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

Andrea JIMÉNEZ-SÁNCHEZ
Área de Paleontología, Departamento de Ciencias de la Tierra,
Universidad de Zaragoza, C/ Pedro Cerbuna 12,
E-50009 Zaragoza (Spain)
andreaj@unizar.es

Jiménez-Sánchez A. 2010. — New monticuliporidae (Bryozoa, Trepostomata) from the Cystoid Limestone Formation (Upper Ordovician) of the Iberian Chains (NE Spain). *Geodiversitas* 32 (2): 177-199.

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 spjeldnaesi* 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 mesozoecia, and number of acanthostyles. Herein a new generic diagnosis of *Monticulipora* is proposed, putting special emphasis on the shape and distribution of cystiphragms. 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.

RÉSUMÉ
Nouveau Monticuliporidae (Bryozoa, Trepostomata) de la Formation des Calcaires à Cystoïdes (Ordovicien Supérieur) dans les Chaînes ibériques (NE de l'Espagne). Les bryozoaires sont un des groupes les plus abondants parmi les fossiles présents dans les calcaires d'eau froide qui caractérisent le Katien terminal (Ordovicien Supérieur) au sud-ouest de l'Europe et au nord de l'Afrique. La Formation des Calcaires à Cystoïdes, l'unité représentative de ces roches très répandues dans les Chaînes ibériques (NE de l'Espagne), a fourni une des faunes de bryozoaires les plus riches et diversifiées dans tout le secteur. La première étude systématique des représentants de la famille Monticuliporidae des Trepostomates est entreprise ici. Il s'agit de l'un des groupes de bryozoaires les plus diversifiés parmi les associations récoltées. Quatre espèces appartenant aux genres *Monticulipora* et *Prasopora* sont décrites, parmi lesquelles les nouvelles espèces *Monticulipora cystiphragmata* n. sp. et *Prasopora spjeldnaesi* n. sp. et un Monticuliporidae indéterminé. Les genres *Monticulipora* et *Prasopora* sont très similaires, et contiennent certaines espèces difficiles à différencier. Leurs diagnoses incluent de nombreux caractères très courants, comme la microstructure de la paroi, la densité de mesozoécies et le nombre d'acanthostyles. Une nouvelle diagnose est proposée ici pour le genre *Monticulipora*, dont la forme et la distribution des cystiphragmes ont une importance spéciale. L'espèce *Monticulipora kolaluensis* est reconnue pour la première fois hors de la Sibérie. Quoique la présence des nouveaux taxons suggère un certain isolement des Chaînes ibériques dans la plate-forme nord gondwanienne, la présence de *Prasopora carnica* montre une relation avec les Alpes Carniques voisines (Italie et Autriche).

MOTS CLÉS
Bryozoa,
Trepostomata,
Monticuliporidae,
Ordovicien supérieur,
Formation des Calcaires à Cystoïdes,
Chaînes ibériques,
espèces nouvelles.

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 (Liñán *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

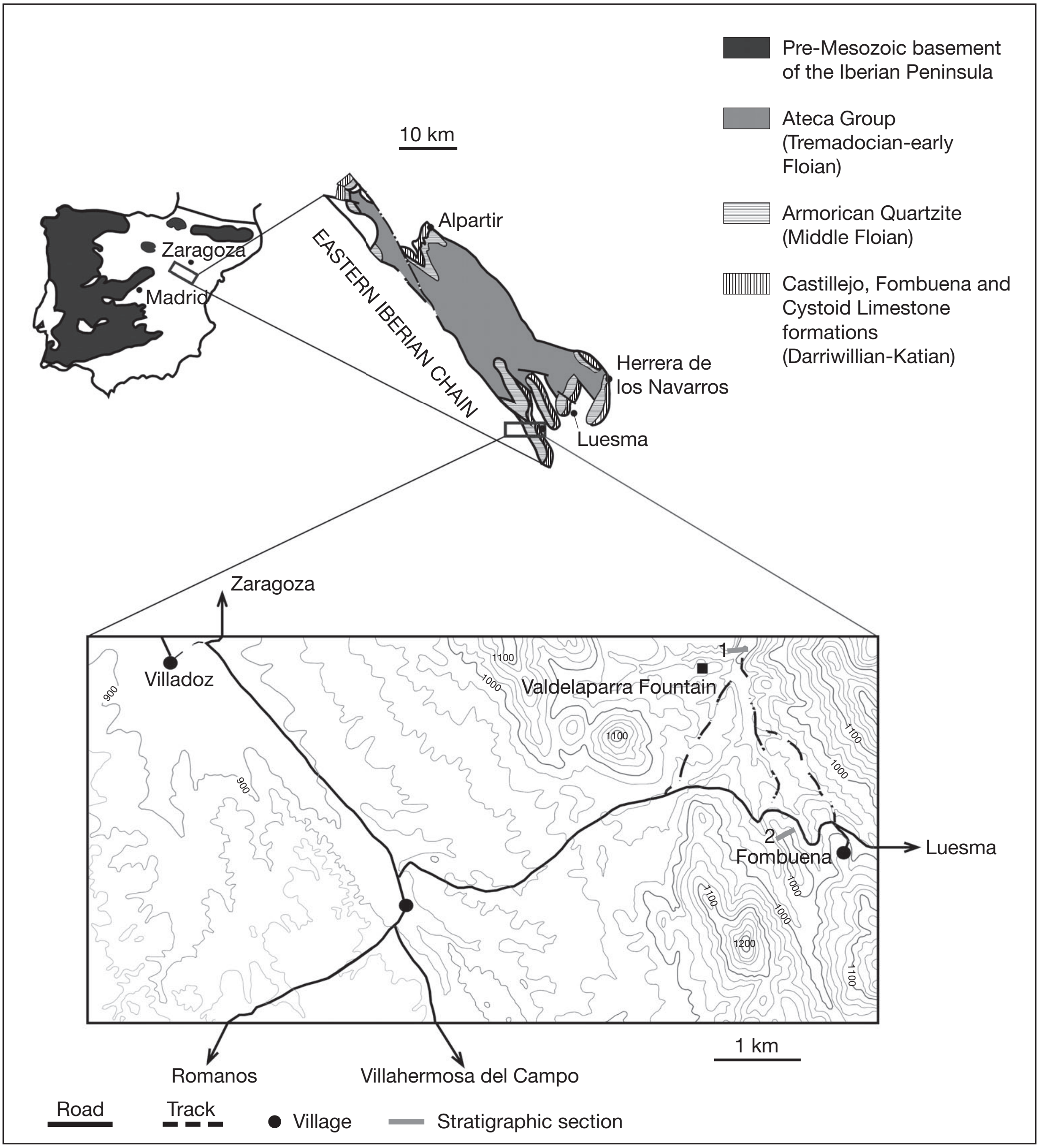

FIG. 1. — Outcrops of Ordovician rocks in the Eastern Iberian Chain and their location in the Iberian Peninsula. The lower rectangle marks the location of the study area and measured sections. **1**, Valdelaparra; **2**, La Peña del Tormo.

