per mm. In deep tangential sections all autozooecial cross sections have one or two curved cystiphragms inside, changing the form and size of the autozooecial aperture and reducing its space up to 75%. Shape of mesozooecial apertures changes according to the level in the colony. In intermacular areas, one or two pairs of square or triangular-shaped mesozooecia are in contact with one or two autozooecial sides (Fig. 4). In macular areas, mesozooecia form either small groups located in the center of a group of autozooecia or are distributed between several autozooecia. In this area, mesozooecia are more abundant and, when forming small groups, their apertures are more irregular. Their average diameter is 0.11 mm, with seven complete mesozooecia per mm² and one complete mesozooecium per linear mm. The difference between the area and linear density is due to differences in the size and shape of the mesozooecia relative to the autozooecia, which result in no mesozooecium per linear mm in the 25% of measures. In specimen MPZ 2006/132 the number of mesozooecia per mm² is much smaller than the general average, with only three mesozooecia on average. Acanthostyles have an
average diameter of 0.03 mm and a density of four complete acanthostyles per mm². Most of them are circular dark masses without a defined microstructure; others are composed of a central light core surrounded by a dark sheath. Both types are located at the junction of three autozoecia. Zooecial walls have a granular microstructure; in distal zone they are 0.014 mm on average thickness and without a zooecial boundary.

**Longitudinal section**

Autozoecia with an initial growth angle of 32° on average; on the proximal zone they curve sharply and intersect the zoarial surface with an angle of 84° on average. They have a tubular shape divided by cystiphragms and diaphragms. Cystiphragms form single series, starting on a basal diaphragm at the beginning of the autozoecial growth and ending in the first part of the outer exozone; these series are always located on the autozoecial side farthest from the center of the colony (centrifugal arrangement). According to the size of the cystiphragms a lower and an upper zone can be recognized in a longitudinal section of autozoecia. The lower one takes up approximately half of the zoarial length and is characterized by the presence of large cystiphragms that extend across almost the entire autozoecial section. The upper or distal zone is characterized by smaller cystiphragms than in the lower section and by the absence of them in the shallower part of the section. Averaging out the two different zones, there are four cystiphragms per mm. Diaphragms are straight and perpendicular to autozoecial walls. They can be basal diaphragms or diaphragms joining cystiphragms to opposite wall. Two autozoecial diaphragms per mm. Mesozoecia start between autozoecia at the point where they curve to become almost perpendicular to the zoarial surface. They are narrow tubes containing on average six diaphragms per mm of their length, with mesozoecial constrictions where diaphragms join the walls. Most acanthostyles are found in the distal zone of the zoarium, but some can also be found proximally. The former are like a thickening of the autozoecial wall and the latter are thin, massive light-coloured carbonate rods. Autozoecial walls are regular in outline and thickness in endozone, but become thicker and more irregular in exozone where acanthostyles are present; in this case the autozoecial walls have a chevron microstructure. Endozone-exozone boundary coincides with a changing of cystiphragms size; their absence marks the inner-outer exozone boundary.

**Remarks**

Vinassa de Regny (1910) studied the bryozoan fauna in Upper Ordovician rocks from the Carnic Alps, identifying nine species of *Monticulipora*, most of them later assigned to other genera. Although these species need a revision, they can be clearly distinguished from the new *Monticulipora* described here considering its growth habit. Schmidt (1931), in his work on the Paleozoic of the Spanish Pyrenees, identified *Monticulipora petropolitana* Pander, 1830, a species that is best placed within *Diplotrypa* Nicholson, 1879. Since there is neither a description nor illustrations of *Monticulipora petropolitana* in Schmidt’s (1931) paper, a comparison of the Iberian specimens with the Pyrenees ones is not possible.

*Monticulipora cystiphragmata* n. sp. is distinguished from all other described *Monticulipora* species by the size and centrifugal arrangement of the cystiphragms. It is similar to the type species *Monticulipora mammulata* revised by Boardman & Utgaard (1966), and to *Monticulipora parallela*, in the structure of maculae. Moreover, with the former it shares the presence of two types of acanthostyles, and with the latter the density and size of them. But *Monticulipora cystiphragmata* n. sp. can be distinguished from both these species by having fewer mesozoecia; and from *Monticulipora mammulata* by having a granular microstructure wall.

*Monticulipora kolaluensis* Jaroshinskaja, 1962
(Figs 3E, F; 5A, B; Table 2)

*Monticulipora kolaluensis* Jaroshinskaja, 1962: 147, pl. 1, fig. 3, text-fig. 4.

**Material examined.** — One complete zoarium (MPZ 2006/109).

**Stratigraphic and geographic range.** — Upper Ordovician of the Altai Mountains, Siberia (Jaroshin-
skaja 1962); and in the La Peña Member from the Cystoid Limestone Formation, in the Valdelaparra section (Zaragoza, Spain).

**EMENDED DIAGNOSIS.** — Hexagonal autozooecial cross sections with one semicircular cystiphragm cross section inside; diaphragms straight and perpendicular to walls in most autozooecia; cystiphragms mainly arranged in single series lining one side of wall; acanthostyles regularly distributed; and walls with laminated microstructure.