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 deposites 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 Tormo 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 Tormo. 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 Tormo and close to the Valdelaparra Fountain (Fig. 1). The La Peña del Tormo 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).

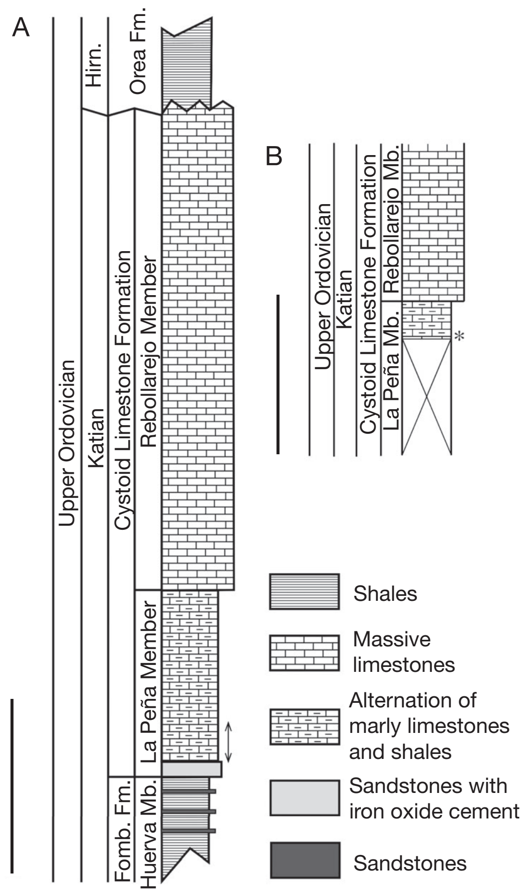

Fig. 2. — Stratigraphic columns of the Cystoid Limestone Formation: **A**, Valdelaparra section; **B**, La Peña del Tormo section. The horizons where bryozoans were collected are marked with a double head arrow in A and with an asterisk in B. Scale bars: A, 10 m; B, 1 m.

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 monticules. 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 cystiphragms 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 autozooecia completely surrounded by mesozooecia, and the other one with mesozooecia located in the corners of some autozooecia. 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 TREPOSTOMATA 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; autozooecia with polygonal or subpolygonal apertures, less commonly subcircular; with simple cystiphragms larger in endozone than in inner exozone; autozooecial diaphragms join cystiphragms to the opposite wall; mesozooecia not abundant, located in autozooecial corners and monticules, and densely tabulated by diaphragms; acanthostyles mainly developed in exozone; monticules present and formed by mesozooecia and autozooecia larger than those in the intermonticular area.

DISCUSSION

Astrova (1978) characterized *Monticulipora* as having autozooecia with polygonal apertures, numerous cystiphragms and diaphragms in all autozooecia, few mesozooecia, presence of acanthostyles, and zooecial walls with granular microstructure. Ross (1967) had described *Prasopora* as having autozooecia with rounded or subpolygonal apertures, isolated and superimposed autozooecial diaphragms and cystiphragms, 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 cystiphragms 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 mm^2 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

TABLE 1. — Summary of the statistical analysis of *Monticulipora cystiphragmata* n. sp. including the observed range (**Or**), the mean value (**X**), the standard deviation (**SD**), the number of measurements (**Nm**), and the number of colonies where these measurement were made (**Nsp**).

Character	**Or**	**X**	**SD**	**Nm**	**Nsp**
Acanthostyle diameter (in mm)	0.015-0.060	0.030	0.005	30	3
Autozooecial angle with basal colony surface	28-35°	32°	3	5	2
Autozooecial angle with exterior colony surface	78-87°	84°	3	11	1
Autozooecial wall thickness in exozone (in mm)	0.005-0.030	0.014	0.006	48	3
Intermacular autozooecial diameter (in mm)	0.20-0.42	0.30	0.07	68	3
Macular autozooecial diameter (in mm)	0.36-0.48	0.43	0.04	38	2
Mesozooecial macular and intermacular diameter (in mm)	0.07-0.18	0.11	0.02	71	3
Number of acanthostyles per mm^2	2.5-5.5	4.0	1.2	18	2
Number of autozooecia per mm	0.5-5.0	2.9	0.2	212	3
Number of autozooecial cystiphragms per mm	2.0-6.0	4.0	0.5	41	3
Number of autozooecial diaphragms per mm	0.0-7.0	2.0	1.2	23	3
Number of autozooecia per mm^2	7.5-11.5	9.2	1.2	60	3
Number of mesozooecial diaphragms per mm	5.0-8.0	6.0	0.3	15	3
Number of mesozooecia per mm	0.0-5.0	1.0	0.2	212	3
Number of mesozooecia per mm^2	2.5-18.5	7.0	3.6	60	3

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.

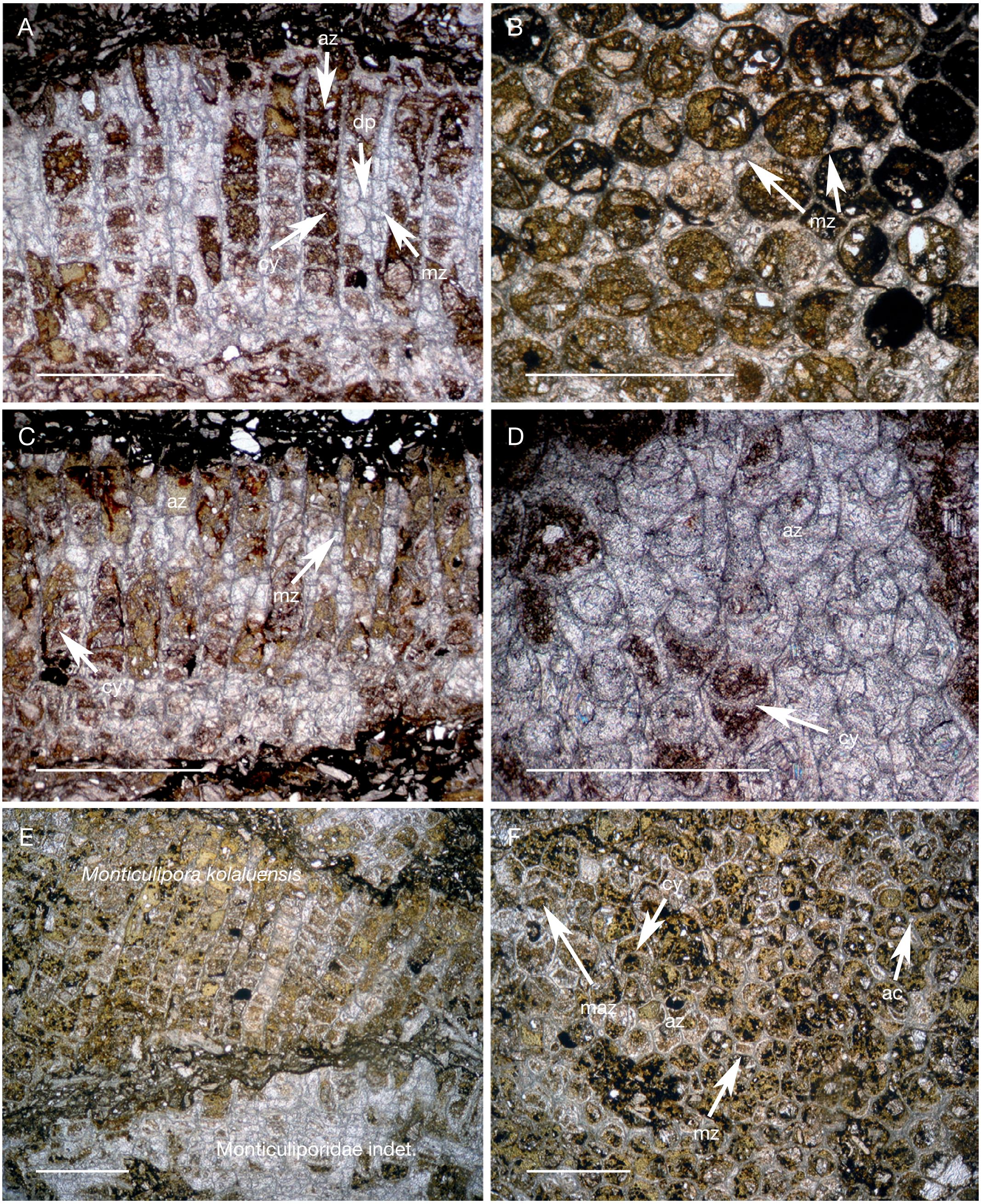

FIG. 3. — **A-D**, *Monticulipora cystiphragmata* n. sp.; **A**, **C**, longitudinal thin sections of the holotype (MPZ 2006/134) and paratype (MPZ 2006/132), respectively, showing the autozooecia (**az**), the large cystiphragms (**cy**) joined in some cases to the opposite wall by diaphragms (**dp**), 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 know 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 endozone 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 mesozoecia on average. Acanthostyles have an

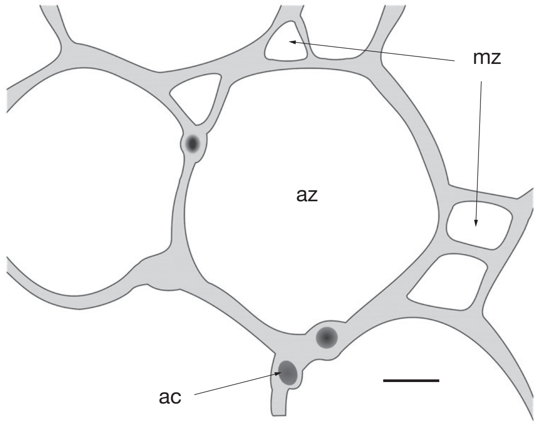

FIG. 4. — *Monticulipora cystiphragmata* n. sp., schematic tangential section of the holotype (MPZ 2006/134). It shows the disposition of the square- and triangular-shaped mesozooecia (**mz**), the location of acanthostyles (**ac**), and the autozooecial aperture shape (**az**). Scale bar: 0.1 mm.

average diameter of 0.03 mm and a density of four complete acanthostyles per mm^2. 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 autozooecia. Zooecial walls have a granular microstructure; in distal zone they are 0.014 mm on average thickness and without a zooecial boundary.

Longitudinal section
Autozooecia 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 autozooecial growth and ending in the first part of the outer exozone; these series are always located on the autozooecial 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 autozooecia. 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 autozooecial 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 autozooecial walls. They can be basal diaphragms or diaphragms joining cystiphragms to opposite wall. Two autozooecial diaphragms per mm. Mesozooecia start between autozooecia 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 mesozooecial 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 autozooecial wall and the latter are thin, massive light-coloured carbonate rods. Autozooecial 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 autozooecial 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 mesozooecia; 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-

TABLE 2. — Summary of the statistical analysis of *Monticulipora kolaluensis* Jaroshinskaja, 1962. Abbreviations: see Table 1.

Character	Or	X	SD	Nm	Nsp
Acanthostyles diameter (in mm)	0.010-0.060	0.027	0.013	21	1
Autozooecial wall thickness in exozone (in mm)	0.015-0.045	0.024	0.009	21	1
Autozooecial angle with exterior colony surface	77.0-87.0°	83.5°	4.4	9	1
Intermacular autozooecial diameter (in mm)	0.15-0.31	0.27	0.04	19	1
Macular autozooecial diameter (in mm)	0.39-0.52	0.44	0.05	17	1
Mesozooecial macular and intermacular diameter (in mm)	0.09-0.22	0.14	0.04	16	1
Number of acanthostyles per mm^2	4.1-4.5	4.2	0.2	11	1
Number of autozooecia per mm	0.0-4.0	2.6	1.0	39	1
Number of autozooecial cystiphragms per mm	3.0-9.5	7.0	2.2	12	1
Number of autozooecial diaphragms per mm	2.0-4.0	3.3	0.8	7	1
Number of autozooecia per mm^2	7.2-7.9	7.5	0.5	34	1
Number of mesozooecial diaphragms per mm	5.0-9.0	7.0	2.0	5	1
Number of mesozooecia per mm	0.0-4.5	1.1	1.2	35	1
Number of mesozooecia per mm^2	2.1-2.4	2.2	0.2	34	1