**DESCRIPTION**

**General characters**

Zoarium massive with free growth habit, composed of two layers of irregular thickness and length, with maximum zoarial height of 4.5 mm, minimum height of 1.5 mm, and maximum apparent diameter of 35.0 mm.

**Tangential section**

Autozooecial apertures regularly and irregularly hexagonal with two distinct ranges of diameter. Smaller apertures with an average diameter of 0.27 mm, more regular in form than larger ones, and with fewer mesozooecia between them. Larger apertures have an average diameter of 0.44 mm and form the maculae with a group of mesozooecia. These maculae are separated from each other by 3.5 mm on average, measured from center to center. Without differentiating between macular and intermacular areas there are on average 7.5 autozooecia per mm² and 2.6 per linear mm. All autozooecia have a maximum of 50% of their section occupied by one single circular or subcircular cystiphragm, commonly touching one or two sides of the hexagonal autozooecial aperture. Mesozooecial apertures polygonal and fitting in the spaces between autozooecia. Mesozooecia abundant in maculae, rare in the intermacular area. Mesozooecia vary greatly in size, from 0.09 to 0.22 mm, with an average of 0.14 mm. Without differentiating between macular and intermacular areas there are on average 2.2 mesozooecia per mm² and one mesozooecium per linear mm. Acanthostyles located in the junction of three autozooecia; on average 4.2 acanthostyles per mm², without differentiating between macular and intermacular areas. Acanthostyles average diameter of 0.027 mm. The largest acanthostyles have two well differentiated zones: 1) a central one composed of a light-coloured core with massive amorphous, hyaline microstructure; and 2) an outer sheath formed by a series of dark-coloured laminae concentrically arranged around the core. The smallest acanthostyles circular with darker colour than zooecial walls. Autozooecial walls 0.024 mm thick on average, having laminated microstructure. Mesozooecial walls with the same microstructure and thickness as autozooecial ones. Zooecial boundaries not discernible.

**Longitudinal section**

Zoarium composed of two layers of variable thickness. Overgrowth surface marked by the develop-

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthostyles diameter (in mm)</td>
<td>0.010-0.060</td>
<td>0.027</td>
<td>0.013</td>
<td>21</td>
<td>1</td>
</tr>
<tr>
<td>Autozooecial wall thickness in exozone (in mm)</td>
<td>0.015-0.045</td>
<td>0.024</td>
<td>0.009</td>
<td>21</td>
<td>1</td>
</tr>
<tr>
<td>Autozooecial angle with exterior colony surface</td>
<td>77.0-87.0°</td>
<td>83.5°</td>
<td>4.4</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Intermacular autozooecial diameter (in mm)</td>
<td>0.15-0.31</td>
<td>0.27</td>
<td>0.04</td>
<td>19</td>
<td>1</td>
</tr>
<tr>
<td>Macular autozooecial diameter (in mm)</td>
<td>0.39-0.52</td>
<td>0.44</td>
<td>0.05</td>
<td>17</td>
<td>1</td>
</tr>
<tr>
<td>Mesozooecial macular and intermacular diameter (in mm)</td>
<td>0.09-0.22</td>
<td>0.14</td>
<td>0.04</td>
<td>16</td>
<td>1</td>
</tr>
<tr>
<td>Number of acanthostyles per mm²</td>
<td>4.1-4.5</td>
<td>4.2</td>
<td>0.2</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooecia per mm</td>
<td>0.0-4.0</td>
<td>2.6</td>
<td>1.0</td>
<td>39</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooecial cystiphragms per mm</td>
<td>3.0-9.5</td>
<td>7.0</td>
<td>2.2</td>
<td>12</td>
<td>1</td>
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<tr>
<td>Number of autozooecial diaphragms per mm</td>
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<td>3.3</td>
<td>0.8</td>
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<td>1</td>
</tr>
<tr>
<td>Number of autozooecia per mm²</td>
<td>7.2-7.9</td>
<td>7.5</td>
<td>0.5</td>
<td>34</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooecial diaphragms per mm</td>
<td>5.0-9.0</td>
<td>7.0</td>
<td>2.0</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooecia per mm</td>
<td>0.0-4.5</td>
<td>1.1</td>
<td>1.2</td>
<td>35</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooecia per mm²</td>
<td>2.1-2.4</td>
<td>2.2</td>
<td>0.2</td>
<td>34</td>
<td>1</td>
</tr>
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</table>
ment of new basal diaphragms. Autozoecia start to growth at an angle of 16° on average (measured only in two autozoecia), sharply bending to intersect the zoarial surface at an angle of 84°. Autozoecia tubular, containing cystiphragms and diaphragms. Cystiphragms generally arranged in a single series on one side of the autozoecial chamber, but can also be seen in both sides of the walls either as a single series or isolated, or as double series in a single side. They occupy from 25 to 50% of the autozoecial tube on average, taking up more space in the proximal part, where they are mainly arranged as a single series in one side of a wall. Most autozoecia lack cystiphragms in their distal part. There is an average of seven complete cystiphragms per mm along the total length of the autozoecia. Diaphragms in the lower part of autozoecia either joining cystiphragms with the opposite wall or spanning the autozoecial tube where cystiphragms are absent; they are straight, perpendicular to the walls and less abundant (mean of 3.3 diaphragms per mm of autozoecial length). Mesozoecia scarce, tubular and smaller than autozoecia. They are tabulated by perpendicular and concave diaphragms, averaging seven diaphragms per mm of length. Some mesozoecia have small cystiphragms attached to one side of the wall that curve and lean on a lower cystiphragm or diaphragm. Acanthostyles commonly recognized as a thickening of the autozoecial wall, but in some cases it is possible to observe the core longitudinally cut. Acanthostyles have variable length, most of them reaching the zoarial surface. In proximal zone autozoecial walls slightly thinner than in distal ones (0.024 mm on average). The difference in thickness increases when the wall contains acanthostyles; in this case the simple laminated microstructure becomes a chevron laminated microstructure. Endozone-exozone boundary marked by disappearance of diaphragms.

Remarks
The specimen described here has tangential sections identical to those of *Monticulipora kolaluensis* Jaroshinskaja, 1962, from the Upper Ordovician of Siberia, displaying regular to irregular hexagonal autozoecial sections with a cystiphragm touching one or two sides of the autozoecial chamber, as well as scarce mesozoecia, mainly concentrated in maculae. Longitudinal sections are similar, with cystiphragms either arranged in series on one or both sides of the autozoecial walls, or isolated. However, the Siberian specimens have more abundant diaphragms in both autozoecia and mesozoecia, an average of 12 and 14 respectively, whereas the Iberian specimens have 3.5 and 7.0 diaphragms, respectively. In spite of this difference the studied material is assigned to *Monticulipora kolaluensis* because the identified similarities appear to predominate. In her description, Jaroshinskaja (1962) did not mention either the presence of acanthostyles or the wall microstructure, and the diagnosis of the species is here emended to include these characters.

*Monticulipora kolaluensis* is clearly distinguished from *Monticulipora cystiphragmata* n. sp. by having thicker walls with laminated microstructure, more regular autozoecial apertures, smaller autozoecial cystiphragms arranged in a single series or isolated on one or both sides of the wall, and less inclined autozoecia in the proximal zone of colony.

*Monticulipora kolaluensis* is not an endemic species as it was thought, having a more extended geographic distribution. This new distribution implies a greater mobility for its larvae and a greater capacity for this species to adapt itself to different conditions of temperature and salinity, since the Mediterranean Region had a latitude of about 60°S (Fortey & Cocks 2002) whereas Siberia was placed in tropical latitudes during the Upper Ordovician (Fortey & Cocks 2002).

Genus *Prasopora* Nicholson & Etheridge, 1877

Type species. — *Prasopora grayae* Nicholson & Etheridge, 1877; Upper Ordovician of Scotland.

*Prasopora carnica* Vinassa de Regny, 1915
(Fig. 5C-E; Table 3)

*Prasopora sp.* — Vinassa de Regny, 1914: 205, 206, text-fg. 4.

Fig. 5. — **A, B**, Monticulipora kolaluensis Jaroshinskaja, 1962, MPZ 2006/109, longitudinal thin sections; **A**, area of the zoarium with large cystiphragsms (cy) attached to one side of the autozooeial (az) wall that are joined to the opposite wall by diaphragms (dp); **B**, an area with smaller cystiphragsms (cy) located in both sides of the wall as single rows or isolated; **C-E**, Prasopora carnica Vinassa de Regny, 1915, MPZ 2006/113; **C**, longitudinal thin section showing the autozooecia (az), the cystiphragsms (cy), and the mesozooecia (mz); **D, E**, two tangential thin sections separated by less than 3 mm and in the same depth of the colony; **D**, the autozooecia (az) are completely surrounded by mesozooecia (mz); **E**, the autozooecia (az) are in contact with other autozooecia in most part of their outline, having two cystiphragsms (cy) inside, and scarce mesozooecia (mz); **F**, Prasopora spjeldnaesi n. sp., MPZ 2006/99, basal surface showing the concentrically wrinkled base and the initial point of growth of the zoarium (ipg). Scale bars: 1 mm.
**Material examined.** — One zoarium (MPZ 2006/113).

**Stratigraphic and geographic range.** — Upper Katian (Upper Ordovician) of the Carnic Alps: Vinassa de Regny (1914, 1915); Upper Katian (Upper Ordovician) of Sardinia (Italy): Conti (1990); Cystoid Limestone Formation, La Peña Member, of the Valdelaparra section (Zaragoza, Spain).

**Description**

**General characters**
Zoarium incrusting a brachiopod valve and incrusted by Monticuliporidae sp. indet described below. Composed of two layers, with colony thickness 0.9-1.9 mm, and minimum diameter of 15.0 mm.