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 mm^2 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 mm^2 and one mesozooecium per linear mm. Acanthostyles located in the junction of three autozooecia; on average 4.2 acanthostyles per mm^2, 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 development of new basal diaphragms. Autozooecia start to growth at an angle of 16° on average (measured only in two autozooecia), sharply bending to intersect the zoarial surface at an angle of 84°. Autozooecia tubular, containing cystiphragms and diaphragms. Cystiphragms generally arranged in a single series on one side of the autozooecial 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 autozooecial 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 autozooecia lack cystiphragms in their distal part. There is an average of seven complete cystiphragms per mm along the total length of the autozooecia. Diaphragms in the lower part of autozooecia either joining cystiphragms with the opposite wall or spanning the autozooecial tube where cystiphragms are absent; they are straight, perpendicular to the walls and less abundant (mean of 3.3 diaphragms per mm of autozooecial length). Mesozooecia scarce, tubular and smaller than autozooecia. They are tabulated by perpendicular and concave diaphragms, averaging seven diaphragms per mm of length. Some mesozooecia 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 autozooecial 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 autozooecial walls slightly thinner than in distal ones (0.024 mm on average). The difference in thickness increases when the wall contains acanthoslyles; 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 autozooecial sections with a cystiphragm touching one or two sides of the autozooecial chamber, as well as scarce mesozooecia, mainly concentrated in maculae. Longitudinal sections are similar, with cystiphragms either arranged in series on one or both sides of the autozooecial walls, or isolated. However, the Siberian specimens have more abundant diaphragms in both autozooecia and mesozooecia, 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 autozooecial apertures, smaller autozooecial cystiphragms arranged in a single series or isolated on one or both sides of the wall, and less inclined autozooecia 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 & Etherigde, 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-fig. 4.

Prasopora carnica Vinassa de Regny, 1915: 101, pl. 12, figs 7-9. Conti 1990: 91, pl. 1, figs 1-4.

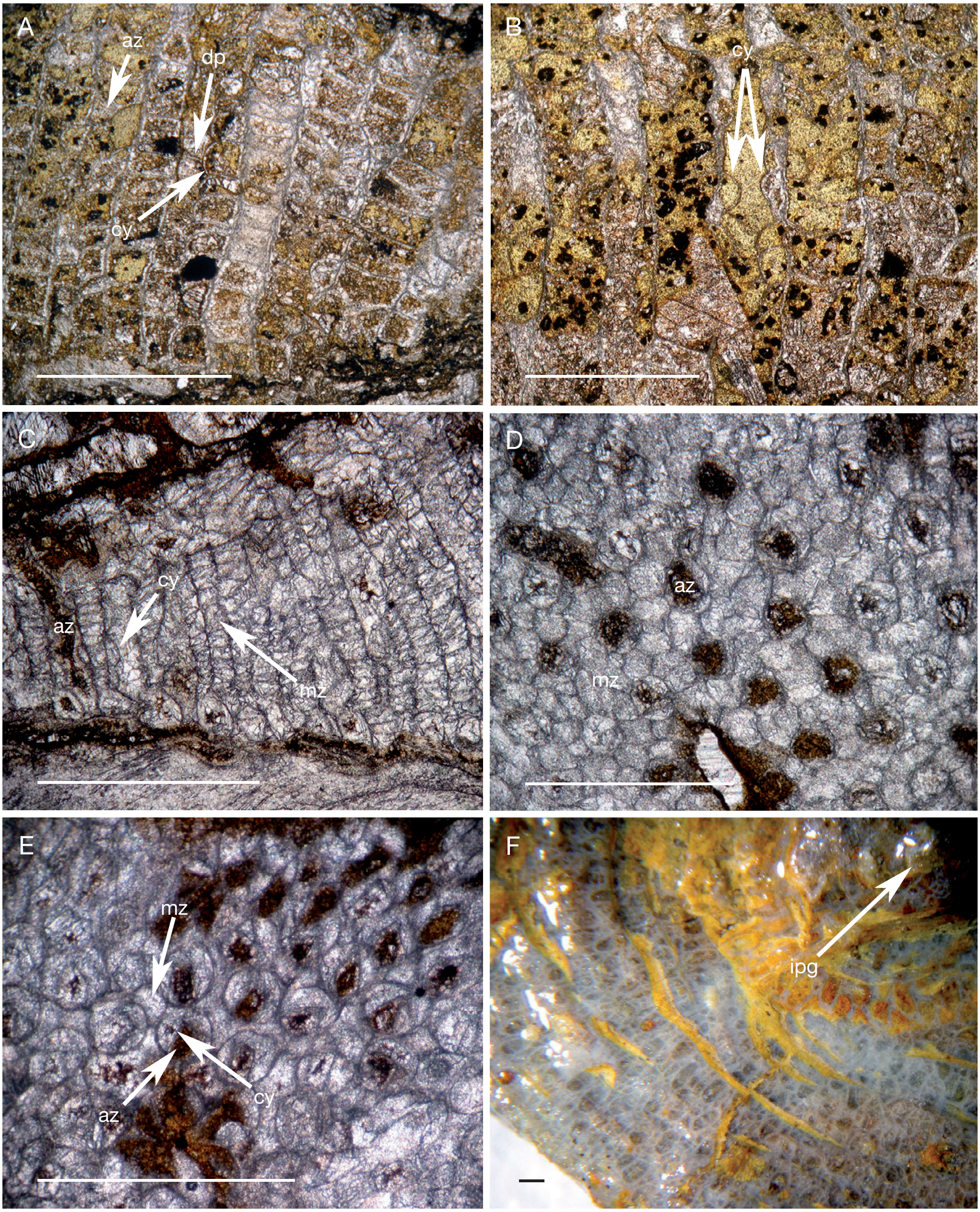

FIG. 5. — **A**, **B**, *Monticulipora kolaluensis* Jaroshinskaja, 1962, MPZ 2006/109, longitudinal thin sections; **A**, area of the zoarium with large cystiphragms (**cy**) attached to one side of the autozooecial (**az**) wall that are joined to the opposite wall by diaphragms (**dp**); **B**, an area with smaller cystiphragms (**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 cystiphragms (**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 cystiphragms (**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.

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

Character	Or	X	SD	Nm	Nsp
Autozooecial angle with exterior colony surface	77-87°	85°	3	7	1
Autozooecial diameter (in mm)	0.12-0.30	0.20	0.03	58	1
Mesozooecial diameter (in mm)	0.08-0.18	0.12	0.02	44	1
Number of autozooecia per mm	1.0-4.0	2.2	1.2	13	1
Number of autozooecial cystiphragms per mm	6-12	9	3	4	1
Number of autozooecia per mm^2	6.0-9.0	7.5	1.0	6	1
Number of mesozooecial diaphragms per mm	12-22	16	3	11	1
Number of mesozooecia per mm	4-9	6	2	13	1
Number of mesozooecia per mm^2	31.0-45.0	41.5	5.2	7	1
Zooecial wall thickness in exozone (in mm)	0.005-0.020	0.011	0.004	35	1

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 autozooecial apertures, completely surrounded by mesozooecia; and the second one composed by more circular autozooecial apertures, in contact with each other in most of their perimeter, and with scarce mesozooecia located in the space between them. The spatial density of autozooecia is almost twice in the second zone than in the first one. Autozooecial sections with an average diameter of 0.20 mm, 7.5 autozooecia per mm^2 and 2.2 autozooecia per linear mm on average (measured in the first zone, where they are less numerous). Most autozooecial sections with two or three cystiphragms leaving an oval cavity between them, located either in a central position in the case of two cystiphragms, or on the periphery in the case of three cystiphragms. Shape of mesozooecial cross sections depends on their position in the colony: irregularly hexagonal when surrounding autozooecia and variably shaped when occupying the spaces between autozooecia. Mesozooecia with an average diameter of 0.12 mm, 41.5 mesozooecia per mm^2 and six mesozooecia per linear mm on average (measured in first zone where they are more abundant). Both, autozooecial and mesozooecial walls thin (mean of 0.011 mm). Wall microstructure laminated, but zooecial 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 autozooecia with respect to basal surface. Autozooecia intersect zoarial surface at an angle of 85°. Autozooecia consist of long tubes with cystiphragms and diaphragms. Cystiphragms 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 cystiphragms can take up three fourths of autozooecial diameter. Nine cystiphragms per linear mm on average. Diaphragms very scarce, always joining the larger isolated cystiphragms to the opposite wall. Mesozooecia are length tubes located between autozooecia or in small groups. Some of them almost as large as autozooecia, distinguish from latter by absence of cystiphragms and by higher density of diaphragms (an average

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

Character	Or	X	SD	Nm	Nsp
Autozooecial angle with basal colony surface	43.0-64.0°	54.5°	5.5	12	1
Autozooecial angle with exterior colony surface	69-81°	76°	4	19	1
Autozooecial-mesozooecial wall thickness in exozone (in mm)	0.005-0.015	0.010	0.002	19	1
Autozooecial major diameter (in mm)	0.45-0.55	0.51	0.02	18	1
Autozooecial minor diameter (in mm)	0.40-0.45	0.43	0.02	18	1
Intermonticular Mesozooecial diameter (in mm)	0.18-0.34	0.25	0.05	14	1
Mesozooecial-mesozooecial wall thickness in exozone (in mm)	0.005-0.010	0.008	0.003	22	1
Monticular mesozooecial diameter (in mm)	0.3-0.4	0.4	0.0	10	1
Number of autozooecia per mm	0.7-1.2	1.0	0.5	13	1
Number of autozooecial cystiphragms per mm	2-8	4	2	15	1
Number of autozooecial diaphragms per mm	2-5	3	1	15	1
Number of autozooecia per mm^2	1.2-2.0	1.7	0.5	10	1
Number of mesozooecial diaphragms per mm	5-13	9	2	45	1
Number of mesozooecia per mm	2.0-3.5	3.0	1.0	13	1
Number of mesozooecia per mm^2	10.5-13.5	12.0	2.0	10	1

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 autozooecial 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 autozooecial cystiphragms and diaphragms as well as by the size of the cystiphragms which occupy less space inside the autozooecial 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 autozooecia and mesozooecia; presence of cystiphragms on one side of the autozooecial wall leaning on lower diaphragms or on other cystiphragms growing from opposite side of wall; autozooecia isolated from each other by mesozooecia; the splitting of largest mesozooecia in two new mesozooecia just above a diaphragm.

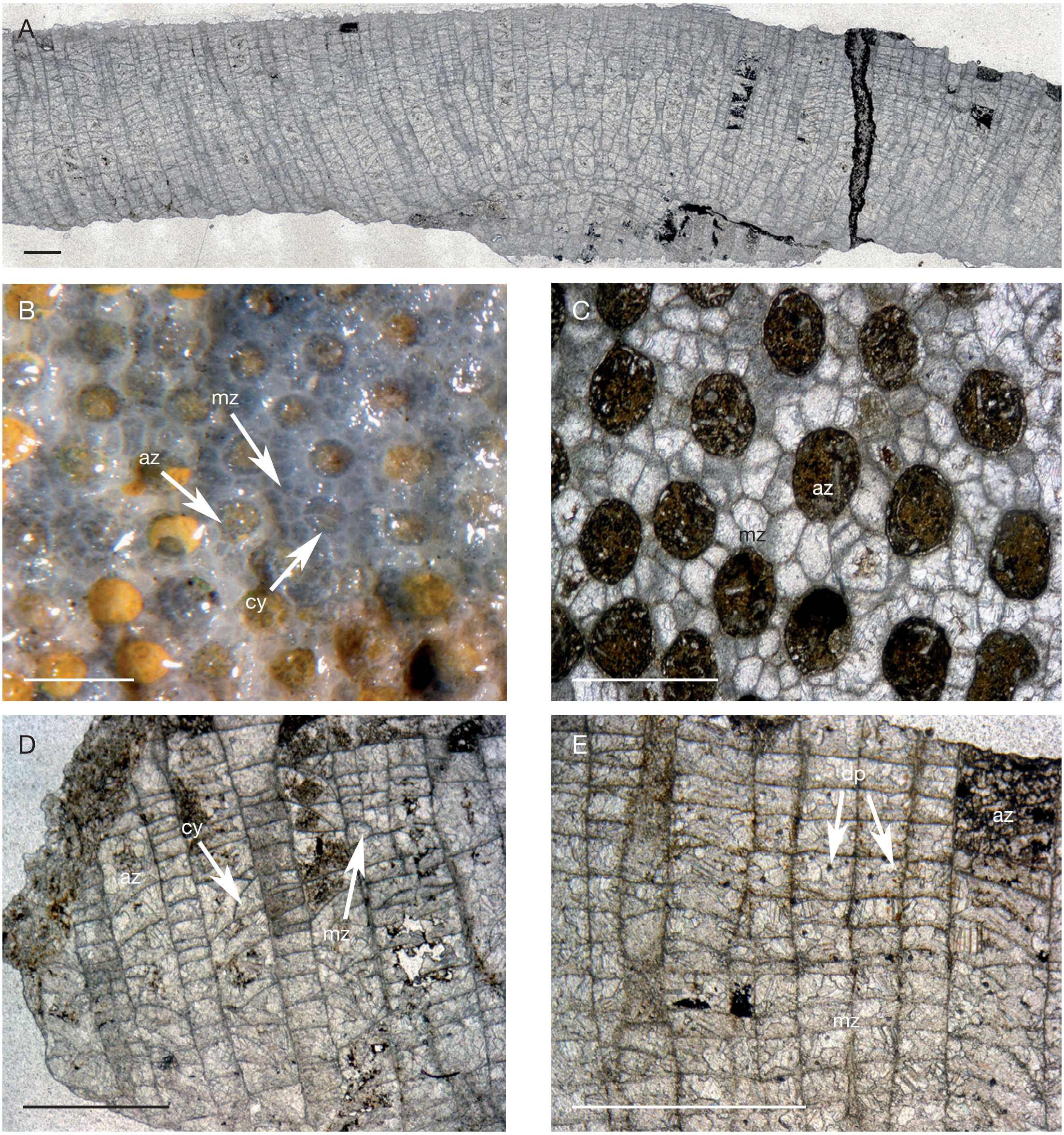

FIG. 6. — *Prasopora spjeldnaesi* n. sp., holotype (MPZ 2006/99): **A**, general view of the colony; **B**, surface of the colony showing autozooecia (**az**) completely surrounded by mesozooecia (**mz**), and a cross section of a cystiphragm (**cy**) inside an autozooecial aperture; **C**, tangential 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.