**Tangential section**
Two zones with gradual transition between them: the first one composed by oval or subpolygonal autozooidal apertures, completely surrounded by mesozooidal; and the second one composed by more circular autozooidal apertures, in contact with each other in most of their perimeter, and with scarce mesozooidal located in the space between them. The spatial density of autozooidal is almost twice in the second zone than in the first one. Autozooidal sections with an average diameter of 0.20 mm, 7.5 autozooidal per mm² and 2.2 autozooidal per linear mm on average (measured in the first zone, where they are less numerous). Most autozooidal sections with two or three cystiphrags leaving an oval cavity between them, located either in a central position in the case of two cystiphrags, or on the periphery in the case of three cystiphrags. Shape of mesozooidal cross sections depends on their position in the colony: irregularly hexagonal when surrounding autozooidal and variably shaped when occupying the spaces between autozooidal. Mesozooidal with an average diameter of 0.12 mm, 41.5 mesozooidal per mm² and six mesozooidal per linear mm on average (measured in first zone where they are more abundant). Both, autozooidal and mesozooidal walls thin (mean of 0.011 mm). Wall microstructure laminated, but zoooidal boundaries not observed. Acanthostyles absent.

**Longitudinal section**
Zoarium composed by two layers of different thickness; lower one with maximum thickness of 1.35 mm; the upper one 0.45 mm, more regular in thickness. Overgrowth marked by development of new basal diaphragms. The oblique orientation of the section does not permit measuring the inclination of autozooidal with respect to basal surface. Autozooidal intersect zoarial surface at an angle of 85°. Autozooidal consist of long tubes with cystiphrags and diaphragms. Cystiphrags with an irregular distribution and size, arranged either in single series lining one or both sides of walls, or isolated, also on one or both sides. Isolated cystiphrags can take up three fourths of autozooidal diameter. Nine cystiphrags per linear mm on average. Diaphragms very scarce, always joining the larger isolated cystiphrags to the opposite wall. Mesozooidal are length tubes located between autozooidal or in small groups. Some of them almost as large as autozooidal, distinguish from latter by absence of cystiphrags and by higher density of diaphragms (an average

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**Table 3.** — Summary of the statistical analysis of *Prasopora carnica* Vinassa de Regny, 1915. Abbreviations: see Table 1.

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooidal angle with exterior colony surface</td>
<td>77-87°</td>
<td>85°</td>
<td>3</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Autozooidal diameter (in mm)</td>
<td>0.12-0.30</td>
<td>0.20</td>
<td>0.03</td>
<td>58</td>
<td>1</td>
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<tr>
<td>Mesozooidal diameter (in mm)</td>
<td>0.08-0.18</td>
<td>0.12</td>
<td>0.02</td>
<td>44</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooidal per mm</td>
<td>1.0-4.0</td>
<td>2.2</td>
<td>1.2</td>
<td>13</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooidal cystiphrags per mm²</td>
<td>6-12</td>
<td>9</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooidal diaphragms per mm</td>
<td>6.0-9.0</td>
<td>7.5</td>
<td>1.0</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooidal per mm</td>
<td>12-22</td>
<td>16</td>
<td>3</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooidal per mm²</td>
<td>4-9</td>
<td>6</td>
<td>2</td>
<td>13</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooidal per mm²</td>
<td>31.0-45.0</td>
<td>41.5</td>
<td>5.2</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Zoooidal wall thickness in exozone (in mm)</td>
<td>0.005-0.020</td>
<td>0.011</td>
<td>0.004</td>
<td>35</td>
<td>1</td>
</tr>
</tbody>
</table>
Monticuliporidae (Bryosoa) from the Iberian Chains (NE Spain)

of 16 per mm). Mesozooecial diaphragms straight or slightly oblique. Zooecial walls sinuous, causing narrowing and widening of zooecia, but with constant thickness throughout zoarium.

REMARKS
The specimen from the Iberian Chains is similar to specimens from the Upper Ordovician of Sardinia (Italy) assigned by Conti (1990) to Prasopora carnica. They have colonies with secondary overgrowths; cystiphragms isolated or in series on one or both sides of the wall, with a similar spatial density in both collections (Conti 1990 and this one); autozooecia that intersect the upper surface with an angle of about 85°; numerous mesozooecia with closely spaced diaphragms; sinuous walls of constant thickness; as well as absence of acanthostyles. But the Iberian zoarium does not reveal either the cystoidal diaphragms or the macula described by Conti (1990) in Sardinian material.

Two other species of Prasopora are known from the Mediterranean Province, but they can be clearly distinguished. The Iberian zoarium is mainly distinguished from Prasopora fistuliporoides (Vinassa de Regny, 1910) because the former has fewer autozoecial diaphragms, more abundant mesozooecia, and has neither cystoidal diaphragms in overgrown areas nor acanthostyles. From Prasopora grayae the present material is distinguished by less abundant autozoecial cystiphragms and diaphragms as well as by the size of the cystiphragms which occupy less space inside the autozoecial tubes.