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 monticules, surrounded by depressed intermonticular areas. Autozooecial apertures oval, completely surrounded by mesozooecial 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 mm^2 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 mm^2 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

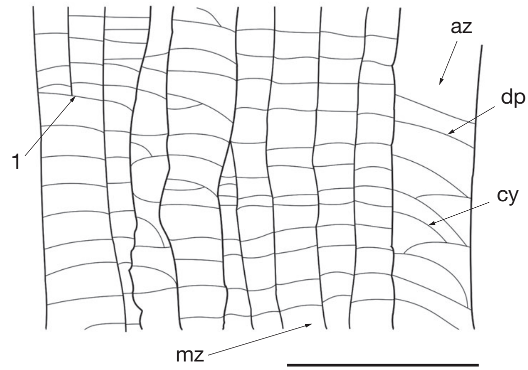

Fig. 7. — *Prasopora spjeldnaesi* n. sp., schematic longitudinal section showing the shape and distribution of autozooecial (**az**) cystiphragms (**cy**) and diaphragms (**dp**) and a group of densely tabulate mesozooecia (**mz**) with diaphragms at the same level. In **1** a large mesozooecium divides to form two smaller mesozooecia. Scale bar: 1 mm.

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 mesozooecia tabulated by straight diaphragms, 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 congeneric 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

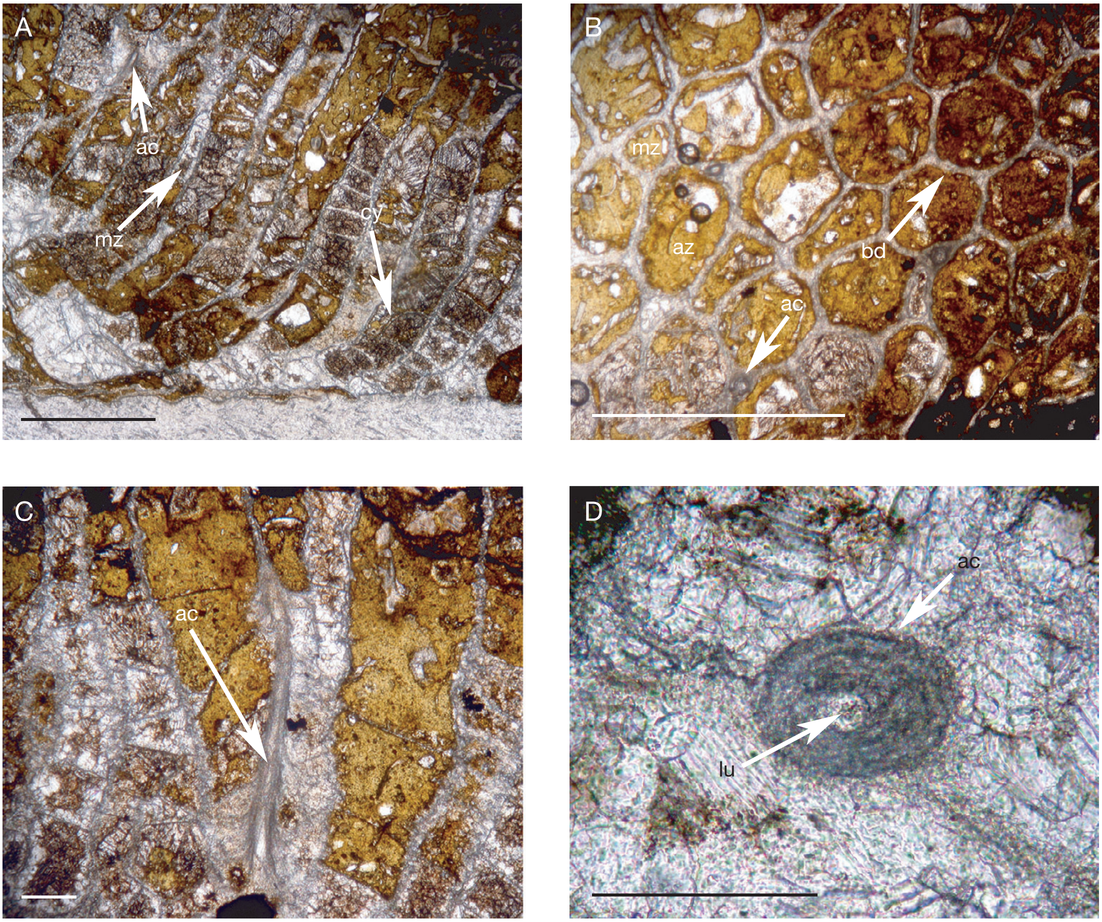

FIG. 8. — Monticuliporidae sp. indet., MPZ 2006/110: **A**, longitudinal thin section showing the large acanthostyles (**ac**), the peculiar cystiphragms (**cy**), and the narrow mesozooecia (**mz**); **B**, tangential thin section showing the regular hexagonal autozooecia (**az**) with wall sections 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.