Prasopora spjeldnaesi n. sp.
(Figs 5F; 6; 7; Table 4)

Prasopora sp. – Jiménez-Sánchez et al. 2007: 694, fig. 8 (5-6).

TYPE MATERIAL. — Complete zoarium, holotype (MPZ 2006/99).

ETYMOLOGY. — This species is named after Nils Spjeldnaes, who introduced me to the bryozoan world.

MATERIAL EXAMINED. — The holotype.

TYPE HORIZON. — La Peña Member of the Cystoid Limestone Formation, Upper Ordovician.

TYPE LOCALITY. — La Peña del Tormo section (Zaragoza, Spain).

STRATIGRAPHIC AND GEOGRAPHIC RANGE. — It is only known from its type locality, at the La Peña Member of the Cystoid Limestone Formation in La Peña del Tormo section (Zaragoza, Spain).

DIAGNOSIS. — Prasopora species characterized by anomalously large autozoecia and mesozooecia; presence of cystiphragms on one side of the autozoecial wall leaning on lower diaphragms or on other cystiphragms growing from opposite side of wall; autozoecia isolated from each other by mesozooecia; the splitting of largest mesozooecia in two new mesozooecia just above a diaphragm.

Table 4. — Summary of statistical analysis of Prasopora spjeldnaesi n. sp. Abbreviations: see Table 1.

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozoecial angle with basal colony surface</td>
<td>43.0-64.0°</td>
<td>54.5°</td>
<td>5.5</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Autozoecial angle with exterior colony surface</td>
<td>69-81°</td>
<td>76°</td>
<td>4</td>
<td>19</td>
<td>1</td>
</tr>
<tr>
<td>Autozoecial-mesozooecial wall thickness in exozone (in mm)</td>
<td>0.005-0.015</td>
<td>0.010</td>
<td>0.002</td>
<td>19</td>
<td>1</td>
</tr>
<tr>
<td>Autozoocelial major diameter (in mm)</td>
<td>0.45-0.55</td>
<td>0.51</td>
<td>0.02</td>
<td>18</td>
<td>1</td>
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<tr>
<td>Autozoocelial minor diameter (in mm)</td>
<td>0.40-0.45</td>
<td>0.43</td>
<td>0.02</td>
<td>18</td>
<td>1</td>
</tr>
<tr>
<td>Intermonticular Mesozooecelial diameter (in mm)</td>
<td>0.18-0.34</td>
<td>0.25</td>
<td>0.05</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>Mesozooecial-mesozooecial wall thickness in exozeone (in mm)</td>
<td>0.005-0.010</td>
<td>0.008</td>
<td>0.003</td>
<td>22</td>
<td>1</td>
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<tr>
<td>Monticular mesozooecial diameter (in mm)</td>
<td>0.3-0.4</td>
<td>0.4</td>
<td>0.0</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozoocelia per mm</td>
<td>0.7-1.2</td>
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<td>1</td>
</tr>
<tr>
<td>Number of autozoocelial cystiphragms per mm</td>
<td>2-8</td>
<td>4</td>
<td>2</td>
<td>15</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozoocelial diaphragms per mm</td>
<td>2-5</td>
<td>3</td>
<td>1</td>
<td>15</td>
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</tr>
<tr>
<td>Number of autozoocelia per mm²</td>
<td>1.2-2.0</td>
<td>1.7</td>
<td>0.5</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooecial diaphragms per mm</td>
<td>5-13</td>
<td>9</td>
<td>2</td>
<td>45</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozooecia per mm</td>
<td>2.0-3.5</td>
<td>3.0</td>
<td>1.0</td>
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</tr>
<tr>
<td>Number of mesozooecia per mm²</td>
<td>10.5-13.5</td>
<td>12.0</td>
<td>2.0</td>
<td>10</td>
<td>1</td>
</tr>
</tbody>
</table>
Jiménez-Sánchez A.

**DESCRIPTION**

**External characters**

Zoarium lens-shaped with apparent maximum diameter of 27.0 mm, thickness of 6.5 mm in its center and of 5.0 mm in the periphery. Convex upper surface with monticles, surrounded by depressed intermonticular areas. Autozooecial apertures oval, completely surrounded by mesozooecial

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**Fig. 6.** — *Prasopora sjeldnaesi* n. sp., holotype (MPZ 2006/99): A, general view of the colony; B, surface of the colony showing autozooecia (az) completely surrounded by mesozooecia (mz), and a cross section of a cystiphragm (cy) inside an autozooecial aperture; C, tangential thin section with abundant mesozooecia (mz) completely isolating autozooecia (az); D, longitudinal thin section showing the autozooecia (az) and mesozooecia (mz) as well as the peculiar cystiphragms (cy); E, a group of mesozooecia (mz) with their diaphragms (dp) at the same level forming a square network. Scale bars: 1 mm.
apertures. Monticular areas composed of slightly smaller and more circular autozooecia than those in intermonticular areas, and by larger mesozooecia. Mean distance between adjacent monticules of 4 mm measured from center to center. Zoarium basal surface concave, with concentrically wrinkled epitheca around ancestrula, with radially arranged autozooecia.

**Tangential section**

Autozooecial apertures oval, with an average major diameter of 0.51 mm and an average minor diameter of 0.43 mm; these values decrease in deeper sections. Almost two autozooecia per mm² and one autozooecia per linear mm on average, always surrounded by mesozooecia. Most autozooecia crossed from side to side by one or two cystiphragms. Intermonticular mesozooecial apertures polygonal (square, rhomboidal, or pentagonal), with an average major diagonal diameter of 0.25 mm, an average of 12 mesozooecia per mm² and 3 mesozooecia per linear mm. Monticular mesozooecia always surrounding autozooecia, with the shape of apertures in form of irregular polygons and an average major diameter of 0.4 mm. Autozooecial-mesozooecial and mesozooecial-mesozooecial walls composed of thin dark lamina; the former with average thickness of 0.01 mm and the latter slightly thinner (0.008 mm on average). Acanthostyles absent.

**Longitudinal section**

Initial autozooecia originated from the ancestrula and located in the central area of the colony, growing at an angle of 90° to the substrate. These autozooecia form a small convex bulge that breaks the concavity of this surface. The other autozooecia growing with an average angle of 54.5° to the basal surface, but bending after a short distance and reaching the zoarial surface with an average angle of 76°. Autozooecia are long tubes, densely tabulated by diaphragms and cystiphragms. Diaphragms very regularly distributed throughout autozooecium length, straight, concave or convex, without a predominance of one type or the other, three per mm of autozooecial length. Cystiphragms grow from one side of wall, and lean on lower diaphragms or on another cystiphragm growing in opposite wall. The junction between a cystiphragm and a diaphragm forms a small wedge or semicircular cavity and the junction between two cystiphragms always forms semicircular-shaped cavities. Number of cystiphragms increases towards the zoarial surface, where an average of four cystiphragms per mm have been counted. Mesozooecia are long tubes either isolated separating autozooecia or forming small clusters. They generally have narrower apertures than autozooecia and are densely tabulated by diaphragms (averaging nine per mm). Most mesozooecial diaphragms are straight, but they can also be slightly concave or convex. In continuous mesozooecial diaphragms develop at the same level, forming a square network. Near zoarial surface the largest mesozooecia split just above the surface of a diaphragm to form two new mesozooecia (Fig. 7).

**Remarks**

This *Prasopora* species shares with most of its congenic species the presence of monticules on the zoarial surface, the distribution and shape of densely tabulated mesozooecia when they are separating autozooecia, and the presence of diaphragms and cystiphragms in the autozooecia.

It is similar to *Prasopora gotlandica* Hennig, 1908. Both species can be distinguished from other *Prasopora* species (including *Prasopora carnica* described above) by the form and distribution of their cystiphragms. All the other known species of
this genus have cystiphragms either blister-shaped and isolated or forming long series superimposing each other, lining one or both sides of the autozooecial wall; in most cases they are joined to each other or to the opposite wall by one straight diaphragm. In *Prasopora sjeldnaesi* n. sp. and *Prasopora gotlandica* the cystiphragms are attached to one side of the wall curving and leaning on the lower diaphragm or on another cystiphragm growing in the opposite wall. They also have in common that the largest mesozooecia divide to form new smaller ones. In spite of these similarities, both species can be clearly distinguished by the different diameters of the autozooecia and mesozooecia (0.25-0.30 mm and 0.10-0.20 mm, respectively, in *Prasopora gotlandica* vs 0.45-0.55 mm and 0.18-0.34 mm, respectively, in *Prasopora sjeldnaesi* n. sp.). The new species can be also discriminated from *Prasopora gotlandica* by its higher mesozooecia number/autozooecia number relation.

**Fig. 8.** — Monticuliporidae sp. indet., MPZ 2006/110: **A**, longitudinal thin section showing the large acanthostyles (ac), the peculiar cystiphragms (cy), and the narrow mesozooecia (mz); **B**, tangential thin section showing the regular hexagonal autozooecia (az) with wall sections having gently beaded (bd) outline, the mesozooecia (mz) in an area where hexagonal autozooecia are not so regular, and large acanthostyles (ac); **C**, a high-magnification detail of the longitudinal section of an acanthostyle (ac) showing the central lumen on the lower part of the figure and lamination around the lumen; **D**, a high-magnification detail of the cross section of an acanthostyle (ac) showing the light coloured central lumen (lu) and surrounding dark lamina. Scale bars: A, B, 1 mm; C, D, 0.1 mm.
According to the discussion above, *Prasopora* spjeldnaesi n. sp. can be clearly discriminated from all the congeneric species. In spite of not being possible, at the moment, to describe the intraspecific variability of the new species, known from a single complete zoarium, it is proposed to erect formally a new species. This will facilitate further comparisons within this widespread genus in the Mediterranean Province.