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 spjeldnaesi* 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 spjeldnaesi* n. sp.). The new species can be also discriminated from *Prasopora gotlandica* by its higher mesozooecia number/autozooecia number relation

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

Character	Or	X	SD	Nm	Nsp
Acanthostyles diameter (in mm)	0.040-0.100	0.065	0.023	10	1
Autozooecial angle with basal colony surface	14-36°	26°	9	6	1
Autozooecial angle with exterior colony surface	90°	90°	0	8	1
Autozooecial diameter (in mm)	0.36-0.55	0.39	0.06	14	
Autozooecial wall thickness in exozone (in mm)	0.030-0.050	0.032	0.006	24	1
Mesozooecial diameter (in mm)	0.18-0.21	0.20	0.01	8	1
Number of acanthostyles per mm2	0.5-1.5	1.0	1.0	6	1
Number of autozooecia per mm	3.0-1.7	2.6	0.5	12	1
Number of autozooecial cystiphragms per mm	1.0-5.0	2.5	1.7	10	1
Number of autozooecial diaphragms per mm	3.0-5.0	3.9	0.6	13	1
Number of autozooecia per mm2	6.5-8.5	7.2	1.8	6	1
Number of mesozooecial diaphragms per mm	3.0-5.0	4.6	0.8	4	1
Number of mesozooecia per mm	0.0-2.0	0.6	0.6	12	1
Number of mesozooecia per mm2	1.1-2.9	2.2	1.8	6	1

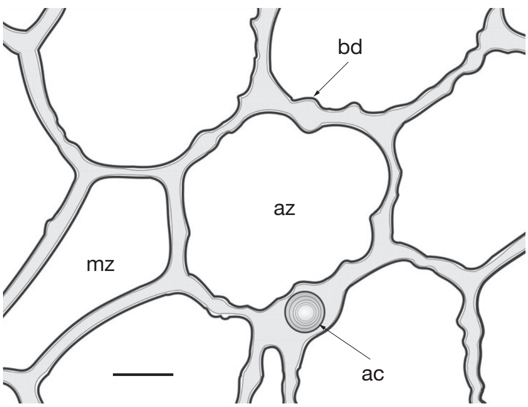

FIG. 9. — Monticuliporidae sp. indet., schematic tangential section showing the shape of autozooecial (**az**) and mesozooecial (**mz**) apertures, the gently beaded (**bd**) outline of the wall setions, as well as the large acanthostyles (**ac**). Scale bar: 0.1 mm.

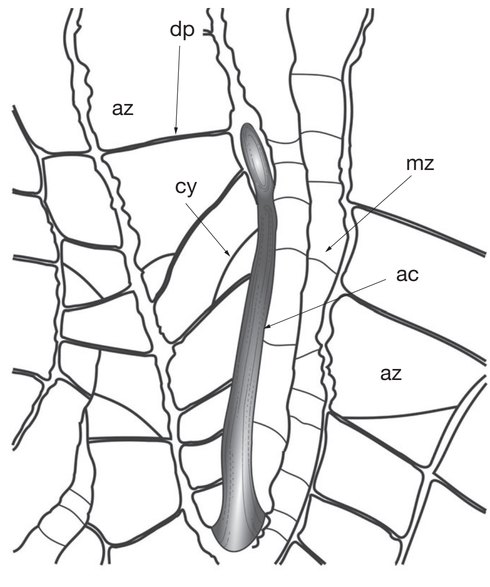

FIG. 10. — Monticuliporidae sp. indet., schematic longitudinal section showing a prominent acanthostyle (**ac**), the shape of diaphragms (**dp**), cystiphragms (**cy**) and autozooecial tubes (**az**), as well as the narrow mesozooecia (**mz**). Scale bar: 0.1 mm.

(2.5 in *Prasopora gotlandica* vs 7.0 in *Prasopora spjeldnaesi* n. sp.).

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 mesozooecia forming characteristic rings around autozooecia; but *Prasopora mesoporosa* has the typical *Prasopora* cystiphragms and much smaller autozooecia and mesozooecia 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.).

Monticuliporidae sp. indet.
(Figs 8; 9; 10; Table 5)

Orbignyella sp. Jiménez-Sánchez *et al.* 2007: 687, fig. 4 (1-2).

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 aparent 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 mm^2 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 mm^2 and 0.6 mesozooecia per linear mm. Mesozooecia located in the space left by less regular hexagonal autozooecia. Acanthostyles rather scarce, averaging one per mm^2, large (mean diameter of 0.065 mm), mainly located in junction of three autozooecia. Acanthostyles with light-coloured cores and dark-coloured laminated sheaths. Zooecial 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). Zooecial 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: encrusting 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 exilazooecia instead of mesozooecia and much smaller acanthostyles 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 autozooecial apertures (polygonal vs oval), the number of mesozooecia (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 Monticuliporidae 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 Mediterranean 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 Mediterranean Region and the Baltica paleocontinent.

Acknowledgements

The author would like to thank the late Niels Spjeldnaes for his help in deciphering the systematic of bryozoans. Thanks also go to Caroline Buttler and Andrej Ernst for reviewing an early version of this manuscript, and to Beatriz Azanza, Javier Gómez and Enrique Villas for improving the standard of English and helpful advice. Finally I would like to thank again Andrej Ernst and Marcus Key who formally reviewed this paper. This research has been funded by the Spanish Ministry of Science, Project CGL 2006-11176. This is a contribution to IGCP 503 Ordovician Paleogeography and Paleoclimatic.

REFERENCES

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

BOARDMAN R. S. & UTGAARD J. 1966. — A revision of the Ordovician bryozoan genera *Monticulipora*, *Peronopora*, *Heterotrypa*, and *Dekayia*. *Journal of Paleontology* 40 (5): 1082-1108.

BORK K. B. & PERRY T. G. 1968. — Bryozoa (Ectoprocta) 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 Paleontology* 42 (4): 1042-1065, pls 133-138.

BROWN G. D. JR & DALY E. J. 1985. — Trepostome Bryozoa from the Dillsboro Formation (Cincinnatian 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. — Bryozoan mud-mounds from the Upper Ordovician Jifarah (Djeffara) Formation of Tripolitania, North-West of Libya. *Palaeontology* 50: 479-494.

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 geography 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 Italica* 77: 85-165.

DEL MORAL B. 2005. — Estudio tafonómico preliminar de los conodontos de la Formación Calizas de Cistideos (Ordovícico 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 Paleontología.* Institución Fernando el Católico, Zaragoza: 109-118.

ERNST A. & KEY M. 2007. — Upper Ordovician bryozoan from the Montagne Noire, Southern France. *Journal of Systematic Palaeontology* 5 (4): 359-428.

ERNST A., TAYLOR P. D. & WILSON M. A. 2007. — Ordovician bryozoans from the Kanosh Formation (Whiterckian) of Utah, USA. *Journal of Paleontology* 81 (5): 998- 1008.

FORTEY R. A. & COCKS L. R. M. 2002. — Paleontological evidence bearing on global Ordovician-Silurian continental reconstructions. *Earth-Science Reviews* 61: 245-307.

FORTEY R. A. & COCKS L. R. M. 2005. — Late Ordovician global warming – The Boda event. *Geological Society of America Bulletin* 33 (5): 405-408.