*Prasopora* spjeldnaesi n. sp. is also similar to *Prasopora mesoporosa* Fritz, 1957. Both have numerous mesozoecia forming characteristic rings around autozooecia; but *Prasopora* mesoporosa has the typical *Prasopora* cystiphragms and much smaller autozooecia and mesozoecia than *Prasopora* spjeldnaesi n. sp. (0.24-0.32 mm and 0.05-0.18 mm, respectively, in *Prasopora* mesoporosa vs 0.45-0.55 mm and 0.18-0.34 mm, respectively, in *Prasopora* spjeldnaesi n. sp.).

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**TABLE 5.** — Summary of the statistical analysis of Monticuliporidae sp. indet. (MPZ 2006/110). Abbreviations: see Table 1.

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthostyles diameter (in mm)</td>
<td>0.040-0.100</td>
<td>0.065</td>
<td>0.023</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>Autozooecial angle with basal colony surface</td>
<td>14-36°</td>
<td>26°</td>
<td>9</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Autozooecial angle with exterior colony surface</td>
<td>90°</td>
<td>90°</td>
<td>0</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Autozooecial diameter (in mm)</td>
<td>0.36-0.55</td>
<td>0.39</td>
<td>0.06</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Autozooecial wall thickness in exozone (in mm)</td>
<td>0.030-0.050</td>
<td>0.032</td>
<td>0.006</td>
<td>24</td>
<td>1</td>
</tr>
<tr>
<td>Mesozoecial diameter (in mm)</td>
<td>0.18-0.21</td>
<td>0.20</td>
<td>0.01</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooecial cystiphragms per mm</td>
<td>1.0-5.0</td>
<td>2.5</td>
<td>1.7</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooecial diaphragms per mm</td>
<td>3.0-5.0</td>
<td>3.9</td>
<td>0.6</td>
<td>13</td>
<td>1</td>
</tr>
<tr>
<td>Number of autozooecia per mm²</td>
<td>6.5-8.5</td>
<td>7.2</td>
<td>1.8</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozoecial diaphragms per mm</td>
<td>3.0-5.0</td>
<td>4.6</td>
<td>0.8</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozoecia per mm</td>
<td>0.0-2.0</td>
<td>0.6</td>
<td>0.6</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Number of mesozoecia per mm²</td>
<td>1.1-2.9</td>
<td>2.2</td>
<td>1.8</td>
<td>6</td>
<td>1</td>
</tr>
</tbody>
</table>
Monticuliporridae sp. indet.
(Figs 8; 9; 10; Table 5)


**MATERIAL EXAMINED.** — Zoarium MPZ 2006/110.

**DESCRIPTION**

**General characters**

Zoarium with incrusting growth habit, composed of two layers with variable thickness in different parts of colony. Zoarium with maximum height of 4.3 mm, minimum height of 1.5 mm and maximum apparent diameter of 32.0 mm. It is incrusting the external and internal surface of a brachiopod shell and the zoarium of *Prasopora carnica* described above.

**Tangential section**

Autozooecial apertures with very regular hexagonal form, giving a high degree of packing, with average diameter of 0.39 mm and average of 7.2 autozooecia per mm² and 2.6 autozooecia per linear mm. Mesozooecial apertures polygonal (rectangular to pentagonal), with average diameter of 0.20 mm and average spacing of 2.2 mesozooecia per mm² and 0.6 mesozooecia per linear mm. Mesozooecia located in the space left by less regular hexagonal autozooecia. Acanthostyles rather scarce, averaging one per mm², large (mean diameter of 0.065 mm), mainly located in junction of three autozooecia. Acanthostyles with light-coloured cores and dark-coloured laminated sheaths. Zoecial walls are thick (0.032 mm) with beaded outline, (Fig. 9). Maculae not observed.

**Longitudinal section**

Zoarium composed of two layers of irregular thickness, with overgrowth surface marked by development of new basal diaphragms. Autozooecia grow at an angle of 26° from the substrate, bending sharply and intersecting zoarial surface at an angle of 90°. Autozooecia with tubular shape, containing diaphragms and cystiphragms. Diaphragms mainly straight and perpendicular to autozooecial walls, but occasionally also oblique, concave or convex; regularly spaced inside autozooecia with an average spacing of 3.9 diaphragms per mm. Cystiphragms developed in upper three quarters of autozooecia with a spacing of 2.5 per mm. They are attached to one side of the wall curving and leaning on a lower diaphragm or on a cystiphragm developed in the opposite wall. Mesozooecia scarce, consisting of narrow tubes originating at the base of the exozone. They have more diaphragms than autozooecia, an average of 4.6 per mm. Acanthostyles long, up to 1.14 mm in length, developed at different levels, but only up to the point where autozooecia curve (Fig. 10). Zoecial walls with irregularities in form of small beads visible at low magnification; their thickness increases upwards in the colony. At higher magnification an exterior dark line that continues in the diaphragms can be observed. Between the two dark lines there is a layer with an obvious granular microstructure. Endozone-exozone boundary marked by change of inclination of autozooecia, development of mesozooecia and acanthostyles, and higher density of cystiphragms in autozooecia.