FRITZ M. A. 1976. — Redescription of type specimens of species of the bryozoan genera *Monticulipora*, *Mesotrypa*, *Peronopora* and *Prasopora* from the Upper Ordovician rocks of Toronto and vicinity, Ontario, Canada. *Life Sciences Contribution, Royal Ontario Museum* 107: 1-24.

HAFENRICHTER M. 1980. — The lower and upper boundary of the Ordovician system of some selected regions (Celtiberia, Eastern Sierra Morena) in Spain. Part II: The Ordovician/Silurian boundary in Spain. *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen* 160: 138-148.

HAMMANN W. 1992. — The Ordovician trilobites from the Iberian Chains in the province of Aragón, NE-Spain. I. The trilobites of the Cystoid Limestone (Ashgill Series). *Beringeria* 6: 219 p.

HU Z. X & WANG Y. F. 1983. — [Upper Silurian Bryozoa from Darhan Mumingan Joint Banner, Inner Mongolia], *in* LI W. G., RONG J. Y. & DONG D. Y. (eds), [*Silurian/Devonian Rocks and Faunas of the Bateobao Area in Darhan Mumingan Joint Banner, Inner Mongolia*]. Peoples' Publishing House of Inner Mongolia, Hohhot: 145-151 (in Chinese).

JAROSHINSKAJA A. M. 1962. — [Some representatives of the bryozoan family Monticuliporidae in the Upper Ordovician of the Altai Mountains]. *Trudy Sibirskogo nauchno-isledovatelskogo instituta geologii, geofiziki i mineralnogo syrya (SNIIGGIMS)* 23: 143-149, 2 pls. (in Russian).

JIMÉNEZ-SÁNCHEZ A. 2009. — The Upper Katian (Ordovician) bryozoans from the Eastern Iberian Chains (NE Spain). *Bulletin of Geosciences* 84 (4): 687-738.

JIMÉNEZ-SÁNCHEZ A., SPJELDNAES N. & VILLAS E. 2007. — Ashgill bryozoans from the Iberian Chains (NE Spain) and their contribution to the late Ordovician biodiversity peak in North Gondwana. *Ameghiniana* 44 (4): 681-696.

LIÑAN E., VILLAS E., GÁMEZ-VINTANED J. A., ÁLVARO J., GONZALO R., PALACIOS T. & SDZUY K. 1996. — Síntesis paleontológica del Cámbrico y Ordovícico del Sistema Ibérico (Cadenas Ibéricas y Cadenas Hespéricas). *Revista Española de Paleontología* nº extraordinario: 21-32.

MODZALEVSKAYA E. A. 1978. — [Bryozoa complexes from the Chergak series in Tuva]. *Ezhegodnik Vsesoiuznogo paleontologicheskogo obshchestva* 21: 119-147 (in Russian).

NELSON C. S., KEANE S. L. & HEAD P. S. 1988. — Non-tropical carbonate deposits on the modern New Zealand shelf, *in* NELSON C. S. (ed.), Non-tropical shelf carbonates – Modern and Ancient. *Sedimentary Geology* 60: 71-94.

NICHOLSON H. A. & ETHERIDGE R. 1877. — On *Prasopora grayae*, a new genus and species of Silurian corals. *Annals and Magazine of Natural History* series 4 (20): 388-392.

NICKLES J. M. & BASSLER R. S. 1900. — A synopsis of American fossil Bryozoa, including bibliography and synonymy. *U. S. Geological Survey Bulletin* 173: 1663 p.

ROSS J. R. P. 1967. — Evolution of ectoproct genus *Prasopora* in Tretonian time (Middle Ordovician) in northern and central United States. *Journal of Paleontology* 41 (2): 403-416.

SARMIENTO G. N. 2002. — Lower Paleozoic of the Iberian Cordillera, *in* GARCÍA-LÓPEZ S. & BASTIDA F. (eds), *Instituto Geológico y Minero de España*, *serie Cuadernos del Museo Geominero*, Madrid 1: 438 p.

SCHMIDT G. 1931. — Das Paläozoikum der spanischen Pyrenäen. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen*. *Mathematisch-Physikalische Klasse*, *KI.3*, *H.5*, 8: 981-1065.

SINGH R. J. 1979. — Trepostomatous bryozoan fauna from the Bellevue Limestone, Upper Ordovician, in the Tri-state area of Ohio, Indiana and Kentucky. *Bulletins of American Paleontology* 76 (307): 288 p.

TUCKEY M. E. 1990. — Biogeography of Ordovician bryozoans. *Palaeogeography, Palaeoclimatology, Palaeoecology* 77: 91-126.

ULRICH E. O. 1882. — American Palaeozoic Bryozoa. *Journal of the Cincinnati Society of Natural History* 5: 121-175, 232-257, pls 6-8, 10, 11.

UTGAARD J. & PERRY T. G. 1964. — Trepostomatous bryozoan fauna of the upper part of the Whiterwater Formation (Cincinnatian) of Eastern Indiana and Western Ohio. Indiana Department of Conservation. *Geological Survey Bulletin* 33: 111 p., pls 1-23.

VENNIN E., ALVARO J. J. & VILLAS E. 1998. — High-latitude pelmatozoan-bryozoan mud-mounds from the late Ordovician northern Gondwana platform. *Geological Journal* 3: 121-140.

VENNIN E., ROUCHY J. M., CHAIX C., BLANC-VALLERON M. M., CARUSO A. & ROMMEVAU V. 2004. — Paleoecological constraints on reef-coral morphologies in the Tortonian-Early Messinian of the Lorca Basin, SE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213: 163-185.

VILLAS E. 1985. — Braquiópodos del Ordovícico Medio y Superior de las Cadenas Ibéricas Orientales. *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 1: 223 p.

VILLAS E., VENNIN E., ÁLVARO J. J., HAMMANN W., HERRERA Z. & PIOVANO E. L. 2002. — The late Ordovician carbonate sedimentation as a major triggering factor of the Hirnantian glaciation. *Bulletin de la Société géologique de France* 173: 569-578.

VINASSA DE REGNY P. 1910. — Fossili Ordoviciani del Nucleo Centrale Carnico. *Atti della Accademia Gioenia di Scienze Naturali in Catania* Serie V, 3, Mem. XII: 1-48.

VINASSA DE REGNY P. 1914. — Fossili Ordoviciani di Uggwa (Alpi Carniche). *Memorie dell'Instituto Geologico della R. Universiteta di Padora* 2: 195-221, pl. 16.

VINASSA DE REGNY P. 1915. — Fossili Ordoviciani del Capolago presso il passo di Volaia (Alpi Carniche). *Palaeontographia Italica* 21: 97-117, pls 12-13.

Submitted on 4 August 2008;
accepted on 25 May 2009.