**REMARKS**

This specimen exhibits the main diagnostic characters of the family Monticuliporidae: incrusting growth habit, polygonal autozooecial apertures, presence of diaphragms and cystiphragms, densely tabulate mesozooecia and presence of acanthostyles. The only diagnostic character not observable are maculae, but it could be the result of the small number of sections studied. This specimen has a combination of features that are not present in any other Monticuliporidae genus: very regular hexagonal apertures, walls with a distinctive beaded outline in cross section, and very large and scarce acanthostyles with a core. These three features have been used in traditional trepostomate systematic to distinguish and classify genera. The occurrence of these characters would merit the erection of a new genus in the family Monticuliporidae. The formal definition should await until more colonies are found.

This Iberian zoarium is similar in the shape of its cystiphragms to *Orbignyella* Ulrich & Bassler, 1904, originally ascribed to the monticuliporids but presently considered to be best placed within the family Atactotoechidae Duncan, 1939. Nevertheless, the Iberian zoarium cannot be included in *Orbignyella*.
which, like the other atactotoechids, has exilazoecia instead of mesozoecia and much smaller acantho-
styles than the studied sample. This zoarium is also
similar to Prasopora spjeldnaesi n. sp., but it can be
clearly distinguished by the shape of its autozoecial
apertures (polygonal vs oval), the number of meso-
azoecia (much less abundant than in the Prasopora
species) and the presence of acanthostyles.

CONCLUSION

In the Iberian Chain, the family Monticuliporidae is
represented by four species belonging to the genera
Monticulipora and Prasopora as well as one Monti-
culiporidae indet.

Monticulipora cystiphragmata n. sp. is described in
this work for the first time. Monticulipora kolaluensis
is identified here for the first time outside its original
area of Siberia (Altai Mountain).

Prasopora carnica is widely distributed in the Medi-
terranean Region, but it is not known outside this
region. The new species Prasopora spjeldnaesi n. sp.
described here is very different to all other Prasopora
species known in the Mediterranean Region. However,
it is very similar to the younger species of Prasopora
gotlandica from the Silurian of Baltica. Ongoing
studies by our group are trying to show which is
the phylogenetic, ecological and paleobiogeographic
relationship between bryozoan faunas of the Medi-
terranean Region and the Baltica paleocontinent.

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REFERENCES

ASTROVA G. G. 1978. — [The history of development,
system, and phylogeny of the Bryozoa: order Trepo-
stromata]. Trudy Paleontologicheskogo Instituta Akademii
Nauk SSSR 169: 1-240, 30 pls. (in Russian, english
translation by Brown, Department of Geology, Aus-
tralian National University).

BOARDMAN R. S. & ÚTGAARD J. 1966. — A revision
of the Ordovician bryozoan genera Monticulipora,
Peronopora, Heterotrypa, and Dekayia. Journal of

BORK K. B. & PERRY T. G. 1968. — Bryozoa (Ecto-
procta) of Champlainian age (Middle Ordovician)
from Northwestern Illinois and adjacent parts of
Iowa and Wisconsin. Part III. Homotrypa, Orbignyella,
Prasopora, Monticulipora and Cyphotrypa. Journal of

Bryozoa from the Dillsboro Formation (Cincinnati
Series) of Southeastern Indiana. Geological Survey
Special Report 33: 1-95.

BUTTLER C. J. 1991. — Bryozoans from the Llanbedrog
Mudstones (Caradoc), North Wales. Bulletin of the
British Museum (National History), Geological Series
47: 153-168.

BUTTLER C. J., CHERNS L. & MASSA D. 2007. — Bryo-
zoan mud-mounds from the Upper Ordovician Jifarah
(Djeffara) Formation of Tripolitania, North-West of

CARLS P. 1975. — The Ordovician of the Eastern Iberian
Chains near Fombuena and Luesma. Neues Jahrbuch
für Geologie und Paläontologie, Abhandlungen 152 (2):
127-146.

COCKS L. R. M. & TORSVIK T. H. 2002. — Earth ge-
ography from 500 to 400 million years ago. A faunal
and palaeomagnetic review. Journal of the Geological
Society of London 159: 631-644.

CONTI S. 1990. — Upper Ordovician Bryozoa from
Sardinia. Palaeontographia Italic a 77: 85-165.

DEL MORAL B. 2005. — Estudio tafonómico prelimi-
nar de los conodontos de la Formación Calizas de
Cistideos (Ordovicico Superior) en la sección Piedra
del Tormo (Cordillera Ibérica, Zaragoza, España), in
GÁMEZ-VINTANED J. A., LIÑÁN E. & VALENZUELA-
RÍOS J. I. (eds), VIII Jornadas de Aragonesas de Pale-
ontología. Institución Fernando el Católico, Zaragoza:
109-118.

ERNST A. & KEY M. 2007. — Upper Ordovician bryozoan
from the Montagne Noire, Southern France. Journal

Ordovician bryozoans from the Kanosh Formation
(Whiterckian) of Utah, USA. Journal of Paleontology
81 (5): 998-1008.

FORTY R. A. & COCKS L. R. M. 2002. — Paleontologi-


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